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# Sex ratio evolution through group selection using diffusion approximation

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Abstract. We consider a haploid, hermaphrodite population subdivided into an infinite number of demes of finite size N. Assuming recurrent mutation, random union of gametes, partial dispersal, genetic drift, and incorporating group competition, a diffusion approximation is used to describe the evolution of sex ratio, corresponding to sex allocation to male versus female functions. The stationary distribution is deduced. In presence of group selection, a female-biased sex ratio in the whole population is found to be optimal in the sense that an allele coding for this sex ratio is always more frequent at equilibrium when segregating with another allele coding for a different sex ratio than for the same sex ratio. Numerical studies are presented to check the validity and accuracy of this prediction.

## 1. Introduction

A one-to-one sex ratio is known to be optimal in an infinite population of haploid or diploid individuals if mating is random and segregation Mendelian. This is supported by a verbal argument due to Fisher (1930) and confirmed by exact analyses (see, e.g., Eshel and Feldman, 1982, Karlin and Lessard, 1986, Lessard, 1990, and references therein).

Among the many factors suggested to explain the occurrence of biased sex ratios in some natural populations, mainly insects and arthropods, local mate competition, LMC (Hamilton 1967), is one of the favorite. In its original formulation, this model assumes an infinite number of colonies on different sites, each founded by a fixed number N of inseminated females chosen at random in the whole population at the beginning of each generation, and a proportion (N - 1)/2N of males is then shown to be optimal. This bias in favor of females was interpreted by Colwell (1981) as a group selection effect although other interpretations based on individual fitness

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were also proposed. See, e.g., Wilson and Colwell (1981), Nunney (1985), Bulmer (1986), Frank (1986a, 1986b), Nunney and Luck (1988), Nishimura (1993), Taylor (1994), Nagelkerke (1996), Nagelkerke and Sabelis (1996), Courteau and Lessard (1999, 2000) for other assumptions and/or interpretations.

In this paper, we extend the LMC model by assuming competition among the colonies to occupy a fixed proportion k of sites that are left vacant, the competitive value of a colony being proportional to its size after reproduction. This introduces an explicit form of group selection. We also assume dispersal and recurrent mutation, both occurring at small rates, along with a large colony size, so that a diffusion approximation is possible. Such an approximation with a similar kind of group competition was considered by Kimura (1984) to explain the evolution of an altruist trait.

The aim of this paper is to find an optimal sex ratio when two distinct sex ratios are segregating in the population in any frequencies. Because no restriction will be made on the frequencies of the sex ratios, we will not search for an optimal sex ratio using the standard definition of an evolutionarily stable strategy, or ESS (Maynard Smith and Price, 1973). This definition would require that one of the two sex ratios, the mutant one, is rare and that the resident one, the ESS sex ratio, is protected against initial invasion by the mutant, whenever it is different. Here is the definition we will use to say that a sex ratio is optimal. Suppose that there exists a stationary distribution such that two alleles A and B coding for two sex ratios a and b, respectively, coexist in the population without extinction of one or the other. If the two associated sex ratios a and b were equal, then neither A nor B should benefit from natural selection, since they are selectively neutral, and, as it will be shown, the frequency of A at equilibrium should then be v/(u + v), where u and v are the mutation probabilities from A to B and from B to A, respectively. Therefore, we will say that the sex ratio *a* is optimal if the equilibrium frequency of its coding allele A is always greater or equal to v/(u+v) whatever the sex ratio b associated to another allele B is.

Thus, we will need to study the equilibrium frequencies of two segregating sex ratios in a population. To do this, we will approximate the discrete-time model by a continuous-time model, and then apply diffusion theory to the approximated process to deduce the stationary distribution and properties of its mean.

#### 2. Model and diffusion approximation

Consider a population of haploid, hermaphrodite individuals subdivided into an infinite number of demes, each of constant size N. Assume two types of individuals: type A individuals, carrying allele A and producing aR male gametes and (1 - a)r female gametes, and type B individuals, carrying allele B and producing bR male gametes and (1 - b)r female gametes. Each individual produces a very large number of male and female gametes (R and r large with R usually larger than r), and then dies. During the production of these gametes, mutation can occur such that a proportion u of A gametes become B gametes and, conversely, a proportion v of B gametes become A gametes. Then, male and female gametes combine, pairwise and at random, within demes and give rise later on to the next generation of haploid individuals who inherit one or the other of the two parental

gametes with equal probabilities. It is supposed that all female gametes combine with male gametes and give birth to the same large number of haploid individuals. Afterward, a small proportion *m* of the newly produced individuals will leave their original deme and be replaced by the same proportion of newly produced individuals taken randomly in the population at large. This corresponds to what has been called proportional dispersal in Courteau and Lessard (2000) as opposed to uniform dispersal as studied in Bulmer (1986), Frank (1986) and Taylor (1988), with all demes receiving the same amount of newly produced individuals taken at random in the whole population. In general, there is a difference between these two types of dispersal, since the amount of newly produced individuals is not the same in all demes. However, under the assumptions of weak selection and weak dispersal, both types of dispersal will lead to the same approximation.

Finally, because of food and/or space constraints, only N of the individuals currently in each deme will survive to reproduction. More importantly, we also suppose that there is competition between demes such that, before population regulation within demes, a proportion k of demes are recolonized by other demes whose competitive values are measured by their relative sizes.

Let state x = i/N, where  $0 \le i \le N$ , be the proportion of type A individuals, that is, the frequency of allele A, in a particular deme. Assume that N is large and take N generations as the unit of time, so that the changes of state occur at times  $\delta t$ ,  $2\delta t$ ,  $3\delta t$ , and so on, where  $\delta t = 1/N$ . If the probability distribution of x in [0, 1] at time t converges, as N goes to infinity, to a continuous density which is twice continuously differentiable with respect to x and continuously differentiable with respect to t, then, for N sufficiently large, we can approximate the discrete-time model by a continuous-time model, actually a diffusion.

Let  $\phi(x, t)$  be the probability density of x at time t. We are interested in the variation of  $\phi$  with respect to time t. This variation can be due to the change of x within the deme and the effect of group competition.

## Change within the deme

The change of  $\phi(x, t)$  within the deme is given by the following Kolmogorov's forward equation (see, e.g., Ewens (1979) or Crow and Kimura (1970) for details):

$$\frac{\partial}{\partial t}\phi(x,t) = \frac{1}{2}\frac{\partial^2}{\partial x^2}\{v(x)\phi(x,t)\} - \frac{\partial}{\partial x}\{m(x)\phi(x,t)\},\tag{1}$$

where m(x) and v(x) are the rates of change for the mean and variance, respectively, of the change of x, that is,

$$E[\delta x|x] = m(x)\delta t + o(\delta t), \qquad (2)$$

$$Var[\delta x|x] = v(x)\delta t + o(\delta t), \tag{3}$$

where  $\delta x$  represents the change of x per generation within the deme and  $o(\delta t)$  denotes any function of  $\delta t$  such that  $o(\delta t)/\delta t$  goes to 0 as  $\delta t$  goes to 0. In order to find the drift parameter (infinitesimal mean m(x)) and the diffusion parameter (infinitesimal variance v(x)), let us decompose the change for the frequency of A from one generation to the next within the deme into changes due to four different factors:

(i) Production of gametes and mutation. Gametes are produced in large numbers and initially the frequency of A is ax/[ax + b(1 − x)] among male gametes and (1 − a)x/[(1 − a)x + (1 − b)(1 − x)] among female gametes, but then a proportion u of A gametes become B gametes and a proportion v of B gametes become A gametes, so that the frequency of A after mutation is

$$x' = \frac{(1-u)ax + vb(1-x)}{ax + b(1-x)}$$
(4)

among male gametes and

$$y' = \frac{(1-u)(1-a)x + v(1-b)(1-x)}{(1-a)x + (1-b)(1-x)}$$
(5)

among female gametes.

(ii) Random union of gametes and production of haploid individuals. All female gametes are united to male gametes chosen at random within the same deme to yield the ordered pairs of male and female gametes AA, AB, BA and BB, respectively, with the frequencies

$$M_{AA} = x'y', (6)$$

$$M_{AB} = x'(1 - y'), (7)$$

$$M_{BA} = (1 - x')y',$$
 (8)

$$M_{BB} = (1 - x')(1 - y').$$
(9)

The proportion of type A individuals among all haploid individuals subsequently produced in the same large number within the deme is

$$x'' = M_{AA} + \frac{1}{2}(M_{AB} + M_{BA}), \tag{10}$$

from which we get

$$x'' = \frac{x' + y'}{2}.$$
 (11)

Moreover, the relative size of the deme is

$$w(x) = (1-a)x + (1-b)(1-x).$$
(12)

(iii) *Partial dispersal*. A proportion *m* of the newly produced individuals disperse. Assuming proportional dispersal, the frequency of *A* within the deme is changed to

$$x''' = (1 - m)x'' + m\frac{x''w(x)}{\overline{w(x)}}.$$
(13)

On the other hand, assuming uniform dispersal, we have

$$x''' = \frac{(1-m)x''w(x) + m\overline{x''w(x)}}{(1-m)w(x) + m\overline{w(x)}}.$$
(14)

(iv) *Random sampling*. *N* haploid individuals chosen at random within the deme survive and the mean and variance of the frequency of *A* following this binomial sampling are

$$E[x^{\star}|x^{\prime\prime\prime}] = x^{\prime\prime\prime} \tag{15}$$

and

$$Var(x^{\star}|x''') = \frac{x'''(1-x''')}{N}.$$
(16)

Now, let us suppose that the parameters u, v, m and the difference |a - b| are all small, actually, functions of order 1/N or smaller. Then, the expectation of the change  $\delta x = x^* - x$  from one generation to the next within the deme, which is given by

$$E[\delta x|x] = x^{\prime\prime\prime} - x, \tag{17}$$

can be expressed, after some algebraic manipulations, as

$$E[\delta x|x] = m(\overline{x} - x) + sx(1 - x) + v(1 - x) - ux + o(1/N), \quad (18)$$

where

$$s = \frac{(a-b)(1/2-b)}{b(1-b)}.$$
(19)

We find also for the variance of the change

$$Var(\delta x|x) = \frac{x(1-x)}{N} + o(1/N).$$
 (20)

The above approximations are valid under proportional dispersal as well as uniform dispersal.

If we define the scaled parameters U = Nu, V = Nv, M = Nm and S = Ns, then we have

$$E[\delta x|x] = m(x)\frac{1}{N} + o\left(\frac{1}{N}\right),\tag{21}$$

$$Var(\delta x|x) = v(x)\frac{1}{N} + o\left(\frac{1}{N}\right),$$
(22)

where

$$m(x) = V(1-x) - Ux + M(\overline{x} - x) + Sx(1-x)$$
(23)

and

$$v(x) = x(1-x).$$
 (24)

If there is no competition between demes, then Kolmogorov's forward equation with the above parameters would be the differential equation associated with the model.

## Change due to group competition

Assuming competition among demes for a proportion k of deme sites and competitive values of demes measured by their relative sizes before population regulation within demes, then the density  $\phi(x, t)$  is transformed into

$$\phi(x, t+\delta t) = \left\{ (1-k) + k \left[ \frac{x(1-a) + (1-x)(1-b)}{\overline{x}(1-a) + (1-\overline{x})(1-b)} \right] \right\} \times \phi(x, t).$$
(25)

Here, we assume that a proportion k of demes go extinct and are recolonized by exact copies of some other demes before random sampling. Then, the change of  $\phi(x, t)$  per generation due to group competition is

$$\delta\phi(x,t) = \left\{\frac{k(\overline{x}-x)(a-b)}{(1-b)-\overline{x}(a-b)}\right\} \times \phi(x,t),\tag{26}$$

that is,

$$\delta\phi(x,t) = c(x-\overline{x})\phi(x,t) + o\left(\frac{1}{N}\right),\tag{27}$$

where

$$\overline{x} = \int_0^1 x \phi(x, t) dx$$
 and  $c = \frac{k(b-a)}{(1-b)}$ . (28)

Defining C = Nc, the variation of  $\phi(x, t)$  associated with group competition is given by

$$\frac{\partial}{\partial t}\phi(x,t) = C(x-\overline{x})\phi(x,t).$$
(29)

Combining the two sources of variation of  $\phi(x, t)$ , we obtain the following reaction-diffusion equation

$$\frac{\partial}{\partial t}\phi(x,t) = \frac{1}{2}\frac{\partial^2}{\partial x^2}\{v(x)\phi(x,t)\} - \frac{\partial}{\partial x}\{m(x)\phi(x,t)\} + C(x-\overline{x})\phi(x,t), \quad (30)$$

where

$$m(x) = V(1-x) - Ux + M(\overline{x} - x) + Sx(1-x),$$
(31)

$$v(x) = x(1-x),$$
 (32)

and C = Nk(b-a)/(1-b), V = Nv, U = Nu, M = Nm and S = N(a-b)(1/2-b)/(b(1-b)). The analysis of the above equation follows closely that of Kimura (1984) for an altruist trait. The main difference here is that the parameters *C* and *S* depend on the types present in the population.

## 3. Stationary distribution

At equilibrium, the function  $\phi(x, t)$  does not depend on t and then we must have

$$\frac{\partial}{\partial t}\phi(x,t) = 0. \tag{33}$$

Thus, the stationary distribution, denoted by  $\phi(x)$ , must be a solution of the equation

$$\frac{1}{2}\frac{\partial^2}{\partial x^2}\{v(x)\phi(x)\} - \frac{\partial}{\partial x}\{m(x)\phi(x)\} + C(x-\overline{x})\phi(x) = 0, \qquad (34)$$

where m(x) and v(x) are given by (31) and (32), respectively. As can be checked directly, the stationary distribution can be written in the form

$$\phi(x) = \phi_0(x) \exp\{y(x)\},$$
(35)

where  $\phi_0(x)$  satisfies

$$\frac{\partial}{\partial x} \{ v(x)\phi_0(x) \} = 2\{ m(x)\phi_0(x) \},\tag{36}$$

and y(x) is a solution of the following differential equation

$$v(x)\left[y''(x) + (y'(x))^2\right] + 2m(x)y'(x) + 2C(x - \overline{x}) = 0,$$
(37)

where

$$m(x) = V(1-x) - Ux + M(\overline{x} - x) + Sx(1-x)$$
(38)

and

$$v(x) = x(1-x).$$
 (39)

We find (see, e.g., Kimura, 1984)

$$\phi_0(x) \propto \frac{1}{v(x)} \exp\left\{2\int \frac{m(x)}{v(x)} dx\right\},\tag{40}$$

where

$$\int \frac{m(x)}{v(x)} dx = V \ln x + U \ln(1-x) + M\overline{x} \ln x - M\overline{x} \ln(1-x) + M \ln(1-x) + Sx.$$
(41)

Therefore, we have

$$\phi_0(x) \propto x^{2(V+M\overline{x})-1}(1-x)^{2(U+M(1-\overline{x}))-1} \exp\left\{2Sx\right\}.$$
(42)

Consequently, the stationary distribution is given by

$$\phi(x) = \frac{\exp\{y(x) + 2Sx\}x^{\alpha - 1}(1 - x)^{\beta - 1}}{\int \exp\{y(x) + 2Sx\}x^{\alpha - 1}(1 - x)^{\beta - 1}dx},$$
(43)

where  $\alpha = 2(V + M\overline{x})$ ,  $\beta = 2(U + M(1 - \overline{x}))$ , and y(x) is a solution of the differential equation (37) with the initial condition y(0) = 0.

Some care must be taken with the singular points x = 0 and x = 1. We can find y(x) in the neighbourhood of these singular points by expanding y(x) in Taylor series. In the neighbourhood of x = 0, we have

$$y(x) = y(0) + y'(0)x + \frac{1}{2}y''(0)x^2 + \dots,$$
(44)

where y'(0) is obtained by taking the limit when x goes to 0 in equation (37), giving

$$y'(0) = \frac{C\overline{x}}{V + M\overline{x}},\tag{45}$$

and y''(0) is obtained by first dividing equation (37) by *x* and then taking the limit when *x* goes to 0. In this case, we find

$$y''(0) + (y'(0))^2 - 2(V + U + M - S)y'(0) + 2C + 2\lim_{x \to 0} \frac{(V + M\overline{x})y'(x) - C\overline{x}}{x} = 0.$$
(46)

But, by L'Hospital's rule, we have

$$\lim_{x \to 0} \frac{(V + M\bar{x})y'(x) - C\bar{x}}{x} = (V + M\bar{x})y''(0), \tag{47}$$

and then

$$y''(0) = \frac{2(V+U+M-S)y'(0) - (y'(0))^2 - 2C}{1 + 2V + 2M\overline{x}}.$$
 (48)

A similar argument leads to

$$y(x) = y(1) - y'(1)(1-x) + \frac{1}{2}y''(1)(1-x)^2 + \dots,$$
(49)

where

$$y'(1) = \frac{C(1-\bar{x})}{U+M(1-\bar{x})}$$
 (50)

and

$$y''(1) = \frac{2C - 2(V + U + M + S)y'(1) - (y'(1))^2}{1 + 2U + 2M(1 - \overline{x})}.$$
 (51)

We have just determined the stationary distribution of x. Notice however that this distribution depends on  $\overline{x}$ , which depends itself on the distribution. To bypass this problem, we use the following procedure. Let us take a starting value for  $\overline{x}$ , say  $\overline{x} = 1/2$ . Then, we calculate the distribution  $\phi(x)$ . To do this, we solve equation (37) numerically for x not too close to 0 or 1, and for x near these extreme values, we simply use equations (44) and (49). It is now possible to calculate the new value for  $\overline{x}$  by the formula

$$\overline{x} = \int_0^1 x\phi(x)dx.$$
(52)

We repeat this procedure until two successive values of  $\overline{x}$  are sufficiently close.

## 4. Optimal sex ratio

First, notice that if a = b, then allele A is neutral, that is, allele A has no selective advantage over allele B and vice versa. In this case, we have

$$y(x) + 2Sx = 0 \tag{53}$$

for all x in [0, 1], and the stationary distribution is given by

$$\phi(x) = \frac{x^{\alpha - 1} (1 - x)^{\beta - 1}}{\int x^{\alpha - 1} (1 - x)^{\beta - 1} dx},$$
(54)

where  $\alpha = 2N(v + m\overline{x})$  and  $\beta = 2N(u + m(1 - \overline{x}))$ . Thus, in this particular situation, the mean  $\overline{x}$  should satisfy

$$\overline{x} = \frac{\alpha}{\alpha + \beta} = \frac{v + m\overline{x}}{v + u + m},\tag{55}$$

that is,

$$\overline{x} = \frac{v}{u+v}.$$
(56)

In this section, we will try to find a sex ratio *a* that will be optimal in the following sense: allele *A* coding for the sex ratio *a* will be more frequent at equilibrium when segregating with an allele *B* coding for a sex ratio  $b \neq a$ , at least close enough to *a*, than it would be if b = a. We are thus searching for a sex ratio *a* such that

$$\overline{x} > \frac{v}{u+v},\tag{57}$$

for all  $b \neq a$  and close enough to a.

From equation (43), we have

$$\phi(x) \propto \exp\{y(x) + 2Sx\}x^{\alpha - 1}(1 - x)^{\beta - 1},$$
(58)

where y(x) satisfies the equation

$$x(1-x)\left[y''(x) + (y'(x))^2 + 2Sy'(x)\right] + 2[V(1-x) - Ux + M(\overline{x}-x)]y'(x) + 2C(x-\overline{x}) = 0.$$
(59)

Moreover, in the neighbourhood of 0, we have

$$y(x) = y'(0)x + \frac{1}{2}y''(0)x^2 + \cdots$$
 (60)

with

$$y'(0) = \frac{C\overline{x}}{V + M\overline{x}} \tag{61}$$

and

$$y''(0) = \frac{2(V+U+M-S)y'(0) - (y'(0))^2 - 2C}{1 + 2V + 2M\overline{x}}.$$
 (62)

First, suppose that the mutation parameters u and v are much lower than the dispersal rate m, so that U and V can be neglected compared to M. Then, equations (59) and (60) become, respectively,

$$x(1-x)\left[y''(x) + (y'(x))^2 + 2Sy'(x)\right] + 2(\overline{x}-x)[My'(x) - C] = 0 \quad (63)$$

and

$$y(x) = \left(\frac{C}{M}\right)x - \frac{C}{M}\left(\frac{C}{M} + 2S\right)\frac{x^2}{2(1+2M\overline{x})} + \cdots$$
(64)

If C/M = -2S, then (C/M)x is a good approximation of y(x) in the neighbourhood of 0. In fact, (C/M)x is an exact solution of the differential equation (63). Thus, nearby the point C/M = -2S, the stationary distribution can be approximated by

$$\phi(x) \propto e^{Dx} x^{\alpha - 1} (1 - x)^{\beta - 1},$$
 (65)

where

$$D = \frac{C}{M} + 2S. \tag{66}$$

If D = 0, then  $e^{Dx} = 1$ , and the stationary distribution is given by (54). The point D = 0 seems to indicate the neutral point in the sense that there is neither benefit nor disadvantage associated with allele A, giving  $\overline{x} = v/(u + v)$ . On the other hand, if D > 0, then  $e^{Dx}$  goes from 1 to  $e^{D}$  as x goes from 0 to 1, giving more weight to larger values of x. This would entail an increase of  $\overline{x}$ . Of course, the opposite would occur if D < 0, because  $e^{Dx}$  would be a decreasing function of x, giving more weight to smaller values of x.

We are looking for a sex ratio *a* such that D > 0 for all  $b \neq a$  and close enough to *a*. Developing the above expression for *D*, we get

$$D = \frac{(b-a)}{(1-b)} \left[ \frac{k}{m} - 2N \frac{(1/2-b)}{b} \right],$$
 (67)

which is close to 0 when b is close enough to a. Moreover, the term in square brackets in the above expression for D is positive if

$$b > \frac{Nm}{k+2Nm} \tag{68}$$

and negative if the inequality is reversed. Then, let

$$a = \frac{Nm}{k + 2Nm}.$$
(69)

In this case, we have D > 0 whenever  $b \neq a$ . Thus, when a is given by (69), we are expecting to have

$$\overline{x} > \frac{v}{u+v} \tag{70}$$

for any  $b \neq a$  and close enough to a.

Now, consider the more general case where U and V are not necessarily negligible compared to M. Near the neutral point, that is, when there is nearly no benefit

associated with allele A, we can approximate  $\overline{x}$  by the neutral value  $\overline{x}_0 = v/(u+v)$ . Thus, in this neighbourhood, we have

$$y'(0) = R \tag{71}$$

and

$$y''(0) = -\frac{R(R+2S)}{1+2V+2M\overline{x}},$$
(72)

where

$$R = \frac{C}{U + V + M}.\tag{73}$$

Thus, when R + 2S is close to 0, y(x) can be approximated by Rx, giving

$$\phi(x) \propto e^{Dx} x^{\alpha - 1} (1 - x)^{\beta - 1},$$
(74)

with

$$D = R + 2S. \tag{75}$$

Therefore, allele A will be advantageous in the sense that  $\overline{x} > v/(u+v)$ , if D > 0. But, if we let

$$a = \frac{N(m+v+u)}{k+2N(m+v+u)},$$
(76)

and we proceed in the same way as previously, we conclude that D > 0 for all  $b \neq a$  and close enough to a.

#### 5. Numerical results

In the previous section, we suggested the following optimal sex ratio

$$a^{\star} = \frac{N(m+v+u)}{k+2N(m+v+u)}.$$
(77)

Then, we expect to find

$$\overline{x} \ge \frac{v}{u+v},\tag{78}$$

for all *b* close enough to  $a^*$ . In order to check the validity of this prediction, we performed two numerical studies for the case k = 1.

The first one consists of an evaluation of  $\overline{x}$  by the continuous-time model which is an approximation of the original discrete-time model when the parameters m, u, v and the difference  $|a^* - b|$  are small enough. The following procedure is used to determine  $\overline{x}$ . First, the differential equation (37) is numerically solved with Mathematica using  $\overline{x} = 0.5$ . For x near 0 and 1, say x < 0.05 and x > 0.95, we calculate the Taylor series (44) and (49) for y(x). Now, y(x) is known to be in [0, 1] and we are able to determine  $\phi(x)$ . We compute the new value of  $\overline{x}$  by the following formula

$$\overline{x} = \int_0^1 x \phi(x) dx. \tag{79}$$

We repeat this procedure with the new value of  $\overline{x}$  until two successive values are sufficiently close (in our case, we repeated the procedure until the absolute difference between two consecutive values was at most  $10^{-5}$ ). Let us denote by  $\overline{x}_c$  the retained value.

We also checked if the continuous-time model is a good approximation of the discrete-time model. To do this, we suppose that the frequency distribution of demes having *i* type *A* individuals at time *t* is  $F_t^{(0)}(i)$ , for i = 0, 1, ..., N. After group competition in the case k = 1, this distribution becomes

$$F_t(i) = \frac{(1-b) - (i/N)(a-b)}{(1-b) - \overline{x}(a-b)} F_t^{(0)}(i),$$
(80)

where  $\bar{x} = \sum_{i=0}^{N} (i/N) F_t^{(0)}(i)$ .

The distribution in the next generation is given by the following relation

$$F_{t+\delta t}(i) = \sum_{j=0}^{N} P_{ji} F_t(j),$$
(81)

where  $P_{ji}$  is the probability that a deme containing *j* type *A* individuals becomes a deme containing *i* type *A* individuals in the next generation. Since we perform a binomial sampling, we have

$$P_{ji} = \binom{N}{i} p_j^i (1 - p_j)^{N-i}, \qquad (82)$$

where  $p_j$  is the frequency of type A individuals in a deme initially composed of j type A individuals after the occurrence of mutation, random union of gametes, production of haploid individuals and partial dispersal. To find  $p_j$ , we follow the steps described in Section 2, starting with a frequency j/N and assuming proportional dispersal. We repeat this procedure until quasi-equilibrium. We then calculate the mean frequency of type A individuals and denote it by  $\overline{x}_d$ .

With Mathematica and Fortran, we performed these two procedures for different values of the parameters and noted the behaviour of the means  $\overline{x}_c$  and  $\overline{x}_d$  around  $a^*$  (given by formula (77)), that is, for *b* near  $a^*$ . The results are shown in Table 1. Notice that  $\overline{x}_c$  is always greater or equal to  $\overline{x}_0 = v/(u + v)$ .

Now, consider the discrete-time model. We identify the optimal sex ratio by taking the value of b corresponding to the minimum of  $\bar{x}_d$ . For example, let N = 10with m = 0.01, u = 0.02 and v = 0.01. The minimum of  $\bar{x}_d$  is 0.329 and the corresponding value of b is 0.21. This means that 0.21 is the best strategy when confronted to  $a^*$ . Thus, we conclude that 0.21 is the optimal sex ratio. Repeating this argument for all the other cases, we notice that the optimal sex ratio is almost always: either equal to  $a^*$ , or lower than  $a^*$  by 0.01. Nevertheless,  $a^*$  is a good approximation of the optimal sex ratio, especially when N is large. This is reasonable since the continuous-time model is a better approximation of the discrete-time model when N is large.

**Table 1.** Mean frequencies of allele A at stationarity obtained in the continuous- and discrete-time models, given by  $\overline{x}_c$  and  $\overline{x}_d$ , respectively. Here  $\overline{x}_0 = v/(u+v)$  represents the neutral value and  $a^*$  is the optimal sex ratio given by (77) in the case k = 1

Ν	m	и	v	$\overline{x}_0$	<i>a</i> *	b	$\overline{x}_c$	$\overline{x}_d$
10	0.1	0.1	0.1	0.500	0.429	0.20	0.678	0.593
						0.30	0.554	0.524
						0.41	0.501	0.499
						0.42	0.500	0.499
						0.43	0.500	0.500
						0.50	0.514	0.516
						0.60	0.573	0.564
10	0.1	0.01	0.02	0.667	0.361	0.20	0.920	0.849
						0.30	0.736	0.681
						0.34	0.675	0.659
						0.36	0.669	0.666
						0.37	0.668	0.673
						0.40	0.690	0.704
						0.50	0.811	0.813
10	0.1	0.001	0.001	0.500	0.336	0.20	0.982	0.967
						0.30	0.800	0.526
						0.32	0.587	0.422
						0.33	0.511	0.458
						0.34	0.507	0.498
						0.36	0.666	0.758
						0.40	0.882	0.902
10	0.01	0.02	0.01	0.333	0.222	0.10	0.939	0.565
						0.21	0.339	0.329
						0.22	0.334	0.332
						0.23	0.335	0.340
						0.25	0.359	0.371
						0.30	0.484	0.484
						0.40	0.659	0.633
20	0.1	0.1	0.1	0.500	0.462	0.20	0.688	0.616
						0.30	0.575	0.546
						0.40	0.511	0.506
						0.45	0.500	0.500
						0.46	0.500	0.500
						0.47	0.500	0.500
						0.50	0.504	0.505
20	0.1	0.01	0.01	0.500	0.414	0.20	0.922	0.867
						0.30	0.773	0.703
						0.40	0.506	0.504
						0.41	0.500	0.501
						0.42	0.501	0.499
						0.43	0.508	0.497
						0.50	0.649	0.651
	1	1	1	1	1	1	1	1

Ν	m	и	υ	$\overline{x}_0$	a*	b	$\overline{x}_c$	$\overline{x}_d$
20	0.1	0.01	0.02	0.667	0.419	0.20	0.927	0.879
						0.30	0.819	0.772
						0.40 0.41	0.672 0.668	0.665 <b>0.665</b>
						0.42	<b>0.667</b> 0.732	0.667
20	0.01	0.02	0.01	0.333	0.308	0.10	0.956	0.897
						0.20	0.740	0.658
						0.29	0.341	0.334 0.332
						0.31	<b>0.334</b> 0.487	0.334
						0.50	0.636	0.598

Table 1. Continued

What about the values of  $\bar{x}_c$  and  $\bar{x}_d$  when  $|a^* - b|$  is large? The gap between these two values is generally less than 1.5%. The only cases where the gap is large are when *u* and *v* are small (0.001 in Table 1). These discrepancies are probably due to the fact that a very large number of generations are needed to reach equilibrium (at least 3000 generations compared to less than 500 in the other cases). Cumulative errors could then be at the origin of these differences.

Finally, we examined the behaviour of the optimal sex ratio for small values of N and large dispersal rates m. Fixing the mutation rates u and v at 0.01, we looked for the optimal sex ratio for N varying from 1 to 5 and m varying from 0.01 to 1. The results are shown in Table 2. Notice first that the optimal sex ratio increases with m. For m = 0.01, formula (77) is a good approximation of the optimal sex ratio large. It is interesting however to note that the optimal sex ratio is always larger than  $a^*$  given by (77). Moreover, when dispersal is complete (m = 1), it seems that the optimal sex ratio approaches the quantity

$$a_H = \frac{N-1}{2N},\tag{83}$$

predicted by Hamilton (1967) for the Local Mate Competition model.

#### 6. Discussion

Colwell (1981) suggested that group selection was behind the bias in favor of females in Hamilton (1967) local mate competition model. In this model, individuals producing as many sons as daughters have a selective advantage over any others within colonies but a selective disadvantage over those producing an excess of females in invading new colonies. This was interpreted as a group selection effect

Ν	a <sub>H</sub>	m = 0.01	m = 0.1	m = 0.5	m = 1
1	0.000	0.02	0.05	0.12	0.16
2	0.250	0.05	0.12	0.23	0.27
3	0.333	0.07	0.17	0.31	0.35
4	0.375	0.09	0.22	0.35	0.38
5	0.400	0.11	0.24	0.38	0.41
10	0.450	0.19	0.35	0.44	0.45
20	0.475	0.27	0.41	0.47	0.48

**Table 2.** Optimal sex ratios obtained in the discrete-time model in the case k = 1. Here, we have u = v = 0.01 and *m* varies from 0.01 to 1.  $a_H = (N - 1)/2N$  is the ESS sex ratio obtained by Hamilton (1967) in the case where m = 1.

even though competition actually occurs between individuals distributed into colonies. As is often the case with group selection arguments, the exact significance of this interpretation is controversial.

In this paper, we studied another form of group competition, a fixed proportion k of colonies being left vacant and recolonized in block by some other colonies with probabilities proportional to their relative sizes. Assuming large colonies, recurrent mutation and partial dispersal, both occurring at small rates, we have deduced a diffusion approximation and shown that the optimal sex ratio is biased in favor of females (see equation (77)) as long as there is some level of group selection (k > 0). The dispersal rate has an effect similar to the mutation rates on the optimal sex ratio, which decreases in the same way when any of these rates decreases and decreases to 0 when all these rates decrease to 0. Then, group selection takes over and leads in the limit to an all female population. This is the case because group selection is essentially based on the number of female gametes produced within demes.

It may be surprising that more dispersal reduces the bias in favor of females in the model studied, since dispersal is a necessary ingredient for the evolution of a female-biased sex ratio in the local mate competition model in absence of group selection (k = 0). Actually, in this model, it is known that the ESS sex ratio does not depend on the dispersal rate when dispersal is uniform (see, e.g., Bulmer, 1986, Frank, 1986, Taylor, 1988), while it decreases with more dispersal when dispersal is proportional at least in the case N = 2 with a value given by (2 - m)/[2(3 - m)] (Courteau and Lessard, 2000). While selection acts solely through dispersal in the classical local mate competition model, there is direct competition between groups in the model studied with dispersal having only a small perturbing effect that lessens the effect of selection by reducing relatedness within groups.

In absence of group selection (k = 0), the optimal sex ratio in the model studied is 1/2 since *m* has been assumed small and *N* large. It is for the same reason of weak dispersal that the optimal sex ratio in the model studied is the same with

uniform dispersal (each deme receiving the same amount of migrants) than with proportional dispersal (each individual leaving a deme being replaced), contrary to the case with complete dispersal in the local mate competition model.

The optimality property used in this paper is defined with respect to the allele frequencies at stationarity. According to Rousset and Billiard (2000) and Leturque and Rousset (2002), there should be a correspondence with an optimality property defined with respect to fixation probabilities in the case of no mutation by letting the mutation rates go to 0. Then, the limiting optimal sex ratio obtained this way should be continuously stable in Eshel's (1983) sense or convergence-stable in Christiansen's (1991) terminology.

We may wonder why we have to resort to the stationary distribution of allele frequencies within demes to find an optimal sex ratio based only on the mean of this distribution. Actually, the dynamics of this mean depends on higher moments and it is more convenient to use the whole distribution.

The numerical results suggest that the diffusion approximation predicts adequately the optimal sex ratio even when the deme size N is as small as 10 and the rates of dispersal (m) and mutation (u and v) are as large as 0.1. Moreover, they confirm that the optimal sex ratio in the exact discrete-time model in the case k = 1increases with the dispersal rate m and is only slightly higher than the optimal sex ratio in Hamilton (1967) local mate competition model in the case of complete dispersal (m = 1) as soon as  $N \ge 2$ . This suggests that the effect of group selection is negligible compared to the effect of dispersal when it is complete, the slightly less biased optimal sex ratio in this case being likely due to the small effect of mutation.

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## References

- Bulmer, M.G.: Sex ratio evolution in geographically structured populations. Heredity 56, 69–73 (1986)
- Colwell, R.K.: Group selection is implicated in the evolution of female-biased sex ratios. Nature **290**, 401–404 (1981)
- Courteau, J., Lessard, S.: Stochastic effects in LMC models. Theoretical Population Biology 55, 127–136 (1999)
- Courteau, J., Lessard, S.: Optimal sex ratios in structured populations. J. Theoretical Biology **207**, 159–175 (2000)
- Crow, J.F., Kimura, M.: An introduction to population genetics theory. New York: Harper and Row, 1970
- Christiansen, F.B.: On conditions for evolutionary stability for a continuously varying character. American Naturalist **138**, 37–50 (1991)
- Eshel, I.: Evolution and continuous stability. J. Theoretical Biology 103, 99-111 (1983)
- Eshel, I., Feldman, M.W.: On evolutionary genetic stability of the sex ratio. Theoretical Population Biology **21**, 430–439 (1982)
- Ewens, W.: Mathematical population genetics. Heidelberg: Springer, 1979
- Hamilton, W.D.: Extraordinary sex ratios. Science 156, 477–488 (1967)
- Fisher, R.A.: The Genetical Theory of Natural Selection. Oxford: Oxford University Press, 1930
- Frank, S.A.: The genetic value of sons and daughters. Heredity 56, 351-354 (1986a)

- Frank, S.A.: Hierarchical selection theory and sex ratios I. General solutions for structured populations. Theoretical Population Biology **29**, 312–342 (1986b)
- Karlin, S., Lessard, S.: Theoretical Studies on Sex Ratio Evolution. Princeton University Press, Princeton, 1986
- Kimura, M.: Diffusion models in population genetics. J. Applied Probability 1, 177–232 (1964)
- Kimura, M.: Evolution of an altruistic trait through group competition as studied by the diffusion equation method. IMA Journal of Mathematics Applied in Medicine and Biology 1, 1–15 (1984)
- Maynard Smith, J., Price, G.R.: The logic of animal conflict. Nature 246, 15-18 (1973)
- Lessard, S.: Evolution du rapport numérique des sexes et modèles dynamiques connexes. In: Mathematical and Statistical Developments of Evolutionry Theory, S. Lessard, (ed.), NATO ASI Series C: Mathematical and Physical Sciences, Vol. 299, Dordrecht, The Netherlands: Kluwer, 1990, pp. 269–325
- Leturque, H., Rousset, F.: Dispersal, kin selection, and the ideal free distribution in a spatially heterogeneous population. Theoretical Population Biology **62**, 169–180 (2002)
- Nagelkerke, C.J.: Discrete clutch sizes, local mate competition and the evolution of precise sex allocation. Theoretical Population Biology 49, 314–343 (1996)
- Nagelkerke, C.J., Sabelis, M.W.: Hierarchical levels of spatial structure and their consequences for the evolution of sex allocation in mites and other arthropods. The American Naturalist **148**, 16–39 (1996)
- Nishimura, K.: Local mate competition in a stochastic environment. Theoretical Population Biology **44**, 189–202 (1993)
- Nunney, L., Luck, R.F.: Factors influencing the optimum sex ratio in a structured population. Theoretical Population Biology **33**, 1–30 (1988)
- Nunney, L.: Group selection, altruism, and structured-deme models. The American Naturalist **126**, 212–230 (1985)
- Rousset, F., Billiard, S.: A theoretical basis for measures of kin selection in subdivided populations: finite populations and localized dispersal. J. Evolutionary Biology 13, 814–825 (2000)
- Taylor, P.D.: Inclusive fitness with two sexes. Theoretical Population Biology **34**, 145–168 (1988)
- Taylor, P.D.: Sex ratio in a stepping-stone population with sex-specific dispersal. Theoretical Population Biology **45**, 203–218 (1994)
- Taylor, P.D., Bulmer, M.G.: Local mate competition and the sex ratio. Journal of Theoretical Biology **86**, 409–419 (1980)
- Wilson, D.S., Colwell, R.K.: The evolution of sex ratio in structured demes. Evolution 35, 882–897 (1981)