Mathematical Biosciences and Engineering

http://www.aimspress.com/journal/mbe

MBE, 21(6): 6407–6424.
DOI: 10.3934/mbe.2024280
Received: 14 February 2024
Revised: 29 May 2024
Accepted: 12 June 2024
Published: 27 June 2024

Research article

Mathematical modeling in semelparous biological species through two-sex branching processes

Manuel Molina[1,2,*], **Manuel Mota**[1,2] **and Alfonso Ramos**[1,3]

[1] Department of Mathematics, University of Extremadura, Badajoz 06006, Spain
[2] Institute of Advanced Scientific Computation, University of Extremadura, Badajoz 06006, Spain
[3] Institute in Livestock and Cynegetic, University of Extremadura, Badajoz 06006, Spain

* **Correspondence:** Email: mmolina@unex.es; Tel: +34924289568; Fax: +34924272911.

Abstract: This research focused its interest on the mathematical modeling of the demographic dynamics of semelparous biological species through branching processes. We continued the research line started in previous papers, providing new methodological contributions of biological and ecological interest. We determined the probability distribution associated with the number of generations elapsed before the possible extinction of the population in its natural habitat. We mathematically modeled the phenomenon of populating or repopulating habitats with semelparous species. We also proposed estimates for the offspring parameters governing the reproductive strategies of the species. To this purpose, we used the maximum likelihood and Bayesian estimation methodologies. The statistical results are illustrated through a simulated example contextualized with Labord chameleon (Furcifer labordi) species.

Keywords: mathematical modeling; branching processes; population dynamics; extinction probability; statistical inference; semelparous biological species

---

1. Introduction

This research focuses its interest on the mathematical modeling of the population dynamics of semelparous biological species. A species is called semelparous when it has a single reproductive episode before dying. Semelparity (sometimes called big-bang reproduction) occurs in very diverse biological species, see [1], including amphibians (e.g., Hyla frogs), arachnids (e.g., Pardosa licosidae spider, australian redback spider, desert spider, or black widow spider), fish (e.g., Pacific salmon, or sockeye salmon), insects (e.g., some butterflies, cicadas, or mayflies), mammals (e.g., some didelphids or dasyurid marsupials), mollusks (some squids or octopuses), reptiles (e.g., Labord chameleon, or some lizards), etc.

Methodologies for modeling dynamic biological systems, such as those based on population viability analysis (see [2, 3]) or compartmental modeling (see [4, 5]) usually require information about environmental variables, mortality rates, growth rates, etc. In practice, such information is difficult to obtain. In this work, we shall consider the methodology based on branching processes. These stochastic processes are appropriate mathematical models to describe the evolution of dynamical systems whose components, after a certain life period, reproduce and die in such a way that the transition from one to another state of the system is made according to a certain probability distribution. For theoretical concepts and applications about such types of processes, we refer the reader to some classical monographs [6–8], where several applications to cell kinetics, cell biology, chemotherapy, gene amplification, human evolution, and molecular biology are presented. See also the contributions, based on branching processes, by [9, 10], in nuclear physics and complex contagion adoption dynamics, respectively.

In fact, branching processes are routinely used to describe the population dynamics of biological species with both asexual and sexual reproduction. We are especially interested in the mathematical modeling of the demographic dynamics of biological species with sexual reproduction. To this end, a fairly rich literature has emerged about discrete-time two-sex branching processes, see the surveys in [11, 12] and the discussions therein. Most of these branching processes assume that all of the progenitor couples have a similar reproductive behavior, see [13–15]. It is also frequently assumed that mating and reproduction depend on the current number of progenitor couples existing in the population, see [16–18]. However, it is known that, due to various environmental factors, e.g., weather conditions, food supply, fertility parameters, or predators, in many biological species mating and reproduction occur in a non-predictable environment influenced by the current number of females and males in the population. For stochastic modeling about the demographic evolution of such species, two-sex branching processes had not been sufficiently developed. With such motivation, in [19], a new class of two-sex branching processes, which takes into account the possibility of various mating and reproduction strategies, both depending on the number of females and males in the population, was introduced. This class of processes is appropriate for the description of the demographic dynamics of semelparous species, which are characterized by having diverse behaviors in the mating and reproduction phases. In [20, 21], some results about such a class of two-sex processes were established. The main purpose of this work is to continue this research line by providing new methodological (probabilistic and statistical) contributions.

The paper is organized as follows. In Section 2, the probability model is mathematically described and interpreted. In Section 3, some probabilistic results are provided. The probability distribution associated with the number of generations elapsed before the possible extinction of the population (time to the extinction) is determined. The class of processes under study is then used to mathematically model phenomena concerning to populate or repopulate habitats with endangered semelparous species. In Section 4, statistical results are derived. By considering maximum likelihood and Bayesian estimation methodologies, approximations for the main reproductive parameters involved in the probability model are proposed. To this purpose, information about the reproduction of the couples is incorporated. As illustration, a simulated example contextualized with a species of chameleons (Labord's chameleon) is presented. Concluding remarks and some questions for research are included in Section 5.

2. Mathematical model and preliminary results

Let us consider the discrete-time two-sex branching process introduced in [19], denoted by $\{X_n\}_{n=0}^{\infty}$, $X_n = (F_n, M_n)$ representing the number of female and male individuals at generation n. The underlying probability model is described as follows, with $\mathbb{N}$ and $\mathbb{N}_+$ denoting the non-negative and the positive integers, respectively:

1) The mating phase is represented by a sequence of $n_m \geq 1$ two arguments integer-valued functions $\{L_l\}_{l\in\mathbb{N}_m}$, $\mathbb{N}_m := \{1, \ldots, n_m\}$. Each L_l is assumed to be non-decreasing and such that $L_l(F, 0) = L_l(0, M) = 0,\ F, M \in \mathbb{N}$. At generation n, according to the lth mating strategy (function), $L_l(F_n, M_n)$ couples female-male are formed.
2) The reproduction phase is modeled by a sequence of $n_r \geq 1$ offspring probability distributions $\{P_h\}_{h\in\mathbb{N}_r}$, $\mathbb{N}_r := \{1, \ldots, n_r\}$, $P_h := \{p^h_{k,s}\}_{(k,s)\in S_h}$, with $S_h \subseteq \mathbb{N}^2$ and $p^h_{k,s}$ being the probability for a given couple to produce exactly k females and s males, when P_h is the reproductive strategy.
3) In each generation, the mating and reproduction strategies are determined through suitable functions φ_m and φ_r, both defined on $\mathbb{N}^2$, taking values on $\mathbb{N}_m$ and $\mathbb{N}_r$, respectively.

Initially, $X_0 = x_0 \in \mathbb{N}^2_+$, and the number of couples originated $L_{\varphi_m(x_0)}(x_0) > 0$. Given that $X_n = x \in \mathbb{N}^2$, it is then derived that, in the nth generation, $L_{\varphi_m(x)}$ and $P_{\varphi_r(x)}$ are the corresponding mating and reproductive strategies, respectively. Hence, at generation $n + 1$,

$$X_{n+1} := \sum_{i=1}^{L_{\varphi_m(x)}(x)} (F^h_{n,i}, M^h_{n,i}),\ \ h = \varphi_r(x),\ \ n \in \mathbb{N}, \tag{2.1}$$

with $F^h_{n,i}$ and $M^h_{n,i}$ denoting, respectively, the number of female and male individuals originated by the ith couple at generation n, providing that the reproductive strategy h has been considered. For each $h \in \mathbb{N}_r$, the random vectors $(F^h_{n,i}, M^h_{n,i})$, $i = 1, \ldots, L_{\varphi_m(x)}(x)$, are assumed to be independent and identically distributed (i.i.d.) with offspring probability distribution P_h, i.e.,

$$P(F^h_{n,1} = k, M^h_{n,1} = s) = p^h_{k,s},\ (k, s) \in S_h.$$

Remark 2.1 Functions L_l, φ_m, and φ_r should be flexible enough in order to fit the main features of the semelparous species we pretend to describe. Usually, such functions will depend of certain biological/ecological parameters of interest in the demographic dynamics of the species.

Remark 2.2 It is verified that $\{X_n\}_{n=0}^{\infty}$ is a homogeneous Markov chain. In fact, given $x_0, \ldots, x_n, x_{n+1} \in \mathbb{N}^2$, taking into account that for each $h \in \mathbb{N}_r$, independent of n, the random vectors $(F^h_{n,i}, M^h_{n,i})$, $i = 1, \ldots, L_{\varphi_m(x)}(x)$, are i.i.d.,

$$P(X_{n+1} = x_{n+1} \mid X_0 = x_0, \ldots, X_n = x_n) = P(X_{n+1} = x_{n+1} \mid X_n = x_n) = P\left(\sum_{i=1}^{L_{\varphi_m(x_n)}(x_n)} \left(F^{\varphi_r(x_n)}_{n,i}, M^{\varphi_r(x_n)}_{n,i}\right) = x_{n+1} \right).$$

Note that if, for some $n \geq 1$, $X_n = (0, 0)$, then $X_{n+j} = (0, 0)$, $j \geq 1$, thus $(0, 0)$ is an absorbing state. Consequently, in such a case, the population will become extinct. Let us denote by:

$$q(x_0) := P(\lim_{n\to\infty} X_n = 0 \mid X_0 = x_0),\ x_0 \in \mathbb{N}^2_+,$$

the extinction probability, associated with $\{X_n\}_{n=0}^{\infty}$, when initially $X_0 = x_0$. Assuming that, for each $h \in \mathbb{N}_r$:

$$\max\left\{P(F^h_{1,1} = 0), P(M^h_{1,1} = 0)\right\} > 0, \tag{2.2}$$

it has been proved in [20] the extinction-explosion property:

$$q(x_0) + P(\lim_{n\to\infty} g(X_n) = \infty \mid X_0 = x_0) = 1, \tag{2.3}$$

where for $F, M \in \mathbb{N}$,

$$g(F, M) := \alpha F + \beta M,\ \alpha \geq 0,\ \beta \geq 0,\ \alpha + \beta > 0.$$

Also, by considering the rate:

$$m_g(x) := g(x)^{-1}E[g(X_{n+1}) \mid X_n = x] = L_l(x)g(\mu^h)g(x)^{-1},$$

sufficient conditions for the extinction/survival of a biological population, described through the model (2.1), have been established in [20].

In particular, the following cases have a special biological significance: $g(F, M) = F$, $g(F, M) = M$, or $g(F; M) = F + M$, namely, the number of females, males, or total individuals in the population, respectively.

Remark 2.3 For each $h \in \mathbb{N}_r$, let us denote by $\mu^h := \left(\mu^h_1,\ \mu^h_2\right)$ and $\Sigma^h = (\sigma^h_{ij})_{i,j=1,2}$ the mean vector and the covariance matrix of $(F^h_{1,1}, M^h_{1,1})$, respectively, i.e.,

$$\mu^h_i := \sum_{(k_1,k_2)\in S_h} k_i p^h_{k_1,k_2}, \quad i = 1, 2, \tag{2.4}$$

$$\sigma^h_{ij} := \sum_{(k_1,k_2)\in S_h} (k_i - \mu^h_i)(k_j - \mu^h_j)p^h_{k_1,k_2}, \quad i, j = 1, 2. \tag{2.5}$$

Given $x \in \mathbb{N}^2$,

$$E[X_{n+1} \mid X_n = x] = E\left[\sum_{i=1}^{L_l(x)}(F^h_{n,i}, M^h_{n,i})\right] = \sum_{i=1}^{L_l(x)} E\left[(F^h_{n,i}, M^h_{n,i})\right] = L_l(x)\mu^h,$$

and

$$Var[X_{n+1} \mid X_n = x] = Var\left[\sum_{i=1}^{L_l(x)}(F^h_{n,i}, M^h_{n,i})\right] = \sum_{i=1}^{L_l(x)} Var\left[(F^h_{n,i}, M^h_{n,i})\right] = L_l(x)\Sigma^h,$$

where $l = \varphi_m(x)$ and $h = \varphi_r(x)$.

The research about this class of two-sex branching processes will now continue investigating new probabilistic and statistical questions of biological/ecological interest.

3. Probabilistic results

From a probabilistic point of view, attention will be focused on two issues of special interest. First, assuming the possible extinction of the population in the habitat, we will look at the determination of the probability distribution associated with the number of generations elapsed before the possible extinction occurs. Second, we will investigate the application of the class of two-sex branching processes under study to the phenomenon of populating or repopulating habitats with endangered semelparous species. We will assume condition (2.2) and $q(x_0) \in (0, 1)$. Note that, taking into account (2.3), the cases $q(x_0) = 0$ or $q(x_0) = 1$ mean the explosion or the extinction of the population, respectively.

3.1. Time to the extinction

Let us denote by $Z_n := L_{\varphi_m(X_n)}(X_n)$ the number of couples formed at generation n. Clearly, if for some $n \geq 1$, $Z_n = 0$, then the population will be extinct. Given that $X_0 = x_0 = (F_0, M_0) \in \mathbb{N}_+^2$, let us introduce the random variable:

$$T(x_0) := \sup\{n \geq 0 : \ Z_n > 0\},$$

representing the number of generations elapsed before the extinction of the population occurs, when there were F_0 females and M_0 males in the population. Assuming that $T(x_0) < \infty$, the next result provides the probability distribution associated with $T(x_0)$, and also its main moments (mean and variance). In the case that the population goes extinct, such probability distribution shows how quickly the extinction will probably occur.

Let $u_n(s) := E[s^{Z_n}],\ 0 \leq s \leq 1$, be the probability generating function of Z_n. By simplicity, it will be denoted by $u_n^*(0) := u_{n+1}(0) - u_n(0),\ n \in \mathbb{N}$.

Theorem 3.1

- (a) $P(T(x_0) = n \mid T(x_0) < \infty) = q(x_0)^{-1} u_n^*(0),\ n \in \mathbb{N}$.
- (b) $E[T(x_0) \mid T(x_0) < \infty] = \sum\limits_{n=1}^{\infty} (1 - q(x_0)^{-1} u_n(0))$.
- (c) $Var[T(x_0) \mid T(x_0) < \infty] = q(x_0)^{-1} \left[\sum\limits_{n=1}^{\infty} n^2 u_n^*(0) - q(x_0)^{-1} \left(\sum\limits_{n=1}^{\infty} (q(x_0) - u_n(0)) \right)^2 \right]$.

Proof. First, note that $P(T(x_0) < \infty) = q(x_0)$.

(a) Using that $Z_0 := L_{\varphi_m(x_0)}(x_0) > 0$, it is derived that $u_0(0) = P(Z_0 = 0) = 0$. Therefore,

$$\begin{aligned} P(T(x_0) = 0 \mid T(x_0) < \infty) &= P(T(x_0) < \infty)^{-1} P(T(x_0) = 0) = q(x_0)^{-1} P(Z_1 = 0) \\ &= q(x_0)^{-1} u_1(0) = q(x_0)^{-1}(u_1(0) - u_0(0)) = q(x_0)^{-1} u_0^*(0). \end{aligned}$$

Now, for $n \in \mathbb{N}_+$,

$$\begin{aligned} P(T(x_0) = n \mid T(x_0) < \infty) &= q(x_0)^{-1} P(T(x_0) = n) \\ &= q(x_0)^{-1}(P(T(x_0) \leq n) - P(T(x_0) \leq n-1)) \\ &= q(x_0)^{-1}(P(Z_{n+1} = 0) - P(Z_n = 0)) \\ &= q(x_0)^{-1}(u_{n+1}(0) - u_n(0)) = q(x_0)^{-1} u_n^*(0). \end{aligned}$$

(b) Using that $T(x_0)$ is a non-negative random variable, it is derived, see [22, pg. 84], that

$$E[T(x_0) \mid T(x_0) < \infty] = \sum_{n=0}^{\infty} (1 - P(T(x_0) \leq n \mid T(x_0) < \infty)).$$

Hence, using that $P(T(x_0) \leq n) = P(Z_{n+1} = 0) = u_{n+1}(0)$,

$$\begin{aligned}E[T(x_0) \mid T(x_0) < \infty] &= \sum_{n=0}^{\infty}(1 - P(T(x_0) \le n \mid T(x_0) < \infty)) \\ &= \sum_{n=0}^{\infty}\left(1 - q(x_0)^{-1}P(T(x_0) \le n)\right) \\ &= \sum_{n=0}^{\infty}\left(1 - q(x_0)^{-1}u_{n+1}(0)\right) = \sum_{n=1}^{\infty}\left(1 - q(x_0)^{-1}u_n(0)\right).\end{aligned}$$

(*c*) The result is derived, from Theorem 3.1(*b*), using that:

$$Var[T(x_0) \mid T(x_0) < \infty] = E[T(x_0)^2 \mid T(x_0) < \infty] - E[T(x_0) \mid T(x_0) < \infty]^2,$$

and taking into account that:

$$\begin{aligned}E[T(x_0)^2 \mid T(x_0) < \infty] &= \sum_{n=1}^{\infty} n^2 P(T(x_0) = n \mid T(x_0) < \infty) \\ &= q(x_0)^{-1}\sum_{n=1}^{\infty} n^2\left(P(T(x_0) \le n) - P(T(x_0) \le n-1)\right) \\ &= q(x_0)^{-1}\sum_{n=1}^{\infty} n^2\left(P(Z_{n+1} = 0) - P(Z_n = 0)\right) \\ &= q(x_0)^{-1}\sum_{n=1}^{\infty} n^2(u_{n+1}(0) - u_n(0)) = q(x_0)^{-1}\sum_{n=1}^{\infty} n^2 u_n^*(0). \qquad (3.1)\end{aligned}$$

3.2. Application to populate or repopulate a habitat

Let us consider a certain habitat in which a semelparous species has become extinct, or it is in serious danger of extinction. The purpose is to populate or repopulate the habitat with such species. To this end, of ecological significance, several attempts to repopulate the species in the habitat will probably be necessary. Next, the class of two-sex branching processes $\{X_n\}_{n=0}^{\infty}$, defined in (2.1), will be used as the mathematical model.

In fact, let $\{X_n^{(j)}\}_{n=0}^{\infty}$, $j \in \mathbb{N}_+$, be independent processes where, for each $j \in \mathbb{N}_+$, $\{X_n^{(j)}\}_{n=0}^{\infty}$ is a two-sex branching process, like the one defined in (2.1), which describes the population dynamics concerning the jth attempt of repopulating. Thus, vector $X_n^{(j)} = (F_n^{(j)}, M_n^{(j)})$ represents the number of female and male individuals in the habitat at generation n, in the jth attempt of repopulating. All processes $\{X_n^{(j)}\}_{n=0}^{\infty}$, $j \in \mathbb{N}_+$, have the same mating and reproductive strategies, i.e., they have the same sequences $\{L_l\}_{l\in\mathbb{N}_m}$ and $\{P_h\}_{h\in\mathbb{N}_r}$. Assume condition (2.2) holds and $q(x_0) \in (0, 1)$.

Initially (attempt $j = 1$), it is assumed that $X_0^{(1)} = x_0 = (F_0, M_0) \in \mathbb{N}_+^2$, i.e., F_0 females and M_0 males of the species under consideration are introduced in the habitat. If, after a certain number of generations, the population becomes extinct, then it will be necessary to restart the repopulating, by introducing again (attempt $j = 2$) F_0 females and M_0 males in the habitat, i.e., $X_0^{(2)} = x_0$, and so on. This iterative procedure continues until a sufficient number of females and males are achieved in the habitat, so that the risk of extinction disappears (for simplicity, this fact will be referred to as implementation of the species in the habitat). It is deduced that

$$P\left(\lim_{n\to\infty} X_n^{(j)} = 0 \mid X_0^{(j)} = x_0\right) = q\left(x_0\right), \ j \in \mathbb{N}_+.$$

Let $T^{(j)}\left(x_0\right) := \sup\left\{n \geq 0 : Z_n^{(j)} > 0\right\}$, $Z_n^{(j)} := L_{\varphi_m(X_n)^{(j)})}(X_n{}^{(j)})$, $j \in \mathbb{N}_+$, namely, the time to the extinction at the jth attempt of repopulation. It is derived that $\{T^{(j)}\left(x_0\right)\}_{j=1}^{\infty}$ is a sequence of i.i.d. random variables with the probability distribution given in Theorem 3.1(a).

Let us denote by $N(x_0)$ the number of attempts until the implementation of the species occurs. It is then verified that $N(x_0)$ is distributed according to a geometric law with parameter $1 - q(x_0)$. Hence,

$$P(N(x_0) = n) = q(x_0)^n(1 - q(x_0)), \ n \in \mathbb{N}, \tag{3.2}$$

and

$$E[N(x_0)] = q(x_0)(1 - q(x_0))^{-1} \text{ and } Var[N(x_0)] = q(x_0)(1 - q(x_0))^{-2}. \tag{3.3}$$

Finally, let us consider the variable:

$$T^*(x_0) := \sum_{j=1}^{N(x_0)} T^{(j)}(x_0), \tag{3.4}$$

representing the total number of generations elapsed until the implementation of the species in the habitat occurs. The next result establishes the probability distribution of $T^*(x_0)$ and its main moments.

Theorem 3.2

(a) $P(T^*(x_0) = n) = q^*(x_0)^{-1}\left(\delta_{n,0} + \sum_{j=1}^{\infty} q(x_0)^j P_n(x_0)^{(*j)}\right)$, $n \in \mathbb{N}$.

(b) $E[T^*(x_0)] = q^*(x_0) \sum_{n=1}^{\infty} (q(x_0) - u_n(0))$.

(c) $Var[T^*(x_0)] = q^*(x_0)\left[(1 + q^*(x_0)) \sum_{n=1}^{\infty} n^2 u_n^*(0) - q(x_0)^{-1}\left(\sum_{n=1}^{\infty}(q(x_0) - u_n(0))\right)^2\right]$,

where

$$q^*(x_0) := (1 - q(x_0))^{-1}, \ \delta_{n,0} := 1 \text{ if } n = 0 \text{ or } 0 \text{ if } n \neq 0,$$

$$P_n(x_0) := P\left(T^{(1)}(x_0) = n \mid T^{(1)}(x_0) < \infty\right), \ P_n(x_0)^{(*j)} := \sum_{i_1+\ldots+i_j=n} P_{i_1}(x_0)\ldots P_{i_j}(x_0).$$

Proof.

(a) Taking into account (3.2) and (3.4),

$$\begin{aligned} P(T^*(x_0) = n) &= \sum_{j=0}^{\infty} P(T^*(x_0) = n \mid N(x_0) = j) P(N(x_0) = j) \\ &= q^*(x_0)^{-1} \left(\delta_{n,0} + \sum_{j=1}^{\infty} q(x_0)^j P\left(\sum_{l=1}^{j} T^{(l)}(x_0) = n \right) \right) \\ &= q^*(x_0)^{-1} \left(\delta_{n,0} + \sum_{j=1}^{\infty} q(x_0)^j P_n(x_0)^{(*j)} \right), \ n \in \mathbb{N}. \end{aligned}$$

(b) From (3.3), (3.4), and Theorem 3.1(b),

$$E[T^*(x_0)] = E[N(x_0)] E\left[T^{(1)}(x_0) \mid T^{(1)}(x_0) < \infty\right] = q^*(x_0) \sum_{n=1}^{\infty} (q(x_0) - u_n(0)).$$

(c) Using (3.3), (3.4), and Theorem 3.1(b),(c), we can obtain that:

$$Var[T^*(x_0)] = E[N(x_0)] Var\left[T^{(1)}(x_0) \mid T^{(1)}(x_0) < \infty\right] + Var[N(x_0)] E\left[(T^{(1)}(x_0))^2 \mid T^{(1)}(x_0) < \infty\right].$$

Remark 3.1 By simplicity in the underlying probabilistic development, it has been assumed that in the proposed iterative procedure, for each $j \in \mathbb{N}_+$, $X_0^{(j)} = x_0 = (F_0, M_0)$, that is, each iteration begins with F_0 females and M_0 males in the habitat. In practice, this assumption is not a problem. It implies that the extinction probability $q(x_0)$ is the same for all iterations. Therefore, it is deduced that $N(x_0)$ is distributed according to a geometric law with parameter $1 - q(x_0)$.

4. Statistical results

With the aim to check some possible changes in the demographic dynamics of the semelparous species, it is important to determine accurate approximations for the main statistical parameters (offspring means, variances, and covariances) specified in (2.4) and (2.5), respectively. The application of estimation methodologies based on population viability analysis requires having information on various variables related to the biological species under consideration. In practice, the information about such variables is difficult to obtain. In this scenario, estimation based in Bayesian methodology provides a reasonable solution. In fact, by considering a parametric statistical context about the reproductive strategies P_h, $h \in \mathbb{N}_r$, estimates for such statistical parameters have been determined in [19]. More recently, by using approximate Bayesian computation techniques, estimates have also been proposed in [21]. The application of such techniques requires a large number of simulations from the mathematical model. Consequently, it involves a significant computational effort. In this section, we shall consider the more general nonparametric framework about the reproductive strategies P_h, $h \in \mathbb{N}_r$, that is, no functional form is assumed for the probabilities $p^h_{k,s}$, $(k, s) \in S_h$. By using maximum likelihood and Bayesian estimation methodologies, we will determine approximations for such probabilities and also for μ^h_i, σ^h_{ij}, $i, j = 1, 2$.

Let $\{X_n\}_{n=0}^{\infty}$ be the two-sex branching process described in the previous section. Assume, for a given n, the following observed information over time in a set of generations, denoted by G_n, up to the nth generation is reached:

$$\mathcal{S}_n := \left\{X_0 = (F_0, M_0),\ Z_{i,(k,s)},\ (k,s) \in S_{\varphi_r(X_i)},\ i \in G_n\right\}, \tag{4.1}$$

where

$$Z_{i,(k,s)} := \sum_{j=1}^{L_{\varphi m(X_i)}(X_i)} \mathbf{I}_{\left\{(F_{i,j}^{\varphi r(X_i)}, M_{i,j}^{\varphi r(X_i)})=(k,s)\right\}}, \tag{4.2}$$

with $\mathbf{I}_A$ denoting the indicator function of A. The variable $Z_{i,(k,s)}$ represents the total number of couples at generation i, which produce exactly k females and s males, $(k,s) \in \bigcup_{h\in\mathbb{N}_r} S_h$.

For $h \in \mathbb{N}_r$, let $G_n^h := \{i \in G_n :\ \varphi_r(X_i) = h\}$, i.e., the set of observed generations of G_n where P_h has been the reproductive strategy. Clearly,

$$\bigcup_{h\in\mathbb{N}_r} G_n^h = G_n, \quad G_n^h \cap G_n^{h'} = \emptyset,\ \ h, h' \in \mathbb{N}_r,\ \ h \neq h'.$$

In what follows, it will be assumed that $G_n^h \neq \emptyset$, $h \in \mathbb{N}_r$. From (4.2), let us introduce the variables:

$$V_{n,(k,s)}^h := \sum_{i\in G_n^h} Z_{i,(k,s)}\ ,\ h \in \mathbb{N}_r.$$

Note that $V_{n,(k,s)}^h$ represents the total number of couples in the observed generations that have originated exactly k females and s males, with P_h being the underlying reproductive strategy.

4.1. Maximum likelihood estimates

According to this estimation methodology, taking into account the sample information given in (4.1) and (4.2), we have to determine, for $h \in \mathbb{N}_r$, the values of $p_{k,s}^h$, $(k,s) \in S_h$ that maximize the corresponding likelihood function.

Theorem 4.1 The maximum likelihood estimates for $p_{k,s}^h$, μ_i^h, and σ_{ij}^h, $i, j = 1, 2$, $h \in \mathbb{N}_r$, are given by:

(a) $\widehat{p_{k,s}^h} = (V_n^h)^{-1} V_{n,(k,s)}^h$, $(k,s) \in S_h$.

(b) $\widehat{\mu_i^h} = (V_n^h)^{-1} \sum_{(k_1,k_2)\in S_h} k_i V_{n,(k_1,k_2)}^h$.

(c) $\widehat{\sigma_{ij}^h} = \left(V_n^h(1 + V_n^h)\right)^{-1} \left[V_n^h \sum_{(k_1,k_2)\in S_h} k_i k_j V_{n,(k_1,k_2)}^h - \sum_{(k_1,k_2),(l_1,l_2)\in S_h} k_i l_j V_{n,(k_1,k_2)}^h V_{n,(l_1,l_2)}^h\right]$,

where $V_n^h := \sum_{(k,s)\in S_h} V_{n,(k,s)}^h$ is assumed to be positive.

Proof. Taking into account (4.1), the corresponding likelihood function is given by:

$$\mathcal{L}(P_1, \ldots, P_{n_r} \mid \mathcal{S}_n) = \prod_{h=1}^{n_r} \prod_{(k,s)\in S_h} (p_{k,s}^h)^{V_{n,(k,s)}^h}. \tag{4.3}$$

From (4.3), the log-likelihood function is then deduced:

$$\ell(P_1, \ldots, P_{n_r} \mid \mathcal{S}_n) := log\left(\mathcal{L}(P_1, \ldots, P_{n_r} \mid \mathcal{S}_n)\right) = \sum_{h=1}^{n_r} \sum_{(k,s)\in S_h} V_{n,(k,s)}^h log(p_{k,s}^h). \tag{4.4}$$

In order to determine the maximum likelihood estimates for $p^h_{k,s}$, $(k,s) \in S_h$, it is necessary to obtain the values that maximize the likelihood function (4.3), or equivalently, the log-likelihood function (4.4), subject to the constraints:

$$\sum_{(k,s)\in S_h} p^h_{k,s} = 1, \quad p^h_{k,s} \geq 0, \quad h = 1, \dots, n_r.$$

Consequently, using the Lagrange multipliers technique, it is required to determine the values of $p^h_{k,s}$ that maximize the function:

$$\Psi(P_1, \dots, P_{n_r}) := \ell(P_1, \dots, P_{n_r} \mid \mathcal{S}_n) + \lambda_h (1 - \sum_{(k,s)\in S_h} p^h_{k,s}),$$

where λ_h, $h = 1, \dots, n_r$ denotes the corresponding Lagrange multipliers. Now, it is obtained:

$$\frac{\partial}{\partial p^h_{k,s}} \left[\ell(P_1, \dots, P_{n_r} \mid \mathcal{S}_n) + \lambda_h (1 - \sum_{(k,s)\in S_h} p^h_{k,s}) \right] = (p^h_{k,s})^{-1} V^h_{n,(k,s)} - \lambda_h = 0. \tag{4.5}$$

From (4.5), it is deduced that $\lambda_h = V^h_n$. Hence, the solutions of the equations given in (4.5) are the expressions given in Theorem 4.1(a). It can be checked that such solutions maximize function (4.4). Intuitively, notice that $\widehat{p^h_{k,s}}$ is the proportion of progenitor couples that generate exactly k females and s males when P_h is the underlying reproductive strategy.

Estimates given in Theorem 4.1(b),(c), are then determined using (2.4), (2.5), and Theorem 4.1(a).

4.2. Bayesian estimates

First, in order to apply the Bayesian estimation methodology, it is necessary to choose a suitable class of prior densities $\pi(P_1, \dots, P_{n_r})$ for $(P_1, \dots, P_{n_r})$. From the mathematical expression given in (4.3), it is derived that an appropriate class of prior densities for $(P_1, \dots, P_{n_r})$ is the product of Dirichlet densities:

$$\pi(P_1, \dots, P_{n_r}) = \prod_{h=1}^{n_r} D_h \prod_{(k,s)\in S_h} (p^h_{k,s})^{\tau^h_{k,s}-1}, \tag{4.6}$$

where for each $h \in \mathbb{N}_r$,

$\tau_h = \left(\tau^h_{k,s},\ (k,s) \in S_h\right)$ is a vector of positive constants,

$D_h = \prod_{(k,s)\in S_h} \Gamma(\tau^h_*) \left(\Gamma(\tau^h_{k,s})\right)^{-1}, \ \tau^h_* = \sum_{(k,s)\in S_h} \tau^h_{k,s}, \ \Gamma(u) := \int_0^\infty e^{-x} x^{u-1} dx, \ u > 0.$

Theorem 4.2 By considering the squared error loss function, the Bayesian estimates for $p^h_{k,l}$, μ^h_i, and σ^h_{ij}, $i, j = 1, 2$, $h \in \mathbb{N}_r$, are given by:

(a) $\widetilde{p^h_{k,s}} = (W^h_*)^{-1} W^h_{k,s}, \ (k,s) \in S_h.$

(b) $\widetilde{\mu^h_i} = (W^h_*)^{-1} \sum_{(k_1,k_2)\in S_h} k_i W^h_{k_1,k_2}.$

$$(c)\ \ \widetilde{\sigma^h_{ij}} = \left(W^h_*(1+W^h_*)\right)^{-1}\left(W^h_* \sum_{(k_1,k_2)\in S_h} k_i k_j W^h_{k_1,k_2} - \sum_{(k_1,k_2),(l_1,l_2)\in S_h} k_i l_j W^h_{k_1,k_2} W^h_{l_1,l_2}\right),$$

where

$$W^h_{k,s} := \tau^h_{k,s} + V^h_{n,(k,s)}, \quad W^h_* := \sum_{(k,s)\in S_h} W^h_{k,s}.$$

Proof. Taking into account (4.6), the posterior density of $(P_1,\dots,P_{n_r})$, incorporating the information provided by (4.1), is given by the product of Dirichlet densities:

$$\pi(P_1,\dots,P_{n_r} \mid \mathcal{S}_n) = \prod_{h=1}^{n_r} D^*_h \prod_{(k,s)\in S_h} (p^h_{k,s})^{W^h_{k,s}-1}, \tag{4.7}$$

where for each $h \in \mathbb{N}_r$,

$$W_h = \left(W^h_{k,s},\ (k,s)\in S_h\right), \quad D^*_h = \prod_{(k,s)\in S_h} \Gamma(W^h_*)(\Gamma(W^h_{k,s}))^{-1}.$$

Given $(k,l)\in S_h$, from (4.7) we deduce, as marginal posterior density for $p^h_{k,s}$, the Beta density:

$$\pi(p^h_{k,s} \mid \mathcal{S}_n) = \frac{\Gamma(W^h_*)}{\Gamma(W^h_{k,s})\Gamma(W^h_* - W^h_{k,s})}(p^h_{k,s})^{W^h_{k,s}-1}(1-p^h_{k,s})^{W^h_*-W^h_{k,s}-1}, \ \ p^h_{k,s}\in(0,1). \tag{4.8}$$

Finally, from (4.8), using the squared error loss function, it is obtained as Bayesian estimate for $p^h_{k,s}$:

$$\widetilde{p^h_{k,s}} := \int_0^1 p^h_{k,l}\pi(p^h_{k,s} \mid \mathcal{S}_n)dp^h_{k,s} = (W^h_*)^{-1}W^h_{k,s}. \tag{4.9}$$

From (2.4), (2.5), and (4.9), the expressions given in Theorem 4.2(b),(c), are deduced as Bayesian estimates for μ^h_i and σ^h_{ij}, $i,j=1,2$, $h\in\mathbb{N}_r$, respectively.

Remark 4.1 From (4.8), we can determine the highest posterior density (HPD) credibility sets for $p^h_{k,s}$, namely, sets of the form:

$$\mathbb{J}(Q) := \left\{p^h_{k,s} : \pi(p^h_{k,s} \mid \mathcal{S}_n) \ge Q\right\}, \ Q > 0,$$

where given a certain credibility coefficient $1-\alpha$, the constant Q is calculated taking into account that:

$$\int_{\mathbb{J}(Q)} \pi(p^h_{k,s} \mid \mathcal{S}_n)dp^h_{k,s} = 1-\alpha.$$

To determine HPD credibility sets for μ^h_i and for σ^h_{ij}, $i,j=1,2$, $h\in\mathbb{N}_r$, it is necessary to approximate the corresponding posterior densities for such parameters. An appropriate procedure is based on the simulation, from $\pi(p^h_{k,s} \mid \mathcal{S}_n)$, of a sufficiently large number of values of $p^h_{k,s}$. Then, from (2.4) and (2.5), the corresponding values for μ^h_i and for σ^h_{ij}, $i,j=1,2$, $h\in\mathbb{N}_r$, are determined. From these values, applying a suitable Gaussian kernel method, see e.g., [23], approximated posterior densities for such parameters can be obtained. Using such approximated densities, we can then determine the corresponding empirical HPD credibility sets.

Remark 4.2 In order to simulate data from model (2.1), to calculate the proposed estimates for the parameters, and to determine the corresponding HPD credibility sets, we have implemented some specific programs using the statistical software R, see [24].

4.3. Illustrative example

Labord's chameleon (Furcifer labordi) is a native reptile of southwestern Madagascar, where it usually lives in dry deciduous forests. It is considered the shortest-lived tetrapod animal. It spends most of its life in the developing embryo phase (8 to 9 months) and, after that, it experiences a very rapid growth. It has a short lifespan (4 to 5 months), reaching its sexual maturity at an early age (2 months). There are no rigorous studies in the specialized scientific literature about their social organization or on their mating and reproduction strategies. The few studies that have been carried out are based on monitoring experiments through radio telemetry. From the information recorded, it has been detected that females exhibit high habitat fidelity, moving small cumulative and linear distances with low dispersion rates. Males move greater distances, in a less predictable manner, with higher dispersal rates than females. This species of chameleon constitutes a particular example of semelparous life (progenitors die shortly after reproducing). Their mating and reproductive strategies, highly conditioned by the number of females and males in the habitat, must adapt to these temporal limitations existing in intense competition and fighting between males. It has been suggested that they possess a wide range of different mating systems, generally polygamous matings. Males can mate with more than one female and females can mate with different males during the same ovarian cycle (the dynamics of male color change could also affect the choice of partner). The female lays a clutch of eggs and the progenitor male and female die. Some studies reported that females can lay between 6 and 8 eggs. Due to various random factors, mainly predators and environmental factors, a high percentage of eggs will not hatch. See [25–28] for more information about this species of chameleon.

Unfortunately, there is no real data available on the demographic dynamics of this reptile species. Next, taking into account the special characteristics of this species of chameleon, a simulated example is presented where mating and reproduction strategies close to reality are assumed. Let us consider a population of chamaleon of Labord with the following population dynamics:

1) Females and males form couples according to the $n_m = 2$ mating strategies:

$$L_1(F,M) = \min\{F,M\},\ \ L_2(F,M) = F\min\{1,M\},\ \ F,M \in \mathbb{N}.$$

According to L_1, the females and males practice fidelity, and they are allowed to have at most one mate. According to L_2, in each generation, a dominant male mates with each female. The other males do not participate in the mating process.

2) Since the number of eggs laid by a female is between 6 and 8, and it is known that a high percentage of eggs do not hatch, it will be assumed in our simulation the $n_r = 2$ reproductive strategies $P_h = \{p^h_{k,s}\}_{(k,s)\in S_h}$, $h = 1,2$, where

$$S_1 = S_2 = \{(0,0),(3,3),(4,3),(3,4),(4,4),(5,3),(3,5)\},$$

$$p^1_{0,0} = 0.71,\ p^1_{3,3} = 0.08,\ p^1_{4,3} = 0.06,\ p^1_{3,4} = 0.05,\ p^1_{4,4} = 0.03,\ p^1_{5,3} = 0.03,\ p^1_{3,5} = 0.04,$$

$$p^2_{0,0} = 0.71,\ p^2_{3,3} = 0.08,\ p^2_{4,3} = 0.05,\ p^2_{3,4} = 0.06,\ p^2_{4,4} = 0.03,\ p^2_{5,3} = 0.04,\ p^2_{3,5} = 0.03.$$

From P_1 and P_2,

$$\mu^1_1 = 1.02,\ \mu^1_2 = 1.03,\ \sigma^1_{11} = 2.679,\ \sigma^1_{22} = 2.749,\ \sigma^1_{12} = 2.519,$$

$$\mu_1^2 = 1.03,\ \mu_2^2 = 1.02,\ \sigma_{11}^2 = 2.749,\ \sigma_{22}^2 = 2.679,\ \sigma_{12}^2 = 2.519.$$

P_1 slightly favors the birth of males, with a ratio of males/females of the means equal to 1.01. This ratio has a value of 0.99 for P_2, which slightly favors the birth of females. From such reproductive strategies, it is deduced that:

$$\max\{P(F_{0,1}^h = 0), P(M_{0,1}^h = 0)\} = 0.71,\ h = 1, 2.$$

Hence, condition (2.2) holds.

3) In each generation, it is assumed that the functions φ_m and φ_r are given by:

$$\varphi_m(F, M) := 1 \cdot \mathbf{I}_{\{M(F+M)^{-1}>K\}} + 2 \cdot \mathbf{I}_{\{M(F+M)^{-1}\leq K\}},\ \ \varphi_r(F, M) := 1 \cdot \mathbf{I}_{\{F\leq M\}} + 2 \cdot \mathbf{I}_{\{F>M\}},\ F, M \in \mathbb{N}.$$

$K < 1$ is a suitable threshold for the proportion of males in the population.

Let $\{X_n\}_{n=0}^{\infty}$ be the two-sex branching process described in (2.1) with the mating and reproduction strategies mentioned previously. By way of illustration, taking $X_0 = (10, 10)$ and $K = 0.8$, we have developed a simulation for the first $n = 100$ generations of such a chameleon Labord population, i.e., in this case, $G_{100} = \{1, 2, \ldots, 100\}$, see Figure 1.

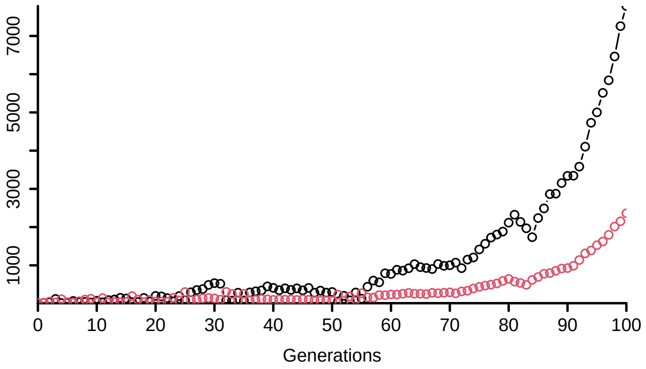

Figure 1. The evolution of the number of females (red color) and males (black color) in the successive generations belonging to G_{100}.

According to the obtained simulation, it is derived that P_2 has been the reproductive strategy in 19 generations and P_1 has been the reproductive strategy in 81 generations. In fact,

$$G_{100}^2 = \{2, 3, 5, 6, 8, 9, 10, 12, 17, 18, 20, 24, 26, 33, 34, 36, 52, 54, 56\}, \quad G_{100}^1 = G_{100} - G_{100}^2.$$

Taking into account the special reproductive characteristics of this biological species, with a high probability of unsuccessful hatching, we have considered the prior density given in (4.7), where

$$\tau_1 = \tau_2 = (29,\ 3.5,\ 3.5,\ 3.5,\ 3.5,\ 3.5,\ 3.5).$$

Using the information provided in the simulation, from Theorems 4.1 and 4.2, we have determined the corresponding maximum likelihood and Bayesian estimates for $p_{k,l}^h$, μ_i^h, and σ_{ij}^h, $i, j, h = 1, 2$, see Tables 1 and 2.

Table 1. The true values of $p^1_{k,l}$, $(k,l) \in S_1$, μ^1_i, σ^1_{ij}, $i, j = 1, 2$, and their maximum likelihood and Bayesian estimates.

	$p^1_{0,0}$	$p^1_{3,3}$	$p^1_{4,3}$	$p^1_{3,4}$	$p^1_{4,4}$	$p^1_{5,3}$	$p^1_{3,5}$
True values	0.71	0.08	0.06	0.05	0.03	0.03	0.04
Maximum likelihood estimates	0.712	0.079	0.061	0.049	0.028	0.029	0.041
Bayesian estimates	0.712	0.079	0.061	0.049	0.028	0.029	0.041
	μ^1_1	μ^1_2	σ^1_{11}	σ^1_{22}	σ^1_{12}		
True values	1.02	1.03	2.679	2.749	2.519		
Maximum likelihood estimates	1.012	1.023	2.664	2.738	2.505		
Bayesian estimates	1.013	1.024	2.666	2.740	2.507		

Table 2. The true values of $p^2_{k,l}$, $(k,l) \in S_2$, μ^2_i, σ^2_{ij}, $i, j = 1, 2$, and their maximum likelihood and Bayesian estimates.

	$p^2_{0,0}$	$p^2_{3,3}$	$p^2_{4,3}$	$p^2_{3,4}$	$p^2_{4,4}$	$p^2_{5,3}$	$p^2_{3,5}$
True values	0.71	0.08	0.05	0.06	0.03	0.04	0.03
Maximum likelihood estimates	0.706	0.072	0.051	0.068	0.028	0.049	0.026
Bayesian estimates	0.700	0.072	0.052	0.068	0.030	0.049	0.028
	μ^2_1	μ^2_2	σ^2_{11}	σ^2_{22}	σ^2_{12}		
True values	1.03	1.02	2.749	2.679	2.519		
Maximum likelihood estimates	1.038	1.030	2.857	2.670	2.556		
Bayesian estimates	1.081	1.054	2.898	2.722	2.595		

From Tables 1 and 2,

$$\max_{h=1,2}\{\max_{(k,l)\in S_h} |p^h_{k,l} - \widehat{p^h_{k,l}}|\} = 0.009, \quad \max_{h=1,2}\{\max_{i=1,2} |\mu^h_i - \widehat{\mu^h_i}|\} = 0.009, \quad \max_{h=1,2}\{\max_{i,j=1,2} |\sigma^h_{ij} - \widehat{\sigma^h_{ij}}|\} = 0.108,$$

$$\max_{h=1,2}\{\max_{(k,l)\in S_h} |p^h_{k,l} - \widetilde{p^h_{k,l}}|\} = 0.008, \quad \max_{h=1,2}\{\max_{i=1,2} |\mu^h_i - \widetilde{\mu^h_i}|\} = 0.051, \quad \max_{h=1,2}\{\max_{i,j=1,2} |\sigma^h_{ij} - \widetilde{\sigma^h_{ij}}|\} = 0.149,$$

which shows good accuracy of the estimators.

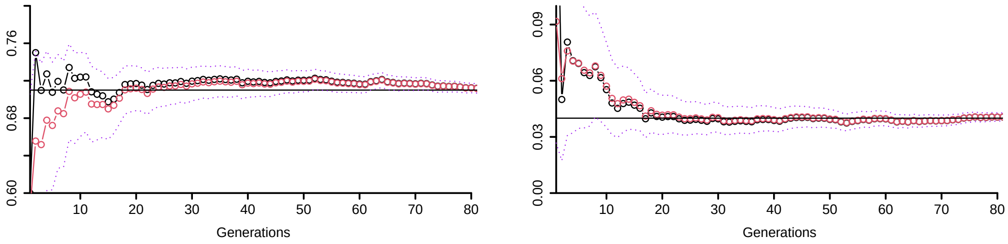

Figure 2. On the left is the evolution of $\widehat{p^1_{0,0}}$ (black color) and $\widetilde{p^1_{0,0}}$ (red color) and on the right is the evolution of $\widehat{p^1_{3,5}}$ (black color) and $\widetilde{p^1_{3,5}}$ (red color) in the successive generations belonging to G^1_{100}.

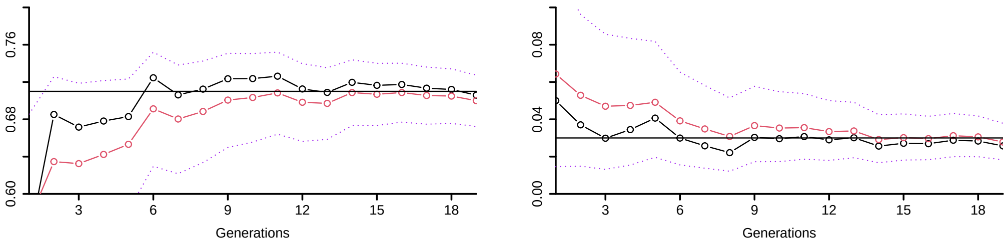

Figure 3. On the left is the evolution of $\widehat{p^2_{0,0}}$ (black color) and $\widetilde{p^2_{0,0}}$ (red color) and on the right is the evolution of $\widehat{p^2_{3,5}}$ (black color) and $\widetilde{p^2_{3,5}}$ (red color) in the successive generations belonging to G^2_{100}.

As an illustration, Figures 2 and 3 show the evolution of the estimates for $p^h_{0,0}$ and $p^h_{3,5}$, in the successive generations belonging to G^h_{100}, $h = 1, 2$, respectively. Similarly, Figures 4 and 5 show the evolution of the estimates for μ^1_i and μ^2_i, $i = 1, 2$, in the successive generations belonging to G^1_{100} and G^2_{100}, respectively. The 95% HPD credibility sets are also included in all figures (the true values for the parameters are represented by horizontal lines). For a better visualization of the graphs, the generations belonging to G^1_{100} and G^2_{100} have been renumbered, from 1 to 81 and from 1 to 19, respectively.

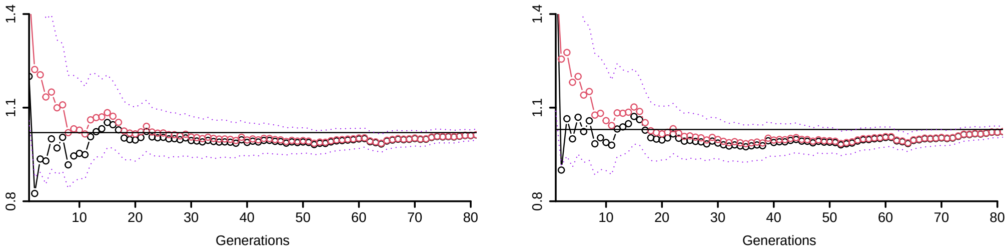

Figure 4. On the left is the evolution of $\widehat{\mu^1_1}$ (black color) and $\widetilde{\mu^1_1}$ (red color) and on the right is the evolution of $\widehat{\mu^1_2}$ (black color) and $\widetilde{\mu^1_2}$ (red color) in the successive generations belonging to G^1_{100}.

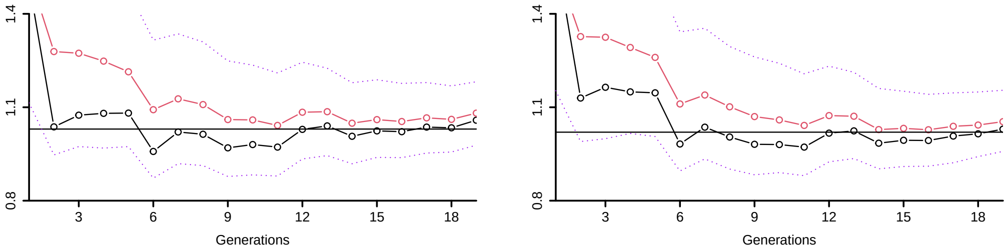

Figure 5. On the left is the evolution of $\widehat{\mu^2_1}$ (black color) and $\widetilde{\mu^2_1}$ (red color) and on the right is the evolution of $\widehat{\mu^2_2}$ (black color) and $\widetilde{\mu^2_2}$ (red color) in the successive generations belonging to G^2_{100}.

5. Conclusions

In this research, we have continued the working line started in previous papers about mathematical modeling concerning the demographic dynamics of semelparous biological species through two-sex branching processes with multiple mating and reproduction strategies. It has been assumed that, in each generation, both phases (mating and reproduction) are influenced by the current number of females and males existing in the population (habitat). Several probabilistic and statistical contributions have been established. In fact, the probability distribution associated to the variable number of generations elapsed before the possible extinction of the population has been derived. Also, the aforementioned two-sex branching processes have been used to mathematically describe the phenomenon of populating or repopulating habitats with a semelparous species that has become extinct, or is in danger of extinction. By considering the most general non-parametric statistical setting on the reproductive strategies associated with the biological species, various inferential questions about the main parameters governing the reproduction phase have been determined. To this purpose, information concerning the reproduction of the couples has been included in the observed data sample. Using this information, estimates for the reproductive parameters have been proposed. To this end, maximum likelihood and Bayesian estimates, and the corresponding 95% HPD credibility sets, have been determined. To simulate data from the mathematical model and also to calculate the estimates and the HPD credibility sets, the necessary computing programs have been developed. By way of illustration, the proposed estimation methodologies have been applied through a simulated example with Labord's chamaleon populations. The simulation performed has showed the accuracy of the proposed estimates.

Some possible direcions for research are, for example, to extend this class of two-sex branching processes, including in the probability model the immigration of females, males, or couples, from external populations; considering mating and/or reproduction in random environments; or assuming multi-type populations. It is also necessary to explore other possible mathematical methodologies that allow modeling the evolution of semelparous biological species with sexual reproduction. In this regard, the survey in [29] provides interesting information to be considered.

Use of AI tools declaration

The authors declare they have not used Artificial Intelligence (AI) tools in the creation of this article.

Acknowledgments

The authors wish to express their gratitude to the referees. Their technical questions, suggestions, and corrections have improved the presentation and understanding of this paper. This research has been supported by the Ministerio de Ciencia e Innovación of Spain (grant PID2019-108211GB-I00/AEI/10.13039/501100011033).

Conflict of interest

The authors declare there is no conflict of interest.

References

1. E. Ranta, D. Tesar, V. Kaitala, Environmental variability and semelparity vs. iteroparity as life histories, *J. Theor. Biol.*, **217** (2002), 391–396. https://doi.org/10.1006/jtb.2002.3029
2. A. Margalida, M. Colomer, D. Oro, R. Arlettaz, J. Donázar, Assesing the impact of removal scenarios on population viability of a threatened long-lived avian scavenger, *Sci. Rep.*, **5** (2015), 16962. https://doi.org/10.1038/srep16962
3. H. Tauler, J. Real, A. Hernández-Matías, P. Aymerich, J. Baucells, C. Martorell, et al., Identifying key demographic parameters for the viability of a growing population of the endangered Egyptian Vulture Neophron pernopterus, *Bird Conserv. Int.*, **25** (2015), 246–439. https://doi.org/10.1017/S0959270914000392
4. M. J. Faddy, Stochastic compartmental models as approximations to more general stochastic systems with the general stochastic epidemic as an example, *Adv. Appl. Probab.*, **9** (1977), 448–461. https://doi.org/10.2307/1426108
5. J. H. Matis, T. E. Wehrly, Stochastic models of compartmental systems, *Biometrics*, **35** (1979), 199–220. https://doi.org/10.2307/2529945
6. K. B. Athreya, P. E. Ney, *Branching Processes*, Springer-Verlag Berlin, Heidelberg, 1972. https://doi.org/10.1007/978-3-642-65371-1
7. P. Guttorp, *Statistical Inference for Branching Processes*, Wiley, New York, 1991.
8. P. Haccou, P. Jagers, V. Vatutin, *Branching Processes: Variation, Growth, and Extinction of Population*, Cambridge University Press, Cambridge, **5** (2005).
9. I. Pázsit, Symmetries and asymmetries in branching processes, *Symmetry*, **15** (2023), 1154. http://doi.org/10.3390/sym15061154
10. L. A. Keating, J. P. Gleeson, D. J. O'Sullivan, Multitype branching process method for modeling complex contagion on clustered networks, *Phys. Rev. E*, **105** (2022), 034306. http://doi.org/10.1103/PhysRevE.105.034306
11. D. M. Hull, A survey of the literature associated with the bisexual Galton-Watson branching process, *Extracta Math.*, **18** (2003), 321–343.
12. M. Molina, Two-sex branching process literature, in *Workshop on Branching Processes and Their Applications*, Springer Berlin Heidelberg, Berlin, **197** (2010), 279–293. https://doi.org/10.1007/978-3-642-11156-3-20
13. D. J. Daley, D. M. Hull, J. M. Taylor, Bisexual Galton-Watson branching processes with superadditive mating functions, *J. Appl. Probab.*, **23** (1986), 585–600. https://doi.org/10.2307/3213999
14. D. M. Hull, A necessary condition for extinction in those bisexual Galton-Watson branching processes governed for superadditive mating functions, *J. Appl. Probab.*, **19** (1982), 847–850. https://doi.org/10.2307/3213838
15. S. Ma, Y. Xing, The asymptotic properties of supercritical bisexual Galton-Watson branching processes with immigration of mating units, *Acta Math. Sci.*, **26** (2006), 603–609. https://doi.org/10.1016/S0252-9602(06)60086-6

16. M. Molina, C. Jacob, A. Ramos, Bisexual branching processes with offspring and mating depending on the number of couples in the population, *Test*, **17** (2008), 265–281. https://doi.org/10.1007/s11749-006-0031-9
17. Y. Xing, Y. Wang, On the extinction of one class of population-size dependent bisexual branching processes, *J. Appl. Probab.*, **42** (2005), 175–184. https://doi.org/10.1239/jap/1110381379
18. Y. Xing, Y. Wang, On the extinction of population-size dependent bisexual Galton-Watson processes, *Acta Math. Sci.*, **42** (2008), 210–216. https://doi.org/10.1016/S0252-9602(08)60022-3
19. M. Molina, M. Mota, A. Ramos, Stochastic modeling in biological populations with sexual reproduction through branching models: application to coho salmon populations, *Math. Biosci.*, **258** (2014), 182–188. https://doi.org/ 10.1016/j.mbs.2014.10.007
20. M. Molina, M. Mota, A. Ramos, Two-sex branching processes with several mating and reproduction strategies: Extinction versus survival, *Branching Processes Appl.*, **219** (2016), 307–317. https://doi.org/10.1007/978-3-319-31641-3-18
21. M. Molina, M. Mota, A. Ramos, Estimation of parameters in biological species with several mating and reproduction alternatives, *Math. Biosci.*, **329** (2020), 108471. https://doi.org/10.1016/j.mbs.2020.108471
22. V. K. Rohatgi, *An Introduction to Probability Theory and Mathematical Statistics*, Wiley, New York, 1976.
23. B. W. Silverman, *Density Estimation for Statistics and Data Analysis*, Monographs on Statistics and Applied Probability, Chapman and Hall, London, 1986.
24. *R Development Core Team, a Language and Enviroment for Statistical Computing*, 2009. Available from: http://www.r-project.org.
25. K. B. Karsten, L. N. Andriamandimbiarisoa, S. F. Fox, C. J. Raxworthy, A unique life history among tetrapods: An annual chameleon living mostly as an egg, *Proc. Natl. Acad. Sci. USA*, **105** (2008), 8980–8984. https://doi.org/10.1073/pnas.0802468105
26. F. Eckhardt, P. M. Kappeler, C. Kraus, Highly variable lifespan in an annual reptile, Labord's chameleon (Furcifer labordi), *Sci. Rep.*, **7** (2017), 11397. https://doi.org/10.1038/s41598-017-11701-3
27. F. Eckhardt, *A Short Story: Senescence in an Annual Reptile, Labord's Cahameleon (Furcifer Labordi)*, Ph.D thesis, Georg-August University School of Science, 2019. Available from: http://dx.doi.org/10.53846/goediss-8355.
28. L. Hudei, P. M. Kappeler, Sex-specific movement ecology of the shortest-lived tetrapod during the mating season, *Sci. Rep.*, **12** (2022), 10053. https://doi.org/10.1038/s41598-022-14156-3
29. J. Ewald, P. Sieber, R. Garde, S. N. Lang, S. Schuster, B. Ibrahim, Trend in mathematical modeling of host-pathogen interactions, *Cell. Mol. Life Sci.*, **77** (2020), 467–480. https://doi.org/10.1007/s00018-019-03382-0

AIMS Press