

Mating Behavior, Population Growth, and the Operational Sex Ratio: A Periodic Two-Sex Model Approach

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ABSTRACT: We present a new approach to modeling two-sex populations, using periodic, nonlinear two-sex matrix models. The models project the population growth rate, the population structure, and any ratio of interest (e.g., operational sex ratio). The periodic formulation permits inclusion of highly seasonal behavioral events. A periodic product of the seasonal matrices describes annual population dynamics. The model is nonlinear because mating probability depends on the structure of the population. To study how the vital rates influence population growth rate, population structure, and operational sex ratio, we used sensitivity analysis of frequency-dependent nonlinear models. In nonlinear two-sex models the vital rates affect growth rate directly and also indirectly through effects on the population structure. The indirect effects can sometimes overwhelm the direct effects and are revealed only by nonlinear analysis. We find that the sensitivity of the population growth rate to female survival is negative for the emperor penguin, a species with highly seasonal breeding behavior. This result could not occur in linear models because changes in population structure have no effect on per capita reproduction. Our approach is applicable to ecological and evolutionary studies of any species in which males and females interact in a seasonal environment.

Keywords: two-sex periodic matrix model, population structure, population growth rate, mating systems, sex ratio, emperor penguin.

Introduction

Two-sex models are important for studying the consequences, both ecological and evolutionary, of sexual dimorphism. If males and females differ, it is important to distinguish them in demographic models (e.g., Caswell and Weeks 1986; Lindstrom and Kokko 1998). The differences may result from environmental factors (e.g., temperature in gonochoristic vertebrates: Ospina-Alvarez and Piferrer 2008), the cost of sexual reproduction (e.g., mate com-

petition; Kokko and Jennions 2008), or human activities (e.g., sex-specific hunting; Milner-Gulland et al. 2003). If reproduction requires both males and females, the lack of suitable mates can affect population growth and viability (Kokko and Rankin 2006). Accounting for such effects requires a two-sex model (Caswell 2001; Iannelli et al. 2005) in which births depend on the relative abundance of males and females through a nonlinear mating function (also called a birth function or a marriage function; McFarland 1972). The “operational sex ratio” (OSR), defined as the ratio of sexually competing males to females that are ready to mate (Kvarnemo and Ahnesjö 1996; Clutton-Brock 2007), can influence the intensity of selection and mate competition (Kokko and Rankin 2006). Other aspects of population structure, such as the availability of males and females of appropriate ages or stages, may also be important (Kokko and Monaghan 2001), and population structure is affected by the sex-specific vital rates.

Reproduction often involves a sequence of behaviors (e.g., mate searching, mate choice, mate competition, and parental investment in offspring). It is important to include those behaviors in demographic models (e.g., Gerber 2006). However, behavioral stages may exist only briefly within an annual projection interval. Here, we present a new approach to two-sex population models that uses a periodic matrix model that (1) maps behaviors onto the annual cycle and (2) projects the intermediate population structure during that cycle, making it easy to incorporate even ephemeral behavioral events.

To understand how population growth rate and structure are influenced by the vital rates, perturbation analysis is required; it provides the sensitivity and elasticity of population growth rate, population structure, and indices (e.g., OSR) derived from the population structure. There are few examples of sensitivity analysis of two-sex models. Caswell (2001, chap. 17) used linear sensitivity analyses on the equilibrium population, but this was incorrect

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(Caswell 2008). Veran and Beissinger (2009) presented an innovative sensitivity analysis of population structure and OSR, but it was based on a linear rather than a nonlinear model. Tuljapurkar et al. (2007) examined the sensitivity of population growth rate in a nonlinear two-sex model using life-table methods. Here, we will present the first application of a new approach that gives a complete perturbation analysis of nonlinear two-sex models (Caswell 2008).

A Two-Sex Model Incorporating Behavior

Two-sex matrix population models can be created by including males and females in the population vector \mathbf{n} and writing

$$\mathbf{n}(t+1) = \mathbf{A}[\mathbf{n}(t)]\mathbf{n}(t) \quad (1)$$

to indicate that the projection matrix $\mathbf{A}[\mathbf{n}]$ depends on the current population vector (Caswell and Weeks 1986; Caswell 2001 [chap. 17], 2008 [sec. 7]). $\mathbf{A}[\mathbf{n}]$ projects the population from time t to $t+1$. If the model depends only on the relative abundance of males and females, it is said to be frequency dependent, and $\mathbf{A}[\mathbf{n}]$ is homogeneous of degree zero in \mathbf{n} , so that $\mathbf{A}[c\mathbf{n}] = \mathbf{A}[\mathbf{n}]$ for any nonzero c .

When the projection interval (say, 1 year) includes multiple behavioral events, $\mathbf{A}[\mathbf{n}]$ may depend on stages that do not appear in the vector $\mathbf{n}(t)$. For example, mating might occur only among those males and females that obtain a territory, but territories may be occupied for only a short period within the year. Such behavioral processes and their dependence on population structure may be of great interest (e.g., Gerber 2006). The only solution to date has been to incorporate all behavioral events, and the transitions among them, into (possibly complicated) expressions for the elements of $\mathbf{A}[\mathbf{n}]$. (e.g., Gerber 2006; Veran and Beissinger 2009). This limits the behavioral complexity that can be included.

As an example of multiple behavioral events, consider the emperor penguin *Aptenodytes forsteri* (fig. 1A), to which we will apply our two-sex model (“Two-Sex Demography of the Emperor Penguin”). Emperor penguins are distributed around Antarctica and reproduce during winter in colonies on sea ice, far from open water. This extreme environment requires finely tuned cooperation between males and females in mating, incubating, and provisioning offspring (Jouventin 1971*b*). Males incubate the egg while females return to sea to feed. Males fast for 4 months and are especially sensitive to environmental change (Jenouvrier et al. 2005*b*). Males and females arrive at the breeding colony in March–April and begin mating. The female lays an egg in May–June, which is incubated by the male in June–July while the female returns to the

sea to forage (Prevost 1961). From July through November, the parents take turns making lengthy foraging trips from the colony to the sea to feed the chicks until fledging. Adults and chicks leave the colony and spend December to March at sea or on sea ice (Zimmer et al. 2008). Individuals that do not reproduce probably remain on the coast all year.

An annual life-cycle graph, projecting from May to May (fig. 1B) distinguishes five stages according to breeding status and sex: male and female prebreeders, male and female nonbreeders, and breeding pairs. Prebreeders have yet to breed for the first time. Nonbreeders have bred at least once, but not in the current year. A breeding pair consists of a female and a male who cooperate over the breeding season to produce offspring.

Although figure 1B appears simple, its transitions are conditional on survival and depend on return to the breeding site, mating, raising offspring to fledging, and leaving the breeding site. When all these intermediate behaviors are included in $\mathbf{A}[\mathbf{n}]$, the resulting expressions are complicated (we show them later) and tricky to derive accurately. We now present a periodic model that explicitly includes these processes and the nonlinearity in the mating process.

Periodic Model Construction

A periodic matrix model divides the year into a series of “phases” (Caswell 2001, chap. 13). The population at each phase may contain different stages, and the phases need not be of the same duration. A (possibly rectangular) matrix \mathbf{M}_i projects the population from phase i to phase $i+1$. If the cycle is of period p , then \mathbf{M}_p projects the population from phase p back to phase 1. The annual dynamics are given by the periodic product of the \mathbf{M}_i :

$$\mathbf{n}(t+1) = \mathbf{M}_p \dots \mathbf{M}_1 \mathbf{n}(t) \quad (2)$$

Note that the sequence of matrix multiplications must be preserved.

Periodic models are extremely flexible. In their simplest form, the \mathbf{M}_i project across fixed intervals of time, including seasonal cycles (e.g., Steets et al. 2007) or interannual cycles (e.g., multiyear fire cycles; Caswell and Kaye 2001). But the phases need not be defined by calendar time. They may instead represent behavioral events, as in the sooty shearwater (*Puffinus griseus*), where the emergence of chicks from their burrows at night defines a demographic change, regardless of its date (Hunter and Caswell 2005). Or phases may be defined by environmental events, such as the recession of spring floods (Smith et al. 2005), regardless of when that recession occurs. More generally, the \mathbf{M}_i need not represent time intervals at all. For

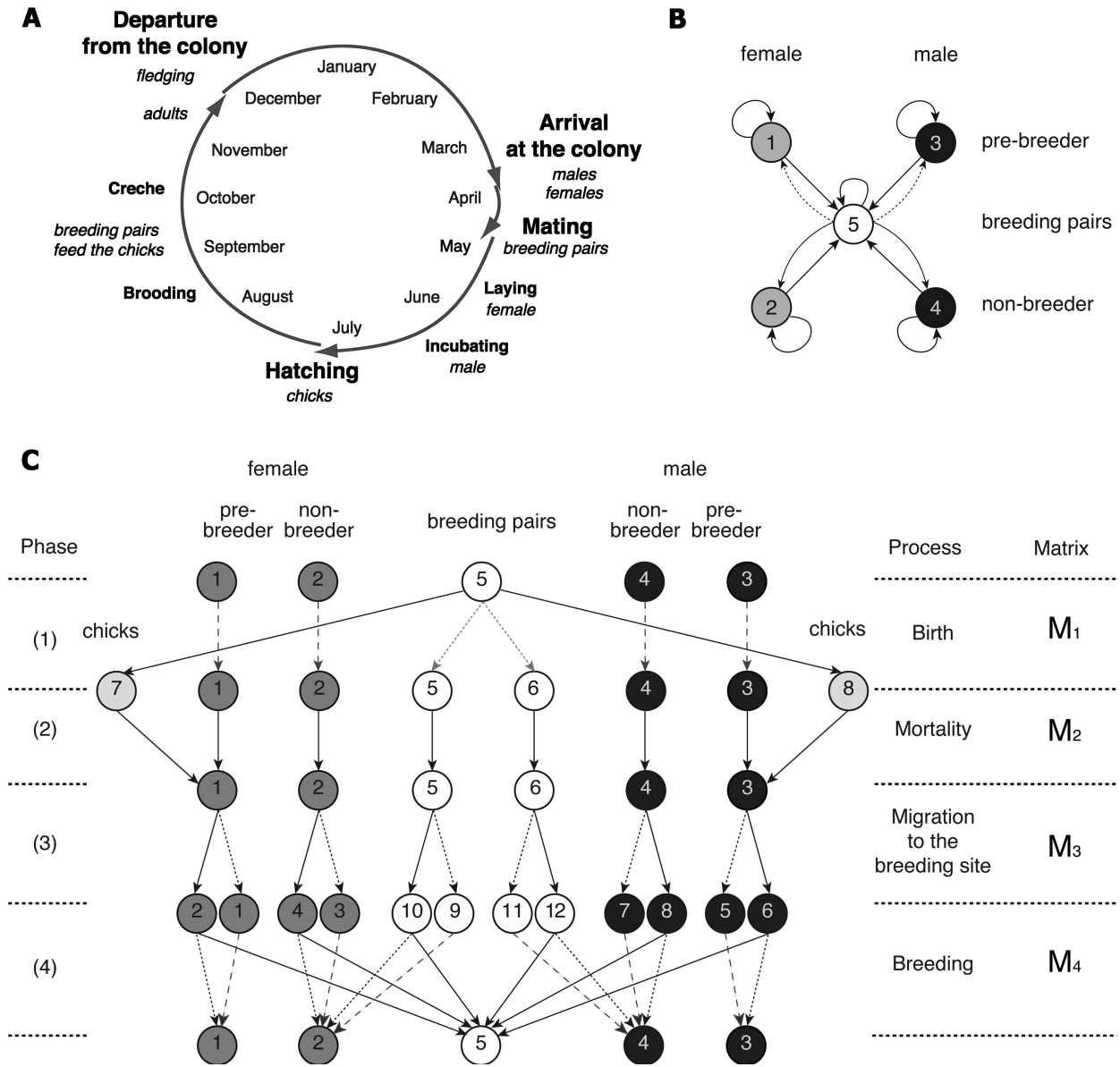


Figure 1: A, Seasonal cycle of the emperor penguin. B, Annual life-cycle graph for a two-sex model with males (black) and females (gray). Fertilities are represented by dotted lines, and the transitions between stages of individuals already present in the population are represented by solid lines. C, Periodic life-cycle graph with $p = 4$ phases within the year. During the year, (1) breeding pairs produce chicks (dark lines, light gray) and separate at the end of the breeding season (dotted lines), (2) individuals survive, (3) individuals either do or do not return to their breeding site (solid lines and dotted lines, respectively), and (4) individuals either do or do not mate to form breeding pairs (solid lines and dotted lines, respectively). The numbering of the nodes on each line of the life-cycle graphs corresponds to the rows and columns of the matrices M_1 – M_4 , and the dashed lines refer to transition probability of 1.

example, in mark-recapture analysis, projection matrices are sometimes written as the product of a survival matrix and a transition matrix (e.g., Choquet et al. 2004, 2009). There is no need to assume that transitions occur during one part of the year and survival during the other; the

matrix multiplication corresponds to a conditional probability calculation, not a temporal sequence.

Regardless of the interpretation of the M_p , formulation and analysis proceed in the same way, taking advantage of the periodic mathematical structure. In our example,

the two-sex dynamics are based on events defined by breeding behavior, not by calendar time. We use the decomposition into annual survival and conditional transitions, partly because we are modeling a population that breeds in one of the most inaccessible habitats on earth, and detailed seasonal variation in survival is unobtainable.

We present our approach in terms of the emperor penguin life cycle (fig. 1C), but it is not limited to this case. (1) At the first phase, starting in May, individuals are classified into the five basic stages. Between May and December, breeding pairs produce chicks and then separate at the end of the breeding season. (2) At the beginning of the second phase, eight stages may be present in the population. Chicks survive from December to May and become prebreeders in May. Adults survive throughout the entire annual life cycle but do not change breeding status. (3) At the beginning of the third phase, six stages are present in the population. During this phase, individuals choose whether to return to the breeding site in March–April. (4) At the beginning of fourth phase, individuals are thus classified into 12 stages. During this phase, individuals at the breeding site may mate to form breeding pairs in late April–May. At the end of phase 4, the cycle is back to phase 1, with five stages present.

Associated with phase i is a matrix \mathbf{M}_i . The numbering of the nodes on each line of figure 1C corresponds to the rows and columns of the \mathbf{M}_i . Matrix \mathbf{M}_1 models the birth process, \mathbf{M}_2 models the mortality process (annual for adult stages but from December to March for fledgings), \mathbf{M}_3 models migration to the breeding site, and \mathbf{M}_4 models the breeding process. Except for the fertilities in \mathbf{M}_1 , the columns of matrices \mathbf{M}_1 , \mathbf{M}_3 and \mathbf{M}_4 sum to 1 and represent transitions conditional on survival, which appears in \mathbf{M}_2 .

The matrix \mathbf{M}_1 projects the population from the five stages of the annual life cycle to eight intermediate stages:

$$\mathbf{M}_1 = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 - \rho_2 \\ 0 & 0 & 0 & 0 & \rho_2 \\ 0 & 0 & 0 & 0 & f_1 \\ 0 & 0 & 0 & 0 & f_3 \end{pmatrix}. \tag{3}$$

In \mathbf{M}_1 , breeding pairs produce female and male offspring with fertilities f_1 and f_3 . Fertility depends on the probability m that a breeding pair raises offspring and is calculated as $f_1 = (1 - \rho_1)m$ and $f_3 = \rho_1 m$, where ρ_1 is the sex ratio at birth. Breeding pairs separate into females and males in proportions $(1 - \rho_2)$ and ρ_2 . If mating is strictly monogamous, $\rho_2 = 0.5$; if not, ρ_2 might depend on the rel-

ative number of males and females in the breeding pair stage. Prebreeders and nonbreeders do not change stage by the processes modeled in \mathbf{M}_1 .

The matrix \mathbf{M}_2 projects the population from the eight stages after phase 1 to six intermediate stages:

$$\mathbf{M}_2 = \begin{pmatrix} s_1 & 0 & 0 & 0 & 0 & 0 & s_0 & 0 \\ 0 & s_2 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_3 & 0 & 0 & 0 & 0 & s_0^* \\ 0 & 0 & 0 & s_4 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & s_5 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & s_6 & 0 & 0 \end{pmatrix}. \tag{4}$$

In \mathbf{M}_2 , s_0 and s_0^* are survival probabilities for female and male chicks from December to May; \mathbf{M}_2 also contains annual survival probabilities of all other stages (s_x ; see table 1). It is not possible to estimate seasonal survival of emperor penguins. In other species, it may be, and appropriate survival matrices could be added to the model.

The matrix \mathbf{M}_3 projects the population from the six stages at the end of phase 2 to 12 stages at the start of phase 3:

$$\mathbf{M}_3 = \begin{pmatrix} 1 - r_1 & 0 & 0 & 0 & 0 & 0 \\ r_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 - r_2 & 0 & 0 & 0 & 0 \\ 0 & r_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 - r_3 & 0 & 0 & 0 \\ 0 & 0 & r_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 - r_4 & 0 & 0 \\ 0 & 0 & 0 & r_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 - r_5 & 0 \\ 0 & 0 & 0 & 0 & r_5 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 - r_6 \\ 0 & 0 & 0 & 0 & 0 & r_6 \end{pmatrix}, \tag{5}$$

where r_x is the probability that individuals of stage x return to the breeding site (table 1).

The matrix $\mathbf{M}_4[\mathbf{n}]$ projects the population from the 12 stages at the end of phase 3 to five stages at the beginning of phase 1:

$$\mathbf{M}_4[\mathbf{n}] = \begin{pmatrix} 1 & 1 - u_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 1 - u_2 & 0 & 0 & 0 & 0 & 1 & 1 - u_3 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 1 - u_3 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 - u_4 & 0 & 0 & 1 & 1 - u_6 \\ 0 & u_1 & 0 & u_2 & 0 & u_3 & 0 & u_4 & 0 & u_5 & 0 & u_6 \end{pmatrix}, \tag{6}$$

where $u_x = u_x[\mathbf{n}]$ depends on the population structure. According to \mathbf{M}_4 , individuals not at the colony remain in

Table 1: Parameters of the model designated according to the breeding status and the sex of the individual

Stage	Survival	Return	Mating
Prebreeder female	s_1	r_1	u_1
Nonbreeder female	s_2	r_2	u_2
Prebreeder male	s_3	r_3	u_3
Nonbreeder male	s_4	r_4	u_4
Breeder female	s_5	r_5	u_5
Breeder male	s_6	r_6	u_6

their state (prebreeders or nonbreeders) with probability 1. Individuals at the colony mate with the probability $u_x[\mathbf{n}]$ (table 1), which depends on the availability of potential mates.

The probability of mating is defined by a mating function (also called a marriage function), which depends on the breeding system. For the emperor penguin, mating is strictly monogamous within a breeding season because incubation and feeding of a chick require both parents. Mate fidelity between years is low; only 15% of individuals stay faithful to their previous partner (Isenmann 1971; Bried et al. 1999). Our model assumes that mating occurs among all males and females at the breeding site, independent of their previous stage (breeder, nonbreeder, or prebreeder). Each individual has a probability u_m (males) or u_f (females) of mating. This is certainly an oversimplification, but no data are available to explore alternatives.

Let N_f and N_m denote the number of potentially breeding females and males, calculated as

$$N_f = \mathbf{c}_f^T \mathbf{n}(t), \tag{7}$$

$$N_m = \mathbf{c}_m^T \mathbf{n}(t), \tag{8}$$

with

$$\mathbf{c}_f^T = [s_1 r_1 \ s_2 r_2 \ 0 \ 0 \ (1 - \rho_2) s_3 r_3], \tag{9}$$

$$\mathbf{c}_m^T = (0 \ 0 \ s_3 r_3 \ s_4 r_4 \ \rho_2 s_6 r_6). \tag{10}$$

The number of mating pairs is $\min(N_f, N_m)$, and the probabilities of mating are

$$u_f = \frac{\min(N_f, N_m)}{N_f}, \tag{11}$$

$$u_m = \frac{\min(N_f, N_m)}{N_m}. \tag{12}$$

The operational sex ratio (OSR) is the ratio of sexually competing males to females that are ready to mate (Kvarnemo and Ahnesjö 1996). In our case, this ratio is

$$\text{OSR} = \frac{N_m}{N_f}. \tag{13}$$

Therefore, in this model, mating probabilities are a direct function of the OSR. When $N_m > N_f$, the OSR is male biased, and the mating probabilities are $u_f = 1$ for females and $u_m = N_f/N_m = 1/\text{OSR}$ for males. When $N_f > N_m$, the OSR is female biased, and the mating probabilities are $u_m = 1$ for males and $u_f = N_m/N_f = \text{OSR}$ for females.

The annual projection matrix is

$$\mathbf{A}[\mathbf{n}] = \mathbf{M}_4[\mathbf{n}] \mathbf{M}_3 \mathbf{M}_2 \mathbf{M}_1. \tag{14}$$

Note the simple structure of the matrices \mathbf{M}_1 – \mathbf{M}_4 and their relation to the periodic life-cycle graph (fig. 1C); $\mathbf{A}[\mathbf{n}]$ is much more complicated than its components (app. A in the online edition of the *American Naturalist*). For example, the behavioral event of returning to the breeding colony (probabilities r_1 – r_6) appears in every nonzero entry of $\mathbf{A}[\mathbf{n}]$ in products and/or sums involving all the other probabilities, each one different. The annual matrices obtained from a different choice of the starting phase are even more complex (app. A). It would be challenging to correctly arrive at these expressions directly, but they are obtained in our approach by a simple periodic permutation of \mathbf{M}_1 – \mathbf{M}_4 .

Model Analysis

Because our model is homogeneous, it eventually converges to an equilibrium proportional structure ($\hat{\mathbf{p}}$) and grows exponentially at a rate $\hat{\lambda}$ given by the dominant eigenvalue of the projection matrix $\hat{\mathbf{A}}[\hat{\mathbf{p}}]$. The equilibrium relative numbers of potentially breeding individuals are $\hat{N}_f = \mathbf{c}_f^T \hat{\mathbf{p}}$ and $\hat{N}_m = \mathbf{c}_m^T \hat{\mathbf{p}}$, and the OSR is therefore

$$\widehat{\text{OSR}} = \frac{\mathbf{c}_f^T \hat{\mathbf{p}}}{\mathbf{c}_m^T \hat{\mathbf{p}}}. \tag{15}$$

Our goal is to explore how the parameters influence $\hat{\mathbf{p}}$, $\hat{\lambda}$, and $\widehat{\text{OSR}}$, using sensitivity and elasticity analysis. It is essential to account for the nonlinearity created by the mating process (Caswell 2008). To do so, we use the matrix calculus approach of Caswell (2008). Let $\boldsymbol{\theta}$ denote a vector of parameters (see table 2 for a list). The sensitivity of the equilibrium structure $\hat{\mathbf{p}}$ to the parameter vector $\boldsymbol{\theta}$ is

Table 2: Description of the parameter vector θ for the emperor penguin

Parameter (θ)	Notation	Value
Sex ratio at birth	ρ_1	.5
Breeding success	β	.55
Prebreeder return probability	$r_1 = r_3$.38
Nonbreeder return probability	$r_2 = r_4$.26
Breeder return probability	$r_5 = r_6$.97
Prebreeder annual survival	$s_1 = s_3$.81
Female annual survival	$s_5 = s_2$.83
Male annual survival	$s_6 = s_4$.79
Newborn survival from December to May	$s_0 = s_0^*$.45

Note: The estimates of return and survival probabilities are based on capture-recapture data and were corrected by a 4.8% tag loss (see app. B in the online edition of the *American Naturalist* for more details)

$$\frac{d\hat{\mathbf{p}}}{d\theta^T} = \left[\hat{\lambda} \mathbf{I} - (\hat{\mathbf{A}} - \hat{\mathbf{p}} \mathbf{e}^T \hat{\mathbf{A}}) - ((\hat{\mathbf{p}}^T \otimes \mathbf{I}) - (\hat{\mathbf{p}}^T \otimes \hat{\mathbf{p}} \mathbf{e}^T)) \frac{\partial \text{vec} \hat{\mathbf{A}}}{\partial \hat{\mathbf{p}}} \right]^{-1} \times ((\hat{\mathbf{p}}^T \otimes \mathbf{I}) - (\hat{\mathbf{p}}^T \otimes \hat{\mathbf{p}} \mathbf{e}^T)) \frac{\partial \text{vec} \hat{\mathbf{A}}}{\partial \theta^T}, \quad (16)$$

where \mathbf{I} is an identity matrix, \mathbf{e} is a vector of ones, vec is the vec operator, and \otimes is the Kronecker product (Caswell 2008, eq. [94]). Because equation (14) is nonlinear, vital rates depend on the parameters θ and on the population structure \mathbf{p} . Thus, the sensitivity of $\hat{\mathbf{p}}$ includes both these effects, as $\partial \text{vec} \hat{\mathbf{A}} / \partial \hat{\mathbf{p}}^T$ in the first term and $\partial \text{vec} \hat{\mathbf{A}} / \partial \theta^T$ in the second term of equation (16).

The sensitivity of the population growth rate $\hat{\lambda}$ at the equilibrium is

$$\frac{d\hat{\lambda}}{d\theta^T} = (\hat{\mathbf{p}}^T \otimes \hat{\mathbf{v}}^T) \left(\frac{\partial \text{vec} \hat{\mathbf{A}}}{\partial \theta^T} + \frac{\partial \hat{\mathbf{A}}}{\partial \hat{\mathbf{p}}^T} \frac{d\hat{\mathbf{p}}}{d\theta^T} \right) \quad (17)$$

(Caswell 2008, eq. [93]), where $\hat{\mathbf{v}}$ is the reproductive value vector, given by the left eigenvector of $\hat{\mathbf{A}}$ corresponding to $\hat{\lambda}$. It includes direct effects of θ on $\hat{\mathbf{A}}$, and indirect effects through the effects of θ on $\hat{\mathbf{p}}$.

The sensitivity of the operational sex ratio is

$$\frac{d\widehat{\text{OSR}}}{d\theta^T} = \frac{1}{\hat{N}_f} \left(\frac{d\hat{N}_m}{d\theta^T} - \widehat{\text{OSR}} \frac{d\hat{N}_f}{d\theta^T} \right), \quad (18)$$

where the derivatives of \hat{N}_f and \hat{N}_m are

$$\frac{d\hat{N}_f}{d\theta^T} = \hat{\mathbf{p}}^T \frac{d\mathbf{c}_f}{d\theta^T} + \mathbf{c}_f^T \frac{d\hat{\mathbf{p}}}{d\theta^T}, \quad (19)$$

$$\frac{d\hat{N}_m}{d\theta^T} = \hat{\mathbf{p}}^T \frac{d\mathbf{c}_m}{d\theta^T} + \mathbf{c}_m^T \frac{d\hat{\mathbf{p}}}{d\theta^T}. \quad (20)$$

Two-Sex Demography of the Emperor Penguin

We will apply our approach to the emperor penguin population in Terre Adélie, East Antarctica (Barbraud and Weimerskirch 2001; Jenouvrier et al. 2005b), using data collected between 1962 and 2005.

Parameter estimates. The parameter estimates are summarized in tables 2 and 3. Survival and return probabilities were estimated using capture-recapture methods (Lebreton et al. 1992, 2009; Lebreton and Pradel 2002; see app. B in the online edition of the *American Naturalist*). Adult survival probabilities differed between sexes but not between nonbreeders and breeders. Thus, in the matrix \mathbf{M}_2 , $s_2 = s_5$ and $s_4 = s_6$. No data are available on sex differences in survival of prebreeders and chicks, so $s_1 = s_3$ and $s_0 = s_0^*$. The return probabilities in matrix \mathbf{M}_3 differed according to breeding status but not between sexes, so prebreeder return probability is $r_1 = r_3$, nonbreeder return probability is $r_2 = r_4$, and breeder return probability is $r_5 = r_6$.

In the absence of data on mating preferences, we assumed that mating among individuals at the colony is independent of prior breeding status (prebreeder, nonbreeder, and breeder). Therefore mating probability depends only on the relative abundance of the sexes, according to equations (11)–(12). In the matrix $\mathbf{M}_4[\mathbf{n}]$, $u_f = u_1 = u_2 = u_5$ for females and $u_m = u_3 = u_4 = u_6$ for males.

The proportion of males among breeding pairs is $\rho_2 = 0.5$ because penguins are monogamous. Based on genetic determination of the sex of dead chicks found in colonies over several years of monitoring, the sex ratio at birth was not biased and was estimated as $\rho_1 = 0.5$ (H. Weimerskirch, unpublished data).

The fertilities in \mathbf{M}_1 depend on the sex ratio at birth ρ_1 and the reproductive output m (chicks per breeding pair):

$$m = \frac{0.5\beta}{s_5^{8/12} s_6^{8/12}}. \quad (21)$$

The breeding success, estimated to be $\beta = 0.55$ (Jenouvrier et al. 2009), is the probability of successfully raising a chick to fledging. The factor 0.5 accounts for the fact that one egg is produced per breeding pair. Breeding suc-

Table 3: Fertilities parameters for the emperor penguin

Fertilities parameters	Notation	Calculation
Breeding success	β	No. fledging chicks over number of eggs
Proportion of male at birth or sex ratio	ρ_1	Fixed at .5
Proportion of male in the breeding pair	ρ_2	.5 for strictly monogamous species
Reproductive output (chicks per breeding pair)	m	$.5\beta/(s_5^{8/12}s_6^{8/12})$
Probability of producing newborn female	f_1	$(1 - \rho_1)m$
Probability of producing newborn male	f_3	$\rho_1 m$

cess includes the probability of survival of both parents, which is already included in the matrix \mathbf{M}_2 , so the term $s_5^{8/12}s_6^{8/12}$ factors out the probability that both parents survive for the 8 months of the breeding season.

Demographic results. The equilibrium population structure in May contains 63% breeding pairs, 16% prebreeders (7% males, 9% females), and 21% nonbreeders (2% males, 19% females) for the parameters shown in tables 2 and 3. The OSR is female biased and equal to 0.83. The population is projected to decline at a rate of 2.33% per year. This value agrees well with the observed average population growth rate of -2.23% per year (bootstrap 95% confidence intervals: $[-2.66\%, -1.85\%]$) obtained as the slope of a linear regression of the log of the numbers of breeding pairs against time.

Effects of Male-Female Survival Differences

Population structure and growth rate reflect the differences between males and females. The only difference observed in the emperor penguin is in adult survival. To study this difference, we express it as a proportional survival differential ΔS . We define a baseline situation where male and female survival are equal at the observed female value $s_5 = s_6 = 0.83$; at this baseline, $\Delta S = 0\%$. When males survive better than females, the survival differential is $\Delta S = (s_6 - 0.83)/0.83 \times 100 > 0\%$, measuring the percent advantage in male survival. When females survive better than males, the survival of males is set to $s_6 = 0.83$ and $\Delta S = (0.83 - s_5)/0.83 \times 100 < 0\%$, measuring the percent disadvantage of males relative to females.

The observed range of variations in ΔS is $[-26\%, 15\%]$ from 1962 to 2005. The average male survival is lower than average female survival by 4.8% ($\Delta S_0 = -4.8\%$). To explore the effect of survival differences, we varied ΔS over the range $-15\% \leq \Delta S \leq 15\%$. We calculated the population structure, OSR, and population growth rate as a function of ΔS and the elasticities of the OSR and of population growth rate when $\Delta S_0 = \pm 4.8\%$.

Population Structure and OSR. At $\Delta S = 0\%$, males and females are equally abundant at equilibrium. There is a high proportion of breeding pairs (78%) and a low pro-

portion of nonbreeders (5%) in the equilibrium population (fig. 2). When female survival is higher than that of males (i.e., $\Delta S < 0$), females are more abundant than males. As the survival disadvantage of males increases (ΔS becomes more negative), the proportion of breeding pairs decreases and the proportion of female nonbreeders increases. When male survival is higher (i.e., $\Delta S > 0$) the opposite occurs: males become more abundant and the proportion of male nonbreeders increases.

When $\Delta S = 0\%$, potentially breeding males and females are equally abundant, and the OSR and mating probabilities are both equal to 1 (fig. 3A). When female survival exceeds that of males (i.e., $\Delta S < 0$), potentially breeding females are more abundant than males, $OSR = u_f < 1$ and $u_m = 1$. As the male disadvantage increases (ΔS becomes more negative), the OSR decreases. When male survival is higher than that of females (i.e., $\Delta S > 0$) the opposite occurs: potentially breeding males become more abundant, $OSR = 1/u_m > 1$ and $u_f = 1$ and the OSR increases. The elasticities of the population structure are shown in appendix C in the online edition of the *American Naturalist*.

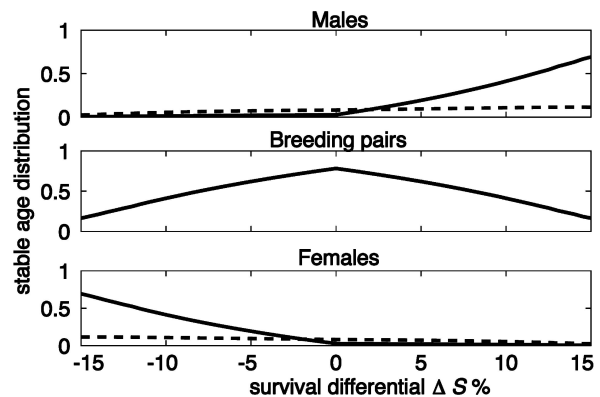


Figure 2: Equilibrium structure of the emperor penguin population as a function of the proportional difference in adult survival between males and females, ΔS (%). There are five stages in the population, according to breeding status and sex (fig. 1B). We show results for males, breeding pairs, and females. Among males and females, the dashed line refers to prebreeders and the solid line to nonbreeders.

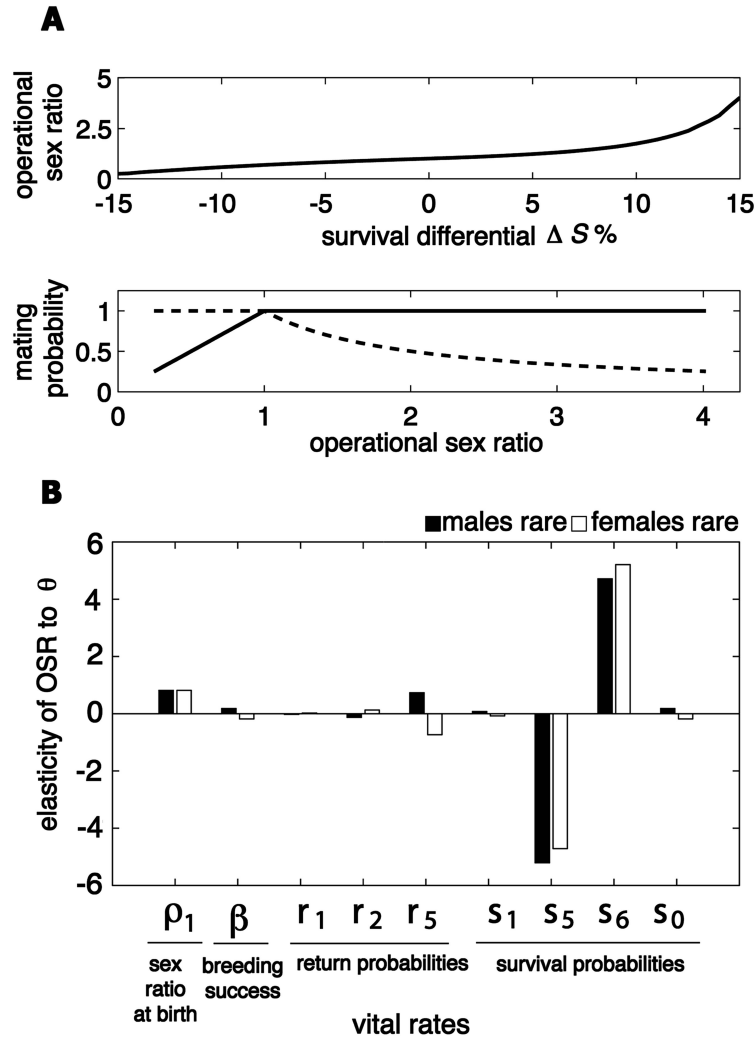


Figure 3: A, Equilibrium operational sex ratio (\widehat{OSR}) and mating probabilities; *upper graph*: \widehat{OSR} as a function of the proportional difference in adult survival between males and females, ΔS (%), and *lower graph*: mating probabilities of males (*dashed line*) and females (*solid line*) are functions of the OSR. B, Elasticity of \widehat{OSR} to the vital rates at $\Delta S = |4.8|\%$. Black bars show results when males are rare ($\Delta S_0 = -4.8\%$). White bars are the opposite case ($\Delta S = 4.8\%$). The vital rates are defined in table 2.

Elasticity of the Operational Sex Ratio to Vital Rates. To study effects of parameter perturbation on the OSR, we maintain the equality of all male and female vital rates except adult survival. Thus, the parameter vector θ in equations (18)–(20) has nine elements (see table 2). For instance, the elasticity of OSR to prebreeder return probability r_1 refers to a perturbation that affects both females (r_1) and males (r_3) equally. We examine two cases: (1) when females survive better than males and the survival differential is $\Delta S_0 = -4.8\%$ (the observed average, in which males are rare) and (2) when $\Delta S = 4.8\%$ (a hypothetical symmetrical situation in which males survive better than females).

In absolute value, the elasticities of the OSR are highest to male and female adult survival, followed by sex ratio at birth, breeder return probability, breeding success, chick survival, and prebreeder survival (fig. 3B). The elasticities of the OSR to male survival and sex ratio at birth are positive, whereas to female survival, they are negative. The effects of perturbations in two-sex models are more complicated than in linear models because they change the relative abundance of stages and the sex ratio within stages. The OSR is a weighted average of male and female proportions in different stages, so the elasticities of the OSR can be counterintuitive. In the penguin, when males are rare, the elasticity of the OSR to the return probability

of nonbreeders (r_2) is negative, while the elasticity to the return probability of breeders (r_5) is positive. Returning breeders and returning nonbreeders are both available to mate, so why should their return rates have opposite effects on OSR? Closer examination shows that the potentially returning nonbreeders include few males. Increasing r_2 thus increases the return of a female-biased set of individuals and reduces the OSR. Among breeding pairs, however, males and females are equally abundant, so r_5 therefore increases the OSR.

Population Growth and Its Elasticity. The equilibrium population growth rate ($\hat{\lambda}$) is maximized when male and female survival are equal (i.e., $\Delta S = 0\%$; fig. 4A); in the absence of any other sex differences, males and females are equally abundant among potential breeders and breeding is not limited by availability of mates. Under these conditions, the population grows at a rate of 1.1%/year. The population growth rate decreases as ΔS increases or decreases from $\Delta S = 0\%$. The population is projected to decline (i.e., $\hat{\lambda} < 1$) when $|\Delta S| > 2\%$ (fig. 4).

We calculated the elasticities of $\hat{\lambda}$ to the parameters using equations (16) and (17), with $\Delta S_0 = -4.8\%$ (the observed average, in which females survive better than males and males are rare) and $\Delta S = 4.8\%$ (the symmetrical situation, in which males survive better than females and females would be rare). In absolute value, the elasticities of $\hat{\lambda}$ to male and female adult survival are the highest, followed by others shown in figure 4B.

The elasticities in nonlinear two-sex models include both direct effects of the parameter and indirect effects through the impact of the parameter on population structure and thus on mating. In the present case, when males are rare, we find that the elasticity of $\hat{\lambda}$ to female adult survival is negative! This is impossible in a linear model, but it happens here because an increase in female survival increases the proportion of females, decreases the OSR, and thus reduces mating probability. The negative effect of reduced mating exceeds, in this case, the positive effect of increased female survival, leading to a net decrease in $\hat{\lambda}$. The balance between these effects depends on the entire set of parameters. It is generally not possible to predict the signs of the elasticities of $\hat{\lambda}$ in a two-sex model.

Penguin Population Dynamics during a Regime Shift

The Terre Adélie population was stable from 1962 to the early 1970s, with an average of 5,733 breeding pairs. It declined to an average of 2,878 pairs during the mid-1970s and has remained approximately stable since then (fig. 5A). This abrupt change from 1972 to 1981 from one stationary population state to another was identified as a regime shift (Jenouvrier et al. 2005a, 2009a).

To see whether our two-sex model could generate these dynamics, we applied equation (1) using two matrices: A_1 during a normal year and A_2 during a regime-shift year. To explore sex differences in adult survival, we set all other vital rates in A_1 and A_2 equal. The observed survival differential was $\Delta S_1 = -1.2\%$ in a normal year and $\Delta S_2 = -10.8\%$ in a regime-shift year (i.e., the regime shift reduced male survival more than female survival; Jenouvrier et al. 2005b). The initial population vector was set to the equilibrium structure calculated from A_1 , with the number of breeding pairs set equal to the mean during 1962–1971.

The projected dynamics of breeding pairs agree well with the observation (fig. 5A), including the rate, magnitude, and duration of the population decline during the regime shift and the stability before and after the regime shift. Although prebreeders and nonbreeders are not observable at the colony, the model predicts these numbers. Before the regime shift (1962–1971), females outnumber males among both prebreeders (667 females vs. 634 males) and nonbreeders (501 females vs. 206 males). During the regime shift (1972–1981), males decrease (to 105 males) but females increase (to 1,474 females) among nonbreeders. After the regime shift (1982–2005), nonbreeding females decrease (to 386 females).

According to the model, before the regime shift the OSR was slightly female biased (OSR = 0.96, fig. 5B). During the regime shift, reduced male adult survival caused a strong female bias in the OSR (OSR = 0.72 in 1981). After the regime shift, male adult survival returned to its pre-regime-shift value and the OSR had almost recovered to its pre-regime-shift value by 2005.

Discussion

Two-Sex Models

The components of any two-sex demographic model include sex, stage structure, the nonlinearities created by mating, and seasonality in breeding behavior. The nonlinear periodic matrix model we present here greatly increases the flexibility of such models. The stages in our example focus on breeding status but could be extended to include age structure (e.g., Jenouvrier et al. 2005b), breeding experience (e.g., Nevoux et al. 2007), or other stages. The penguin forms monogamous breeding pairs, but other mating systems could be incorporated, by accounting for harems or by separating breeding individuals into females and males.

In most animals and many plants, breeding behaviors are highly seasonal. The periodic matrix model makes it possible to include complex sequences of behavioral events coupled with seasons within the year. We focused on return

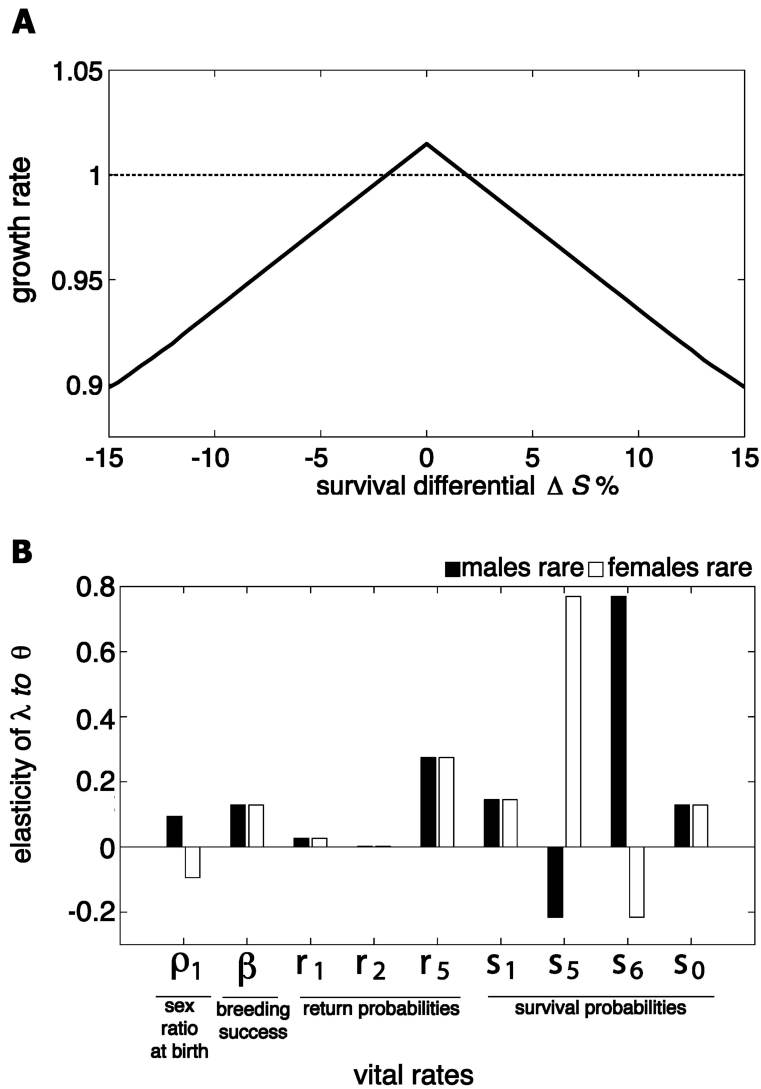


Figure 4: A, Equilibrium population growth rate $\hat{\lambda}$ as a function of the proportional difference in adult survival between males and females, ΔS (%). B, Elasticity of the population growth rate to the vital rates at $\Delta S = |4.8|\%$.

to the breeding site, mating, raising offspring, and leaving the breeding site; however, the approach could be applied to any behaviors occurring during the annual seasonal cycle (e.g., Gerber 2006). One or more of the seasonal matrices will be nonlinear to account for the dependence of mating on the availability of males and females. In our case, mating appeared in only one matrix but could appear in more than one.

The calculation of population structure and growth rate, two important measures in evolution and population ecology, must take the nonlinearity of the mating function into account. We analyzed the OSR, which is commonly used in evolutionary studies. However, the approach could

be applied to any other ratio of interest (Caswell 2008), such as the relative number of breeding individuals to adults.

A new general perturbation analysis for nonlinear models (Caswell 2008) makes it possible for the first time to calculate the sensitivity and elasticity of nonlinear two-sex models. The results can be quite different from those expected in linear two-sex models (see Veran and Beissinger 2009, for a sensitivity analysis of a linear two-sex model). For example, in the case of penguins, increases in adult female survival actually reduce population growth rate. This surprising result happens because of indirect negative effects through the impact on population structure. These

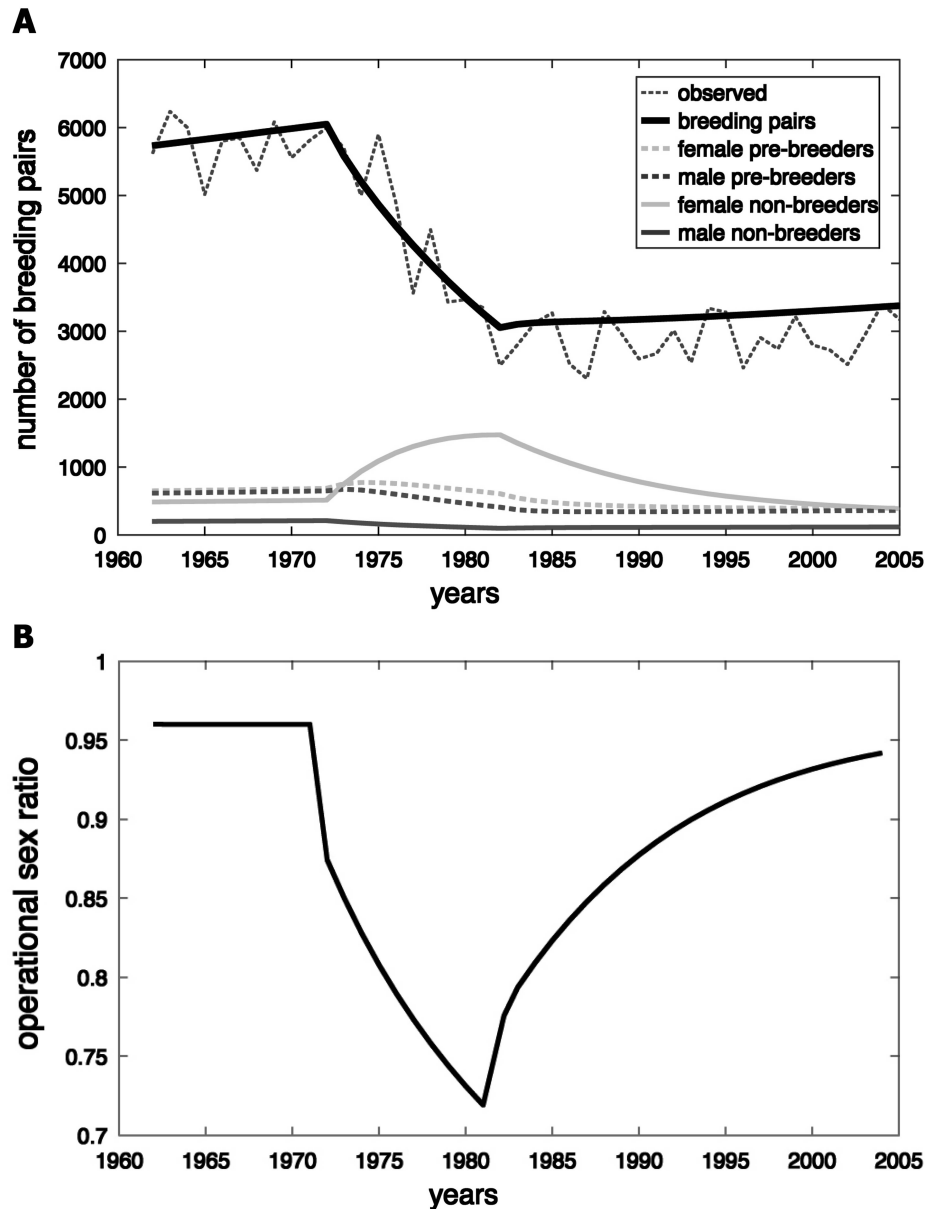


Figure 5: Population dynamics (A) and the operational sex ratio (B) of the emperor penguin breeding in Terre Adélie from 1962 to 2005. A, Number of breeding pairs observed and the number of breeding pairs calculated by the two-sex model. The number of male and female prebreeders and nonbreeders as calculated by the two-sex model are also shown.

can be stronger that the positive direct effects of survival on population growth. In contrast, in linear models per capita fertility is independent of population structure, and increases in survival cannot have negative effects. Nonlinear models are thus crucial in studying how the interaction of the sexes affects the sensitivity of the OSR and population growth rate to demographic parameters.

The Emperor Penguin

The emperor penguin is interesting because its extreme environment enforces strict monogamy. The only sexual demographic difference apparent in the data is that survival of adult males is lower than that of females, because males are more strongly affected by environmental vari-

ations, especially winter sea ice extent (SIE; Jenouvrier et al. 2005b). Winter SIE affects krill populations (Loeb et al. 1997) on which the food web is based (Olaso et al. 2004). Males must accumulate body fat before the breeding season to be able to incubate the egg while fasting and awaiting the return of their mate. In years with reduced winter SIE, resources may decrease, and males may be unable to cope with a long fast. This may result in higher mortality rates for males than for females.

Over the entire study period (1962–2005), we project a growth rate of -2.33% per year, which agrees well with the observed average growth rate. We project an equilibrium OSR of 0.96 during normal years (i.e., 1962–1971 and 1982–2005). The few observations of adult sex ratio suggest that females outnumber males during the mating season (OSR estimated in 1968 is 0.91 [Isenmann 1971] and in 1969 is 0.91 [Jouventin 1971a]; C. Barbraud and H. Weimerskirch, unpublished data).

During the regime shift in the mid-1970s, the number of breeding pairs decreased by approximately 50% due to a higher male mortality related to a decrease in SIE (Jenouvrier et al. 2005b). The projected number of nonbreeding females increased, and the projected OSR dropped to 72%. These results illustrate the strong effect that reduced SIE during the regime shift has on population structure, OSR, and population growth rate. They show that such climate effects may last for decades after the perturbation. Recently, using a single-sex model, we showed that an increased frequency of reduced SIE would reduce penguin population viability (Jenouvrier et al. 2009a). Including mating processes in that analysis would reduce population viability even more, as previously suggested for monogamous species (Bessa-Gomes et al. 2004).

Other Mating Systems

Our approach can be extended beyond monogamous mating by using appropriate mating functions in the matrix \mathbf{M}_4 . Previous studies discussed some mating functions that are included in fertility (e.g., Caswell and Weeks 1986; Legendre et al. 1999; Caswell 2001; Iannelli et al. 2005). In our case, mating is described by probabilities that are bounded between 0 and 1, and the mating functions must be modified to suit this limit.

Polygynous species, in which a single male mates with several females, can be described in terms of the average harem size h (Caswell and Weeks 1986). The number of potential harems is N_f/h , and the number of mated harems is $\min(N_f/h, N_m)$. The male and female mating probabilities would be

$$u_m = \frac{\min(N_f/h, N_m)}{N_m}, \quad (22)$$

$$u_f = \frac{h \min(N_f/h, N_m)}{N_f}. \quad (23)$$

If males are scarce, mating will be limited by male abundance. For example, poaching of male saiga antelope (*Saiga tatarica*), selected for their horns, reduced the number of adult males in this harem-breeding ungulate to the point that many females became unable to find a mate (Milner-Gulland et al. 2003). As a result, fecundity and population size decreased, leading to a “critically endangered” listing of the saiga antelope on the 2002 International Union for Conservation of Nature and Natural Resources Red List.

Sexual conflict and male harassment can be included in the model by making survival of the harassed sex a function of the number of males and females (e.g., Le Galliard et al. 2005). In this case, the matrix \mathbf{M}_2 would be frequency dependent. A similar approach could be used to study the risk for a female to contract a sexual disease (Rankin and Kokko 2007).

Conclusion

The interaction of the sexes has important implications in management and conservation. Some studies have proposed manipulating the sex ratio to change the population growth rate to control invasive species (Barclay 2005; Ferguson et al. 2005) or in reintroduction programs (Milner-Gulland et al. 2003; Sæther et al. 2004; Robertson et al. 2006; Lenz et al. 2007). Periodic two-sex models will permit study of such manipulations in more details, and the results from perturbation analysis may provide new guidelines for managers.

In studies of sexual evolution, it is essential to include demographic processes because reproduction is limited by the relative abundance of both sexes, eventually affecting the OSR (Kokko and Jennions 2008) and the fitness of different breeding strategies. Nonlinear perturbation analysis permits the study of the factors affecting any aspect of population structure, including but not limited to the OSR.

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Emperor penguin colony at the end of the breeding season in Terre Adélie. Photograph by Christophe Barbraud.