



Original Research Article

Statistical inference in two-sex biological populations with reproduction in a random environment

Manuel Molina^{a,b,*}, Manuel Mota^{a,b}, Alfonso Ramos^{a,c}^a Department of Mathematics, University of Extremadura, Spain^b Institute of Advanced Scientific Computation, University of Extremadura, Spain^c Institute in Livestock and Cynetic, University of Extremadura, Spain

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ABSTRACT

We mathematically model the demographic dynamics of biological populations with sexual reproduction where mating and reproduction can be influenced by the current number of couples in the population. We assume the more realistic situation where the reproduction process occurs in a non-predictable environment. We also consider the immigration/emigration of couples in the population. In this work, we continue the research about the class of two-sex models introduced in [Ma et al. \(2016\)](#) where the offspring distribution changes over time in a random environment influenced by the number of progenitor couples in the population. By considering the more general non-parametric statistical setting, we study several inferential problems of ecological interest. As illustration, we present an application to Pacific salmon populations.

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1. Introduction

Branching models are appropriate to describe the probabilistic evolution of dynamical systems whose components, after certain life period, reproduce and die, in such a way that the transition from one to other state of the system is made according to a certain probability law. For background see, e.g., [Asmussen and Hering \(1983\)](#), [Guttorp \(1991\)](#) or [Sankaranarayanan \(1989\)](#). They have been especially developed to model biological phenomena, playing a major role in studies on population dynamics of great interest in population ecology, wildlife management, or conservation biology, see e.g., [Haccou et al. \(2005\)](#), [Jagers \(1975\)](#) or [Kimmel and Axelrod \(2002\)](#). In particular, using some asexual branching models, ecological applications have been considered in [Bruss and Slatvchova-Bojkova \(1999\)](#) and [Slatvchova-Bojkova \(2000\)](#).

We focus here our interest on the development of branching models to describe the demographic dynamics of biological populations with sexual reproduction. This research line was

initiated in [Daley \(1968\)](#) where the bisexual Galton–Watson model was introduced. In this model, the population of the species under consideration consists of two disjoint types of individuals (females and males) and two biological processes are carried out: mating and reproduction. In the mating process the couples female–male are formed. In the reproduction process, such couples produce new female and male descendants. In [Daley \(1968\)](#), using two specific mating strategies, conditions for the extinction of biological populations with dynamics described through the bisexual Galton–Watson model were derived. By considering more general mating strategies, several contributions about the probabilistic evolution of such populations were also established, see e.g., [Alsmeyer and Rösler \(2002\)](#), [Bagley \(1986\)](#), [Bruss \(1984\)](#), [Daley et al. \(1986\)](#), [González and Molina \(1996\)](#), or [Hull \(1982\)](#). From these works, the interest in this issue increased and new classes of two-sex (bisexual) branching models have been studied, see for details [Molina \(2010\)](#) and the references cited therein.

Significant efforts have been made to develop two-sex models based on the assumption that the couples which take part in the reproduction process (progenitor couples) behave over time identically with respect to the reproduction, see e.g., [Ma and Xing \(2006\)](#), [Molina et al. \(2008\)](#), or [Molina et al. \(2002\)](#). Moreover, in such models, the number of progenitor couples is determined in a

* Corresponding author at: Department of Mathematics, University of Extremadura, Spain.

E-mail address: mmolina@unex.es (M. Molina).

predictable environment. In many biological species due to random factors, for instance, weather conditions, food supply, fertility parameters, predators, or human activities, the reproduction process occurs in a non-predictable environment. Mathematical models to describe the demographic dynamics of such species have not been sufficiently investigated. In an attempt to contribute some solution to this issue, a new class of two-sex models where reproduction occurs in a non-predictable environment has been introduced in [Ma et al. \(2016\)](#). In each generation, the number of progenitor couples is randomly determined and they reproduce according to certain probability law which changes over time depending on the current number of progenitor couples in the population. In [Ma et al. \(2016\)](#), several general results about the demographic dynamics of the population have been obtained. In fact, some probabilistic properties have been determined, conditions which guarantee the classical extinction/explosion property in branching models have been derived, and sufficient conditions about the extinction of the population or its survival with a positive probability have been established.

The motivation behind the present work is to continue the research on this class of models, studying several inferential problems of ecological interest. In particular, it is of great practical importance to develop suitable statistical methods to provide close approximations for the probability laws governing the reproduction and for their main parameters. To this end, we propose appropriate inferential procedures.

The work is organized as follows: In Section 2, we provide the mathematical description about the class of two-sex models considered. In Section 3, assuming the more general non-parametric statistical framework, we determine estimators for the probability laws involved in the reproduction process and for their most important parameters. In order to obtain optimal credibility sets for such parameters, we also suggest a computational algorithm. Section 4 is devoted to presenting an ecological application to salmonid populations. The conclusions and some open questions for research are included in Section 5.

2. Two-sex model

We assume biological populations where mating and reproduction can be affected by the current number of couples in the population. In each generation both the number of progenitor couples and the probability law governing the reproductive process are randomly determined. The progenitor couples, independently of the others, produce new female and male descendants and then disappear. In [Ma et al. \(2016\)](#), the demographic dynamics of such populations has been mathematically described through the following class of two-sex model:

$$(F_{n+1}, M_{n+1}) := \sum_{i=1}^{\phi_{n,Z_n}} (f_{n,i}^{(\phi_{n,Z_n})}, m_{n,i}^{(\phi_{n,Z_n})}), \tag{1}$$

$$Z_{n+1} := L_{Z_n}(F_{n+1}, M_{n+1}), \quad n \in \mathbb{N}$$

where \mathbb{N} denotes the set of non-negative integers and the empty sum is assumed to be $(0, 0)$. For $n \in \mathbb{N}$, the variables F_{n+1} , M_{n+1} , and Z_{n+1} represent, respectively, the current numbers of females, males, and couples in the population at time (generation) $n + 1$. Initially, we assume a positive number k_0 of couples in the population. If in the n th generation there are k couples in the population, i.e., $Z_n = k$ then, the following sequences are involved in the probability model (1):

1. $\{\phi_{n,k}\}_{k=0}^\infty$, sequence of random variables taking values in \mathbb{N} . For each $k \in \mathbb{N}$, the variables $\phi_{n,k}$, $n \in \mathbb{N}$, are assumed to be independent and identically distributed (i.i.d.). Since $Z_n = k$, the total number of progenitor couples in the n th generation is

randomly determined by the variable $\phi_{n,k}$. The immigration/emigration of couples in the population is considered. In fact, when $\phi_{n,k} > k$ then $\phi_{n,k} - k$ immigrant couples come to the population and they take part in the reproduction. When $\phi_{n,k} < k$ then $k - \phi_{n,k}$ couples leave the population and they do not take part in the reproduction. It is assumed that $P(\phi_{n,0} = 0) = 1$, $P(\phi_{n,k} = 0) < 1$, $k > 0$.

Given that $\phi_{n,k} = j$ then, irrespectively of n , $(f_{n,i}^{(j)}, m_{n,i}^{(j)})$, $i = 1, \dots, j$, are i.i.d. random vectors, $(f_{n,i}^{(j)}, m_{n,i}^{(j)})$ representing the numbers of females and males descending from the i th progenitor couple in the n th generation. Its probability law, denoted by $P^{(j)} := (p_{f,m}^{(j)}, (f, m) \in S_j)$, $S_j \subseteq \mathbb{N}^2$, is referred to as the offspring distribution when j progenitor couples take part in the reproduction process:

$$p_{f,m}^{(j)} := P(f_{n,1}^{(j)} = f, m_{n,1}^{(j)} = m), \quad (f, m) \in S_j.$$

Clearly, $p_{0,0}^{(0)} = 1$.

2. $\{L_k\}_{k=0}^\infty$, sequence of functions defined on \mathbb{N}^2 and taking values in \mathbb{N} . The role of these functions, referred to as mating functions, is to determine, in each generation, the total number of couples formed in the mating process. Each L_k is assumed to be non-decreasing and such that:

$$L_k(0, m) = L_k(f, 0) = 0, \quad f, m \in \mathbb{N}.$$

Note that $\{(F_n, M_n)\}_{n=1}^\infty$, given in (1), is a class of two-sex models representing the evolution of the numbers of females and males in the population in an environment which changes, stochastically in time, influenced by the current number of couples in the population. In fact, if at time n , k couples have been formed in the population then the offspring distribution and the mating function governing the reproduction and mating processes are given by $P^{(\phi_{n,k})}$ and L_k , respectively. This general class of models includes, as particular cases, the two-sex models studied in [Daley \(1968\)](#), [Molina et al. \(2008\)](#), [Molina et al. \(2002\)](#), and [Xing and Wang \(2005\)](#). In addition to its theoretical interest, it has also ecological applications. In particular, it can be used as mathematical model to describe the probabilistic evolution of semelparous species, namely, biological species characterized by a single reproductive episode before death, see for details [Fleming \(1996\)](#) or [Laufle et al. \(1986\)](#).

3. Estimation

Let $\{(F_n, M_n)\}_{n=1}^\infty$ be the class of models defined in (1) with offspring distributions:

$$P^{(j)} = (p_{f,m}^{(j)}, (f, m) \in S_j), \quad j \in \mathbb{N}.$$

In this section, by considering the more general non-parametric statistical setting, we will determine close approximations for such distributions and for their main parameters. The section is organized in three subsections: Section 3.1 is devoted to determining Bayes estimators for the offspring distributions. Estimators for the main parameters of the offspring distributions are derived in Section 3.2. Finally, the problem of obtaining optimal credibility sets for such parameters is considered in Section 3.3.

3.1. Estimation of the offspring distributions

We assume the observation of the entire family tree in the population up to the n th generation is reached, i.e., we know the values concerning the set of variables:

$$\mathcal{V}_n := \{Z_l, \phi_{l,Z_l}, (f_{l,i}^{(\phi_{l,Z_l})}, m_{l,i}^{(\phi_{l,Z_l})}), i = 1, \dots, \phi_{l,Z_l}, l = 0, \dots, n\}$$

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