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# Accounting for Management Costs in Sensitivity Analyses of Matrix Population Models

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**Abstract:** *Traditional sensitivity and elasticity analyses of matrix population models have been used to inform management decisions, but they ignore the economic costs of manipulating vital rates. For example, the growth rate of a population is often most sensitive to changes in adult survival rate, but this does not mean that increasing that rate is the best option for managing the population because it may be much more expensive than other options. To explore how managers should optimize their manipulation of vital rates, we incorporated the cost of changing those rates into matrix population models. We derived analytic expressions for locations in parameter space where managers should shift between management of fecundity and survival, for the balance between fecundity and survival management at those boundaries, and for the allocation of management resources to sustain that optimal balance. For simple matrices, the optimal budget allocation can often be expressed as simple functions of vital rates and the relative costs of changing them. We applied our method to management of the Helmeted Honeyeater (*Lichenostomus melanops cassidix*; an endangered Australian bird) and the koala (*Phascolarctos cinereus*) as examples. Our method showed that cost-efficient management of the Helmeted Honeyeater should focus on increasing fecundity via nest protection, whereas optimal koala management should focus on manipulating both fecundity and survival simultaneously. These findings are contrary to the cost-negligent recommendations of elasticity analysis, which would suggest focusing on managing survival in both cases. A further investigation of Helmeted Honeyeater management options, based on an individual-based model incorporating density dependence, spatial structure, and environmental stochasticity, confirmed that fecundity management was the most cost-effective strategy. Our results demonstrate that decisions that ignore economic factors will reduce management efficiency.*

**Keywords:** conservation, elasticity, marginal costs, marginal efficiency, optimization, perturbation analysis, population management, stochastic model

Representación de Gastos de Administración en el Análisis de Sensibilidad de Modelos Poblacionales Matriciales

**Resumen:** *Los tradicionales análisis de sensibilidad y elasticidad de los modelos poblacionales matriciales han sido utilizados para informar a las decisiones de gestión, pero ignoran los costos económicos de la manipulación de las tasas vitales. Por ejemplo, la tasa de crecimiento de una población a menudo es más sensible a los cambios en la tasa de supervivencia de adultos, pero esto no significa que el incremento de esta tasa es la mejor opción para la gestión de la población porque puede ser mucho más cara que otras opciones. Para explorar como los gestores deberían optimizar su manipulación de las tasas vitales, incorporamos el*

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Paper submitted April 7, 2005; revised manuscript accepted for publication July 12, 2005.

costo del cambio de esas tasas en modelos poblacionales matriciales. Derivamos expresiones analíticas en puntos del parámetro espacio en los que los gestores deben alternar entre la gestión de fecundidad y de supervivencia para el balance entre la gestión de la fecundidad y la supervivencia en esos límites y para la asignación de recursos para sostener ese balance óptimo. En matrices simples, la asignación presupuestaria óptima se puede expresar a menudo como funciones simples de las tasas vitales así como los costos relativos de cambiarlos. Como ejemplos, aplicamos nuestro método en la gestión de *Lichenostomus melanops cassidix* (una ave australiana en peligro) y del koala (*Phascolarctos cinereus*). Nuestro método mostró que la gestión rentable de *L. m. cassidix* debería enfocar el incremento de la fecundidad por medio de la protección de nidos, mientras que la gestión óptima del koala debería centrarse en la manipulación simultánea de la fecundidad y de la supervivencia. Estos hallazgos son contrarios a las recomendaciones que no consideran a los costos del análisis de elasticidad, que sugerirían centrar la gestión en la supervivencia en ambos casos. Una investigación posterior de las opciones de gestión de *L. m. cassidix*, con base en un modelo que incorporó densa dependencia, estructura especial y estocasticidad ambiental, confirmó que la gestión de la fecundidad era la estrategia más rentable. Nuestros resultados demuestran que las decisiones que ignoran factores económicos reducen la eficiencia de la gestión.

**Palabras Clave:** análisis de perturbación, conservación, costos marginales, eficiencia marginal, elasticidad, gestión de la población, modelo estocástico, optimización

## Introduction

Stage- and age-structured population models are widely used tools for the conservation of threatened species, harvesting of species for products, and the eradication of pest populations (Getz & Haight 1989; Shea & Kelly 1998; Caswell 2001). For threatened species management, matrix population models may provide a more elegant understanding of species viability than Monte Carlo simulation models (Beissinger & Westphal 1998; Benton & Grant 1999) and can be a valuable first step in any analysis of population viability (Heppell et al. 2000). They are particularly useful with respect to the declining-population paradigm (Caughley 1994; Caswell 2001). Despite their broad application to applied population management problems, these models have not been placed within an economic framework.

In matrix models, a population is classified according to age, life stage, or some other characteristic. Matrix elements denote transition rates between classes, and the dominant eigenvalue,  $\lambda$ , gives the asymptotic population growth rate (Caswell 2001). The value of  $\lambda$  is often used as an indicator of population status ( $\lambda > 1$  signals an increasing population) rather than as a predictive result. Recommendations for species management that use matrix population models are frequently based on a perturbation (sensitivity or elasticity) analysis. These analyses involve comparing sensitivities ( $\partial\lambda/\partial p$ ) of  $\lambda$  to changes in the different matrix parameters ( $p$ ) or comparing elasticities ( $\partial \ln \lambda / \partial \ln p$ ), which measure proportional changes in  $\lambda$  relative to proportional parameter changes. Elasticities have the appealing property of summing to unity, which allows more direct comparison of the effects of parameter changes (de Kroon et al. 1986). As a result, researchers commonly state that management efforts should focus

on the vital rate producing the highest elasticity value where practical because small changes in vital rates with high elasticity values are likely to result in relatively larger changes in  $\lambda$  (e.g., Crouse et al. 1987; Wootton & Bell 1992; Hunt 2001). Although the relative merits of managing other vital rates are often also discussed, we think that such evaluations would be better informed by the inclusion of the costs of such actions.

Biological (Caswell 2000) and mathematical (Benton & Grant 1999) constraints on parameter values that describe vital rates can lead to a trade-off between elasticity values and parameter variation, with parameters yielding high elasticity values often having the least range of natural or management-induced variation (Cross & Beissinger 2001 and references therein). For most long-lived species the dominant eigenvalue is most sensitive to changes in the adult survival rate (e.g., Heppell et al. 1996; Fisher et al. 2000; Hunt 2001; Hebblewhite et al. 2003). Increasing adult survival to maximize population growth rates, however, may not always be affordable or even possible.

The use of perturbation analysis to choose between population management actions has been criticized on several counts: for example, dependence of elasticity values on the long-term population growth rate,  $\lambda$  (Oostermeijer et al. 1996; Silvertown et al. 1996; de Kroon et al. 2000; but see Heppell et al. 2000); lack of information on the performance of elasticities in realistic settings (de Kroon et al. 2000); and exclusion of density-dependence and nonequilibrium dynamics (Grant & Benton 2003). Ehrlén et al. (2001) recommend confining the use of elasticities to projecting changes in  $\lambda$  rather than producing a prioritized ranking of vital rates for management (but see also Mills et al. 2001). However, elasticity values and their application (such as ranking of parameters in terms of management importance) seem to be robust to large

changes in parameter values (Mills et al. 1999; Caswell 2000; de Kroon et al. 2000), and there is widespread approval of their judicious use as a management tool.

Given the limited financial resources of most conservation endeavors, one needs to consider the economic aspects of conservation management (Possingham et al. 2001). For example, the vital rate that gives the greatest elasticity may be impossible, or very expensive, to manage, whereas a parameter giving a low elasticity may provide a cheaper means of increasing the long-term population growth rate. Some authors note the need for considering the economic cost of changing parameters (e.g., Goodman 1980; Crooks et al. 1998; Heppell 1998; Link & Doherty 2002), whereas others discuss the overall and relative feasibility of implementing recommendations from elasticity analysis (Crouse et al. 1987; Hiraldo et al. 1996; Caswell 2001). Nichols and Hines (2002) propose deciding between  $k$  different management options by using the expression

$$\frac{\partial \ln \lambda}{\partial \ln p} \frac{\partial \ln p}{\partial x_k} \frac{\partial x_k}{\partial y_k},$$

where  $p$  is a parameter altered by management action  $x_k$  of unit cost  $y_k$ . Here we included cost factors in matrix population models in a similar fashion to couch sensitivity in the economic framework to which conservation is ultimately subjected.

In considering the allocation of conservation funds in an economic context, one examines the relative efficiency of management strategies, where the benefit is an increase (or decrease) in the long-term population growth rate. Cost is the amount to be paid for a good or service, in this case, for attaining a certain parameter value. In particular, one looks at the marginal cost, which is the increase in total costs associated with a unitary increase in output (in our case, one of the components of population growth, e.g., survival or fecundity). This is important because it allows comparison between different management strategies that produce a standard level of output and thus provides information on how to invest each (additional) unit of conservation funding. For conservationists limited by budget constraints, the preferable management strategy is the one with the highest marginal benefit. If the marginal benefits of two alternative strategies are equal, then it is optimal to follow both strategies at once (until the marginal costs change). Most introductory economic textbooks (e.g., Pindyck & Rubinfeld 2001; McTaggart et al. 2003) contain further information on how to account for costs in management decisions.

Although most conservation practitioners already consider costs implicitly (if not explicitly) and researchers discuss relative pros and cons of the feasibility of elasticity recommendations (above), there are a number of benefits to making the economic considerations explicit. The methods we introduce here will increase rigor and transparency in conservation decision making and vali-

date and enhance a manager's intuition with relatively little additional effort.

## Methods

Given some age- or stage-based population projection matrix  $\mathbf{M}$ , we obtained an expression for its dominant eigenvalue  $\lambda$ , which allowed us to calculate the sensitivity ( $\partial \lambda / \partial p$ ) of  $\lambda$  to changes in the value of parameter  $p$ . If  $p$  is a "lower-level" parameter contributing to multiple matrix elements ( $a_{ij}$ ) the sensitivity of  $\lambda$  to  $p$  can be expressed as

$$\frac{\partial \lambda}{\partial p} = \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial p}$$

(Caswell 2001). For example, in stage-structured models, the growth rates of individuals can affect both stasis rates (survival within a class; diagonal elements) and transition rates between classes (subdiagonal elements). We assumed the cost ( $C_p$ ) of attaining a parameter value (e.g., the cost of some level of adult survival) changes linearly with small changes in the parameter value. By dividing  $\partial \lambda / \partial p$  by the marginal cost ( $\partial C_p / \partial p$ ) of changing parameter  $p$ , we obtained the "marginal efficiency" of managing each parameter,  $\epsilon_p = \partial \lambda / \partial C_p$ , which represents the change in population growth rate caused by management investment in life-history parameter  $p$ . The relationships between values of the marginal efficiency of a management strategy that alters parameter  $p$ ,  $\epsilon_p$ , can then provide general management rules for when to invest more effort into, say, changing fecundity ( $p = f$ ) or survival ( $p = s$ ). These relationships can be calculated for any management action and any population model.

We derived analytical solutions for eight matrix models of varying complexity (Table 1). We obtained "critical parameter values," indicating states in  $sf$  (survival-fecundity) parameter space where optimal management should switch between focuses on survival and fecundity by setting the marginal efficiencies of managing survival and fecundity to be equal,  $\epsilon_s = \epsilon_f$ . We then calculated the relative marginal efficiency of investing in fecundity versus survival (or "relative marginal efficiency" for conciseness),  $\chi = \epsilon_f / \epsilon_s (= \partial C_s / \partial C_f)$ . When the relative marginal efficiency is  $> 1$  ( $\chi > 1$ ), it is more efficient to manage fecundity alone, and when  $\chi < 1$  it is more efficient to manage survival alone. The boundary in  $sf$  space along which the marginal efficiencies are equal,  $\chi = 1$ , is where investment in neither parameter is exclusively preferable to the other, and therefore further investment in the population requires both parameters to be managed at once. The slope of the curve representing this boundary thus gave the relative increases needed for fecundity and survival and (multiplying again by the marginal costs)

Table 1. Results of applying the procedure for incorporating management costs into sensitivity analysis (outlined in the Methods section) to matrices of varying complexity.

Matrix	Dominant eigenvalue $\lambda$	Sensitivity of $\lambda$ to changes in fecundity $\partial\lambda/\partial f$	Sensitivity of $\lambda$ to changes in (adult) survival $\partial\lambda/\partial s$	Relative marginal efficiency $\chi = \epsilon_r/\epsilon_s$	Fecundity: survival investment split in optimal state $\$f_x : \$s_x$
$A = \begin{pmatrix} 0 & f \\ s & 0 \end{pmatrix}$	$\sqrt{sf}$	$\sqrt{s/4f}$	$\sqrt{f/4s}$	$s/\phi f$	1 : 1
$B^a = \begin{pmatrix} 0 & f \\ s & s \end{pmatrix}$	$\frac{s + \sqrt{s^2 + 4sf}}{2}$	$\frac{s}{\sqrt{s^2 + 4sf}}$	$\frac{1}{2} \left( 1 + \frac{s + 2f}{\sqrt{s^2 + 4sf}} \right)$	$\frac{2s}{\phi(s + 2f + \sqrt{s^2 + 4sf})}$	$(1 - \sqrt{\phi}) : 1$
$C = \begin{pmatrix} 0 & f \\ \alpha s & s \end{pmatrix}$	$\frac{s + \sqrt{s^2 + 4\alpha sf}}{2}$	$\frac{\alpha s}{\sqrt{s^2 + 4\alpha sf}}$	$\frac{1}{2} \left( 1 + \frac{s + 2\alpha f}{\sqrt{s^2 + 4\alpha sf}} \right)$	$\frac{2\alpha s}{\phi(s + 2\alpha f + \sqrt{s^2 + 4\alpha sf})}$	$(1 - \sqrt{\frac{\phi}{\alpha}}) : 1$
$D^b = \begin{pmatrix} 0 & f \\ j & s \end{pmatrix}$	$\frac{s + \sqrt{s^2 + 4jf}}{2}$	$\frac{j}{\sqrt{s^2 + 4jf}}$	$\frac{1}{2} \left( 1 + \frac{s}{\sqrt{s^2 + 4jf}} \right)$	$\Xi = \left\{ \frac{j}{\phi}, \frac{f}{\sigma}, \frac{s + \sqrt{s^2 + 4jf}}{2} \right\}^c$	see Expr. D <sup>d</sup>
$E = \begin{pmatrix} 0 & 0 & \dots & 0 & f \\ \alpha_1 s & 0 & \dots & 0 & 0 \\ 0 & \alpha_2 s & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \alpha_{n-1} s & 0 \end{pmatrix}$	$\left( f s^{\alpha_1 - 1} \prod_{i=1}^{n-1} \alpha_i \right)^{\frac{1}{n}}$	$\frac{1}{n} \left( f^{1-n} s^{\alpha_1 - 1} \prod_{i=1}^{n-1} \alpha_i \right)^{\frac{1}{n}}$	$\frac{n-1}{n} \left( \frac{f}{s} \prod_{i=1}^{n-1} \alpha_i \right)^{\frac{1}{n}}$	$\frac{s}{(n-1)\phi f}$	$\left( \frac{1}{n-1} \right) : 1$
$F = \begin{pmatrix} 0 & 0 & f \\ s & 0 & 0 \\ 0 & s & s \end{pmatrix}$	see Eq. F1 <sup>d</sup>	$\frac{s^2}{3\lambda^2 - 2s\lambda}$	$\frac{2sf + \lambda^2}{3\lambda^2 - 2s\lambda}$	$\frac{s^2}{\phi(2sf + \lambda^2)}$	solve Eq. F2 <sup>d</sup> to get s in terms of f and $\phi$ , divide out by $\phi$ to get ratio
$G = \begin{pmatrix} 0 & f & f \\ s & 0 & 0 \\ 0 & s & 0 \end{pmatrix}$	see Eq. G1 <sup>d</sup>	$\frac{s^2 + s\lambda}{3\lambda^2 - sf}$	$\frac{2sf + f\lambda}{3\lambda^2 - sf}$	$\frac{s^2 + s\lambda}{\phi(2sf + f\lambda)}$	solve Eq. G2 <sup>d</sup> to get s in terms of f and $\phi$ , divide out by $\phi$ to get ratio
$H = \begin{pmatrix} 0 & f & f \\ \alpha s & 0 & 0 \\ 0 & \beta s & s \end{pmatrix}$	see Eq. H1 <sup>d</sup>	$\frac{\alpha(\alpha-1)s^2 - \alpha s\lambda}{3\lambda^2 - 2s\lambda - \alpha sf}$	$\frac{2\alpha(\alpha-1)s - \alpha f\lambda + \lambda^2}{3\lambda^2 - 2s\lambda - \alpha sf}$	$\frac{\alpha(\alpha-1)s^2 - \alpha s\lambda}{\phi(2\alpha(\alpha-1)s - \alpha f\lambda + \lambda^2)}$	solve Eq. H2 <sup>d</sup> (solving Eq. H1 <sup>d</sup> for $\lambda$ ), get s in terms of f and $\phi$ , divide out by $\phi$ to get ratio

<sup>a</sup> Results are consistent for all matrices  $X_n$  with elements  $x_{i+1,i} = x_{n,n} = s(1 \leq i \leq n-1)$ ,  $x_{i,h} = f(2 \leq h \leq n)$  and all other  $x_{i,h} = 0$ .

<sup>b</sup>  $\partial\lambda/\partial j = f/(s^2 + 4f)^{1/2}$ ;  $\sigma$  is the relative (to adult survival) marginal cost of changing juvenile survival ( $\partial C_j/\partial j = \sigma k$ ).

<sup>c</sup> Management should focus on the (Expr.) vital rate associated with the highest value in  $\Xi(i, j, s)$ .

<sup>d</sup> Expressions and equations: expression D,  $1:1/2\phi s/(1 - \phi\sigma s^2)^2$  (fecundity/juvenile survival/adult survival); Eq. F1,  $\lambda^3 - s\lambda^2 - fs^2 = 0$ ; Eq. F2,  $2(\beta\phi + D)s^3 + (f - 4\phi - 12\phi^2 D)s^2 + 4(2\phi^2 f - 1)\phi sf - 4\phi^2 f = 0$ ; Eq. G1,  $\lambda^3 - fs\lambda - fs^2 = 0$ ; Eq. G2,  $s^4 - 6\phi s^3 f + (12\phi + D)\phi s^2 f^2 - 2(4\phi + D)\phi^2 s^3 f + \phi^3 f^4 = 0$ ; Eq. H1,  $\lambda^3 - s\lambda^2 + \alpha fs\lambda - (\alpha - 1)\alpha fs^2 = 0$ ; Eq. H2,  $(\alpha - 1)\alpha fs^2 = 0$ ; Eq. H2,  $(\alpha - 1)\alpha fs^2 = 0$ ; Eq. H2,  $(\alpha - 1)\alpha fs^2 = 0$ ;  $\pm [(\alpha^2 s^2 - 2\alpha^2 \phi fs + \alpha^2 \phi^2 f^2 + 4(\alpha^2 \phi s^2 - \alpha \phi s^2 - 2\alpha^2 \phi^2 s + 2\alpha \phi^2 s))^{1/2}]/2\phi$ .

indicated how money should be allocated between the two vital rates to maintain an optimal balance between the two management activities. To obtain these solutions, we could also use implicit differentiation, solving solely in terms of  $\partial\lambda/\partial p$  if  $\lambda$  could not be found directly (see also Goodman 1980; Oli & Zinner 2001). This broadens the approach to larger and more complex matrices. We followed this procedure to explore the effect of including economic constraints in a range of population projection matrices (Table 1).

**Example: Proportional Juvenile and Adult Survival**

We applied our procedure to a relatively simple matrix of two stage classes with juvenile survival proportional to adult survival (matrix C, Table 1). We discuss management in terms of increasing vital rates, bearing in mind that the same procedure can be applied to decreasing vital rates if the management objective is population reduction.

In the case of matrix C (Table 1), the juvenile and adult survival rates are proportional to each other,  $\alpha s$  and  $s$ , respectively (with  $\alpha > 0$ ). This implies managers can alter the underlying survival rate  $s$  or the fecundity  $f$  but cannot separately manage juvenile and adult survival. This will often occur when management involves removal of a predator or disease that affects both juveniles and adults equally. Matrix D in Table 1 is the more complicated case in which adult and juvenile survival rates are managed independently. The matrix

$$C = \begin{pmatrix} 0 & f \\ \alpha s & s \end{pmatrix}$$

has a dominant eigenvalue (and long-term population growth rate) of  $\lambda = 1/2(s + \sqrt{s^2 + 4\alpha s f})$ . Differentiating, we obtained the following sensitivities of  $\lambda$  to changes in fecundity and survival:

$$\frac{\partial\lambda}{\partial f} = \frac{\alpha s}{\sqrt{s^2 + 4\alpha s f}},$$

$$\frac{\partial\lambda}{\partial s} = \frac{1}{2} \left( 1 + \frac{s + 2\alpha f}{\sqrt{s^2 + 4\alpha s f}} \right).$$

To consider the cost ( $C_s$ ) of attaining the survival rate  $s$ , for simplicity we assumed this cost increases linearly with small changes to the current survival rate so that the marginal cost was  $\partial C_s/\partial s = k$ . Similarly we assumed that the marginal cost for increasing fecundity was  $\partial C_f/\partial f = \kappa$  or (letting  $\phi = \kappa/k$ ),  $\partial C_f/\partial f = \phi k$ . The parameter  $\phi$  thus represents the marginal cost of managing fecundity relative to that of managing survival. We calculated the sensitivity of  $\lambda$  to the marginal cost of changing parameter  $p$  ( $= f$  or  $s$ ), which we called the ‘‘marginal efficiency’’ of managing  $p$ :  $\epsilon_p = \partial\lambda/\partial C_p = (\partial\lambda/\partial p) \div (\partial C_p/\partial p)$ . Hence,

the marginal efficiencies of managing fecundity and survival were

$$\epsilon_f = \frac{\partial\lambda}{\partial C_f} = \frac{\alpha s}{\phi k \sqrt{s^2 + 4\alpha s f}}$$

and

$$\epsilon_s = \frac{\partial\lambda}{\partial C_s} = \frac{1}{2k} \left( 1 + \frac{s + 2\alpha f}{\sqrt{s^2 + 4\alpha s f}} \right).$$

Under these assumptions, therefore, managers should focus on fecundity whenever  $\epsilon_f > \epsilon_s$  (i.e., when

$$\chi = \frac{\partial\lambda}{\partial f} \frac{\partial f}{\partial C_f} \bigg/ \frac{\partial\lambda}{\partial s} \frac{\partial s}{\partial C_s} = \frac{2\alpha s}{\phi (s + 2\alpha f + \sqrt{s^2 + 4\alpha s f})} > 1).$$

If the marginal efficiency of managing fecundity is greater than that of managing survival,  $\chi > 1$ , fecundity management is relatively less expensive (i.e., more efficient) than survival management. Alternatively, we could have used elasticities (de Kroon et al. 1986; Caswell 2001) and followed the same procedure (with a little extra effort),

$$\chi = \frac{\partial \ln \lambda}{\partial \ln f} \frac{\partial \ln f}{\partial C_f} \bigg/ \frac{\partial \ln \lambda}{\partial \ln s} \frac{\partial \ln s}{\partial C_s},$$

to arrive at the same result (see also Nichols & Hines 2002). Note that  $k$  dropped out of the expression for relative marginal efficiency  $\chi$ . The actual steepness of the slopes of survival and fecundity costs are irrelevant because they are assumed linear for small changes in  $s$  and  $f$ ; only the relative marginal cost ( $\phi$ ) counts. The case  $\chi = 1$  corresponds to where it is equally efficient to manage survival and fecundity. Solving for  $\chi = 1$  (producing the quadratic equation  $[\alpha - \phi]s^2 - 2\alpha\phi fs + \alpha\phi^2 f^2 = 0$ ) gave expressions for ‘‘critical’’ values of a parameter in terms of the other parameters. For example, the critical survival value, which gave  $\chi = 1$ , can be expressed as

$$s_\chi = f \frac{\phi}{1 - \sqrt{\phi/\alpha}}.$$

The expression can be rearranged to obtain critical values for the other parameters. From these expressions it follows that it is more efficient to manage fecundity ( $\chi > 1$ ) whenever  $f < f_\chi$ ,  $s > s_\chi$ ,  $\phi < \phi_\chi$  or  $\alpha > \alpha_\chi$ . However, constraining the parameters to be nonnegative meant that when the relative marginal cost of managing fecundity was greater than or equal to the juvenile:adult survival ratio,  $\phi \geq \alpha$ , it was always optimal to manage survival.

When the marginal efficiencies were equal for both survival and fecundity management ( $\chi = 1$ ), it technically did not matter whether we invested in survival or fecundity

but signaled a possible change in management strategy depending on whether the parameters were changing and in which direction. The state of the system could be mapped in *sf* space, in which case the condition  $\chi = 1$  describes a line  $s = mf$  of slope  $m = \phi / (1 - (\phi/\alpha)^{1/2})$ . Increasing fecundity alone resulted in moving below this line in *sf* space, which advised an increase in survival management. Similarly, increasing survival alone resulted in moving above the line, directing an increase in fecundity management. Therefore, optimal management entailed remaining on the  $s = f\phi / (1 - (\phi/\alpha)^{1/2})$  line, once it was reached. This required changing *f* and *s* in the ratio  $(1 - (\phi/\alpha)^{1/2})/\phi : 1$ . Because a unit change in *f* costs  $\phi$  times as much as a unit change in *s*, this required that future investment be divided in the ratio (fecundity:survival)

$$\left(1 - \sqrt{\phi/\alpha}\right) : 1,$$

when the marginal efficiencies of managing survival and fecundity are equal.

This simple rule is sensible for values of relative marginal costs that are less than the juvenile:adult survival ratio ( $\phi < \alpha$ ) when fecundity management is sometimes optimal. For low values of the ratio  $\phi/\alpha$  (as fecundity gets cheaper than survival to manage, or as juvenile survival increases relative to adult survival), one should invest more in fecundity. As  $\phi/\alpha$  increases (fecundity costs increase, relative survival of juveniles declines), one should invest more in survival. The proportion of the total budget invested in survival is always at least 50% (for  $\phi = 0$ ) and can be as high 100% (when  $\phi = \alpha$ , or  $\phi > \alpha$  as noted above). Conversely, the proportion invested in fecundity is between 0% and 50%. This investment split is only optimal when the vital rates are already in the optimal proportions for management. At other points in *sf* space, the optimal management strategy would be to invest in one rate or the other.

### Results and Discussion

We applied the approach to population projection matrices of varying complexity. We present the results in Table 1 and below explore further the implications of our method for some of the matrices.

For matrix **B** (or **C**, with  $\alpha = 1$ ), the critical survival values ( $s_\chi = \frac{\phi}{1 - \sqrt{\phi}} f$ , giving  $\chi = 1$ ) increased with increasing values of fecundity (*f*) and relative marginal cost ( $\phi$ ) of managing fecundity versus survival. We examined how the frequency of recommendations to manage either fecundity (*f*) or survival (*s*) changed for each parameter ( $f = 0.1, 0.2, \dots, 2.0$ ;  $s = 0.025, 0.050, \dots, 1.000$ ; and  $\phi = 2^{-4}, -3, -4$ ) over all factorial combinations of the other two parameters. As fecundity, *f*, or the relative cost of chang-

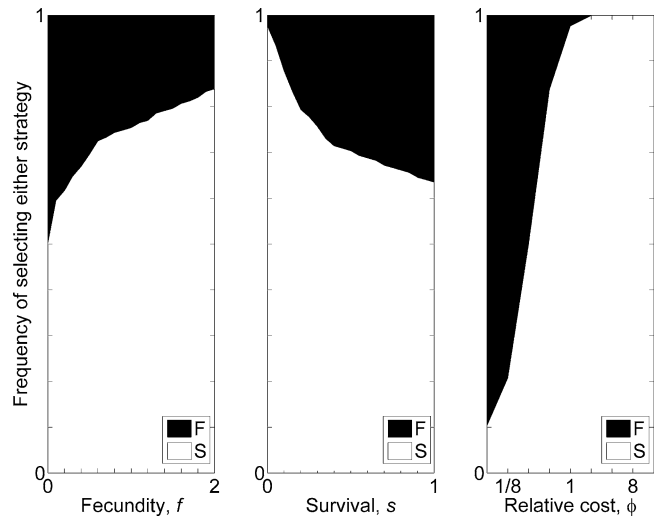
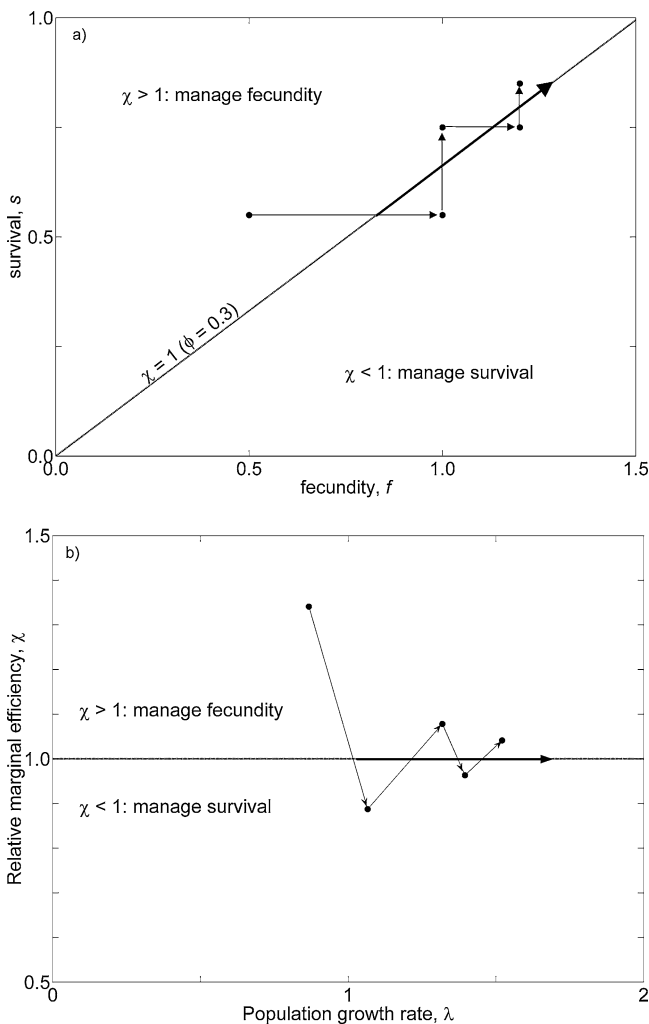


Figure 1. Frequency of choosing to manipulate fecundity (*f*, management denoted by F) or survival (*s*, S) for various parameter values (*f*, *s*) and relative marginal costs ( $\phi$ ) for matrix **B** in Table 1. For each parameter value, the graphs depict the frequency of choosing either management option, based on the relative marginal efficiency of fecundity versus survival management ( $\chi$ ), for all factorial combinations of the other parameters:  $f = 0.00, 0.25, \dots, 2.00$ ;  $s = 0.0, 0.1, \dots, 1.0$ ;  $\phi = 1/16, 1/8, \dots, 16$ .

ing it,  $\phi$ , increased, one was less likely to manage fecundity, and as survival (*s*) increased one was more likely to manage fecundity (Fig. 1).

A progression of management decisions can be followed for a hypothetical population (Fig. 2). We assumed matrix **B** applies, relative marginal costs are constant throughout,  $\phi = 0.3$ , and that the population starts with fecundity  $f = 0.55$  and survival  $s = 0.5$ . These assumptions give a long-term population growth rate of  $\lambda = 0.867$  and relative marginal efficiency (of fecundity vs. survival management) of  $\chi = 1.341$ . The first management step would therefore be to increase fecundity. Once the  $\chi = 1$  line (denoting equal marginal efficiencies) was crossed, managers would increase survival (second point), and so on. If population management was precise enough so that the  $\chi = 1$  line was reached exactly, optimal management would then require staying on this line (thick arrows, Fig. 2) by managing both parameters together in the fecundity:survival investment ratio of  $(1 - \phi^{1/2}) : 1$  (see worked example, above). Similar tactics have been prescribed for endangered species management, with the fund allocation between two or more species chosen to maintain the same marginal decrease in extinction probability (Possingham et al. 2002). In practice, parameter management costs should be reassessed periodically, and the relative marginal cost  $\phi$  recalculated, but we assumed  $\phi$  remains



**Figure 2.** Hypothetical trajectory of parameters under efficient strategies of population management, assuming a relative marginal cost of fecundity ( $\phi$ ) versus survival ( $s$ ) management of  $\phi = 0.3$  throughout, for matrix **B** in Table 1. (a) Population management depicted in  $sf$  parameter space. Either fecundity or survival is managed depending on which side of the  $\chi = 1$  line (where marginal efficiencies are equal) the actual parameter combination lies. When the parameter combination lies exactly on the  $\chi = 1$  line, optimal management requires staying on this line (thick arrow). (b) Same trajectory as (a) but mapped in  $\chi\lambda$  parameter space. In all cases shown, cost-exclusive elasticity analysis recommends managing survival.

constant here for purposes of demonstration. In this example, although both management actions resulted in increases in  $\lambda$  (i.e., the horizontal component), fecundity management decreased the value of relative marginal efficiency  $\chi$ , making survival management more likely to be optimal, and survival management increased  $\chi$ , making fecundity management more desirable (Fig. 2b). In con-

trast, for all points shown, a naïve application of elasticity analysis would advise focusing on survival management alone.

Assuming a proportional nonidentical relationship between juvenile and adult survival (the juvenile:adult survival ratio  $\alpha$  has been constrained to be  $\geq \phi$  as above), critical values of fecundity ( $f_\chi$ ) increased with increasing values of  $\alpha$  and survival ( $s$ ) and decreasing relative marginal costs of fecundity  $\phi$  (Fig. 3). Fecundity management is preferable in the parameter space below the surfaces in Fig. 3, becoming more attractive with lower values of  $\alpha$  (juvenile survival much less than adult survival) and with higher  $s$  and lower  $f$  and  $\phi$ , as seen in Fig. 1. This reveals an interesting dichotomy between juvenile and adult survival, attributable to their occurrence in separate life-history pathways (“loops”; van Groenendael et al. 1994). If juvenile survival is low relative to adult survival (low  $\alpha$ ), then fecundity management is likely to be preferable to survival management.

Management strategies for a species that has independent juvenile and adult survival rates (matrix **D** in Table 1) are summarized in Fig. 4, with  $\sigma$  as the relative marginal cost of managing juvenile versus adult survival (i.e.,  $\partial C_j / \partial j = \sigma k$ ; see Table 1). For each parameter, the figure depicts the relative frequency of choosing to manage fecundity ( $f$ ), juvenile survival ( $j$ ), or adult survival ( $s$ ) for factorial combinations of the other parameter values. As either fecundity or juvenile survival increased, management effort to increase that parameter decreased on average. In contrast, management investment in adult survival increased with adult survival rate. This contrasts with the combined-survival cases above where management investment into survival decreased with increasing survival rate (cf. Fig. 1b). Again we see the dichotomy between juvenile and adult survival suggested in the case of matrix **C** (above and Fig. 3): as  $f$  and  $j$  increase, one should be focusing more on juvenile survival and fecundity, respectively, with less focus on adult survival and whichever vital rate is increasing.

As the marginal costs of managing fecundity and juvenile survival increase relative to adult-survival management cost, management focus on fecundity and juvenile survival should decrease. This concept is also demonstrated in the unimodal nature of adult-survival management in the bottom-right graph of Fig. 4. An intriguing insight gained from partitioning juvenile and adult survival is that as fecundity got more expensive to manage, the vital rate managed in preference to fecundity depended on whether its cost was increased relative to that of adult survival (top-right graph Fig. 4; manage adult survival more) or juvenile survival (bottom-right Fig. 4; manage juvenile survival more). Although the changes were reasonably self-explanatory, the overall proportions of management effort between the three vital rates demonstrated that automatic application of sensitivity/elasticity results may turn out to be inappropriate in many circumstances.

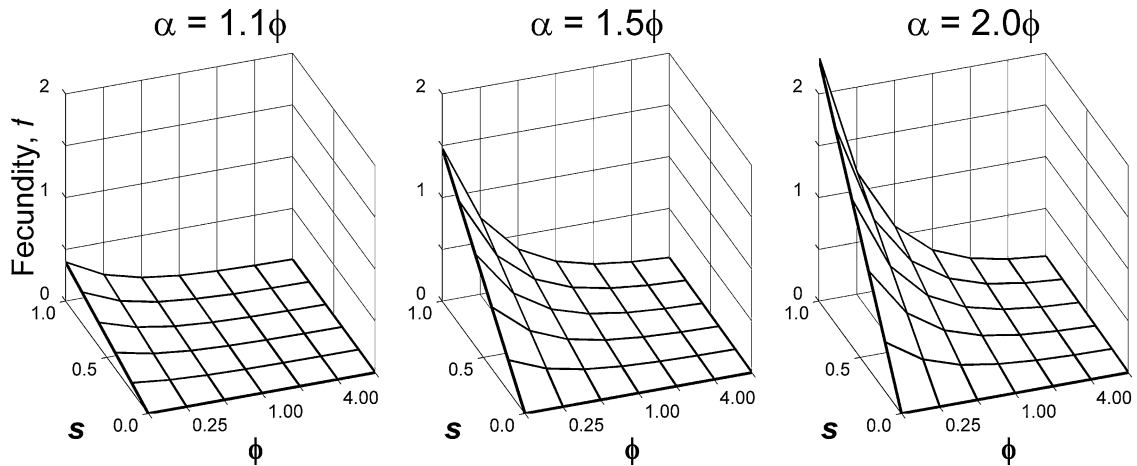


Figure 3. Critical fecundity values ( $f_c$ ), at which fecundity management and survival management are equally efficient strategies for effecting population change, for matrix  $C$  in Table 1. The critical values are shown as functions of survival ( $s$ ) and the relative marginal costs of fecundity versus survival management ( $\phi$ ) for different levels of juvenile:adult survival ratio ( $\alpha$ ) relative to  $\phi$ . Fecundity management is preferable to survival management if the fecundity value lies below the surfaces shown.

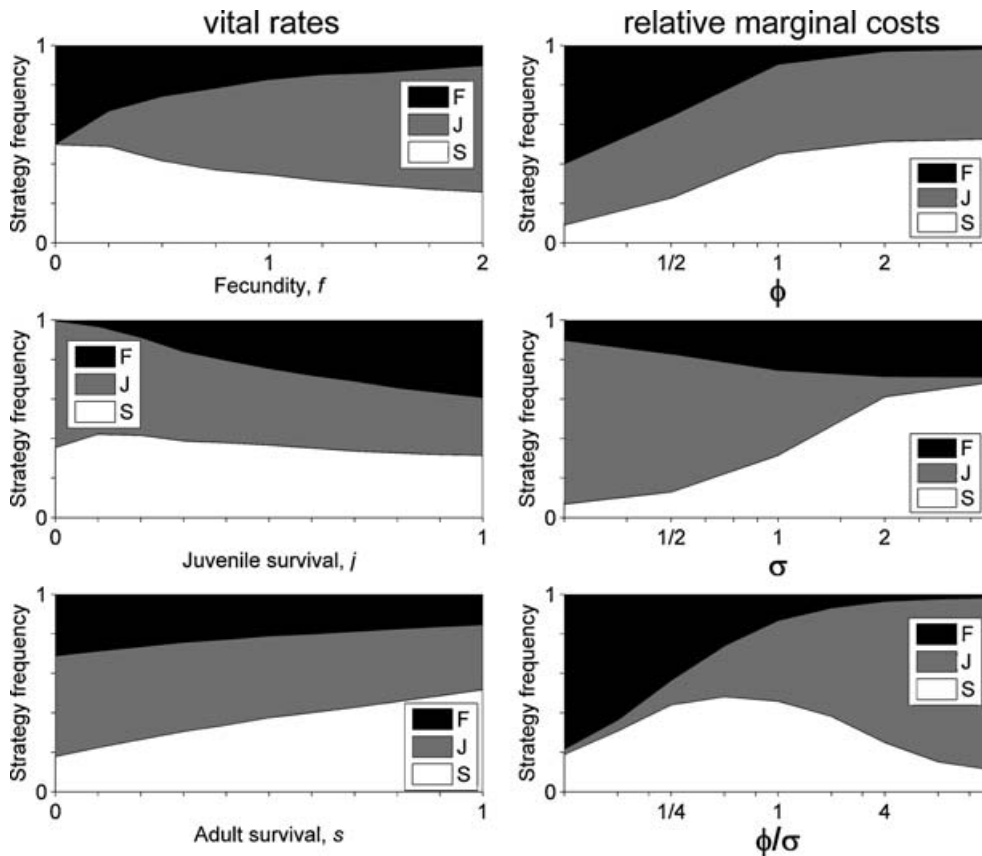


Figure 4. Frequency of choosing to manipulate fecundity ( $f$ , management denoted by  $F$ ), juvenile survival ( $j$ ,  $J$ ), or adult survival ( $s$ ,  $S$ ) for various values and population-management costs of matrix  $D$  parameters. Each graph depicts the frequency of choosing each management option at a given parameter value for all combinations of the other parameters:  $f = 0.00, 0.25, \dots, 2.00$ ;  $j = 0.0, 0.1, \dots, 1.0$ ;  $s = 0.0, 0.1, \dots, 1.0$ ; relative marginal cost of fecundity versus adult survival management  $\phi = 0.25, 0.50, 1.00, 2.00, 4.00$ ; relative marginal cost of juvenile versus adult survival management  $\sigma = 0.25, 0.50, 1.00, 2.00, 4.00$ . The ratio  $\phi/\sigma$  ( $= 0.0625, 0.125, \dots, 8, 16$ ) gives the marginal costs of fecundity management relative to juvenile survival management (high  $\phi/\sigma$  implies more expensive fecundity management). Relative marginal costs are plotted on a  $\log_2$  scale.



### Application to Conservation

To demonstrate the methods we developed, we applied them to investigate management strategies for the Helmeted Honeyeater (*Lichenostomus melanops cassidix*, Meliphagidae), an endangered bird of southeastern Australia. We first consider a simplified heuristic treatment, describing a more realistic analysis below. McCarthy et al. (2004) outline the biology of *L. m. cassidix* and provide a population projection matrix corresponding to our matrix **B** with  $s = 0.8$  and  $f = 0.4$ . Previous management efforts increased fledging rate by 16%, at a cost of \$5112 (supply and installation of 12 nest protectors; Helmeted Honeyeater recovery team, unpublished data); a 16% increase in fecundity increases  $f$  by 0.064. It is almost impossible to directly increase survival rate, but \$50,000 would finance revegetation of habitat that could be used as breeding habitat by young dispersers and thus “buy” an extra pair (albeit with a 15-year delay for maturation of the woodland). On the basis of a current population of around 20 breeding females (McCarthy et al. 2004), one extra female approximately translates to an equivalent increase in  $s$  of  $0.8(1/20) = 0.04$ .

To standardize the parameter increases to a small amount, we considered the costs of increasing  $f$  and  $s$  by 0.01 each; these were  $\$5112 \times (0.01/0.064) = \$798.75$  and  $\$50,000 \times (0.01/0.04) = \$12,500$ , respectively (assuming linearity) or relative marginal costs of  $\phi = 0.0639$ . This yielded a relative marginal efficiency of  $\chi = 8.3865$ , which is substantially greater than 1, indicating that fecundity should be the focus of management efforts. Put another way, spending \$10,000 on fecundity management would increase  $f$  to 0.5252 and  $\lambda$  from 1.093 to 1.162 (+6.3%), and spending this amount on survival ( $s$ ) would increase  $s$  to 0.808 and  $\lambda$  to just 1.101 (+0.7%). The cost of revegetating habitat for one pair would need to be at most \$5961.95 ( $= 50,000/8.3865$ ) to make survival management optimal (at  $\chi \leq 1$ ). At this value,  $\phi = 0.5359$  ( $= 0.0639 \times 8.3865$ ), so fecundity would still be rela-

tively cheap to manage but only just as efficient as survival management at increasing the population growth rate. In contrast, elasticity analysis excluding costs would clearly recommend focusing on survival management:  $\partial\lambda/\partial f = 0.5774$ , elasticity for fecundity = 0.2113; and  $\partial\lambda/\partial s = 1.0774$ , elasticity for survival = 0.7887. In this case the naïve use of elasticity values to guide management would have yielded a very poor result, whereas a rash decision is avoided by explicitly including costs in the calculations.

For a more detailed analytic example, we applied our method to management of the koala (*Phascolarctos cinereus*). Although declining in parts of its range, other populations are thriving and are considered overabundant (Melzer et al. 2000; McLean 2003; Department of Sustainability and Environment 2004). This example deals with a management goal of population reduction, with the explicit objective of decreasing the long-term population growth rate given by the dominant eigenvalue  $\lambda$ . We used data from the koala population at Snake Island, Victoria, Australia, with a population projection matrix as shown in Table 2 (McLean 2003). We considered subdermal contraception (Middleton et al. 2003) and translocation as alternative management strategies, both of which we assumed are targeted equally across all stage classes except the first (i.e., equal probability of capture across all stage classes 2–9). Management costs per (female) koala were estimated as \$100–\$120 for contraception and \$300–\$400 for translocation (Harbutt 2004). We assumed the stage distributions of fecundity and survival rates are preserved due to the equal management effort across stage classes and are expressed relative to the final-stage vital rates (similar to matrix **H** in Table 1).

With these assumptions, the average per-capita costs of contraception and translocation (\$110 and \$350, respectively) gave marginal costs of changes in vital rates of  $\partial C_f/\partial f = 9338N_{2-9}$  and  $\partial C_s/\partial s = 574.7N_{2-9}$  (where  $f$  and  $s$  are the underlying fecundity and survival rates and  $N_{2-9}$  is the number of individuals in stage classes 2–9; full details of the calculations are given in the Appendix). The

**Table 2.** Stage-based population projection matrix for the koala population on Snake Island, Victoria, Australia (data from McLean 2003).\*

Stage at time $t + 1$	Life stage (tooth-wear class) at time $t$								
	1	2	3	4	5	6	7	8	9
1	0	0.3026	0.1663	0.1244	0.0891	0.0556	0.0394	0.0226	0.0118
2	0.9908	0.5359	0	0	0	0	0	0	0
3	0	0.4580	0.4550	0	0	0	0	0	0
4	0	0	0.5000	0.0655	0	0	0	0	0
5	0	0	0	0.7272	0.2216	0	0	0	0
6	0	0	0	0	0.4617	0.2265	0	0	0
7	0	0	0	0	0	0.3538	0.1267	0	0
8	0	0	0	0	0	0	0.4693	0.4247	0
9	0	0	0	0	0	0	0	0.1762	0.6090

\*The population is divided into stages based on tooth wear. Top row elements give production of young by each older stage class, diagonal elements represent the proportion staying within a stageclass, and subdiagonal elements represent the proportion advancing to the next stageclass.

relative marginal cost of contraception versus translocation was  $\phi = 16.2480$ . The population projection matrix had a dominant eigenvalue (long-term growth rate) of  $\lambda = 1.0407$ , with sensitivities to changes in fecundity and survival of  $\partial\lambda/\partial f = 21.0844$  and  $\partial\lambda/\partial s = 1.3010$ , respectively (following methods in Caswell [2001]). This gave marginal efficiencies of contraception and translocation of  $\epsilon_f = 0.002258/N_{2-9}$  and  $\epsilon_s = 0.002264/N_{2-9}$ , respectively, or a relative marginal efficiency of  $\chi = 0.9974$ . This value is very close to unity, indicating that it is optimal to undertake contraception and translocation simultaneously. To maintain the underlying fecundity and survival rates close to the optimal ratio (as at present), future management should focus on both fecundity and survival simultaneously in the investment ratio of 110:350 (the ratio of their per-capita costs: this apparently simple expression arises from our assumption of equal management effort across stage classes for both strategies). At first it may seem counterintuitive to invest more than three times as much money in survival as fecundity when the two strategies are almost equally efficient, but this recommendation integrates costs with sensitivities to maintain the optimal fecundity: survival ratio and thus ensure the greatest effect on  $\lambda$ . For example, investing exclusively in contraception would quickly result in translocation becoming relatively more efficient (as fecundity dropped) so that any additional investment in contraception is relatively wasteful (cf. Fig. 2a).

Unsurprisingly, the management recommendation changed with changes to the estimated costs for either strategy. The most translocation-favorable combination of estimated costs (\$120 per koala for contraception, \$300 per translocated individual) gave a relative marginal efficiency of  $\chi = 0.7837$ , indicating that translocation is the better option in this situation, whereas the most contraception-favorable cost estimates (\$100/contraception, \$400/translocation) gave  $\chi = 1.2539$ , which supports contraception. In contrast, the combined elasticities of fecundity and survival were 0.2387 and 0.7613, respectively, leading to a cost-negligent conclusion that translocation would always be more than three times as desirable as contraception.

To demonstrate our method numerically, we revisited the Helmeted Honeyeater case study, which included many broad assumptions in our first example (above). For example, the dominant eigenvalue  $\lambda = 1.093$  predicts a growing population when the population is density independent and at its stable-stage distribution. In the case of the Helmeted Honeyeater, however, density dependence may take effect through juveniles remaining as nonbreeding birds in the absence of vacant territories for them to occupy. Density dependence can be incorporated into perturbation analysis of matrix models by examining elasticities of equilibrium and mean population sizes to changes in vital rates (Grant & Benton 2003). In the first example we also ignored the time delay that

would occur before changes in habitat would lead to an increase in survival. If this delay was taken into account, the benefit of increasing fecundity would be even greater relative to that of increasing survival. The recommendations could also change, however, if recurring year-to-year costs of ongoing fecundity or survival management were included with some element of economic discounting.

McCarthy (1996) describes an individual-based model of the Helmeted Honeyeater population, which includes spatial structure, density dependence, and demographic and environmental stochasticity. We used this model to investigate the relative efficiency of management decisions to invest in survival or fecundity, and thus the robustness of our earlier heuristic result to inclusion of more realistic factors. We assumed a total management budget of \$50,000, which could be used either for planting habitat for one extra pair (to mature 15 years later) or buying nest protectors over a 50-year period. A lump sum of \$50,000 is equivalent to a 50-year annual payment stream of \$2238 (discounted at 4% per annum), which we assumed would increase fecundity by 7% ( $= 0.16[\$2238]/\$5112$ ; see above).

We ran the model for 10,000 stochastic iterations and measured how the expected minimum population size (EMP; McCarthy & Thompson 2001) over the 50-year time frame changed with each strategy. Buying extra habitat produced an EMP of 44.0 birds, an increase of 1.5 birds compared with no management (EMP = 42.5). Investing in fecundity produced a more favorable outcome for the same financial outlay (EMP = 45.1, an increase of 2.6 birds compared with no management). Expressing these results in terms of the efficiency of each strategy, efficiency of fecundity management was 0.052 (increase in EMP from fecundity management  $[\Delta\text{EMP}/\Delta f]$ , per \$1000 spent on fecundity  $[\Delta f/\Delta C_f]$ , analogous to our  $[\partial\lambda/\partial f]/[\partial f/\partial C_f]$  above) and efficiency of survival management was 0.030, giving a relative marginal efficiency of  $\chi = 1.73$ . Further simulations showed that the increase in fecundity would have to be as low as 2.7% (i.e., investing \$19,400 rather than \$50,000 in nest protection) to produce an EMP of 44.0. This suggests a nonlinear response of EMP to changes in fecundity, resulting in nest protection being preferable to habitat provision over an even greater range of costs than suggested by the initial value of relative marginal efficiency.

In this more realistic model, fecundity management outperformed survival management by 73% when the performance measure (improvement in EMP) was standardized for cost. Our simpler first example favored fecundity management by a factor of 8.4, whereas elasticity analysis favored survival management by a factor of 3.7. Therefore, the choice of model will favor different parameters for management (e.g., fecundity or survival) to different extents in different situations. In this case, the recommendations resulting from the first heuristic example, which were later supported by the realistic model,

provided a valuable first guideline, not least by questioning the elasticity-based indication that survival would be the best management target. Given the importance of the choice of model, we argue that models that neglect cost altogether are likely to be unsuitable for making conservation decisions.

The estimation of management costs, and other economic assumptions that may affect the model, such as the appropriate discount rate, should be given careful consideration. In the absence of cost information for a particular species, one approach could be to conduct a metaanalysis of management costs for similar species and then test the robustness of the recommendations to changes in the cost structure. Additionally, the marginal costs of managing parameters could be made nonlinear with each parameter, but here we restricted our analysis to decisions regarding what the managers should do immediately. Because perturbation analysis is based on the local behavior of changes in parameters and growth rate, the linearity of marginal costs is therefore a reasonable assumption for this exercise. Preliminary work indicates that, for nonlinear cost structures, the relative marginal cost ( $\phi$  in the linear case) remains the crucial variable. Nonetheless, the assumption of linear marginal costs should be critically evaluated before application of this method to management. Nonlinearities would likely occur particularly as biological limits are approached, for example as the survival rate  $s$  approaches 1. Over a prolonged period of survival or fecundity management, therefore, further changes may become increasingly expensive to produce, thus modifying  $\phi$  over time.

Alternatively, managers could experience economies of scale whereby the marginal cost decreases as the managed vital rate is increased, perhaps due to high setup or training costs for a given management strategy. The state of equal marginal efficiencies,  $\chi = 1$  (where dual management is optimal) can therefore be reached not only by changes in vital rates but also by the changes in the relative marginal cost as management proceeds, and managers should regularly reassess their cost-based decisions in this light. Following one fixed strategy for an extended period may lead to increasing inefficiency if the ranking of marginal efficiencies changes (Fig. 2b). The knife-edge result of the koala example further demonstrates that awareness of costs, and ongoing awareness of possible future changes in costs, can be critical to optimal management.

In practice, rather than focusing on individual matrix elements, managers must often target an underlying parameter that can affect more than one matrix element. For example, translocation of koalas affected both the stasis (diagonal) and growth (subdiagonal) elements. Our analytic results (Table 1) have a reasonably simple form partly because the matrix elements are usually the same as (or proportional to) the underlying vital rates. Although our analytic method requires relatively simplistic matrices to

produce amenable analytical solutions, the procedure can also be followed numerically if the vital rates and the relative costs of managing them can be estimated, as seen above. Indeed, any of the range of methods of calculating sensitivity coefficients (e.g., McCarthy et al. 1995; Cross & Beissinger 2001) could be modified to incorporate management costs by dividing the coefficients by the marginal costs of management. In a similar vein, the method can be adapted to pursue objectives other than the maximization of a deterministic population's growth rate. For example, in a stochastic system this could involve using stochastic growth rate  $\log \lambda_s$  (Benton & Grant 1996; Caswell 2001; Tuljapurkar et al. 2003), mean geometric growth rate, mean time to extinction, expected minimum population size (McCarthy & Thompson 2001) or probability of extinction (Lande 1993), and following the same approach.

This procedure may also have application to conservation decisions based on the metapopulation capacity concept (Hanski & Ovaskainen 2000), wherein the viability of a metapopulation can be expressed as the dominant eigenvalue of a landscape matrix, the elements of which reflect patch areas, distance between patches, and mean migration distances. Managers of metapopulations could use the procedure outlined here to determine, for example, whether it is more efficient to improve interpatch dispersal, or the size of patches, based on the relative costs of managing those particular landscape elements. In essence the strategy becomes one of including cost structures within any modeling exercise, and what we advocate is the explicit consideration of costs in making decisions regarding the management of populations for conservation purposes.

## Acknowledgments

We thank B. Brook, C. Catterall, H. Caswell, J. Elith, S. Heppell, E. Main, W. Getz, C. Thompson, B. Wintle, P. Zuidema, and an anonymous reviewer for fruitful discussion and comments on earlier versions of the manuscript. This research was funded by an Australian Research Council grant to H.P.P. and M.A.M.C.C.

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### Appendix. Calculations for Koala Management Case Study

We assumed koalas are captured with equal probability across all stage classes 2-9 (i.e., nondependent individuals) and therefore that the two management strategies (manage fecundity via subdermal contraception; manage survival within the population via translocation) are targeted equally across all stage classes except the first. However, individuals in the first stage class (dependent young) are translocated with their mothers at no additional cost. We therefore expressed the matrix elements as functions of underlying fecundity ( $f$ ) and survival ( $s$ ) rates. Specifically, the Snake Island koala population projection matrix (Table 2) was expressed as

$$\begin{pmatrix} 0 & p_2f & p_3f & \dots & p_8f & p_9f \\ \gamma_1q_1s & (1-\gamma_2)q_2s & 0 & \dots & 0 & 0 \\ 0 & \gamma_2q_2s & (1-\gamma_3)q_3s & \dots & 0 & 0 \\ \vdots & \ddots & \ddots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & (1-\gamma_8)q_8s & 0 \\ 0 & 0 & 0 & \dots & \gamma_8q_8s & (1-\gamma_9)q_9s \end{pmatrix}$$

where  $p_i$  and  $q_i$  relate the stage-specific matrix elements to the underlying fecundity ( $f$ ) and survival ( $s$ ) rates, respectively, and  $\gamma_i$  is the proportion of survivors in class  $i$  advancing to class  $i + 1$  the following year (with  $\gamma_1 = 1$  and  $\gamma_9 = 0$ ). For convenience we set the underlying vital rates ( $f$  and  $s$ ) equal to those of the oldest stage class in our calculations (i.e.,  $p_9 = q_9 = 1$ ).

Let  $N$  be the total population with  $N_i$  the number in each stage class, and let  $\$M$  be the available management budget. For fecundity management, if it costs  $c_F$  to dart one individual, then an overall investment of  $\$M$  in fecundity management will give an allocation to class  $i$  of  $\$M_i = MN/N_i$  (i.e., distributed pro rata across stage classes), treating  $M_i/c_F$  individuals. Without contraception, the number of young born to class  $i$  mothers would be  $p_{if}N_i$ , becoming  $p_{if}(N_i - M_i/c_F)$  after contraception, a reduction in number of newborns of  $p_{if}M_i/c_F$ , or a reduction in the class  $i$  fecundity rate of  $\Delta f_i = p_i M_i / c_F N_i$ . The marginal cost of

contraception in class  $i$  is thus  $\partial C_{f_i} / \partial f_i = M_i / \Delta f_i = c_F N_i / p_i f$ , and the marginal cost of contraception in all classes is

$$\frac{\partial C_f}{\partial f} = \sum_{i=2}^9 \frac{\partial C_{f_i}}{\partial f_i} \frac{\partial f_i}{\partial f} = \sum_{i=2}^9 \frac{c_F N_i}{p_i f} p_i = c_F N_F / f,$$

where the total manageable population is given by  $N_F = N_2 + N_3 + \dots + N_9$ .

For managing survival within the population ( $q_i s$ ) of an individual in stage class  $i$ , we treat growth  $\gamma_i q_i s$  and stasis  $(1 - \gamma_i) q_i s$  separately. As with fecundity management, above, if it costs  $c_S$  to remove one individual, then a translocation budget of  $\$M$  acting pro rata among stage classes will remove  $M_i/c_S$  individuals from class  $i$ . Without translocation, the number in stage class  $i$  advancing to class  $i + 1$  would be  $\gamma_i q_i s N_i$ , becoming  $\gamma_i q_i s (N_i - M_i/c_S)$  with translocation, a reduction in the number advancing of  $\gamma_i q_i s M_i/c_S$  or a reduction in the class  $i$  growth rate of  $\Delta s_{i,\gamma} = \gamma_i q_i M_i s / c_S N_i$ . Similarly, the reduction in class  $i$  stasis is  $\Delta s_{i,1-\gamma} = (1-\gamma_i) q_i M_i s / c_S N_i$ , giving an overall reduction in class  $i$  survival of  $\Delta s_i (= \Delta s_{i,\gamma} + \Delta s_{i,1-\gamma}) = q_i M_i s / c_S N_i$ . The marginal cost of translocating class  $i$  is thus  $\partial C_{s_i} / \partial s_i = M_i / \Delta s_i = c_S N_i / q_i s$ , and the marginal cost of translocating all classes is  $\partial C_s / \partial s = c_S N_S / s$  (letting  $N_S = N_2 + N_3 + \dots + N_9 = N_F$  as above).

The relative marginal cost of fecundity versus survival management is  $\phi = (\partial C_f / \partial f) / (\partial C_s / \partial s)$ , or  $\phi = \frac{c_F N_F s}{c_S N_S f}$ . The marginal efficiency of contraception is  $\epsilon_f = (\partial \lambda / \partial f) / (\partial C_f / \partial f) = (\partial \lambda / \partial f) (f / c_F N_F)$  and similarly the marginal efficiency of translocation is  $\epsilon_s = (\partial \lambda / \partial s) (s / c_S N_S)$ . The relative marginal efficiency of fecundity versus survival management is therefore  $\chi = \epsilon_f / \epsilon_s = \frac{f c_S N_S}{s c_F N_F} \frac{\partial \lambda / \partial f}{\partial \lambda / \partial s}$  or, for  $N_S = N_F$ , the cost of a proportional change in  $s$  ( $c_S / s \Delta s$ ) divided by the cost of a proportional change in  $f$ .

Using the values given in Table 2, and sensitivity analysis methods described in Caswell (2001), we calculated the sensitivities  $\partial \lambda / \partial f = 21.0844$  and  $\partial \lambda / \partial s = 1.3010$ . Per-capita management costs of  $c_F = \$110$  and  $c_S = \$350$  (see text) give marginal costs of  $\partial C_f / \partial f = 9338 N_F$  and  $\partial C_s / \partial s = 574.7 N_S$  for fecundity and survival management, respectively. The marginal efficiencies are thus  $\epsilon_f = 21.0844 / 9338 N_F = 0.002258 / N_F$  and  $\epsilon_s = 0.002264 / N_S$ , giving (as  $N_F = N_S$  here) a relative marginal efficiency of fecundity versus survival management of  $\chi = 0.9974$ .

