J. theor. Biol. (2000) **207,** 159–175
doi:10.1006/jtbi.2000.2160, available online at http://www.idealibrary.com on IDEAL®

Optimal Sex Ratios in Structured Populations*

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(*Received on* 17 *May* 1999, *Accepted in revised form on* 1 *August* 2000)

In this paper, we develop a general method to determine evolutionary equilibrium sex ratios and to check evolutionary stability, continuous stability and invadability in exact genetic models with or without dominance. This method is then applied to three kinds of models for structured populations: the first one concerns Hamilton's LMC model, except that only a fraction β of female offspring mate with male offspring born in the same colonies, while a fraction $1-\beta$ mate with male offspring chosen at random within the whole population; in the second model, it is assumed that partial dispersal of inseminated females occurs after mating; in the third model, partial dispersal of male and female offspring occurs before mating. In the first model, the effect of population regulation is studied while, in the other models, two kinds of dispersal are considered: proportional and uniform.

Introduction

Sex ratio evolution has been a major topic in theoretical population biology since Fisher (1958) presented a verbal argument for the predominance of an even sex ratio in random mating populations (see, e.g. Karlin & Lessard, 1986, and references therein). The subject has deserved much attention because sex ratio is an easily measurable trait and its evolution, though sensitive to some general factors, seems not to depend on the exact genetic background.

One of the first factors to have been considered to explain biased sex ratios in some natural populations is *local mate competition*, LMC (Hamilton, 1967), which occurs when female offspring mate exclusively or mostly with male offspring born within the same confined niches or colonies and then disperse to found new colonies, as commonly observed in parasitic insects, mites and other arthropods. In such a case, it has been argued that a female-biased sex ratio evolves in order to reduce competition among sons. Some have suggested that the main feature in the LMC model responsible for a female-biased sex ratio is partial sib-mating or inbreeding (Maynard Smith, 1978; Stenseth, 1978); others group selection (Colwell, 1981; Wilson & Colwell, 1981), the colonies producing more female offspring contributing more foundresses to the next generation. But there may be also competition among daughters for limited resources within colonies, called *local resource competition* (LRC, Clark, 1978), leading to a male-biased sex ratio if male offspring disperse before mating. More generally, a bias of the sex ratio towards the sex dispersing more widely or more evenly in geographically structured populations has been predicted (Bulmer & Taylor, 1980). It has been suggested that the mechanism underlying biased sex ratios

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0022–5193/00/220159 + 17 $35.00/0

in structured populations is differential sib competition, actually intra-sex as well as inter-sex sibling interactions over reproductive success (Taylor, 1981).

A relationship between biased sex ratios and asymmetrical degrees of relatedness among relatives have also been proposed with particular reference to the social *hymenoptera* and a possible worker–queen conflict over the sex ratio (Hamilton, 1972; Trivers & Hare, 1976; Oster *et al*., 1977; Uyenoyama & Bengtsson, 1981; Matessi & Eshel, 1992; see also Lessard, 1996). The role of relatedness in the evolution of the sex ratio has been studied for partial sib-mating models (Uyenoyama & Bengtsson, 1982; Lessard, 1990) and LMC models (Herre, 1985; Frank, 1986a, b, Taylor, 1988; Taylor & Frank, 1996). In particular, maximization of inclusive fitnesses (Hamilton, 1964) that measure contributions to future generations through male and female offspring weighted by coefficients of relatedness, has proved to be a powerful approach to predict optimal sex ratios. But the approach is applicable only to a first approximation when selection is weak.

From an evolutionary perspective, the main problem is the existence of some population sex ratio that can be maintained through time. Considering Y-linked drive with local mate competition, Hamilton (1967) found out a brood sex ratio that would have a selective advantage over any other at any frequency and called it an *unbeatable sex ratio*. He also presented an approximate analysis in the case of non-sex linked control. Analysing diploid and haplodiploid models, Taylor & Bulmer (1980) looked for a fixed sex ratio determined by some allele at a single locus that can resist invasion by any mutant allele when rare, either dominant or recessive. Such a sex ratio corresponds to an *evolutionarily stable strategy*, ESS, in the Maynard Smith & Price (1973) terminology, originally introduced in a purely ecological context of animal conflict. But actually, Taylor & Bulmer (1980) only checked evolutionary equilibrium, not evolutionary stability (see also Taylor, 1985). Karlin & Lessard (1986) studied in a similar way the effect of partial outbreeding and population regulation within colonies in diploid populations. Bulmer (1986) obtained by numerical methods ESS sex ratios in LMC models with limited but uniform dispersal of males and females before or after mating for haploid, diploid and haplodiploid populations, assuming recessive, additive or dominant gene action. Applying the Price (1970, 1972) covariance form for hierarchical selection to a haploid model or diploid model with additive gene action and using the expected number of grand progeny as fitness, Frank (1986a, b) deduced Bulmer's results. He also considered more realistic assumptions (Frank, 1985). A more rigorous treatment linking exact genetic models with Price's covariance approach, and with inclusive fitness formulations based on regression (relatedness) coefficients was proposed by Taylor (1988) to get the evolutionary equilibrium sex ratio under weak selection. A "direct fitness" approach for inclusive fitness yielded an even more straightforward derivation by simple differentiation and replacement of derivatives by appropriate relatedness terms (Taylor & Frank, 1996). See, e.g. the Frank (1998) book for a review of sex ratio evolution theory in the context of kin selection theory.

In this paper, we first extend the Taylor & Bulmer (1980) condition for a strategy as the sex ratio to be an evolutionary equilibrium, in order to get a tractable condition for local evolutionary stability. These are conditions on the characteristic polynomial of the linearized transformation for the population state near fixation and its first and second partial derivatives. We consider the case of a mutant allele that is neither recessive nor dominant, which leads to a situation where a resident strategy is confronted to two mutant strategies. We also consider continuous stability. A *continuously stable strategy*, CSS, is a strategy such that, "if a large enough majority of the population chooses a strategy close enough to [it], then only those mutant strategies which are even closer to [it] will be selectively advantageous" (Eshel, 1983). A related property considered for a strategy is the property of invading, when rare, any other strategy at least sufficiently close to it and once fixed in the population, which will be called the *invadability property*. Note that, in a population genetic framework, a population strategy has been said to possess the *evolutionary genetic stability* (EGS) property if, within a given genetic system, a mutant allele introduced in small frequency into any deviant population at

equilibrium, monomorphic or polymorphic, is selectively favored if and only if it renders the population strategy closer to it, at least initially after enough generations have passed, and this has been applied to sex ratio evolution in random mating populations (Eshel & Feldman, 1982).

We study optimal sex ratios in structured populations, actually LMC models, in the case of partial outbreeding with or without regulation on the number of inseminated females within colonies, in the cases of partial dispersal of inseminated females after mating and partial dispersal of male and female offspring before mating, with two types of dispersal, proportional and uniform. Haploid, diploid and haplodiploid populations are considered.

Framework

Consider an infinite population subdivided into an infinite number of colonies in which two genes, a resident gene R and a mutant gene S, are segregating at a single locus. Assume that there are n colony types in the population among which $n-1$ contain the mutant gene S. These are called mutant colonies. Let

$$\mathbf{x} = (x_1, x_2, \ldots, x_{n-1})^{\mathrm{t}}$$

be the vector of the frequencies of the different mutant colonies in the population and let $x_n = 1 - x_1 - x_2 - \cdots - x_{n-1}$ be the frequency of the non-mutant colonies. Suppose discrete, non-overlapping generations and let $\mathbf{x}$ at the current generation become $\mathbf{x}'$ at the next generation, according to the following transformation:

$$\begin{aligned}\mathbf{x}' &= \mathscr{T}(\mathbf{x}) \\ &= \mathscr{M}\mathbf{x} + \text{higher-order terms in } \mathbf{x},\end{aligned}$$

where

$$\mathscr{M} = \left(\left.\frac{\partial x_i'}{\partial x_j}\right|_{\mathbf{x}=0}\right)_{i,j=1}^{n-1}$$

is the linearized matrix around $\mathbf{0} = (0, \ldots, 0)$ of the transformation $\mathscr{T}$.

The mutant gene S will *disappear when rare* if, for all $\mathbf{x} \geqslant \mathbf{0}$ sufficiently close to $\mathbf{0}$ (meaning $x_i \geqslant 0$ small enough for $i = 1, \ldots, n-1$), we have

$$\mathscr{T}^k\mathbf{x} \to \mathbf{0} \quad \text{as } k \to \infty,$$

where $\mathscr{T}^k$ represents the k-th iterate of $\mathscr{T}$.

On the contrary, the mutant gene S will *invade when rare* if, for all $\mathbf{x} > \mathbf{0}$ sufficiently close to $\mathbf{0}$ (meaning $x_i > 0$ small enough for $i = 1, \ldots, n-1$), we have

$$\mathscr{T}^k\mathbf{x} \nrightarrow \mathbf{0} \quad \text{as } k \to \infty.$$

Now, suppose that the genes R and S, with S either dominant or recessive on R, determine some individual strategy as a progeny sex ratio represented by a real number between 0 and 1, and that we are interested in finding a resident strategy r, governed by gene R, which is protected once fixed in the population against any mutant strategy s, governed by gene S, when S is introduced in very low frequency into the population. Then, whatever is the strategy s (with $s \neq r$) adopted by all individuals carrying at least one mutant gene S, this gene will have to disappear when rare. Denote by $\lambda(r, s)$ the spectral radius of the linearized matrix $\mathscr{M} = \mathscr{M}(r, s)$. This means that $\lambda(r, s)$ is the greatest modulus of the eigenvalues of $\mathscr{M}$. Assume that for every (r, s), we have $\mathscr{M} \geqslant 0$ with $\mathscr{M}^k > 0$ for at least one $k \geqslant 1$ (that is, all entries of the matrix $\mathscr{M}$ are nonnegative and there exists an integer k such that all entries of the matrix $\mathscr{M}^k$ are positive). Then the Perron–Frobenius theory (see, e.g. Karlin & Taylor, 1975) tells us that $\lambda(r, s)$ is a simple positive eigenvalue of $\mathscr{M}$ and that there exist two positive vectors $\boldsymbol{\eta}(r, s)$ and $\boldsymbol{\xi}(r, s)$ satisfying $\boldsymbol{\eta}^{\mathrm{t}}(r, s)\boldsymbol{\xi}(r, s) = 1$ (t for transpose) and

$$\boldsymbol{\eta}(r, s)^{\mathrm{t}}\mathscr{M}(r, s) = \lambda(r, s)\boldsymbol{\eta}(r, s)^{\mathrm{t}}, \tag{1}$$

$$\mathscr{M}(r, s)\boldsymbol{\xi}(r, s) = \lambda(r, s)\boldsymbol{\xi}(r, s). \tag{2}$$

Moreover, we have

$$\frac{\mathscr{M}^k}{\lambda(r, s)^k} \to \boldsymbol{\eta}(r, s)\boldsymbol{\xi}(r, s)^{\mathrm{t}} \quad \text{as } k \to \infty.$$

It is known (see, e.g. Lessard & Karlin, 1982) that the condition $\lambda(r, s) < 1$ is sufficient (and

necessary in non-degenerate cases) for the gene S to disappear when rare. We are thus looking for a strategy r such that

$$\lambda(r, s) < 1 \quad \text{for all } s \neq r.$$

Since $\lambda(r, r) = 1$, we must have, assuming the function $\lambda(r, s)$ regular enough and r in the interior of $[0, 1]$,

$$\frac{\partial}{\partial s}\lambda(r, s)\bigg|_{s=r} = 0 \tag{3}$$

and

$$\frac{\partial^2}{\partial s^2}\lambda(r, s)\bigg|_{s=r} < 0. \tag{4}$$

Evolutionary Equilibrium

Following Taylor (1985), the *evolutionary equilibrium strategies* are defined as the interior strategies which satisfy eqn (3). Unfortunately, in most practical cases, this condition is useless because it is difficult to find an explicit expression for $\lambda(r, s)$, especially when the matrix $\mathcal{M}$ is large. For this reason, we look for another condition equivalent to eqn (3).

First, let us take the derivative with respect to s on both sides of eqn (1) and, then, let us multiply each term on the right by $\boldsymbol{\xi}(r, s)$. We obtain

$$\begin{aligned}\left[\frac{\partial}{\partial s}\boldsymbol{\eta}(r, s)^{\mathrm{t}}\right]\mathcal{M}(r, s)\boldsymbol{\xi}(r, s)&\\ + \boldsymbol{\eta}(r, s)^{\mathrm{t}}\left[\frac{\partial}{\partial s}\mathcal{M}(r, s)\right]\boldsymbol{\xi}(r, s)&\\ = \left[\frac{\partial}{\partial s}\lambda(r, s)\right]\boldsymbol{\eta}(r, s)^{\mathrm{t}}\boldsymbol{\xi}(r, s)&\\ + \lambda(r, s)\left[\frac{\partial}{\partial s}\boldsymbol{\eta}(r, s)^{\mathrm{t}}\right]\boldsymbol{\xi}(r, s).&\end{aligned}$$

Using eqn (2) and the fact that $\boldsymbol{\eta}(r, s)^{\mathrm{t}}\boldsymbol{\xi}(r, s) = 1$, we have

$$\frac{\partial}{\partial s}\lambda(r, s) = \boldsymbol{\eta}(r, s)^{\mathrm{t}}\left[\frac{\partial}{\partial s}\mathcal{M}(r, s)\right]\boldsymbol{\xi}(r, s),$$

which gives, by continuity, the equation

$$\frac{\partial}{\partial s}\lambda(r, s)\bigg|_{s=r} = \boldsymbol{\eta}^{\mathrm{t}}\left[\frac{\partial}{\partial s}\mathcal{M}(r, s)\bigg|_{s=r}\right]\boldsymbol{\xi},$$

where

$$\boldsymbol{\eta} = \boldsymbol{\eta}(r, r) \quad \text{and } \boldsymbol{\xi} = \boldsymbol{\xi}(r, r)$$

are positive left and right eigenvectors associated with the eigenvalue 1 of the matrix $\mathcal{M}(r, r)$, and satisfying $\boldsymbol{\eta}^{\mathrm{t}}\boldsymbol{\xi} = 1$.

Thus, the evolutionary equilibrium strategies are characterized by the equation (Taylor, 1985)

$$\boldsymbol{\eta}^{\mathrm{t}}\left[\frac{\partial}{\partial s}\mathcal{M}(r, s)\bigg|_{s=r}\right]\boldsymbol{\xi} = 0. \tag{5}$$

Evolutionary Stability

Let r^* be an evolutionary equilibrium strategy. We say that r^* is a local ESS or, simply, an ESS (*evolutionarily stable strategy*, following Maynard Smith & Price, 1973), if r^* satisfies eqn (4).

We look for an equivalent condition easier to use. To find such a condition, we develop further an approach suggested by Taylor & Bulmer (1980). Since $\lambda(r, s)$ is an eigenvalue of the matrix $\mathcal{M}(r, s)$ (by the Perron–Frobenius theory), then $\lambda(r, s)$ is a solution to the equation

$$f(r, s, \lambda) = 0,$$

where

$$f(r, s, \lambda) = det(\lambda I - \mathcal{M}(r, s))$$

is the characteristic polynomial of $\mathcal{M}(r, s)$. Taking the derivative of the characteristic polynomial with respect to s, we obtain

$$\frac{\partial f}{\partial s} + \frac{\partial f}{\partial \lambda}\frac{\partial \lambda}{\partial s} = 0, \tag{6}$$

where the first term represents the derivative of f with respect to s, keeping λ constant. Then, we have

$$\frac{\partial \lambda}{\partial s}\bigg|_{s=r=r^*} = 0$$

if and only if

$$\left.\frac{\partial f}{\partial s}\right|_{s=r=r^*} = 0,$$

unless $(\partial f/\partial\lambda)|_{s=r=r^*} = 0$. But (see Appendix A), we always have

$$\left.\frac{\partial f}{\partial \lambda}\right|_{s=r=r^*} > 0. \tag{7}$$

Thus, the condition

$$\left.\frac{\partial f}{\partial s}\right|_{s=r=r^*} = \frac{\partial}{\partial\lambda}\, det(I - \mathscr{M}(r, s))|_{s=r=r^*} = 0,$$

which is equivalent to eqns (3) and (5), can be used to determine evolutionary equilibrium strategies (Taylor & Bulmer, 1980).

Now, let us take once more the derivative with respect to s on both sides of eqn (6). We get

$$\frac{\partial}{\partial s}\left[\frac{\partial f}{\partial s} + \frac{\partial f}{\partial \lambda}\frac{\partial \lambda}{\partial s}\right] + \frac{\partial \lambda}{\partial s} \times \frac{\partial}{\partial \lambda}\left[\frac{\partial f}{\partial s} + \frac{\partial f}{\partial \lambda}\frac{\partial \lambda}{\partial s}\right] = 0.$$

When $s = r = r^*$, we have $\partial\lambda/\partial s = 0$, and then, at this point, the above equation becomes

$$\frac{\partial^2 f}{\partial s^2} + \frac{\partial^2 \lambda}{\partial s^2}\frac{\partial f}{\partial \lambda} = 0.$$

Thus, when $s = r = r^*$, we have

$$\frac{\partial^2 \lambda}{\partial s^2} = -\frac{(\partial^2 f/\partial s^2)}{(\partial f/\partial \lambda)}. \tag{8}$$

Since $\partial f/\partial\lambda|_{s=r} > 0$ (see Appendix A), then

$$\left.\frac{\partial^2 \lambda}{\partial s^2}\right|_{s=r=r^*} \quad \text{and} \quad -\left.\frac{\partial^2 f}{\partial s^2}\right|_{s=r=r^*}$$

have the same sign. This proves the following result.

Result 1. *If a resident strategy r is confronted to one mutant strategy s, then an evolutionary equilibrium strategy r^* is an ESS if*

$$\left.\frac{\partial^2 f}{\partial s^2}\right|_{s=r=r^*} > 0, \tag{9}$$

where $f = det(I - \mathscr{M}(r, s))$.

Continuous Stability

Suppose that the population is fixed for a strategy r near an ESS strategy r^*. Will it be selectively advantageous for a mutant individual to adopt a strategy closer to r^*? If this is the case, then we say that r^* is a *continuously stable strategy* or, simply, a CSS (Eshel, 1983).

More formally, an ESS strategy r^* will be a CSS if there exists an $\varepsilon > 0$ such that, for any strategy r in the ε-neighborhood of r^* (which means that r is within the range $[r^* - \varepsilon, r^* + \varepsilon]$), there exists some $\delta > 0$ such that for any strategy s in the δ-neighborhood of r, we have

$$\lambda(r, s) > 1 \quad \text{if and only if } |s - r^*| < |r - r^*|.$$

Eshel (1983) derived the following condition for an ESS to be a CSS. Let r^* be an ESS.

(i) If r^* is a CSS, then, for $s = r = r^*$, we have

$$\frac{\partial^2}{\partial r\, \partial s}\lambda(r, s) + \frac{\partial^2}{\partial s^2}\lambda(r, s) \leqslant 0.$$

(ii) If, for $s = r = r^*$, we have

$$\frac{\partial^2}{\partial r\, \partial s}\lambda(r, s) + \frac{\partial^2}{\partial s^2}\lambda(r, s) < 0, \tag{10}$$

then r^* is a CSS.

For the same reason as before, we wish to find an equivalent condition for an ESS to be a CSS. To do this, we consider the following Taylor series around the point $s = r = r^*$:

$$\left.\frac{\partial}{\partial s}\lambda(r, s)\right|_{s=r=r^*+\theta} = \left.\frac{\partial}{\partial s}\lambda(r, s)\right|_{s=r=r^*}$$

$$+ \theta\left[\frac{\partial^2}{\partial s^2}\lambda(r, s) + \frac{\partial^2}{\partial r\, \partial s}\lambda(r, s)\right]_{s=r=r^*} + o(\theta)$$

and

$$\frac{\partial}{\partial r}\lambda(r,s)\Big|_{s=r=r^*+\theta} = \frac{\partial}{\partial r}\lambda(r,s)\Big|_{s=r=r^*}$$

$$+\theta\left[\frac{\partial^2}{\partial r^2}\lambda(r,s)+\frac{\partial^2}{\partial s\,\partial r}\lambda(r,s)\right]_{s=r=r^*}+o(\theta),$$

where $o(\theta)$ designates any function such that $o(\theta)/\theta$ goes to 0 as θ goes to 0. Combining the above two expressions, we get

$$\frac{\partial}{\partial s}\lambda(r,s)\Big|_{s=r=r^*+\theta}+\frac{\partial}{\partial r}\lambda(r,s)\Big|_{s=r=r^*+\theta}$$

$$=\frac{\partial}{\partial s}\lambda(r,s)\Big|_{s=r=r^*}+\frac{\partial}{\partial r}\lambda(r,s)\Big|_{s=r=r^*}$$

$$+\theta\left[\frac{\partial^2}{\partial s^2}\lambda(r,s)+\frac{\partial^2}{\partial r\,\partial s}\lambda(r,s)\right.$$

$$\left.+\frac{\partial^2}{\partial r^2}\lambda(r,s)\right.$$

$$\left.+\frac{\partial^2}{\partial s\,\partial r}\lambda(r,s)\right]_{s=r=r^*}+o(\theta).$$

Since $\lambda(r,r)=1$ for all r in (0, 1), then the derivative of $\lambda(r,s)$ in the direction of the diagonal evaluated on the diagonal (that is, when $s=r$) is 0. Moreover, this directional derivative, denoted by $D\lambda(r,s)$, is given by

$$D\lambda(r,s)|_{s=r}=\cos(\pi/4)\frac{\partial}{\partial r}\lambda(r,s)\Big|_{s=r}$$

$$+\sin(\pi/4)\frac{\partial}{\partial s}\lambda(r,s)\Big|_{s=r}$$

$$=\frac{\sqrt{2}}{2}\left[\frac{\partial}{\partial r}\lambda(r,s)\Big|_{s=r}+\frac{\partial}{\partial s}\lambda(r,s)\Big|_{s=r}\right]$$

$$=0.$$

Since r^* is an ESS, then

$$\frac{\partial}{\partial s}\lambda(r,s)\Big|_{s=r=r^*}=0,$$

which implies

$$\frac{\partial}{\partial r}\lambda(r,s)\Big|_{s=r=r^*}=0.$$

Thus, we have

$$0=\theta\left[\frac{\partial^2}{\partial s^2}\lambda(r,s)+\frac{\partial^2}{\partial r\,\partial s}\lambda(r,s)+\frac{\partial^2}{\partial r^2}\lambda(r,s)\right.$$

$$\left.+\frac{\partial^2}{\partial s\,\partial r}\lambda(r,s)\right]_{s=r=r^*}+o(\theta)$$

for θ sufficiently small. Therefore, we obtain the following equality:

$$\left[\frac{\partial^2}{\partial s^2}\lambda(r,s)+\frac{\partial^2}{\partial r\,\partial s}\lambda(r,s)\right]_{s=r=r^*}$$

$$=-\left[\frac{\partial^2}{\partial r^2}\lambda(r,s)+\frac{\partial^2}{\partial s\,\partial r}\lambda(r,s)\right]_{s=r=r^*} \tag{11}$$

On the other hand, for $s=r=r^*$, we have

$$\frac{\partial^2}{\partial r^2}\lambda(r,s)=-\frac{(\partial^2 f/\partial r^2)}{(\partial f/\partial\lambda)} \quad \text{and}$$

$$\frac{\partial^2}{\partial r\,\partial s}\lambda(r,s)=-\frac{(\partial^2 f/\partial r\,\partial s)}{(\partial f/\partial\lambda)}. \tag{12}$$

Finally, using eqns (8), (11) and (12), we obtain the following result.

Result 2. *Let r^* be an ESS and $f=det(I-\mathscr{M}(r,s))$.*

(i) *If r^* is a CSS, then, for $s = r = r^*$, we have*

$$\frac{\partial^2 f}{\partial s^2} + \frac{\partial^2 f}{\partial r \partial s} \geqslant 0$$

$$\left(\textit{or, in an equivalent form, } \frac{\partial^2 f}{\partial r^2} + \frac{\partial^2 f}{\partial s \partial r} \leqslant 0 \right).$$

(ii) *If, for $s = r = r^*$, we have*

$$\frac{\partial^2 f}{\partial s^2} + \frac{\partial^2 f}{\partial r \partial s} > 0$$

$$\left(\textit{or, in an equivalent form, } \frac{\partial^2 f}{\partial r^2} + \frac{\partial^2 f}{\partial s \partial r} < 0 \right), \tag{13}$$

then r^* is a CSS.

Invadability Property

Let r^* be a CSS strategy. Then, we would like to know if r^* has also the property of *invading, when rare, any other fixed strategy* at least sufficiently close to it. Proceeding as previously, we get that this will be the case if we have the inequality

$$\frac{\partial^2}{\partial r^2} \lambda(r, s)\bigg|_{s=r=r^*} > 0,$$

which is equivalent to the converse inequality for the corresponding partial derivative of the characteristic polynomial.

Result 3. *A CSS strategy r^* will invade, when rare, any other fixed strategy sufficiently close to it if*

$$\frac{\partial^2 f}{\partial r^2}\bigg|_{s=r=r^*} < 0, \tag{14}$$

where $f = det(I - \mathcal{M}(r, s))$.

Note that, in the case where r^* is not a CSS, the above condition cannot be satisfied by r^*. Indeed, using eqns (10) and (11), we have

$$\frac{\partial^2}{\partial s^2} \lambda(r, s)\bigg|_{s=r=r^*} \geqslant -\frac{\partial^2}{\partial r \partial s} \lambda(r, s)\bigg|_{s=r=r^*}$$

and

$$\frac{\partial^2}{\partial r^2} \lambda(r, s)\bigg|_{s=r=r^*} \leqslant -\frac{\partial^2}{\partial r \partial s} \lambda(r, s)\bigg|_{s=r=r^*}.$$

Thus, we have

$$\frac{\partial^2}{\partial r^2} \lambda(r, s)\bigg|_{s=r=r^*} \leqslant \frac{\partial^2}{\partial s^2} \lambda(r, s)\bigg|_{s=r=r^*}.$$

But, since r^* is an ESS, then

$$\frac{\partial^2}{\partial s^2} \lambda(r, s)\bigg|_{s=r=r^*} < 0$$

and, consequently, we get

$$\frac{\partial^2}{\partial r^2} \lambda(r, s)\bigg|_{s=r=r^*} < 0.$$

Case without Dominance

If there is no dominance, diploid individuals will adopt different strategies according to the number of mutant genes that they will carry at a single locus. Suppose that *RR* individuals adopt strategy r, *SS* individuals adopt strategy s and *SR* individuals adopt strategy t.

The linearized matrix associated with the recurrence equation $\mathbf{x}' = \mathcal{T}(\mathbf{x})$ will now depend on r, s and t. This time we are looking for a strategy r which satisfies

$$\lambda(r, s, t) < 1 \quad \text{for all } s \neq r \text{ and } t \neq r,$$

where $\lambda(r, s, t)$ is the spectral radius of the matrix $\mathcal{M}(r, s, t)$. Assuming the function $\lambda(r, s, t)$ regular enough, we must have

$$\frac{\partial}{\partial s} \lambda(r, s, t)\bigg|_{s=t=r} = 0 \tag{15}$$

and

$$\frac{\partial}{\partial t}\lambda(r, s, t)\Big|_{s=t=r} = 0, \tag{16}$$

for r to be an evolutionary equilibrium strategy. Proceeding as before, these conditions become, respectively,

$$\boldsymbol{\eta}^{t}\left[\frac{\partial}{\partial s}\mathcal{M}(r, s, t)\Big|_{s=t=r}\right]\boldsymbol{\xi} = 0 \tag{17}$$

and

$$\boldsymbol{\eta}^{t}\left[\frac{\partial}{\partial t}\mathcal{M}(r, s, t)\Big|_{s=t=r}\right]\boldsymbol{\xi} = 0, \tag{18}$$

where $\boldsymbol{\eta}$ and $\boldsymbol{\xi}$ are positive left and right eigenvectors associated with the eigenvalue $\lambda(r, r, r) = 1$ of the matrix $\mathcal{M}(r, r, r)$, and satisfying $\boldsymbol{\eta}^{t}\boldsymbol{\xi} = 1$.

Furthermore, $\lambda(r, s, t)$ has to be actually maximum when $s = t = r$ for an evolutionary equilibrium strategy r to be an ESS strategy. This leads to the extra conditions

$$\frac{\partial^2}{\partial s^2}\lambda(r, s, t)\Big|_{s=t=r=r^*} = 0 \tag{19}$$

and

$$\left[\frac{\partial^2}{\partial s^2}\lambda(r, s, t)\frac{\partial^2}{\partial t^2}\lambda(r, s, t) - \left(\frac{\partial^2}{\partial t\,\partial s}\lambda(r, s, t)\right)^2\right]_{s=t=r=r^*}$$

$$> 0. \tag{20}$$

Proceeding as before, we get the following identities:

$$\frac{\partial^2\lambda}{\partial s^2} = -\frac{(\partial^2 f/\partial s^2)}{(\partial f/\partial\lambda)}, \qquad \frac{\partial^2\lambda}{\partial t^2} = -\frac{(\partial^2 f/\partial t^2)}{(\partial f/\partial\lambda)},$$

and

$$\frac{\partial^2\lambda}{\partial t\,\partial s} = -\frac{(\partial^2 f/\partial t\,\partial s)}{(\partial f/\partial\lambda)}.$$

This leads to the result below.

Result 4. *If a resident strategy r is confronted to two mutant strategies s and t, then an evolutionary equilibrium strategy r^* is an ESS if*

$$\frac{\partial^2 f}{\partial s^2}\Big|_{s=r=r^*} > 0 \quad \textit{and}$$

$$\left[\frac{\partial^2 f}{\partial s^2}\frac{\partial^2 f}{\partial t^2} - \left(\frac{\partial^2 f}{\partial t\,\partial s}\right)^2\right]_{s=r=r^*} > 0, \tag{21}$$

where $f = det(I - \mathcal{M}(r, s, t))$.

Model I: LMC Model with Partial Outbreeding

We consider a very large number of colonies founded by N inseminated females. Following reproduction, a female offspring mate with a male offspring within the same colony with probability β and mate with a male offspring chosen at random in the population at large with probability $1 - \beta$. The newly inseminated females randomly disperse and form colonies of size N. If we assume that the newly inseminated females compete between themselves before dispersal such that the contribution of every colony to the next generation is the same, then we will say that there is *regulation*, actually local population regulation. Otherwise, we will say that there is *no regulation*. We also assume that each inseminated female has a very large number of offspring and that generations are non-overlapping. The sex ratio among the offspring is determined either by the mother or the father (*maternal control* or *paternal control*).

With the method developed in the previous sections, we have determined evolutionary equilibrium sex ratios in the general case, without any assumption on the dominance of gene S. Then we have checked whether or not these sex ratios were optimal in the ESS and CSS senses and if they were invading any other fixed sex ratio sufficiently close to them. Symbolic calculations were performed using softwares as MATHEMATICA and MAPLE. For haploid and diploid populations, a shortcut is available because of symmetry in gene transmission to male and female offspring, as in Taylor & Bulmer (1980) and Karlin & Lessard (1986). Some details on the models are presented in Appendices B and C.

TABLE 1
Evolutionary equilibrium sex ratios for model I

	Control	Regulation	$0 \leqslant \beta \leqslant 1$	$\beta = 0$	$\beta = 1$
Haplodiploid	Maternal	No	$\frac{(2N-\beta)(N-\beta)}{N(4N-\beta)}$	$\frac{1}{2}$*	$\frac{(2N-1)(N-1)}{N(4N-1)}$†
		Yes	$\frac{(2N-\beta)(N-\beta)}{(2N-\beta)(N-\beta)+2N(N-1)}$	$\frac{N}{2N-1}$	$\frac{2N-1}{4N-1}$‡
	Paternal	No	$\frac{\beta(N-\beta)}{N(4N-\beta)}$	0§	$\frac{N-1}{N(4N-1)}$†
		Yes	$\frac{\beta(N-\beta)}{\beta(N-\beta)+2(N-1)(2N-\beta)}$	0	$\frac{1}{4N-1}$
Haploid or diploid	Maternal or paternal	No	$\frac{N-\beta}{2N}$‖	$\frac{1}{2}$*	$\frac{N-1}{2N}$†§
		Yes	$\frac{N-\beta}{2N-\beta-1}$‖	$\frac{N}{2N-1}$¶‖	$\frac{1}{2}$**

*Fisher (1958).
†Taylor & Bulmer (1980).
‡Herre (1985).
§Hamilton (1967).
‖Karlin & Lessard (1986).
¶Charnov (1982).
**Wilson & Colwell (1981).

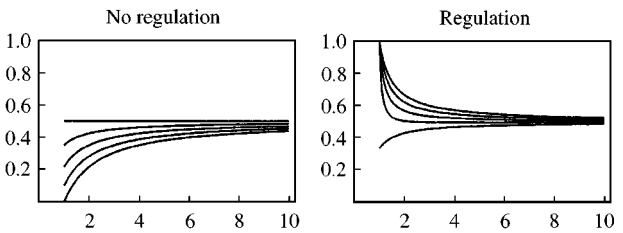

FIG. 1. Evolutionary equilibrium sex ratios for model I as functions of N for $\beta = 0$, 1/4, 1/2, 3/4 and 1: haplodiploid populations with maternal control.

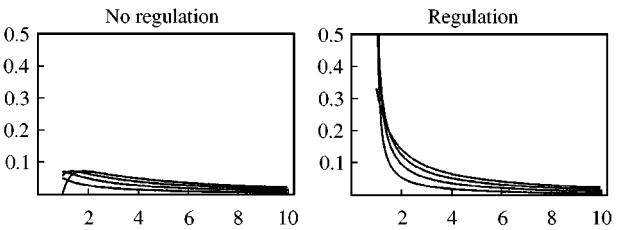

FIG. 2. Evolutionary equilibrium sex ratios for model I as functions of N for $\beta = 0$, 1/4, 1/2, 3/4 and 1: haplodiploid populations with paternal control.

Result 5. *The evolutionary equilibrium sex ratios for model I with or without regulation* (*Table* 1 *and Figs* 1–3) *are ESS and CSS sex ratios for at least* $N \geqslant 2$. *Moreover, they invade, when rare, any other fixed sex ratio sufficiently close to them.*

Model II: LMC Model with Partial Dispersal after Mating

We consider a very large number of colonies founded by N inseminated females. Following

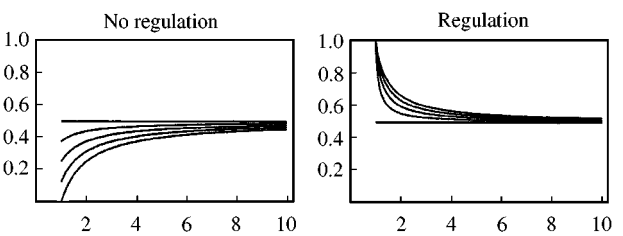

FIG. 3. Evolutionary equilibrium sex ratios for model I as functions of N for $\beta = 0$, 1/4, 1/2, 3/4 and 1: haploid and diploid populations with maternal or paternal control.

reproduction and mating within colonies, a proportion d (with $d > 0$) of the newly inseminated females disperse randomly in the population, while the others stay in their own colony. The newly inseminated females then compete within colonies such that N survive in each colony. Two types of dispersal are considered: *proportional dispersal*, which means that every inseminated female who quits her own colony is replaced by an inseminated female taken at random in the population; and *uniform dispersal*, which means that every colony receives the same amount of inseminated females taken at random in the population. The latter case has already been analysed numerically for small values of N ($N = 2, 3, 4$) by Bulmer (1986) and analytically for any N but in a special case (additive gene action in a diploid population) by Frank (1986b) and Taylor (1988).

Since not all inseminated females disperse, we cannot suppose that a colony is formed by no more than one mutant female and at least $N - 1$ resident females. In the previous model, this assumption was legitimate because of total dispersal of inseminated females. We have been able, using MATHEMATICA and MAPLE, to determine the evolutionary equilibrium sex ratio and its optimality properties for a population of haploid individuals in the case $N = 2$.

Result 6. *Consider model II for a haploid population in the case $N = 2$. In the case of proportional dispersal, the evolutionary equilibrium sex ratio is*

$$r^* = \frac{2 - d}{2(3 - d)},$$

which is optimal in the ESS and CSS senses and which invades when rare any other fixed sex ratio. In the case of uniform dispersal, the sex ratio which has the same properties is

$$r^* = \frac{1}{4},$$

which does not depend on the parameter d, in agreement with previous studies.

Some details on the models are provided in Appendix D. Note that the evolutionary equilibrium sex ratio in the case of proportional dispersal decreases from 1/3 to 1/4 as the dispersal rate d goes from 0 to 1.

Model III: LMC Model with Partial Dispersal before Mating

In this model, we suppose that dispersal of male and female offspring occurs before mating. More precisely, we assume that a proportion d_1 of female offspring and a proportion d_2 of male offspring randomly disperse and then mate within their colony. The newly inseminated females compete within the colonies and N survive in each colony. We also suppose that sex ratio control is maternal.

We consider two types of dispersal for males and females: *proportional dispersal* and *uniform dispersal*. As for model II, we concentrate on small values of N ($N = 1, 2$) and use MATHEMATICA and MAPLE. The evolutionary equilibrium sex ratios are shown in Table 2 and some details for the analysis are given in Appendix E.

Bulmer (1986) has already determined numerically the evolutionary equilibrium sex ratio for this model in the case of uniform dispersal. The haploid model with uniform dispersal for any N has been analysed by Frank (1986b). Our results are in agreement with Bulmer's results except for a haplodiploid population. Bulmer's results show a little difference on the evolutionary equilibrium sex ratio according to S recessive, dominant or additive (this means that the heterozygote RS produces a sex ratio $(s + r)/2$) in the haplodiploid case, even for $N = 1$. With the method developed in this paper, we have determined exactly the evolutionary equilibrium sex ratio in the more general case where S is codominant (this means that the heterozygote RS produces a sex ratio t). Our results show, however, no influence of the degree of dominance of the mutant gene S on the evolutionary equilibrium sex ratio at least in the case $N = 1$. On the other hand, our analytical results for the haploid model with uniform dispersal correspond to the Frank (1986b) results in the cases $N = 1, 2$. But there are differences in the evolutionary equilibrium sex ratios and their optimality properties when dispersal is proportional.

TABLE 2
Evolutionary equilibrium sex ratios for model III

	Dispersal	$0 \leqslant d_1 \leqslant 1$ $0 \leqslant d_2 \leqslant 1$	$d_1 = 1$ $d_2 = 0$	$d_1 = 0$ $d_2 = 1$
$N = 1$ haploid and diploid	Prop.	$\frac{d_2}{d_1 + d_2}$	0	1
	Uniform	$\frac{d_2(2 - d_2)}{d_1(2 - d_1) + d_2(2 - d_2)}$*	0†	1†
$N = 1$ haplodiploid	Prop.	$\frac{d_2(1 + d_1 + d_2 - d_1 d_2)}{2d_1 + d_2(1 + d_1 + d_2 - d_1 d_2)}$	0	1
	Uniform	$\frac{d_2(2 - d_2)(1 + d_1 + d_2 - d_1 d_2)}{2d_1(2 - d_1) + d_2(2 - d_2)(1 + d_1 + d_2 - d_1 d_2)}$	0	1
$N = 2$ haploid	Prop.	$\frac{d_1(10 - 3d_1) + 14d_2 + d_2^2(1 - d_2) - d_1 d_2(6 - d_1)}{4d_1(7 - 2d_1) + d_1^3 + 20d_2 - d_2^3 - d_1 d_2(8 - d_1 + d_2)}$	1/3	14/19
	Uniform	$\frac{d_1(10 - 3d_1) + d_2(22 - 5d_2) - d_2^3(4 - d_2) - d_1 d_2(8 - 2d_1 - 2d_2 + d_1 d_2)}{18d_1(2 - d_1) + 2d_2(14 - 3d_2) + d_1^3(4 - d_1) - d_2^3(4 - d_2) - 8d_1 d_2}$*	1/3†	14/19†

*Frank (1986b) in the haploid case for any N.
†Bulmer (1986) in the haploid case.

Result 7. *For $N = 1$ and at least for uniform dispersal, all evolutionary equilibrium sex ratios for model III (Table 2) are ESS and CSS besides invading, when rare, any other nearby fixed sex ratio. For proportional dispersal, in the haploid and diploid cases, stability analysis of the evolutionary equilibrium sex ratio degenerates, while in the haplodiploid case, the evolutionary equilibrium sex ratio is not ESS. For $N = 2$, the evolutionary equilibrium sex ratios in the haploid case with uniform dispersal and proportional dispersal are different when $d_1 \neq d_2$ (Table 2).*

In fact, in the haplodiploid case for $N = 1$, the evolutionary equilibrium sex ratio is the worst strategy a haplodiploid can adopt, since it will be invaded by any other strategy. For $N = 2$, we did not manage to do the calculations necessary to verify stability in the haploid case and to determine the evolutionary equilibrium sex ratios in the diploid and haplodiploid cases. See Appendix E for some details on the models.

Discussion

We have made effort to bring completeness and mathematical rigor in the study of sex ratio evolution in the structured populations. We have developed tractable algebraic criteria for optimal properties such as evolutionary equilibrium, evolutionary stability, continuous stability and invadability. These criteria bear on the characteristic polynomial of the linearized transformation for the population state near fixation and its first and second partial derivatives. With the assistance of computer softwares for symbolic calculations (MATHEMATICA and MAPLE), we have been able to get analytical results on optimal sex ratios in LMC models taking into account several factors such as population ploidy, paternal or maternal control, co-dominant gene action, regulation of colony size, partial dispersal, proportional or uniform. Three breeding assumptions have been considered: partial outbreeding (model I), partial dispersal after mating (model II), partial dispersal before mating (model III).

With complete dispersal after mating (Table 1), the case of complete outbreeding ($\beta = 0$) without regulation corresponds to a panmictic situation and the evolutionary equilibrium sex ratio is $\frac{1}{2}$ except in a haplodiploid population with paternal control of the sex ratio for which it is 0. The case of no outbreeding ($\beta = 1$) without regulation

corresponds to the original LMC situation (Hamilton, 1967). It is interesting to note that the evolutionary equilibrium sex ratio in this case is always equal to $(N-1)/N$ times the evolutionary equilibrium sex ratio in the case of no outbreeding ($\beta = 1$) but with regulation, which removes the LMC advantage of a female-biased sex ratio, competition of males for mates being counterbalanced by competition of females for limited resources. But the evolutionary equilibrium sex ratio in haplodiploid populations remains female-biased in the case of maternal control and positive in the case of paternal control as an effect of non-symmetric but always positive relatedness of the controlling parent to its male and female offspring as noted by Herre (1985). In the case of complete outbreeding ($\beta = 0$) with regulation, the evolutionary equilibrium sex ratio is male-biased in order to reduce LRC except in haplodiploid populations with paternal control for which it is 0, fathers being unrelated to their sons. As a function of β, the evolutionary equilibrium sex ratio is monotome. As the proportion of outbreeding increases (β decreases), the evolutionary equilibrium sex ratio increases or decreases when $N \geqslant 2$, but there is little difference as soon as $N \geqslant 10$ (Figs 1–3). West & Herre (1998) studied 17 species of fig wasps, ten with wingless males, who must mate within their natal patch before dispersal of females, and seven with winged males who can practice partial outbreeding. As expected for haplodiploid species with maternal control and no regulation, species with winged males had less female-biased sex ratios than species with wingless males.

Introducing limited but uniform dispersal, Bulmer (1986) obtained little or no effect on the evolutionary equilibrium sex ratio if dispersal occurs after mating, but a bias of the sex ratio towards the sex with the highest dispersal rate to lower competition between sibs of that sex if dispersal occurs before mating. The conclusion in the first case challenged the Grafen (1984) prediction for a more female-biased sex ratio with decreasing dispersal explained by a kin selection factor when females in each breeding colony are related. But it seems that the increase in reproductive success of ones relatives' sons is exactly counterbalanced by the decrease in reproductive success of ones relatives' daughters who do not disperse. With proportional dispersal after mating, there is a kind of regulation after dispersal which favors a less female-biased sex ratio. In the case of dispersal before mating with $N = 1$, proportional dispersal favors a more pronounced bias of the sex ratio towards the sex with the highest dispersal rate than uniform dispersal, but this is not always true when $N = 2$.

Note that, in several cases (model I, models II and III in the case of proportional dispersal), the evolutionary equilibrium sex ratios have been obtained for the first time, in others (models II and III in the case of uniform dispersal), previous numerical results (Bulmer, 1986) or analytical results (Frank, 1986b; Taylor, 1988; Taylor & Frank, 1996) have been complemented. Among our most valuable findings is the rather robust result that the evolutionary equilibrium sex ratios, in all cases considered, are independent of the degree of dominance of the mutant genes. This challenges different numerical findings, at least for haplodiploid populations, in the case of partial uniform dispersal before mating. Another particularly interesting result is the fact that the evolutionary equilibrium sex ratio obtained in the case of partial dispersal after mating, depends on the dispersal rate when dispersal is proportional, but not when it is uniform.

Finally, all the evolutionary equilibrium sex ratios obtained, except those in model III with partial proportional dispersal before mating, have been shown for the first time to be evolutionarily stable (ESS) and continuously stable (CSS) besides to invade, at least when rare, any other closeby strategy once fixed in the population. However, in the haplodiploid case considered with partial proportional dispersal before mating, we have shown that the evolutionary equilibrium sex ratio is not an ESS and is actually invaded by any other rare mutant. Therefore, it is not sufficient to check evolutionary equilibrium to conclude about evolutionary stability.

This paper is part of a Ph.D. thesis defended by Josiane Courteau supervised by Sabin Lessard. More details on the appendices can be found on the web page ⟨http://www.dms.umontreal.ca/~courteau/⟩.
The authors thank the external examiner, Prof. Carlo Matessi, for very helpful comments. They also thank Dr S. A. West and an anonymous referee for pertinent references and constructive comments on an earlier draft of this paper.

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APPENDIX A

Property of the Characteristic Polynomial

Let us determine the sign of $\partial f/\partial\lambda$ when $s = r$, where $f = det(\lambda I - \mathscr{M}(r, s))$ is the characteristic polynomial of the matrix $\mathscr{M}(r, s)$. This determinant can be written as

$$(\lambda - \lambda_1)(\lambda - \lambda_2)\ldots(\lambda - \lambda_{n-1}),$$

where $\lambda_1, \ldots, \lambda_{n-1}$ are the $n - 1$ eigenvalues of the matrix $\mathscr{M}(r, s)$. Without loss of generality, we can suppose that $\lambda_1 = \lambda(r, s)$, the spectral radius of $\mathscr{M}(r, s)$. Taking the derivative of f with respect

to λ yields

$$\frac{\partial f}{\partial \lambda} = (\lambda - \lambda_2)\dots(\lambda - \lambda_{n-1})$$

$$+ (\lambda - \lambda_1)\frac{\partial}{\partial \lambda}[(\lambda - \lambda_2)\dots(\lambda - \lambda_{n-1})].$$

When $s = r$, we have $\lambda = \lambda(r, r) = \lambda_1 = 1$ and, therefore,

$$\left.\frac{\partial f}{\partial \lambda}\right|_{s=r} = (1 - \lambda_2)\dots(1 - \lambda_{n-1}).$$

On the other hand, $\lambda_1 = 1 \geqslant |\lambda_j|$ for $j = 2, \dots, n-1$ by the definition of the spectral radius. Moreover, since the eigenvalue 1 is simple, then the other eigenvalues are all different from 1. This ensures that the above derivative is non-zero when $s = r$. If λ_j is a real eigenvalue, then $(1 - \lambda_j) > 0$. If $\lambda_j = a + ib$, with $b \neq 0$, that is, λ_j is a complex eigenvalue, then necessarily $\bar{\lambda}_j = a - ib$ is also a complex eigenvalue. Then

$$(1 - \lambda_j)(1 - \bar{\lambda}_j) = (1 - a)^2 + b^2 > 0.$$

Thus,

$$\left.\frac{\partial f}{\partial \lambda}\right|_{s=r} > 0.$$

APPENDIX B

Model I for Haplodiploid Populations

Assuming the mutant gene S rare, most of the mutant colonies will be of the types

$$(2, 1), (2, 0), (1, 1), (1, 0), (0, 1),$$

where (i, j) means a colony founded by $N - 1$ non-mutant inseminated females and one mutant inseminated female (i, j), where i and j are the numbers of gene S carried by the female and her mate, respectively, with $i + j \geqslant 1$. Let $x(i, j)$ be the frequency of the mutant colonies (i, j) and

$$\mathbf{x} = (x(2, 1), x(2, 0), x(1, 1), x(1, 0), x(0, 1)).$$

A non-mutant colony is represented by $(0, 0)$ and the frequency of all non-mutant colonies is given by

$$x(0, 0) = 1 - x(2, 1) - x(2, 0) - x(1, 1)$$

$$- x(1, 0) - x(0, 1).$$

At the next generation, the frequency of the mutant colonies (i, j) becomes

$$x'(i, j) = N[P^{(i,j)}_{(2,1)}C(2, 1) + \dots + P^{(i,j)}_{(0,0)}C(0, 0)]$$

$$+ \text{higher-order terms in } \mathbf{x},$$

where

$$P^{(i,j)}_{(k,l)} = \text{proportion of mutant inseminated females } (i, j) \text{ coming from colonies } (k, l)$$

and

$$C(k, l) = \text{proportion of inseminated females coming from colonies } (k, l).$$

APPENDIX C

Model I for Haploid Populations

C.1. CASE OF NO REGULATION

We suppose that the inseminated females $(1, j)$ and $(0, j)$ have a sex ratio given, respectively, by s and r. Let $\psi(\mathrm{i}, j)$ be the frequency of gene S transmitted to the next generation by all inseminated females of type (i, j) and $f(i, j)$ be the frequency of females of type (i, j) in the population. The frequency of S in females (i, j) is $[(i + j)/2] f(i, j)$. We are looking for r satisfying

$$\psi(i, j) \leqslant \left(\frac{i + j}{2}\right) f(i, j) \quad \text{for all } s \neq r \quad \text{(A.1)}$$

with strict inequality for at least one (i, j). We have

$$\psi(i, j) = \tfrac{1}{2}\phi_1(i, j) + \tfrac{1}{2}\phi_2(i, j),$$

where

$\phi_1(i,j)$ = expected frequency of S transmitted to the next generation by the female offspring of (i,j)

$$= \left(\frac{i+j}{2}\right) f(i,j) k_1(r,s,i)$$

and

$\phi_2(i,j)$ = expected frequency of S transmitted to the next generation by the male offspring of (i,j)

$$= \left(\frac{i+j}{2}\right) f(i,j) k_2(r,s,i),$$

where

$$k_1(r,s,i) = \begin{cases} (1-s)/(1-r) & \text{if } i=1, \\ 1 & \text{if } i=0 \end{cases}$$

find the solution

$$r = \frac{N-\beta}{2N}.$$

C.2. CASE OF REGULATION

In this case, we have

$$\psi(i,j) = \tfrac{1}{2}\phi_1(i,j) + \tfrac{1}{2}\phi_2(i,j),$$

where

$$\phi_1(i,j) = \begin{cases} \left(\frac{i+j}{2}\right)\left[\frac{Nf(i,j)(1-s)}{(1-s)+(N-1)(1-r)}\right] & \text{if } i=1, \\ \left(\frac{i+j}{2}\right) f(i,j) & \text{if } i=0 \end{cases}$$

and

$$\phi_2(i,j) = \begin{cases} \left(\frac{i+j}{2}\right) f(i,j)\left[\beta\frac{Ns}{s+(N-1)r} + (1-\beta)\frac{s}{r}\right] & \text{if } i=1, \\ \left(\frac{i+j}{2}\right) f(i,j) & \text{if } i=0. \end{cases}$$

and

$$k_2(r,s,i) = \begin{cases} \beta\frac{s}{s+(N-1)r}\frac{(1-s)+(N-1)(1-r)}{(1-r)} + (1-\beta)\frac{s}{r} & \text{if } i=1, \\ 1 & \text{if } i=0. \end{cases}$$

Then,

$$\psi(i,j) = \left(\frac{i+j}{4}\right) f(i,j) g(r,s,i),$$

where

$$g(r,s,i) = k_1(r,s,i) + k_2(r,s,i).$$

Therefore, we are looking for r such that $g(r,s,i) < 2$ for all $s \neq r$, for at least one (i,j). We

The equation

$$\psi(i,j) < \left(\frac{i+j}{2}\right) f(i,j) \quad \text{for all } s \neq r$$

is satisfied for at least one (i,j) if and only if

$$g(r,s) = \frac{N(1-s)}{(1-s)+(N-1)(1-r)} + \beta\frac{Ns}{s+(N-1)r} + (1-\beta)\frac{s}{r} < 2.$$

This is true if and only if

$$r = \frac{(N-\beta)}{2N-\beta-1}.$$

APPENDIX D

Model II for Haploid Populations in the case $N = 2$

An inseminated female is of type (i, j) if she has i mutant genes S in her genotype and j genes S in her mate's genotype. When individuals are haploid with two inseminated females by colony, there are ten types of colonies:

$\{(1,1),(1,1)\}$	$\{(1,1),(1,0)\}$	$\{(1,1),(0,1)\}$	$\{(1,1),(0,0)\}$	$\{(1,0),(1,0)\}$
↓	↓	↓	↓	↓
1	2	3	4	5
$\{(1,0),(0,1)\}$	$\{(1,0),(0,0)\}$	$\{(0,1),(0,1)\}$	$\{(0,1),(0,0)\}$	$\{(0,0),(0,0)\}$,
↓	↓	↓	↓	↓
6	7	8	9	10

where $\{(i_1, i_2), (i_3, i_4)\}$ is a colony founded by one inseminated female of type (i_1, i_2) and one of type (i_3, i_4). Let x_j be the frequency of all colonies of type j at a given generation and x_i' be the corresponding frequency at the next generation for $j = 1, 2, \ldots, 10$.

D.1. CASE OF PROPORTIONAL DISPERSAL

We have

$$x_i' = \sum_{j=1}^{10} P_j^i x_j,$$

where P_j^i represents the probability that a colony of type j becomes a colony of type i at the next generation, and

$$P_j^i = (1 + I((i_1, i_2) \neq (i_3, i_4)))[dP^{(i_1, i_2)} + (1-d)P_j^{(i_1, i_2)}][dP^{(i_3, i_4)} + (1-d)P_j^{(i_3, i_4)}],$$

where $P_j^{(i_k, i_{k+1})}$ is the proportion of inseminated females of type (i_k, i_{k+1}) of the new generation produced by a colony of type j, $P^{(i_k, i_{k+1})}$ is the proportion of inseminated females type (i_k, i_{k+1}) of the new generation of migrant females and

$$I(E) = \begin{cases} 1 & \text{if } E \text{ is realized,} \\ 0 & \text{otherwise.} \end{cases}$$

On the other hand, if C_n represents the weighted size of colonies of type n before dispersal, then

$$C_n = \begin{cases} \dfrac{2(1-s)x_n}{K[\mathbf{x}]}, & i = 1,\ 2,\ 5, \\ \dfrac{[(1-s)+(1-r)]x_n}{K[\mathbf{x}]}, & i = 3,\ 4,\ 6,\ 7, \\ \dfrac{2(1-r)x_n}{K[\mathbf{x}]}, & i = 8,\ 9,\ 10 \end{cases}$$

with

$$K[\mathbf{x}] = 2(1-s)[x_1 + x_2 + x_5] + [(1-s) + (1-r)][x_3 + x_4 + x_6 + x_7] + 2(1-r)[x_8 + x_9 + x_{10}]$$

and

$$P^{(i_k, i_{k+1})} = \sum_{n=1}^{10} P_n^{(i_k, i_{k+1})} C_n.$$

Then, for $i = \{(i_1, i_2), (i_3, i_4)\}$, we have

$$x_i' = (1 + I((i_1, i_2) \neq (i_3, i_4)))$$
$$\times \sum_{j=1}^{10} \left[\left(d \sum_{n=1}^{10} P_n^{(i_1, i_2)} C_n + (1-d) P_j^{(i_1, i_2)} \right) \right.$$
$$\left. \times \left(d \sum_{n=1}^{10} P_n^{(i_3, i_4)} C_n + (1-d) P_j^{(i_3, i_4)} \right) \right].$$

D.2. CASE OF UNIFORM DISPERSAL

Let

$$f_j(d) = \frac{d\bar{M}}{d\bar{M} + (1-d) M_j},$$

where

$$M_j = \begin{cases} 2(1-s) & \text{if } j = 1,\ 2,\ 5, \\ (1-s) + (1-r) & \text{if } j = 3,\ 4,\ 6,\ 7, \\ 2(1-r) & \text{if } j = 8,\ 9,\ 10 \end{cases}$$

and

$$\bar{M} = \sum_{k=1}^{10} M_k x_k.$$

Proceeding as before, we have

$$P_j^i = (1 + I((i_1, i_2) \neq (i_3, i_4)))[f_j(d) P^{(i_1, i_2)}$$
$$+ (1 - f_j(d)) P_j^{(i_1, i_2)}][f_j(d) P^{(i_3, i_4)}$$
$$+ (1 - f_j(d)) P_j^{(i_3, i_4)}]$$

and for $i = \{(i_1, i_2), (i_3, i_4)\}$,

$$x_i' = (1 + I((i_1, i_2) \neq (i_3, i_4)))$$
$$\times \sum_{j=1}^{10} \left[\left(f_j(d) \sum_{n=1}^{10} P_n^{(i_1, i_2)} C_n + (1 - f_j(d)) P_j^{(i_1, i_2)} \right) \right.$$
$$\left. \times \left(f_j(d) \sum_{n=1}^{10} P_n^{(i_3, i_4)} C_n + (1 - f_j(d)) P_j^{(i_3, i_4)} \right) \right] x_j.$$

APPENDIX E

Model III

For $N = 1$ and $n - 1$ types of mutant inseminated females represented by $i = (i_1, i_2)$, with $i_1 + i_2 \geqslant 1$, we have, from one generation to the next,

$$x_i' = \sum_{k=1}^{n-1} (f_k(d_1) P^{i_1} + (1 - f_k(d_1)) P_k^{i_1})$$
$$\times (g_k(d_2) Q^{i_2} + (1 - g_k(d_2)) Q_k^{i_2}) x_k,$$

where $P_k^{i_1}$ and P^{i_1} represent the proportions of female offspring i_1 among the females produced by a colony of type k and those produced by the migrant females, $Q_k^{i_2}$ and Q^{i_2} represent the proportions of male offspring i_2 among the males produced by a colony of type k and those produced by the migrant males, $f_k(d_1)$ and $g_k(d_2)$ correspond to the proportions of female and male migrants in a colony of type k, after dispersion.

For $N = 2$ and for i from 1 to $n - 1$ representing a colony founded by inseminated females of types (i_1, i_2) and (i_3, i_4), we have

$$x_i' = (1 + I((i_1, i_2) \neq (i_3, i_4))) \sum_{k=1}^{n-1} (f_k(d_1) P^{i_1}$$
$$+ (1 - f_k(d_1)) P_k^{i_1})(g_k(d_2) Q^{i_2} + (1 - g_k(d_2)) Q_k^{i_2})$$
$$\times (f_k(d_1) P^{i_3} + (1 - f_k(d_1)) P_k^{i_3})(g_k(d_2) Q^{i_4}$$
$$+ (1 - g_k(d_2)) Q_k^{i_4}) x_k,$$

where, as for the case $N = 1$, $P_k^{i_1}$ and P^{i_1} represent the proportions of female offspring i_1 among all the females produced by a colony of type k and among the immigrant females, $Q_k^{i_2}$ and Q^{i_2} represent the proportions of male offspring i_2 among all the males produced by a colony of type k and among the immigrant males.