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## SEX-RATIO BIAS WITH ASYMMETRIC EXCHANGE OF POLLEN BETWEEN DEMES

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**Abstract.**—In a patch of hermaphroditic plants, with a low level of pollen migration between patches, a prevailing wind creates a gradient, within the patch, in the strength of local competition among pollen for reproductive success. This leads to a sex ratio gradient, with a male (pollen) bias in downwind individuals, which can be quite strong even for large patches. The effect can be understood as follows: downwind individuals have relatively low reproductive value and respond by putting more resources into the gamete (pollen) with the best long-range (extra-patch) reproductive success.

**Key words.**—Asymmetric pollen flow, hermaphrodites, migration, population subdivision, sex ratio.

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Consider a local population (a patch) of hermaphroditic plants subject to a prevailing wind, such that downwind individuals receive much more pollen from the patch than do upwind individuals. If individuals are able to respond to their position in the patch, relative to the wind, how should they adjust the allocation of their resources to pollen or ovules to take account of the variation in local pollen competition within the patch?

To tackle this problem mathematically, I break the patch into two demes, D1 upwind and D2 downwind, with asymmetric partial pollen flow between demes (but with no exchange of ovules or of seeds) followed by random mating within each deme, and I allow the gametic sex ratio to be different in each deme. Kirkpatrick and Bull (1987) were the first to study this model. They remarked that because pollen produced by D2 must experience strong competition from D1 pollen at home, but with no such competition among ovules, “one might conjecture that selection would favor a shift towards increased female reproductive function (ovules) and decreased male function (pollen)” (Kirkpatrick and Bull 1987, p. 218) in D2. However, they show with a two-allele model that if the demes are large, then Fisher's (1930) result holds—the evolutionarily stable strategy (ESS) sex ratio is  $1/2$ .

Here I consider this problem in the context of small local populations (e.g., 200 individuals). I show that if there is a possibility, no matter how slight, of long-range pollen migration to other similar populations, then there is a sex-ratio bias in the downwind deme D2 that can be quite strong, but which, contrary to the above intuition, favors pollen production. We can understand this phenomenon by allowing the long-range migrants to be ovules instead of pollen. In this case, we still get a sex-ratio bias in D2, but towards ovule production. We conclude that the gamete with the better chance of long-range migration determines the sign of the bias (male vs. female) and that the amount of asymmetry in the exchange of pollen between the two demes (the strength of the wind) determines the strength of the bias.

I first consider the case in which the patch is not subdivided. This simplifies the inclusive fitness argument and gives

some insight into the unexpected behavior of the sex ratio as the long-range migration rate approaches zero.

### ONE DEME PER PATCH

Consider an isolated population of diploid hermaphrodites, with nonoverlapping generations, each generation consisting of  $N$  individuals and formed by random fusion of pollen and ovules from the previous generation. To calculate the evolutionarily stable strategy (ESS) sex ratio, a standard argument introduces two alleles, a normal allele  $S$  and a mutant allele  $\hat{S}$ , coding for sex ratios  $s$  and  $\hat{s}$ , and looks at the average change in the frequency  $p$  of  $\hat{S}$  over one generation. The result is that if  $s \neq 1/2$  and  $\hat{s} = 1/2$  then  $p$  increases, and if  $s = 1/2$  and  $\hat{s} \neq 1/2$ , then  $p$  decreases; we conclude that the ESS sex ratio is  $s = 1/2$ . This argument uses the average frequency of  $\hat{S}$  and will be reasonable only when  $N$  is large. For small  $N$ , we expect genetic drift to be important, and it is not clear, in general, when deterministic arguments will be valid.

A standard way to treat the small- $N$  problem is to embed the population in an infinite collection of similar populations (called patches), with a small rate of long-range migration between patches. For many purposes, such migration is formally equivalent to mutation (Crow and Kimura 1970; Hartl and Clark 1989). However, this equivalence breaks down where genotypes vary in their effective migration rates, because migration presents an opportunity for increased fitness at the expense of unrelated genotypes (those in destination patches). Where male and female gametes have different average rates of migration, they benefit directly from this effect. The ESS sex ratio may be strongly biased as a consequence, *even in the limit as the migration rates approach zero*.

Assume that pollen and ovule migration both take place before fertilization, which occurs randomly on each patch, and assume that there is no migration of seeds (fertilized ovules). If  $\mu$  (respectively,  $\nu$ ) is the ratio of immigrant to native pollen (respectively, ovules) competing on a random patch, then to first order in  $\mu$  and  $\nu$ , the ESS sex ratio (proportion of resources invested in pollen) is

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

Appendix A derives this surprising and counterintuitive result from an inclusive fitness argument. Equation (1) shows that for small  $\mu$  and  $v$ , the sex ratio  $s$  depends only on their ratio and varies between

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

when pollen is the exclusive migratory agent, and

$$s = \frac{1}{2} \frac{N - 1}{N} \tag{3}$$

when ovules are the exclusive migratory agent. When  $\mu = v$ , then  $s = 1/2$ , as expected.

It is important to note that the sex-ratio bias due to asymmetry in gamete migration remains even as the migration rates approach 0. In other words, under a fixed migration asymmetry (e.g.  $\mu/v = 100$ ), the limiting sex ratio as the migration rates approach 0 is not the same as the sex ratio of the limiting population—the latter being a finite isolated population with Fisherian sex ratio 1/2.

This important point may be seen more clearly by considering the case in which there is no ovule migration, such that  $v = 0$ . Then  $\mu$  cancels out of equation (1), and to see how  $s$  depends on  $\mu$ , we have to look at the quadratic ( $\mu^2$ ) terms in the equilibrium equation (Appendix A, eq. A4). If we do this, we get

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

which is male-biased, as expected, for all  $N$  and  $\mu$ , and has limit  $s = (N + 1)/2N$  as  $\mu$  approaches zero, as found above for the case  $v = 0$ . Equation (4) shows again that as  $\mu$  approaches zero (and the population approaches isolation), the limiting sex ratio is not 1/2, but retains a male bias.

TWO DEMES PER PATCH

Now consider a pair of demes between which there is partial exchange of pollen. As above, assume an infinite population of diploid hermaphrodites, organized into discrete patches, with the possibility of long-range migration of gametes between patches. Although in nature we expect pollen to be the principal long-range migratory agent, I will also consider migration of (unfertilized) ovules, because a comparison of the results in these two cases allows us to more fully understand the effect of long-range gametic migration on the sex ratio.

Suppose each patch is divided into two equal demes, an upwind deme D1 and a downwind deme D2, with  $N$  individuals each, and with exchange of pollen, but not of ovules, between the two demes. The dispersal rates are diagrammed in figure 1. Note that the rate  $n$  refers to unfertilized ovules and not to (fertilized) seeds, which do not disperse. Individuals in D1 and D2 can produce different sex ratios  $s_1$  and  $s_2$ , and the inclusive fitness argument outlined in Appendix B calculates the evolutionarily stable strategy (ESS) values of these ratios. The main task is to solve a set of recursion

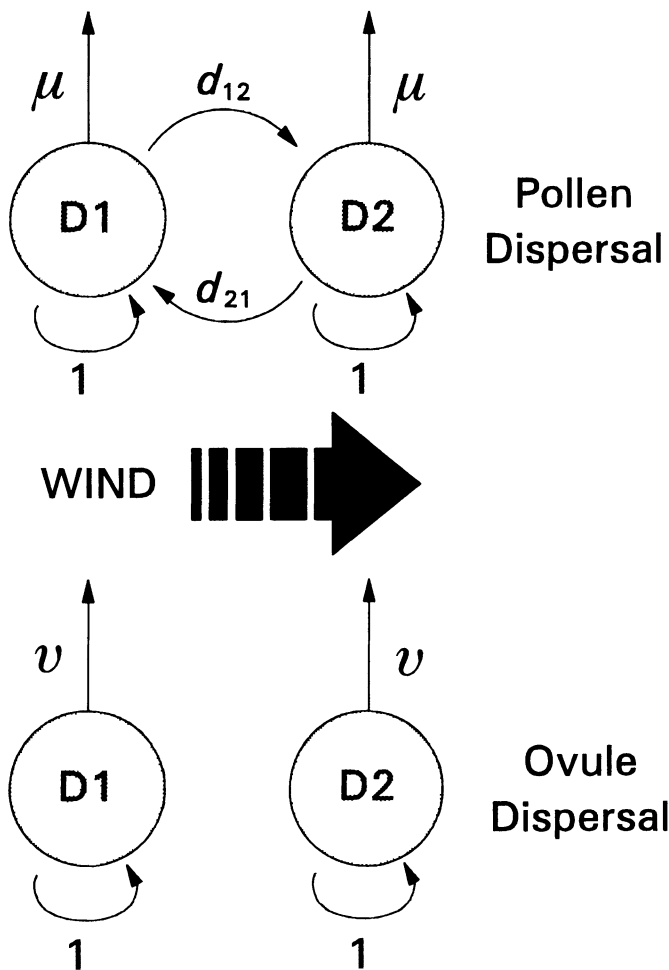


FIG. 1. Gamete dispersal rates. The pollen produced by  $D_i$  will, with relative probabilities  $1:d_{ij}\mu$ , remain on its home deme  $D_i$ , land on the neighbouring deme  $D_j$ , and migrate to a random patch (at infinity). Because D2 is the downwind deme, we expect  $d_{12} \geq d_{21}$ . The ovules produced on  $D_i$  will, with relative probabilities  $1:v$ , remain on  $D_i$  or migrate to a random patch.

equations for the relatedness coefficients within and between demes; this must be done numerically because the equations involve the sex ratios for each deme, which cannot be calculated without the relatedness coefficients.

Symmetric Pollen Exchange

There is one special case in which the calculations are tractable—the symmetric case  $d_{12} = d_{21} = d$ , for in this case the two sex ratios are the same ( $s_1 = s_2 = s$ ), and  $s$  drops out of the recursion equations for relatedness. In this case, to first order in  $\mu$  and  $v$ , the sex ratio is

$$s = \frac{\mu[N(2 + d) + 2] + v(1 + d)[N(2 + d) - d]}{[\mu + v(1 + d)][2N(2 + d) - d]} \tag{5}$$

This gives the following two subcases:

long-range pollen migration ( $v = 0$ ):

TABLE 1. Variation of the sex ratio in demes D1 and D2 with the pollen-exchange rates between demes.

Line	Deme size $N$	Interdeme pollen exchange		Sex ratio		RV ratio $\nu v_i$
		$d_{12}$	$d_{21}$	$r_1$	$r_2$	
Long-range pollen migration ( $\mu = 10^{-5}$ , $\nu = 0$ )						
1	100	0	0	.505	.505	1
2		0.1	0.1	.505	.505	1
3		1	1	.504	.504	1
4		1	0.1	.504	.510	5.4
5		1	0.01	.504	.554	44
6		1	0.001	.504	.729	281
7		1	0.0001	.503	.929	1813
8		10	0.01	.504	.593	77
9		0.1	0.0001	.504	.760	392
10	10	1	0.01	.537	.751	30
11	1000	1	0.001	.500	.550	432
12	1000	1	0.0001	.500	.722	2701
Long-range ovule migration ( $\mu = 0$ , $\nu = 10^{-5}$ )						
13	100	1	1	.499	.499	1
14		1	0.1	.498	.494	5.6
15		1	0.01	.496	.428	63
16		1	0.005	.496	.330	181
17		1	0.001	.496	0	$10^5$

$$s = \frac{N(2 + d) + 2}{2N(2 + d) - d}; \quad (6)$$

long-range ovule migration ( $\mu = 0$ ):

$$s = \frac{N(2 + d) - d}{2N(2 + d) - d}. \quad (7)$$

These formulae give the limiting sex ratios as  $\mu$  and  $\nu$  approach zero. The calculations assume that  $\mu$  and  $\nu$  are much smaller than  $d$ , and thus one cannot set  $d = 0$  in (5) and recover (1). As expected from the single-deme results, we get a male bias with long-range pollen migration and a female bias with long-range ovule migration. It might be noted that the ratio given by (6) is always greater than that given by (2), with  $N$  replaced by  $2N$ . Thus, in a patch model, with a low level of long-range migration of pollen between patches, breaking each patch into two equal demes with symmetric partial exchange of pollen between demes has the effect of increasing the male bias in the sex ratio.

#### Asymmetric Pollen Exchange

Some results for the asymmetric case are given in table 1. The table is designed to illustrate several patterns. Note that line 1 of the table illustrates equation (2) ( $s = 101/200$ ), lines 2 and 3 illustrate equation (6) ( $s = 212/419.9$  and  $302/599$ ), and line 13 illustrates equation (7) ( $s = 299/599$ ). The important qualitative features are as follows. (1) Long-range migration of pollen (lines 1–12) creates a male bias in both demes, and long-range migration of ovules (lines 13–17) creates a female bias. (2) The smaller the deme size  $N$ , the greater is the sex ratio bias. For example, compare lines 10–12 with lines 5–7. (3) Asymmetry in the exchange of pollen between demes (lines 4–12 and 14–17), has the effect of increasing the sex-ratio bias in the downwind deme. (4) When the exchange-rate ratio between demes is fixed, the sex ratio bias

is generally greater for smaller exchange rates. This is illustrated in lines 6 and 8–9 with an exchange rate ratio of 1000. For the case of symmetric exchange rates, this can be verified analytically from equation (5).

The last column of table 1 records the ratio of the reproductive values of the two demes. The reproductive value  $\nu v_i$  ( $i = 1, 2$ ) is the (asymptotic) probability that a random gene in the distant future of the population derives, in the current generation, from  $D_i$ . As expected, the effect of asymmetric exchange of pollen between demes is to increase the relative reproductive value (RV) of the upwind deme.

#### DISCUSSION

How are we to understand these rather strange results? The key is to note that much of the potential fitness variation in this system is associated with migration, even when the absolute migration rates are very small. As an example, consider an infinite population of diploid hermaphrodites, organized into discrete patches of 200 individuals. Each individual produces pollen and ovules, and there is a small probability of long-range migration of pollen between patches. The following sex-ratio results apply to the limiting case in which the pollen migration rate approaches zero.

First, suppose the patch is not subdivided, and the next generation is formed by random fusion of the pollen (some of which is immigrant) and the ovules on each patch. In this case, the evolutionarily stable strategy (ESS) sex ratio is  $s = 201/400 = 0.5025$  given by equation (2) with  $N = 200$ . The male bias can be understood as a response to the pollen migration, which reduces the local competition among pollen for ovules. The bias is slight because the population is relatively large.

Now suppose each patch is subdivided into two demes of size 100 with symmetric partial exchange of pollen between demes. This slightly increases the male bias. For example, if as much pollen is exchanged as is retained on each deme ( $d = 1$ ), then  $s = 302/599 \approx 0.5042$  (eq. 6 with  $N = 100$ ). The bias is still small, but it has almost doubled. This is expected for small exchange rates, because the configuration should approximate the case of undivided patches of half the size.

Now suppose the exchange rate is asymmetric. This has little effect on the sex ratio in the upwind deme but can produce a substantial increase in the male bias in the downwind deme. For example, with a ratio of 1000 between the downwind and upwind exchange rates, we can get a sex ratio of 0.729 for the downwind deme, and for a ratio of 10,000, this rises to 0.929 (table 1, lines 6–7). If we multiply the population size by 10 ( $N = 1000$ ), with an exchange rate ratio of 10,000, we can still get a substantial bias (table 1, line 12:  $s = 0.722$  in the downwind deme).

It is unusual to find such large sex-ratio biases in relatively large local populations. Standard models of local mate or local resource competition typically predict sex-ratio biases of the order of  $1/N$ , (e.g., eqs. 2 and 3), and therefore require small patch sizes to produce a noticeable effect.

We gain further insight into the effect of asymmetric gene flow by replacing the long-range migration of pollen with that of ovules, while still retaining pollen as the within-patch

exchange gamete between D1 and D2 (table 1, lines 13–17). The results described above all still hold but with a female instead of a male bias in the sex ratio. In particular, the downwind deme can now exhibit a strong female bias. What happens here is that as the pollen exchange becomes increasingly one-sided, the long-term reproductive prospects of downwind individuals become increasingly poor (see the reproductive value ratios of table 1), and their best response is to put increasingly more of their resources into long-range migration (whose payoff is little affected by local pollen flow). Typically, this will lead to a pollen bias, not because pollen is the gamete that is exchanged between demes, but because it is the gamete with the better long-range migratory potential.

It is important to note that this effect remains even as the long-range migration rate approaches zero. The long-range migration rate in table 1 is  $10^{-5}$ , but the entries all appear to be very close to the limiting values as  $\mu$  and  $\nu$  approach zero. For example, changing the pollen rate  $\mu$  to  $10^{-6}$  affects the resulting sex ratios only in their third decimal places, at most.

This is surprising because the sex-ratio effect hinges on the fraction of resources directed to the long-range strategy. To see how this works, consider the marginal inclusive fitnesses, and for simplicity return to the case of one deme per patch. The marginal inclusive fitness through pollen (Appendix A, eq. A3) is proportional to

$$\Delta W_p = a(x - y) + cx, \quad (8)$$

where the notation is defined in Appendix A. The first term represents the inclusive fitness return through pollen that remains on the patch, and the second term measures the return through pollen migration. Now if we cut the migration rate  $\mu$  by a factor of 10, the migration probability  $c$  is cut by about the same factor, but the stay-at-home probability  $a$  is hardly affected. Does this not severely alter the balance of the two terms of equation (8)? The answer is no. Although the parameter  $a$  is essentially unchanged, the relatedness difference  $x - y$  is also cut by a factor of about 10, because both terms,  $x$  and  $y$  differ from 1 by an amount that is first-order in  $\mu$ . The same analysis applies to the marginal returns through ovules. In short, although the sex-ratio bias is driven by the migration rate, cutting the migration rate by a factor of 10 (when it is small) does not significantly change the equilibrium equation, because it cuts all components of the marginal inclusive fitness by about the same factor, not only those terms that describe fitness returns through migration.

In all cases, the sex-ratio bias is more pronounced for smaller demes and disappears as the deme size approaches infinity. This concurs with the result of Kirkpatrick and Bull (1987), that for effectively infinite demes the sex ratio should be 1/2 regardless of the pollen-exchange pattern. Nordborg (1991) has generalized this result to a multideme model with an arbitrary pattern of pollen exchange between demes and an arbitrary number of sex-ratio alleles.

With a fixed exchange ratio  $d_{12}/d_{21}$ , the bias increases as the exchange rates  $d_{ij}$  decrease. In particular, for the case of symmetric exchange, the bias predicted by equation (6) decreases as  $d$  increases. This is closely connected with the variation in bias with deme size discussed above. Large ex-

change rates make the demes behave more like a random mating patch of size  $2N$ , and this decreases the sex-ratio bias.

What if the demes making up each patch were not of equal size? With the idea that, in a continuous model, there should be a sex-ratio gradient within the patch, we would expect that if more individuals were grouped in the upwind patch this should increase the bias in the downwind patch, and perhaps decrease the bias slightly in the upwind patch. However, with more individuals downwind, the bias in the downwind deme should be less, and in the upwind deme, slightly greater. This reasoning is confirmed by some numerical calculations. For example, consider line 6 of table 1, in which there are 200 individuals in the patch. With 100 in each deme, the upwind and downwind sex ratios are 0.504 and 0.729, as reported in table 1. With a split of 150:50 in the upwind and downwind deme, we get sex ratios of 0.503 and 0.801, and with a split of 50:150, we get sex ratios of 0.506 and 0.649.

In natural populations, we also expect a certain amount of migration of seeds (fertilized ovules) both within and between patches, and this can be expected to shift the results somewhat towards increased ovule production. I conjecture that if we had long-range migration of both pollen and seeds, then we would get a slight female bias in the upwind deme and a possibly substantial male bias in the downwind deme (similar to table 1).

For the case in which there is no patch subdivision and no interpatch migration of gametes, but partial long-range migration of seeds, a standard argument shows that the sex ratio is independent of the seed migration rate and is slightly female biased (as given by eq. 3). A similar result holds for the analogous case of dispersal of mated female offspring (Hamilton 1967), even when such dispersal is only partial (Frank 1986; Taylor 1988).

We have considered long-range dispersal of ovules as a theoretical device, but it is interesting to ask whether there might be any examples in which a plant disperses both male and female gametes before fertilization. I know of one candidate, the lycophyte *Selaginella* (Raven et al. 1986), whose diploid sporophyte bears haploid microspores and megaspores that mature into micro- and megagametophytes that disperse before sperm are released by the microgametophyte.

In summary, we might say that asymmetric exchange of pollen between demes in a nearly isolated population does not in itself lead to a male-biased sex ratio in the downwind deme but that it amplifies a male bias that is already there because of the possibility, no matter how small, of long-range pollen migration. The surprising result is that highly asymmetric exchange rates can generate large male biases, even in fairly large local populations.

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## APPENDIX A

An inclusive fitness model for the case of one deme per patch. Recall that the coefficient of consanguinity (CC) between two individuals or gametes is the probability that alleles chosen randomly from each of the two individuals are identical by descent (Crow and Kimura 1970).

## Summary of Notation

- a* The probability a random pollen grain competing for the next generation is native to the patch. Then,  $a = 1/(1 + \mu)$ .
- b* The probability a random ovule competing for the next generation is native to the patch. Then  $b = 1/(1 + \nu)$ .
- c* The probability a random pollen grain competing for the next generation comes from a distant patch. Then  $c = 1 - a$ .
- e* The probability a random ovule competing for the next generation comes from a distant patch. Then  $e = 1 - b$ .
- f* The inbreeding coefficient, the CC between two gametes of the same individual.
- g* The CC between two gametes native to the same patch.
- x* The CC between an individual and its own gamete. Then,  $x = (1 + f)/2$ .
- y* The CC between an individual and a random pollen grain competing for the next generation on the individual's native patch. Then  $y = ag$ .
- z* The CC between an individual and a random ovule competing for the next generation on the individual's native patch. Then  $z = bg$ .
- s* The sex ratio.

$\Delta W_O$  Marginal inclusive fitness gain through ovule allocation.

$\Delta W_P$  Marginal inclusive fitness gain through pollen allocation.

The one-generation recursion equation for *g* is

$$g' = \frac{1}{N}x' + \frac{N-1}{N}\left[\frac{1}{4}a^2g + \frac{1}{2}abg + \frac{1}{4}b^2g\right], \quad (A1)$$

where  $g'$  and  $x'$  are the next generation values of  $g$  and  $x$ . The two terms represent the probabilities that the two gametes come from the same individual or different individuals. In the latter case, the expression in the square brackets displays the three cases in which the gametes are both pollen, pollen and ovules, and both ovule. At equilibrium, we set  $g' = g$  and  $x' = x$  and rewrite this to get an expression for  $g/x$ :

$$\frac{g}{x} = \frac{4}{4N - (N-1)(a+b)^2}. \quad (A2)$$

The sex-allocation model assumes that each individual has one unit of reproductive resource and allocates  $s$  to pollen production and  $1 - s$  to ovule production. Choose units of fitness such that each individual expects to gain one unit through pollen and one unit through ovules.

Then an individual who allocates an extra  $\epsilon$  units of energy to ovule or pollen production can expect a fitness increase through ovules of  $\epsilon/(1 - s)$  or through pollen of  $\epsilon/s$ . To get the inclusive fitness change of the individual (Hamilton 1964), we must calculate the resulting change in overall relatedness of the individual to next-generation individuals. This is

pollen allocation:

$$\Delta W_P = \frac{\epsilon}{s}[a(x - y) + cx] = \frac{\epsilon}{s}[x - a^2g];$$

ovule allocation:

$$\Delta W_O = \frac{\epsilon}{1-s}[b(x - z) + ex] = \frac{\epsilon}{1-s}[x - b^2g]. \quad (A3)$$

Note that in case the gamete stays to compete at home (probability  $a$  and  $b$ ), we must deduct the relatedness of the parent to the competitors of the gamete ( $y$  and  $z$ ). I have used coefficients of consanguinity here to represent relatedness, though it is more common to normalize these by dividing by  $x$ , the CC of the parent to its own gametes.

At sex-ratio equilibrium the marginal inclusive fitnesses must be equal

$$\frac{s}{1-s} = \frac{x - a^2g}{x - b^2g} = \frac{4N - (N-1)(a+b)^2 - 4a^2}{4N - (N-1)(a+b)^2 - 4b^2} \quad (A4)$$

using (A2). Equations (1) and (4) follow from this, setting  $b = 1/(1 + \nu)$  and  $a = 1/(1 + \mu)$ .

## APPENDIX B

An inclusive fitness model for the case of two demes per patch. The notation follows that of Appendix A. Allow the demes to have different sizes, with  $N_i$  individuals in deme  $Di$  ( $i = 1, 2$ ). Thus,

$$a_{ii} + a_{ji} + c_{ii} + c_{ji} = 1, \quad (B1)$$

where the four terms on the left are, in order, the probabilities that a random pollen grain competing for  $Di$  in a certain patch comes from  $Di$  and  $Dj$  of the same patch, and from  $Di$  and  $Dj$  of an infinitely distant patch. Similarly,

$$b_i + e_{ii} + e_{ji} = 1, \quad (B2)$$

where the three terms on the left are, in order, the probabilities that a random ovule competing for deme  $Di$  in a certain patch comes from that same deme, and from  $Di$  and  $Dj$  of an infinitely distant patch. The coefficients of consanguinity are

- $f_i$  The inbreeding coefficient in deme  $i$ .
- $g_{ij}$  The coefficient of consanguinity (CC) between two gametes native to  $Di$  and  $Dj$  of the same patch.
- $x_i$  The CC between an individual on  $Di$  and its own gamete. Then,  $x_i = (1 + f_i)/2$ .
- $y_{ij}$  The CC between a  $Di$  individual and a random pollen grain competing for the next generation on  $Dj$  of the individual's native patch. Then,  $y_{ij} = \sum_k a_{kj}g_{ki}$ .
- $z_i$  The CC between a  $Di$  individual and a random ovule competing for the next generation on  $Di$  of the individual's native patch. Then  $z_i = b_i g_i$ .
- $s$  The sex ratio on  $Di$ .
- $v_i$  The reproductive value of  $Di$ , defined as the probability that a random gamete in the distant future descends from a  $Di$  individual in the current generation.

As in Appendix A, the marginal inclusive fitnesses of a  $Di$  individual, using sex ratio  $s_i$  through pollen and ovule production are

$$\Delta W_P = \frac{\epsilon}{N_i s_i} [a_{ii}(x_i - y_{ii})v_i + a_{ij}(x_i - y_{ij})v_j + c_{ii}x_i v_i + c_{ij}x_i v_j],$$

$$\Delta W_O = \frac{\epsilon}{N_i(1-s_i)} [b_i(x_i - z_i)v_i + e_{ii}x_i v_i + e_{ij}x_i v_j]. \quad (B3)$$

At sex-ratio equilibrium, these must be equal.

We now need to calculate the parameters defined above. The source probabilities for pollen and ovules are

$$\begin{aligned}
 a_{ij} &= N_i s_i d_{ij} / A_j, \\
 c_{ij} &= \frac{N_j}{N_1 + N_2} N_i s_i \mu / A_j, \\
 b_j &= N_j (1 - s_j) / B_j, \\
 e_{ij} &= \frac{N_j}{N_1 + N_2} N_i (1 - s_i) v / B_j,
 \end{aligned}$$

where it is convenient to introduce  $d_{ij} = 1$ , and the denominators  $A_j$  and  $B_j$  are chosen so that the sums in equations (B1) and (B2) equal 1. Here we make the assumption that pollen and ovules that migrate to a distant patch land on demes D1 and D2 with probabilities proportional to the deme sizes  $N_1$  and  $N_2$ .

The reproductive values  $v_i$  are determined from the "backward equation"

$$\bar{v}_1 = \frac{1}{2} [v_1(a_{11} + c_{11}) + v_2(a_{12} + c_{12})] + \frac{1}{2} [v_1(b_1 + e_{11}) + v_2(e_{12})].$$

Here,  $v_i$  applies to generation  $n$  and  $\bar{v}_1$  applies to generation  $n - 1$ . To

find the probability  $\bar{v}_1$  that a random allele in the distant future comes from D1 in generation  $n - 1$ , ask what and where it was in generation  $n$ . With probability 1/2 it was either pollen or ovule, and these possibilities correspond to the two square brackets. The two terms in each bracket correspond to the probabilities that it came from D1 given that in generation  $n$  it was in D1 and D2, respectively. At equilibrium,  $\bar{v}_1 = v_1$ , and we can solve for the ratio  $v_1/v_2$ . There is an analogous equation for  $\bar{v}_2$ .

To calculate the relatedness coefficients, the next-generation recursion equations are

$$\begin{aligned}
 F_j &= b_j \sum_i a_{ij} g_{ij}, \\
 g_{kk} &= \frac{1}{N_k} x_k + \frac{N_k - 1}{4N_k} \left[ \sum_{i,j} a_{ik} a_{jk} g_{ij} + 2b_k \sum_i a_{ik} g_{ik} + b_k^2 g_{kk} \right],
 \end{aligned}$$

and if  $j \neq k$ ,

$$g_{jk} = \frac{1}{4} \left[ \sum_{h,t} a_{hj} a_{tk} g_{ht} + b_j \sum_i a_{ik} g_{ij} + b_k \sum_i a_{ij} g_{ik} + b_j b_k g_{jk} \right].$$