

LOCAL RESOURCE COMPETITION AND THE SKEWNESS OF THE SEX RATIO: A DEMOGRAPHIC MODEL

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ABSTRACT. Most animal populations are characterized by balanced sex ratios, but there exist several exceptions in which the sex ratio at birth is skewed. An interesting hypothesis proposed by Clark (1978) to explain male-biased sex ratios is the local resource competition theory: the bias may be expected in those species in which males disperse more than females, which are thus more prone to local competition for resources. Here we discuss some of the ideas underlying Clark's theory using a spatially explicit approach. In particular, we focus on the role of spatiotemporal heterogeneity as a possible determinant of biased sex ratios. We model spatially structured semelparous populations where either Ricker density dependence or environmental stochasticity can generate irregular spatiotemporal patterns. The proposed discrete-time model describes both genetic and complex population dynamics assuming that (1) sex ratio is genetically determined, (2) only young males can disperse, and (3) individuals locally compete for resources. The analysis of the model shows that no skewed sex ratios can arise in homogeneous habitats. Temporal asynchronized fluctuations between two distinct patches coupled with dispersal of young males is the minimum requirement for obtaining skewed sex ratios of demographic nature in local adult populations. However, the establishment of a male-biased sex ratio at birth in the long run is possible if dispersal is genetically determined and there is genetic linkage between sex ratio determination and dispersal.

1. Introduction. Sex ratio is determined in nature via a wide range of mechanisms, varying between chromosome-mediated and environmental determination [34]. Nevertheless, independently of the underlying processes, in most animal species the sex ratio resulting from reproduction is balanced, i.e., individuals generate an approximatively equal number of male and female newborns in each reproductive event. Although the study of the sex ratio evolution goes back to Charles Darwin's work, the first formal explanation of the optimality of a balanced sex ratio is due to Fisher [18].

Fisher's explanation is fairly simple: if males [females] of a population had a greater reproductive value than females [males], then parents should bias the sex ratio of their offspring and produce more males [females] than females [males]; as a result, this skewed sex ratio at birth would eventually lead to a skewed sex ratio

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in the adult population, as there would be more adult males [females] than females [males]; therefore, the excess of males [females] would decrease their own reproductive value, and parents should consequently bias their energetic investment towards a female- [male-] skewed sex ratio. The only possible outcome of this recursive process is a balanced sex ratio [18, 19].

There are cases, however, in which Fisher's argument does not hold. In fact, in several animal species the sex ratio at birth is skewed. Examples range from insects to mammals and even to non-human primates [34]. The simplest case is that of species with a marked sexual dimorphism. In this case, Fisher's theory can be simply extended by assuming that parents invest the same amount of energy for giving birth to males and females, rather than produce the same number of newborns of each sex. This phenomenon has been widely reported in the literature [40].

On the other hand, sexual dimorphism is not present in many species that do reproduce with skewed sex ratios. In such cases, Fisher's theory of sex allocation in its basic formulation cannot explain the bias. As a matter of fact, in some species a difference in males' and females' reproductive values may indeed persist even if male and female abundances in the population are balanced: as a consequence, evolution should shape the sex ratio accordingly [10]. This has been widely verified in insects (in particular in parasitoid wasps and eusocial hymenoptera [10, 21, 2, 68, 26, 69]). As for vertebrates (like birds, ungulates, and primates), the outcomes of similar analyses are far more controversial [13, 14, 69].

Several alternative theories have been proposed in the literature to explain the emergence of skewed sex ratios. The best known are:

1. Hamilton's theory of local mate competition [24], in which males are subject to local competition for mating (see [65, 66, 57, 51, 52, 53] for experimental tests);
2. the so-called Trivers & Willard hypothesis [61], according to which the sex ratio of the offspring is influenced by the nutrition condition of the mother [30, 31, 4, 5, 49, 50];
3. the helper repayment hypothesis, in which newborns of a given sex eventually help their own parent (e.g., in building the nest), thus promoting a bias towards the sex of the helpers [20, 17, 43, 23];
4. the local resource competition theory, originally proposed by Clark [11], which assumes male dispersal and competition between females for local resources and is the focus of the present work.

Interestingly, some recent works attempt to combine some of these theories in order to achieve a greater realism [73].

Clark's theory applies to animal species in which males disperse from the native site, while females are subject to competition for access to local resources. As a result of these two conditions, evolution should favor the emergence of a male-biased sex ratio. The birth of non-dispersing daughters, in fact, increases the strength of local competition for resources in the native patch. On the contrary, young males can avoid local competition through dispersal. Like all its predecessors, the local resource competition theory opened a very fruitful research line, from both a theoretical and an experimental standpoint, and has been applied to a variety of animal species, from insects to birds, ungulates, and primates [12, 13, 54, 29, 42].

Several mathematical models have been proposed to formally discuss some of the ideas underlying the local resource competition theory. In particular, sex-specific

dispersal has been proved necessary to the establishment of biased sex ratios in finite subpopulations [6]. The effects of different mating and dispersal systems have been explored [7], also in a spatially explicit context [58]. In particular, many arguments are based on kin selection [56, 58, 59, 71] and evolution of dispersal [47, 39, 41, 60, 44, 35, 32]. Other studies tackle the difficult problem of the coevolution of dispersal and sex ratio [36, 37, 70, 72] using kin selection or the heterogeneity of the landscape (patterns of either low or high quality) as basic mechanisms.

However, all these approaches have typically used fairly simple descriptions of population dynamics. Therefore, they have not explored the potential role of demographic processes (and, in particular, of demographic fluctuations) in promoting the establishment of biased sex ratios [36]. Demographic fluctuations can profoundly affect patch quality, as more crowded sites provide less resources per capita. Although some studies have already tackled the topic of differential habitat quality, (e.g., [72] and references therein), this heterogeneity has been typically described in a static way, thus disregarding its dependence on the density of individuals actually inhabiting the habitat, as implicitly assumed by Clark in her seminal paper.

If demographic fluctuations in different patches are not synchronized, it is conceivable that male dispersal from crowded patches can be advantageous, as individuals migrate to patches that are likely to be less crowded, namely with lower competition. In a density-dependent context, the spatiotemporal heterogeneity required for dispersal to be potentially advantageous can be basically produced by two different mechanisms: an overcompensatory demography implying oscillations or chaos, or a compensatory demography with environmental stochasticity. As for the former, non-equilibrial behavior of logistic or Ricker maps may produce so called out-of-phase dynamics (i.e., dynamics in which different spatial patches have different population densities at a given time; see [16, 15]). As for the latter, spatially uncorrelated stochasticity may act so as to break the dynamical coherence of the habitat (*sensu* [16]), thus leading to spatiotemporal heterogeneity as well.

The paper is organized as follows. In the next section we describe a local model for the demography and genetic dynamics of a population in which the sex ratio is genetically determined. Then, we make the model spatially explicit in order to investigate the role of spatiotemporal heterogeneity generated by desynchronized population dynamics in promoting genotypes with biased sex ratios. After that, we analyze the consequences on the establishment of skewed sex ratios of letting dispersal be genetically determined and linked to sex ratio determination. Finally, the biological implications of our theoretical analysis are discussed.

2. A local model for the demography and sex ratio genetic dynamics of a population.

We consider a diploid animal population in which the sex ratio at birth is genetically determined by means of a single autosomal gene with two alleles, the resident allele A and the mutant allele a (genotypes AA , Aa , and aa). We limit our analysis to semelparous species and suppose that only females are responsible for the determination of the sex of the offspring. In addition, we assume that the population size is so large that kin selection mechanisms are negligible [72]. All females produce on average $E_0 = E_m + E_f$ offspring, where E_m and E_f denote the abundances of male and female newborns, respectively. However, while AA females produce sons and daughters according to a balanced sex ratio ($E_m/E_f = 1$), aa females procreate with a male-biased sex ratio $s = E_m/E_f \geq 1$, and Aa females are characterized by an intermediate (skewed) sex ratio r (with $s \geq r \geq 1$). Such

Offspring genotype	AA mothers	Aa mothers	aa mothers
m_t^{AA}	$\frac{E_0}{2} p_t^M$	$\frac{r}{r+1} \frac{E_0}{2} p_t^M$	-
m_t^{Aa}	$\frac{E_0}{2} (1 - p_t^M)$	$\frac{r}{r+1} \frac{E_0}{2}$	$\frac{s}{s+1} E_0 p_t^M$
m_t^{aa}	-	$\frac{r}{r+1} \frac{E_0}{2} (1 - p_t^M)$	$\frac{s}{s+1} E_0 (1 - p_t^M)$
f_t^{AA}	$\frac{E_0}{2} p_t^M$	$\frac{1}{r+1} \frac{E_0}{2} p_t^M$	-
f_t^{Aa}	$\frac{E_0}{2} (1 - p_t^M)$	$\frac{1}{r+1} \frac{E_0}{2}$	$\frac{1}{s+1} E_0 p_t^M$
f_t^{aa}	-	$\frac{1}{r+1} \frac{E_0}{2} (1 - p_t^M)$	$\frac{1}{s+1} E_0 (1 - p_t^M)$

TABLE 1. Abundance of male (m_t) and female newborns (f_t) of each genotype generated by mothers of different genotypes at time t . E_0 is the mean offspring production of mothers, while p_t^M is the allelic frequency of allele A in males at time t .

a mechanism for the determination of the sex ratio is rather common, for instance, in wasp species [65, 55, 67, 53].

Under these hypotheses, it is straightforward [48] to compute abundance, sex, and genotype of the offspring produced by mothers of any given genotype. Consider, for instance, aa females. Since they reproduce according to the unbalanced sex ratio s , during a single reproductive event they produce $E_0 (s/(s+1))$ gametes (eggs) that will become male offspring and $E_0 (1/(s+1))$ gametes that will become female offspring. If we denote by p_t^M [p_t^F] the frequency of the resident allele in the genetic pool of adult males [females] at generation t and assume random mixing for gametes, we find that eggs are fertilized by A and a male gametes with probability p_t^M and $(1 - p_t^M)$, respectively. In this way we are implicitly assuming that the frequencies of A and a gametes correspond to the allelic frequencies. Therefore, during one reproductive event aa mothers generate $E_0 p_t^M (s/(s+1))$ aa sons, $E_0 (1 - p_t^M) (s/(s+1))$ Aa sons, $E_0 p_t^M (1/(s+1))$ aa daughters and $E_0 (1 - p_t^M) (1/(s+1))$ Aa daughters. The computation for the other genotypes is reported in Table 1.

In order to describe the population demography, we have to define the relationships between two subsequent generations of adult males (M) and females (F). Two-sex models are relatively complex and thus quite rare in the ecological literature (see [9] for an example and a discussion on this). However, since we aim at studying the skewness of the sex ratio, we must account for population densities of both sexes. The abundance of the newborns of each sex can be easily deduced from Table 1 after suitable algebraic manipulations. As a consequence of a reproductive event, the density of male newborns (or young males) m_t is

$$m_t = m_t^{AA} + m_t^{Aa} + m_t^{aa} = E_0 \left(\frac{1}{2} F_t^{AA} + \frac{r}{r+1} F_t^{Aa} + \frac{s}{s+1} F_t^{aa} \right), \quad (1)$$

where m_t^X and F_t^X are the densities of male newborns and of mothers with genotype X , respectively. In a similar way, the abundance of female newborns (or young females) f_t can be computed as

$$f_t = f_t^{AA} + f_t^{Aa} + f_t^{aa} = E_0 \left(\frac{1}{2} F_t^{AA} + \frac{1}{r+1} F_t^{Aa} + \frac{1}{s+1} F_t^{aa} \right),$$

where f_t^X is the density of female newborns with genotype X .

In this paper we want to explore whether differences of patch quality caused by temporal variations of local population densities can lead to skewed sex ratios. There are basically two mechanisms that can provide these kinds of spatiotemporal fluctuations: either strong density-dependent local demography or spatially uncorrelated environmental stochasticity. We will use the Ricker model [46] as a prototype of the first mechanism and the stochastic version of the Beverton-Holt model [1] as a prototype of the second. In fact, the Ricker model can exhibit self-sustained oscillations of both regular (cyclic) and irregular (chaotic) nature. By contrast, the Beverton-Holt model predicts stationary dynamics no matter what values are attributed to model parameters [27], but a stochastic version accounting for demographic fluctuations can be easily derived by assuming that exogenous drivers act as a multiplicative noise.

Let us first consider the case in which there is no metapopulation structure. If we introduce density-dependent fertilities and assume that only a fraction σ_M [σ_F] of male [female] newborns survive and become reproductive adults after one year, the dynamical relationships between subsequent adult generations are given by

$$M_{t+1} = \sigma_M E_0 g(F_t, M_t) \left(\frac{1}{2} F_t^{AA} + \frac{r}{r+1} F_t^{Aa} + \frac{s}{s+1} F_t^{aa} \right) \tag{2a}$$

$$F_{t+1} = \sigma_F E_0 g(F_t, M_t) \left(\frac{1}{2} F_t^{AA} + \frac{1}{r+1} F_t^{Aa} + \frac{1}{s+1} F_t^{aa} \right), \tag{2b}$$

where $g(F_t, M_t)$ is the function used to describe density dependence. In particular, in the case of the Ricker model we have

$$g(F_t, M_t) = g_R(F_t, M_t) = e^{-\beta(F_t+M_t)},$$

while for the Beverton-Holt model with environmental stochasticity we have

$$g(F_t, M_t) = g_{BH}(F_t, M_t) = \frac{e^{z(t)}}{1 + \beta(F_t + M_t)},$$

where $z(t)$ follows a normal distribution with mean 0 and standard deviation ξ . In both formulations β is a positive parameter scaling the intensity of density dependence. To avoid confounding effects, we assume that the survival parameters of males and females in Eqs. (2) are equal ($\sigma_F = \sigma_M$). Any difference in the survivals would in fact result in a bias towards the favored sex.

Eqs. (2) do not constitute *per se* a well-defined dynamical system, because they do not allow the computation of the density of the various genotypes in the next generation. To formalize the genetic dynamics, we start by computing the frequency p_t^m of the dominant allele A in the young males of the population as

$$p_t^m = \frac{2m_t^{AA} + m_t^{Aa}}{2m_t}.$$

The assumption of semelparous species implies that the allelic frequencies in offspring after a reproductive event transcribe to the adult individuals of the next generation, i.e., $p_{t+1}^M = p_t^m$. Similar relations hold for the allelic frequency p_t^f of the dominant allele A in the young females (i.e., $p_{t+1}^F = p_t^f = (2f_t^{AA} + f_t^{Aa})/2f_t$).

Therefore, using data from Table 1, we get

$$p_{t+1}^M = \frac{\frac{1}{2}(1+p_t^M)F_t^{AA} + \frac{r}{r+1}\left(\frac{1}{2}+p_t^M\right)F_t^{Aa} + \frac{s}{s+1}p_t^M F_t^{aa}}{F_t^{AA} + \frac{2r}{r+1}F_t^{Aa} + \frac{2s}{s+1}F_t^{aa}} \quad (3a)$$

$$p_{t+1}^F = \frac{\frac{1}{2}(1+p_t^M)F_t^{AA} + \frac{1}{r+1}\left(\frac{1}{2}+p_t^M\right)F_t^{Aa} + \frac{1}{s+1}p_t^M F_t^{aa}}{F_t^{AA} + \frac{2}{r+1}F_t^{Aa} + \frac{2}{s+1}F_t^{aa}}. \quad (3b)$$

Taken together, the two sets of equations (2) and (3) fully describe the demographic and genetic processes in the population provided we invoke the Hardy-Weinberg principle [25, 64]. In fact, in this case we can obtain genotype abundances as

$$\begin{aligned} F_t^{AA} &= (p_t^F)^2 F_t \\ F_t^{Aa} &= 2p_t^F (1-p_t^F) F_t \\ F_t^{aa} &= (1-p_t^F)^2 F_t. \end{aligned} \quad (4)$$

Thus, the proposed population model is as follows:

$$M_{t+1} = \sigma_M \frac{E_0}{2} g(F_t, M_t) \left[(p_t^F)^2 + \frac{4r}{r+1} p_t^F (1-p_t^F) + \frac{2s}{s+1} (1-p_t^F)^2 \right] F_t \quad (5a)$$

$$F_{t+1} = \sigma_F \frac{E_0}{2} g(F_t, M_t) \left[(p_t^F)^2 + \frac{4}{r+1} p_t^F (1-p_t^F) + \frac{2}{s+1} (1-p_t^F)^2 \right] F_t \quad (5b)$$

$$p_{t+1}^M = \frac{p_t^F \left(\frac{1-r}{1+r} p_t^F + \frac{2r}{r+1} \right)}{2 \left[(p_t^F)^2 + \frac{4r}{r+1} p_t^F (1-p_t^F) + \frac{2s}{s+1} (1-p_t^F)^2 \right]} + \frac{p_t^M}{2} \quad (5c)$$

$$p_{t+1}^F = \frac{p_t^F \left(\frac{r-1}{r+1} p_t^F + \frac{2}{r+1} \right)}{2 \left[(p_t^F)^2 + \frac{4}{r+1} p_t^F (1-p_t^F) + \frac{2}{s+1} (1-p_t^F)^2 \right]} + \frac{p_t^M}{2}. \quad (5d)$$

The underlying hypotheses of the Hardy-Weinberg principle do not always hold [48], therefore one might wonder whether the introduction of (4) may lead to significant errors in our analysis. We have analyzed the behavior of an extended model obtained without invoking the Hardy-Weinberg principle. This model requires an additional equation for the dynamics of the frequency of genotype Aa . Our numerical investigations (not reported here for brevity) have shown that the errors introduced by using the Hardy-Weinberg principle are very small and temporally limited to the first iteration of the model. Thus, the results presented in the remainder of the paper refer to the more compact model (5) derived by taking advantage of (4).

It is interesting to note that model (5) has a cascade structure, i.e., its Jacobian matrix is block upper triangular. This means that Eqs. (5c-5d) are decoupled from Eqs. (5a-5b), thus forming a genetic submodel. Extensive simulations of this submodel (not shown for brevity) make clear that the genetic pool of the population slowly, but systematically, evolves towards a monomorphic condition in which the only existing allele is A ($p_t^{M,F} = 1$) and all individuals share the same genotype AA . As a consequence, the sex ratio is obviously balanced both at birth and in the adult population, independently of the values attributed to the parameters r and s . Because genetics and demography are decoupled in model (5), this result is robust

to changes in the functional form used to describe density dependence and, in turn, in population demographic dynamics.

All these results are summarized in Fig. 1, which shows how the attractors of the population model (5) typically vary with respect to the mean fertility E_0 . For increasing values of the parameter, the behavior of the model obtained with the Ricker density dependence (left panels) undergoes several qualitative changes. For very low values of E_0 , both males and females in the population are doomed to extinction, while at higher fertilities they can coexist at a stationary equilibrium, along a cycle or along a chaotic attractor (panel A). However, for any value of E_0 , male and female densities remain identical. In the long run the frequencies of the dominant allele approach unity whatever the value of E_0 (panel C). In the case of the Beverton-Holt density dependence with environmental stochasticity (right panels), increasing values of E_0 (beyond the extinction threshold) produce larger and larger demographic oscillations (panel B) but no genetic polymorphism (panel D). To sum up, the analysis of population model (5) confirms the evidence (see *Introduction*) that no skewed sex ratios can be found in a non-spatial context.

3. The model for spatially explicit populations. We turn now to describing populations living in a spatially structured habitat, which is the main goal of our analysis. The simplest way for making our demographic and genetic approach spatially explicit is by coupling via dispersal two identical patches whose local dynamics in isolation can be described by model (5). Two-patch models with undifferentiated sexes have been extensively studied in the literature as simple, yet insightful, models for spatial interactions [28, 38, 62, 63]. The complexity of demographic behaviors that emerges from such one-sex models is so rich that very rare are the analyses of two-sex maps (see [45] for a counterexample).

However, to investigate the theory of local resource competition [11], it is necessary to separately account for the abundance of the two sexes. We assume that (1) only young males disperse and (2) dispersal takes place just after the reproductive season [22]. These hypotheses imply that young males are still subject to competition for accessing local resources, but they have the chance of escaping from low quality, densely populated sites. As a consequence of the introduction of young male dispersal, equations (5a) and (5c) in our model have to be modified accordingly. To this purpose, we need to reconsider Eq. (1). If the density of young males in patch 1 (\mathcal{M}_t^1) is measured just after dispersal has occurred, we have

$$\begin{aligned} \mathcal{M}_t^1 = & (1 - D) \left(m_t^{AA^1} + m_t^{Aa^1} + m_t^{aa^1} \right) + \\ & + \alpha D \left(m_t^{AA^2} + m_t^{Aa^2} + m_t^{aa^2} \right), \end{aligned}$$

where D is the dispersal coefficient (i.e., the proportion of young males dispersing each year) and α is the fraction of individuals that survive dispersal. Notice that if $\alpha < 1$, dispersal comes along with an extra-mortality term, which is a rather common hypothesis in the literature on fragmented habitats [8]. Therefore, Eqs. (5a) and (5c) for patch 1 read respectively as

$$\begin{aligned} M_{t+1}^1 &= \sigma_M \mathcal{M}_t^1, \\ p_{t+1}^M &= \frac{(1 - D) \left(2m_t^{AA^1} + m_t^{Aa^1} \right) + \alpha D \left(2m_t^{AA^2} + m_t^{Aa^2} \right)}{2\mathcal{M}_t^1}. \end{aligned}$$

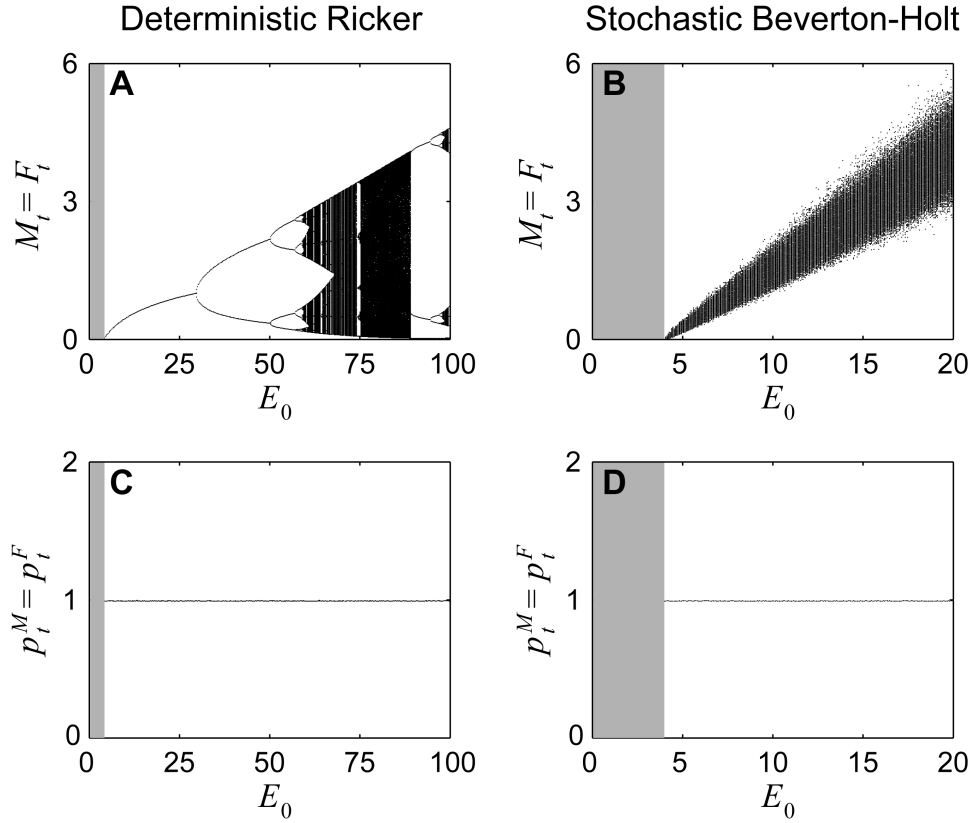


FIGURE 1. Attractors of model (5) with respect to the mean fertility E_0 . Top panels (A) and (B) are the population densities of either sex; bottom panels (C) and (D) are the frequencies of the resident alleles in males and females. Left panels (A) and (C) have been obtained with a deterministic Ricker demography ($g = g_R$), while right panels (B) and (D) with a stochastic Beverton-Holt model ($g = g_{BH}$, see text for details). For each value of E_0 model (5) has been iterated for 10000 time steps with 10 randomly generated initial conditions. The gray stripes mark the region in the parameter space in which the population goes extinct. Parameter values: $s = 1.6$, $r = 1.3$, $\sigma_M = \sigma_F = 0.5$, and $\beta = 1$ (left panels), or $\beta = 0.5$ and $\xi = 0.1$ (right panels).

These equations, together with Eq. (5b) and (5d) for female dynamics, and the four relevant counterparts for patch 2, describe the demography and the genetic dynamics of the metapopulation living in the two-patch habitat. It is interesting to notice that, when spatial interactions are accounted for, the genetic and demographic dynamics of the local populations are interdependent and can no longer be studied separately. In other words, the cascade structure found in the non-spatial model is destroyed by spatial coupling. With more than one patch, thus, the absolute abundances of the individuals of each genotype do matter and must be explicitly considered.

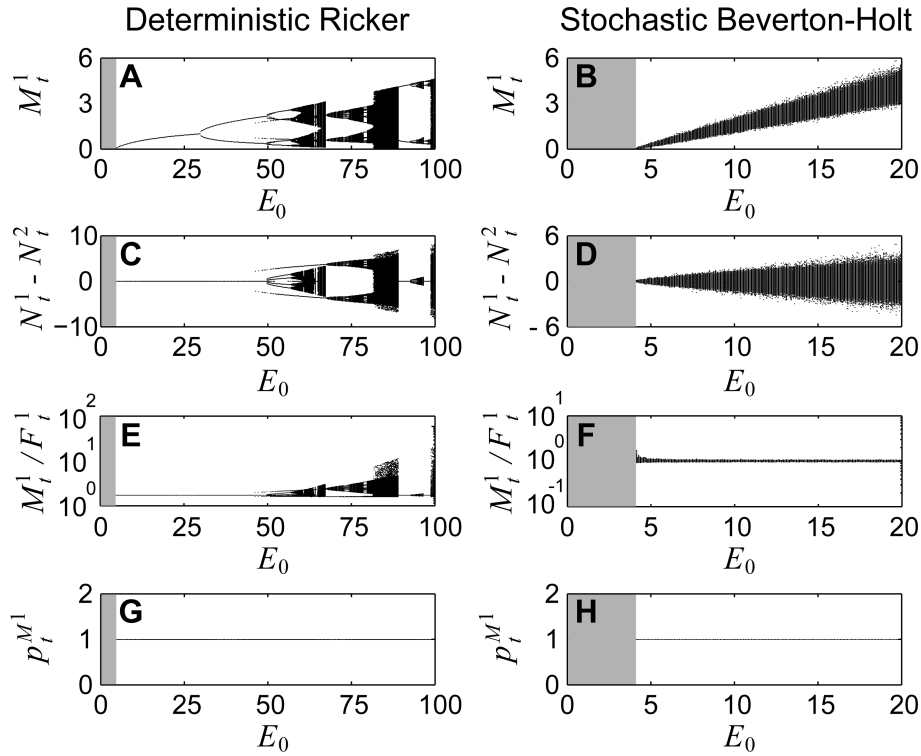


FIGURE 2. Attractors of the two-patch metapopulation model for different values of the mean fecundity E_0 . Left [right] panels have been obtained with the Ricker ($g = g_R$) [Beverton-Holt ($g = g_{BH}$)] model for density dependence. In particular, panels (A) and (B) show the density of males in patch 1; (C) and (D) display the differences between the total densities in the two patches ($N_t^1 - N_t^2 = F_t^1 + M_t^1 - F_t^2 - M_t^2$); (E) and (F) represent the demographic sex ratio in patch 1 (note the logarithmic scale); (G) and (H) show the frequency of the resident allele in males of the same patch. Parameter values: $D = 0.1$ and $\alpha = 1$. Other parameters and technical details as in Fig. 1.

The analysis of the metapopulation model, performed via extensive model simulation over wide regions of the parameter space, shows that in the long run no alleles other than the dominant allele A can persist in the genetic pool of the population (i.e., $p_t^{M, F^{1,2}} = 1$). As an example, Fig. 2 reports how some representative variables of our spatially explicit model typically vary with the mean fecundity E_0 , both with deterministic Ricker and stochastic Beverton-Holt demographies.

In the first case (Fig. 2, left panels), the demography of the two local populations can be periodic or chaotic at high E_0 (panel A). As shown in panel C, the dynamics of the two subpopulations can be either in-phase (i.e., $N_t^1 - N_t^2 = F_t^1 + M_t^1 - F_t^2 - M_t^2 = 0 \forall t$) or out-of-phase ($N_t^1 \neq N_t^2$). In particular, out-of-phase attractors can emerge for high values of E_0 if the local dynamics is periodic or chaotic. Interestingly, if the dynamics is out-of-phase, the sex ratio in local

adult subpopulations—the so called demographic sex ratio [69]—can be biased towards males (panel E). We remark that this bias has only a demographic origin, as it is apparent from the correlation between the emergence, crisis, and disappearance of either periodic or chaotic out-of-phase invariants (panels A and C) and the relevant modifications of the demographic sex ratio (panel E). However, the genetic pool of the population remains monomorphic and all the individuals in the population share the same genotype AA (panel G). Also, the demographic sex ratio of the metapopulation as a whole is still balanced, i.e., $(M_t^1 + M_t^2)/(F_t^1 + F_t^2) = 1$. Qualitatively similar results hold in the case of the stochastic Beverton-Holt demography (Fig. 2, right panels), in which spatially uncorrelated environmental stochasticity can produce demographic fluctuations (panel B), out-of-phase dynamics (panel D) and skewed demographic sex ratios (panel F), but no biases in the sex ratio at birth (panel H). All these result remains true also if some extra-mortality is added to dispersal (i.e., if $\alpha < 1$).

In summary, we have found that in a two-patch system the population is always monomorphic and the sex ratio at birth remains balanced. The result is very robust not only to changes in the values attributed to genetic and demographic parameters other than E_0 , but also to the weight given to sex and age in the functional forms used for density dependence. In particular, we have alternatively assumed that fertility might depend on the density of (1) females only, (2) young of both sexes, or (3) young females only. Also, introducing a dependence of the genetic parameters s and r on the density of (young) males and females in the population or the sex ratio itself is not sufficient to originate polymorphisms. In any of the above cases, we have obtained results that are qualitatively similar to those reported in Fig. 2. Therefore, even if we explicitly account for space, we can obtain skewed demographic sex ratios at the local scale, but we cannot find genetic polymorphism in the population, even less fixation of a skewed sex ratio at birth. This result shows that Clark's theory does not work when an explicit description of density dependence in a metapopulation structure is introduced.

4. Genotype-dependent dispersal. Since dispersal can be genotype dependent (e.g., [47, 44, 32] and references therein), we may wonder whether coevolution of dispersal and sex ratio can lead to the fixation of genes that codify for skewed sex ratios at birth. A complete analysis of this coevolution problem in two-sex spatially explicit models with complex demographies is a quite difficult task. To keep the problem affordable, we study a simpler problem, namely whether skewed sex ratios at birth can arise if there exists a correlation between the genetic information codifying the sex ratio and the propensity of males to disperse. In other words, we investigate whether a linkage [48] between two distinct genes, one regulating the skewness of the sex ratio and the other controlling the propensity to disperse, can lead to genetic polymorphism or substitution of the resident allele.

To this end, we introduce genotype-dependent dispersal into our model by simply differentiating the dispersal coefficients corresponding to different genotypes. Specifically, we assume that (1) aa young males disperse more than AA males ($D_{aa} \geq D_{AA}$), and (2) the dispersal ability of the heterozygote Aa males is intermediate between those of the homozygotes ($D_{Aa} = (D_{AA} + D_{aa})/2$). The abundance \mathcal{M}_t^1 of young males in patch 1 immediately after dispersal has occurred can now be

computed as

$$\begin{aligned} \mathcal{M}_t^1 &= (1 - D_{AA})m_t^{AA^1} + (1 - D_{Aa})m_t^{Aa^1} + (1 - D_{aa})m_t^{aa^1} + \\ &+ \alpha \left(D_{AA}m_t^{AA^2} + D_{Aa}m_t^{Aa^2} + D_{aa}m_t^{aa^2} \right). \end{aligned}$$

The model equations for allelic frequencies in males have also to be modified. For instance, in patch 1 we have that

$$p_{t+1}^{M^1} = \frac{2(1 - D_{AA})m_t^{AA^1} + (1 - D_{Aa})m_t^{Aa^1} + \alpha \left(2D_{AA}m_t^{AA^2} + D_{Aa}m_t^{Aa^2} \right)}{2\mathcal{M}_t^1}.$$

Similar relationships obviously hold for patch 2. The equations describing female dynamics do not need any modification.

Fig. 3 shows the results in a two-patch metapopulation with genotype-dependent dispersal as the fertility parameter E_0 is varied over a broad range of values, with both endogenous heterogeneity (Ricker demography) and exogenous spatial diversification (Beverton-Holt density dependence and environmental stochasticity). As for the Ricker case (left panels of Fig. 3), if fertilities are low ($E_0 \lesssim 50$ in the example), then either stationary or periodic dynamics arise (panel A) and only the dominant allele persists in the long run (panel E). A similar result holds for the stochastic Beverton-Holt model. However, for higher fertilities genotypes corresponding to skewed sex ratios can establish.

More specifically, the mutant allele a can invade the genetic pool of the population as soon as E_0 exceeds the threshold value ($E_0 \approx 50$, Fig. 3E) at which out-of-phase attractors emerge (panel C). Therefore, for intermediate fertilities ($50 \lesssim E_0 \lesssim 115$ in Fig. 3) we can have polymorphic populations in which the frequency of the resident allele A is smaller than unity. It is thus possible for the mutant allele to persist in the long run, and, correspondingly, the sex ratio at birth is skewed.

Also, for intermediate to high fertilities ($E_0 \gtrsim 75$, Fig. 3E) the resident allele A can be excluded from the genetic pool of the population and completely replaced by the mutant allele a . For these parameter settings, in fact, the homozygote aa may prevail in the long run. In these cases, the sex ratio at birth is simply s . We notice that the detection of the attractor leading to substitution in the parametric interval $75 \lesssim E_0 \lesssim 115$ is made difficult by the presence of a chaotic invariant leading to genetic polymorphism in the population.

On the other hand, for intermediate fertilities $50 \lesssim E_0 \lesssim 115$ there can be coexistence of multiple different attractors, each giving rise to a different genetic outcome (Fig. 3E). In the example of Fig. 3, for $50 \lesssim E_0 \lesssim 75$ one of the attractors leads to a balanced sex ratio, while the other leads to genetic polymorphism (and, thus, to a skewed sex ratio). For $75 \lesssim E_0 \lesssim 115$ one attractor determines polymorphism, while the other is responsible for complete substitution of the resident allele. Multi-stability is ecologically interesting because it implies that populations characterized by the same survival and fertility parameters, as well as by the same dispersal abilities, may be genetically different depending upon the relative abundance of different genotypes among the founders or the ancestral subpopulation densities.

Results for exogenous heterogeneity (stochastic Beverton-Holt model) have some significant differences (Fig. 3, right panels). In fact, demographic oscillations may arise also in this case and, as a consequence, out-of-phase dynamics may be generated (panel D). However, genotype evolution is rather different with respect to the case of Ricker density dependence in a deterministic context. In fact, we have found

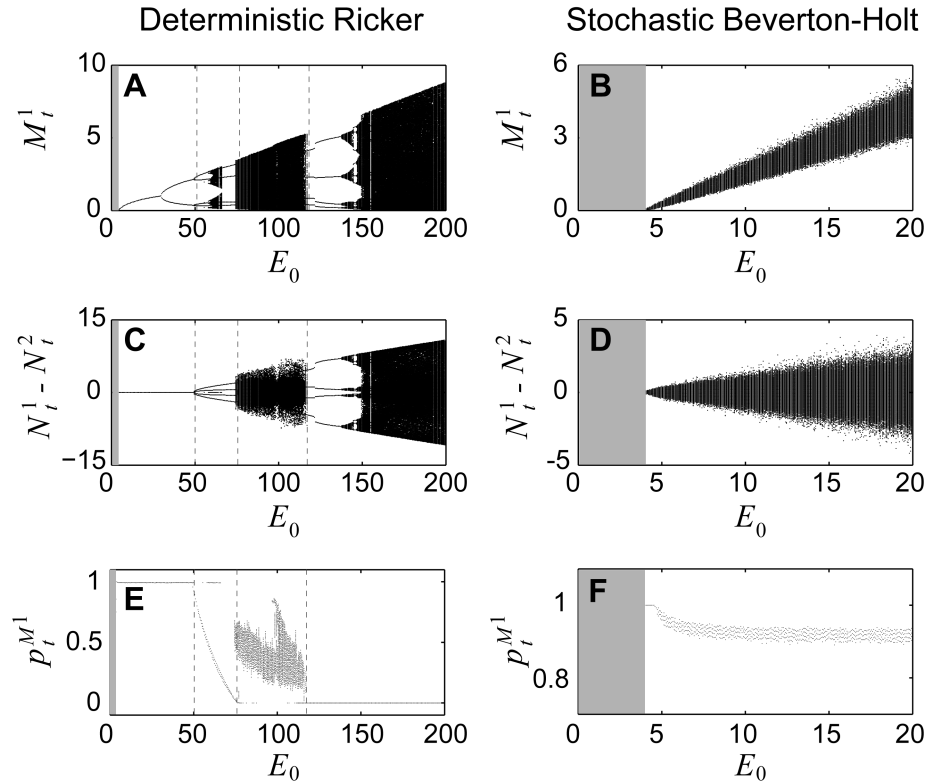


FIGURE 3. Attractors of the spatially explicit two-patch system with genotype-dependent dispersal for different values of the mean fertility E_0 . Left [right] panels have been obtained with the Ricker ($g = g_R$) [Beverton-Holt ($g = g_{BH}$)] model for density dependence. In particular, panels (A) and (B) show male density in patch 1; (C) and (D) display the difference between the total densities in the two patches ($N_t^1 - N_t^2 = F_t^1 + M_t^1 - F_t^2 - M_t^2$); (E) and (F) report the frequency of the resident allele in males in patch 1. Parameter values: $\alpha = 1$, $D_{AA} = 0.1$, $D_{Aa} = 0.2$ (left panels), $D_{Aa} = 0.5$ (right panels), $D_{aa} = 0.3$ (left panels), $D_{aa} = 0.9$ (right panels). For other parameter values and technical details see Fig. 1.

that, although the genetic pool of the population can be polymorphic, neither coexistence between multiple attractors nor complete substitution of the mutant allele is possible, for any of the parametric combinations we have explored.

To sum up, our model shows that the emergence of male-biased sex ratios at birth is possible if dispersal is genotype-dependent in cases where demography is fluctuating in an out-of-phase manner between different patches. In general, this condition may be satisfied with strong-density dependence if the fertility parameter E_0 is sufficiently high. The E_0 threshold depends on the other parameters defining the metapopulation, in particular on the dispersal rates. It is thus interesting to numerically evaluate in the parameter space (D_{AA}, D_{aa}) the minimum value of E_0 for which genetic polymorphism and substitution may arise. To this end, we have

used the following condition

$$E_0^* = \arg \min_{0 \leq E_0 \leq 200} \left[\max \left(p_{T, \dots, T+100}^{M^1}, p_{T, \dots, T+100}^{F^1}, p_{T, \dots, T+100}^{M^2}, p_{T, \dots, T+100}^{F^2} \right) < \gamma \right], \quad (6)$$

where T is a suitably large number of time steps that lets us avoid transient dynamics and γ is a convenient numerical threshold. We have set $\gamma = 0.99$ to detect the emergence of polymorphism and $\gamma = 0.01$ for the complete substitution of the resident allele.

Fig. 4 shows the results obtained with Ricker density dependence in terms of polymorphism (left panels) and substitution (right panels) for two different values of dispersal success α (no mortality during dispersal in top panels and 10% mortality in bottom panels). As already discussed in the previous section, in the scenario of genotype-independent dispersal (that is $D_{AA} = D_{aa} = D_{Aa}$) the mutant allele cannot invade the population, which still remains monomorphic ($p_t^{M,F^{1,2}} = 1$). Nevertheless, both polymorphism (panel A) and substitution of the resident allele (panel B) are possible for suitable combinations of dispersal and fertility parameters. In particular, polymorphism can occur if the value of the dispersal coefficient D_{AA} does not exceed a threshold which is given by $D_{AA} \approx 0.5$. As it is obvious from Eq. (6), the parametric region where substitution can take place is completely included in the region where polymorphism can arise. Quite interestingly, though, the complete substitution of the resident allele can occur only for sufficiently small values of both D_{AA} and D_{aa} . The addition of a small extra-mortality term during dispersal (panels C and D of Fig. 4) does not qualitatively alter the results obtained with $\alpha = 1$.

The analysis just performed with endogenous heterogeneity can be repeated for Beverton-Holt demography with environmental stochasticity. As shown in Fig. 5, polymorphism is possible even in this case and in a way that is qualitatively similar to the outcome obtained with Ricker density dependence (see again Fig. 4A). As already pointed out in Fig. 3F, substitution has not been found in the same region of the parameter space. Also, even a small mortality due to dispersal (as little as 1%, $\alpha = 0.99$) turns out to be sufficient to prevent the emergence of genetic polymorphism. This suggests that exogenous heterogeneity is much less favorable than endogenous heterogeneity to the establishment of genes codifying for skewed sex ratios at birth.

5. Discussion and conclusions. In this paper we have described a demographic and genetic model aimed at formalizing some features of Clark's local resource competition theory [11]. We have derived a simple metapopulation model (a nonlinear map) to describe both the genetic and the demographic dynamics of a semelparous animal population characterized by strong density dependence at the local scale and male dispersal. Sex ratio at birth is genetically determined by the mother's genotype. The spatial and sex structure of the model, together with nonlinearity and environmental stochasticity have made the analysis amenable to numerical simulations only. We have introduced genotype-dependent dispersal and, specifically, we have considered the simple case in which there exists a correlation between the genetic information codifying for skewed sex ratios and the propensity of males to disperse. Then, we have performed a sensitivity analysis of the model outcomes with respect to dispersal parameters.

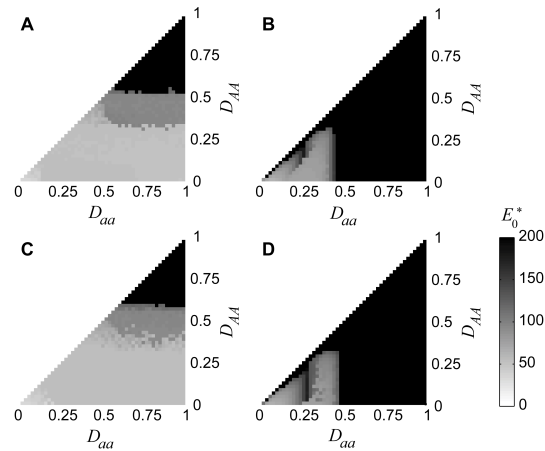


FIGURE 4. Conditions in the dispersal parameter space (D_{aa} , D_{AA}) for which polymorphism (panels A and C) and substitution of the resident allele (panels B and D) can arise in the genotype-dependent dispersal model with Ricker density dependence ($g = g_R$). For each point of the parameters space we have evaluated the minimum value of the fertility parameter E_0 that gives rise to polymorphism and substitution (condition (6)). Black areas correspond to no polymorphism or no substitution in the interval $0 \leq E_0 \leq 200$. Top panels are obtained with $\alpha = 1$, bottom panels with $\alpha = 0.9$. For each parameter setting model equations have been iterated for 10000 time steps with 10 randomly generated initial conditions. Unspecified parameter values as in Fig. 1.

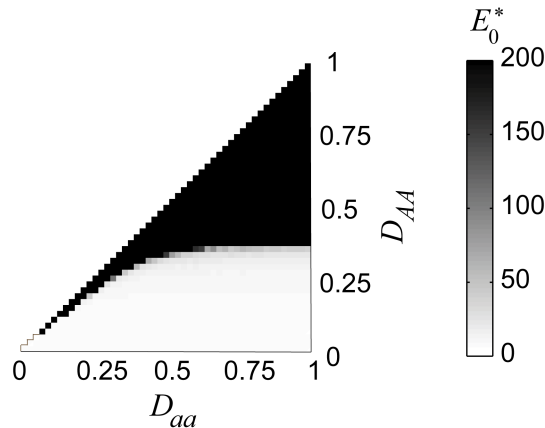


FIGURE 5. Conditions in the dispersal parameter space (D_{aa} , D_{AA}) for which polymorphism can arise in the genotype-dependent dispersal model with stochastic Beverton-Holt demography ($g = g_{BH}$). All simulations have been performed with $\alpha = 1$. Other parameter values and technical details as in Fig. 1.

The model analysis shows that no biased sex ratio at birth can evolve in a spatially homogeneous setting (Fig. 1). More interestingly, we show that in a spatially structured population subject to local resource competition (*sensu* Clark [11]) the sex ratio in local adult populations may be skewed. However, this bias is only due to demographic dynamics (Fig. 2). Without further hypotheses on the genetic characteristics of the species, the skewness of the sex ratio cannot establish in a metapopulation at birth. In contrast, the linkage between genotype-dependent sex ratio and genotype-dependent dispersal in a spatially heterogeneous habitat is a sufficient mechanism for the establishment of male-biased sex ratio at birth in the population (Fig. 3). In any case, the mutant allele can invade the resident only in presence of out-of-phase demographic fluctuations or with spatially uncorrelated environmental stochasticity. The region in the parameter space occupied by combinations of genotype-dependent dispersal coefficients leading to skewed sex ratios can be found with the model and turns out to be fairly large (Figs. 4 and 5). Therefore, our findings are robust and do not depend on a very particular choice of the parameter setting.

The model proposed in this work is flexible and may be easily modified so as to increase the realism of genetic, demographic and dispersal processes. With regard to genetics, a natural extension of our work would be that of studying the interplay between the evolution of the dispersal ability and the sex ratio transmission. This would require the study of the genetic dynamics for two different phenotypic traits with different degrees of genetic linkage. From a demographic viewpoint, our hypothesis of semelparous species clearly limits the applicability of our model; therefore, a useful extension could be that of removing this hypothesis in order to study how age structure could possibly influence the emergence of a bias in the sex ratio. Also, the mathematical description of the dispersal process could be enhanced, for instance by considering the possibility of performing directed movements. Finally, the spatial structure of the model itself could be easily extended to introduce more than two patches. From a technical viewpoint, this would require the study of a coupled map lattice [33].

Thanks to its simplicity, however, our model represents in its current form a first step towards a better understanding of the demographic mechanisms that may promote the establishment of biased sex ratios at birth in spatially structured populations subject to local intraspecific competition for resources.

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