



# The long-run distribution of births across environments under environmental stochasticity and its use in the calculation of unconditional life-history parameters



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## ABSTRACT

Matrix population models assume individuals develop in time along different stages that may include age, size or degree of maturity to name a few. Once in a given stage, an individual's ability to survive, reproduce or move to another stage are fixed for that stage. Some demographic models consider that environmental conditions may change, and thus the chances of reproducing, dying or developing to another stage depend on the current stage and environmental conditions. That is, models have evolved from a single transition matrix to a set of several transition matrices, each accounting for the properties of a given environment. These models require information on the transition between environments, which is in general assumed to be Markovian. Although great progress has been made in the analysis of these models, they present new challenges and some new parameters need to be calculated, mainly the ones related to how births are distributed among environments. These parameters may help in population management and to calculate unconditional life history parameters. We derive for the first time an expression for the long-run distribution of births across environments, and show that it does not depend only on the long-range frequency of different environments, but also on the set of all transition and fertility matrices. We also derive the long-run distribution of deaths across environments. We provide an example using a real data set of the dynamics of Saiga antelope. Theoretical values closely match the observed values obtained in a large set of stochastic simulations.

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## 1. Introduction

Modern demography theory goes back to Lotka (1924). Most population models describe the dynamics of a population whose individuals are classified by their current stage, where stage is a label to indicate a particular life period or condition of an individual, such as age (Milner-Gulland, 1994), size (Aberg, 1992) or a given period of the life cycle (Caswell, 2009). These models are discrete state, discrete time models because the number of stages is finite and they evolve in time at discrete steps of unitary size, for instance a year (Aberg, 1992) or a month period (Gotelli, 1991). These models analyze the dynamics of vector  $\mathbf{X}_t$ , that contains

the number of individuals in each stage category at time  $t$ . The relationship between the composition of the population at time  $t$  and  $t + 1$  is given by

$$\mathbf{X}_{t+1} = \mathbf{A} \mathbf{X}_t$$

where  $\mathbf{A}$  is called the *projection matrix*. A common type of projection matrix is the so called Lefkovich matrix, which, for 4 stages has the form

$$\mathbf{A} = \begin{pmatrix} G_1 & 0 & f_3 & f_4 \\ P_1 & G_2 & 0 & 0 \\ 0 & P_2 & G_3 & 0 \\ 0 & 0 & P_3 & G_4 \end{pmatrix}.$$

Each column (or row) of  $\mathbf{A}$  contains information on a given stage. For instance,  $G_i$  is the probability that an individual in stage  $i$  will remain in stage  $i$  at the next unit of time, and  $P_i$  is the probability that an individual in stage  $i$  will move to the next stage at the next unit of time. The remaining  $1 - P_i - G_i$  is the probability

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that the individual will die. Also,  $f_i$  is the fertility per unit of time by an individual in stage  $i$ . We use fertility following Caswell (2001) to indicate actual reproductive performance, as opposed to fecundity as an indicator of physiological maximum reproductive output, although in the entomological literature fecundity is used as number of eggs laid and fertility as the hatching rate of those eggs. In matrix  $\mathbf{A}$  of the previous example, only stages 3 and 4 can reproduce. Matrix  $\mathbf{A}$  can be adapted to reflect movements between stages not necessarily in sequential order, for instance, when stages include pregnancy status, and individuals may enter and leave this stage several times (Caswell, 2001, 2009). Something similar happens with fertility: assuming that fertility is the production of newborns and these are labeled as stage 1, then the  $f_i$ 's should be placed in the first row of matrix  $\mathbf{A}$ . Nevertheless, and depending on the particular biological meaning of the stages, fertility may be considered more generally as the production of individuals of any stage; for instance, Aberg (1992) classified plants of *Ascophyllum nodosum* in six categories of increasing content of dry mass where a large plant may be broken in smaller pieces due to environmental factors and thus it would produce two plants in categories that may be different to category 1. For a compendium of basic results and concepts for these models see Caswell (2009).

What matrix models consider is how and when individuals reproduce and how they develop across stages. Most models use a transition matrix  $\mathbf{U}$  to describe transitions between stages, and a fertility matrix  $\mathbf{F}$  to describe the fertility of individuals in every stage. Matrix  $\mathbf{A}$  is constructed as  $\mathbf{A} = \mathbf{U} + \mathbf{F}$ , thus,  $\mathbf{X}_{t+1} = \mathbf{A} \mathbf{X}_t$  includes in the next unit of time the sum of survivors and newborns in each stage.

Lotka's seminal work had to wait fifty years for the development of models that included dispersal of populations (Hamilton and May, 1977) and 75 years to include populations living under fluctuating environments, but there is a growing interest in the field (Tuljapurkar and Orzack, 1980; Tuljapurkar, 1982a,b, 1986, 1990; Horvitz and Schemske, 1995; Nakaoka, 1997; Pascarella and Horvitz, 1998; Tuljapurkar et al., 2003; Haridas and Tuljapurkar, 2005; Horvitz et al., 2005; Tuljapurkar and Horvitz, 2006; Tuljapurkar et al., 2009).

Consider four different seasons within a year as different environments. Then the sequence of environments is always  $\{1, 2, 3, 4, 1, 2, 3, 4, 1, 2, 3, 4, \dots\}$  therefore we can make  $\mathbf{B} = \mathbf{A}^{(1)}\mathbf{A}^{(2)}\mathbf{A}^{(3)}\mathbf{A}^{(4)}$  and the composition of the population after 5 years of transitions is

$$\mathbf{X}_5 = \mathbf{BBBBB} \mathbf{X}_0 = \mathbf{B}^5 \mathbf{X}_0.$$

Nevertheless, this is not the general case since not all seasons are alike, for instance, fertility and reproduction may depend on the summer or winter type. Environmental disturbance due for instance to meteorological phenomena (Tuljapurkar et al., 2003; Pascarella and Horvitz, 1998) or forest fires (Silva et al., 1991) may also be driving factors that should be represented in stochastic models of environmental variation. Life history parameters (LHPs) measure some biological properties at the individual level. Among the most important LHPs we find the average offspring size per individual, the average age at reproduction, the average age at first reproduction, life expectancy, survivorship, etc. Harvesting or natural disasters affect these parameters and their estimation can be used to assess the fitness of the population. Observe that life history parameters refer to *average* behavior of *average* individuals, thus, in order to derive analytical expressions for these parameters we first need to find the distribution of births among environments, which is currently missing from the literature. Once the distribution of births across environments is found, it can be used to transform known conditional LHP into unconditional LHP.

Models that include environmental stochasticity need to incorporate rules of transition for environments. This requires

an additional matrix  $\mathbf{P}$ , with elements  $p_{ij}$  for the probability that if the current environment is  $i$ , at the next unit of time the environment will be  $j$ . In demography literature for variable environments the transition between environments is classified in three types (Tuljapurkar and Orzack, 1980; Tuljapurkar and Horvitz, 2006; Caswell, 2009): *Periodic, Independent and identically distributed* and *Markovian*. The latter is the most general case, where every  $p_{ij}$  is only limited to  $0 \leq p_{ij} \leq 1$ . An example matrix for four environments is

$$P = \begin{pmatrix} & 1 & 2 & 3 & 4 \\ p_{11} & p_{12} & p_{13} & p_{14} \\ p_{21} & p_{22} & p_{23} & p_{24} \\ p_{31} & p_{32} & p_{33} & p_{34} \\ p_{41} & p_{42} & p_{43} & p_{44} \end{pmatrix}.$$

The theory to study the dynamics of populations under stochastic environments was developed by Tuljapurkar and Orzack (1980), Tuljapurkar (1982a,b), Tuljapurkar et al. (2003), analyzed the growth rates of three kinds of population growth under stochastic environments: one is the *stochastic* growth arising from a model that uses the theory of random matrix products; other is the *mean growth*, arising from models that use the mean matrix, which is a weighted average of the projection matrices and the *megamatrix* growth rate, arising from the construction of a megamatrix, a matrix that describes the dynamics of a population of individuals classified by stage and environment.

The main approaches to analyze life history parameters under stochastic environments were given by Tuljapurkar and Horvitz (2006) and Caswell (2006). Tuljapurkar and Horvitz (2006) derived expressions for the age-specific mortality, survivorship and life expectancy for periodic, iid and Markovian environments, using theory of random matrix products, although for the Markovian case, the results are based in the use of square megamatrices of dimension  $S \times K$  where  $S$  is the number of stages and  $K$  is the number of environments. These megamatrices can be seen as a matrix of size  $K \times K$  where each element is itself a matrix of size  $S \times S$  containing the stage transitions. The expressions for life-history parameters depended on the initial state, and the unconditional distributions were constructed by weighting the initial state by the stationary distribution of environments, that is, it is implied under this approach that the probability that an individual is born in a particular environment is the same as the long-run relative frequency of that environment.

The problem of calculating LHPs was approached by Caswell (2009) by proposing the calculation of a matrix  $\mathbf{X}_t$  of size  $S \times K$  with entries  $x_{ij}$  containing the expected number of individuals in every combination of stage  $\times$  environment at time  $t$ . The expressions for the calculation of mean and variance of longevity were given using vec-permutation models (Hunter and Caswell, 2005) but, similarly to Tuljapurkar and Horvitz (2006), the derived expressions were conditional distributions, and the unconditional ones were calculated assuming again that the distribution of births was identical to the long run distribution of environments.

For the single environment case, Cochran and Ellner (1992) suggested the use of the distribution of newborns at the stable state distribution as weight to construct the different life history parameters. The distribution of newborns at the steady state can be found by normalizing the product of the fertility matrix  $\mathbf{F}$  and the eigenvector  $\mathbf{v}$ , associated to the dominant eigenvalue of  $\mathbf{A}$ , which contains the steady state distribution, that is

$$\mathbf{b} = \mathbf{Fv}/(\mathbf{1}'\mathbf{Fv}). \tag{1}$$

The rationale behind this approach is very simple and effective: in the long run, the population will reach a stable stage distribution  $\mathbf{v}$  and then the offspring will be produced according to  $\mathbf{Fv}$ , and the normalization of this vector gives the long run offspring

distribution across stages. Nevertheless, under environmental stochasticity, populations never reach a steady state, meaning a population structure  $\mathbf{v}$  such that at the next unit of time, the relative frequencies of  $\mathbf{v}$  are kept constant. We will deal with this topic in the discussion section.

Here we first derive an expression for the distribution of births across environments or *birth distribution*, and use it to derive unconditional expressions for some life history parameters.

## 2. Model construction

### 2.1. The transition and fertility matrices for each environment

Recall the transition matrix for environment  $k$ ,  $\mathbf{U}^{(k)}$ , for an example with 5 stages is

$$\mathbf{U}^{(k)} = \begin{pmatrix} G_1 & 0 & 0 & 0 & 0 \\ P_1 & G_2 & 0 & 0 & 0 \\ 0 & P_2 & G_3 & 0 & 0 \\ 0 & 0 & P_3 & G_4 & 0 \\ 0 & 0 & 0 & P_4 & G_5 \end{pmatrix}.$$

Also, the associated fertility matrix for environment  $k$ :

$$\mathbf{F}^{(k)} = \begin{pmatrix} 0 & f_2^{(k)} & f_3^{(k)} & f_4^{(k)} & f_5^{(k)} \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{pmatrix}$$

where  $f_i^{(k)}$  = number of stage 1 individuals produced per unit time by an individual in stage  $i$  when the environment is  $k$ .

### 2.2. The stationary distribution for environments

In the long run, environment  $k$  occurs a proportion  $\pi_k$  of the time. If the matrix  $\mathbf{P}$  providing the rules of transition between stochastic environments is not periodic, the long run proportion of each environment is obtained from the stationary distribution of the process under which environments evolved, and that can be calculated as

$$\boldsymbol{\pi}' = \mathbf{1}'(\mathbf{P} + \mathbf{J} - \mathbf{I})^{-1}$$

where  $\mathbf{J}$  is a matrix of ones of the appropriate dimension (Resnick, 1992). However, if  $\mathbf{P}$  is periodic,  $\boldsymbol{\pi}$  then is

$$\boldsymbol{\pi}' = K^{-1}\mathbf{1}'$$

where  $K$  is the number of environments. If  $\mathbf{P}$  is iid, the stationary distribution of  $\mathbf{P}$  is given by any of its rows

$$\boldsymbol{\pi}' = [p_1 p_2 p_3 \cdots p_K].$$

### 2.3. The transition among stages and environments

We define every possible combination of stage  $\times$  environment as a *state*. Clearly, if there are  $K$  environments and  $S$  stages there are  $S \times K$  possible states. We can construct a *megamatrix*  $\mathbf{U}$  describing the transition between states:

$$\mathbf{U} = \begin{pmatrix} p_{(1,1)}\mathbf{U}^{(1)} & p_{(2,1)}\mathbf{U}^{(2)} & \cdots & p_{(K,1)}\mathbf{U}^{(K)} \\ p_{(1,2)}\mathbf{U}^{(1)} & p_{(2,2)}\mathbf{U}^{(2)} & \cdots & p_{(K,2)}\mathbf{U}^{(K)} \\ \vdots & \vdots & \ddots & \vdots \\ p_{(1,K)}\mathbf{U}^{(1)} & p_{(2,K)}\mathbf{U}^{(2)} & \cdots & p_{(K,K)}\mathbf{U}^{(K)} \end{pmatrix} \quad (2)$$

where  $p_{(i,j)}$  is the probability that the next environment will be  $j$  given that current environment is  $i$ . Cohen (1977a,b), Horvitz and

Schemske (1986), Pascarella and Horvitz (1998) and Tuljapurkar et al. (2003) among others used these types of megamatrices.

Let  $\mathbf{A}^{(i)} = \mathbf{U}^{(i)} + \mathbf{F}^{(i)}$  and define matrix  $\mathbf{A}$  as

$$\mathbf{A} = \begin{pmatrix} p_{(1,1)}\mathbf{A}^{(1)} & p_{(2,1)}\mathbf{A}^{(2)} & \cdots & p_{(K,1)}\mathbf{A}^{(K)} \\ p_{(1,2)}\mathbf{A}^{(1)} & p_{(2,2)}\mathbf{A}^{(2)} & \cdots & p_{(K,2)}\mathbf{A}^{(K)} \\ \vdots & \vdots & \ddots & \vdots \\ p_{(1,K)}\mathbf{A}^{(1)} & p_{(2,K)}\mathbf{A}^{(2)} & \cdots & p_{(K,K)}\mathbf{A}^{(K)} \end{pmatrix}.$$

This is the projection matrix with entries as the per-capita production of individuals at the different stages and environments at time  $t + 1$  by the individuals of all other stages and environments at time  $t$ . For instance, the sub-matrix

$$P_{(n,m)}\mathbf{A}^{(m)}$$

contains in the  $i$ -th row and  $j$ -th column, the per-capita production of individuals of stage  $j$  and environment  $m$  at time  $t + 1$ , produced by individuals of stage  $i$  and environment  $n$  at time  $t$ .

### 2.4. On the interpretation of $\mathbf{U}$ and $\mathbf{A}$

The first column of  $\mathbf{U}$  contains the probabilities that an individual in stage 1 and environment 1 moves to all other stages through the different environments at the next time step. The second column contains the probabilities that an individual in stage 2 and environment 1 moves to all other stages through the different environments at the next time step, and so on. The first  $S$  columns contain the information on transitions from every stage of the first environment, to all other stages and environments. The second group of  $S$  columns contain the information on transitions from every stage of the second environment, to all other stages and environments, and so on.

Since  $\mathbf{A}$  is a projection matrix and  $\mathbf{P}$  a probability transition matrix, the expected composition of  $\mathbf{X}_t$ , the number of individuals in each of the  $S \times K$  states at time  $t$ , can be obtained with

$$\mathbf{X}_t = \mathbf{A}\mathbf{X}_{t-1}.$$

Observe that  $\mathbf{X}_t$  is a column vector of dimension  $S \times K$  containing the expected number of individuals in each of the  $S \times K$  combinations of stage  $\times$  environment at time  $t$ , which is equivalent to the one obtained after applying the *vec* operator to the transpose of  $\mathbf{X}_t$  suggested by Caswell (2009).

Matrix  $\mathbf{A}$  allows us to calculate the expected number of individuals for each combination of stage  $\times$  environment at a given time. As Caswell (2009) points out, the eigenvalues of matrix  $\mathbf{A}$  will yield the growth rate of the mean population, but not the stochastic growth rate, which is always less or equal to the growth rate of the mean population. Nevertheless, this does not affect parameters that depend on average times on every state Caswell (2009).

It is known (Iosifescu, 1980) that matrix  $\mathbf{N}$  calculated as

$$\mathbf{N} = (\mathbf{I} - \mathbf{U})^{-1} \quad (3)$$

contains the expected time an individual spends on each of the  $S \times K$  stages (rows), for every one of the possible  $S \times K$  initial stages (columns). The variance of the time spent on each state is contained in matrix  $\mathbf{V}$ :

$$\mathbf{V} = (2\mathbf{N}_{\text{diag}} - \mathbf{I})\mathbf{N} - \mathbf{N} \circ \mathbf{N} \quad (4)$$

where  $\circ$  is the Hadamard product. The average longevity of an individual that starts in every possible state is

$$E(\eta) = \mathbf{1}'\mathbf{N} \quad (5)$$

with variance

$$V(\eta) = \mathbf{1}'\mathbf{N}(2\mathbf{N} - \mathbf{I}) - E(\eta)' \circ E(\eta') \quad (6)$$

(see Iosifescu, 1980, Section 3.2).

### 3. Calculation of unconditional life-history parameters

Expressions (5) and (6) give the mean and variance of longevity starting from every possible initial state. Assuming that every newborn belongs to stage 1, the conditional expressions given in the previous section must be weighted by the probability of starting at environment  $j$ . For instance, even if an environment occurs at a high frequency on the long run, if the population's growth rate of individuals in that environment is small, then the relative contribution of births of that environment to the overall population size may be low. Therefore, the chances that a newborn is born under environment  $k$  are not completely dependent on  $\pi$ , the stationary distribution of the environments, but, as we will show later, on the population's growth rate under each environment. These considerations were not taken into account in Tuljapurkar and Horvitz (2006) and Caswell (2009), where these parameters were calculated by weighting the estimates by the stationary distribution of environments. As previously mentioned, this latter approach assumes that the probability that an individual is born under environment  $k$  is the same as the long run frequency at which environment  $k$  occurs. Unconditional life history parameters refer to average individuals, thus the initial state has to be weighted by the probability that an individual is born at every initial environment, which justifies the need to find the distribution of births across environments.

Consider for instance the net reproductive rate or  $R_0$ , which is the average number of individuals produced by an individual during its lifetime, that is, the per-generation growth rate (Cushing and Zhou, 1994). Although individuals born in a particular environment may have a larger expected offspring size than if born in another environment,  $R_0$  relates to the offspring size averaging over all individuals, and this is where the distribution of births across environments becomes useful. This is specially relevant in periodic environments (Hunter and Caswell, 2005) where births are concentrated in one or two environments, or in spatially regularly distributed environments (e.g., patches of trees and grasses in savannas). The next section deals with the derivation of expressions to calculate unconditional life history parameters.

#### 3.1. The distribution of births across states and the net reproductive rate, $R_0$

The main goal of this paper is to derive an expression for the long-run distribution of births across environments. In order to achieve this, we need to derive the long-run distribution of births across states. We first construct a fertility matrix  $\mathbf{W}$  such that  $\mathbf{WN}$  gives the expected offspring size for an individual born in every combination of stage  $\times$  environment. Define

$$\mathbf{W} = \text{diag}(\mathbf{F}^{(1)}, \mathbf{F}^{(2)}, \mathbf{F}^{(3)}, \dots, \mathbf{F}^{(K)})$$

$$= \begin{pmatrix} \mathbf{F}^{(1)} & \mathbf{0} & \mathbf{0} & \dots & \mathbf{0} \\ \mathbf{0} & \mathbf{F}^{(2)} & \mathbf{0} & \dots & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{F}^{(3)} & \dots & \mathbf{0} \\ \cdot & \cdot & \cdot & \dots & \cdot \\ \cdot & \cdot & \cdot & \dots & \cdot \\ \cdot & \cdot & \cdot & \dots & \cdot \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \dots & \mathbf{F}^{(K)} \end{pmatrix} \quad (7)$$

where  $\mathbf{F}^{(k)}$  is the fertility matrix for environment  $k$  and  $\mathbf{0}$  is a matrix of zeros of dimension  $S$ , thus,  $\mathbf{WN}$  is a square matrix of dimension  $S \times K$ , whose columns contain the average offspring size produced in every combination of stage  $\times$  environment for an individual born at every one of these  $S \times K$  combinations, thus, it is the well-known generation distribution.

Let  $\mathbf{e}_j$  be a column vector of zeros of dimension  $S \times K$  with a one at position  $j$ . The average offspring size produced in every state by

an individual born in state  $j$  is contained in the  $j$ -th column of  $\mathbf{WN}$ , that is,  $\mathbf{WNe}_j$ .

Let  $\theta_j$  be the fraction of individuals born in state  $j$ , and define  $\theta$  as

$$\theta = [\theta_1 \ \theta_2 \ \theta_3 \ \dots \ \theta_{S \times K}].$$

Let also  $n_i(t)$  be the number of individuals born in state  $i$  up to time  $t$ . Thus, in the long run, the average number of individuals produced on each state is

$$\lim_{t \rightarrow \infty} \frac{n_1(t)\mathbf{WNe}_1 + n_2(t)\mathbf{WNe}_2 + n_3(t)\mathbf{WNe}_3 + \dots + n_{SK}(t)\mathbf{WNe}_{SK}}{n_1(t) + n_2(t) + n_3(t) + \dots + n_{SK}(t)}$$

since  $\lim_{t \rightarrow \infty} n_i(t) / \sum_{i=1}^{SK} n_i(t) = \theta_i$ , we can write the last expression as:

$$\theta_1\mathbf{WNe}_1 + \theta_2\mathbf{WNe}_2 + \dots + \theta_{SK}\mathbf{WNe}_{SK} = \mathbf{WN}\theta. \quad (8)$$

Nevertheless, observe that the relationship  $\mathbf{X}_t = \mathbf{A}\mathbf{X}_{t-1}$  assumes an individual born in a given environment starts its life cycle in the environment that occurs next. Thus, even although individuals are born across states according to the birth distribution  $\theta$ , they will start their life cycle in the next (random) environment, yielding a distribution that we call the starting distribution  $\phi$ . To derive  $\phi$ , the matrix  $\mathbf{WN}$  must be premultiplied by a matrix  $\mathbf{E}$  where  $\mathbf{E} = \mathbf{P} \otimes \mathbf{I}_s$  with  $\mathbf{P}$  the matrix of transition probabilities between environments,  $\otimes$  the Kronecker product and  $\mathbf{I}_s$  the identity matrix of size equal to the number of stages,  $s$ . Premultiplying by  $\mathbf{E}$  weights the rows of  $\mathbf{WN}$  to reflect the fact that newborns start their life cycle in the environment following that in which they were born.

The distribution of the environments in which individuals start their life cycle is the relevant weighting distribution to calculate life history traits.

Observe  $\mathbf{EWN}\phi$  is the average offspring size produced on each state from one generation to the next, thus, it must be a constant times the average offspring distribution across states, that is

$$\mathbf{EWN}\phi = c \phi. \quad (9)$$

It follows  $\phi$ , the starting distribution is the normalized left eigenvector of the dominant eigenvalue of  $\mathbf{EWN}$  and  $R_0$ , the expected offspring size of an individual in one generation or net reproductive rate, is obtained by adding the rows of  $\mathbf{EWN}\phi$ , that is

$$\mathbf{1}'\mathbf{EWN}\phi = \mathbf{1}'c \phi = c \quad (10)$$

that is, the dominant eigenvalue of  $\mathbf{EWN}$ . Since individuals start their life cycle according to  $\phi$ , the offspring will be born across states according to the birth distribution:

$$\theta = \mathbf{WN}\phi. \quad (11)$$

#### 3.2. The distribution of deaths across states

Similarly to the birth distribution, it may be useful to derive an expression for how deaths are distributed along states in the long run. We call this distribution  $\omega$ . As with the birth distribution,  $\omega$  should depend on a mixture of survivorship and frequency of environments. If an individual dies while in state  $i$ , it is absorbed by state  $D_i$ . The calculation of probabilities of absorption requires the construction of a matrix  $\mathbf{R}$  as

$$\mathbf{R} = \text{diag}(\mathbf{S}^{(1)}, \mathbf{S}^{(2)}, \mathbf{S}^{(3)}, \dots, \mathbf{S}^{(K)})$$

$$= \begin{pmatrix} \mathbf{S}^{(1)} & \mathbf{0} & \mathbf{0} & \dots & \mathbf{0} \\ \mathbf{0} & \mathbf{S}^{(2)} & \mathbf{0} & \dots & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{S}^{(3)} & \dots & \mathbf{0} \\ \cdot & \cdot & \cdot & \dots & \cdot \\ \cdot & \cdot & \cdot & \dots & \cdot \\ \cdot & \cdot & \cdot & \dots & \cdot \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \dots & \mathbf{S}^{(K)} \end{pmatrix} \quad (12)$$



where

$$\mathbf{S}^{(i)} = \text{diag}(1 - \mathbf{1}'\mathbf{U}^{(i)})$$

that is,  $\mathbf{S}^{(i)}$  is a diagonal matrix with its diagonal elements equal to one minus the sum of the columns of  $\mathbf{U}^{(i)}$ , which is the probability of dying at the next unit of time while in state  $i$ . The probability of dying on every state given that an individual starts in every state is  $\mathbf{RN}$ , and since the probability of starting the life cycle on each one of the possible is  $SK$  combinations stage  $\times$  environment is  $\phi$ , we arrive to the following expression for the distribution of deaths across environments:

$$\omega = \mathbf{RN}\phi.$$

### 3.3. Distributions of births and deaths across environments

We finally arrive to the long-run distribution of births and deaths across environments. Vector  $\phi$  contains the probability of starting the life cycle in every state. Adding the first  $S$  values of  $\phi$  yields the probability of being born in the first environment, and in general, adding the  $j$ -th set of  $S$  consecutive values yields the probability of being born in environment  $j$ . Let  $\mathbf{u}$  be a column vector of ones of size  $S$ . Define the matrix  $\mathbf{H}$  of size  $S \times K$  as:

$$\mathbf{H} = \text{diag}(\mathbf{u}', \mathbf{u}', \mathbf{u}' \dots \mathbf{u}') = \begin{pmatrix} \mathbf{u}' & \mathbf{0} & \mathbf{0} & \dots & \mathbf{0} \\ \mathbf{0} & \mathbf{u}' & \mathbf{0} & \dots & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{u}' & \dots & \mathbf{0} \\ \cdot & \cdot & \cdot & \dots & \cdot \\ \cdot & \cdot & \cdot & \dots & \cdot \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \dots & \mathbf{u}' \end{pmatrix} \quad (13)$$

then

$$\phi^* = \mathbf{H}\phi$$

is a column vector of size  $S$  that contains the probability of being born on each environment. Similarly,

$$\omega^* = \mathbf{H}\omega$$

contains the probability of dying on each environment.

We now derive expressions for some life-history parameters. Since vector  $\phi$  contains the probability of starting the life cycle in each of the  $S \times K$  states, all calculations that involve conditioning on the initial state must be weighted by  $\phi$ .

### 3.4. Average longevity

The unconditional average lifetime of an individual is then

$$E(T) = E(\eta')\phi \quad (14)$$

with variance

$$V(T) = V(\eta')\phi \quad (15)$$

with  $E(\eta')$  and  $V(\eta')$  in (5) and (6) respectively.

### 3.5. Generation time, $\mu_1$

This type of generation time measures the average age of parents at offspring production. This is calculated as

$$\mu_1 = R_0^{-1}\mathbf{1}'\mathbf{WNUN}\phi + c \quad (16)$$

where  $c$  is the time at which births occur in every time interval  $(t, t + 1)$ . If births are credited to occur at the beginning of the interval,  $c = 0$ , whereas if at the end,  $c = 1$  (Hernandez-Suarez, 2011).

**Table 1**

Observed frequencies for the four types of years for the Saiga antelope example.

Year type (Environment)	Label	Observed frequency
Summer normal, Winter normal	SnWn	0.63
Summer normal, Winter drought	SnWd	0.07
Summer drought, Winter normal	SdWn	0.27
Summer drought, Winter drought	SdWd	0.03

### Generation time, $\bar{A}$

This parameter measures the average age of parents of the offspring produced in the current time period, once the population has reached stable stage distribution (Cochran and Ellner, 1992). Let  $\mathbf{V} = \lambda^{-1}\mathbf{U}$  and  $\mathbf{M} = (\mathbf{I} - \mathbf{V})^{-1}$ , where  $\lambda$  is the dominant eigenvalue of  $\mathbf{A}$ , then

$$\bar{A} = \mathbf{1}'\mathbf{WMVM}\phi + c \quad (17)$$

where  $c$  has similar interpretation than in (16).

## 4. Simulations

In this section we compare the expressions obtained for the calculation of life-history parameters (Eqs. (14)–(17)) against the values obtained from stochastic simulations of these models. The data set is a population model for the management of the Saiga antelope *Saiga tatarica* (Milner-Gulland, 1994, ). There are three age categories of females: 1-year old, 2-year old and 3–10 years old. Females only reproduce in summer. There are only two seasons, summer and winter, and each one of them could be normal or drought, giving a total of four possible types of years, with their frequencies shown in Table 1. There was no information on the transition between the four environments, so we use here an *iid* distribution whose stationary distribution is the same as the observed. This is

$$P = \begin{pmatrix} \text{SnWn} & \text{SnWd} & \text{SdWn} & \text{SdWd} \\ 0.63 & 0.07 & 0.27 & 0.03 \\ 0.63 & 0.07 & 0.27 & 0.03 \\ 0.63 & 0.07 & 0.27 & 0.03 \\ 0.63 & 0.07 & 0.27 & 0.03 \end{pmatrix}$$

with  $S =$  Summer,  $W =$  Winter,  $n =$  normal, and  $d =$  drought. Thus, SnWd means a normal Summer with a drought Winter.

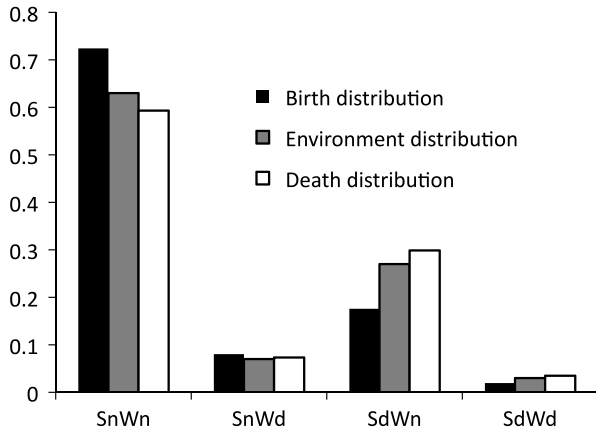
Fertility and mortality depend on the year type. The transition and fertility matrices calculated from the data are as follows:

$$\begin{aligned} \mathbf{U}^{(1)} &= \begin{pmatrix} 0 & 0 & 0 \\ 0.671 & 0 & 0 \\ 0 & 0.81 & 0.875 \end{pmatrix} & \mathbf{F}^{(1)} &= \begin{pmatrix} 0.525 & 0.875 & 0.875 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix} \\ \mathbf{U}^{(2)} &= \begin{pmatrix} 0 & 0 & 0 \\ 0.624 & 0 & 0 \\ 0 & 0.72 & 0.875 \end{pmatrix} & \mathbf{F}^{(2)} &= \begin{pmatrix} 0.525 & 0.875 & 0.875 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix} \\ \mathbf{U}^{(3)} &= \begin{pmatrix} 0 & 0 & 0 \\ 0.206 & 0 & 0 \\ 0 & 0.765 & 0.875 \end{pmatrix} & \mathbf{F}^{(3)} &= \begin{pmatrix} 0.5 & 0.5 & 0.5 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix} \\ \mathbf{U}^{(4)} &= \begin{pmatrix} 0 & 0 & 0 \\ 0.192 & 0 & 0 \\ 0 & 0.68 & 0.875 \end{pmatrix} & \mathbf{F}^{(4)} &= \begin{pmatrix} 0.5 & 0.5 & 0.5 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}. \end{aligned}$$

**Table 2**

Comparison of theoretical vs. simulated values of birth distribution  $\theta^*$ , death distribution  $\omega^*$ , and the environment distribution  $\pi$ . Results from  $25 \times 10^4$  individual trajectories, for the Saiga antelope example.

Distribution	Label	Type	Results			
Birth distribution	$\theta^*$	Theoretical	0.7241	0.0804	0.1759	0.0195
		Simulated	0.7235	0.0807	0.1764	0.0194
Death distribution	$\omega^*$	Theoretical	0.5931	0.0733	0.2987	0.0349
		Simulated	0.5939	0.0726	0.2989	0.0346
Starting distribution	$\phi^*$	Theoretical	0.6300	0.0700	0.2700	0.0300
		Simulated	0.6301	0.0692	0.2689	0.0318
Environment distribution	$\pi$	Theoretical	0.6300	0.0700	0.2700	0.0300
		Simulated	0.6320	0.0688	0.2706	0.0286



**Fig. 1.** Comparison of theoretical values of birth distribution ( $\theta^*$ ), environment frequency ( $\pi$ ) and death distribution ( $\omega^*$ ), for the Saiga antelope example.

In Appendix A.1 we provide the procedure on how the transition and fertility matrices were constructed from the data, and a step by step calculation of mathematical expressions for this data set.

The details of the simulation are as follows: since life history parameters pertain to individual properties, we first let the population evolve through a long series of stochastic environments and select a newborn at random. Call this individual  $I_0$  and call the current environment  $k$  (the environment following that in which  $I_0$  was born). We then decide according to  $\mathbf{U}^{(k)}$  and  $\mathbf{F}^{(k)}$  if  $I_0$  reproduces, dies or moves to the next stage as follows: reproduction takes place according to  $\mathbf{F}^{(k)}$ . With probability  $G_k$ ,  $I_0$  stays in its current stage one more unit of time; with probability  $P_k$ ,  $I_0$  moves to the next stage, and with probability  $1 - G_k - P_k$   $I_0$  dies in environment  $k$ . If  $I_0$  did not die at this environment, then we chose the next environment at random according to the  $k$ -th row of matrix  $\mathbf{P}$  and repeat the process until  $I_0$  dies. Throughout  $I_0$ 's lifetime, all the events pertaining this individual are recorded: the number of times it goes through every possible environment, the times at which it gives births (if any), and its time of death. We also record how its newborns are distributed across the environments.

Next, we select one of the descendants of  $I_0$  at random and follow it in the same way and repeat this process following up a total of  $25 \times 10^4$  individuals. The individual selected for follow up is one of the cumulated descendants of  $I_0$  through time, which ensures that we are sampling from the distribution of births across the environments. At the end, we obtain a detailed collection of lifetime events of a large number of individuals, which we use to calculate average lifetime, distribution of births across environments, distribution of deaths across the environments, net reproductive rate and two measures of generation time, averaging over all  $25 \times 10^4$  individuals.

Table 2 shows the comparison between the theoretical and simulated offspring distribution across environments for each popu-

**Table 3**

Comparison of theoretical vs. simulated values for Expectation  $E(T)$  and Variance  $V(T)$  of longevity, as well as the net reproductive rate ( $R_0$ ) and two measures of generation time ( $\mu$  and  $\bar{A}$ ). Results from averaging  $25 \times 10^4$  individual trajectories, for the Saiga antelope example.

	$E(T)$	$V(T)$	$R_0$	$\mu_1$	$\bar{A}$
Theoretical	4.853	39.821	3.455	7.720	3.315
Simulated	4.852	42.450	3.455	7.746	3.326

lation. The table also shows the comparison between theoretical and simulated distribution of deaths across environments, and the theoretical and simulated environment distribution. Fig. 1 shows a comparison of the three theoretical distributions: birth, death and environmental. Table 3 shows the comparison of the theoretical and simulated values for some life-history parameters as mean and variance of lifetime,  $R_0$ ,  $\mu$  and  $\bar{A}$ .

### 5. Discussion

The main result of this research is the derivation of the distribution of births across environments when the population is subjected to stochastic environmental fluctuation, which allowed the derivation of unconditional life history parameters. We showed that the birth distribution does not depend only on  $\mathbf{P}$ , the transition matrix for the environments, but also on the transition and fertility matrices for each environment.

To obtain  $R_0$ , the average offspring size produced by an average individual during a generation time period, we first constructed the generation matrix  $\mathbf{EWN}$  under environmental stochasticity, and showed that the dominant eigenvalue of  $\mathbf{EWN}$  is this average, and represents the average growth rate from one generation to the next. The derivation was based on considering individual trajectories and thus the dynamics of the population was not implied.

$R_0$ , the dominant eigenvalue of  $\mathbf{EWN}$  is indeed the average offspring size produced by an individual since individuals starting in stage  $j$  will produce on average  $\mathbf{1}^T \mathbf{EWN} \mathbf{e}_j$  individuals and a proportion  $\phi_j$  of individuals starts their life cycles in state  $j$ , thus the overall average offspring size is  $\sum_{j=1}^{SK} \mathbf{1}^T \mathbf{EWN} \mathbf{e}_j \phi_j = \mathbf{1}^T \mathbf{WN} \boldsymbol{\phi}$  which we have shown is the dominant eigenvalue of  $\mathbf{EWN}$ .

Since  $\mathbf{EWN}$  is the generation matrix, given an initial cohort  $\mathbf{x}_0$ ,  $\mathbf{EWN} \mathbf{x}_0$  shows how the individuals will start their life cycle at the next generation, and thus the normalized left eigenvector of the dominant eigenvalue of  $\mathbf{EWN}$  is  $\boldsymbol{\phi}$ , the starting distribution. It is interesting to notice that although the dominant eigenvalue of the generation matrix has received much recognition as the net reproductive rate, little attention has been made to the interpretation of its associated normalized left eigenvector, which is the long-run newborn distribution across states, or, in the case of a single environment, the distribution of births across stages.

**Table 4**

The relative frequencies of the population structure across the 12 combinations of stage  $\times$  environment (states). The table shows last ten of  $1 \times 10^6$  generations. The environment is shown in brackets next to the generation, for the Saiga antelope example.

State	Generation [Environment]									
	1 [3]	2 [1]	3 [1]	4 [2]	5 [1]	6 [3]	7 [1]	8 [2]	9 [3]	10 [1]
1	0	0.478	0.481	0	0.479	0	0.478	0	0	0.477
2	0	0.220	0.218	0	0.227	0	0.221	0	0	0.223
3	0	0.301	0.300	0	0.292	0	0.300	0	0	0.298
4	0	0	0	0.495	0	0	0	0.495	0	0
5	0	0	0	0.210	0	0	0	0.208	0	0
6	0	0	0	0.294	0	0	0	0.295	0	0
7	0.485	0	0	0	0	0.485	0	0	0.489	0
8	0.095	0	0	0	0	0.096	0	0	0.100	0
9	0.419	0	0	0	0	0.417	0	0	0.410	0
10	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0

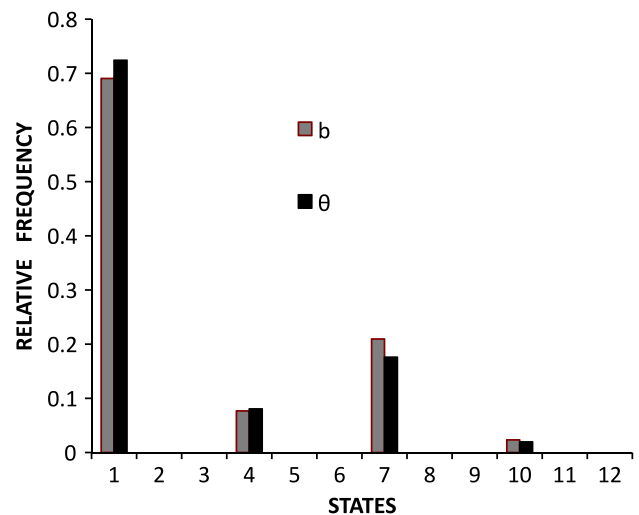
The differences between the observed (simulated) values for the birth distribution across environments and those calculated with the expressions suggested, are minimal. The similarity between theoretical and simulated values extends to the death distribution and net reproductive rate, average longevity and the two measures of generation time.

Among the *birth*, *death* and *starting* distributions, the first two are the ones with a biological meaning and are the relevant ones for planning conservation, harvesting or in general, managing purposes, since they can indicate where most births or deaths occur. The *starting distribution* is only a tool to calculate the different life history traits. Since the unconditional expressions for life-history parameters are new, the sensitivity analysis for these parameters has to be reconsidered, since we can see now that the different demographic parameters depend on a wider set of factors than those up to now considered.

Cochran and Ellner's approach (1992) of using the long run stable stage distribution to find how births are distributed at the next unit of time, although effective for a single environment, does not work for the stochastic environment setup. Recall Cochran and Ellner (1992) suggested using the long run stable stage distribution  $\mathbf{v}$  and then normalizing the product  $\mathbf{W}\mathbf{v}$ , which gives the fraction of births produced in every stage the next unit of time. Nevertheless,  $\mathbf{v}$  has the property that  $\mathbf{A}\mathbf{v} = \lambda\mathbf{v}$ , that is, if at some time  $t$  population reaches the composition  $\mathbf{v}$  at time  $t + 1$  the stage relative frequencies will not change. But in the stochastic environment set up,  $\mathbf{A}$  is a square matrix of dimension  $S \times K$  therefore  $\mathbf{v}$  has  $S \times K$  elements, and any  $\mathbf{v}$  that fulfills  $\mathbf{A}\mathbf{v} = \lambda\mathbf{v}$  will have all entries positive, nevertheless, such population structure can never be reached in real life if environments fluctuate, since for any  $t$ , the population structure  $\mathbf{X}_t$  contains at most  $S$  positive entries corresponding to the number of individuals in each one of the  $S$  possible stages of the current environment, while other  $S(K - 1)$  entries will be zero. At the next unit of time, the set of positive entries may change place, corresponding to the new environment.

For instance, we let the example population of the *Saiga antelope* for  $1 \times 10^6$  units of time and built Table 4, where the relative frequencies of the last ten generations are shown. In this table it is evident how the relative frequencies of the  $S$  stages change places, according to the environment. Fig. 2 shows a comparison of both birth distributions, Cochran and Ellner's  $\mathbf{b}$  as in (1) and the distribution of births across states derived in this paper,  $\theta$ , for the *Saiga antelope* data.

The offspring distribution becomes an important factor on the dynamics of the population, which is the matter of future research. For instance, if one environment has zero growth rate, and the transition matrix for this environment  $\mathbf{U}^{(k)}$  is  $G_i = 0$  for every stage, then the transition between environments must be periodic,



**Fig. 2.** Comparison of the birth distributions  $\mathbf{b}$  and  $\theta$  where  $\mathbf{b} = \mathbf{W}\mathbf{v}/(\mathbf{1}'\mathbf{W}\mathbf{v})$  with  $\mathbf{v}$  as the left eigenvector of the dominant eigenvalue of  $\mathbf{A}$ , while  $\theta$  is the normalized eigenvector of the dominant eigenvalue of  $\mathbf{EWN}$ , for the *Saiga antelope* example.

otherwise, extinction is certain (see proof in Appendix A.2). This is due to the fact that eventually a long sequence of environments with zero growth rate will occur with probability one if transitions between environments are Markovian or *iid*, but this possibility is ruled out if transition between environments is periodic.

Sometimes we may suspect that by including environmental stochasticity we could improve our population models. If environments are not that influent on the dynamic of the population, which is the case when the matrices  $\mathbf{A}^{(i)}$  are very similar, then the birth distribution  $\theta^*$  and the environment distribution  $\pi$  will look very similar. The similarity between these two distributions is a clue that there was no need to include environmental variability as a driving factor on the dynamics of the population.

In the particular case of periodic environments, the net reproductive rate  $R_0$  (the dominant eigenvalue of  $\mathbf{EWN}$ ) is equal to the definition used by Bacaër (2009, 2012), where  $R_0$  is the dominant eigenvalue of a matrix product of the form  $\mathbf{W}\mathbf{B}^{-1}$  (see Bacaër, 2009, eqn. 8). Indeed,  $R_0$  is the spectral radius of  $\mathbf{EWN}$ , which is equal to that of  $\mathbf{WNE}$ . It is then easily checked that  $\mathbf{EB} = \mathbf{N}^{-1}$ , so that  $\mathbf{NE} = \mathbf{B}^{-1}$ .

In the case of *iid* environments, the *starting distribution*  $\phi$  is the same as the long-run environment distribution, which is any of the rows of  $\mathbf{P}$ . This is because regardless of the environment in which an individual is born, the probability that it will start its life cycle in a given environment  $j$  is constant.

**Acknowledgments**

We want to thank Nicolas Bacaër for helpful discussions leading to improve the manuscript.

**Appendix**

*A.1. Example calculation for Saiga antelope data*

*A.1.1. Calculation of the long run frequency of environments*

The long run frequency of environments for iid matrices is any of its rows, that is  $\pi = \{0.63, 0.07, 0.27, 0.03\}$  for the environments {SnWn, SnWd, SdWn, SdWd} respectively. According to field observations, the proportion of bad summers is 0.3 and that of bad winters is 0.1

Due to the way the megamatrices were constructed, columns (or rows) of these megamatrices always have the following order: {SnWn[1], SnWn[2], SnWn[3], SnWd[1], SnWd[2], SnWd[3], SdWn[1], SdWn[2], SdWn[3], SdWd[1], SdWd[2], SdWd[3]}

where the number in brackets indicates the stage the individual is in. We label these 12 combinations of environment  $\times$  stage as the states 1 to 12.

*A.1.2. Calculation of birth and death distributions*

The megamatrix  $\mathbf{U}$  as in (2) is given in Box I.

The fundamental matrix  $\mathbf{N} = (\mathbf{I} - \mathbf{U})^{-1}$  as in (3) is given in Box II. Matrix  $\mathbf{V} = (2\mathbf{N}_{\text{diag}} - \mathbf{I})\mathbf{N} - \mathbf{N} \circ \mathbf{N}$  as in (4) is given in Box III.

The average lifetime of an individual that starts in every possible state is  $E(\eta)$  and its variance  $V(\eta)$  (Eqs. (5)–(6)) are as follows:

$$E(\eta) = [5.9 \ 7.48 \ 8 \ 5.56 \ 6.76 \ 8 \ 2.51 \ 7.12 \ 8 \ 2.4 \ 6.44 \ 8]$$

$$V(\eta) = [48.5 \ 55.2 \ 56 \ 46.7 \ 53.2 \ 56 \ 20 \ 54.3 \ 56 \ 18.8 \ 52 \ 56]$$

Matrix  $\mathbf{W}$  as in (7) is given in Box IV.

The matrix product  $\mathbf{E}$  is  $\mathbf{P}' \otimes \mathbf{I}_s$  is given in Box V.

Thus the matrix product  $\mathbf{EWN}$  is given in Box VI:

We now have all the elements to calculate  $\phi$ , the birth distribution as a normalization of the left eigenvector of the dominant eigenvalue of  $\mathbf{EWN}$ . The dominant eigenvalue of  $\mathbf{EWN}$  is 3.455, and its left eigenvector is

$$\phi = [21 \ 0 \ 0 \ 2.33 \ 0 \ 0 \ 9 \ 0 \ 0 \ 1 \ 0 \ 0]^T.$$

Normalizing this yields

$$\phi = [0.63 \ 0 \ 0 \ 0.07 \ 0 \ 0 \ 0.27 \ 0 \ 0 \ 0.003 \ 0 \ 0]^T.$$

Now  $\theta$ , the birth distribution is the normalization of  $\mathbf{WN}\phi$ , that is

$$\theta = [0.71 \ 0 \ 0 \ 0.079 \ 0 \ 0 \ 0.189 \ 0 \ 0 \ 0.021 \ 0 \ 0]^T.$$

To derive the distribution of deaths across environments,  $\omega$ , we start calculating  $s_i$ :

$$\mathbf{S}^{(1)} = 1 - \mathbf{1}'\mathbf{U}^{(1)} = [0.329 \ 0.190 \ 0.125]$$

$$\mathbf{S}^{(2)} = 1 - \mathbf{1}'\mathbf{U}^{(2)} = [0.376 \ 0.280 \ 0.125]$$

$$\mathbf{S}^{(3)} = 1 - \mathbf{1}'\mathbf{U}^{(3)} = [0.794 \ 0.235 \ 0.125]$$

$$\mathbf{S}^{(4)} = 1 - \mathbf{1}'\mathbf{U}^{(4)} = [0.808 \ 0.320 \ 0.125].$$

Matrix  $\mathbf{R}$  is as in Box VII.

Finally, we arrive to the distribution of deaths across states is given in Box VIII:

Now we calculate the starting distribution across environments. Let:

$$\mathbf{H} = \begin{pmatrix} 1 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 1 \end{pmatrix}$$

thus the starting distribution across environments is:

$$\phi^* = \mathbf{H}\phi = [0.63 \ 0.07 \ 0.27 \ 0.03]^T$$

whereas the birth distribution is

$$\theta^* = \mathbf{H}\theta = [0.71 \ 0.0789 \ 0.189 \ 0.021]^T$$

and the distribution of deaths across environments is:

$$\omega^* = \mathbf{H}\omega = [0.532 \ 0.065 \ 0.360 \ 0.041]^T$$

*A.1.3. Calculation of life history parameters*

*A.1.3.1. Longevity.* The unconditional average lifetime of an individual is

$$E(T) = E(\eta')\phi = 4.853$$

with variance:

$$V(T) = V(\eta')\phi = 39.821.$$

*A.1.3.2. Net reproductive rate.*

$$R_0 = \mathbf{1}'\mathbf{WN}\phi = 3.455$$

observe  $\mathbf{WN}\phi$  is column vector that contains the average number of newborns on each environment for an average individual. The sum of the terms is  $R_0$ .

*A.1.3.3. Generation time,  $\mu_1$ .* Here we use (16) with  $c = 1$ , that is, we assume births occur at the end of each unit of time.

$$\begin{aligned} \mu_1 &= (\mathbf{1}'\mathbf{WN}\phi)^{-1}\mathbf{1}'\mathbf{WNUN}\phi + 1 \\ &= R_0^{-1}\mathbf{1}'\mathbf{WNUN}\phi + 1 \\ &= 7.720. \end{aligned}$$

*A.1.3.4. Generation time,  $\bar{A}$ .* Let  $\mathbf{V} = \lambda^{-1}\mathbf{U}$  and  $\mathbf{M} = (\mathbf{I} - \mathbf{V})^{-1}$  and  $c = 1$

$$\begin{aligned} \bar{A} &= \mathbf{1}'\mathbf{WMVM}\phi + 1 \\ &= 3.315. \end{aligned}$$

*A.2. Example calculation for Saiga antelope data*

Here we show that if one environment has zero growth rate, and the transition matrix for this environment  $\mathbf{U}^{(k)}$  is has  $G_i = 0$  for every stage, then the transition between environments must be periodic, otherwise, extinction is certain.

Let  $\mathbf{X}_t$  be the  $S \times 1$  vector of population sizes on each category at time  $t$ . Assume there are  $K$  environments and that transition among them is Markovian. Let  $\mathbf{A}$  be an environment with zero growth rate and with  $G_i = 0$  for every stage. This implies that

$$\mathbf{A}^n \mathbf{X}_t = \mathbf{0}$$

for any  $n \geq S$ . This is because  $G_i = 0$  and zero growth rate implies all individuals of each class leave that class at the next time step and there are no newborns. Thus, it takes at most  $S$  time steps for all individuals of all classes to disappear. That is, if a sequence of  $S$  environments or more of type  $\mathbf{A}$  occurs in a row, the population will vanish. But since it is a well known fact that if the transition matrix is stochastic, a sequence of size  $n$  of any given environment will occur with probability one, the population will vanish eventually.



$$\mathbf{U} = \begin{pmatrix}
 1 & 2 & 3 & 4 & 5 & 6 & 7 & 8 & 9 & 10 & 11 & 12 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0.42 & 0 & 0 & 0.39 & 0 & 0 & 0.13 & 0 & 0 & 0.12 & 0 & 0 \\
 0 & 0.51 & 0.55 & 0 & 0.45 & 0.55 & 0 & 0.48 & 0.55 & 0 & 0.43 & 0.55 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0.048 & 0 & 0 & 0.04 & 0 & 0 & 0.01 & 0 & 0 & 0.01 & 0 & 0 \\
 0 & 0.06 & 0.06 & 0 & 0.05 & 0.06 & 0 & 0.05 & 0.06 & 0 & 0.05 & 0.06 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0.18 & 0 & 0 & 0.17 & 0 & 0 & 0.06 & 0 & 0 & 0.052 & 0 & 0 \\
 0 & 0.22 & 0.24 & 0 & 0.19 & 0.24 & 0 & 0.21 & 0.24 & 0 & 0.18 & 0.24 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0.02 & 0 & 0 & 0.02 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0.02 & 0.03 & 0 & 0.02 & 0.03 & 0 & 0.02 & 0.03 & 0 & 0.02 & 0.03
 \end{pmatrix}$$

Box I.

$$\mathbf{N} = \begin{pmatrix}
 1.0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0.42 & 1.0 & 0 & 0.39 & 0 & 0 & 0.13 & 0 & 0 & 0.12 & 0 & 0 \\
 2.7 & 4.1 & 5.4 & 2.5 & 3.6 & 4.4 & 0.82 & 3.9 & 4.4 & 0.76 & 3.4 & 4.4 \\
 0 & 0 & 0 & 1.0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0.05 & 0 & 0 & 0.04 & 1 & 0 & 0.01 & 0 & 0 & 0.01 & 0 & 0 \\
 0.3 & 0.45 & 0.49 & 0.28 & 0.40 & 1.5 & 0.09 & 0.43 & 0.49 & 0.08 & 0.38 & 0.49 \\
 0 & 0 & 0 & 0 & 0 & 0 & 1.0 & 0 & 0 & 0 & 0 & 0 \\
 0.18 & 0 & 0 & 0.17 & 0 & 0 & 0.06 & 1.0 & 0 & 0.05 & 0 & 0 \\
 1.1 & 1.7 & 1.9 & 1.1 & 1.6 & 1.9 & 0.35 & 1.7 & 2.9 & 0.33 & 1.5 & 1.9 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1.0 & 0 & 0 \\
 0.02 & 0 & 0 & 0.02 & 0 & 0 & 0 & 0 & 0 & 0 & 1.0 & 0 \\
 0.13 & 0.19 & 0.21 & 0.12 & 0.17 & 0.21 & 0.04 & 0.18 & 0.21 & 0.04 & 0.16 & 1.2
 \end{pmatrix}$$

Box II.

$$\mathbf{V} = \begin{pmatrix}
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0.67 & 0 & 0 & 0.63 & 0 & 0 & 0.24 & 0 & 0 & 0.23 & 0 & 0 \\
 22.0 & 28.0 & 24.0 & 21.0 & 26.0 & 28.0 & 8.2 & 27.0 & 27.0 & 7.7 & 25.0 & 28.0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0.09 & 0 & 0 & 0.08 & 0 & 0 & 0.03 & 0 & 0 & 0.03 & 0 & 0 \\
 0.79 & 1.1 & 1.2 & 0.74 & 1.0 & 0.73 & 0.26 & 1.1 & 1.2 & 0.25 & 0.99 & 1.2 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0.33 & 0 & 0 & 0.31 & 0 & 0 & 0.11 & 0 & 0 & 0.10 & 0 & 0 \\
 5.3 & 7.1 & 7.4 & 5.0 & 6.6 & 7.4 & 1.9 & 6.8 & 5.5 & 1.8 & 6.3 & 7.4 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0.04 & 0 & 0 & 0.04 & 0 & 0 & 0.01 & 0 & 0 & 0.01 & 0 & 0 \\
 0.29 & 0.43 & 0.46 & 0.27 & 0.39 & 0.46 & 0.09 & 0.41 & 0.46 & 0.08 & 0.37 & 0.25
 \end{pmatrix}$$

Box III.

$$\mathbf{W} = \begin{pmatrix}
 0.525 & 0.875 & 0.875 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0.525 & 0.875 & 0.875 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0.5 & 0.5 & 0.5 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.5 & 0.5 & 0.5 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0
 \end{pmatrix}$$

Box IV.

$$E = \begin{pmatrix} 0.63 & 0 & 0 & 0.63 & 0 & 0 & 0.63 & 0 & 0 & 0.63 & 0 & 0 \\ 0 & 0.63 & 0 & 0 & 0.63 & 0 & 0 & 0.63 & 0 & 0 & 0.63 & 0 \\ 0 & 0 & 0.63 & 0 & 0 & 0.63 & 0 & 0 & 0.63 & 0 & 0 & 0.63 \\ 0.07 & 0 & 0 & 0.07 & 0 & 0 & 0.07 & 0 & 0 & 0.07 & 0 & 0 \\ 0 & 0.07 & 0 & 0 & 0.07 & 0 & 0 & 0.07 & 0 & 0 & 0.07 & 0 \\ 0 & 0 & 0.07 & 0 & 0 & 0.07 & 0 & 0 & 0.07 & 0 & 0 & 0.07 \\ 0.27 & 0 & 0 & 0.27 & 0 & 0 & 0.27 & 0 & 0 & 0.27 & 0 & 0 \\ 0 & 0.27 & 0 & 0 & 0.27 & 0 & 0 & 0.27 & 0 & 0 & 0.27 & 0 \\ 0 & 0 & 0.27 & 0 & 0 & 0.27 & 0 & 0 & 0.27 & 0 & 0 & 0.27 \\ 0.03 & 0 & 0 & 0.03 & 0 & 0 & 0.03 & 0 & 0 & 0.03 & 0 & 0 \\ 0 & 0.03 & 0 & 0 & 0.03 & 0 & 0 & 0.03 & 0 & 0 & 0.03 & 0 \\ 0 & 0 & 0.03 & 0 & 0 & 0.03 & 0 & 0 & 0.03 & 0 & 0 & 0.03 \end{pmatrix}$$

Box V.

$$EWN = \begin{pmatrix} 2.7 & 3.7 & 3.9 & 2.5 & 3.3 & 3.9 & 1.0 & 3.3 & 3.7 & 0.99 & 2.9 & 3.7 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0.30 & 0.41 & 0.43 & 0.28 & 0.37 & 0.43 & 0.12 & 0.36 & 0.41 & 0.11 & 0.33 & 0.41 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1.2 & 1.6 & 1.7 & 1.1 & 1.4 & 1.7 & 0.44 & 1.4 & 1.6 & 0.42 & 1.3 & 1.6 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0.13 & 0.17 & 0.19 & 0.12 & 0.16 & 0.19 & 0.049 & 0.15 & 0.18 & 0.047 & 0.14 & 0.18 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}$$

Box VI.

$$R = \begin{pmatrix} 0.33 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.19 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.12 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.38 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.28 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.12 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.79 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.23 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.12 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.81 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.32 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.12 \end{pmatrix}$$

Box VII.

$$\omega = RN\phi = [0.207 \ 0.063 \ 0.262 \ 0.026 \ 0.0103 \ 0.029 \ 0.214 \ 0.033 \ 0.112 \ 0.024 \ 0.005 \ 0.012]^T.$$

Box VIII.

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