# Kin selection models for the co-evolution of the sex ratio and sex-specific dispersal

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## ABSTRACT

We investigate the co-evolutionary relationship between sex-ratio bias and sex-specific dispersal behaviour using an inclusive fitness approach. We consider two models: (i) DDM, in which dispersal of both sexes occurs before mating; and (ii) DMD, in which male dispersal precedes mating and female dispersal follows mating. Under DDM, at equilibrium, there is no bias in either the sex ratio or the sex-specific dispersal rates unless the sex-specific dispersal costs are different. However, under DMD, and at equilibrium, equal sex-specific dispersal costs imply a female bias in the sex ratio and a female dispersal rate at least as great as that of males. The present work highlights the role of sex differences – in either dispersal costs or the timing of dispersal – to the co-evolution of the sex ratio and dispersal.

*Keywords*: co-evolution, inclusive fitness, kin selection, local competition, sex ratio, sex-specific dispersal, stability.

## INTRODUCTION

The proportion of a fixed parental resource devoted to sons is a social behaviour known, by convention, as the 'sex ratio'. The adaptive nature of sex-ratio decisions has occupied many researchers (see Charnov, 1982). In particular, the evolution of resource allocation strategies that favour one or the other sex (i.e. 'sex-ratio' bias) has received much attention.

In geographically structured populations, local competition among same-sex relatives is known to be a major determinant of sex-ratio bias. Optimal sex ratios favour females when local competition occurs only among males (Hamilton, 1967), but favour males when the local competition occurs exclusively among females (Clark, 1978). Overall, sex ratios in geographically structured populations appear to be biased towards the sex that suffers less from local competition (see Perrin and Mazalov, 2000, and references therein).

Dispersal from one's natal site is another remarkable social behaviour, especially when that dispersal is costly. Like the sex ratio, local competition (or rather, avoiding local competition) provides an incentive for adaptive adjustment of the dispersal rate (Hamilton and May, 1977; Frank, 1986; Taylor, 1988a; Motro, 1991). With a greater likelihood of kin competition comes a higher rate of dispersal.

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Of course, a situation might arise where local competitive pressures are different for males than they are for females. These situations represent a sort of 'asymmetry' between the sexes that encourages the evolution of dispersal conditional upon sex – that is, 'sex-specific' dispersal (Perrin and Mazalov, 2000). In this way, the evolution of sex-specific dispersal parallels the evolution of sex-ratio bias.

Theoretical models have traditionally considered the evolution of the sex ratio or dispersal independently. That is, when investigating the evolution of one of these behaviours, the other is fixed. Given the parallels described above, investigating the co-evolution of both sex ratio and dispersal seems especially important.

In this paper, we explore kin selection models for the co-evolution of the sex ratio and dispersal under two different life histories. The first life history assumes that both sexes disperse before mating takes place. The second assumes that males disperse before mating, whereas females disperse after mating. In the first scenario, both sex-ratio bias and sex-specific dispersal behaviour are possible at equilibrium – but only when the cost of dispersal differs between the sexes. In the second scenario, equal sex-specific dispersal costs imply a female bias in the equilibrium sex ratio, and an equilibrium female dispersal rate that is at least as great as that of males.

## AN INCLUSIVE FITNESS MODEL

### Basic model

We have tabulated all notation and symbols used for easy reference (see Table 1).

We consider a dioecious diploid organism undergoing discrete, non-overlapping generations. Our model assumes an infinite patch-structured population. Each patch is identical, supporting $N$ breeding females and their mates.

**Table 1.** Summary of symbols used in the main text

| Symbol | Explanation |
| --- | --- |
| * | indicates the equilibrium level of a particular behaviour |
| $\alpha_i$ | proportion of any brood devoted to sex-$i$ offspring |
| $c_i$ | probability that a sex-$i$ offspring perishes during dispersal |
| $d_i$ | proportion of sex-$i$ offspring that disperse |
| $\delta$ | small positive deviation from 'normal' behaviour |
| $\Delta W_{\alpha_m}$ | $= \Delta W_m - \Delta W_f$ |
| $\Delta W_i$ | inclusive fitness effect of a sex-$i$ offspring |
| $\Delta W_{d_i}$ | inclusive fitness effect of sex-$i$ dispersal |
| $k_i$ | $= (1 - d_i)/(1 - c_i d_i)$, the probability that a random sex-$i$ competes on its native patch |
| $N$ | number of fertilized adult females on any patch |
| $r$ | $= \bar{R}_i/R_j$ for $i, j = $ m, f |
| $R_i$ | relatedness of mother to her own sex-$i$ offspring |
| $\bar{R}_i$ | relatedness of mother to a random sex-$i$ offspring born on her patch |
| $\sigma_X^2$ | genetic variance of trait $X$ |
| $\sigma_{XY}$ | genetic covariance between traits $X$ and $Y$, assumed to be 0 |
| $t$ | unit of evolutionary time |

At the beginning of a season, each breeding female produces a brood of large but constant size. A proportion $\alpha_m$ of the brood is male, and a proportion $\alpha_f (= 1 - \alpha_m)$ is female. We refer to $\alpha_m$ as the sex-ratio strategy (or simply sex ratio). It is assumed that $\alpha_m$ is under maternal control (i.e. dependent only on the genotype of the mother).

Dispersal of offspring occurs soon after birth. The quantity $d_m$ (or $d_f$) denotes the proportion of sons (or daughters) that disperse. Like the sex ratio, sex-specific dispersal is assumed to be under maternal control.

Dispersal is assumed to be costly: a proportion $c_m$ of males and a proportion $c_f$ of females are removed from the dispersal pool. In a patch-structured model, such as this one, individuals that disperse do not encounter any relatives.

Males compete at random with one another for mates, whereas fertilized females compete at random with one another for breeding sites on a patch. We consider two basic life histories characterized by the order in which mating and intrasexual competition occur:

1. DDM model: mating follows dispersal by both sexes.
2. DMD model: males disperse before mating, whereas (fertilized) females disperse after mating.

The kin selection model we develop below is based on a classical inclusive fitness argument (Hamilton, 1964). The genetic validity of the inclusive fitness approach has been demonstrated elsewhere (see Taylor, 1988b, 1989, 1996a, and references therein). An equivalent model can be constructed using the more recent 'direct fitness' approach (Taylor and Frank, 1996). Unfortunately, the direct fitness approach can obscure biological interpretation of the model. In contrast, a biological narrative forms the basis of the classical approach; and so the classical approach is often the more desirable one.

An inclusive fitness argument estimates the fitness of a rare, nearly neutral mutant in a 'normal' population (i.e. 'mutant fitness'). Mathematically speaking, this estimate is made accurate to first-order in mutant frequency and in the deviation in mutant behaviour (Taylor, 1988b). That is to say, the estimate considers only the additive effects of deviant behaviour.

The difference between (estimated) mutant fitness and normal fitness determines whether mutant behaviour is increasing or decreasing in the population, and so this difference, the so-called 'inclusive fitness effect', is the object of our interest.

## Sex ratio: the inclusive fitness effect of a son

To develop our model for sex-ratio evolution, we fix the sex-specific dispersal rates, $d_m$ and $d_f$, at arbitrary levels. Our approach, typical of sex-ratio models (Charnov, 1982), is to compare the inclusive fitness effect of a son with the inclusive fitness effect of a daughter.

Consider a mutant mother (the 'actor') in a population using normal sex-ratio strategy, $\alpha_m$. The mutant's 'deviation' comes in the form of an extra $\delta$ units of a reproductive resource, to be allocated either entirely to the production of more sons or entirely to the production of more daughters. We suppose $\delta$ is small compared with brood size. The inclusive fitness effect of a son, $\Delta W_m$, describes the net benefit to the mutant who puts those $\delta$ units towards sons.

We will express the costs and benefits of a behaviour in units of reproductive success. We measure reproductive success in terms of numbers of offspring that reach breeding age,

weighted by genetic contribution to the future population. In a diploid sexual organism, males (as a group) and females (as a group) make equal genetic contributions to future populations (Fisher, 1930). The expected genetic contribution made by any individual male (or female) offspring, then, will be proportional to $1/\alpha_m$ (or $1/\alpha_f$). Readers familiar with sex-ratio theory will recognize $1/\alpha_m$ and $1/\alpha_f$ as the individual reproductive value of a male and female, respectively (Taylor and Frank, 1996). Individual reproductive value is precisely the weighting we need to use in our units of reproductive success.

Under DDM and DMD, the benefit of the mutant sex-ratio strategy is, of course, the reproductive success of extra male offspring. Our first-order method of estimation allows us to assume that these extra offspring have normal reproductive success equal to 1. Allocating the extra reproductive resource to sons, then, contributes $\delta/\alpha_m$ units of reproductive success to the actor's fitness. However, we only wish to count the actor's 'genetic share' of this reproductive success. That is to say, before we count the benefit $\delta/\alpha_m$, it must be multiplied by $R_m$, the relatedness of the actor to her own male offspring (see Appendix 1).

The cost of allocating reproductive resources to sons is due to male–male competition for mates. Because there are only a fixed number of matings, the extra $\delta/\alpha_m$ units of reproductive success must displace exactly the same amount. We are again interested only in the actor's genetic share of this cost. Let $k_m = (1 - d_m)/(1 - c_m d_m)$ be the probability that a random male is competing on his native patch. Under DDM or DMD, then, a proportion $k_m$ of the extra reproductive success will be won on the native patch; and here other native males will be displaced with probability $k_m$. If $\bar{R}_m$ is the relatedness of the actor to a random male offspring born on her patch, we can summarize the cost of the mutant behaviour under DDM and DMD as $\bar{R}_m k_m^2 \delta/\alpha_m$.

To compute $\Delta W_m$ we subtract the costs from the benefits. In the final calculation we omit $\delta$, simply writing

$$\text{DDM or DMD:} \quad \Delta W_m = (R_m - \bar{R}_m k_m^2)/\alpha_m \tag{1}$$

## Sex ratio: the inclusive fitness effect of a daughter

We use a similar approach to determine $\Delta W_f$, the inclusive fitness effect of a daughter. Now, the actor allocates the $\delta$ units of resource to the production of daughters.

As above, the direct benefit to the actor is extra female reproductive success. This direct benefit is described by $R_f \delta/\alpha_f$, where $R_f$ is the relatedness of the actor to her own female offspring.

Since males compete for mates, there is also an indirect benefit: more daughters provide more mating opportunities for related males. Let $k_f = (1 - d_f)/(1 - c_f d_f)$ denote the probability that a random female is competing on her native patch. Under DDM only $k_f \delta/\alpha_f$ units of female reproductive success are available to related males, whereas under DMD all $\delta/\alpha_f$ units are available to native males. Of the available female reproductive success, only a proportion $k_m$ is won by native males. It follows that the indirect benefit of the deviant behaviour is $\bar{R}_m k_m k_f \delta/\alpha_f$ under DDM and $R_m k_m \delta/\alpha_f$ under DMD.

We can summarize the overall benefit to the actor as

$$\text{DDM:} \quad \delta(R_f + \bar{R}_m k_m k_f)/\alpha_f \tag{2}$$

$$\text{DMD:} \quad \delta(R_f + \bar{R}_m k_m)/\alpha_f \tag{3}$$

We now focus attention on costs. As above, direct costs include displaced female competitors: under both DDM and DMD, $k_f \delta / \alpha_f$ units of reproductive success are displaced on the native patch, and these belonged to a native female with probability $k_f$. If $\bar{R}_f$ is the relatedness of the actor to a random female offspring born on her patch, then the direct cost to the actor is $\bar{R}_f k_f^2 \delta / \alpha_f$.

We must also account for the indirect cost due to displaced mates of competitors. Under DDM the displaced reproductive success belonged to native males with probability $k_m$, whereas under DMD the displaced reproductive success belonged to native males with probability $k_m k_f$.

The overall cost to the actor can be summarized as

$$\text{DDM:} \quad \delta(\bar{R}_f k_f^2 + \bar{R}_m k_m k_f)/\alpha_f \tag{4}$$

$$\text{DMD:} \quad \delta(\bar{R}_f k_f^2 + \bar{R}_m k_m k_f^2)/\alpha_f \tag{5}$$

We subtract costs (4) or (5) from benefits (2) or (3) and omit $\delta$ to get

$$\text{DDM:} \quad \Delta W_f = (R_f - \bar{R}_f k_f^2)/\alpha_f \tag{6}$$

$$\text{DMD:} \quad \Delta W_f = (R_f + \bar{R}_m k_m - \bar{R}_f k_f^2 - \bar{R}_m k_f^2 k_m)/\alpha_f \tag{7}$$

## Sex-specific dispersal

In this subsection, we fix $\alpha_m$ at some arbitrary level and we seek expressions for $\Delta W_{d_m}$, the inclusive fitness effect of male dispersal, and $\Delta W_{d_f}$, the inclusive fitness effect of female dispersal. In the case of sex-specific dispersal, we need not include reproductive value as part of our units for reproductive success.

To calculate $\Delta W_{d_m}$, we consider a mother who uses deviant male-dispersal strategy $d_m + \delta$ in a population of $d_m$-strategists. As with the sex ratio, $\delta$ is considered to be positive and small.

Under both DDM and DMD, the deviant actor loses an additional $c_m \delta$ sons during dispersal. Her genetic share of this cost is given by $R_m c_m \delta$. The benefit of the deviant dispersal behaviour is reduced male–male competition. The dispersed sons effectively give a gift of $\delta$ units of reproductive success to a random competitor on the actor's patch. This random competitor is a native with probability $k_m$. The benefit to the actor is given by $\bar{R}_m k_m \delta$ under DDM and under DMD. It follows that

$$\text{DDM or DMD:} \quad \Delta W_{d_m} = \bar{R}_m k_m - R_m c_m \tag{8}$$

where we have again omitted the behavioural deviation in the final expression.

Now we look at female dispersal. An argument similar to the one for male dispersal gives us

$$\text{DDM:} \quad \Delta W_{d_f} = \bar{R}_f k_f - R_f c_f \tag{9}$$

Under DMD, a female disperses after mating; hence the consequences of dispersal for her mate and the mate of a random competitor must be included in our calculation. Using reasoning analogous to that used above, we see that the benefits of a small, positive behavioural deviation, $\delta$, in a normal $d_f$-population are

$$\delta(\bar{R}_f k_f + \bar{R}_m k_f k_m) \tag{10}$$

and the costs are

$$\delta(R_f c_f + \bar{R}_m k_m c_f) \tag{11}$$

It follows that

$$\text{DMD:} \quad \Delta W_{d_f} = \bar{R}_f k_f + \bar{R}_m k_f k_m - R_f c_f - \bar{R}_m k_m c_f \tag{12}$$

## EQUILIBRIUM STRATEGIES

### Equilibrium condition

Our analysis in this section will focus on 'equilibrium strategies'. Formally, a particular strategy $(\alpha_m^*, d_m^*, d_f^*)$ is said to be an equilibrium strategy provided

$$\Delta W_m = \Delta W_f \qquad \Delta W_{d_m} = 0 \qquad \Delta W_{d_f} = 0 \tag{13}$$

when $\alpha_m = \alpha_m^*$, $d_m = d_m^*$ and $d_f = d_f^*$. Note that $\alpha_f^* = 1 - \alpha_m^*$.

### DDM

We are primarily interested in the relationship (if any) between (a) the direction of sex-ratio bias and (b) the relative extent of sex-specific dispersal. As outlined in the following proposition, sex-specific dispersal costs play a crucial role in this relationship, at equilibrium.

**Proposition 1.** *Suppose* $c_m$, $c_f < 1$. *If* $(\alpha_m^*, d_m^*, d_f^*)$ *is an equilibrium strategy under DDM, then* (i) $\alpha_m^* - \alpha_f^*$, (ii) $d_m^* - d_f^*$ *and* (iii) $c_f - c_m$ *all have the same sign* (*Fig. 1*).

Proposition 1 sheds some light on previous work on the (independent) evolution of dispersal and the (independent) evolution of the sex ratio.

Taylor (1988a) has considered the evolution of dispersal under DDM, setting $c_m = c_f$. To simplify his analysis, he assumed a fixed, 1 : 1 sex ratio, and did not allow dispersal rates to be conditional on sex. Proposition 1 provides the appropriate justification for these simplifications. As one might expect, setting $c_m = c_f = c$ in our co-evolutionary model yields $\alpha_m^* = \alpha_f^*$. We also find

$$d_m = d_f = d = 2/(1 + \sqrt{1 + 4N(N-1)c^2} + 2Nc) \tag{14}$$

an expression for equilibrium dispersal rate that is equal to that presented in Taylor (1988a).

Kirkpatrick and Bull (1987) and Nordborg (1991) have established that unbiased sex ratios are to be expected in geographically structured populations – as long as patch sizes are very large. When patch sizes are small, Proposition 1 indicates that $c_m = c_f$ guarantees an even equilibrium sex ratio – as long as sex-specific dispersal rates are allowed to co-evolve.

The proof of Proposition 1 relies on the fact that, under DDM, an equilibrium strategy $(\alpha_m^*, d_m^*, d_f^*)$ satisfies

$$\alpha_m^*/\alpha_f^* = (1 - rk_m^2)/(1 - rk_f^2) \tag{15}$$

$$c_m = rk_m \tag{16}$$

$$c_f = rk_f \tag{17}$$
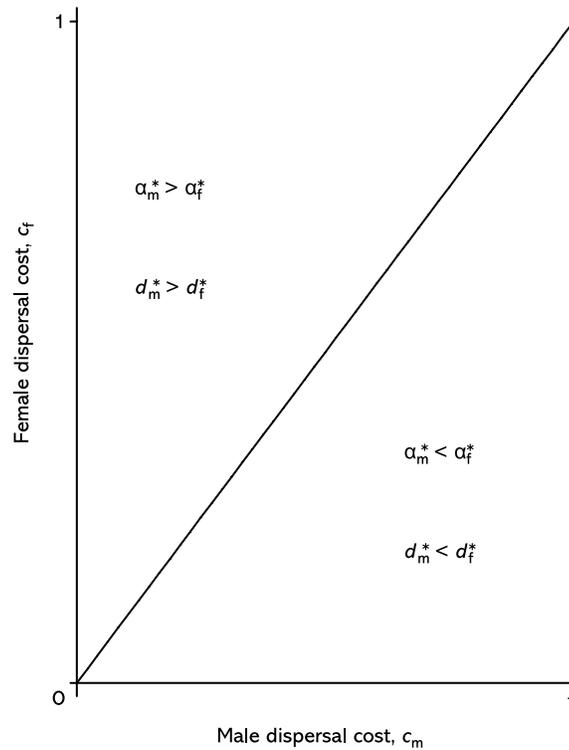
**Fig. 1.** Direction of sex-ratio bias and relative rates of sex-specific dispersal for all combinations of sex-specific dispersal costs, $c_m$ and $c_f$, under the DDM model. Along the solid line, $c_m = c_f$ and so $\alpha_m^* = \alpha_f^*$ and $d_m^* = d_f^*$. By Proposition 1, we may also label the vertical axis $k_f$ and the horizontal axis $k_m$.

where $r = \bar{R}_i/R_j$ for $i, j = m, f$ is a ratio of relatedness coefficients (see Appendix 1). The complete proof of Proposition 1 is presented in Appendix 2.

It has been proposed that optimal sex ratios are biased towards the more dispersive sex (Bulmer and Taylor, 1980; Bulmer, 1986; Taylor, 1994). If $\alpha_m^*$ is the result of co-evolution with dispersal, then this is certainly true (Proposition 1). However, if dispersal is not at evolutionary equilibrium, there is no guarantee that sex-ratio bias follows this principle. Consider the following proposition, whose proof is obvious from (15).

**Proposition 2.** *If the sex ratio is at evolutionary equilibrium under DDM, then* (i) $\alpha_m^* - \alpha_f^*$ *and* (ii) $k_f - k_m$ *have the same sign (Fig. 1). This statement holds for arbitrary dispersal rates, $d_m$ and $d_f$.*

Proposition 2 tells us that the equilibrium sex ratio, under a DDM life history, is biased towards the sex that is less likely to compete on its natal patch. This is not the same as saying that sex-ratio bias favours the more dispersive sex. Consider the following example of sex-ratio evolution with fixed dispersal rates and a DDM life history. We set $d_f > 0$ and $c_f = 0$, hence $k_f = 1 - d_f < 1$. By choosing $c_m$ sufficiently close to one, we can get $k_m > k_f$, even when

$d_{\mathrm{m}} > d_{\mathrm{f}}$. It is possible, then, for selection to produce a sex-ratio bias that actually favours the less dispersive sex.

An alternative principle suggests that sex ratios in geographically structured populations are biased toward the sex that 'suffers' less from competition with relatives (Perrin and Mazalov, 2000). Still, this alternative formulation, itself, suffers from a measure of imprecision. If there are more females than males, is it true that female–female competition, even among relatives, is less 'intense'? The answer is not clear.

We simply suggest that the most 'universal' principle of sex-ratio evolution (or sex-ratio/dispersal co-evolution) in geographically structured populations is set out in Proposition 2: optimal sex ratios, under DDM, should be biased towards the sex that is less likely to compete on its natal patch.

## DMD

Setting (1) equal to (7), routine algebra shows that under DMD and at equilibrium

$$\frac{\alpha_{\mathrm{m}}^*}{\alpha_{\mathrm{f}}^*} = \frac{1 - rk_{\mathrm{m}}^2}{1 - r(k_{\mathrm{f}}^2 - k_{\mathrm{m}}) - rk_{\mathrm{m}}k_{\mathrm{f}}^2} \tag{18}$$

We rely primarily on equation (18) to prove the following proposition about sex-ratio evolution, an analogue to Proposition 2.

**Proposition 3.** *If the sex ratio is at evolutionary equilibrium under DMD, then* (i) $\alpha_{\mathrm{m}}^* - \alpha_{\mathrm{f}}^*$ *and* (ii) $k_{\mathrm{f}}^2 - k_{\mathrm{m}}$ *have the same sign* (*Fig. 2*). *This statement holds for arbitrary dispersal rates, $d_{\mathrm{m}}$ and $d_{\mathrm{f}}$.*

Sex-ratio evolution under DMD is not as clear-cut as it is under DDM. The fact that a female is less likely than a male to compete on her native patch is still sufficient to produce a female-biased sex ratio under DMD. However, the same cannot be said for males (Fig. 2). For a male-biased sex ratio to evolve under DMD, $k_{\mathrm{m}}$ must be less than $k_{\mathrm{f}}^2$, the probability that two randomly chosen females are competing on their native patch.

How are we to understand this seemingly strange condition for the evolution of male-biased sex ratios? Consider equation (18). We are actually interested in understanding why the numerator in (18) is greater than the denominator. If $k_{\mathrm{m}} < k_{\mathrm{f}}^2$, there are two reasons why this is so (a similar argument demonstrates why female-biased sex ratios are expected when $k_{\mathrm{m}} > k_{\mathrm{f}}^2$, but $k_{\mathrm{m}} < k_{\mathrm{f}}$).

First, consider the last terms in both the numerator and denominator of (18). If $k_{\mathrm{m}} < k_{\mathrm{f}}^2$, then $rk_{\mathrm{m}}^2 < rk_{\mathrm{m}}k_{\mathrm{f}}^2$ (the converse is also true). In biological terms, $k_{\mathrm{m}} < k_{\mathrm{f}}^2$ means an actor is less likely to be related to her son's competitor than she is to be related to the mate of her daughter's competitor. In this case, an actor considers male fitness lost through increased female–female competition a more serious expense than that lost through increased male–male competition. As a result, the investment in sons is favoured.

Next, focusing attention on the second term in the denominator of (18), we note that $k_{\mathrm{m}} < k_{\mathrm{f}}^2$ is equivalent to $r(k_{\mathrm{f}}^2 - k_{\mathrm{m}}) > 0$ – a mathematical fact that diminishes the size of the denominator further. Biological interpretation requires us to recall that one benefit of producing a daughter is that she provides a mate to a related male. However, $k_{\mathrm{m}} < k_{\mathrm{f}}^2$ means that this benefit does not outweigh the loss of inclusive fitness – through daughters –
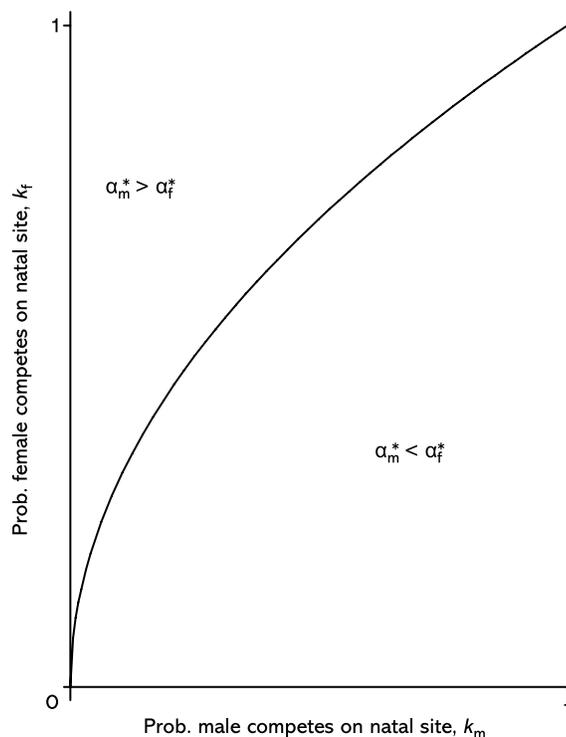
**Fig. 2.** Direction of sex-ratio bias under the DMD model for all combinations of $k_m$ and $k_f$, the sex-specific probabilities of competing on the native patch. Along the solid line, $k_m = k_f^2$ and so $\alpha_m^* = \alpha_f^*$.

due to increased female–female competition. Again we see that investment in sons is favoured.

Let us now consider sex-specific dispersal under DMD. Referring to equations (8) and (12) we see that $\Delta W_{d_m} = 0$ if, and only if,

$$c_m = rk_m \tag{19}$$

and $\Delta W_{d_f} = 0$ if, and only if,

$$c_f = r(k_f + k_f k_m - k_m c_f) \tag{20}$$

In general, we cannot solve (19) and (20) explicitly for $d_m^*$ and $d_f^*$. The case $N = 1$, however, is exceptional. When $N = 1$, the ratio $r = 1$, and so

$$\frac{\alpha_m^*}{\alpha_f^*} = \frac{1 - c_m}{1 - c_f^2} \qquad d_m^* = \frac{1}{1 + c_m} \qquad d_f^* = \frac{1}{1 + c_f} \tag{21}$$

It follows from equations (21) that we may choose values of $c_m$ and $c_f$ such that $d_m^* > d_f^*$, while $\alpha_m^* < \alpha_f^*$. Thus, under DMD, sex-ratio bias does not always favour the more dispersive sex.

Equations (21) also demonstrate that a strong sex-ratio bias can be the product of sex-ratio/dispersal co-evolution under DMD – even without strong differences between

sex-specific rates of dispersal. For example, in the extreme situation where $c_m$ and $c_f$ are both very close to one, equations (21) show that (a) $d_m^*$ and $d_f^*$ are about 1/2 but (b) daughters make up almost 2/3 of a brood!

Of course, we are interested in understanding co-evolution under DMD for arbitrary $N$. The following proposition addresses the case $c_m = c_f$, in which timing of dispersal is the only sexual asymmetry present in the model.

**Proposition 4.** *Suppose* $(\alpha_m^*, d_m^*, d_f^*)$ *is an equilibrium strategy under DMD. If* $0 < c_m = c_f = c < 1$, *then* (i) $\alpha_m^* \leq \alpha_f^*$ *and* (ii) $d_m^* \leq d_f^*$, *with equality in either case if, and only if,* $N = 1$.

In simple terms, without sex differences in the cost of dispersal, selection under DMD favours female-biased sex ratios and relatively higher rates of female dispersal (what we term 'female-biased dispersal').

In the most general of DMD cases, equations (18–20) were solved numerically. We investigated various parameter combinations, and observed both $\alpha_m^* > \alpha_f^*$ and $\alpha_m^* < \alpha_f^*$, as well as $d_f^* > d_m^*$ and vice versa (e.g. Figs. 3 and 4). There are cases where $c_m < c_f$, but $d_m^* < d_f^*$ (Fig. 3); and there are cases where $c_m < c_f$, and $d_m^* > d_f^*$, but $\alpha_m^* < \alpha_f^*$ (Fig. 4).
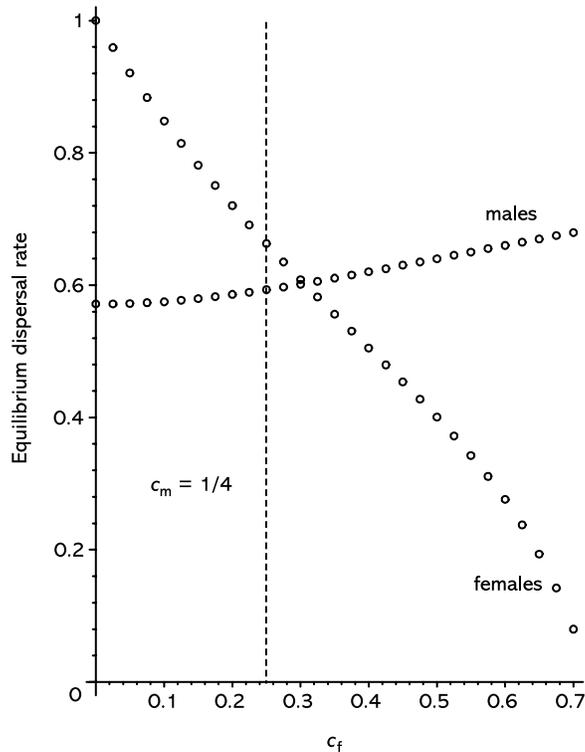


**Fig. 3.** Equilibrium rate of male dispersal, $d_m^*$, and equilibrium rate of female dispersal, $d_f^*$, under the DMD model as the cost of female dispersal, $c_f$, varies. Results are based on numerical solution of the equilibrium condition using $N = 2$ and $c_m = 1/4$. The dashed line indicates $c_f = c_m$.
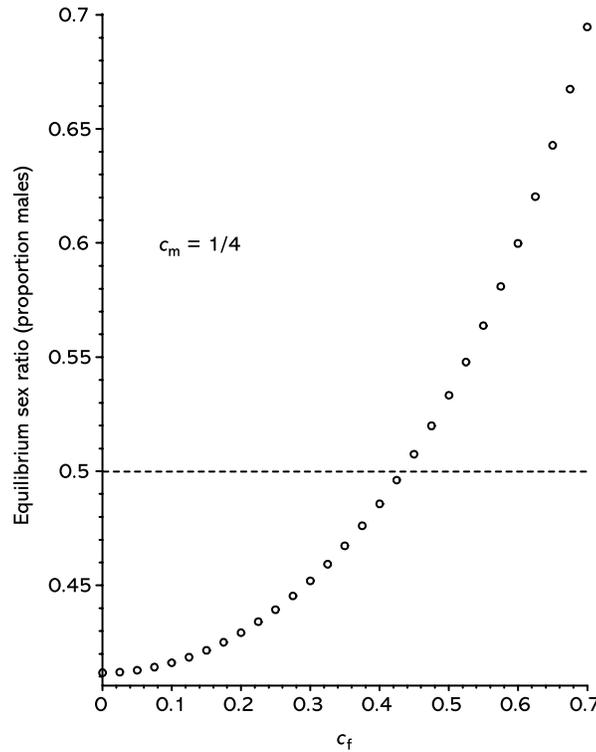
**Fig. 4.** Equilibrium sex ratio, $\alpha_m^*$, under the DMD model as the cost of female dispersal, $c_f$, varies. Results are based on numerical solution of the equilibrium condition using $N = 2$ and $c_m = 1/4$. The dashed line indicates $\alpha_m^* = \alpha_f^*$.

It should be noted, however, that in no instance did we observe $d_m^* < d_f^*$ and $\alpha_m^* > \alpha_f^*$ simultaneously.

Since unequal dispersal costs $c_i$ are not the only source of sexual asymmetry in the DMD model, we are not surprised that the relative size of these costs does not always predict the direction of bias in equilibrium strategies. Still, there may be specific cases where dispersal costs alone tell us something about the bias (if any) in $(\alpha_m^*, d_m^*, d_f^*)$. We propose the following:

**Conjecture 1.** *Suppose* $(\alpha_m^*, d_m^*, d_f^*)$ *is an equilibrium strategy under DMD. If* $c_f \leq c_m$, *then* (i) $\alpha_m^* \leq \alpha_f^*$ *and* (ii) $d_m^* \leq d_f^*$.

Our efforts to prove Conjecture 1 have been unsuccessful. We have been unable to demonstrate, rigorously, (a) that $d_m^*$ decreases with increasing $c_m$, and (b) that $d_f^*$ decreases with increasing $c_f$. At least one of (a), (b) appears to be a prerequisite for the proof of Conjecture 1.

Instead of Conjecture 1, we have settled for a result that assumes costs of dispersal are arbitrarily small.

**Proposition 5.** *Suppose* $(\alpha_m^*, d_m^*, d_f^*)$ *is an equilibrium strategy under DMD. If* $c_m$ *and* $c_f$ *are sufficiently small, then* (i) $d_m^* - d_f^*$ *and* (ii) $c_f - c_m$ *have the same sign. Furthermore, if* $c_m > c_f$, *then* $\alpha_m^* < \alpha_f^*$.

Proposition 5 is the DMD-analogue to Proposition 1. Interestingly, if dispersal cost is small, the behaviour of the DMD model is quite similar to that of the DDM model.


## STABILITY

We have been working under the tacit assumption that the equilibrium strategy $(\alpha_m^*, d_m^*, d_f^*)$ is the endpoint of co-evolution by natural selection. This may not be the case, and in this section we address the stability of $(\alpha_m^*, d_m^*, d_f^*)$.

   We adopt the following dynamical description of evolution:

$$\frac{\mathrm{d}}{\mathrm{d}t}\begin{bmatrix} \alpha_m \\ d_m \\ d_f \end{bmatrix} = \begin{bmatrix} \sigma_{\alpha_m}^2 & \sigma_{\alpha_m d_m} & \sigma_{\alpha_m d_f} \\ \sigma_{\alpha_m d_m} & \sigma_{d_m}^2 & \sigma_{d_m d_f} \\ \sigma_{\alpha_m d_f} & \sigma_{d_m d_f} & \sigma_{d_f}^2 \end{bmatrix}\begin{bmatrix} \Delta W_{\alpha_m} \\ \Delta W_{d_m} \\ \Delta W_{d_f} \end{bmatrix} \tag{22}$$

The notation $\mathrm{d}/\mathrm{d}t$ signifies differentiation with respect to evolutionary time; the constant $\sigma_x^2$ gives the genetic variance of trait $X$; the constant $\sigma_{XY}$ gives the genetic covariance between traits $X$ and $Y$; and $\Delta W_{\alpha_m} = \Delta W_m - \Delta W_f$ (Abrams *et al.*, 1993; Greenwood-Lee *et al.*, 2001). We will assume that $\sigma_{XY} = 0$.

   We have adopted a continuous-time dynamic primarily for mathematical convenience. There are discrete-time versions of (22) available (Iwasa *et al.*, 1991; Taylor, 1996b), but demonstrating stability under these dynamics is substantially more difficult. Since life histories have been cast in discrete time, the validity of (22) rests on the assumption that $t$ measures time on a scale that is much longer than one generation.

   By definition, an equilibrium strategy is also a rest point of (22). Equilibria that correspond to asymptotically stable rest points of (22) are considered to be the end result of selection. We call such equilibria 'dynamically stable strategies' (DSSs).

   The DSS differs from the concept of stability perhaps most familiar to biologists, the so-called evolutionarily stable strategy (ESS; Maynard Smith and Price, 1973). We have not pursued the ESS concept here, because inclusive fitness effects do not, in general, yield genetically valid ESS conditions (Taylor, 1989; Day and Taylor, 1998).

   The DSS also differs from the concept of convergence stability (Taylor, 1989; Christiansen, 1991; Day and Taylor, 2003, and references therein). Although inclusive fitness effects can be used to test for convergence stability, our preference for a dynamical description of evolution makes this 'static' concept unattractive.

   With stability properly defined, we may now state the main result of this section.


**Proposition 6.** *If* $c_m$, $c_f < 1$, *then all equilibrium strategies under DDM are DSSs.*

Proposition 6 tells us that the results of the previous section about equilibria under DDM can also be stated for DSSs under DDM – provided dispersal is not lethal. Proposition 6 does not necessarily hold when we assume $\sigma_{XY} \neq 0$.

   Unfortunately, no similar result can be found for equilibrium strategies under DMD. Dynamic stability for DMD equilibria can be verified for the special case, $N = 1$ (see

Appendix 2). Dynamic stability has been verified numerically for all DMD equilibria identified in the previous section.

## DISCUSSION

This is not the first paper to consider the co-evolution of the sex ratio and sex-specific dispersal. Leturque and Rousset (2003) have also addressed the present co-evolutionary problem, but in the context of a spatially heterogeneous model. Although Leturque and Rousset (2003) use a kin selection approach, their results are based on numerical investigations and are limited to the case of DDM. This leaves open the question of the precise effect of life-history asymmetries on sex ratio/dispersal co-evolution.

The present work establishes, in a formal way, the importance of such asymmetries to the joint evolution of sex-ratio bias and sex-specific dispersal. Our models account for two basic types of asymmetry between the sexes: (i) sex-specific costs of dispersal and (ii) a difference in timing of life-history events, namely dispersal.

The result of co-evolution of the sex ratio and sex-specific dispersal is not immediately clear. Using models similar to ones used here, Perrin and Mazalov (2000) demonstrated that optimal dispersal rates are higher in the sex that suffers more from local competition. An analogous result has been shown, herein, to hold for the sex ratio under a DDM life history: optimal sex ratios are biased towards the sex that is less likely to compete on its natal patch (Proposition 2). At first glance, it appears that sex-ratio bias and sex-specific dispersal respond to local competitive influences in different and opposite ways. One might wonder, then, whether sex-ratio bias and dispersal bias could ever co-evolve so as to favour the same sex. Clearly, a careful co-evolutionary argument is necessary.

Our model shows that dispersal and the sex ratio do not respond oppositely to local competition. The sex ratio does not figure in the equilibrium condition for either $d_{\mathrm{m}}^*$ or $d_{\mathrm{f}}^*$, but both $d_{\mathrm{m}}^*$ and $d_{\mathrm{f}}^*$ are required for the calculation of $\alpha_{\mathrm{m}}^*$. The sexual asymmetries that influence the optimal level of sex-specific dispersal are modified by dispersal rates themselves. The optimal sex ratio is then based on this modified asymmetry.

We have demonstrated that, in the absence of both forms of sexual asymmetry considered, neither sex-ratio bias nor sex-specific dispersal is to be expected. Furthermore, when only one source of asymmetry is present, sex-ratio bias and dispersal bias favour the same sex. Interestingly, when both sex-specific dispersal costs and sex-specific timing of dispersal are considered simultaneously, almost any combination of sex-ratio bias and dispersal bias seems possible (the exception being the joint occurrence of female-biased dispersal and male-biased sex ratios).

Given the importance of sex-specific costs and sex-specific timing of dispersal in the present work, it is reasonable to ask for biological examples of these asymmetries.

Although dispersal costs are often impossible to measure in the field (Wolff, 1994), we might reasonably expect unequal sex-specific dispersal costs when dispersal of the sexes occurs under different environmental or physiological conditions. For instance, dispersal by a large or gravid female may naturally be more costly than dispersal by a smaller or otherwise unencumbered male.

Sex-specific dispersal costs might also be prevalent in some plants. In plants, dispersal of pollen corresponds to male dispersal, and dispersal of seeds corresponds to female dispersal. Most wind-dispersed pollen falls within 100 m of the parent plant, and so wind

dispersal is quite costly when suitable patches (i.e. available stigmas) are sparse (Raven *et al.*, 1992). If seeds disperse to another patch via an animal, for instance, the cost of seed dispersal may be markedly cheaper than that of pollen.

The dispersal of pollen and seeds by plants is also a good example of a DMD life cycle. Sex-specific timing of dispersal is also widespread among birds and mammals, though these species do not adhere to a strict DMD life history (Greenwood, 1980). It is interesting to note that in both plants and birds/mammals, the predictions of sex-ratio theory are often at odds with data (Frank, 1990; Cockburn *et al.*, 2002; de Jong and Klinkhamer, 2002). It is also interesting to note that the effects of sex-specific timing of dispersal have not been adequately incorporated into those predictions (see Campbell, 2000; Cockburn *et al.*, 2002; de Jong and Klinkhamer, 2002, and references therein). We have already established that under DMD, sex ratios do not necessarily follow widely accepted principles. Certainly, predictions based on these principles are likely to fail.

To see the value of applying the DMD model, consider dioecious plants. Some researchers have argued that sex-ratio theory predicts female-biased or 1 : 1 sex ratios for this group (de Jong and Klinkhamer, 2002). The prediction, however, is not supported by data. Data for dioecious plants show a wide variety of sex ratios, both within and among species; and these often include male-biased sex ratios (de Jong and Klinkhamer, 2002).

The DMD model offers a different theoretical perspective. In fact, the model predicts a wide variety of sex ratios (including instances of male bias) when traits like dispersal vary appropriately among populations and among species. Selection that alters dispersal also indirectly influences the sex ratio. Dioecious plants no doubt experience diverse environmental conditions relevant to the evolution of dispersal. The DMD model suggests that sex-ratio variation among dioecious plants may simply be a reflection of this diversity.

There is a breadth of opportunity for new research. In particular, we are interested in cases where $\alpha_m^*$ influences the level of both $d_m^*$ and $d_f^*$ – not just the other way around. Such a situation would occur, for example, if sex-ratio decisions are costly to parental survival (e.g. Charnov, 1982, Ch. 6). A costly sex-ratio decision, in this case, would influence the extent to which generations overlap, and ultimately the equilibrium level of dispersal (Irwin and Taylor, 2000). We are, at present, trying to understand how the co-evolution of these traits proceeds in a population with age-structure.

Inbreeding depression and inbreeding avoidance are prominent theoretical explanations for both the evolution of dispersal (Motro, 1991; Gandon, 1999) and the evolution of sex-specific dispersal (Johnson and Gaines, 1990; Wolff and Plissner, 1998). Understanding the importance of such mechanisms to the joint evolution of the sex ratio and dispersal is, therefore, critical to the development of a complete co-evolutionary picture. Under DMD we expect inbreeding avoidance to influence only male dispersal. Since both male and female dispersal occur before mating under DDM, the influence of inbreeding in this case should be symmetric. The contrast presented by the two models, DDM and DMD, is worth further consideration.

## ACKNOWLEDGEMENTS

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## APPENDIX 1: RELATEDNESS CALCULATIONS

In this appendix, we outline the calculation of relatedness for the inclusive fitness effects developed in the main text.

Recall that the coefficient of consanguinity (CC) between two individuals, $X$ and $Y$, is defined as the probability that a random allele belonging to $X$ and a random allele belonging to $Y$ are identical by descent (IBD). Let $f_{XY}$ denote the CC between $X$ and $Y$. Following Michod and Hamilton (1980), we define the relatedness of $X$ to $Y$ as

$$R_{XY} = f_{XY}/f_{XX} \tag{A1}$$

Individual $X$ is the actor and has control over the behaviour under consideration.

To compute the necessary relatedness coefficients, we first determine expressions for a variety of CCs. The standard way to do this involves building a system of recursive equations for each CC needed. Once the recursions are constructed, a steady-state solution is found.

We will need the following definitions:

- $F$, the inbreeding coefficient, i.e. the probability that homologous alleles of a diploid zygote are IBD;
- $G$, the CC between a breeding female and her mate;
- $H_{ff}$, the CC between a breeding female and a random breeding female patchmate (taken with replacement);
- $H_{mm}$, the CC between a breeding male and a random breeding male patchmate (taken with replacement);
- $H_{fm}$, the CC between a breeding female and a random breeding male patchmate;
- $\bar{H} = H_{ff}/4 + H_{fm}/2 + H_{mm}/4$, the CC between two offspring born on the same patch.

The system of equations we investigate depends on the details of the life cycle. Consequently, we require two sets of calculations: one for the DDM model and another for the DMD model. We use a 'prime' to denote the next-generation value of a particular probability. Under DDM,

$$F' = G \tag{A2}$$

$$G' = k_f k_m \bar{H} \tag{A3}$$

$$H'_{ff} = [1/N](1 + F)/2 + [(N - 1)/N]k_f^2\bar{H} \tag{A4}$$

$$H'_{mm} = [1/N](1 + F)/2 + [(N - 1)/N]k_m^2\bar{H} \tag{A5}$$

$$H'_{fm} = G' \tag{A6}$$

Under DMD,

$$F' = G \tag{A7}$$

$$G' = k_m\bar{H} \tag{A8}$$

$$H'_{ff} = [1/N](1 + F)/2 + [(N - 1)/N]k_f^2\bar{H} \tag{A9}$$

$$H'_{mm} = [1/N](1 + F)/2 + [(N - 1)/N]k_m^2 k_f^2\bar{H} \tag{A10}$$

$$H'_{fm} = [1/N]G' + [(N - 1)/N]k_m k_f^2\bar{H} \tag{A11}$$

We will not detail the solutions to equations (A2–A6) and equations (A7–A11). We only note that each system has a unique, steady-state solution that can be found easily using a computer algebra package.

With solutions to the recursions in hand, relatedness coefficients are easy to determine. Recall that we have assumed maternal control of all behaviours. It follows that relatedness ought to be computed from the perspective of a breeding female on a given patch (see equation A1). Under either model,

- $R_m = R_f = [(1 + 3F)/4]/[(1 + F)/2]$
- $\bar{R}_m = \bar{R}_f = \bar{H}/[(1 + F)/2]$

For later calculations we need more detailed expressions of relatedness. Under DDM,

$$R_m = R_f = \frac{1}{2}\left[\frac{2k_f k_m + 4N - 2Nk_f k_m - (k_f^2 + k_m^2)(N - 1)}{4N - 2Nk_f k_m - (k_f^2 + k_m^2)(N - 1)}\right] \tag{A12}$$

$$\bar{R}_m = \bar{R}_f = \frac{2}{4N - 2Nk_f k_m - (k_f^2 + k_m^2)(N - 1)} \tag{A13}$$

Under DMD,

$$R_m = R_f = \frac{1}{2}\left[\frac{4N - k_f^2(1 + k_m)^2(N - 1)}{4N - 2k_m - k_f^2(1 + k_m)^2(N - 1)}\right] \tag{A14}$$

$$\bar{R}_m = \bar{R}_f = \frac{2}{4N - 2k_m - k_f^2(1 + k_m)^2(N - 1)} \tag{A15}$$

Since $R_m = R_f$ and $\bar{R}_m = \bar{R}_f$ always hold, we get

$$r = \frac{\bar{R}_m}{R_m} = \frac{\bar{R}_f}{R_f} = \frac{\bar{R}_m}{R_f} = \frac{\bar{R}_f}{R_m} \tag{A16}$$

The ratio $r$ has its own interpretation as a relatedness coefficient (see Taylor, 1988a).

## APPENDIX 2: PROOFS AND MATHEMATICAL DETAILS

The proof of Proposition 1 will use the following lemma.

**Lemma 1.** *Suppose* $(\alpha_m^*, d_m^*, d_f^*)$ *is an equilibrium strategy under DDM and* $c_m$, $c_f < 1$. *Then* $d_f^*$ *does not decrease with increasing* $c_m$, *and* $d_m^*$ *does not decrease with increasing* $c_f$.

**Proof of Lemma 1.** By symmetry, it is enough to prove the lemma for one sex. We shall prove that $d_f^*$ does not decrease with increasing $c_m$.

The equilibrium conditions (16, 17) implicitly define the relatedness ratio and sex-specific dispersal rates as functions of a single variable, $c_m$. We call these functions $r^*$, $d_m^*$ and $d_f^*$, respectively. Implicit differentiation of (16, 17) with respect to $c_m$ gives a system of two equations in $dd_f^*/dc_m$ and $dd_m^*/dc_m$. When this system is solved we see that

$$\frac{dd_f^*}{dc_m} = 2\, \frac{k_f(1 - c_f d_f^*)^2 (N-1)(k_m + k_f)}{(1 - c_f)r^*(4N + (N-1)(k_m + k_f)^2)} \geq 0 \tag{A17}$$

Since $c_f < 1$, the derivative $dd_f^*/dc_m$ exists and $d_f^*$ is a differentiable function of $c_f$, and since $dd_f^*/dc_m \geq 0$, we have the first conclusion.

**Proof of Proposition 1.** From equations (16, 17), $c_m < c_f$ is equivalent to $k_m < k_f$, at equilibrium. Elementary algebra gives us $1 - k_m^2 > 1 - k_f^2$; and from equation (15) this is equivalent to $\alpha_m^* > a_f^*$. We conclude that $c_m < c_f$ if, and only if, $\alpha_m^* > a_f^*$.

We now show that $c_m < c_f$ if, and only if, $d_m^* > d_f^*$. First, note that if $c_m = c_f = c$, the equilibrium rate of dispersal under DDM, $d^*$, is not sex-specific. Equation (14) shows that $d^*$ is a decreasing function of $c$.

As in the proof of Lemma 1, we also note that sex-specific dispersal is a function of $c_m$ and $c_f$. For the purposes of this proof, we write $d_m^*(c_m; c_f)$ and $d_f^*(c_f; c_m)$, where the semi-colon is intended to remind us that we change only one variable at a time – not simultaneously. Observe that $d^*(c) = d_m^*(c_m; c_f) = d_f^*(c_f; c_m)$.

By Lemma 1, $c_m < c_f$ is equivalent to

$$d_f^*(c_f; c_m) < d_f^*(c_f; c_f) = d^*(c_f) \tag{A18}$$

Since $d^*$ is decreasing in its argument we have (A18) if, and only if,

$$d_f^*(c_f; c_m) < d^*(c_m) = d_m^*(c_m; c_m) \tag{A19}$$

Applying Lemma 1 again yields $d_f^* < d_m^*$. We conclude that $c_m < c_f$ if, and only if, $d_m^* > d_f^*$.

The proof that $c_m > c_f$ if, and only if, $d_m^* < d_f^*$ if, and only if, $\alpha_m^* < a_f^*$ is similar.

**Proof of Proposition 2.** Obvious from equation (15).

**Proof of Proposition 3.** (i) The assumption $\alpha_m^* > a_f^*$ is equivalent to

$$k_m^2 < k_f^2 - k_m + k_m k_f^2 \tag{A20}$$

by equation (18). In turn, (A20) is equivalent to $(1 + k_m)(k_m - k_f^2) < 0$, which holds if, and only if, $k_m < k_f^2$. Proof that $\alpha_m^* < a_f^*$ if, and only if, $k_m < k_f^2$ is similar.

To prove Proposition 4 we need the following lemma.

**Lemma 2.** *If* $(\alpha_m^*, d_m^*, d_f^*)$ *is an equilibrium strategy under DMD and* $c_m$, $c_f < 1$, *then* $d_f^*$ *does not increase with increasing patch size,* $N$. *Furthermore, if* $c_f > 0$, *then* $d_f^*$ *is strictly increasing in* $N$.

**Proof of Lemma 2.** We use an approach similar to that used to prove Lemma 1. Implicit differentiation of (19, 20) with respect to $N$ gives two equations in two unknowns, $dd_f^*/dN$ and $dd_m^*/dN$. Solving these equations gives us

$$\frac{dd_f^*}{dN} = \frac{k_f(1 - c_f d_f^*)^2(k_m k_f + k_f + 2)(k_m k_f + k_f - 2)}{(1 + k_m)(1 - c_f)(4N + k_f^2(1 + k_m)^2(N - 1))} \leq 0 \tag{A21}$$

where equality implies either $k_m = k_f = 1$, or $d_f^* = 1$. For $N < \infty$, we have $d_f^* > 0$, hence $k_m = k_f = 1$ if, and only if, $c_m = c_f = 1$. By assumption, $c_f < 1$, hence $d_f^* = 1$ is the sole necessary condition. However, $d_f^* = 1$ if, and only if, $c_f = 0$; so when $c_f > 0$, the derivative $dd_f^*/dN$ must be strictly negative.

**Proof of Proposition 4.** We shall prove (ii) first.

Suppose $0 < c_m = c_f = c < 1$. By equation (21) and Lemma 2, $d_f^* \leq 1/(1 + c)$, where the weak inequality is an equality if, and only if, $N = 1$. It follows that

$$(d_f^* - 1)(d_f^* - 1/(1 + c)) \geq 0 \tag{A22}$$

with equality if, and only if, $N = 1$. In equality (A22) is equivalent to

$$d_m^* \geq \frac{(2 + c)d_f^* - 1}{(1 + c)d_f^*} \tag{A23}$$

with equality if, and only if, $N = 1$.

Now, it follows from the assumption that $c_m = c_f$ and equations (19, 20) that

$$k_m = k_f \left[ \frac{1 - c d_f^*}{c - c^2 d_f^* + d_f^* - c d_f^*} \right] \tag{A24}$$

or equivalently

$$d_m^* = \frac{(2 + c)d_f^* - 1}{(1 + c)d_f^*} \tag{A25}$$

The conclusion (ii) then follows immediately from inequality (A23).

We shall use Proposition 3 to prove part (i). Define $\kappa(c, d) = (1 - d)/(1 - cd)$ and observe that $\kappa(c_f, d_f^*) = k_f$ and $\kappa(c_m, d_m^*) = k_m$. We restrict $\kappa$ to values of $c$ and $d$ on the unit square, and observe that $\kappa$ is decreasing in $d$. It follows from part (ii) that $k_m \geq k_f \geq k_f^2$ with equality if, and only if, $N = 1$. This yields (i).

**Proof of Proposition 5.** We first show that $d_f^* - d_m^*$ and $c_m - c_f$ have the same sign. Define

$$f(c_m, c_f, d_m, d_f) : [0,1] \times [0,1] \times [0,1] \times [0,1] \rightarrow \mathbf{R}^2 \tag{A26}$$

as $f = (f_1, f_2)$, where

$$f_1(c_m, c_f, d_m, d_f) = c_m - r k_m \tag{A27}$$

$$f_2(c_m, c_f, d_m, d_f) = c_f - r(k_f + k_f k_m - c_f k_m) \tag{A28}$$

The function $f$ is infinitely differentiable (i.e. of class $C^\infty$) on the set

$$E := [0,1]^2 \times [0,1]^2 \tag{A29}$$

At $(0,0,1,1) \in E$, we get $f(0,0,1,1) = 0$ and

$$\begin{vmatrix} \dfrac{\partial f_1}{\partial d_m} & \dfrac{\partial f_1}{\partial d_f} \\[2mm] \dfrac{\partial f_2}{\partial d_m} & \dfrac{\partial f_2}{\partial d_f} \end{vmatrix} = \dfrac{1}{N^2} \tag{A30}$$

when evaluated at $(0,0,1,1)$. It follows from the Implicit Function Theorem that there is a neighbourhood $U \subset [0,1]^2$ of $(0,0)$, a neighbourhood $V \subset [0,1]^2$ of $(1,1)$, and a unique function

$$(d_m^*, d_f^*) : U \to V \tag{A31}$$

such that

$$f(c_m, c_f, d_m^*(c_m, c_f), d_f^*(c_m, c_f)) = 0 \tag{A32}$$

for all $(c_m, c_f) \in U$. Furthermore $(d_m^*, d_f^*) \in C^\infty(U)$.

The partial derivatives $\partial d_i^*/\partial c_j$ are given by the matrix

$$-\begin{bmatrix} \dfrac{\partial f_1}{\partial d_m} & \dfrac{\partial f_1}{\partial d_f} \\[2mm] \dfrac{\partial f_2}{\partial d_m} & \dfrac{\partial f_2}{\partial d_f} \end{bmatrix}^{-1} \begin{bmatrix} \dfrac{\partial f_1}{\partial c_m} & \dfrac{\partial f_1}{\partial c_f} \\[2mm] \dfrac{\partial f_2}{\partial c_m} & \dfrac{\partial f_2}{\partial c_f} \end{bmatrix} \tag{A33}$$

and when this is evaluated at $(0,0,1,1)$

$$\begin{bmatrix} \dfrac{\partial d_m^*}{\partial c_m} & \dfrac{\partial d_m^*}{\partial c_f} \\[2mm] \dfrac{\partial d_f^*}{\partial c_m} & \dfrac{\partial d_f^*}{\partial c_f} \end{bmatrix}_{(0,0,1,1)} = -\begin{bmatrix} N & 0 \\ 0 & N \end{bmatrix} \tag{A34}$$

Now define $\Delta(c_m, c_f) = d_f^*(c_m, c_f) - d_m^*(c_m, c_f)$. The new function, $\Delta$ is $C^\infty(U)$ and

$$\Delta(0,0) = 0 \tag{A35}$$

$$\left( \dfrac{\partial \Delta}{\partial c_m}, \dfrac{\partial \Delta}{\partial c_f} \right)_{(0,0)} = (N, -N) \tag{A36}$$

By Taylor's Theorem, for $\mathbf{c} = (c_m, c_f) \in U$

$$\Delta(c_m, c_f) = N(c_m - c_f) + o(\|\mathbf{c}\|) \tag{A37}$$

It follows that by choosing $c_m$ sufficiently small and $c_f < c_m$, we get $\Delta > 0$ (i.e. $d_f^* > d_m^*$). Similarly, if $c_f$ is small and $c_m < c_f$, we get $d_m^* > d_f^*$.

Now suppose $c_f < c_m$. By the comments above, this implies $d_f^* > d_m^*$. Now define $\kappa(c, d) = (1 - d)/(1 - cd)$ and observe that $\kappa(c_f, d_f^*) = k_f$ and $\kappa(c_m, d_m^*) = k_m$. Restricting $\kappa$ to the unit square, we see that $\kappa$ is increasing in $c$, but decreasing in $d$. Since $c_f < c_m$ and $d_f^* > d_m^*$, we get $k_f < k_m$. The conclusion that $\alpha_f^* > \alpha_m^*$ follows from Proposition 3.

**Proof of Proposition 6.** Suppose $(\alpha_m^*, d_m^*, d_f^*)$ is an equilibrium strategy under DDM. For $(\alpha_m^*, d_m^*, d_f^*)$ to also be a DSS, it is enough to show that the eigenvalues of the Jacobian matrix

$$\mathbf{J} = \begin{bmatrix} \sigma_{\alpha_m}^2 & 0 & 0 \\ 0 & \sigma_{d_m}^2 & 0 \\ 0 & 0 & \sigma_{d_f}^2 \end{bmatrix} \begin{bmatrix} \dfrac{\partial \Delta W_{\alpha_m}}{\partial \alpha_m} & \dfrac{\partial \Delta W_{\alpha_m}}{\partial d_m} & \dfrac{\partial \Delta W_{\alpha_m}}{\partial d_f} \\ \dfrac{\partial \Delta W_{d_m}}{\partial \alpha_m} & \dfrac{\partial \Delta W_{d_m}}{\partial d_m} & \dfrac{\partial \Delta W_{d_m}}{\partial d_f} \\ \dfrac{\partial \Delta W_{d_f}}{\partial \alpha_m} & \dfrac{\partial \Delta W_{d_f}}{\partial d_m} & \dfrac{\partial \Delta W_{d_f}}{\partial d_f} \end{bmatrix} \tag{A38}$$

all have negative real part when $\mathbf{J}$ is evaluated at equilibrium.

Observe that $\mathbf{J}|_*$ is an upper block-triangular matrix with

$$\sigma_{\alpha_m}^2 \left.\frac{\partial \Delta W_{\alpha_m}}{\partial \alpha_m}\right|_* \tag{A39}$$

and

$$\mathbf{J}_d|_* = \begin{bmatrix} \sigma_{d_m}^2 \dfrac{\partial \Delta W_{d_m}}{\partial d_m} & \sigma_{d_m}^2 \dfrac{\partial \Delta W_{d_m}}{\partial d_f} \\ \sigma_{d_f}^2 \dfrac{\partial \Delta W_{d_f}}{\partial d_m} & \sigma_{d_f}^2 \dfrac{\partial \Delta W_{d_f}}{\partial d_f} \end{bmatrix}_* \tag{A40}$$

on its diagonal.

It can be shown that

$$\left.\frac{\partial \Delta W_{\alpha_m}}{\partial \alpha_m}\right|_* = -\Delta W_m \left(\frac{1}{\alpha_m^*} + \frac{1}{\alpha_f^*}\right) < 0 \tag{A41}$$

Therefore, we now only need to show that the real parts of the eigenvalues of $\mathbf{J}_d|_*$ are negative.

By the Routh-Hurwitz Theorem, the eigenvalues of $\mathbf{J}_d|_*$ have negative real parts if $Tr\mathbf{J}_d|_* < 0$ and $\det \mathbf{J}_d|_* > 0$. Now,

$$Tr\mathbf{J}_d|_* = -\left[\sigma_{d_m}^2 \frac{(1-c_m)\bar{R}_m^2}{2(1-c_m d_m)^2} T_f \left(1 - \frac{k_f c_m}{2}\right) + \sigma_{d_f}^2 \frac{(1-c_f)\bar{R}_f^2}{2(1-c_f d_f)^2} T_m \left(1 - \frac{k_m c_f}{2}\right)\right]_* \tag{A42}$$

where

$$T_i = 4N - (k_i - k_j)(k_m + k_f)(N - 1) \qquad i \neq j \tag{A43}$$

$Tr\mathbf{J}_d|_*$ is always negative since $c_m$, $c_f < 1$.

The product of off-diagonal terms, $\partial \Delta W_{d_m}/\partial d_f$ and $\partial \Delta W_{d_f}/\partial d_m$, can be written as

$$\sigma_{d_m}^2 \sigma_{d_f}^2 \left(\frac{(1-c_m)\bar{R}_m^2}{2(1-c_m d_m)^2}\right) \left(\frac{(1-c_f)\bar{R}_f^2}{2(1-c_f d_f)^2}\right) k_m k_f \left(S_m - \frac{c_m T_m}{2}\right) \left(S_f - \frac{c_f T_f}{2}\right) \tag{A44}$$

where

$$S_i = 2\left(Nk_i + k_j(N - 1)\right) \qquad i \neq j \tag{A45}$$

We can now see that det $\mathbf{J}_d|_*$ has the same sign as

$$T_\mathrm{m}T_\mathrm{f}\left(1-\frac{k_\mathrm{f}c_\mathrm{m}}{2}\right)\left(1-\frac{k_\mathrm{m}c_\mathrm{f}}{2}\right)-k_\mathrm{m}k_\mathrm{f}\left(S_\mathrm{m}-\frac{c_\mathrm{m}T_\mathrm{m}}{2}\right)\left(S_\mathrm{f}-\frac{c_\mathrm{f}T_\mathrm{f}}{2}\right) \tag{A46}$$

which is equivalent to

$$\left(T_\mathrm{m}-\frac{k_\mathrm{f}c_\mathrm{m}T_\mathrm{m}}{2}\right)\left(T_\mathrm{f}-\frac{k_\mathrm{m}c_\mathrm{f}T_\mathrm{f}}{2}\right)-\left(k_\mathrm{f}S_\mathrm{m}-\frac{k_\mathrm{f}c_\mathrm{m}T_\mathrm{m}}{2}\right)\left(k_\mathrm{m}S_\mathrm{f}-\frac{k_\mathrm{m}c_\mathrm{f}T_\mathrm{f}}{2}\right) \tag{A47}$$

Observe that

$$T_i-k_jS_i=(4-(k_\mathrm{m}+k_\mathrm{f})^2)\,N>0 \qquad i\neq j \tag{A48}$$

hence $T_i>k_jS_i$ for $i\neq j$. It follows from (A47) that det $\mathbf{J}_d|_* > 0$. We conclude that $(\alpha_\mathrm{m}^*, d_\mathrm{m}^*, d_\mathrm{f}^*)$ is a DSS.

**Remark.** Under DMD, the dynamic stability of an equilibrium strategy also rests upon the sign of det $\mathbf{J}_d|_*$. If det $\mathbf{J}_d|_* > 0$, then $(\alpha_\mathrm{m}^*, d_\mathrm{m}^*, d_\mathrm{f}^*)$ is a DSS. When $N=1$, the entry $\partial \Delta W_{d_\mathrm{m}}/\partial d_\mathrm{f}|_* = 0$. The dynamic stability of a DMD equilibrium then follows from the fact that the product of diagonal elements of $\mathbf{J}_d|_*$ is positive.