Average sex ratio and population maintenance cost

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Abstract

In this work, we propose a dynamic-programming-based explanation for the reported stability of the female and male ratios in biological populations. Using tools of variational theory applied to the study of ground states in one-dimensional crystal, we introduce the notion of historically adapted populations as global minimizers of maintenance cost functions, and prove that historically adapted populations typically present an observable stability in the sex ratio. This mathematical formulation suggests that stable observable sex ratio is an intrinsic feature of populations that are efficient in the use of the resources.

Keywords: population dynamics, finite-resource environment, sex ratio, dynamic programming, ground state.

Mathematical subject classification: 37N25, 49L20, 49L25, 91B80.

1 Introduction

It seems to be Charles Darwin who first pointed out the real challenge behind the development of a sex-ratio theory (see the conclusion of Chapter 8 in [4]). Sex-ratio studies today form a fascinating topic in evolutionary biology, which underline the impact of natural selection on the allocation of resources to male and female progeny. Using a frequency-dependent argument, Fisher provided [6] a theoretical explanation for the prevalence of near 1:1 sex ratio under natural selection. The effort to understand the stability of biased sex ratios has enabled the central theory to find successive and fruitful extensions. For instance, Hamilton's local mate competition hypothesis [8] was originally introduced to clarify how the interactions between siblings produce very female-biased sex ratios in parasitic wasps.

In sex-ratio theory the point of view that consists in describing collective phenomena from the actions and expectations of individuals has been very useful. Charnov's book on sex allocation [3] is an extremely successful illustration of this tendency. By considering nonlinear and unequal returns from parental investment in sons and daughters, Charnov has developed a mathematical formulation, able not only to conceptually explain cases of both Fisherian and non-Fisherian sex ratios but also to provide predictions to be tested in experiments. Another example of a fundamental contribution from the philosophical approach based on methodological individualism is the so-called Trivers–Willard hypothesis [11], which suggests that natural selection should favor parental ability to adjust the sex ratio of their offspring in response to environmental conditions.

The focus on individual behavior leads to the important discussion about selection criteria for reproductive strategies. Nowadays questions arising from parent-offspring conflict, parental investment, sibling antagonism, and mate choice may be mathematically addressed by evolutionary game dynamics (see, for instance, [9]).

We will adopt here a different and, to the best of our knowledge, novel point of view, which consists mostly in a global perspective by proposing a population-based optimization model. Focusing on the entire population as a dynamical agent without directly paying attention to specific biological parameters, the consideration of an implicit maintenance cost function will give qualitative insights for a common biological feature: an observable sex ratio. As a matter of fact, our main result will argue in favor of the hypothesis that the very possibility of a sex ratio being recognized in nature may reflect a balance between the size of the population and the finiteness of resources.

The tools used in this work can be applied to study many other situations where some population (not necessarily biological) is partitioned in a finite number of classes and a cost function on the size of the classes is assigned (for example, to study social and economical behaviors, mean field games, etc.). We remark that the mathematical techniques developed here have foundations in common with dynamic programming and the variational theory applied to the study of ground states of generalized Frenkel–Kontorova models on a one-dimensional crystal (see, for example, [1, 2]). Actually, statistical physics methods have already been successfully exploited in evolutionary games on graphs, especially when social networks are seen as the result of individual interactions governed by some kind of interdependency, such as sexual relationships (see, for example, [10]).

In order to be more concrete, suppose we periodically census the size of each gender in some biological population. Let $\binom{x_i}{y_i} \in \mathbb{N}^2$ be the $(i+1)^{th}$ census, where x_i and y_i indicate the number of females and males, respectively. An infinite list $\omega = (\binom{x_0}{y_0}, \binom{x_1}{y_1}, \binom{x_2}{y_2}, \ldots)$ can be viewed as a possible (yet maybe unlikely) historical record of each gender of a particular population. Obviously, not all ω has a biological meaning: This could be the case, for instance, of $\omega = (\binom{1}{0}, \binom{0}{0}, \binom{0}{0}, \binom{0}{99}, \binom{99}{0}, \ldots)$. Hence one evidently needs some criteria to select among all registers those that may indeed represent a possible history of some population. This can be obtained by considering a function that associates some maintenance cost with any finite register of a population history. Such a cost function shall necessarily capture chief features[1] of the biological population to be modeled.

A cost function leads us to the notion of historically adapted populations, which intuitively correspond to those populations more efficient in the use of available resources. The concept of "historically adapted population" shall not be understood as "survival of the fittest." In fact, we are not focusing on competition either between species or among individuals, but only looking for the

[1]In particular, it must assign a high cost to finite population histories that should be unlikely.

optimal rates for each gender in populations under certain environmental conditions. In particular, we neither claim that actual populations are historically adapted nor assume the existence of natural selection criteria acting on populations. Even so, the mathematical proof of profuseness of historically adapted populations with an identifiable sex ratio might insinuate why sex-ratio random variations in a given population seem to be a very rare phenomenon in nature.

The paper is organized as follows. In section 2, we present the mathematical model we shall study. In section 3, we introduce the notion of historically adapted populations and show some of their properties. In section 4, we present arguments for the existence of an asymptotic average sex ratio for historically adapted populations. Concluding remarks are discussed in section 5. In Appendix A, one can find the mathematical proofs of the results used in the paper.

2 The model

In this section, we shall present a mathematical formulation to model two-sex populations in a finite-resource environment. As far as we know, such a theoretical strategy to deal with sex-ratio questions is totally original.

Denote the set of all nonnegative integers by $\mathbb{N}$. Define then

$$\Omega := \left(\mathbb{N}^2\right)^{\mathbb{N}} := \left\{ \begin{pmatrix} x_i \\ y_i \end{pmatrix}_{i \in \mathbb{N}} : \ x_i, y_i \in \mathbb{N}, \ \forall\, i \in \mathbb{N} \right\}.$$

The elements of Ω will be called the (possible) histories for the population. Each history $\omega \in \Omega$ can be interpreted as a list of consecutive censuses of female and male populations. Given $\omega = \binom{x_i}{y_i}_{i \in \mathbb{N}} \in \Omega$ and $m, n \in \mathbb{N}$ with $m \le n$, we set $\omega[m] := \binom{x_m}{y_m}$ and $\omega[m,n] := \binom{x_i}{y_i}_{m \le i \le n}$, which are the restrictions of the infinite history ω to the moment m and to the finite history from the moment m until the moment n, respectively.

We will now define a class of cost functions that shall be used to select those censuses that may, in fact, be realized. First of all, we would like to emphasize that, although we will explicitly express only the dependence on population sizes, a maintenance cost function must depend on several biological and physical variables. We will just omit this multiple dependence in our analysis. Thus, let $C : \mathbb{N}^2 \times \mathbb{N}^2 \to \mathbb{R}$ be a function bounded from below, which means

$$\inf_{\left(\binom{x}{y}, \binom{\bar{x}}{\bar{y}}\right) \in \mathbb{N}^2 \times \mathbb{N}^2} C\left(\begin{pmatrix} x \\ y \end{pmatrix}, \begin{pmatrix} \bar{x} \\ \bar{y} \end{pmatrix} \right) > -\infty. \tag{1}$$

The value $C(\binom{x}{y}, \binom{\bar{x}}{\bar{y}})$ shall be interpreted as the maintenance cost to have a population with x females and y males, followed by a population with $\bar{x}$ females and $\bar{y}$ males. In particular, we are assuming that the maintenance cost takes into account only two successive population censuses. This assumption is made for simplicity and can be justified by observing that this model captures the main features of the general case, when the maintenance cost is a function of a finite number of consecutive censused-population sizes (see section 5).

In a finite-resource environment, it is reasonable to assume that, uniformly and independently of the initial population size, the cost to generate and maintain a new population tends to infinity as its size increases. In mathematical terms, the latter hypothesis can be expressed as follows:

$$\lim_{\bar{x}+\bar{y}\to+\infty} \inf_{\binom{x}{y}\in\mathbb{N}^2} C\left(\begin{pmatrix} x \\ y \end{pmatrix}, \begin{pmatrix} \bar{x} \\ \bar{y} \end{pmatrix}\right) = +\infty. \tag{2}$$

On the other hand, it is also reasonable to suppose that the population maintenance cost is, in some sense, more affected by the current population than by the former one. Roughly speaking, such an assumption means that, although the cost for a small initial population generating a very numerous new one may be high, the maintenance of a numerous population has a high cost by itself, independently of its previous size. Therefore, we shall assume that there exists a constant $\mathfrak{K}_C > 0$ such that the cost of having $\binom{\bar{x}}{\bar{y}}$ in any census does not vary more than $\mathfrak{K}_C$ as a function of the possible values for the former population, or more precisely, we assume

$$\mathfrak{K}_C := \sup_{\binom{\bar{x}}{\bar{y}}\in\mathbb{N}^2} \left[\sup_{\binom{x}{y}\in\mathbb{N}^2} C\left(\begin{pmatrix} x \\ y \end{pmatrix}, \begin{pmatrix} \bar{x} \\ \bar{y} \end{pmatrix}\right) - \inf_{\binom{x}{y}\in\mathbb{N}^2} C\left(\begin{pmatrix} x \\ y \end{pmatrix}, \begin{pmatrix} \bar{x} \\ \bar{y} \end{pmatrix}\right)\right] < +\infty. \tag{3}$$

3 Historically adapted populations

The intuitive idea is that a historically adapted population should minimize the maintenance cost along the time. Although, in most of the cases, there is no meaning in talking about a minimum cost for infinite histories, the idea of histories minimizing the cost along the time will be useful. As a matter of fact, this heuristic motivation will allow us to highlight a central functional equation that will lead us to a rigorous definition of historically adapted populations.

3.1 Heuristic motivation

In order to explore heuristically a definition of historically adapted populations, consider that the function C is nonnegative[2]. Note that the total maintenance cost of a population history $\bar{\omega} = \binom{\bar{x}_i}{\bar{y}_i}_{i\in\mathbb{N}}$ is given by $\sum_{k\geq 1} C(\binom{\bar{x}_{k-1}}{\bar{y}_{k-1}}, \binom{\bar{x}_k}{\bar{y}_k})$, which may clearly diverge. Assume for now that there exists a history with finite total maintenance cost (that is, for which the series converges). Thus, the smallest total cost for some history beginning from a given initial population $\binom{x_0}{y_0}$ is just

$$u\begin{pmatrix} x_0 \\ y_0 \end{pmatrix} := \inf_{\left(\binom{x_1}{y_1},\binom{x_2}{y_2},\ldots\right)} \left[\sum_{k\geq 1} C\left(\begin{pmatrix} x_{k-1} \\ y_{k-1} \end{pmatrix}, \begin{pmatrix} x_k \\ y_k \end{pmatrix}\right)\right]. \tag{4}$$

Since we are assuming that the total cost is finite for some history, then $u\binom{x_0}{y_0} \in \mathbb{R}$ for any $\binom{x_0}{y_0} \in \mathbb{N}^2$. Moreover, as the cost function C is supposed to be nonnegative, obviously $u \geq 0$

[2]Mathematically there is no loss of generality with such an assumption, since C is bounded from below.

everywhere. Now, note that the above equation can be rewritten as

$$
\begin{aligned}
u\binom{x_0}{y_0} &= \inf_{\binom{x_1}{y_1}} \inf_{\left(\binom{x_2}{y_2},\binom{x_3}{y_3},\dots\right)} \left[C\left(\binom{x_0}{y_0},\binom{x_1}{y_1}\right) + \sum_{k\geq 2} C\left(\binom{x_{k-1}}{y_{k-1}},\binom{x_k}{y_k}\right)\right] \\
&= \inf_{\binom{x_1}{y_1}} \left[C\left(\binom{x_0}{y_0},\binom{x_1}{y_1}\right) + \inf_{\left(\binom{x_2}{y_2},\binom{x_3}{y_3},\dots\right)} \sum_{k\geq 2} C\left(\binom{x_{k-1}}{y_{k-1}},\binom{x_k}{y_k}\right)\right] \\
&= \inf_{\binom{x_1}{y_1}} \left[C\left(\binom{x_0}{y_0},\binom{x_1}{y_1}\right) + u\binom{x_1}{y_1}\right]. \qquad (5)
\end{aligned}
$$

Hypothesis (2) implies that the infimum in the above equation is actually a minimum. Therefore, for each $\binom{x_0}{y_0} \in \mathbb{N}^2$, there exists $\binom{x_1}{y_1} \in \mathbb{N}^2$ such that

$$
u\binom{x_0}{y_0} = C\left(\binom{x_0}{y_0},\binom{x_1}{y_1}\right) + u\binom{x_1}{y_1}. \qquad (6)
$$

One now has a recursive way to construct an interesting history. Indeed, given an initial population $\binom{x_0}{y_0}$, we find $\binom{x_1}{y_1}$, which satisfies (6), and, inductively, from the population $\binom{x_{i-1}}{y_{i-1}}$ at the moment $i-1$, we obtain a population $\binom{x_i}{y_i}$ at the subsequent moment such that $u\binom{x_{i-1}}{y_{i-1}} = C(\binom{x_{i-1}}{y_{i-1}},\binom{x_i}{y_i}) + u\binom{x_i}{y_i}$. Since its total maintenance cost is equal to the smallest one we could expect for some history beginning from $\binom{x_0}{y_0}$, the history $\omega = \binom{x_i}{y_i}_{i\in\mathbb{N}}$ constructed by the above procedure will be called an adapted history. We remark that there is not necessarily uniqueness and there might exist infinitely many adapted histories starting from a given initial population.

3.2 Rigorous definition

The existence of histories with finite total maintenance cost is a very strong demand made for our heuristic definition of historically adapted populations. Besides being a tremendous restriction for the model, such an assumption implies counterintuitively that the maintenance cost of these populations vanishes as time goes by. Anyway, the observation is not totally naive that an adapted history should be one for which in some sense $C(\binom{x_{k-1}}{y_{k-1}},\binom{x_k}{y_k})$ goes to the infimum of the cost function C as k tends to $+\infty$. More important, the previous heuristic discussion leads us to propose a general definition of adapted histories, which extends the intuitive idea of global minimizing histories for situations where the notion of finite total maintenance cost has no meaning.

It is straightforward that whenever a function $u : \mathbb{N}^2 \to \mathbb{R}$ is bounded from below and verifies an equation like (5), we can use it to construct adapted histories. If the maintenance cost function C satisfies hypotheses (1), (2), and (3), then one can show that there exist a bounded function[3] $u : \mathbb{N}^2 \to \mathbb{R}$ and a real constant γ (both depending on the function C) such that

$$
u\binom{x}{y} = \inf_{\binom{\bar{x}}{\bar{y}}\in\mathbb{N}^2} \left[C\left(\binom{x}{y},\binom{\bar{x}}{\bar{y}}\right) + u\binom{\bar{x}}{\bar{y}}\right] - \gamma, \quad \text{for all } \binom{x}{y} \in \mathbb{N}^2. \qquad (7)
$$

[3]Such a function is a fixed point for a suitable Lax-Oleinik operator (see Definition 2, Theorem 3, and Remark 4 in Appendix A).

Since C satisfies (2) and u is bounded, we can again deduce that for each $\binom{x_0}{y_0}$ there exists $\binom{x_1}{y_1}$ such that $u\binom{x_0}{y_0} = C(\binom{x_0}{y_0}, \binom{x_1}{y_1}) + u\binom{x_1}{y_1} - \gamma$. Hence, given any initial population $\binom{x_0}{y_0}$, we define in a recursive way adapted histories starting from $\binom{x_0}{y_0}$ as we have made in section 3.1.

Definition 1. *Let $u : \mathbb{N}^2 \to \mathbb{R}$ be a bounded function satisfying the functional equation* (7) *for some constant γ. Then $\omega = \binom{x_i}{y_i}_{i\in\mathbb{N}}$ is said to be an adapted history for the maintenance cost C if*

$$u\begin{pmatrix} x_{i-1} \\ y_{i-1} \end{pmatrix} = C\left(\begin{pmatrix} x_{i-1} \\ y_{i-1} \end{pmatrix}, \begin{pmatrix} x_i \\ y_i \end{pmatrix}\right) + u\begin{pmatrix} x_i \\ y_i \end{pmatrix} - \gamma, \quad \text{for all } i \geq 1. \tag{8}$$

We remark that in this context the quantity $u\binom{x_0}{y_0}$ is not necessarily given by the expression (4), and then it cannot be interpreted as the smallest total cost we would expect for any history starting from $\binom{x_0}{y_0}$. Anyway, if $\omega = \binom{x_i}{y_i}_{i\in\mathbb{N}}$ is an adapted history, then it is easy to see that its average maintenance cost tends to γ as time goes by, or in mathematical terms

$$\lim_{n\to\infty} \frac{1}{n} \sum_{k=1}^{n} C\left(\begin{pmatrix} x_{k-1} \\ y_{k-1} \end{pmatrix}, \begin{pmatrix} x_k \\ y_k \end{pmatrix}\right) = \gamma. \tag{9}$$

Therefore, it follows from the functional equation (7) that γ can be interpreted as the minimum asymptotic average maintenance cost we can expect for arbitrary histories, and this minimum value γ is necessarily attained by any adapted history. Thus, even without uniqueness of adapted histories, we have uniqueness of the quantity γ (see Remark 4 in appendix A).

If $\omega = \binom{x_i}{y_i}_{i\in\mathbb{N}}$ is an adapted history, we can recover the global minimizing property, since any finite history $\omega[m,n] = \binom{x_i}{y_i}_{m\leq i\leq n}$ minimizes the maintenance cost among all finite histories with the same initial and final populations[4]. More precisely, for all $m, n \in \mathbb{N}$ with $m < n$ and for any other population history $\bar{\omega} = \binom{\bar{x}_i}{\bar{y}_i}_{i\in\mathbb{N}} \in \Omega$ verifying $\omega[m] = \bar{\omega}[m]$ and $\omega[n] = \bar{\omega}[n]$, it follows that

$$\begin{aligned}
\sum_{k=m+1}^{n} C\left(\begin{pmatrix} x_{k-1} \\ y_{k-1} \end{pmatrix}, \begin{pmatrix} x_k \\ y_k \end{pmatrix}\right) &=_{(1)} \sum_{k=m+1}^{n} \left[u\begin{pmatrix} x_{k-1} \\ y_{k-1} \end{pmatrix} - u\begin{pmatrix} x_k \\ y_k \end{pmatrix} + \gamma\right] \\
&=_{(2)} u\begin{pmatrix} x_m \\ y_m \end{pmatrix} - u\begin{pmatrix} x_n \\ y_n \end{pmatrix} + (n-m)\gamma =_{(3)} \sum_{k=m+1}^{n} \left[u\begin{pmatrix} \bar{x}_{k-1} \\ \bar{y}_{k-1} \end{pmatrix} - u\begin{pmatrix} \bar{x}_k \\ \bar{y}_k \end{pmatrix} + \gamma\right] \\
&=_{(4)} \sum_{k=m+1}^{n} \left[\inf_{\binom{\bar{x}}{\bar{y}}} \left[C\left(\begin{pmatrix} \bar{x}_{k-1} \\ \bar{y}_{k-1} \end{pmatrix}, \begin{pmatrix} \bar{x} \\ \bar{y} \end{pmatrix}\right) + u\begin{pmatrix} \bar{x} \\ \bar{y} \end{pmatrix}\right] - u\begin{pmatrix} \bar{x}_k \\ \bar{y}_k \end{pmatrix}\right] \leq_{(5)} \sum_{k=m+1}^{n} C\left(\begin{pmatrix} \bar{x}_{k-1} \\ \bar{y}_{k-1} \end{pmatrix}, \begin{pmatrix} \bar{x}_k \\ \bar{y}_k \end{pmatrix}\right),
\end{aligned}$$

where $=_{(1)}$ is due to (8); $=_{(2)}$ comes from a telescopic series; $=_{(3)}$ follows again from a telescopic series, as well as from the fact that $\omega[m] = \bar{\omega}[m]$ and $\omega[n] = \bar{\omega}[n]$; $=_{(4)}$ is due to (7); and $\leq_{(5)}$ follows from $\inf_{\binom{\bar{x}}{\bar{y}}}[C(\binom{\bar{x}_{k-1}}{\bar{y}_{k-1}}, \binom{\bar{x}}{\bar{y}}) + u\binom{\bar{x}}{\bar{y}}] \leq C(\binom{\bar{x}_{k-1}}{\bar{y}_{k-1}}, \binom{\bar{x}_k}{\bar{y}_k}) + u\binom{\bar{x}_k}{\bar{y}_k}$.

A more pertinent point about historically adapted populations is that, as we will see in the next section, they provide a theoretical argument in favor of the hypothesis of prevalence of stable sex ratios for populations under stable environmental conditions.

[4]In the language of solid state physics, such a property means that the adapted histories behave like ground states of one-dimensional crystal models (see, for instance, [1]).

4 On the existence of the asymptotic average sex ratio

Investigating the identification of a sex ratio, we will find that when the population maintenance cost takes into account the gender proportions, then a sex ratio will be observed in historically adapted populations. In fact, since those populations are global minimizers of cost functions, one may argue that a sex ratio will emerge as a consequence of the finiteness of available resources whenever gender densities have a linear influence on the maintenance cost.

The gender proportions of the $(i+1)^{th}$ censused population $\binom{x_i}{y_i}$ correspond obviously to the quantities $x_i/(x_i+y_i)$ and $y_i/(x_i+y_i)$. Nevertheless, we have seen that there exists at least one historically adapted population starting from any arbitrary population. Such a fact means that all first values for a sex ratio can then be achieved, and it shows that the analysis of initial data may be ineffective. Anyway, one can still ask whether later generations tend toward a sex-ratio equilibrium. Mathematically, it corresponds to looking for some asymptotic sex ratio, that is, given an adapted history $\omega = \binom{x_i}{y_i}_{i\in\mathbb{N}}$, to ask for the existence of the limits

$$\lim_{i\to\infty} \frac{x_i}{x_i+y_i} \qquad \text{and} \qquad \lim_{i\to\infty} \frac{y_i}{x_i+y_i}.$$

The historically-adapted-population approach does not guarantee that convergence, but it will allow one to ensure the convergence in average of sex ratio, namely, the existence of the limits

$$\lim_{n\to\infty} \frac{1}{n}\sum_{k=1}^{n} \frac{x_k}{x_k+y_k} \qquad \text{and} \qquad \lim_{n\to\infty} \frac{1}{n}\sum_{k=1}^{n} \frac{y_k}{x_k+y_k}.$$

More important, if the sex ratio converges in average, then there are infinitely many arbitrarily long periods of time for which it remains as close as one wants to the average limit. This mathematical property might therefore explain the documented stability of sex ratio in nature.

4.1 Linearly perturbed maintenance cost functions

Let $C : \mathbb{N}^2 \times \mathbb{N}^2 \to \mathbb{R}$ be a cost function verifying hypotheses (1), (2), and (3). Given a vector $A = (a_1, a_2) \in \mathbb{R}^2$, the linearly perturbed maintenance cost function with weights a_1 and a_2 on the gender densities is the function $C_A : \mathbb{N}^2 \times \mathbb{N}^2 \to \mathbb{R}$ given by

$$\begin{aligned} C_A\left(\begin{pmatrix}x\\y\end{pmatrix}, \begin{pmatrix}0\\0\end{pmatrix}\right) &= C\left(\begin{pmatrix}x\\y\end{pmatrix}, \begin{pmatrix}0\\0\end{pmatrix}\right), \quad \text{and} \\ C_A\left(\begin{pmatrix}x\\y\end{pmatrix}, \begin{pmatrix}\bar{x}\\\bar{y}\end{pmatrix}\right) &= C\left(\begin{pmatrix}x\\y\end{pmatrix}, \begin{pmatrix}\bar{x}\\\bar{y}\end{pmatrix}\right) + a_1\frac{\bar{x}}{\bar{x}+\bar{y}} + a_2\frac{\bar{y}}{\bar{x}+\bar{y}}, \quad \text{if } \bar{x}+\bar{y} > 0. \end{aligned}$$

Notice that a_1 and a_2 assign cost (or benefits if negative) on the latest gender densities of the population. Besides, the original maintenance cost function C could include linear and nonlinear feedbacks for the gender densities. We shall study the asymptotic average sex ratio for historically adapted populations with respect to perturbed maintenance cost functions in the above form.

It is straightforward that $C_{(0,0)} = C$. Besides, C_A converges uniformly to C as the vector A tends to $(0,0)$ (see (12)). Much more crucial is the fact that hypotheses (1), (2), and (3) also hold for the perturbed cost C_A. Thus, we can apply the result of section 3.2 to get the existence of $\omega^A = \binom{x_i^A}{y_i^A}_{i\in\mathbb{N}} \in \Omega$, an adapted history for the maintenance cost C_A. Therefore, for a fixed cost function C, we can consider the map $\Gamma_C : \mathbb{R}^2 \to \mathbb{R}$ given by

$$\Gamma_C(A) = \lim_{n\to\infty} \frac{1}{n} \sum_{k=1}^{n} C_A\left(\begin{pmatrix} x_{k-1}^A \\ y_{k-1}^A \end{pmatrix}, \begin{pmatrix} x_k^A \\ y_k^A \end{pmatrix}\right), \qquad \text{for all } A \in \mathbb{R}^2.$$

(The above function is well defined due to (9).)

Notice that if γ is the minimum asymptotic average maintenance cost with respect to C, then clearly $\Gamma_C(0,0) = \gamma$. Furthermore, one can easily show that Γ_C is a concave application, which, in particular, means that Γ_C is continuous everywhere and differentiable almost everywhere with respect to the Lebesgue measure[5]. As a matter of fact, one may say a little more on the differentiable behavior of the map Γ_C, since one can show that

$$\Gamma_C(a_1, a_2) = f_C(a_1 - a_2) + \gamma + a_2, \quad \forall\ (a_1, a_2) \in \mathbb{R}^2, \tag{10}$$

where $f_C : \mathbb{R} \to \mathbb{R}$ is a concave function such that $f_C(0) = 0$ (see Remark 6). Thus, for almost all $\Delta \in \mathbb{R}$, the map Γ_C is actually differentiable along the straight line $\{(a, a - \Delta) : a \in \mathbb{R}\}$.

The points of differentiability of Γ_C are essential for the discussion on the existence of an asymptotic average sex ratio for historically adapted populations. Let then $\nabla\Gamma_C(A)$ denote the gradient vector of the function Γ_C at the point $A \in \mathbb{R}^2$. We are able to show that, whenever $A = (a_1, a_2)$ is a point of differentiability of Γ_C, one necessarily has

$$\lim_{n\to\infty} \frac{1}{n} \sum_{k=1}^{n} \left(\frac{x_k^A}{x_k^A + y_k^A}, \frac{y_k^A}{x_k^A + y_k^A}\right) = \nabla\Gamma_C(A) = \big(f_C'(a_1 - a_2), 1 - f_C'(a_1 - a_2)\big), \tag{11}$$

for any adapted history $\omega^A = \binom{x_i^A}{y_i^A}_{i\in\mathbb{N}} \in \Omega$ with respect to the maintenance cost function C_A. This is precisely the statement of Theorem 7 in appendix A.

First of all, (11) means that, for almost all linearly perturbed maintenance cost functions, the respective historically adapted populations do share the same asymptotic average sex ratio. Moreover, this common value is constant for each family of cost functions $\{C_{(a,a-\Delta)}\}_{a\in\mathbb{R}}$, when Δ is a point of differentiability of f_C. In particular, since f_C is concave, then f_C' is nonincreasing whenever it is defined. Therefore, if $\Delta_1 < \Delta_2$ are two points of differentiability of f_C, then the asymptotic average female proportion in historically adapted populations with respect to $C_{(a,a-\Delta_1)}$ will not be less than the one in historically adapted populations with respect to $C_{(b,b-\Delta_2)}$.

The convergence in average of the sex ratio has a main consequence: a recurrent stability along time for this biological feature. In fact, a simple lemma (see Lemma 8) ensures that there will exist infinitely many arbitrarily long periods of time for which sex ratios must be as close as desired to the average limit. In more mathematical terms, suppose $A = (a_1, a_2) \in \mathbb{R}^2$ is a point of differentiability of the map Γ_C, and $\omega^A = \binom{x_i^A}{y_i^A}_{i\in\mathbb{N}} \in \Omega$ is an adapted history with respect to the

[5] See Proposition 5 and Remark 6 in Appendix A.

maintenance cost function C_A. Hence, given $\epsilon > 0$ arbitrarily small and $M > 0$ as large as one wants, there are infinitely many finite histories $\omega^A[m,n] = \binom{x_i^A}{y_i^A}_{m \leq i \leq n}$ such that $n - m \geq M$ and

$$\left| \sum_{k=m+1}^{n} \left(\frac{x_k^A}{x_k^A + y_k^A} - f_C'(a_1 - a_2) \right) \right| < \epsilon.$$

This property might clearly provide a reasonable explanation for the observed stability of sex ratio in nature, underlying the major role of the nontrivial interaction between a finite-resource environment and the growth and maintenance of a two-sex population.

4.2 From perturbed to nonperturbed maintenance costs

We have an asymptotic average sex ratio for historically adapted populations with respect to almost all linearly perturbed maintenance cost functions. However, Γ_C may be nondifferentiable along countably many straight lines $\{(b, b - \Delta) : b \in \mathbb{R}\}$, and the limit (11) is guaranteed only if $A \in \mathbb{R}^2$ is a point of differentiability of Γ_C. Note that this limit could exist for some point of nondifferentiability of Γ_C, but the argumentation in the proof of Theorem 7 cannot be used to decide if this is the case. In particular, one cannot ensure that Γ_C is differentiable at $A = (0,0)$, which would imply the existence of an asymptotic average sex ratio for historically adapted populations with respect to the original nonperturbed maintenance cost function C.

Although we cannot always guarantee the existence of an asymptotic average sex ratio, the characterization of Γ_C given in (10) allows us to deduce that even in the worst case the average sex ratio takes values in some fixed interval (see Theorem 10). As a matter of fact, for all $B = (b, b - \Delta) \in \mathbb{R}^2$, there exist real constants L_Δ and R_Δ (depending only on the cost function C and on the real parameter Δ) such that

$$0 \leq L_\Delta \leq \liminf_{n \to \infty} \frac{1}{n} \sum_{k=1}^{n} \frac{x_k^B}{x_k^B + y_k^B} \leq \limsup_{n \to \infty} \frac{1}{n} \sum_{k=1}^{n} \frac{x_k^B}{x_k^B + y_k^B} \leq R_\Delta \leq 1,$$

whenever $\omega^B = \binom{x_i^B}{y_i^B}_{i \in \mathbb{N}} \in \Omega$ is an adapted history for the maintenance cost function C_B.

For any points $B = (b, b - \Delta)$ and $\bar{B} = (\beta, \beta - \bar{\Delta})$ with $\Delta < \bar{\Delta}$, one can show that $R_{\bar{\Delta}} \leq L_\Delta$ (see Remark 11). Hence the respective intervals $[L_\Delta,\ R_\Delta]$ and $[L_{\bar{\Delta}},\ R_{\bar{\Delta}}]$ may intersect each other only at their common boundary. In particular, a small perturbation, let us say, on $\bar{\Delta}$ will imply that the corresponding average sex ratios of historically adapted populations must take its values outside the interval $(L_{\bar{\Delta}},\ R_{\bar{\Delta}})$. One might interpret this fact as a kind of instability of average sex ratios for points of nondifferentiability of Γ_C.

To illustrate the above discussion, let us consider an extreme situation. Suppose that there exists some point $\bar{B} = (\beta, \beta - \bar{\Delta})$ such that $L_{\bar{\Delta}} = 0$ and $R_{\bar{\Delta}} = 1$. It is straightforward that, for any other point $B = (b, b - \Delta)$ with $\Delta \neq \bar{\Delta}$, we have

$$\text{either} \qquad \lim_{n \to \infty} \frac{1}{n} \sum_{k=1}^{n} \frac{x_k^B}{x_k^B + y_k^B} = 0 \qquad \text{or} \qquad \lim_{n \to \infty} \frac{1}{n} \sum_{k=1}^{n} \frac{x_k^B}{x_k^B + y_k^B} = 1,$$

for all adapted history $\omega^B = \binom{x_i^B}{y_i^B}_{i\in\mathbb{N}} \in \Omega$ with respect to C_B. So only for cost functions $C_{(\bar{b},\bar{b}-\bar{\Delta})}$, there could exist historically adapted populations with two genders coexisting as time goes by.

A brief concluding remark is that, for the special case of the nonperturbed maintenance cost function $C = C_{(0,0)}$, there always exist constants $0 \leq L_0 \leq R_0 \leq 1$ such that average sex ratios of historically adapted populations for C either converge to some point of the interval $[L_0,\ R_0]$ or take values in this interval in a periodic or random way, without convergence.

5 Discussion

We proposed a new theoretical paradigm for sex-ratio problems: Reproductive interactions are supposed to have interconnectedness governed by a maintenance cost function depending explicitly on the size of male and female populations. By considering an environment with finite resources, we are compelled to take three hypotheses on the maintenance cost function: There exists a minimum cost (or a maximum benefit) that could be achieved by some population; the cost diverges to infinity as the latest population increases; the cost is dominated by the current population size. In this framework, we were able to show that there always exist historically adapted populations, which are populations minimizing the maintenance cost along time. Furthermore, the main result established here has guaranteed that, for almost all linearly perturbed maintenance cost functions, the average sex ratios of the respective historically adapted populations do converge.

We notice that formalism developed in previous sections and its consequences can be immediately generalized to various other situations. We would like to briefly discuss some of them.

Cost dependence on a finite number of consecutive censuses. One may consider a maintenance cost function $C : \mathbb{N}^{2L} \to \mathbb{R}$ depending on $L \geq 2$ consecutive population census, which can be seen again depending on two coordinates $C : \mathbb{N}^{2(L-1)} \times \mathbb{N}^{2(L-1)} \to \mathbb{R}$ via the identification

$$C\left(\binom{x_1}{y_1}, \binom{x_2}{y_2}, \ldots, \binom{x_L}{y_L}\right) = C\Big(\left(\binom{x_1}{y_1}\ \ \binom{x_2}{y_2}\ \ \ldots\ \ \binom{x_{L-1}}{y_{L-1}}\right)^T, \left(\binom{x_2}{y_2}\ \ \binom{x_3}{y_3}\ \ \ldots\ \ \binom{x_L}{y_L}\right)^T\Big).$$

One may now use such a point of view to rewrite the assumptions on the cost function and to easily obtain the analogous results for historically adapted populations.

Age-structured population models. We can introduce, for instance, the quantities of newborns of each gender. Hence, if newborns are included as a cost factor, then, for almost all perturbed cost functions, there shall exist an identifiable primary sex ratio in historically adapted populations. More generally, one may analyze a maintenance cost function depending on $M \geq 2$ age classes for both genders, namely, a function $C : \mathbb{N}^{2M} \times \mathbb{N}^{2M} \to \mathbb{R}$, $C\Big(\binom{(x_1,x_2,\ldots,x_M)}{(y_1,y_2,\ldots,y_M)}, \binom{(\bar{x}_1,\bar{x}_2,\ldots,\bar{x}_M)}{(\bar{y}_1,\bar{y}_2,\ldots,\bar{y}_M)}\Big)$.

Sequential and simultaneous hermaphroditism. By adding variables in our model, we can without difficulty extend our study to the occurrence at the same time of separate and combined sexes in some biological system. For instance, if X and Y denote the sizes of the dioecious part of the population, concerning the sex reversal part, let h_x and H_y be the number of sequential hermaphrodites reproducing early in life, respectively, as females and as males. The number of individuals after sex changes will be indicated then by h^y and H^x, respectively. At last, let Z denote the number of individuals having simultaneously both male and female reproductive organs. Therefore, the distribution of dioecy versus hermaphroditism can be investigated, for example, by the means of a maintenance cost function $C : \mathbb{N}^7 \times \mathbb{N}^7 \to \mathbb{R}$,

$$C\Big(\big(X \;\; Y \;\; h_x \;\; h^y \;\; H_y \;\; H^x \;\; Z\big)^T, \big(\bar{X} \;\; \bar{Y} \;\; \overline{h_x} \;\; \overline{h^y} \;\; \overline{H_y} \;\; \overline{H^x} \;\; \bar{Z}\big)^T\Big).$$

Periodic cost functions. The population maintenance cost may vary periodically along time. Such a situation corresponds to considering a family of cost functions $C_1, C_2, \ldots, C_N : \mathbb{N}^2 \times \mathbb{N}^2 \to \mathbb{R}$ and, for any finite history $\omega[m,n] = \binom{x_i}{y_i}_{m \le i \le n}$, a total cost $\sum_{k=m+1}^{n} C_{k-1 \,(\mathrm{mod}\; N)}\big(\binom{x_{k-1}}{y_{k-1}}, \binom{x_k}{y_k}\big)$. The analysis of the periodic case may be reduced to our time-independent case just by introducing a conjunction cost map

$$C\left(\tbinom{x}{y}, \tbinom{\bar{x}}{\bar{y}}\right) := \inf_{\binom{x_1}{y_1}, \binom{x_2}{y_2}, \ldots, \binom{x_{N-1}}{x_{N-1}} \in \mathbb{N}^2} \left[C_1\left(\tbinom{x}{y}, \tbinom{x_1}{y_1}\right) + C_2\left(\tbinom{x_1}{y_1}, \tbinom{x_2}{y_2}\right) + \ldots + C_N\left(\tbinom{x_{N-1}}{y_{N-1}}, \tbinom{\bar{x}}{\bar{y}}\right)\right].$$

It would certainly be very interesting to take into account two or more generalizations at the same application. For instance, an age-structured model with sex reversal individuals might help to understand whether there should exist a special age for sex change. Here again, from the biological perspective, in this particular situation as well as in many other potential applications (for example, to study social or economical characteristics), such a form of modeling requires one first to describe more explicitly the properties of a maintenance cost function regulating the reproductive interactions of a given population.

Appendix A

In this appendix we shall give the mathematical proofs of the results previously discussed. From now on, let $C : \mathbb{N}^2 \times \mathbb{N}^2 \to \mathbb{R}$ be a function verifying assumptions (1), (2), and (3). The main idea is to associate with such a maintenance cost function a suitable Lax-Oleinik operator and use its fixed points to construct historically adapted populations as well as to study their asymptotic properties. Lax-Oleinik fixed point techniques have been successfully explored in several areas. A very important example comes from calculus of variations: the Lax-Oleinik semigroup, which is essential in Fathi's weak KAM theory for Lagrangian mechanics (see [5]).

First of all, we need to introduce the spaces on which our Lax-Oleinik operator will act. Denote by $\ell^\infty(\mathbb{N}^2)$ the set of all real valued bounded functions on $\mathbb{N}^2$, and denote by $\ell^\infty(\mathbb{N}^2)/\mathbb{R}$ the set of all real valued bounded functions on $\mathbb{N}^2$ modulo constants, that is, the set of equivalence classes $[f] := \{g \in \ell^\infty(\mathbb{N}^2) : \; f - g \equiv cte\}$. Both $\ell^\infty(\mathbb{N}^2)$ and $\ell^\infty(\mathbb{N}^2)/\mathbb{R}$ are Banach spaces with norms $\|f\|_\infty := \sup_{\binom{x}{y} \in \mathbb{N}^2} |f\binom{x}{y}|$ and $\|[f]\|_\# := \inf_{\kappa \in \mathbb{R}} \|f + \kappa\|_\infty$, respectively.

Definition 2 (The Lax-Oleinik operator)**.** *Let T_C be the operator acting on $\ell^\infty(\mathbb{N}^2)$ by*

$$T_C f\begin{pmatrix} x \\ y \end{pmatrix} := \inf_{\binom{\bar{x}}{\bar{y}} \in \mathbb{N}^2} \left[C\left(\begin{pmatrix} x \\ y \end{pmatrix}, \begin{pmatrix} \bar{x} \\ \bar{y} \end{pmatrix}\right) + f\begin{pmatrix} \bar{x} \\ \bar{y} \end{pmatrix}\right], \quad \forall \begin{pmatrix} x \\ y \end{pmatrix} \in \mathbb{N}^2,$$

whenever f is a real valued bounded function on $\mathbb{N}^2$.

Notice that the operator T_C is well defined, since

$$\inf C - \|f\|_\infty \le T_C f \le \sup_{\binom{x}{y}\in\mathbb{N}^2} C\left(\begin{pmatrix}x\\y\end{pmatrix},\begin{pmatrix}0\\0\end{pmatrix}\right) + \|f\|_\infty \le \mathfrak{K}_C + C\left(\begin{pmatrix}0\\0\end{pmatrix},\begin{pmatrix}0\\0\end{pmatrix}\right) + \|f\|_\infty.$$

The above upper bound also implies that the infimum in the definition of the Lax-Oleinik operator is actually a minimum. Indeed, as the cost function C verifies hypothesis (2), $T_C f\binom{x}{y}$ will be selected among a finite number of values. Furthermore, note that $T_C(f+\kappa) = T_C(f)+\kappa$ for any $\kappa \in \mathbb{R}$. Thus, we can consider T_C acting on $\ell^\infty(\mathbb{N}^2)/\mathbb{R}$.

Theorem 3. *The operator $T_C : \ell^\infty(\mathbb{N}^2)/\mathbb{R} \to \ell^\infty(\mathbb{N}^2)/\mathbb{R}$ has a fixed point.*

Proof. We remark first that

$$2\big\|[f]\big\|_\# = \operatorname{osc}(f) := \sup_{\binom{x}{y},\binom{\bar x}{\bar y}\in\mathbb{N}^2}\left[f\begin{pmatrix}x\\y\end{pmatrix} - f\begin{pmatrix}\bar x\\\bar y\end{pmatrix}\right],$$

where f is any element of the equivalence class $[f]$.

Given $\lambda \in (0,1)$, let M_λ be the multiplication by $1-\lambda$ acting on $\ell^\infty(\mathbb{N}^2)/\mathbb{R}$. The operator $T_C \circ M_\lambda$ is a contraction and has therefore a fixed point $[u_\lambda] \in \ell^\infty(\mathbb{N}^2)/\mathbb{R}$, that is, $(T_C\circ M_\lambda)[u_\lambda] = T_C[(1-\lambda)u_\lambda] = [u_\lambda]$. Hence, observe that

$$\big\|[u_\lambda]\big\|_\# = \frac{1}{2}\operatorname{osc}\left((T_C\circ M_\lambda)u_\lambda\right) = \frac{1}{2}\operatorname{osc}\left(T_C(1-\lambda)u_\lambda\right) \le \frac{\mathfrak{K}_C}{2}.$$

In particular, the family $\{[u_\lambda]\}_{\lambda\in(0,1)}$ has an accumulation point $[u] \in \ell^\infty(\mathbb{N}^2)/\mathbb{R}$ as λ goes to zero. Choose $\lambda_i \to 0$ such that $[u_{\lambda_i}] \to [u]$ as $i \to \infty$. Since T_C is 1-Lipschitz, we have

$$T_C[u] = \lim_{i\to+\infty} T_C[(1-\lambda_i)u_{\lambda_i}] = \lim_{i\to+\infty}[u_{\lambda_i}] = [u].$$

□

Remark 4. *We have $T_C[u] = [u]$ for some equivalence class $[u] \in \ell^\infty(\mathbb{N}^2)/\mathbb{R}$. Therefore, if $u \in \ell^\infty(\mathbb{N}^2)$ is an element of the equivalence class $[u]$, it follows that*

$$u\begin{pmatrix}x\\y\end{pmatrix} + \gamma = T_C u\begin{pmatrix}x\\y\end{pmatrix} = \min_{\binom{\bar x}{\bar y}\in\mathbb{N}^2}\left[C\left(\begin{pmatrix}x\\y\end{pmatrix},\begin{pmatrix}\bar x\\\bar y\end{pmatrix}\right) + u\begin{pmatrix}\bar x\\\bar y\end{pmatrix}\right], \quad \forall \begin{pmatrix}x\\y\end{pmatrix}\in\mathbb{N}^2,$$

for some real constant γ. Recall that such a functional equation allows one to construct an adapted history $\omega = \binom{x_i}{y_i}_{i\in\mathbb{N}}$ starting with any given initial population $\binom{x_0}{y_0}$. In particular, it is easy to see that, for any adapted history $\omega = \binom{x_i}{y_i}_{i\in\mathbb{N}}$ and all arbitrary history $\bar\omega = \binom{\bar x_i}{\bar y_i}_{i\in\mathbb{N}}$,

$$\lim_{n\to\infty}\frac{1}{n}\sum_{k=1}^{n}\left[C\left(\begin{pmatrix}x_{k-1}\\y_{k-1}\end{pmatrix},\begin{pmatrix}x_k\\y_k\end{pmatrix}\right) + u\begin{pmatrix}x_k\\y_k\end{pmatrix} - u\begin{pmatrix}x_{k-1}\\y_{k-1}\end{pmatrix}\right] =$$

$$= \gamma \le \liminf_{n\to\infty}\frac{1}{n}\sum_{k=1}^{n}\left[C\left(\begin{pmatrix}\bar x_{k-1}\\\bar y_{k-1}\end{pmatrix},\begin{pmatrix}\bar x_k\\\bar y_k\end{pmatrix}\right) + u\begin{pmatrix}\bar x_k\\\bar y_k\end{pmatrix} - u\begin{pmatrix}\bar x_{k-1}\\\bar y_{k-1}\end{pmatrix}\right].$$

Thus, one clearly has (9) *and*

$$\gamma = \inf_{\binom{\bar{x}_i}{\bar{y}_i}_{i\in\mathbb{N}}\in\Omega} \liminf_{n\to\infty} \frac{1}{n}\sum_{k=1}^{n} C\left(\begin{pmatrix}\bar{x}_{k-1}\\ \bar{y}_{k-1}\end{pmatrix}, \begin{pmatrix}\bar{x}_k\\ \bar{y}_k\end{pmatrix}\right).$$

Now, given $A \in \mathbb{R}^2$, consider the perturbed maintenance cost

$$C_A\left(\begin{pmatrix}x\\ y\end{pmatrix}, \begin{pmatrix}\bar{x}\\ \bar{y}\end{pmatrix}\right) := C\left(\begin{pmatrix}x\\ y\end{pmatrix}, \begin{pmatrix}\bar{x}\\ \bar{y}\end{pmatrix}\right) + \left\langle A, \left(\frac{\bar{x}}{\bar{x}+\bar{y}}, \frac{\bar{y}}{\bar{x}+\bar{y}}\right)\right\rangle,$$

with the convention that zero over zero is equal to zero. It is straightforward that C_A verifies (1), (2), and (3), and $\mathfrak{K}_{C_A} = \mathfrak{K}_C$. Furthermore

$$\|C_A - C_B\|_\infty = \sup_{\binom{\bar{x}}{\bar{y}}\in\mathbb{N}^2} \left|\left\langle A - B, \left(\frac{\bar{x}}{\bar{x}+\bar{y}}, \frac{\bar{y}}{\bar{x}+\bar{y}}\right)\right\rangle\right| \leq \|A - B\|, \quad \forall\, A, B \in \mathbb{R}^2. \tag{12}$$

Let $\Gamma_C : \mathbb{R}^2 \to \mathbb{R}$ be the map defined by

$$\Gamma_C(A) := \inf_{\binom{\bar{x}_i}{\bar{y}_i}_{i\in\mathbb{N}}\in\Omega} \liminf_{n\to\infty} \frac{1}{n}\sum_{k=1}^{n} C_A\left(\begin{pmatrix}\bar{x}_{k-1}\\ \bar{y}_{k-1}\end{pmatrix}, \begin{pmatrix}\bar{x}_k\\ \bar{y}_k\end{pmatrix}\right).$$

Obviously $\Gamma_C(0,0) = \gamma$. Moreover, we have the following proposition.

Proposition 5. *The function Γ_C is concave.*

Proof. Given $A, B \in \mathbb{R}^2$ and $t \in [0,1]$, let $\omega = \binom{x_i}{y_i}_{i\in\mathbb{N}}$ be an adapted history with respect to the cost function $C_{tA+(1-t)B}$. Therefore, by the very definition of Γ_C, we get

$$\begin{aligned} t\Gamma_C(A) + (1-t)\Gamma_C(B) &\leq \lim_{n\to\infty} \frac{1}{n}\sum_{k=1}^{n} \left[tC_A\left(\begin{pmatrix}x_{k-1}\\ y_{k-1}\end{pmatrix}, \begin{pmatrix}x_k\\ y_k\end{pmatrix}\right) + (1-t)C_B\left(\begin{pmatrix}x_{k-1}\\ y_{k-1}\end{pmatrix}, \begin{pmatrix}x_k\\ y_k\end{pmatrix}\right)\right] \\ &= \lim_{n\to\infty} \frac{1}{n}\sum_{k=1}^{n} C_{tA+(1-t)B}\left(\begin{pmatrix}x_{k-1}\\ y_{k-1}\end{pmatrix}, \begin{pmatrix}x_k\\ y_k\end{pmatrix}\right) = \Gamma_C(tA + (1-t)B). \end{aligned}$$

□

Remark 6. *A real valued concave function on $\mathbb{R}^n$ is locally Lipschitz continuous*[6] *and hence, by Rademacher's theorem, differentiable almost everywhere with respect to the Lebesgue measure. Thus, Theorem 5 implies that Lebesgue-almost every $A \in \mathbb{R}^2$ is a point of differentiability of the map Γ_C. As a matter of fact, one may be a little more precise on the description of the points of differentiability of Γ_C. To that end, notice that we can write*

$$\Gamma_C(a_1, a_2) = f_C(a_1 - a_2) + \gamma + a_2, \quad \forall\, (a_1, a_2) \in \mathbb{R}^2,$$

[6] Actually, it is not hard to directly check that, for all $A, B \in \mathbb{R}^2$, we have $|\Gamma_C(A) - \Gamma_C(B)| \leq \|A - B\|$.

with $f_C : \mathbb{R} \to \mathbb{R}$ defined by

$$f_C(\Delta) := \inf_{\binom{\bar{x}_i}{\bar{y}_i}_{i\in\mathbb{N}} \in \Omega} \liminf_{n\to\infty} \frac{1}{n} \sum_{k=1}^{n} \left[C\left(\begin{pmatrix} \bar{x}_{k-1} \\ \bar{y}_{k-1} \end{pmatrix}, \begin{pmatrix} \bar{x}_k \\ \bar{y}_k \end{pmatrix} \right) + \frac{\bar{x}_k}{\bar{x}_k + \bar{y}_k} \Delta - \gamma \right], \quad \forall\, \Delta \in \mathbb{R}.$$

Certainly $f_C(0) = 0$. Moreover, as in the proof of Proposition 5, one may immediately verify that the function f_C is concave and therefore differentiable almost everywhere with respect to the Lebesgue measure on the real line. So we conclude that, for Lebesgue-almost every $\Delta \in \mathbb{R}$, the map Γ_C is indeed differentiable along the straight line $\{(a, a-\Delta) : a \in \mathbb{R}\}$.

The next theorem shows that points of differentiability of Γ_C play a crucial role on the study of average sex ratio for historically adapted populations. Its proof is very similar to Gomes's argument for the asymptotic behavior of optimal trajectories defined by discrete viscosity solutions (see [7]).

Theorem 7. *Let $A = (a_1, a_2) \in \mathbb{R}^2$ be a point of differentiability of Γ_C, and let $\omega^A = \binom{x_i^A}{y_i^A}_{i\in\mathbb{N}}$ be an adapted history for the maintenance cost C_A. Then, one has*

$$\lim_{n\to\infty} \frac{1}{n} \sum_{k=1}^{n} \left(\frac{x_k^A}{x_k^A + y_k^A}, \frac{y_k^A}{x_k^A + y_k^A} \right) = \nabla\Gamma_C(A) = \big(f_C'(a_1 - a_2), 1 - f_C'(a_1 - a_2)\big).$$

Proof. Let $u_A \in \ell^\infty(\mathbb{N}^2)$ be such that $u_A\binom{x_i^A}{y_i^A} + \Gamma_C(A) = T_{C_A} u_A\binom{x_i^A}{y_i^A} = C_A(\binom{x_i^A}{y_i^A}, \binom{x_{i+1}^A}{y_{i+1}^A}) + u_A\binom{x_{i+1}^A}{y_{i+1}^A}$, for all $i \in \mathbb{N}$. Therefore, for all $n \geq 1$, we obtain

$$u_A\begin{pmatrix} x_0^A \\ y_0^A \end{pmatrix} = \sum_{k=1}^{n} C_A\left(\begin{pmatrix} x_{k-1}^A \\ y_{k-1}^A \end{pmatrix}, \begin{pmatrix} x_k^A \\ y_k^A \end{pmatrix} \right) + u_A\begin{pmatrix} x_n^A \\ y_n^A \end{pmatrix} - n\Gamma_C(A).$$

For $h > 0$ and $B \in \mathbb{R}^2$, let $u_{A+hB} \in \ell^\infty(\mathbb{N}^2)$ be such that $T_{C_{A+hB}} u_{A+hB} = u_{A+hB} + \Gamma_C(A + hB)$. It is straightforward that

$$u_{A+hB}\begin{pmatrix} x_0^A \\ y_0^A \end{pmatrix} \leq \sum_{k=1}^{n} C_{A+hB}\left(\begin{pmatrix} x_{k-1}^A \\ y_{k-1}^A \end{pmatrix}, \begin{pmatrix} x_k^A \\ y_k^A \end{pmatrix} \right) + u_{A+hB}\begin{pmatrix} x_n^A \\ y_n^A \end{pmatrix} - n\Gamma_C(A + hB), \quad \forall\, n \geq 1.$$

Thus, clearly

$$\begin{aligned} &u_{A+hB}\begin{pmatrix} x_0^A \\ y_0^A \end{pmatrix} - u_A\begin{pmatrix} x_0^A \\ y_0^A \end{pmatrix} \leq \\ &\leq h \sum_{k=1}^{n} \left\langle B, \left(\frac{x_k^A}{x_k^A + y_k^A}, \frac{y_k^A}{x_k^A + y_k^A} \right) \right\rangle - n\big(\Gamma_C(A + hB) - \Gamma_C(A)\big) + u_{A+hB}\begin{pmatrix} x_n^A \\ y_n^A \end{pmatrix} - u_A\begin{pmatrix} x_n^A \\ y_n^A \end{pmatrix}. \end{aligned}$$

Since $u_{A+hB}\binom{x_0^A}{y_0^A} - u_{A+hB}\binom{x_n^A}{y_n^A} + u_A\binom{x_n^A}{y_n^A} - u_A\binom{x_0^A}{y_0^A} \geq -\mathrm{osc}(T_{C_{A+hB}} u_{A+hB}) - \mathrm{osc}(T_{C_A} u_A) \geq -2\mathfrak{K}_C$, it follows that

$$-\frac{2\mathfrak{K}_C}{hn} + \frac{\Gamma_C(A + hB) - \Gamma_C(A)}{h} \leq \left\langle B, \frac{1}{n} \sum_{k=1}^{n} \left(\frac{x_k^A}{x_k^A + y_k^A}, \frac{y_k^A}{x_k^A + y_k^A} \right) \right\rangle.$$

The same argument can be applied to $-B$, and hence we also deduce that

$$\left\langle B, \frac{1}{n}\sum_{k=1}^{n}\left(\frac{x_k^A}{x_k^A+y_k^A}, \frac{y_k^A}{x_k^A+y_k^A}\right)\right\rangle \leq \frac{2\mathfrak{K}_C}{hn} - \frac{\Gamma_C(A-hB)-\Gamma_C(A)}{h}.$$

So setting $h = m/n$ for a fixed $m > 0$ and taking $n \to \infty$, as A is a point of differentiability of Γ_C, from the last two inequalities we get that

$$-\frac{2\mathfrak{K}_C}{m} + \langle B, \nabla\Gamma_C(A)\rangle \leq \left\langle B, \liminf_{n\to\infty}\frac{1}{n}\sum_{k=1}^{n}\left(\frac{x_k^A}{x_k^A+y_k^A}, \frac{y_k^A}{x_k^A+y_k^A}\right)\right\rangle \leq$$
$$\leq \left\langle B, \limsup_{n\to\infty}\frac{1}{n}\sum_{k=1}^{n}\left(\frac{x_k^A}{x_k^A+y_k^A}, \frac{y_k^A}{x_k^A+y_k^A}\right)\right\rangle \leq \frac{2\mathfrak{K}_C}{m} + \langle B, \nabla\Gamma_C(A)\rangle.$$

Finally, taking $m \to +\infty$, we obtain

$$\left\langle B, \lim_{n\to\infty}\frac{1}{n}\sum_{k=1}^{n}\left(\frac{x_k^A}{x_k^A+y_k^A}, \frac{y_k^A}{x_k^A+y_k^A}\right)\right\rangle = \langle B, \nabla\Gamma_C(A)\rangle,$$

and then, since the equality holds for all $B \in \mathbb{R}^2$, we conclude that

$$\lim_{n\to\infty}\frac{1}{n}\sum_{k=1}^{n}\left(\frac{x_k^A}{x_k^A+y_k^A}, \frac{y_k^A}{x_k^A+y_k^A}\right) = \nabla\Gamma_C(A).$$

$\square$

Despite being a weak form of convergence, in fact, convergence in average underlines a recurrence property of the sequence. More precisely, we have the following result from real analysis.

Lemma 8. *Let $\{\alpha_i\} \subset \mathbb{R}$ be a sequence such that $\lim_{n\to\infty}(1/n)\sum_{k=1}^{n}\alpha_k = \alpha \in \mathbb{R}$. Let $\mathbb{I} \subset \mathbb{N}$ be a subset of positive density, that is,*

$$\lim_{n\to\infty}\frac{\#\{k \in \mathbb{I} : 1 \leq k \leq n\}}{n} =: \beta > 0.$$

Then, for all $\epsilon > 0$ and for any integer $L > 0$, there exist $m, n \in \mathbb{I}$, with $n > m \geq L$, such that

$$\left|\sum_{k=m+1}^{n}(\alpha_k - \alpha)\right| < \epsilon.$$

For the convenience of the reader, we give a short proof of this lemma.

Proof. Without loss of generality, we can assume that $\alpha = 0$. Fix $\rho \in (0, \epsilon\beta/8)$. There exists then a positive integer $n_0 \in \mathbb{I}$ such that

$$\#\{k \in \mathbb{I} : 1 \leq k \leq n\} \geq \frac{\beta n}{2} \quad \text{and} \quad \left|\sum_{k=1}^{n}\alpha_k\right| \leq \rho n, \quad \forall\, n \geq n_0.$$

We may suppose that $n_0 \geq L$. Clearly $\{\sum_{k=1}^{n} \alpha_k : n_0 \leq n \leq n_1\} \subset [-\rho n_1, \rho n_1]$. Considering thus

$$n_1 \in \mathbb{N} \quad \text{with} \quad n_1 > \max\left\{n_0,\ \frac{4}{\beta}\#\{k \in \mathbb{I} : 1 \leq k \leq n_0\}\right\},$$

we ensure that

$$\#\{k \in \mathbb{I} : n_0 < k \leq n_1\} = \#\{k \in \mathbb{I} : 1 \leq k \leq n_1\} - \#\{k \in \mathbb{I} : 1 \leq k \leq n_0\} > \frac{\beta n_1}{2} - \frac{\beta n_1}{4} = \frac{\beta n_1}{4}.$$

By the pigeonhole principle, there must be $m, n \in \mathbb{I} \cap \{n_0, n_0 + 1, \ldots, n_1\}$, with $n > m$, such that

$$\left|\sum_{k=m+1}^{n} \alpha_k\right| = \left|\sum_{k=1}^{m} \alpha_k - \sum_{k=1}^{n} \alpha_k\right| \leq \frac{2\rho n_1}{\#\{k \in \mathbb{I} : n_0 \leq k \leq n_1\} - 1} =$$

$$= \frac{2\rho n_1}{\#\{k \in \mathbb{I} : n_0 < k \leq n_1\}} < \frac{2\rho n_1}{\beta n_1/4} = \frac{8\rho}{\beta} < \epsilon.$$

□

Concerning then the stability of the average sex ratio for historically adapted populations, one obtains an immediate consequence.

Corollary 9. *Let $A = (a_1, a_2) \in \mathbb{R}^2$ be a point of differentiability of Γ_C, and let $\omega^A = \binom{x_i^A}{y_i^A}_{i \in \mathbb{N}}$ be an adapted history for the maintenance cost function C_A. Then, for all $\epsilon > 0$ and $M > 0$, there exist infinitely many finite histories $\omega^A[m, n] = \binom{x_i^A}{y_i^A}_{m \leq i \leq n}$, with $n - m \geq M$, such that*

$$\left|\sum_{k=m+1}^{n} \left(\frac{y_k^A}{x_k^A + y_k^A} - \left(1 - f_C'(a_1 - a_2)\right)\right)\right| = \left|\sum_{k=m+1}^{n} \left(\frac{x_k^A}{x_k^A + y_k^A} - f_C'(a_1 - a_2)\right)\right| < \epsilon.$$

Proof. Just apply the previous lemma to $\alpha_i = \frac{x_i^A}{x_i^A + y_i^A}$ and $\mathbb{I} = \{\lceil M \rceil, 2\lceil M \rceil, 3\lceil M \rceil, \ldots\}$, where $\lceil M \rceil$ denotes the smallest integer greater than or equal to M. □

We recall that the one-sided derivatives of f_C at a point Δ are given by

$$f_C'(\Delta+) := \lim_{H \to 0^+} \frac{f_C(\Delta + H) - f_C(\Delta)}{H} \qquad \text{and} \qquad f_C'(\Delta-) := \lim_{H \to 0^-} \frac{f_C(\Delta + H) - f_C(\Delta)}{H}.$$

Since f_C is a real valued concave function, its one-sided derivatives are defined everywhere. The next theorem uses the one-sided derivatives of f_C to find an estimate for the asymptotic average sex ratio even when it does not converge.

Theorem 10. *Given $B = (b, b - \Delta) \in \mathbb{R}^2$, define $L_\Delta := f_C'(\Delta+)$ and $R_\Delta := f_C'(\Delta-)$. Then, for all adapted history $\omega^B = \binom{x_i^B}{y_i^B}_{i \in \mathbb{N}} \in \Omega$ with respect to C_B, one has*

$$L_\Delta \leq \liminf_{n \to \infty} \frac{1}{n} \sum_{k=1}^{n} \frac{x_k^B}{x_k^B + y_k^B} \leq \limsup_{n \to \infty} \frac{1}{n} \sum_{k=1}^{n} \frac{x_k^B}{x_k^B + y_k^B} \leq R_\Delta.$$

Proof. We will prove the result only for the point $B = (0,0)$, since the proof for any other point is analogous. Let $\omega = \binom{x_i}{y_i}_{i\in\mathbb{N}} \in \Omega$ be an adapted history with respect to the cost function C. For any point $A = (a, a-H)$ with $H > 0$, we clearly have

$$\frac{1}{n}\sum_{k=1}^{n} C_A\left(\begin{pmatrix}x_{k-1}\\ y_{k-1}\end{pmatrix}, \begin{pmatrix}x_k\\ y_k\end{pmatrix}\right) = \frac{1}{n}\sum_{k=1}^{n} C\left(\begin{pmatrix}x_{k-1}\\ y_{k-1}\end{pmatrix}, \begin{pmatrix}x_k\\ y_k\end{pmatrix}\right) + \frac{H}{n}\sum_{k=1}^{n}\frac{x_k}{x_k+y_k} + a - H.$$

Since $\liminf_{n\to\infty}(1/n)\sum_{k=1}^{n} C_A\left(\binom{x_{k-1}}{y_{k-1}}, \binom{x_k}{y_k}\right) \geq \Gamma_C(A)$ and $\lim_{n\to\infty}(1/n)\sum_{k=1}^{n} C\left(\binom{x_{k-1}}{y_{k-1}}, \binom{x_k}{y_k}\right) = \Gamma_C(0,0) = \gamma$, we obtain

$$\Gamma_C(A) \leq \gamma + H \liminf_{n\to\infty}\frac{1}{n}\sum_{k=1}^{n}\frac{x_k}{x_k+y_k} + a - H.$$

Therefore, as $f_C(H) = \Gamma_C(A) - \gamma - (a-H)$, we get that

$$\frac{f_C(H) - f_C(0)}{H} = \frac{f_C(H)}{H} \leq \liminf_{n\to\infty}\frac{1}{n}\sum_{k=1}^{n}\frac{x_k}{x_k+y_k},$$

which yields

$$f_C'(0+) \leq \liminf_{n\to\infty}\frac{1}{n}\sum_{k=1}^{n}\frac{x_k}{x_k+y_k}.$$

One obtains the inequality $\limsup_{n\to\infty}(1/n)\sum_{k=1}^{n} x_k/(x_k+y_k) \leq f_C'(0-)$ in a similar way, using points $A = (a, a-H)$ with $H < 0$. □

Remark 11. *If B is a point of differentiability of Γ_C, then the left-sided and right-sided derivatives coincide and we clearly recuperate the statement of Theorem 7. Notice also that, since f_C is concave, then both maps $\Delta \mapsto f_C'(\Delta+)$ and $\Delta \mapsto f_C'(\Delta-)$ are nonincreasing functions and verify $0 \leq f_C'(\Delta+) \leq f_C'(\Delta-) \leq 1$ for all $\Delta \in \mathbb{R}$. For any points $B = (b, b-\Delta)$ and $\bar{B} = (\beta, \beta - \bar{\Delta})$, with $\Delta < \bar{\Delta}$, it follows that*

$$R_{\bar{\Delta}} = f_C'(\bar{\Delta}+) \leq f_C'(\Delta-) = L_\Delta,$$

which implies that the respective intervals $[L_\Delta,\ R_\Delta]$ and $[L_{\bar{\Delta}},\ R_{\bar{\Delta}}]$ may intersect each other only at their common boundary.

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