

Dynamics of populations with two sexes

M. Cecilia Pérez

*Facultad de Ingeniería, Universidad Nacional de la Patagonia San Juan Bosco
Esquel, Chubut, Argentina*

E. Adriana Saavedra

*Facultad de Ingeniería, Universidad Nacional de la Patagonia San Juan Bosco
Trelew, Chubut, Argentina*

Mariano A. Ferrari*

*Facultad de Ingeniería, Universidad Nacional de la Patagonia San Juan Bosco
Puerto Madryn, Chubut, Argentina*

*Centro Nacional Patagónico, CONICET, Puerto Madryn, Chubut, Argentina
mferrari7@gmail.com*

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A mathematical model is presented in order to describe the dynamics of polygamous populations, bearing in mind single individuals of both sexes and the development of reproductive groups. In this context, the description leads us to consider positive homogeneous dynamical systems, establishing conditions for the stationary state existence and its local stability. A fourth pre-reproductive stage was considered, i.e. males and females spend part of their lives before being in condition to reproduce, as a first step to consider more general models. Finally, we parametrized the proposed model using southern elephant seal data, to analyze the direct applicability to a real population.

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1. Introduction

Differential equation and dynamical system theory has been developed in straight linking with other disciplines, particularly the description of population dynamics in continuous time. In this context, the description of a population with both sexes leads to the consideration of a certain kind of nonlinear autonomous systems [11, 6]. The two-sex problem is well known in demography and population biology since

*Corresponding author.

classical linear population models are not appropriate for description of changes in the sex ratio and its consequences, see [19] and references therein. Moreover, mating models are particularly relevant for the study of sexually transmitted diseases [2], and endangered populations with skewed sex ratios, due, for example, to sex-selective hunting [14, 18].

A simple two-sex model was described by Hadelér *et al.* [10], taking into account a population with three stages of reproductive individuals: solitary males, solitary females and pairs; and conditions for the existence of a stationary state were given. In the stationary solution, sex ratio becomes stable and the population increases (or decreases) exponentially. This model presents some limitations and offers the possibility to consider some interesting generalizations. On the one hand, the concept of pairs can only be applied to monogamous populations while polygamy is a common characteristic in wild populations. Moreover, the three-stage model implies that individuals reach the reproductive state immediately, without a previous maturation period.

In this work, we generalized the Hadelér *et al.* model [10] in two ways. First, we considered reproductive groups with a mean number of males and females. Results about stationary state existence and its local stability were the same as that in [10], but analysis was different and we focused on sexual proportion of the groups, that is, the social structure of the population. Then we extended our analysis to a four-stage model, with a pre-reproductive stage. Finally, we applied the model with elephant seal population parameters and compared the results with data from the social structure observed in the field.

Positive homogeneous equations. The positivity and stability of differential systems are very important issues since they are, in many situations, the first step to consider the applicability to some real processes like dynamics of populations or ecological models. In this work, we consider systems of the form $\dot{X} = F(X)$, where $F : \mathbb{R}^n \rightarrow \mathbb{R}^n$ is homogeneous of degree 1, that is $F(\alpha X) = \alpha F(X)$ for all $\alpha \geq 0$, and we will assume that

$$F_i(X) \geq 0 \quad \text{for } X \geq 0, \quad X_i = 0,$$

so the system flow leaves the positive cone \mathbb{R}_+^n invariant. The positivity is guaranteed for that type of systems and we will restrict our analysis to the positive cone since the vector X describes population densities in the considered models. On the other hand, homogeneous assumption is usual when we are interested in the so-called frequency-dependent models, as a first generalization of classical linear population models. That is, we discard population regulation considering the possibility of unlimited population growth. Demographic properties of such models depend only on the relative magnitudes of the X_i , and not on their absolute magnitudes [3]. We refer the reader to [5] for a study of positivity in the linear case and to [4] for an approach to density-dependent models like the Beverton–Holt equation.

For general positive homogeneous systems we will recall the framework developed by Hadelér *et al.* [10] in Secs. 2 and 3. We know that $X = 0$ is the only

stationary point and that $X(t) > 0$ for all t if $X(0) > 0$. Stationary solutions have exponential growth, just like in the linear case, and we know that a stationary exponential solution with growth rate λ^* and stationary structure \bar{X} :

$$X(t) = \bar{X} \exp(\lambda^* t),$$

corresponds to a solution of the nonlinear eigenvalue problem: $F(\bar{X}) = \lambda^* \bar{X}$. Moreover, let $F'(\bar{X})$ be the Jacobian matrix at \bar{X} , then $F'(\bar{X}) \cdot \bar{X} = \lambda^* \bar{X}$ and the stationary solution is locally stable if and only if the numbers $\lambda - \lambda^*$ have negative real part, for every λ eigenvalue of $F'(\bar{X})$, $\lambda \neq \lambda^*$.

2. Population Model with Three Stages

Following Haderler *et al.* [10], we will expose a two-sex model with reproductive group formation. The model is given by a system of three differential equations:

$$\begin{aligned} \dot{x} &= (k_x h + \mu_y h + \sigma h)g - \mu_x x - \varphi\left(\frac{x}{h}, \frac{y}{m}\right)h, \\ \dot{y} &= (k_y h + \mu_x m + \sigma m)g - \mu_y y - \varphi\left(\frac{x}{h}, \frac{y}{m}\right)m, \\ \dot{g} &= -(\mu_x + \mu_y + \sigma)g + \varphi\left(\frac{x}{h}, \frac{y}{m}\right). \end{aligned} \tag{2.1}$$

System variables x, y and g represent unmated females, unmated males and reproductive groups' densities respectively. Population parameters are given by positive constants: the rates of births, k_x, k_y ; the death rates, μ_x, μ_y ; and a separation rate of reproductive groups, σ . Reproductive groups are formed by m males and h females in average and we would assume that these quantities remain constant. Group formation rate is represented by φ . When a new group is formed, this subtracts h females and m males from the unmated population, thus the coefficients $-h, -m$ and 1 that join φ in the three equations of system (2.1). We remark that we related newborns linearly to the number of mated females hg , then $k_x hg$ represents the number of newborn females whereas $k_y hg$ the number of newborn males. This introduces a kind of asymmetry in the first two equations of system (2.1), with consequences on population dynamics. Group formation is a nonlinear process determined by the mating function $\varphi : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+$. As usual in two-sex models [19], we assume that φ is a homogeneous monotone function that satisfies:

$$\begin{aligned} \varphi(x, 0) &= \varphi(0, y) = 0, \\ \varphi(\alpha x, \alpha y) &= \alpha \varphi(x, y), \quad \text{for } \alpha \geq 0, \\ \varphi(x + u, y + v) &\geq \varphi(x, y), \quad \text{for } u \geq 0; v \geq 0. \end{aligned}$$

We have then a positive homogeneous system in \mathbb{R}^3 of the form $\dot{X} = F(X)$. We know then that the system flow leaves the positive cone \mathbb{R}_+^3 invariant and we would like to characterize the exponential stationary solutions. The following analysis is basically the same as [10], but some modifications introduced will facilitate the generalization to a four-stage model.

2.1. Stationary solutions

Consider the nonlinear eigenvalue problem associated to (2.1):

$$\begin{aligned} \lambda \bar{x} &= (k_x h + \mu_y h + \sigma h) \bar{g} - \mu_x \bar{x} - \varphi\left(\frac{\bar{x}}{h}, \frac{\bar{y}}{m}\right) h, \\ \lambda \bar{y} &= (k_y h + \mu_x m + \sigma m) \bar{g} - \mu_y \bar{y} - \varphi\left(\frac{\bar{x}}{h}, \frac{\bar{y}}{m}\right) m, \\ \lambda \bar{g} &= -(\mu_x + \mu_y + \sigma) \bar{g} + \varphi\left(\frac{\bar{x}}{h}, \frac{\bar{y}}{m}\right). \end{aligned} \tag{2.2}$$

The system admits two trivial solutions:

$$\begin{aligned} v_1 &= (1, 0, 0) \quad \text{for } \lambda = -\mu_x, \\ v_2 &= (0, 1, 0) \quad \text{for } \lambda = -\mu_y. \end{aligned}$$

In these solutions, the lack of group formation leads to the population extinction since there are no births. Therefore, we are interested in the existence of positive solutions of (2.2) with $\bar{g} \neq 0$, which correspond to stationary solutions of (2.1) with positive stationary structure. Dividing by \bar{g} we can assume that $\bar{g} = 1$, solving for $\varphi\left(\frac{\bar{x}}{h}, \frac{\bar{y}}{m}\right)$ in the last equation of (2.2) and substituting in the previous two we have:

$$\frac{\bar{x}}{h} = \frac{k_x}{\mu_x + \lambda} - 1; \quad \frac{\bar{y}}{m} = \frac{k_y}{(\mu_y + \lambda)} \frac{h}{m} - 1.$$

Then, replacing in the last equation of (2.2) we find:

$$\varphi\left(\frac{k_x - \mu_x - \lambda}{\mu_x + \lambda}, \frac{k_y h/m - \mu_y - \lambda}{(\mu_y + \lambda)}\right) = \mu_x + \mu_y + \sigma + \lambda, \tag{2.3}$$

with the condition that the right-hand side and both arguments of φ on the left-hand side must be positive. We define:

$$\begin{aligned} \underline{\lambda} &= \max(-\mu_x, -\mu_y), \\ \bar{\lambda} &= \min(k_x - \mu_x, (k_y h/m) - \mu_y) \end{aligned}$$

and we will characterize conditions for the existence and stability of stationary solutions with positive structure in terms of $\underline{\lambda}$ and $\bar{\lambda}$.

Theorem 2.1. *If $\underline{\lambda} > \bar{\lambda}$, then the nonlinear eigenvalue problem (2.2) has no positive solution. If $\underline{\lambda} < \bar{\lambda}$, there are two cases:*

- (i) *If $-\mu_y \leq -\mu_x$, there exists only one nontrivial positive solution, associated to an eigenvalue $\lambda^* > -\mu_x$, if and only if*

$$\frac{k_y \varphi_y(1, 0)}{(\mu_y + \sigma + \varphi_y(1, 0))} \frac{h}{m} > \mu_y - \mu_x. \tag{2.4}$$

- (ii) *If $-\mu_x < -\mu_y$, there exists only one nontrivial solution, associated to $\lambda^* > -\mu_y$, if and only if*

$$\frac{k_x \varphi_x(0, 1)}{(\mu_x + \sigma + \varphi_x(0, 1))} > \mu_x - \mu_y. \tag{2.5}$$

Proof. If $\underline{\lambda} > \bar{\lambda}$, there is no λ such that the left-hand side of (2.3) has positive arguments. Hence, the system only admits trivial solutions. On the other hand, when $\underline{\lambda} < \lambda < \bar{\lambda}$, the left-hand side of (2.3) continuously decreases from a positive value K (possibly $+\infty$) to zero:

$$K = \lim_{\substack{\lambda \rightarrow \underline{\lambda} \\ \lambda > \underline{\lambda}}} \varphi \left(\frac{k_x - \mu_x - \lambda}{\mu_x + \lambda}, \frac{k_y h - (\mu_y + \lambda) m}{(\mu_y + \lambda) m} \right),$$

while the right-hand side of (2.3) increases linearly from $\mu_x + \mu_y + \sigma + \underline{\lambda}$ to $\mu_x + \mu_y + \sigma + \bar{\lambda}$. In the case of (2.3) there will be only one solution λ^* , $\underline{\lambda} < \lambda^* < \bar{\lambda}$, if and only if $K > \mu_x + \mu_y + \sigma + \underline{\lambda}$.

Now, we remark that $\varphi(\omega, y)$ tends to $\varphi_y(1, 0)y$ and $\varphi(x, \omega)$ tends to $\varphi_x(0, 1)x$ when $\omega \rightarrow \infty$, then:

$$K = \begin{cases} \varphi_y(1, 0) \left(\frac{k_y h - (\mu_y - \mu_x) m}{(\mu_y - \mu_x) m} \right) & \text{if } \underline{\lambda} = -\mu_x, \\ \varphi_x(0, 1) \left(\frac{k_x - \mu_x + \mu_y}{\mu_x - \mu_y} \right) & \text{if } \underline{\lambda} = -\mu_y \end{cases}$$

and theorem follows. □

The following corollary summarizes conditions for the existence of the nontrivial solution and corresponds to the existence result in [10].

Corollary 2.2. *The system (2.1) admits a nontrivial stationary solution with positive stationary structure if and only if inequalities (2.4) and (2.5) are satisfied.*

2.2. Local stability

To analyze the conditions for local stability of the solutions we will recall some results from [10]. When the positive solution exists, we can apply the following change of variables:

$$\xi = \frac{x}{(h/m)g}; \quad \eta = \frac{y}{(h/m)g},$$

reducing (2.1) to a system of dimension two. Analyzing the trace and determinant of the resultant system, we can infer that positive stationary state is always locally stable.

To analyze the stability of trivial solutions we will consider the Jacobian of the right-hand side of (2.1):

$$f'(x, y, g) = \begin{pmatrix} -\mu_x - \varphi_x \left(\frac{x}{h}, \frac{y}{m} \right) & -\varphi_y \left(\frac{x}{h}, \frac{y}{m} \right) \frac{h}{m} & k_x h + \mu_y h + \sigma h \\ -\varphi_x \left(\frac{x}{h}, \frac{y}{m} \right) \frac{m}{h} & -\mu_y - \varphi_y \left(\frac{x}{h}, \frac{y}{m} \right) & k_y h + \mu_x m + \sigma m \\ \varphi_x \left(\frac{x}{h}, \frac{y}{m} \right) \frac{1}{h} & \varphi_y \left(\frac{x}{h}, \frac{y}{m} \right) \frac{1}{m} & -(\mu_x + \mu_y + \sigma) \end{pmatrix}$$

and its characteristic polynomial

$$P(\lambda, (x, y, g)) = \det(f'(x, y, g) - \lambda I_3).$$

Theorem 2.3. *Given the system (2.1) and considering the associated nonlinear eigenvalue problem, let $\underline{\lambda} = \max(-\mu_x, -\mu_y)$ corresponding to a trivial solution and \underline{v} be the associated eigenvector. We assume that $\underline{\lambda}$ is not a double root of the characteristic polynomial $P(\lambda, \underline{v})$, then:*

- (a) *If there is a nontrivial stationary solution, this is locally stable while the two trivial solutions are unstable.*
- (b) *If there does not exist the positive solution, then the trivial solution corresponding to $\underline{\lambda}$ is stable, while the one corresponding to $\min(-\mu_x, -\mu_y)$ is unstable.*

Proof. Assume first that $\underline{\lambda} = -\mu_x > -\mu_y$, we can see that:

$$P(-\mu_x, (x, y, g)) = k_x \varphi_x \left(\frac{x}{h}, \frac{y}{m} \right) (\mu_y - \mu_x) \geq 0,$$

$$P(-\mu_y, (x, y, g)) = -\frac{h}{m} k_y \varphi_y \left(\frac{x}{h}, \frac{y}{m} \right) (\mu_y - \mu_x) \leq 0.$$

We have then, for every (x, y, g) , that the characteristic polynomial has a real root greater than or equal to $-\mu_x$, since $P(\lambda, (x, y, g))$ tends to $-\infty$ when $\lambda \rightarrow +\infty$. In particular $P(\lambda, (0, 1, 0))$ would have a real root greater than $-\mu_y$, and then we are able to affirm that the solution corresponding to $(0, 1, 0)$ is unstable.

To analyze the stability of $(1, 0, 0)$ let us consider $P(\lambda, (1, 0, 0)) = (\mu_x + \lambda)Q(\lambda)$, being Q the quadratic polynomial

$$Q(\lambda) = \frac{h}{m} k_y \varphi_y(1, 0) - (\mu_x + \mu_y + \varphi_y(1, 0) + \sigma + \lambda)(\mu_y + \lambda).$$

Then $Q(-\mu_x) = \frac{h}{m} k_y \varphi_y(1, 0) + (\mu_y + \varphi_y(1, 0) + \sigma)(\mu_x - \mu_y)$, being $Q(-\mu_x) \neq 0$ by hypothesis. If $Q(-\mu_x) > 0$, then (2.4) is fulfilled, positive stationary solution exists and $Q(\lambda)$ has a real root greater than $-\mu_x$, in consequence $(1, 0, 0)$ is unstable. On the other hand, if $Q(-\mu_x) < 0$, then positive stationary solution does not exist and we can see that $Q(\lambda)$ has two real roots less than $-\mu_x$, thus the trivial solution $(1, 0, 0)$ is stable.

When $\underline{\lambda} = -\mu_y > -\mu_x$ the analysis is similar, we have that $(1, 0, 0)$ is unstable, while $(0, 1, 0)$ is stable if positive stationary solution does not exist, and unstable if it does exist. In the case of $\underline{\lambda} = -\mu_x = -\mu_y$, we can see, bearing in mind the previous analysis, that positive stationary solution exists and is stable while other trivial solutions are unstable. □

To illustrate solutions behavior we plot the stationary sex ratio $r_x = \bar{x}/(\bar{x} + \bar{y})$ when varying a key population parameter, the female death rate, and keep fixed the rest of the parameters. A sex ratio $r_x = 1$ corresponds to lack of males and $r_x = 0$ corresponds to lack of females, whereas $0 < r_x < 1$ indicates the existence

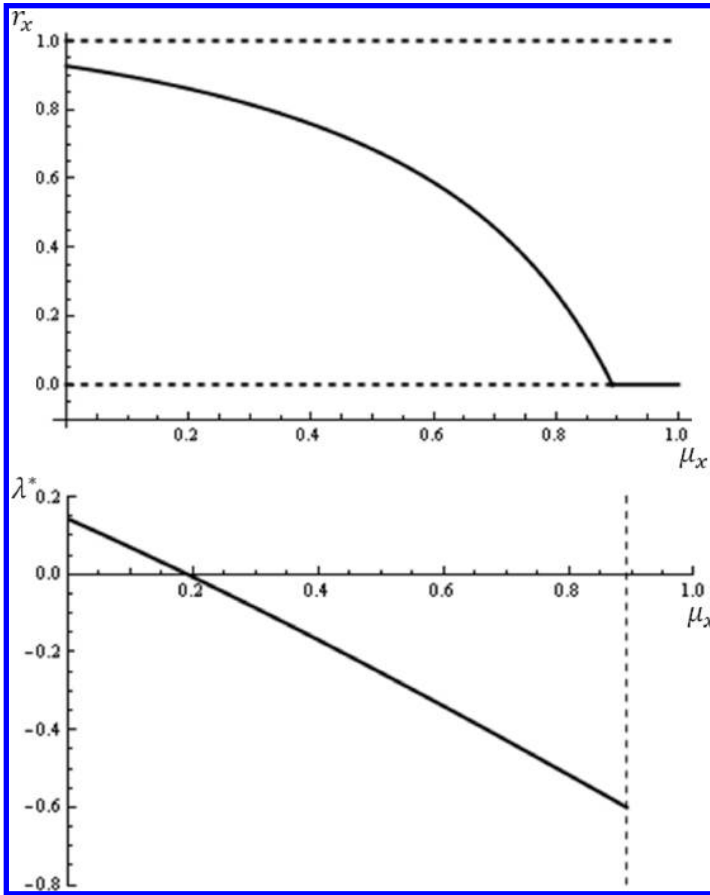


Fig. 1. Stationary sex ratio and population growth for system (2.1) when varying female death rate. The rest of the parameters were fixed: $k_x = 0.7, k_y = 0.35, \mu_y = 0.6, \sigma = 0.5, h = 6, m = 1$ and the mating function was proportional to the harmonic mean $\varphi(x, y) = xy/(x+y)$. Dashed lines in the upper panel indicate unstable solutions. Population is increasing with positive stationary sex ratio for $0 < \mu_x < 0.191$, decreasing with positive stationary sex ratio for $0.191 < \mu_x < 0.893$ and collapses due to lack of females if $\mu_x > 0.893$.

of the positive solution, in such case we can consider the stationary growth rate λ^* to distinguish between a decreasing or increasing population, see Fig. 1.

Regarding the structure of reproductive groups, we remark that if $\mu_x \leq \mu_y$, there is a critical ratio between h and m , $H_0 \geq 0$ given by (2.4) such that the positive stationary state exists if and only if $h/m > H_0$:

$$H_0 = \frac{(\mu_y - \mu_x)(\mu_y + \sigma + \varphi_y(1, 0))}{k_y \varphi_y(1, 0)}. \quad (2.6)$$

On the other hand, if $\mu_x > \mu_y$, the stationary state existence depends on (2.5), and is not dependent on the structure of reproductive groups. That is, a lack of males could be compensated with a higher proportion of males in reproductive

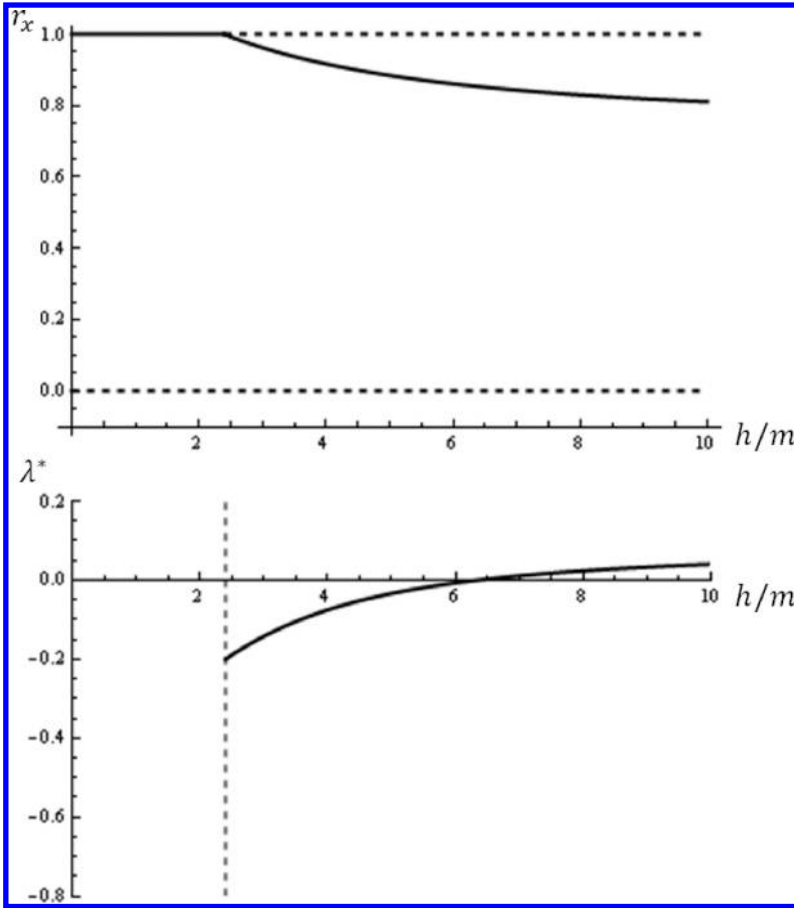


Fig. 2. Stationary sex ratio and population growth for system (2.1) when varying the sexual proportion of reproductive groups. The rest of the parameters were fixed: $k_x = 0.7$, $k_y = 0.35$, $\mu_y = 0.6$, $\sigma = 0.5$, $\mu_x = 0.2$ and the mating function was proportional to the harmonic mean $\varphi(x, y) = xy/(x+y)$. Population collapses due to lack of males if $h/m < 2.4$, whereas population is decreasing with positive stationary sex ratio for $2.4 < h/m < 6.36$ and increasing with positive stationary sex ratio for $h/m > 6.36$.

groups whereas a lack of females could not be compensated. In Fig. 2, we show the stationary sex ratio and growth rate when varying the sexual proportion of the reproductive groups: h/m .

3. Population Model with Four Stages

We propose a model with four stages, including a pre-reproductive stage s . That is, individuals spend part of their life before changing into reproductive males or females. In our model, the difference between both sexes will be based on the death rates (μ_x, μ_y) and the recruitment rates (k_x, k_y), that is the transition rates from the pre-reproductive stage to the reproductive ones. This model is a first approximation

and it is important to mention that, for a more realistic description, it should be considered one or more pre-reproductive stages for each sex and delayed equations to model the different maturation times. Now, our four-stage system is described by:

$$\begin{aligned} \dot{x} &= k_x s + \sigma h g + \mu_y h g - \mu_x x - \varphi\left(\frac{x}{h}, \frac{y}{m}\right) h, \\ \dot{y} &= k_y s + \sigma m g + \mu_x m g - \mu_y y - \varphi\left(\frac{x}{h}, \frac{y}{m}\right) m, \\ \dot{s} &= k_s h g - (\mu_s + k_x + k_y) s, \\ \dot{g} &= -(\mu_x + \mu_y + \sigma) g + \varphi\left(\frac{x}{h}, \frac{y}{m}\right). \end{aligned} \tag{3.1}$$

Again, the associated nonlinear eigenvalue problem admits two trivial solutions:

$$v_1 = (1, 0, 0, 0) \quad \text{for } \lambda = -\mu_x,$$

$$v_2 = (0, 1, 0, 0) \quad \text{for } \lambda = -\mu_y.$$

If $\bar{z} = (\bar{x}, \bar{y}, \bar{s}, \bar{g})$ is a positive solution, of the nonlinear eigenvalue problem, associated to an eigenvalue λ it must satisfy, assuming $\bar{g} = 1$, that: $\bar{s} = \frac{hk_s}{(\mu_s + k_x + k_y + \lambda)}$ and:

$$\begin{aligned} \frac{\bar{x}}{h} &= \frac{k_x k_s - (\mu_s + k_x + k_y + \lambda)(\mu_x + \lambda)}{(\mu_s + k_x + k_y + \lambda)(\mu_x + \lambda)}, \\ \frac{\bar{y}}{m} &= \frac{k_y k_s h - (\mu_s + k_x + k_y + \lambda)(\mu_y + \lambda)m}{(\mu_s + k_x + k_y + \lambda)(\mu_y + \lambda)m}. \end{aligned}$$

Moreover, from the last equation of (3.1) we have that

$$\varphi(\bar{x}/h, \bar{y}/m) = \mu_x + \mu_y + \sigma + \lambda. \tag{3.2}$$

Thus, from $\bar{s} > 0$ we have that $\lambda > -(\mu_s + k_x + k_y)$ and then, from $\bar{x}, \bar{y} > 0$ we have that $\lambda > -\mu_x$ and $\lambda > -\mu_y$. If we call $\underline{\lambda}_1 = \max(-\mu_x, -\mu_y, -(\mu_s + k_x + k_y))$ and

$$\bar{\lambda}_1 = \max(\lambda \geq -(\mu_s + k_x + k_y) : \bar{x} \geq 0 \text{ and } \bar{y} \geq 0),$$

then we can characterize the existence of the nontrivial solution as in the three stages case.

From what follows, let us denote $\varphi_x = \varphi_x(0, 1)$ and $\varphi_y = \varphi_y(1, 0)$.

Theorem 3.1. *Given the two-sex model with pre-reproductive stage (3.1), we have that $\underline{\lambda}_1 < \bar{\lambda}_1$ is a necessary condition for the existence of a nontrivial positive solution. When it exists, the positive solution is unique and has an associated growth rate $\lambda^* > \max(-\mu_x, -\mu_y, -(\mu_s + k_x + k_y))$. Furthermore, if $\underline{\lambda}_1 < \bar{\lambda}_1$ three cases are presented:*

(i) *If $\underline{\lambda}_1 = -\mu_x$, then the nontrivial solution exists if and only if*

$$\frac{k_y k_s \varphi_y}{(\mu_y + \sigma + \varphi_y) m} h > (\mu_y - \mu_x)(\mu_s - \mu_x + k_x + k_y). \tag{3.3}$$

(ii) If $\underline{\lambda}_1 = -\mu_y$, then the nontrivial solution exists if and only if

$$\frac{k_x k_s \varphi_x}{(\mu_x + \sigma + \varphi_x)} > (\mu_x - \mu_y)(\mu_s - \mu_y + k_x + k_y). \tag{3.4}$$

(iii) If $\underline{\lambda}_1 = -(\mu_s + k_x + k_y)$, then the nontrivial solution always exists.

Proof. If $\underline{\lambda}_1 \geq \bar{\lambda}_1$ there is no positive solution since there is no λ such that $\bar{s}, \bar{x}, \bar{y} > 0$. Now let $\underline{\lambda}_1 < \lambda < \bar{\lambda}_1$, then $\varphi(\bar{x}/h, \bar{y}/m)$ is a decreasing function. Let

$$K = \lim_{\substack{\lambda \rightarrow \underline{\lambda}_1 \\ \underline{\lambda}_1 < \lambda}} \varphi(\bar{x}/h, \bar{y}/m),$$

it results that (3.2) have only one solution λ^* if and only if $K > \mu_x + \mu_y + \sigma + \underline{\lambda}_1$. Now, we observe that:

$$K = \begin{cases} \varphi_y \left[\frac{k_y k_s h - (\mu_y - \mu_x)(\mu_s - \mu_x + k_x + k_y)m}{(\mu_y - \mu_x)(\mu_s - \mu_x + k_x + k_y)m} \right] & \text{if } \underline{\lambda}_1 = -\mu_x, \\ \varphi_x \left[\frac{k_x k_s - (\mu_x - \mu_y)(\mu_s - \mu_y + k_x + k_y)}{(\mu_x - \mu_y)(\mu_s - \mu_y + k_x + k_y)} \right] & \text{if } \underline{\lambda}_1 = -\mu_y, \\ \infty & \text{if } \underline{\lambda}_1 = -(\mu_s + k_x + k_y) \end{cases}$$

and we obtain the three cases of the theorem. □

We remark here that the three cases of Theorem 3.1 cannot be synthesized in two inequalities, as we summarized the cases of Theorem 2.1 in Corollary 2.2. On the other hand, the model still provides a critical proportion of reproductive groups for the existence of the positive stationary solution. In fact, if $\mu_x < \mu_y$ and $\mu_x < \mu_s + k_x + k_y$ we have from (3.3) that the positive stationary solution exists if and only if $h/m > H_0$:

$$H_0 = \frac{(\mu_y - \mu_x)(\mu_s - \mu_x + k_x + k_y)(\mu_y + \sigma + \varphi_y(1, 0))}{k_y k_s \varphi_y(1, 0)}.$$

Conditions for the local stability of solutions can be analyzed as in the previous section. We will consider the Jacobian of the right-hand side of (3.1):

$$f'(x, y, s, g) = \begin{pmatrix} -\mu_x - \varphi_x \left(\frac{x}{h}, \frac{y}{m} \right) & -\varphi_y \left(\frac{x}{h}, \frac{y}{m} \right) \frac{h}{m} & k_x & \sigma h + \mu_y h \\ -\varphi_x \left(\frac{x}{h}, \frac{y}{m} \right) \frac{m}{h} & -\mu_y - \varphi_y \left(\frac{x}{h}, \frac{y}{m} \right) & k_y & \sigma m + \mu_x m \\ 0 & 0 & -(\mu_s + k_x + k_y) & k_s h \\ \varphi_x \left(\frac{x}{h}, \frac{y}{m} \right) \frac{1}{h} & \varphi_y \left(\frac{x}{h}, \frac{y}{m} \right) \frac{1}{m} & 0 & -(\mu_x + \mu_y + \sigma) \end{pmatrix}$$

and the characteristic polynomial:

$$P(\lambda, (x, y, s, g)) = \det(f'(x, y, s, g) - \lambda I_4).$$

In particular:

$$f'(1, 0, 0, 0) = \begin{pmatrix} -\mu_x & -\varphi_y \frac{h}{m} & k_x & \sigma h + \mu_y h \\ 0 & -\mu_y - \varphi_y & k_y & \sigma m + \mu_x m \\ 0 & 0 & -(\mu_s + k_x + k_y) & k_s h \\ 0 & \varphi_y \frac{1}{m} & 0 & -(\mu_x + \mu_y + \sigma) \end{pmatrix}$$

since $\varphi_x(\frac{1}{h}, 0) = \varphi_x(1, 0) = 0$, $\varphi_y(\frac{1}{h}, 0) = \varphi_y(1, 0) = \varphi_y$ and

$$f'(0, 1, 0, 0) = \begin{pmatrix} -\mu_x - \varphi_x & 0 & k_x & \sigma h + \mu_y h \\ -\varphi_x \frac{m}{h} & -\mu_y & k_y & \sigma m + \mu_x m \\ 0 & 0 & -(\mu_s + k_x + k_y) & k_s h \\ \varphi_x \frac{1}{h} & 0 & 0 & -(\mu_x + \mu_y + \sigma) \end{pmatrix},$$

since $\varphi_y(0, \frac{1}{m}) = \varphi_y(0, 1) = 0$ and $\varphi_x(0, \frac{1}{m}) = \varphi_x(0, 1) = \varphi_x$. We remark here that we do not use $f'(1, 0, 0, 0)$ and $f'(0, 1, 0, 0)$ to study stability around $(1, 0, 0, 0)$ and $(0, 1, 0, 0)$ since there is no equilibrium points in system (3.1) other than $(0, 0, 0, 0)$. The non-negativity of solutions is guaranteed although $f'(1, 0, 0, 0)$ and $f'(0, 1, 0, 0)$ are not Metzler matrices [5] and eigenvalues determine here the stability of exponential solutions with stationary structure $(1, 0, 0, 0)$ and $(0, 1, 0, 0)$ respectively.

Now, we can rewrite Theorem 2.3.

Theorem 3.2. *The statements of Theorem 2.3 remain valid replacing system (2.1) by system (3.1).*

Proof. To analyze the local stability of the nontrivial solution we consider the following change of variables, valid for $g > 0$:

$$\xi = \frac{x}{(h/m)g}; \quad \eta = \frac{y}{(h/m)g}; \quad \gamma = \frac{s}{(h/m)g}.$$

We then applied the Routh–Hurwitz’s method [17] to the resultant system of dimension three to verify that the real parts of the roots of its characteristic polynomial are negative (we omit here the calculations). Thus we reached the conclusion that, if there is a positive stationary state, it is stable.

For the trivial solutions stability, let us observe that:

$$\begin{aligned} P(-\mu_x, (x, y, s, g)) &= k_s k_x \varphi_x \left(\frac{x}{h}, \frac{y}{m} \right) (\mu_x - \mu_y), \\ P(-\mu_y, (x, y, s, g)) &= \frac{h}{m} k_s k_y \varphi_y \left(\frac{x}{h}, \frac{y}{m} \right) (\mu_y - \mu_x). \end{aligned} \tag{3.5}$$

We assume first that $-\mu_x \neq -\mu_y$, and consider the three cases of Theorem 3.1.

(i) $-\mu_x = \max(-\mu_x, -\mu_y, -(\mu_s + k_x + k_y))$

From (3.5), $P(-\mu_x, (x, y, s, g)) < 0$ and $P(\lambda, (x, y, s, g))$ has a real root greater than or equal to $-\mu_x$. In particular, $P(\lambda, (0, 1, 0, 0))$ will have a real root greater than $-\mu_y$, hence the point $(0, 1, 0, 0)$ corresponds to an unstable solution. To evaluate the stability at $(1, 0, 0, 0)$, we calculate $P(\lambda, (1, 0, 0, 0)) = (\mu_x + \lambda)Q(\lambda)$, being Q a cubic polynomial:

$$Q(\lambda) = (\mu_x + \mu_y + \varphi_y + \sigma + \lambda)(\mu_y + \lambda)(\mu_s + k_x + k_y + \lambda) - \frac{h}{m}k_yk_s\varphi_y \quad (3.6)$$

and

$$Q(-\mu_x) = (\mu_y + \varphi_y + \sigma)(\mu_y - \mu_x)(\mu_s - \mu_x + k_x + k_y) - \frac{h}{m}k_yk_s\varphi_y,$$

different from zero by hypothesis. If $Q(-\mu_x) < 0$ then (3.3) is verified, there exists a positive, stable, stationary solution and $Q(\lambda)$ has a real root greater than $-\mu_x$, since $Q(\lambda) \rightarrow +\infty$ when $\lambda \rightarrow \infty$. Hence $(1, 0, 0, 0)$ is unstable. On the other hand, if $Q(-\mu_x) > 0$, then the positive stationary state does not exist. We consider:

$$Q(\lambda) + \frac{h}{m}k_yk_s\varphi_y = (\mu_x + \mu_y + \varphi_y + \sigma + \lambda)(\mu_y + \lambda)(\mu_s + k_x + k_y + \lambda),$$

the roots of the right-hand side satisfy the inequalities:

$$-(\mu_x + \mu_y + \varphi_y + \sigma) < -\mu_y < -\mu_x \quad \text{and} \quad -(\mu_s + k_x + k_y) < -\mu_x.$$

If we put in order these roots, we have $r_1 \leq r_2 \leq r_3 < -\mu_x$, where some of the inequalities between $r_1 \leq r_2 \leq r_3$ must be strict. Then we see that, depending on the magnitude of $\frac{h}{m}k_yk_s\varphi_y$, $Q(\lambda)$ has three real roots to the left of $-\mu_x$ or one real root between r_3 and $-\mu_x$ and two complex conjugated roots with real part less than r_2 , see Fig. 3. Thus the trivial solution corresponding to $(1, 0, 0, 0)$, and associated to the eigenvalue $-\mu_x$, is locally stable.

(ii) $-\mu_y = \max(-\mu_x, -\mu_y, -(\mu_s + k_x + k_y))$

The analysis is similar to the case (i). The solution $(1, 0, 0, 0)$ is unstable, since $P(-\mu_y, (x, y, s, g)) < 0$ and then $P(\lambda, (1, 0, 0, 0))$ has a real root greater than $-\mu_x$. On the other hand, $P(\lambda, (0, 1, 0, 0)) = (\mu_y + \lambda)Q'(\lambda)$, being Q' a cubic polynomial

$$Q'(\lambda) = (\mu_x + \mu_y + \varphi_x + \sigma + \lambda)(\mu_x + \lambda)(\mu_s + k_x + k_y + \lambda) - k_xk_s\varphi_x.$$

If $Q'(-\mu_y) < 0$ then (3.4) is verified, the positive stable solution exists and $(0, 1, 0, 0)$ is unstable while if $Q'(-\mu_y) > 0$, positive solution does not exist and $(0, 1, 0, 0)$ is stable.

(iii) $-(\mu_s + k_x + k_y) = \max(-\mu_x, -\mu_y, -(\mu_s + k_x + k_y))$

The nontrivial solution exists and it is stable. To show the instability of the trivial solutions, let us suppose that $-(\mu_s + k_x + k_y) > -\mu_x > -\mu_y$. From what was analyzed on (i), we have that the trivial solution corresponding to $(0, 1, 0, 0)$ is unstable by (3.5). In addition, $Q(-\mu_x) < 0$ and then the trivial

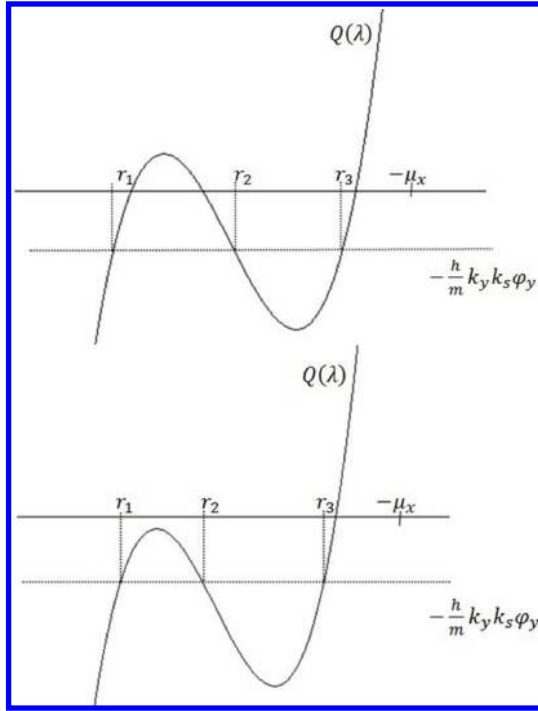


Fig. 3. The cubic polynomial $Q(\lambda)$ from (3.6) with $Q(-\mu_x) > 0$. $Q(\lambda)$ has three or one real root but, in any case, the real parts of all roots are less than $-\mu_x$.

solution $(1, 0, 0, 0)$ is unstable too. A similar argument is valid for the case $-(\mu_s + k_x + k_y) > -\mu_y > -\mu_x$. Then we have completed all the cases if $-\mu_x \neq -\mu_y$.

Considering now $-\mu_x = -\mu_y$, we have that the nontrivial solution exists and we can see that $Q(-\mu_x), Q'(-\mu_y) < 0$, hence both trivial solutions are unstable. \square

4. A Southern Elephant Seal Population

We consider an example of parametrization just to take the flavor of the applicability of the model in a preliminary test and motivate future developments. The southern elephant seal is a polygamous species in which males and females show different life cycles and spend part of their life in a subadult stage until they reach the sexual maturity. Thus, this species is an example where the three-stage model would be an extreme simplification whereas the four-stage model, although still corresponding to a simplified approximation, provides more flexibility to describe the life cycle.

The reproductive season of this species spans two months from the beginning of August to early November. During this period, animals distribute themselves along the beach forming reproductive groups called harems. Each harem consists

of one dominant male, a group of females which can vary between two to hundred individuals and some peripheral males. Females reproduce for the first time around the age of four, while males do not participate actively in the reproductive season until they reach the age of six [1, 13].

To parametrize our model, we based on life tables of southern elephant seals which present survival values of males and females until the age of 20 [16]. From life tables we obtained $lf(i)$ and $lm(i)$, which represent the probability that a female (respectively male) pup will survive to age i . We will assume that adult females are those within the age of four or older and adult males within the age of seven or older. In consequence, the pre-reproductive stage corresponds to females that are three years old or younger and males that are six years old or younger. The life table was estimated for a population close to stability, which means that the number of births remains constant year after year. Likewise, $lf(i)$ represents the proportion of females in the age group i per born female and, because the sex ratio at births is one-to-one, $lf(i)$ is the proportion of females in age group i , with respect to all individuals in the population.

Adult female annual survival can be estimated as the proportion of adult females that remains as adults from a year to another:

$$p_x = \frac{lf(5) + lf(6) + \dots + lf(20)}{lf(4) + lf(5) + \dots + lf(20)}.$$

The female death rate can then be estimated by $p_x = \exp(-\mu_x)$, as it is usual for life table and matrix models [3, 12]. In the same way, we can calculate the annual survival of adult males and pre-reproductive individuals, with the corresponding death rates:

$$p_y = \frac{lm(8) + \dots + lm(20)}{lm(7) + \dots + lm(20)} = \exp(-\mu_y),$$

$$p_s = \frac{lf(2) + lf(3) + lf(4) + lm(2) + \dots + lm(7)}{lf(1) + lf(2) + lf(3) + lm(1) + \dots + lm(6)} = \exp(-\mu_s).$$

On the other hand, the female recruitment rate k_x can be estimated as the proportion of pre-reproductive individuals that will be adult females the next year and, in the same way, we calculated the transition rate k_y from pre-reproductive individuals to adult males:

$$k_x = \frac{lf(4)}{lf(1) + lf(2) + lf(3) + lm(1) + \dots + lm(6)},$$

$$k_y = \frac{lm(7)}{lf(1) + lf(2) + lf(3) + lm(1) + \dots + lm(6)}.$$

The birth rate is given by the product of female fecundity (pregnancy rate in [16]) and the adult survival: $k_s = 0.88p_x$, calculated as birth pulse fertility in populations with post-breeding censuses [12].

Finally, as a reference of the social structure, we have data from the population of Peninsula Valdes, a population that was near stability during the last decade.

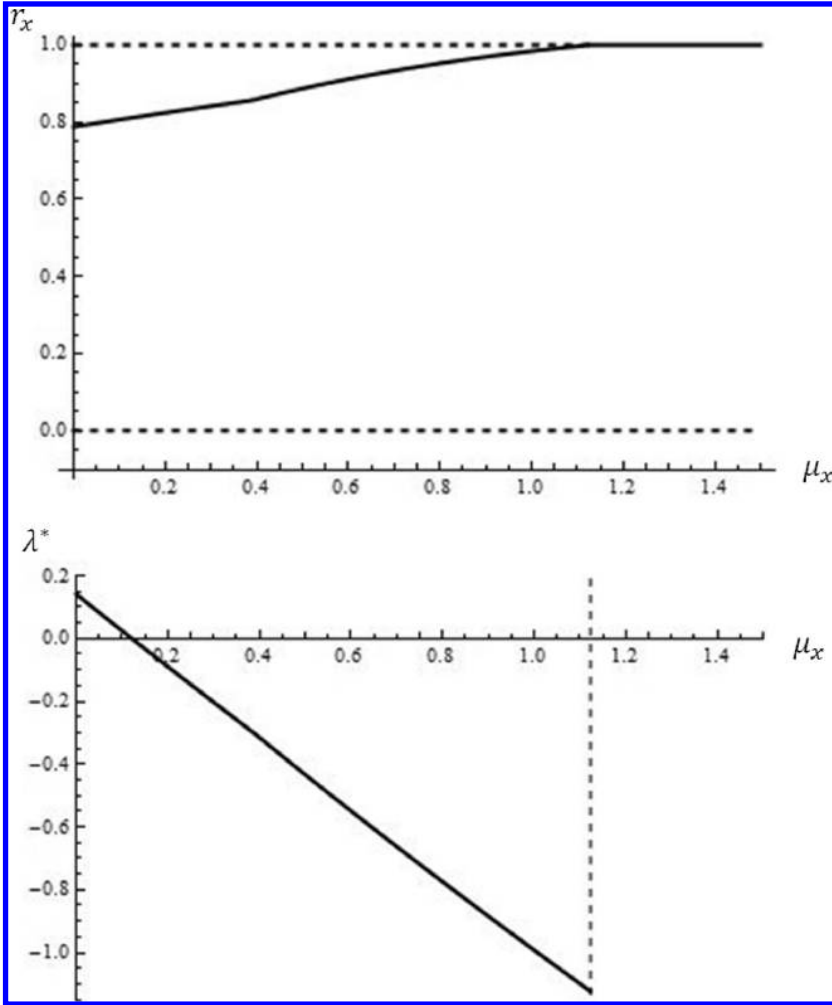


Fig. 4. Stationary sex ratio and population growth for the southern elephant seal population model. Female death rate varies from 0 to 1.5 and the rest of the vital rates vary proportionally according to life table estimates. We used a minimum mating function $\varphi(x, y) = \min(x, y)$, and a small harem size $h/m = 6$. Population is stable, with growth rate = 0, for $\mu_x = 0.121$ and collapses for $\mu_x \geq 1.123$.

There the adult sex ratio, during the breeding season, is close to six females per male and the median of the harem size around 13, with annual mean varying between 11 and 35 females per male [8, 15]. The reproductive groups are formed again each season but we do not have any estimation of the separation rate, corresponding to model parameter σ , thus we set $\sigma = 1$ as a reference value.

Although population parameters were estimated from stable populations according to life tables, when we evaluated these parameters in our continuous time model we obtained a decreasing population. To analyze a stable population we increase p_x

varying the rest of the vital rates proportionally according to life table estimates: $p_y/p_x = 0.84$, $p_s/p_x = 1.001$, $k_x/p_x = 0.118$, $k_y/p_x = 0.059$ and $k_s/p_x = 0.88$. We analyze stationary solutions using a minimum mating function, $\varphi(x, y) = \min(x, y)$, and small harem size, $h/m = 6$ corresponding to the adult sex ratio observed in the field, Fig. 4. With this setting we are in case (i) of Theorem 3.1 and the population collapses when $\mu_x = 1.123$, which corresponds to very low annual survivals: $p_x = 0.325$ and $p_y = 0.273$. If we set $\mu_x = 0.121$, corresponding to a stable population, and we vary the harem size, Fig. 5, we find the critical harem size $H_0 = 1.534$. The break points in Fig. 5, which occur at H_0 and $H_1 \approx 4.9$, show us how the minimum function works on the model. For h/m below H_0 , there does not exist the positive stationary solution; for $H_0 < h/m < H_1$, there exists the positive stationary solution but $hy < mx$ in the stationary state, that is, the number of males

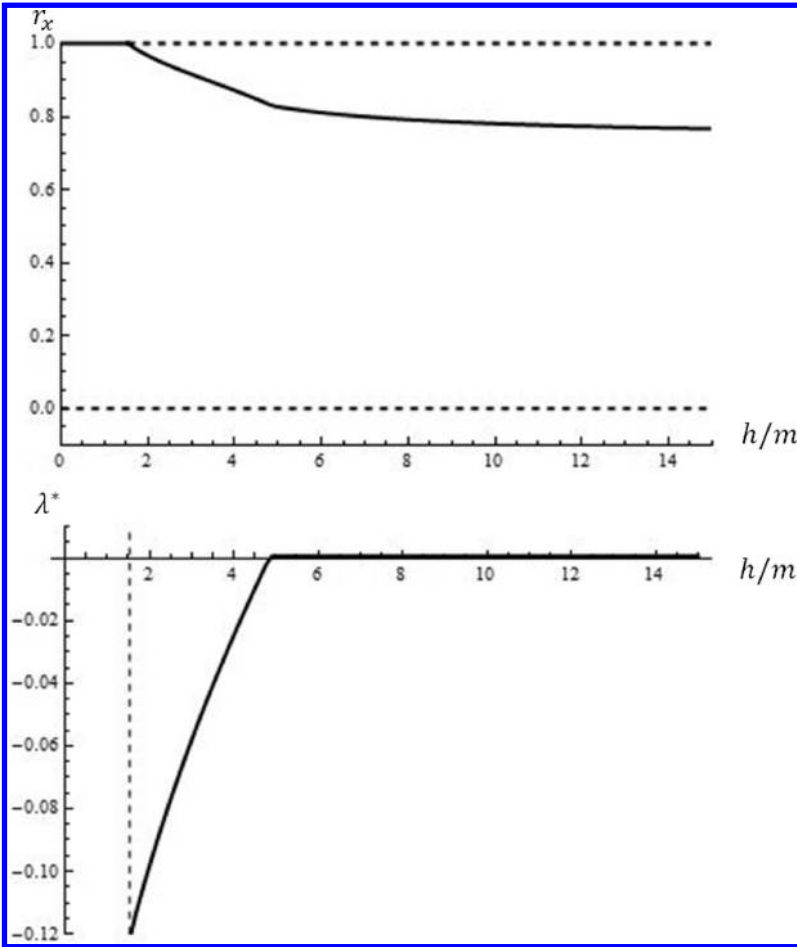


Fig. 5. Stationary sex ratio and population growth for a potentially stable southern elephant seal population when varying the sexual proportion of reproductive groups.

is limiting the population growth, moreover the population is decreasing ($\lambda^* < 0$); finally for $h/m > H_1$ we have that $hy > mx$ in the stationary state, and population is stable ($\lambda^* = 0$).

5. Conclusions and Discussion

The modification on a simple two-sex three-dimensional model allowed us to consider the social structure in polygamous populations. An alternative approach was presented in order to analyze the model in a way that it was possible to generalize the results for a four-dimensional model, as a first step toward the study of more general and complex systems.

The model's solutions resulted in three possible situations: the existence of a stationary state where the population's structure stabilizes increasing or decreasing exponentially and other two solutions, which lead to the population's collapse by means of lack of males or females.

The conditions were established for the existence of the stationary state and its local stability, determining in this manner the critical sexual proportion of the reproductive groups. The adult sex ratio and the structure of reproductive groups are key variables in population dynamics and, in some cases can be directly estimated [9, 15]. This kind of models could be applied on wildlife populations with a pre-reproductive stage and can help, as a first approximation, to assess the population status according to its demographic and social parameters, in relation to the critical structure.

When we parametrize the model for a southern elephant seal population, we find threshold values for the harem size, H_0 and H_1 , which determine the existence of the stationary solution and the population stability respectively. These results could be confronted with similar analyses based on discrete-time models [7]. The critical harem size, $H_0 < 2$, is below observed values, as we expect for a healthy population. And, although small harems are observed in populations of southern elephant seals, the collapse of a population due to small harems would not be a possibility according to our model. On the other hand, the harem size needed for a stable population H_1 is close to the adult sex ratio, observed at the breeding season, but still below from the population's mean harem size. We believe that more complex population models and, specially a better description of the mating function, would be needed to understand these big observed harems and, in general, to analyze the breeding behavior in wildlife populations.

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