Sensitivity analysis of equilibrium population size in a density-dependent model for Short-tailed Shearwaters

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Abstract

Population models are often used to guide conservation management decisions. Sensitivity analysis of such models can be useful in setting research priorities, by highlighting those parameters that have the most influence on population growth rate. Much of the work on sensitivity analysis in this context has been for density-independent models. We present a sensitivity analysis of a density-dependent model for a population of Short-tailed Shearwaters (*Puffinus tenuirostris*), in which the output of interest is the equilibrium population size, N_e. We calculate the sensitivity and elasticity of N_e to both the equilibrium parameter value and the strength of density-dependence associated with each input parameter. The rankings of the sensitivities and elasticities associated with the strength of density-dependence are of particular interest, as they cannot be predicted from a sensitivity analysis for the corresponding density-independent model. In calculating sensitivities we make use of the characteristic equation of the model, rather than the left and right eigenvectors of the projection matrix. In order to check the robustness of our conclusions to the strength of density-dependence specified for each input parameter, we consider a range of relative strengths. Within this range there are no major effects on the rankings. The largest sensitivities of N_e to the strength of density-dependence were for breeder survival, emigration and immigration; the largest corresponding elasticities were for emigration, immigration and breeder skipping rate.
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1. Introduction

In using a population model to guide management of a species, perturbation analysis is a valuable tool for evaluating the relative effectiveness of conservation management decisions and highlighting those parameters that have the greatest influence on model outputs, such as population growth rate. This type of analysis can be carried out mathematically using sensitivities and elasticities, or numerically by analysing simulation output (Burgman et al., 1993; Caswell, 2001; Hamby, 1994; Slooten et al., 2000; Swartzman and Kaluzny, 1987). Perturbation analysis is particularly valuable when our knowledge of a species life-history and the potential costs and benefits of various management alternatives is limited, when research budgets are constrained and when decisions must be made quickly.

Linear deterministic models are relatively easy to construct, analyse and interpret, and much of the published work that uses perturbation analysis for population management involves models that are

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density-independent (Caswell, 2001; Russell, 1999; Slooten et al., 2000). However, these models forego much of the complexity that we know exists in the real world. Populations do not increase without limit, abundance being determined by a number of factors and processes, including those that are density-dependent. Density-dependent processes may play an important role in population regulation, although there is still debate on this issue. The fact that density-dependence can be difficult to detect in natural populations has prolonged this debate.

Given that density-dependence can be difficult to estimate, it is important to explore how our assessment of the form and strength of density-dependence will affect our interpretation of population models. This will help us decide whether we need to include density-dependence in a model, and how accurately it needs to be specified. The probability of extinction has been shown to be sensitive to the presence and form of density-dependence chosen (Ginzburg et al., 1990; Beissinger and Westphal, 1998). Neubert and Caswell (2000) explored the effects of density-dependence on population dynamics in terms of model equilibria and bifurcations. Grant and Benton (2000) considered the extent to which a standard density-independent sensitivity analysis would provide reliable conclusions for a population that is density-dependent and experiencing environmental stochasticity.

The purpose of this paper is to show how sensitivities and elasticities can be used to help set research priorities for management of a species when the population model is density-dependent. In particular, we aim to determine for which parameters it may be important to measure density-dependence. We focus on the same population as that was considered in Hunter et al. (2000), namely the Short-tailed Shearwaters (*Puffinus tenuirostris*) on Fisher Island, in the Bass Strait, Australia.

2. Density-independent model

The Short-tailed Shearwaters is a medium-sized, burrow-nesting procellariiform seabird. They breed annually in south-eastern Australia, mainly on islands around Tasmania, and migrate to northern Pacific waters for the Australian winter. They are the most abundant seabird in Australia, with individual colonies

ranging in size from a few hundred to several million pairs (Serventy, 1967; Serventy and Curry, 1984; Marchant and Higgins, 1990; Wooller and Bradley, 1999).

The deterministic population model we consider is based on the one described in Hunter et al. (2000), which also provides background to the study. The model is for females only, and is stage-structured. Prebreeders are classified by age (1–15) and postbreeding females by "breeding age" (0–25), which is the number of years *since* an individual's first breeding attempt (Fig. 1). In each year following the initial breeding attempt, fecund females are classified as breeders and non-breeders. Each breeding female is assumed to lay one egg. The number of eggs that survive to fledging is determined by a parameter for breeding success. Survival from fledging to 1 year is determined by a parameter for juvenile re-appearance rate. Immigrants enter the model at prebreeder age 3. Prebreeders are allowed to begin breeding between the ages of 2 and 15 and are also subject to emigration from age 3. A parameter for "probability of first breeding" controls the rate of flow of females from each prebreeder age cohort into the breeding part of the population. Breeders and non-breeders that reach breeding age 25 and survive another year are cycled back into the year-25 breeding and non-breeding age classes. We assume here that skipping rate, breeding success, breeder survival and non-breeder survival do not depend on age.

If the number of females of breeding age i that can potentially breed at time t is written as $N_i(t)$, the projection equations for the model are

$$N_0(t+1) = m \sum_{\alpha=0}^{15} \mu_\alpha \sum_{i=0}^{25} N_i(t-\alpha), \qquad (1)$$

$$N_{i+1}(t+1) = sN_i(t), \quad i = 0, 1, \ldots, 23, \qquad (2)$$

$$N_{25}(t+1) = s\{N_{24}(t) + N_{25}(t)\}, \qquad (3)$$

where m is fecundity (female chicks per female), μ_α is the probability that a fledged chick will survive α years as a prebreeder before entering the breeding population, and s is the annual survival rate for a breeding female.

For consistency, we use the same notation for the input parameters as in Hunter et al. (2000), and as shown in Table 1. The parameters m, s and μ_α can be
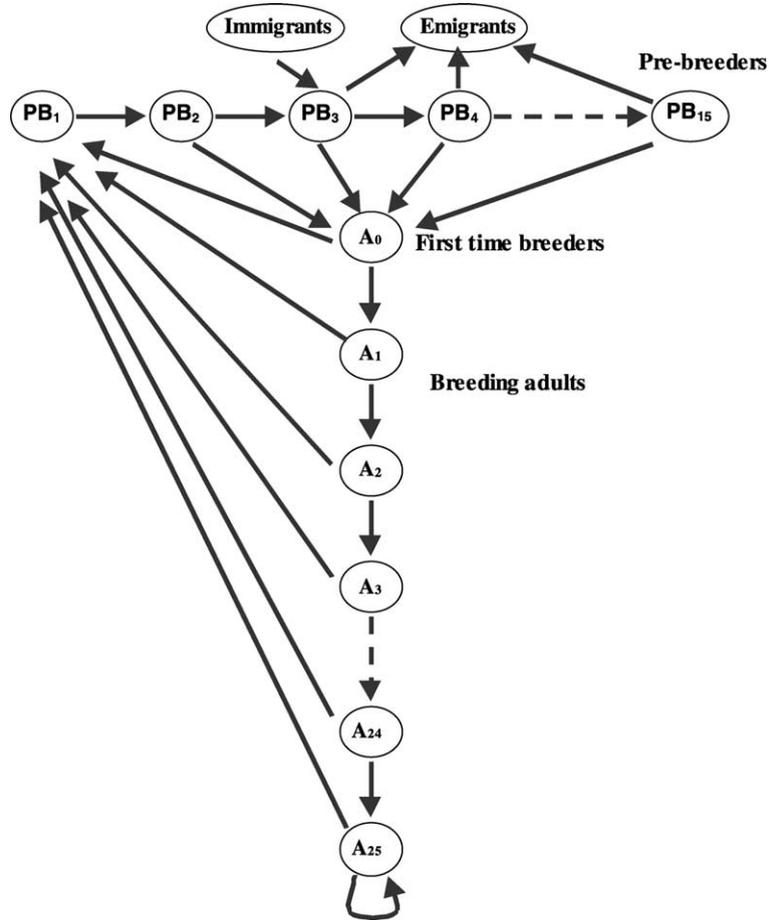
Fig. 1. Life-cycle graph for the Short-tailed Shearwater model. PB_x: prebreeder of age x and A_x: adult of breeding age x.

Table 1
Notation for the model parameters, together with their estimated values (Hunter et al., 2000)

Name	Parameter	Estimate
PFB	Scaling factor for the probability of first breeding	1.000
PST	Probability prebreeders stay at colony each year after prebreeding age class 3	0.755
IMM	Ratio of immigrants to year 2 natal prebreeders entering prebreeder age class 3	1.222
BRK	Probability that a breeding bird skips a breeding season	0.314
BS	Breeding success	0.306
JR	Juvenile reappearance rate from fledging to year 1	0.583
BRS	Breeder survival	0.912
NBRS	Non-breeder survival	0.912
PBR1	Prebreeder reappearance probability from year 1–2	0.867
PBR2	Prebreeder reappearance probability from year 2–3	0.923
PBR3	Prebreeder reappearance probability from year 3 onwards	0.912

The mean of the estimated population size was approximately 150.

written in terms of the input parameters as follows

$$m = \text{BS} \, (1 - \text{BRK}) \, \text{JR}, \tag{4}$$

$$s = \text{BRS} \, (1 - \text{BRK}) + \text{NBRS} \, \text{BRK}, \tag{5}$$

$$\mu_0 = \text{PFB} \, P_1, \tag{6}$$

$$\mu_1 = \mu_0 \, \text{PBR1} \, \left(\frac{1 - P_1}{P_1} \right) P_2, \tag{7}$$

$$\mu_2 = \mu_1 \, \text{PBR2} \, (1 + \text{IMM}) \left(\frac{1 - P_2}{P_2} \right) P_3, \tag{8}$$

$$\mu_3 = \mu_2 \, \text{PBR3} \, \left(\frac{1 - P_3}{P_3} \right) P_4, \tag{9}$$

$$\mu_\alpha = \mu_{\alpha-1} \, \text{PBR3} \, \text{PST} \, \left(\frac{1 - P_\alpha}{P_\alpha} \right) P_{\alpha+1},$$
$$\alpha = 4, 5, \ldots, 15, \tag{10}$$

where P_α is the probability that a prebreeder of age $\alpha-1$ enters the breeding population the following year.

The model we use differs slightly from the "average breeder" model of Hunter et al. (2000) in two ways. First, non-breeders are not explicitly modelled: they are allowed for by assuming that a fraction of each breeding age class does not breed (see Eq. (4)). Second, the manner in which we calculate the sensitivity coefficient for the parameter PFB differs from the approach adopted by Hunter et al. (2000). Hunter et al. (2000) varied the parameter PFB whilst keeping the expected age of first breeding constant. We vary the parameter PFB and make no attempt to control the expected age of first breeding: this leads to fewer constraints on the model dynamics, at the expense of not matching the data so closely.

3. density-dependent model

Suppose the value of each input parameter at time t is a function of the number of female breeders, $N(t) = \sum_{i=0}^{25} N_i(t)$. Specifying the form of this dependence for each parameter will to some extent be arbitrary, due to the lack of data. Indeed, one of the key motivations for carrying out this analysis is to assess which of the density-dependent relationships are the most important to quantify. Even if such data are difficult or impossible to collect, it might still be important to

assess this dependence. In a review of seven possible functional forms for density-dependence in survival, Bellows (1981) recommended one that has a flexible form and involves only two parameters (Model 5 therein; see Maynard Smith and Slatkin, 1973). Using a slightly different notation from Bellows (1981), we write this function as

$$\ln \left(\frac{X(N)}{1 - X(N)} \right) = a + b \ln(N), \tag{11}$$

where $X(N)$ is the value of the parameter X at population size N (from hereon we do not explicitly show the dependence of N upon time). Note that use of N rather than $\ln(N)$ in this equation would lead to a function that is less flexible (Bellows, 1981; Usher, 1972). Eq. (11) is a reparametrisation of the generalised Beverton and Holt function (Beverton and Holt, 1957; Maynard Smith and Slatkin, 1973), and can be rewritten to explicitly show the form of density-dependence as

$$X(N) = \frac{1}{1 + e^{-a} N^{-b}}. \tag{12}$$

Eq. (11) can be used directly for those parameters that vary between zero and one. The parameters IMM, BS and PFB do not satisfy these constraints, so we rewrite them in terms of parameters that do, as follows

$$\text{IMM} = \frac{P_{\text{IMM}}}{1 + P_{\text{IMM}}}, \qquad \text{BS} = \frac{P_{\text{BS}}}{2},$$
$$\text{PFB} = \frac{P_{\text{PFB}}}{\max(P_\alpha)}. \tag{13}$$

Density-dependence for each of these parameters is then achieved by applying the relationship in Eq. (11) to the parameters P_{IMM}, P_{BS} and P_{PFB}.

For each parameter X, we can specify a value for a in Eq. (11) by substituting the estimates of X and N that have been obtained for the study population on Fisher Island. This leads to

$$a = \ln \left\{ \frac{X(N_{\text{FI}})}{1 - X(N_{\text{FI}})} \right\} - b \ln(N_{\text{FI}}), \tag{14}$$

where N_{FI} is the population size on Fisher Island. Estimates of $X(N_{\text{FI}})$ are given in Table 1, and we chose the value of N_{FI} to be the mean of the annual estimates of population size, which was approximately 150.

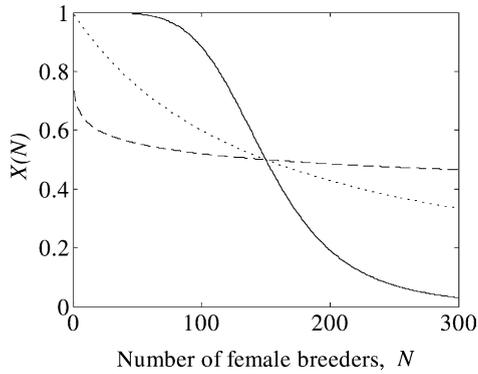The value of b in Eq. (11) determines the strength of the density-dependence in the region of N_{FI}: the

Fig. 2. An illustration of the form of the relationship between an input parameter $X(N)$ and the number of female breeders N. The parameter b takes the values -0.2 (dashed line), -1.0 (dotted line) and -5.0 (solid line). The parameter a is specified by Eq. (14), using $N_{\mathrm{FI}} = 150$ and $X(N_{\mathrm{FI}}) = 0.5$.

greater the value of $|b|$, the stronger the dependence in this region, as illustrated in Figs. 2 and 3. In order to specify b, we summarised the likely form and strength that density-dependence might take for each parameter (Table 2), with the strength being specified as

low, moderate or high. Moderate density-dependence was arbitrarily defined as having $|b| = 1$. In order to allow the difference between low and high density-dependence to vary, they were specified as having $|b| = 1/\delta$ and $|b| = \delta$ respectively, for $\delta = 2$, 5 and 10 (Fig. 3). Note that the form of Eq. (11) does not allow us to include the Allee-type effects thought plausible for PFB, IMM, JR, BRS and PBR. For these parameters, density-dependence has been assumed to be negative.

4. Sensitivities and elasticities

When vital rates are influenced by density, population dynamics become non-linear. The population is characterised not by a growth rate but by the existence and stability of equilibria, the bifurcations that may occur when stability is lost, and the patterns (cycles, quasicycles, chaos) that follow bifurcations (Neubert and Caswell, 2000). Assessment of the sensitivity and elasticity of several different types of model output has been suggested for density-dependent models

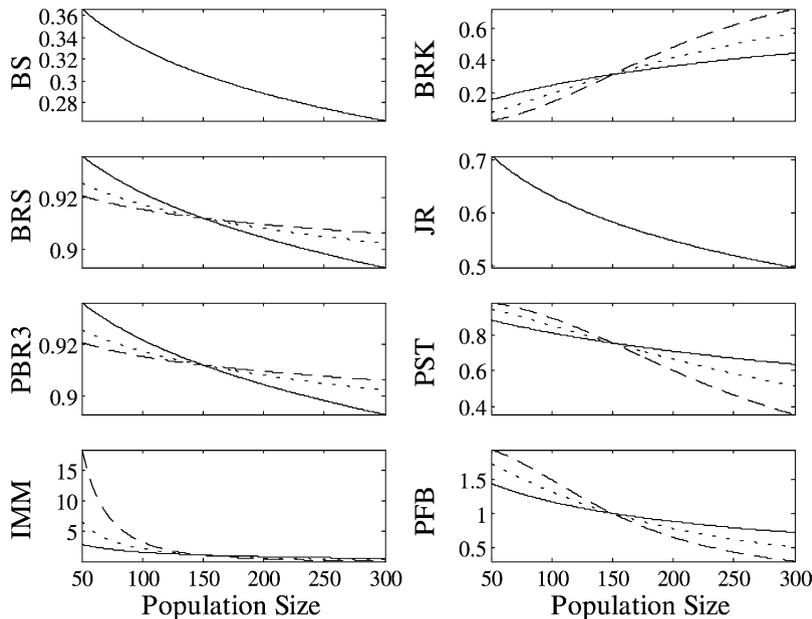Fig. 3. The input parameters as a function of the number of female breeders, for different relative strengths of density-dependence (δ). The parameters PBR1 and PBR2 have the same behaviour as PBR3, and NBRS has the same behaviour as BRS. Where a graph has three lines, solid, dotted and dashed lines correspond to $\delta = 2$, 5, 10 respectively. Parameters with intermediate density-dependence (JR and BS) have $\delta = 1$.

Table 2
Estimates for the functional forms of density-dependence

Parameter	Form	Importance	Possible mechanism
PFB	$+ \rightarrow -$	High	Younger birds are less likely to secure burrows as density increases
PST	$-$	High	As density increases prebreeders are less likely to secure a burrow, and so are more likely to prospect and breed elsewhere
IMM	$+ \rightarrow -$	High	A minimum density is needed to provide stimuli to attract immigrants to a colony, but as density increases immigrants are less likely to secure a burrow and stay at a colony
BRK	$+$	High	Increased disturbance as density increases results in failed breeding attempts, increased divorce rates and higher probability of skipping breeding
BS	$-$	Moderate	Increased disturbance as density increases can result in an increase in failed breeding attempts
JR	$+ \rightarrow -$	Moderate	Protection from predation at low densities, but lower survival as density increases due to competition for food
BRS	$+ \rightarrow -$	Low	Benefits from group foraging at low densities but increased competition for food at high densities
NBRS	$-$	Low	Increased competition for food at high densities
PBR1	$+ \rightarrow -$	Low	Protection from predation at low densities, but lower survival as density increases due to competition for food
PBR2	$+ \rightarrow -$	Low	Protection from predation at low densities, but lower survival as density increases due to competition for food
PBR3	$+ \rightarrow -$	Low	Protection from predation at low densities, but lower survival as density increases due to competition for food

$+$ indicates purely positive density-dependence, $-$ indicates purely negative density-dependence, and $+ \rightarrow -$ indicates an Allee-type effect where density-dependence is positive at low N and becomes negative at higher N.

(Caswell, 2001; Grant and Benton, 2000). We focus on the effect of changes in parameter values on the equilibrium population size, N_e. Previous work has either used the concept of an invasion exponent (Rand et al., 1994; Grant, 1997; Grant and Benton, 2000) or extended the standard density-independent sensitivity analysis, which involves eigenvalues of the projection matrix, to the density-dependent case (Takada and Nakajima, 1992, 1998; Takada and Nakashizuka, 1996). Here we show how the characteristic equation of the model (Caswell, 2001) can be used to provide an alternative expression for the sensitivity of N_e. A disadvantage is that it can be complicated to derive and difficult to use. However, if the life-cycle is such that all individuals must share a common life-history stage (e.g. a juvenile stage), then the characteristic equation is particularly simple (Caswell, 2001). This approach has been used by others in the context of density-independent models (Keyfitz, 1971; Lebreton, 1996) and may provide some advantages by simplifying the derivation of analytical expressions for the sensitivities and elasticities of the equilibrium population size.

When equilibrium is reached, the population growth rate is zero and the characteristic equation for the model is

$$\sum_{\alpha=0}^{15} \mu_\alpha(N) \sum_{i=0}^{25} m_i(N) \, l_i(N) = R_0(N) = 1, \qquad (15)$$

where $l_i = \prod_{j=0}^{i-1} s_j$ and $R_0(N)$ is the net reproductive rate at N (Caswell, 2001). Note that m_i, μ_α and l_i are all functions of N. We can differentiate this equation with respect to any parameter X and rearrange terms to give the sensitivity, s_X, of N_e to the parameter X as

$$s_X = \frac{\partial N_e}{\partial X} = -\frac{\partial R_0/\partial X}{\partial R_0/\partial N}\bigg|_{N=N_e}. \qquad (16)$$

The corresponding elasticity is given by

$$e_X = \frac{\partial \ln(N_e)}{\partial \ln(X)} = \frac{X}{N_e} s_X. \qquad (17)$$

An example of the calculation of sensitivity (for breeding success) is provided in the Appendix A. The sensitivity of N_e to a change in $X(N_e)$ will be proportional to the sensitivity of population growth to a change in X in the corresponding density-independent model (Takada and Nakashizuka, 1996; Caswell, 2001). The key additional information provided here is the sensitivity and

Table 3
Values of b used for calculation of the sensitivities and elasticities, where δ was chosen to have the values 2, 5 and 10

Parameter	Value of b
PFB	$-\delta$
PST	$-\delta$
IMM	$-\delta$
BRK	$+\delta$
BS	-1
JR	-1
BRS	$-1/\delta$
NBRS	$-1/\delta$
PBR1	$-1/\delta$
PBR2	$-1/\delta$
PBR3	$-1/\delta$

elasticity for the strength of the density-dependence (b) associated with each input parameter.

Note that sensitivity analysis with respect to N_e is only relevant when an equilibrium population size exists: if density-dependence is too strong population size may become unstable, leading to stable oscillations or chaos.

5. Results

Using the values of b in Table 3 leads to equilibrium population sizes of breeding females of 146, 143 and 137 for $\delta = 10$, 5 and 2 respectively. The absolute values for the sensitivities and elasticities

of N_e to changes in $X(N_e)$ for the case $\delta = 2$ are given in Table 4. We distinguish between two types of sensitivity/elasticity: those which we label "equilibrium parameter value" refer to the response when a parameter's value at the equilibrium population size, $X(N_e)$, is varied, whilst those labelled "value of b" refer to the response when a parameter's density-dependence, b, is varied. The sensitivities and elasticities of N_e to the equilibrium parameter values are proportional to what we would obtain from the equivalent density-independent model, i.e. with b set to zero for each parameter (Takada and Nakajima, 1998). As Takada and Nakajima (1998) suggest, changing the equilibrium value of breeder survival has by far the largest effect on N_e, a common finding with density-independent models for long-lived species (Goodman, 1980; Brault and Caswell, 1993; Weimerskirsch et al., 1996; Crook et al., 1998; Heppell, 1998; Russell, 1999; Heppell et al., 2000; Slooten et al., 2000). The largest sensitivities of N_e to the value of b are for breeder survival (BRS), emigration (PST) and immigration (IMM), whereas the largest corresponding elasticities are for emigration (PST), followed by those for the immigration (IMM) and breeder skipping rate (BRK). Table 5 shows the absolute relative values of the sensitivities, for the three values of δ, for both the equilibrium value and the strength of density-dependence. These suggest that the rankings of the sensitivities are almost independent of the quantification of low and high density-dependence.

Table 4
The absolute values for the sensitivities and elasticities, and their rankings, of the equilibrium population size (N_e), to the equilibrium parameter value and the strength of density-dependence associated with each parameter (b), using $\delta = 2$ in Table 3 ($N_e = 137$)

Parameter	Equilibrium parameter value				Value of b			
	|Sensitivity|		|Elasticity|		|Sensitivity|		|Elasticity|	
BRS	239	1	1.60	1	1.70	1	0.00623	7
PBR3	122	2	0.820	2	0.873	6	0.00319	8
PST	107	3	0.617	3	1.65	2	0.0242	1
BS	87.8	4	0.204	6	0.941	5	0.00688	6
NBRS	80.7	5	0.540	4	0.575	9	0.00210	9
JR	46.0	6	0.204	5	1.01	4	0.00742	5
BRK	34.1	7	0.0687	11	0.628	7	0.00919	3
PBR1	31.9	8	0.204	7	0.114	10	0.000416	10
PBR2	30.1	9	0.204	8	0.0657	11	0.000240	11
PFB	13.9	10	0.111	10	0.603	8	0.00882	4
IMM	11.3	11	0.121	9	1.53	3	0.0224	2

Rankings are based on the absolute values of the coefficients. Sensitivities and elasticities are shown to three significant figures.

Table 5
The absolute values for the relative sensitivities, and their rankings, of equilibrium population size (N_e) to the equilibrium parameter value and strength of density-dependence associated with each parameter (b), for the three values of δ in Table 3

| Parameter | Equilibrium parameter value | | | | | | Value of b | | | | | |
| | δ | | | | | | δ | | | | | |
	10		5		2		10		5		2	
BRS	1	1	1	1	1	1	1	1	1	1	1	1
PBR3	0.525	2	0.523	2	0.512	2	0.525	6	0.523	6	0.512	6
PST	0.451	3	0.452	3	0.448	3	0.905	3	0.921	2	0.971	2
BS	0.385	4	0.381	4	0.368	4	0.568	5	0.562	5	0.552	5
NBRS	0.315	5	0.32	5	0.338	5	0.315	9	0.32	9	0.338	9
JR	0.202	6	0.2	6	0.192	6	0.611	4	0.605	4	0.595	4
BRK	0.143	7	0.143	7	0.143	7	0.345	7	0.35	7	0.369	7
PBR1	0.137	8	0.137	8	0.134	8	0.0793	10	0.0761	10	0.0667	10
PBR2	0.129	9	0.129	9	0.126	9	0.0459	11	0.044	11	0.0385	11
PFB	0.0573	10	0.0577	10	0.0581	10	0.324	8	0.332	8	0.354	8
IMM	0.0463	11	0.0466	11	0.0472	11	0.908	2	0.906	3	0.897	3

The scaling is relative to the sensitivity of N_e to breeder survival probability (BRS). $N_e = 146$, 143 and 137 for $\delta = 10$, 5 and 2 respectively. Rankings are based on the absolute values of the sensitivities. The relative sensitivities are shown to three significant figures.

It is also of interest to consider which parameters are relatively unimportant in terms of the strength of their density-dependence. Overall, the sensitivities and elasticities of N_e, both to the parameters and to the strength of density-dependence associated with each parameter, suggest that we can effectively ignore the possibility of density-dependence in the probability of first breeding, prebreeder reappearance rate from both year 1–2 (PBR1) and year 2–3 (PBR2), and non-breeder survival (NBRS) (Tables 4 and 5).

6. Discussion

There are a number of possible measures of model output for which the sensitivity to changes in parameters can be calculated for density-dependent models (Grant and Benton, 2000). We have considered the sensitivity of the equilibrium population size to changes in both the equilibrium value and the strength of the density-dependence for each parameter. The former of these two sensitivities is commonly calculated, in some form, for density-dependent models. For example, Grant (1998) uses this type of sensitivity to investigate the effect of density-dependence in a model of a toxicant's effect upon a population, and Takada and Nakashizuka (1996) calculate this sensitivity for a density-dependent model of a broad-leaved

forest. Both our analysis, and that of Takada and Nakashizuka (1996) show that the sensitivity of N_e to changes in the equilibrium parameter values is directly proportional to the results of a sensitivity analysis of a density-independent model evaluated at N_e (Caswell, 2001). This implies that the rankings of the sensitivities will be identical for density-dependent and density-independent models.

Our focus here is clearly on the sensitivity of the equilibrium population size to changes in the strength of density-dependence, which has received far less attention in the literature. The only application which we are aware of is by Tanner (1999), who developed a model of clonal zoanthids, and numerically investigated its sensitivity to changes in the strength of density-dependence. Uncertainty in the strength of density-dependence associated with a parameter may have a large effect upon N_e, even when the equilibrium value for that parameter is relatively unimportant. Thus, in the model of Short-tailed Shearwaters the strength of density-dependence in both breeder skipping rate and immigration had a relatively large effect upon the predicted equilibrium population size, even though their equilibrium values were unimportant (see Table 4).

In this paper we have shown how the characteristic equation for a density-dependent model of a biological population can be used to perform a sensitivity

analysis. The characteristic equation can be derived from the life-cycle graph for a broad range of species. This derivation is particularly simple for large vertebrates, for which models tend to be age-structured, but is likely to be more involved for plants. Unlike other methods, it allows us to use explicit formulae for the sensitivities (Appendix A). Previous work in this area has mainly focussed on the use of the left and right eigenvectors of the Lefkovitch matrix, and its extensions (Takada and Nakajima, 1998; Caswell, 2001). Such an approach can be applied to quite general life-cycles and benefits from the power of matrix algebra, but the link between the eigenvectors of the matrix and the parameters of the model is not always clear. A recent development has been the use of invasion exponents to study the stability and sensitivity of density-dependent and stochastic models (Metz et al., 1992; Rand et al., 1994; Ferriére and Gatto, 1995). For a model at equilibrium, this approach is equivalent to the analysis of left and right eigenvectors. However, invasion exponents can be calculated for cyclic, quasi-periodic and chaotic attractors, making their use more general.

Inclusion of density-dependence in a population model brings with it both increased reality and increased uncertainty. Although few ecologists would argue against the idea that density-dependence is likely to be important in regulating some populations, quantifying this density-dependence is fraught with difficulties. We need to specify both the form and strength of density-dependence. Several functional forms for density-dependence have been suggested (Bellows, 1981), different measures of density may be appropriate (Charlesworth, 1994), and both the strength and direction of density-dependence for a parameter may be open to debate. These uncertainties emphasise the importance of sensitivity analyses for density-dependent models. In our approach a particular functional form of density-dependence has been assumed, and sensitivities and elasticities of N_e to changes in the strength of density-dependence were calculated for a broad range of possible strengths of density-dependence (Tables 2 and 3). Our approach has also assumed that female breeding population is the relevant density, but our approach can be extended to different definitions of density (e.g. the density of a particular stage). A more complete analysis would assess the robustness of our conclusions to different forms of density-dependence and assess whether the values used for b cover the possible range of strengths of density-dependence likely to be observed in real populations.

Alternative functional forms for density-dependence, such as the Ricker, generalised Ricker, or Hassell functions could have been used here (Getz, 1996). The form of the density-dependence function may affect some model conclusions, such as extinction probability estimates (Beissinger and Westphal, 1998), but its impact upon our analysis has not been investigated. Our choice of function constrains the density-dependence to be monotonic, which may not always be realistic. This could be overcome by adding one or more parameters to the function, at the cost of making the analysis more complicated. Runge and Johnson (2002) have recently highlighted the importance of functional form in population models, and shown that the functional forms used in a model can have a significant impact on a models results, such as predictions of optimal harvest rates.

The importance of considering alternative functional forms for density-dependence will depend on the robustness of our analysis to changes in this form. The robustness of our sensitivity analysis is likely to boil down to the robustness of our estimate for N_e: because the sensitivity analysis is local, it would be expected to be fairly insensitive to the functional form of the density-dependence at the equilibrium. On the other hand, the equilibrium population size will depend to a certain extent on the form and strength of density-dependence (as can be seen from the components of the characteristic equation), and may show sensitivity in certain situations: here, we attempted to address this problem by considering different relative strengths for the density-dependence.

If density-dependent models are to usefully inform conservation and wildlife management decisions then the conclusions drawn from a model should be robust and relevant. Robustness of N_e, to both parameters and the strength of density-dependence in parameters, can be addressed using sensitivity analysis and rankings of the sensitivities are often sufficient to guide management. Sensitivity analysis of density-independent models has served as a useful tool, even though such models involve the unrealistic assumption of exponential population growth (Caswell, 2001). The relevance of the use of a density-dependent model may be diminished if the population is not at equilibrium, but

it might be hoped that sensitivity rankings are robust to this problem. Our analysis suggests that sensitivity analysis of density-dependent models will be robust to the strength of density-dependence associated with the parameters.

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Appendix A. Calculation of sensitivities and elasticities using the characteristic equation

To calculate the sensitivity and elasticity of N_e to the parameter $X(N_e)$, we differentiate the characteristic equation (Eq. (14)) with respect to X, giving

$$\frac{\partial R_0}{\partial X} + \frac{\mathrm{d}N}{\mathrm{d}X}\frac{\partial R_0}{\partial N} = 0, \tag{A.1}$$

which can be rearranged and evaluated at N_e to give Eq. (16) for the sensitivity of N_e to any parameter. Evaluating Eq. (A.1) at N_e for our model gives,

$$\sum_{\alpha=0}^{15}\sum_{i=0}^{25}\frac{\partial}{\partial X}(\mu_\alpha(N_e)\,m_i(N_e)\,l_i(N_e))$$
$$= -s_X\sum_{\alpha=0}^{15}\sum_{i=0}^{25}\frac{\partial}{\partial N}(\mu_\alpha(N)\,m_i(N)\,l_i(N))\Big|_{N=N_e} \tag{A.2}$$

where s_X is the sensitivity of N_e to parameter X (Eq. (16)). Rearranging Eq. (A.2) gives,

$$s_X = -\frac{1}{D}\sum_{\alpha=0}^{15}\sum_{i=0}^{25}\frac{\partial}{\partial X}(\mu_\alpha(N_e)\,m_i(N_e)\,l_i(N_e)) \tag{A.3}$$

where $D=\sum_{\alpha=0}^{15}\sum_{i=0}^{25}\frac{\partial}{\partial N}(\mu_\alpha(N)\,m_i(N)\,l_i(N))\big|_{N=N_e}$ has no effect upon the relative values of the sensitivities.

In order to illustrate the use of this approach, consider the sensitivity of N_e to the strength of density-dependence in breeding success. The dependence of BS on N is specified as

$$\mathrm{BS}(N) = 0.5\left\{1 + \frac{0.5 - \mathrm{BS_{FI}}}{\mathrm{BS_{FI}}}\left(\frac{N}{N_{\mathrm{FI}}}\right)^{b_{\mathrm{BS}}}\right\}^{-1}. \tag{A.4}$$

This relationship involves two parameters; the breeding success estimate for Fisher Island, $\mathrm{BS_{FI}}$, and the strength of the density-dependence, b_{BS}. We will write the sensitivity of N_e to changes in $\mathrm{BS}(N_e)$ and b_{BS} as s_{BS} and s_b respectively. From Eq. (10), it can be seen that the breeding success only enters into the expression for fecundity, m_i, giving

$$s_{\mathrm{BS}} = -\frac{1}{D}\sum_{\alpha=0}^{15}\sum_{i=0}^{25}\frac{\mu_\alpha(N_e)\,m_i(N_e)\,l_i(N_e)}{\mathrm{BS}(N_e)} \tag{A.5}$$

and

$$s_b = -\frac{1}{D}\sum_{\alpha=0}^{15}\sum_{i=0}^{25}\frac{\mu_\alpha(N_e)\,m_i(N_e)\,l_i(N_e)}{\mathrm{BS}(N_e)}\frac{\partial\mathrm{BS}(N)}{\partial b_{\mathrm{BS}}}$$
$$= \frac{1}{D}\sum_{\alpha=0}^{15}\sum_{i=0}^{25}\mu_\alpha(N_e)\,m_i(N_e)\,l_i(N_e)$$
$$\times \frac{\mathrm{BS}(N_e)}{\mathrm{BS_{FI}}}\frac{0.5 - \mathrm{BS_{FI}}}{0.5}b_{\mathrm{BS}}\left(\frac{N_e}{N_{\mathrm{FI}}}\right)^{b_{\mathrm{BS}}-1}. \tag{A.6}$$

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