

## Sex Ratio in a Stepping-Stone Population with Sex-Specific Dispersal

PETER D. TAYLOR\*

*Department of Mathematics and Statistics, Queen's University,  
Kingston, Ontario K7L 3N6, Canada*

Received September 9, 1992

The theoretical hypothesis that the sex-ratio should be biased towards the sex with the wider and/or more even dispersal pattern is tested and confirmed with an inclusive fitness model in a one-dimensional diploid stepping-stone population in which offspring can remain on their home site or disperse one site to the right or left. Two models are examined, dispersal of both sexes before mating and male dispersal before mating followed by dispersal of mated females. © 1994 Academic Press, Inc.

### INTRODUCTION

Consider a diploid geographically structured sexual population with sex-specific dispersal of offspring from their native site before mating. If this dispersal is only partial, or is spatially limited, then, in the formation of the next generation, we expect a certain amount of competition between same-sex relatives for reproductive resources (referred to as LRC, local resource competition). In this situation, a parent should act to minimize the amount of LRC experienced by her offspring, and in case she has control over her progeny sex-ratio she should bias this ratio toward the sex that experiences the least amount of intrasex LRC. In a homogeneous environment, in which the offspring disperse and then simply compete with their neighbours, if the male and female dispersal patterns differ, we expect different levels of LRC among males and females. This should create a selective force on the sex-ratio and it is this force that I study here. I use an inclusive fitness argument in a population with a stepping-stone pattern of dispersal.

I study here two different dispersal scenarios: one in which both sexes disperse before mating (DDM) and the other in which males disperse before mating and females disperse after mating (DMD). These scenarios

\* E-mail: TAYLORP@QUCDN.QUEENSU.CA.

differ mathematically: in the second, male gametes disperse twice, first with the male and second as part of the mated female. In both cases we ask how the sex-specific dispersal patterns affect the allocation of resources to male and female production.

As a preliminary test of your intuition, I pose at this point the following question. If the male and female dispersal patterns are identical, then in the DDM model, symmetry will dictate that the sex-ratio should be unbiased: but what is the case for the DMD model? Should the sex-ratio still be unbiased, or should it be male-biased or female-biased? (The answer is obtained by looking along the diagonal  $\alpha = \beta$  line in Fig. 3.)

## THE MODEL

### *The Inclusive Fitness Argument*

There are two types of populations one might consider here: dioecious populations of male and female individuals who produce male and female offspring and monoecious populations of hermaphrodites who produce male and female gametes. In an inclusive fitness analysis there is a formal mathematical equivalence between these two cases, and the results obtained below apply to both types of population. I use dioecious language, but if "offspring" is replaced by "gamete" and "mated female" by "seed" or "individual," the results can be interpreted for a monoecious population. Both dispersal scenarios are appropriate for a dioecious animal population, whereas in plant populations, ovules rarely disperse before fertilization, and the DMD scenario is more appropriate. There is one mathematical difference between population types, which has to do with the mechanism of sex-ratio control. In dioecy, this is usually determined by the genotype of only one parent (often the mother), whereas in monoecy, it is typically determined jointly by the two contributing gametes. Here, I in fact make only the latter assumption and suppose sex-ratio control is determined additively by both parental genotypes. This assumption is mathematically convenient in that it provides for the simplest calculation of the relatedness coefficients and gives us a simple formula [Eq. (5)] in the DDM case. As a check on the sensitivity of my results to this assumption, I have compared my DDM results (with biparental control—Fig. 2) with those obtained with the assumption of maternal control and have found them indistinguishable. That is, the source of sex-ratio control seems to have negligible effect on the ESS sex-ratio.

The equation for sex-ratio equilibrium is obtained with an inclusive fitness argument (Hamilton, 1964). According to this approach, the selective effect of an action is calculated as the sum of the fitness on all individuals

in the population who are affected by the action, each such effect weighted by the relatedness of the actor to the individual. The sex-ratio equation is obtained as the condition that, at equilibrium, the inclusive fitness of the parents through male and female offspring must be equal:

$$W_m = W_f. \tag{1}$$

The relatedness of an actor  $x$  to a recipient  $y$  (Hamilton, 1972; Michod and Hamilton, 1980) is defined as

$$R_{xy} = \frac{f_{xy}}{f_{xx}},$$

where  $f_{xy}$  is the coefficient of consanguinity between  $x$  and  $y$  defined as the probability that random alleles at a neutral locus in  $x$  and  $y$  are identical by descent (Crow and Kimura, 1970). I define the following relatedness coefficients.

- $r_i$ : mated pair to its own sex  $i$  offspring ( $= 1$ )
- $R_i$ : mated pair to a random competitor of its own sex  $i$  offspring
- $r_m^\wedge$ : mated pair to a random mate of its own daughter
- $R_m^\wedge$ : mated pair to a random competitor of its daughter's mate.

Then, for both models, the effect on inclusive fitness through a male offspring is

$$\text{DDM and DMD: } W_m = (r_m - R_m) \frac{1-s}{s}, \tag{2}$$

where  $s$  is the sex-ratio (proportion of males) and the last term represents the number of matings that each male can expect. The effect on inclusive fitness through a female offspring is

$$\text{DDM: } W_f = r_f - R_f \tag{3}$$

$$\text{DMD: } W_f = (r_f - R_f) + (r_m^\wedge - R_m^\wedge). \tag{4}$$

The difference between (3) and (4) is explained as follows. In both cases, an extra daughter provides an extra mating for a related male, and this ( $r_m^\wedge$ ) must be added to the inclusive fitness, but the relatedness of the parents to the competitors of that male ( $R_m^\wedge$ ) must be subtracted. In the DDM model,  $r_m^\wedge = R_m^\wedge$ , and this term drops out.

In a spatially structured population with only local dispersal, there is a technical problem with this argument—even when the population is infinite, the equilibrium value of all relatedness coefficients is 1, and  $W_m$

and  $W_f$  both equal zero. This problem is typically resolved with the introduction of long-range migration with the assumption that long-range migrants are unrelated to those they encounter. Alternatively, a mutation rate has the same effect (Crow and Kimura, 1970, p. 470). My approach here is to assume a small long-range migration rate for males or females or both. Thus, in these models, there are two types of offspring movement, *dispersal*, which is local, and *migration*, which is long-range. The sex-ratio results I report below are obtained by taking the limit as the migration rate approaches zero.

*Population Structure: The Stepping-Stone Model*

Bulmer and Taylor (1980) analyzed the DDM model for a one-dimensional population arranged in a circle; they used a one-locus gene-frequency argument and found that the sex-ratio should be biased towards the sex with the wider and/or more even dispersal pattern. Here I propose to use also a one-dimensional configuration, but with an infinite population arranged along a straight line, the so-called stepping-stone model. I verify the qualitative conclusion of Bulmer and Taylor (1980) and compare the results for the DDM and the DMD models.

In the stepping-stone model there is a site at every lattice point in space (1-, 2-, or 3-dimensional) and a single mated female at each site. The female produces a large number of offspring, who may disperse to neighbouring sites, or may migrate to a distant site. After the mating and dispersal phases (following the DDM or the DMD pattern) the mated females on each site

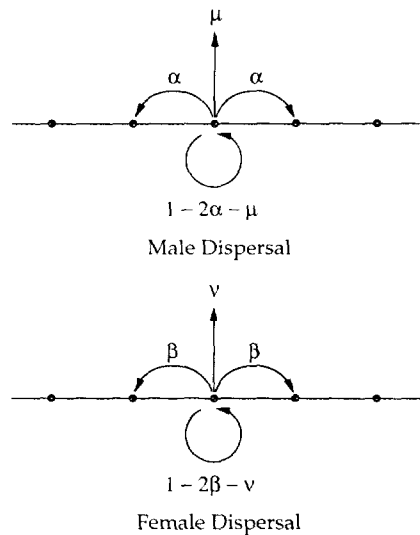


FIG. 1. Male and female dispersal probabilities for both models.

compete for next-generation occupancy. I assume there are always enough females to occupy every site.

I analyze the 1-dimensional model, with sex-specific dispersal to adjacent sites. Specifically I assume that male offspring disperse one site to the right or left each with probability  $\alpha$ , migrate to a distant site with probability  $\mu$ , and remain on their natal site with probability  $1 - 2\alpha - \mu$ . The corresponding probabilities for female offspring are  $\beta$ ,  $\nu$ , and  $1 - 2\beta - \nu$ , respectively (Fig. 1). In the DDM model, these female offspring are unmated, and in the DMD model, they are mated.

RESULTS

For both models the calculation of the relatedness coefficients is discussed in the Appendix. In the limit, as the long-range migration rates  $\mu$  and  $\nu$  approach zero, Eq. (1) yields the following results.

*Dispersal of Both Sexes before Mating (DDM)*

The sex-ratio  $s$  (proportion of males) is given by the formula

$$\frac{s}{1-s} = \frac{\alpha(\beta - \alpha + 2\alpha\sqrt{1-\beta-\alpha})}{\beta(\alpha - \beta + 2\beta\sqrt{1-\beta-\alpha})} \tag{5}$$

and level  $s$ -curves for this equation are plotted in Fig. 2. One immediate and expected feature of this equation is the symmetry in  $\alpha$  and  $\beta$ . If  $\alpha = \beta$ , we get a sex ratio of  $s = \frac{1}{2}$ .

If  $\alpha > \beta$  (wider male dispersal), we might expect (5) to give a male bias, but this is not always the case. The condition for a male bias is

$$\alpha(\beta - \alpha + 2\alpha\sqrt{1-\alpha-\beta}) > \beta(\alpha - \beta + 2\beta\sqrt{1-\alpha-\beta}),$$

which reduces to

$$(\alpha^2 - \beta^2)(2\sqrt{1-\alpha-\beta} - 1) > 0. \tag{6}$$

The inequality holds if both factors have the same sign. The factor on the right is positive if  $\alpha + \beta < \frac{3}{4}$ . Thus, we have the following conditions, illustrated in Fig. 2:

- $\alpha + \beta < \frac{3}{4}$ : male bias when  $\alpha > \beta$
- $\alpha + \beta > \frac{3}{4}$ : female bias when  $\alpha > \beta$
- $\alpha + \beta = \frac{3}{4}$ : sex-ratio  $s = 0.5$  for all  $\alpha$  and  $\beta$ .

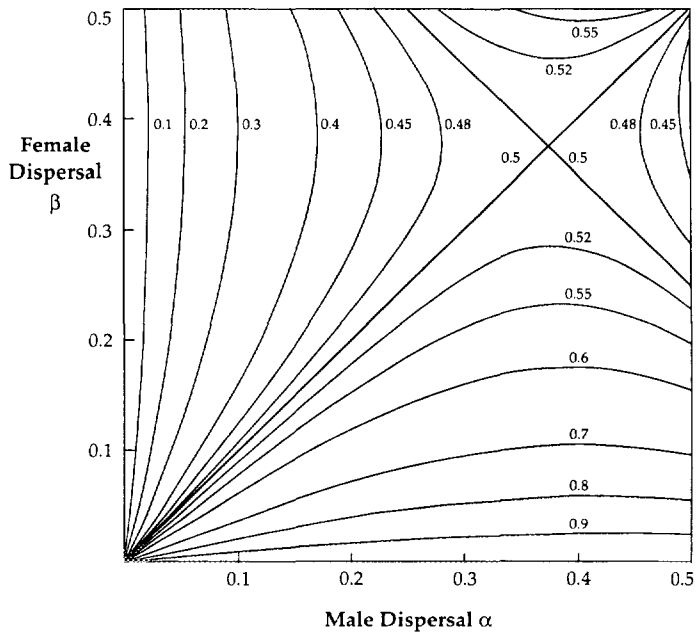


FIG. 2. Level curves for the equilibrium sex-ratio  $s$  for the DDM model: dispersal of both sexes before mating.

Thus, supposing that males have the wider local dispersal ( $\alpha > \beta$ ), as long as  $\alpha + \beta$  is less than  $\frac{3}{4}$ , the sex ratio is male biased, as expected, but for  $\alpha + \beta$  greater than  $\frac{3}{4}$ , we get a female bias. To explain this, I recall the results of Bulmer and Taylor (1980) that there are two factors that promote a bias in favour of a particular sex: the width and the evenness of the dispersal. It is not so clear how to define evenness in general, but for our purposes, an even dispersal would be one that fell off monotonely with dispersal distance (e.g., a normal curve), whereas any non-monotone behavior (e.g., a U-shaped curve) would contribute to the unevenness of the dispersal. In this case, when  $\alpha$  is large (say, greater than  $\frac{1}{3}$ ) any increase in  $\alpha$  increases both the width and the unevenness of male dispersal, and these affect the male bias in opposite ways. It is clear from the slopes of the level curves in Fig. 2 that for  $\alpha$  greater than approximately  $\frac{3}{8}$ , further increase in  $\alpha$  (for fixed  $\beta$ ) moves the sex-ratio towards increased female production, and thus the effect of greater unevenness overbalances the effect of increased width of dispersal.

If the one-step dispersal probabilities  $\alpha$  and  $\beta$  are small, then

$$\frac{\beta}{\alpha} \approx \frac{1-s}{s} \quad (8)$$

and this is interpreted in Fig. 2 as the slope of the level  $s$ -curve at the origin. For example, if there is little local dispersal, but those few offspring who do move to an adjacent patch are 10 times more likely to be male than female, then the male:female ratio should be 10:1. This relationship is also found in the numerical results of Bulmer (1986, Table 2) for a patch-structured population. As  $\alpha$  and  $\beta$  increase, with a constant ratio, the sex ratio bias predicted by (5) becomes much less extreme.

*Male Dispersal before Mating followed by Dispersal of Mated Females (DMD)*

The mathematics for this case is more complicated, and a formula for  $s$  is not available. Level  $s$ -curves are plotted in Fig. 3. We no longer have, nor do we expect, the symmetry in  $\alpha$  and  $\beta$  that we obtained in the DDM model.

If we do the analysis to first order in  $\alpha$  and  $\beta$  (Appendix) we get the formula

$$s = \frac{\alpha + \beta}{\alpha + 3\beta}, \tag{9}$$

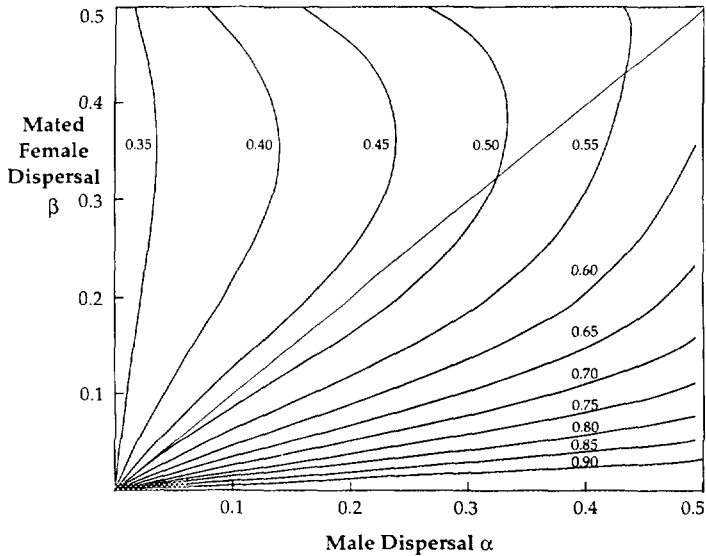


FIG. 3. Level curves for the equilibrium sex-ratio  $s$  for the DMD model: male dispersal before mating followed by dispersal of mated females.

which should be a good approximation when the one-step dispersal probabilities  $\alpha$  and  $\beta$  are small. Solving (9) for  $\beta/\alpha$ , the level  $s$ -curves at the origin should approximate straight lines of slope

$$\frac{\beta}{\alpha} = \frac{1-s}{3s-1} \quad (10)$$

and this can be verified from Fig. 3. If only males disperse ( $\beta=0$ ), Eq. (10) gives us a complete male bias ( $s=1$ ); if only mated females disperse ( $\alpha=0$ ), we get a modest female bias ( $s=\frac{1}{3}$ ); and if dispersal rates are equal ( $\alpha=\beta$ ), we get an unbiased ratio ( $s=0.5$ ).

It is interesting to look more carefully at the case  $\alpha=\beta$ , which is found along the diagonal line in Fig. 3. For small  $\alpha$  and  $\beta$ ,  $s$  is near 0.5, as remarked above. As  $\alpha$  and  $\beta$  increase,  $s$  becomes slightly female biased; but further increase in  $\alpha$  and  $\beta$  brings the sex-ratio back to 0.5 (at  $\alpha=\beta=\frac{1}{3}$ ), and for  $\alpha=\beta>\frac{1}{3}$ , the sex-ratio becomes male biased. How are we to understand these opposite effects? An examination of Eqs. (2) and (4) shows that the double male dispersal can promote a sex-ratio bias in two opposite ways. First of all, the wider male dispersal tends to make my sons' competitors less closely related to me than those of my daughter ( $R_m < R_f$ ), which means  $r_m - R_m > r_f - R_f$  and this increases  $W_m$  over  $W_f$  and promotes a male bias. On the other hand, the tendency of my daughter to disperse after mating, makes her mate more closely related to me than his competitors, making  $r_m^{\wedge} - R_m^{\wedge}$  positive, and this increases  $W_f$  over  $W_m$  and promotes a female bias. For  $\alpha$  and  $\beta$  near zero, the sex ratio is unbiased, and these two factors must cancel one another out. As  $\alpha$  and  $\beta$  increase, the second factor must predominate, giving a female bias; but for large  $\alpha$  and  $\beta$ , the first factor must predominate, giving a male bias.

#### DISCUSSION

The idea that parents should bias their sex ratio towards the sex that competes less intensely goes back to Hamilton (1967) and has since been widely discussed (for example, Maynard Smith, 1978; Bulmer and Taylor, 1980; Taylor, 1981; Charnov, 1982; Silk, 1983, 1984; Frank, 1986; Bulmer, 1986; Kirkpatrick and Bull, 1987; Taylor, 1988). An important force generating differential LRC is sex-specific dispersal, but there are very few field studies which focus on the relationship between dispersal patterns and the sex ratio (Clutton-Brock and Iason, 1986). An exception to this is perhaps found in studies of primate populations. In a now classic study by Clark (1978) an observed male bias in populations of African galagos was



credited to a wider dispersal pattern by young males than by females. More recently Johnson (1988) examined 15 genera of primates and found that the birth sex ratio was more male biased in genera in which philopatry was female biased. And Chapman *et al.* (1989b) examined data from five groups of primates and showed that in those groups in which females dispersed (spider monkeys and chimpanzees) the sex ratio was female biased, and in those groups with male dispersal (baboons, vervets, and langurs) the sex ratio was male biased only in the langurs. They point out that the negative results for the other two groups can easily be explained by the possibility that intrasex interactions may be positive (predator warning, grooming) as well as competitive and this violates the basic assumption of the LRC model (Taylor, 1981).

I have assumed that the environment is inelastic (Hamilton, 1971; Taylor, 1992) in the sense that it does not "expand" in response to changes in offspring density. For example, in terms of the stepping-stone model considered here, an increased production of offspring does not create new breeding sites or mating opportunities. Were this to be the case, we expect a reduction in LRC, which should particularly affect the sex with the higher level of competition and consequently reduce the bias in the sex ratio. Chapman *et al.* (1989a), in a study of a species of spider monkey with female dispersal, report a less female-biased sex ratio in areas of high productivity.

The models examined here confirm the results of Bulmer and Taylor (1980) and Bulmer (1986) that the sex ratio should be biased in favour of the sex which disperses more widely and/or more evenly. This is illustrated in both Figs. 2 and 3, if one of  $\alpha$  or  $\beta$  is held constant and the other is increased; geometrically, this corresponds to tracking along horizontal or vertical lines. For small dispersal rates  $\alpha$  and  $\beta$  (say less than 0.3), as each rate increases, so does the 'width' of dispersal, and so does the allocation towards that sex. But for large dispersal rates (say greater than 0.4) this is not usually the case, and in fact there is a difference between the two models. In the DDM model (Fig. 2) as the rate increases past 0.4 the allocation towards that sex decreases, and this can be explained as the effect of a less even dispersal pattern. In the DMD model (Fig. 3) we get this same effect for increases in the dispersal rate  $\beta$  of mated females (for  $\alpha \leq 0.4$ ), but not for increases in the rate  $\alpha$  of males: as  $\alpha$  increases, the allocation towards males always increases. This is explained by noting that the overall male dispersal pattern is much more even than the female pattern, because of the double dispersal of males. In fact, the effect of this greater overall evenness of male dispersal can be seen in Fig. 3 by simply noting that the region of male bias (to the right of and below the  $s = 0.5$  curve) is somewhat larger than the region of female bias.

The DMD model has formal application to sex allocation in hermaphroditic plants, with  $\alpha$  and  $\beta$  denoting the dispersal rates of pollen and (fertilized) seeds, respectively. However, it is important to note that the basic assumption of the stepping-stone model, of a tradeoff between the pollen dispersed to other sides and that used for self-fertilization, is not usually considered to apply to plant populations (Charlesworth and Charlesworth, 1981), rather it is often supposed that negligible pollen is required for selfing. Another point to note is the standard assumption in the modelling of plant populations that selfed offspring are on average less fit than outcrossed offspring. In both models analyzed here, there is a positive probability of sibmating, but I have assumed no fitness penalty for such matings. I note that there are also practical problems in applying sex allocation models to hermaphroditic plant populations such as the problem of deciding how to measure sex allocation in the field (Lovett Doust and Lovett Doust, 1987).

Possibly of as much interest as the sex ratio results themselves are the technical considerations which arise in the analysis of the model. Foremost among these are the techniques of inclusive fitness (Hamilton, 1964); the analysis here illustrates the power of this approach, which is known, under fairly general conditions (e.g., weak selection and additivity of gene action), to give the same equilibrium results as a one-locus genetic model (Taylor, 1989). In the stepping-stone model, each site is ultimately "connected" to every other site, requiring us to work with an infinite collection of relatedness coefficients  $x_k$ . However, there is an elegant eigenvector approach to the analysis, outlined in the Appendix for the DDM model. I propose that stepping-stone models deserve more prominence in the study of spatially structured social behaviour. Generalizations of this model to higher dimensions or to more general local dispersal patterns are mathematically more complex.

The sex ratio results obtained here are stable from an inclusive fitness point of view. That is, if the population sex ratio  $s$  deviates from the equilibrium value given, for example, by Eq. (5), then the inclusive fitness of a female through sons and daughters will no longer be equal, and by making the sex with the higher inclusive fitness, she will be helping to restore the population sex ratio to the equilibrium value. This can be seen from (2): an increase in the population sex ratio  $s$  causes a decrease in  $W_m$ , which favors female production and promotes a decrease in  $s$ . I have shown (Taylor, 1989) that this implies that, in a one-locus genetic model, the equilibrium will be "m-stable," that is, stable to fluctuations in the population sex ratio.

Another interesting technical device is the introduction of a small long-range migration rate to prevent the relatedness coefficients from all being unity. What I mean here by "small" is that the sex ratio results are

obtained by taking the limit as the migration rate approaches zero. This limiting technique is important, and I illustrate it with a mathematically simpler example of an infinite population organized into discrete patches of  $N$  mated females. After breeding, male offspring migrate with probability  $\mu$  to a random patch, and female offspring remain at home. Mating then takes place at random on each patch, and the mated females compete for the  $N$  breeding spots. A standard inclusive fitness argument provides the equilibrium sex ratio (proportion of males)

$$s = \frac{1}{2} \frac{4(N+1) - \mu(N+3)}{4N - \mu(N+1)} \tag{11}$$

The limit of this as  $\mu$  approaches zero is

$$s = \frac{1}{2} \frac{N+1}{N} \tag{12}$$

and is male biased. Note that if we set  $\mu = 0$  in the original model, each patch is a closed finite population, and the equilibrium sex ratio, by Fisher's (1930) standard argument, should be  $\frac{1}{2}$ ; that is, the limiting sex ratio (12) is not the same as the sex ratio,  $\frac{1}{2}$ , of the population with no long-range migration. This behaviour is typical of this type of limiting process; for a similar example of dispersal of mated females in a haplodiploid population see Taylor (1988, p. 162). For our purposes, this is a nice property; it gives us a candidate for the sex ratio which does not require us to specify the long-range migration rate and which applies as long as this rate is small and non-zero.

APPENDIX

I use the integers to index the sites and let  $a_k^*$  denote the probability that a male will disperse from site  $j$  to site  $j+k$ , with  $b_k^*$  the corresponding probability for a (mated) female. Thus, for both models,  $a_1^* = a_{-1}^* = \alpha$ ,  $a_0^* = 1 - 2\alpha - \mu$ ,  $b_1^* = b_{-1}^* = \beta$ , and  $b_0^* = 1 - 2\beta - v$ . Now I let  $a_k$  or  $b_k$  be the probability that a male or (mated) female native to site  $j$  will arrive at site  $j+k$  after all dispersal has occurred. Then, for the two models:

$$\text{DDM:} \quad a_k = a_k^* \quad b_k = b_k^* \tag{13}$$

$$\text{DMD:} \quad a_k = \sum_j a_{k-j}^* b_j^* \quad b_k = b_k^* \tag{14}$$

I define the following relatedness coefficients.

- $x_k$  mated pair on any site  $j$  to the mated female on site  $j+k$   
 $y_k$  mated pair on any site  $j$  to the next-generation male on site  $j+k$   
 $z_k$  mated pair on any site  $j$  to the next-generation female on site  $j+k$ .

Then

$$y_k = \sum_j x_{k-j} a_j$$

$$z_k = \sum_j x_{k-j} b_j$$

and the  $x_k$  are determined as solutions to the one-generation recursion equations

$$x_0 = 1 \tag{15}$$

$$x_k = \frac{1}{4} \sum_{j,h} (a_j a_h + a_j b_h + b_j a_h + b_j b_h) x_{k+j-h} \quad (k \neq 0).$$

In terms of these geographical coefficients, the parent-offspring coefficients defined in the text are obtained as follows:

$$r_i = x_0$$

$$R_m = \sum_j a_j y_j \tag{16}$$

$$R_f = \sum_j b_j z_j.$$

And for the DMD model

$$\hat{r}_i = \sum_j a_j^* x_j \tag{17}$$

$$\hat{R}_m = \sum_j b_j y_j.$$

#### *Dispersal of Both Sexes before Mating (DDM)*

I follow the approach of Kimura and Weiss (1964) and I restrict attention to the index set  $k \geq 0$ . The recursion (15) for the  $x_k$  has the form

$$x_k = A(x_{k-2} + x_{k+2}) + B(x_{k-1} + x_{k+1}) + Cx_k \quad (k \geq 1) \tag{18}$$

with the convention that  $x_{-1} = x_1$ , where  $4A = (\alpha + \beta)^2$ ,  $B = (\alpha + \beta)(1 - \alpha - \beta - \mu - \nu)$ , and  $2C = (\alpha + \beta)^2 + 2(1 - \alpha - \beta - \mu - \nu)^2$ . I now show

that, with the condition  $x_0 = 1$ , Eq. (18) has a unique bounded solution. I first write Eq. (18) in the matrix form

$$\begin{bmatrix} x_{k+2} \\ x_{k+1} \\ x_k \\ x_{k-1} \end{bmatrix} = \frac{1}{A} \begin{bmatrix} -B & (1-C) & -B & -A \\ A & 0 & 0 & 0 \\ 0 & A & 0 & 0 \\ 0 & 0 & A & 0 \end{bmatrix} \begin{bmatrix} x_{k+1} \\ x_k \\ x_{k-1} \\ x_{k-2} \end{bmatrix}. \tag{19}$$

The solutions of (19) are linear combinations of the eigenvectors of the matrix. Because of the structure of the matrix (the subdiagonal 1's) the eigenvectors are of the form  $x_k = \lambda^k$ , where  $\lambda$  is the corresponding eigenvalue. To get a bounded solution of (18) we must have  $|\lambda| \leq 1$ . The characteristic polynomial of the matrix is

$$p(\lambda) = A\lambda^4 + B\lambda^3 + (C-1)\lambda^2 + B\lambda + A. \tag{20}$$

When  $\mu = \nu = 0$ ,  $\lambda = 1$  is a root of  $p(\lambda)$ , as expected ( $x_k = 1$  is a solution), and in fact it is a double root—at  $\mu = \nu = 0$ ,  $p$  factors as

$$p(\lambda) = (\lambda - 1)^2 q(\lambda), \tag{21}$$

where

$$q(\lambda) = A\lambda^2 + (B + 2A)\lambda + A.$$

The roots of  $q(\lambda)$  are both negative (use the quadratic formula), and one of them, which I denote by  $\phi$ , is between  $-1$  and  $0$ . Now what happens to these four roots as  $\mu + \nu$  increases from  $0$ ? It is not hard to show, from (20), that when  $\mu + \nu > 0$ ,  $p(1) < 0$ ; it follows that the double root  $\lambda = 1$  resolves into two roots, one just above  $1$  and the other, which I denote by  $\theta$ , just below  $1$ . Of course,  $\phi$  will also change, but since the  $p$ -graph has nonzero slope at  $\phi$ , the change in  $\phi$  will be first order in  $\mu + \nu$ . Thus, for  $\mu + \nu$  close to zero, there will be two roots of (20) for which  $|\lambda| < 1$ , and these are

$$\theta = 1 - O(\sqrt{\mu + \nu})$$

and

$$\phi = \frac{1}{\alpha + \beta} (2\sqrt{1 - \alpha - \beta} - 2 + \alpha + \beta) + O(\mu + \nu). \tag{22}$$

A standard technical argument is used to show that  $\theta$  differs from  $1$  by a quantity that is first order, not in  $\mu + \nu$ , but in its square root. This reflects the parabolic nature of the  $p$ -graph in a neighbourhood of  $\lambda = 1$ , displayed

in the quadratic dependence of  $p$  on  $\lambda - 1$  in (21). Since  $x_k$  can only use eigenvalues which are absolutely less than 1, it must have the form

$$x_k = c\theta^k + d\phi^k. \quad (23)$$

The boundary conditions  $x_0 = 1$  and  $x_{-1} = x_1$  allow us to find  $c$  and  $d$ . We get

$$x_1 = 1 - \frac{(1-\theta)(1-\phi)}{1+\theta\phi} \approx 1 - \frac{(1-\theta)(1-\phi)}{1+\phi}$$

and (24)

$$x_2 = 1 - \frac{(1-\theta^2)(1-\phi^2)}{1+\theta\phi} \approx 1 - 2(1-\theta)(1-\phi),$$

where the approximations are first order in  $1 - \theta$ . Put these into (23), and then calculate the relatedness coefficients (16). When these are put into (2) and (3), the equilibrium equation (1) yields the sex-ratio formula (5).

*Male Dispersal before Mating followed by Dispersal of Mated Females (DMD)*

In this case the recursion equations (15) were solved numerically for each value of  $\alpha$  and  $\beta$ . Of course, the solution  $\{x_k\}$  is a vector of infinite length, and the computer could only work with a truncated version. My calculations were performed with an 11-vector; that is, I set  $x_k = 0$  except in the range  $-6 \leq k \leq 6$ . To check my results, I repeated a number of calculations with 21-vectors and 41-vectors. The  $x$ -values obtained in each case were of course quite different, but the resulting sex-ratio equilibria, for each  $\alpha$  and  $\beta$ , differed from the 11-vector calculation by no more than 0.001. The finding that the results are robust to variations in the effective dimension of  $x$  was happy (and unexpected).

Now I do the analysis to first order in the dispersal probabilities  $\alpha$  and  $\beta$ . I assume  $\mu = \nu = 0$ . Then from (14)

$$\begin{aligned} a_0 &= 1 - 2(\alpha + \beta) & a_1 &= a_{-1} = \alpha + \beta \\ b_0 &= 1 - 2\beta & b_1 &= b_{-1} = \beta \\ y_0 &= x_0 - 2(\alpha + \beta)(1 - x_1) & y_1 &= y_{-1} = x_1 - (\alpha + \beta)(2x_1 - x_0 - x_2) \\ z_0 &= x_0 - 2\beta(1 - x_1) & z_1 &= z_{-1} = x_1 - \beta(2x_1 - x_0 - x_2). \end{aligned}$$

When these are put into (16) and (17), we get

$$R_m = 1 - 4(\alpha + \beta)(1 - x_1)$$

$$R_f = 1 - 4\beta(1 - x_1)$$

$$r_m^{\wedge} = 1 - 2\alpha(1 - x_1)$$

$$R_m^{\wedge} = 1 - (2\alpha + 4\beta)(1 - x_1).$$

When these are put into Eqs. (3) and (4), the equilibrium equation (1) gives us (9).

#### ACKNOWLEDGMENTS

This work was partially supported by a grant from the Natural Sciences and Engineering Research Council of Canada. I am grateful for the valuable comments of three referees.

#### REFERENCES

- BULMER, M. G. 1986. Sex ratio theory in geographically structured populations, *Heredity* **56**, 69-73.
- BULMER, M. G., AND TAYLOR, P. D. 1980. Dispersal and the sex ratio, *Nature* **284**, 448-449.
- CHAPMAN, C. A., FEDIGAN, L. M., FEDIGAN, L., AND CHAPMAN, L. J., 1989a. Post-weaning resource competition and sex ratios in spider monkeys, *Oikos* **54**, 315-319.
- CHAPMAN, C. A., CHAPMAN, L. J., AND RICHARDSON, K. S. 1989b. Sex ratio in primates: A test of the local resource competition hypothesis, *Oikos* **56**, 132-134.
- CHARLESWORTH, D., AND CHARLESWORTH, B. 1981. Allocation of resources to male and female functions in hermaphrodites. *Biol. J. Linn. Soc.* **14**, 57-74.
- CHARNOV, E. L. 1982. "The Theory of Sex Allocation," Princeton Univ. Press, Princeton, NJ.
- CLARK, A. B. 1978. Sex ratio and local resource competition in a prosimian primate, *Science* **201**, 163-165.
- CLUTTON-BROCK, T. H., AND IASON, G. R. 1986. Sex ratio variation in mammals, *Quart. Rev. Biol.* **61**, 339-374.
- CROW, J. F., AND KIMURA, M. 1970. "An introduction to Population Genetics Theory," Harper & Row, New York.
- FISHER, R. A. 1930. "The Genetical Theory of Natural Selection," Clarendon Press, Oxford. [Reprinted and revised, 1958, 1981, Dover, New York.]
- FRANK, S. A. 1986. Hierarchical selection theory and sex ratios. I. General solutions for structured populations, *Theor. Popul. Biol.* **29**, 312-342.
- HAMILTON, W. D. 1964. The genetical evolution of social behaviour, I and II, *J. Theor. Biol.* **7**, 1-52.
- HAMILTON, W. D. 1967. Extraordinary sex ratios, *Science* **156**, 477-488.
- HAMILTON, W. D. 1971. Selection of selfish and altruistic behaviour in some extreme models, in "Man and Beast: Comparative Social Behavior" (J. F. Eisenberg and W. S. Dillon, Eds.), pp. 59-91, Smithsonian Inst. Press; Washington, DC.
- HAMILTON, W. D. 1972. Altruism and related phenomena, mainly in social insects, *Ann. Rev. Ecol. Syst.* **3**, 192-232.

- JOHNSON, C. N. 1988. Dispersal and the sex ratio at birth in primates. *Nature* **332**, 726-728.
- KIMURA, M., AND WEISS, G. H. 1964. The stepping-stone model of population structure and the decrease of genetic correlation with distance. *Genetics* **49**, 561-576.
- KIRKPATRICK, M., AND BULL, J. J. 1987. Sex ratio selection with migration: Does Fisher's result hold? *Evolution* **41**, 218-221.
- LOVETT DOUST, J., AND LOVETT DOUST, L. 1987. Sociobiology of plants: An emerging synthesis, in "Plant Reproductive Ecology" (J. Lovett Doust and L. Louvett Doust, Eds.), Oxford Univ. Press, London/New York.
- MAYNARD SMITH, J. 1978. "The Evolution of Sex," Cambridge Univ. Press, Cambridge.
- MICHOD, R. E., AND HAMILTON, W. D. 1980. Coefficients of relatedness in sociobiology, *Nature* **288**, 694-697.
- SILK, J. B. 1983. Local resource competition and facultative adjustment of sex ratio in relation to competitive abilities, *Am. Nat.* **121**, 56-66.
- SILK, J. B. 1984. Local resource competition and the evolution of male-biased sex ratio, *J. Theor. Biol.* **108**, 203-213.
- TAYLOR, P. D. 1981. Intra-sex and inter-sex sibling interactions as sex ratio determinants, *Nature* **291**, 64-66.
- TAYLOR, P. D. 1988. An inclusive fitness model for dispersal of offspring, *J. Theor. Biol.* **130**, 363-378.
- TAYLOR, P. D. 1989. Evolutionary stability in one-parameter models under weak selection, *Theor. Popul. Biol.* **36**, 125-143.
- TAYLOR, P. D. 1992. Inclusive fitness in a homogeneous environment, *Proc. R. Soc. Ser. B* **249**, 299-302.