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ORIGINAL PAPER

Sex ratio evolution when fitness and dispersal vary

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Abstract In a heterogeneous environment, when the fitness of males and females are differently influenced by habitat quality, habitat-dependent sex ratios may evolve to favor the production of the sex that benefits more (or loses less) from the local habitat. Similarly, sex-biased dispersal favors the evolution of habitat-dependent sex ratios. The present study documents the convergence stable sex ratios expected in the presence of sex-specific fitness gains when dispersal is partial, sex-biased or costly, using a simple model with patches of two qualities. Results show that partial dispersal reduces the sex ratio bias expected with sex-specific fitness gains. The direction of the sex ratio bias can be reversed by sex-biased dispersal or the existence of sex-specific dispersal costs, provided that fitness gains for the two sexes are not too different. The reversal of the sex ratio bias is more readily observed when sex-specific dispersal rates are opposite and extreme. Both dispersal and fitness gains, especially when they are sex-specific, should thus be considered when making predictions about sex ratio evolution in a heterogeneous environment.

Keywords Sex allocation · Spatial heterogeneity · Dispersal · Fitness gain · Environmental sex determination · Trivers and Willard hypothesis

Introduction

Sex allocation theory addresses the question of how best to allocate resources to male and female production. In a verbal model, Fisher (1930) proposed that frequency-dependent selection should favor an equal investment in male and female offspring. This theory was then formalized mathematically by Shaw and Mohler (1953). However, this central theory

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is based on a number of assumptions that may not be satisfied in all populations. Since the work of Hamilton (1967), assumptions of Fisher's theory have been relaxed to account for the biased sex ratios commonly observed in the populations of certain species (Bull and Charnov 1988). One extension of sex allocation theory that has received much attention was formulated by Trivers and Willard (1973): when (1) females in better condition produce higher-quality offspring, (2) higher-quality offspring become higher-quality adults, and (3) sons gain a greater fitness benefit from more resources than daughters do, then high-quality mothers should invest more in sons than in daughters. More generally, the hypothesis may be formulated as such: high-quality females should prefer offspring of the sex whose reproductive value is most strongly influenced by maternal investment (Leimar 1996).

The reasoning behind the Trivers and Willard hypothesis may be applied to different situations, including the case of a heterogeneous environment, when the fitness of one sex is more adversely affected by a decrease in habitat quality than the fitness of the other sex. Selection then favors the production of the sex that is less affected in poor-quality habitats and more affected in higher-quality habitats (Charnov 1979; Werren and Simbolotti 1989). In this context, Charnov and Bull (1977) proposed that environmental sex determination may evolve when offspring are better able to assess the relevant variation in the environment than their parents are. Sex ratios expected in such heterogeneous environments were investigated by Charnov (1979), Freeman et al. (1980), and Bull (1981). In a two-patch model, they found analytical expressions for the evolutionarily stable strategy of sex ratio. This is a formalization of the theory outlined by Trivers and Willard (1973) in the case where maternal condition is determined by the quality of the breeding patch, and fitness returns on parental investment increase linearly (Wild and West 2007).

The original models of Charnov and Bull as well as later analyses (Leimar 1996; Wade et al. 2003) assumed a panmictic population (with total dispersal). One salient aspect of sex ratio evolution in such panmictic populations is that models generally predict an abrupt shift from all male to all female offspring at a critical value of an environmental variable (Bull 1981, 1983; Charnov and Dawson 1989). However, the observed pattern in nature is usually a gradual shift in response to environment quality (West et al. 2002; West 2009). A number of factors have been considered to account for these gradual sex ratio shifts, including partial dispersal. Without kin competition, models predict that partial dispersal selects gradual shifts in habitat-dependent sex ratios (Van Dooren and Leimar 2003; Leimar et al. 2004). In the presence of kin competition for local resources, partial female dispersal could also disfavor the evolution of extreme sex ratio biases (Wild and West 2007).

Sex-biased dispersal is widespread in animals (Bowler and Benton 2005) and the norm in Spermatophyta, for which pollen and not ovules disperse, while zygotes disperse through seeds. Dispersal often incurs costs that may be sex-specific (Ronce 2007; Gros et al. 2008). In bird or mammal populations living in a spatially variable environment, sex-biased dispersal has sometimes been found to be associated with biased primary sex ratios (e.g., Komdeur et al. 1997; Goltsman et al. 2005; Banks et al. 2008; Hjernquist et al. 2009; Romano et al. 2012). Models have shown that the sex ratios expected under sex-biased dispersal may sometimes be extreme, even in the absence of interactions between kin to access mates or resources (Reinhold 1998; Julliard 2000; Guillon et al. 2006; Hulin and Guillon 2007).

This study focuses on two factors already known to influence sex ratio evolution, sex-specific dispersal and sex-specific effects of habitat quality on fitness, and examines their interaction while excluding other selective forces such as kin competition. I study the

effects of partial dispersal, sex-biased dispersal, and dispersal costs on the evolution of habitat-dependent sex ratios in a two-patch model when fitness gains according to patch type, defined as the ratio between survival rates in the two patches, differ for males and females. Considering different timings of female dispersal (before and after mating), I show that sex-biased dispersal and dispersal costs alone can considerably modify the predictions of the model with total dispersal. When male and female dispersal rates differ, the sex ratio bias may be opposite to that predicted under total dispersal. The reversal of the sex ratio bias is more readily observed when there is a large difference between effective (cost-corrected) dispersal rates, and when fitness gains for the two sexes are not too different. Sex-specific dispersal costs are able to reverse the sex ratio bias regardless of whether fitness gains differ between sexes. Results of the model are qualitatively but not always quantitatively similar for female dispersal occurring before or after mating.

The model

The studied population is divided into patches of very large sizes. In each generation, (1) zygotes develop into male or female reproductive adults, (2) adults disperse, (3) mating occurs, (4) zygotes disperse, and finally (5) adults die and are replaced by zygotes for the next generation. The number of zygotes developing in each category of habitat quality remains constant: the density regulation of the population thus occurs immediately after zygote dispersal. Two particular cases are studied here (Taylor 1994; Wild and Taylor 2004): both females and males disperse before mating and zygotes do not disperse (DDM model, for male Dispersal-female Dispersal-Mating), or only males disperse before mating and then zygotes disperse (DMD model, for male Dispersal-Mating-zygote Dispersal). The first case describes the typical life cycle of an animal, while the second case describes the life cycle of a plant or that of an animal species in which female dispersal occurs after mating.

I consider a metapopulation of patches large enough to ignore kin effects (relatedness coefficients are assumed to be very low in each patch) and demographic stochasticity (numbers of males and females are equal to their expectations). The environment comprises two qualities of habitat patches. Habitats 1 and 2 occur in proportions $1-g$ and g, respectively. Habitat quality determines F_i^m and F_i^f, the survival rates of adults developing in habitat i, for males and females respectively. F_m and F_f are the fitness gains, i.e., the ratios of survival rate in habitat 2 over survival rate in habitat 1 for males and females, respectively. The probability of a zygote developing into a male or female in habitat i is determined by a single genetic locus, with additive effects of alleles. When homozygous, zygotes produced in habitat i have a probability of r_i and $1 - r_i$ of developing into females and males, respectively. A sex ratio strategy is thus defined by the vector $r = (r_1, r_2)$. Then, a fraction d_m and d_f of males and females attempts dispersal, entering a dispersal pool from which they are redistributed at random among patches (Wright 1931), with dispersal cost being c_m and c_f, respectively. The cost is the proportion of dispersing individuals that do not reach a patch. Dispersal rates are not conditional on habitat: the same proportion of individuals disperses from habitats 1 and 2. Dispersing individuals are distributed according to patch-type frequencies, $1 - g$ and g. Following dispersal, mating occurs at random within patches, with the number of resulting zygotes dependent on the number of females present in the patch. A fraction d_z of zygotes disperses with cost c_z. Again, zygote dispersal is not conditional on habitat, and dispersing zygotes are distributed

according to habitat frequencies. Finally, adults die, and zygotes are drawn at random within patches for the next generation (it is assumed that fertilization events are sufficiently numerous for patches to be saturated with zygotes). A summary of notations is shown in Table 1.

To determine candidate convergence stable strategies, I used the direct fitness method (Taylor and Frank 1996) involving the following steps:

1. Computing $W_{ji}(r_i^\circ,r)$, the expected number of gene copies transmitted in habitat j to the next generation per gene of a focal zygote developing in habitat i (carrying allele r_i°), knowing the mean strategy in the population (r) (see Appendix 1). For the future, it is not the same to transmit a gene copy in habitats 1 and 2, so the next step is:
2. Computing V_i, the reproductive value of a gene present in a zygote developing in habitat i, defined as its asymptotic contribution to the gene pool of the population (Taylor 1990; Rousset 2004). The vector of the reproductive values (V_1,V_2) is the left eigenvector associated with the largest eigenvalue 1 of the W_{ji} matrix evaluated in the neutral model (i.e., when $r_1^\circ = r_1$ and $r_2^\circ = r_2$), such that:

$$(V_1, V_2)\begin{pmatrix} W_{11}(r_1,r) & W_{12}(r_2,r) \\ W_{21}(r_1,r) & W_{22}(r_2,r) \end{pmatrix} = (V_1, V_2). \tag{1}$$

   To solve Eq. (1), I used the normalization of reproductive values $Q_1V_1 + Q_2V_2 = 1$, Q_i being the proportion of zygotes developing in habitat i: $Q_1 = 1-g$ and $Q_2 = g$.
3. Establishing the criterion for singular points (Taylor and Frank 1996). Selection measures evaluate the probability of fixation of a rare allele r_i°, weakly different from the resident strategy r in the population (Rousset and Billiard 2000). In the present case, these are defined as follows:

$$S_1(r_1^\circ, r) = V_1\frac{\partial W_{11}(r_1^\circ, r)}{\partial r_1^\circ} + V_2\frac{\partial W_{21}(r_1^\circ, r)}{\partial r_1^\circ} \tag{2}$$

$$S_2(r_2^\circ, r) = V_1\frac{\partial W_{12}(r_2^\circ, r)}{\partial r_2^\circ} + V_2\frac{\partial W_{22}(r_2^\circ, r)}{\partial r_2^\circ}$$

It can be seen that the $S_i(r_i^\circ,r)$'s measure the marginal benefit of producing extra females (and less males) in habitat i when the resident strategy is r (see Eq. (5); Appendix 1). To take kin selection effects into account, Taylor and Frank's (1996) selection criterion also includes derivatives with respect to the strategy of a focal individual's neighbors within a patch. These derivatives are weighted by the relatedness coefficient between the focal individual and its neighbors. However, as I assume a very large patch size, the relatedness coefficients are very low and these derivatives cancel.

Table 1 Summary of notations

g, $1-g$	Proportion of habitat 2 and habitat 1 patches
F_i^m and F_i^f	Survival rate in habitat i for males and females
F_m and F_f	Fitness gains: ratio of survival rate in habitat 2 over survival rate in habitat 1 for males and females
d_m, d_f, d_z	Dispersal rate for males, females, and zygotes
c_m, c_f, c_z	Dispersal cost for males, females, and zygotes
r_1, r_2	Probability of a zygote developing into a female in habitats 1 and 2

The probabilities $S_i(r_i°,r)$ vanish at singular points (Metz et al. 1996; Geritz et al. 1998), i.e., convergence stable strategies $r^* = (r_1^*, r_2^*)$ necessarily satisfy:

$$\begin{aligned} S_1(r_1*, r*) &= 0 \\ S_2(r_2*, r*) &= 0 \end{aligned} \tag{3}$$

Here, I numerically verified that for $r = r^*$:

$$\frac{\partial S_1(r_1*, r)}{\partial r_1} < 0 \quad \text{and} \quad \frac{\partial S_2(r_2*, r)}{\partial r_2} < 0, \tag{4}$$

indicating that the singular points are convergence stable. Convergence stability was independently attested using individual-based simulations as described in Guillon and Bottein (2011): starting with a random mixture of possible strategies (values at two unlinked loci governing the sex ratio), mean allele values in the population converge toward the singular points.

The convergence stable strategies of habitat-dependent sex ratios (r_1^*, r_2^*, proportion of females produced in habitats 1 and 2, respectively) were determined as a function of male, female, and zygote dispersal rates (d_m, d_f, d_z) and dispersal costs (c_m, c_f, c_z). Two cases are studied here (Taylor 1994): (1) both males and females disperse before mating ($d_z = 0$, DDM model), or (2) only males disperse before mating and then zygotes disperse ($d_f = 0$, DMD model). In the particular case where both dispersal rates are equal to 1 and dispersal is costless, the model is similar to those described by Bull (1981; DDM model) and Freeman et al. (1980; DMD model). When male and female fitness gains are equal ($F_m = F_f$) and dispersal is costless, the model is similar to that described by Guillon et al. (2006).

Except for particular values of F_m, F_f, d_m, d_f, d_z, c_m, c_f, and c_z, there are no simple expressions for r_1^* and r_2^*. Roots of Eq. (3) were determined numerically using Mathematica (Wolfram Research Inc. 2005). Multiple solutions are found in the case where $F_m = F_f$ and $d_m = d_f = 1$ (DDM model) or $F_m = F_f$ and $d_m = d_z = 1$ (DMD model): all strategies with unbiased sex ratio at the scale of the entire population can coexist. For all other values of the parameters, a single solution is found. When dispersal rates are all nil ($d_m = d_f = d_z = 0$) or dispersal costs are total ($c_m = c_f = c_z = 1$), different patches function as separate populations, and the sex ratio in each patch is unbiased.

Results

Three selective forces at play

In the case of non-sex-specific fitness gains ($F_m = F_f$) with different dispersal rates between sexes ($d_m \neq d_f$ or $d_m \neq d_z$), two opposing selective forces affect the evolution of the sex ratio, as described by Guillon et al. (2006). The first (hereafter, SSR, for Secondary Sex Ratios) aims to equilibrate secondary sex ratios within patches after dispersal, by overproducing the more dispersing sex in good habitats and the less dispersing sex in poor habitats. The second (hereafter, HS, for Habitat Selection) increases the number of offspring establishing in good habitats by favoring the production of the less dispersing sex in good habitats and the more dispersing sex in poor habitats (Julliard 2000). In the DDM model, the HS force always dominates the SSR force. In the DMD model, males are always the more dispersing sex because $d_f = 0$. In this case, the HS force dominates only when

$d_m > d_z$, while the SSR force dominates when $d_m < d_z$ (Guillon et al. 2006). When fitness gains are sex-specific ($F_m \neq F_f$), a third selective force is at play (hereafter C&B, after Charnov and Bull), which stems from the competition between individuals of the same sex produced in different habitats. The C&B force favors the production of the sex with the higher fitness gain in habitat 2, and the production of the sex with the lower fitness gain in habitat 1 (Freeman et al. 1980; Bull 1981).

Partial dispersal

I first study the evolution of sex ratios when male and female dispersal rates are equal ($d_m = d_f$, DDM), or when male and zygote dispersal rates are equal ($d_m = d_z$, DMD). Figure 1a shows that when all males and females disperse, in the case when $g = 0.5$ and $F_f = 1$, the sex ratios are completely biased as soon as $F_m \neq F_f$. This is an example of the standard result obtained by Bull (1981). The same result is obtained when all males and zygotes disperse (Freeman et al. 1980; Fig. 1b). If $F_m \neq 1$, the competition is unequal between males, while the competition is equal between females when $F_f = 1$. As a result, habitat 2 produces only the sex with the higher fitness gain, and habitat 1 produces only the sex with the lower fitness gain. However, as the dispersal rate decreases, so does the sex ratio bias in both habitats (Fig. 1). For values of F_m very different from F_f, the sex ratio is still completely biased in one habitat. Qualitatively identical results are obtained for the DDM and DMD models (cf. Fig 1a, b). Overall, partial dispersal yields sex ratios that are biased in the direction predicted by Charnov and Bull, but less biased than with total dispersal.

As shown in Appendix 2, the predicted sex ratio in the presence of a cost to dispersal is identical to that predicted without cost for a lower dispersal rate value. When the dispersal rate is d and dispersal cost c, then $(1 - c)d$ of dispersing individuals reach a patch. The situation is then equivalent to an effective (costless) dispersal rate $d_e = (1 - c)d/(1 - cd)$. This general result applies to male, female, and zygote dispersal in both DDM and DMD

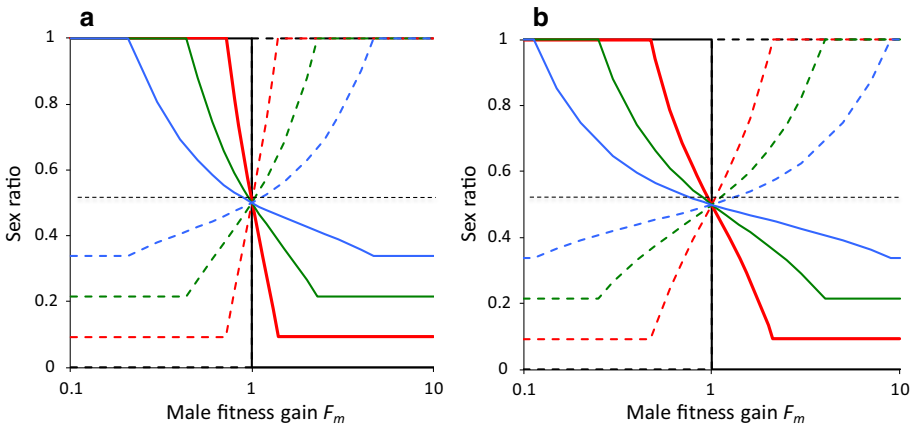

Fig. 1 Sex ratio as a function of male fitness gain (F_m) for different dispersal rate values. $g = 0.5$, $F_f = 1$, and $c_m = c_f = c_z = 0$ throughout. r_1: *dashed line*, r_2: *solid line*. **a** DDM model, *black*: $d_m = d_f = 1$, *red*: $d_m = d_f = 0.7$, *green*: $d_m = d_f = 0.5$, *blue*: $d_m = d_f = 0.3$. **b** DMD model, *black*: $d_m = d_z = 1$, *red*: $d_m = d_z = 0.7$, *green:* $d_m = d_z = 0.5$, *blue*: $d_m = d_z = 0.3$. Note the logarithmic scale on the *x*-axis. (Color figure online)

models. When dispersal rates are equal ($d_m = d_f$ or $d_m = d_z$) and male and female dispersal costs are equal ($c_m = c_f$), costly dispersal thus has the effect of diminishing the effective dispersal rate, which, in turn, lessens the sex ratio bias. Note that for the original Charnov and Bull model (when $d_f = d_m = 1$ or $d_z = d_m = 1$), the introduction of a cost to dispersal does not change the effective dispersal rate. In this special case, the predicted sex ratio is the same with or without cost.

Sex-biased dispersal, when dispersal rates vary

When fitness gains between habitats differ for males and females ($F_m \neq F_f$) and dispersal rates differ between sexes, various cases can be described. In the DDM model, suppose that $F_f > 1$ and $F_m > 1$. Results from previous models (Bull 1981; Guillon et al. 2006) show that the dominant selective forces push the sex ratio in the same direction when $d_f > d_m$ and $F_m > F_f$, or when $d_f < d_m$ and $F_m < F_f$ (Table 2). The dominant selective forces have opposite directions when $d_f < d_m$ and $F_m > F_f$ or when $d_f > d_m$ and $F_m < F_f$. Figure 2a shows the predicted sex ratios as a function of d_m for two values of d_f, when $g = 0.5$, $F_f = 2$, and $F_m = 2.5$. In the case of $d_f = 0.8$, the sex ratio is always biased toward females in habitat 1 and males in habitat 2, even when $d_f < d_m$, as expected when the C&B force dominates the HS force. In the case of $d_f = 0.4$, a different picture emerges: females are produced in excess in habitat 1 only when $d_m < 0.788$. For $d_m > 0.788$, the sex ratio in habitat 1 is biased toward the more dispersing sex (males), as expected if the HS force dominates the C&B force. The direction of the sex ratio bias can thus be reversed, depending on male and female dispersal rates. Noticeably, when d_m or d_f is nil, the predicted sex ratio is always balanced ($r_1 = r_2 = ½$).

In the DMD model, the pattern is very similar (Freeman et al. 1980; Guillon et al. 2006). Suppose that $F_f > 1$, $F_m > 1$. The dominant selective forces push the sex ratio in the same direction when $d_z > d_m$ and $F_m > F_f$, or when $d_z < d_m$ and $F_m < F_f$ (Table 3). The

Table 2 Direction of the sex ratio bias expected from sex-biased dispersal (row) and fitness gains for males and females (column)

DDM	$F_m>F_f>1$ (C&B)	$1<F_m<F_f$ (C&B)
$d_f>d_m$ (HS)	$r_1>0.5>r_2$ / $r_1>0.5>r_2$	$r_2>0.5>r_1$ / $r_1>0.5>r_2$
$d_f<d_m$ (HS)	$r_1>0.5>r_2$ / $r_2>0.5>r_1$	$r_2>0.5>r_1$ / $r_2>0.5>r_1$

The dominant selective force is shown after the dispersal rates and fitness gains

DDM male Dispersal-female Dispersal-Mating model (Taylor 1994), *C&B* Charnov and Bull (Bull 1981), *HS* Habitat Selection (Guillon et al. 2006)

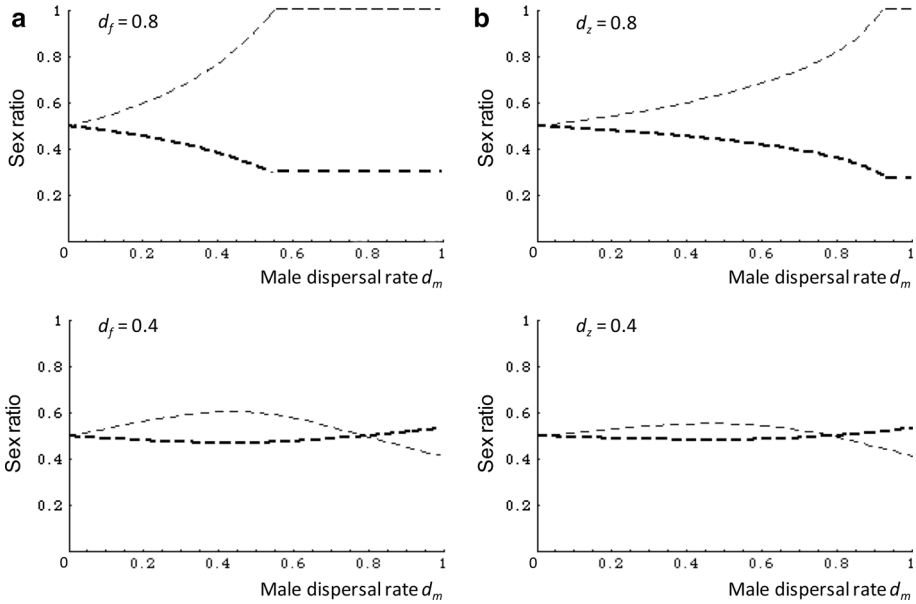

Fig. 2 Sex ratio as a function of male dispersal rate (d_m) for different values of **a** female dispersal rate (DDM model), and **b** zygote dispersal rate (DMD model). r_1: *thin line*, r_2: *bold line*. $g = 0.5$, $F_f = 2$, $F_m = 2.5$ and $c_m = c_f = c_z = 0$ throughout

Table 3 Direction of the sex ratio bias expected from sex-biased dispersal (row) and fitness gains for males and females (column)

DMD	$F_m > F_f > 1$ (C&B)	$1 < F_m < F_f$ (C&B)
$d_z > d_m$ (SSR)	$r_1 > 0.5 > r_2$ / $r_1 > 0.5 > r_2$	$r_2 > 0.5 > r_1$ / $r_1 > 0.5 > r_2$
$d_z < d_m$ (HS)	$r_1 > 0.5 > r_2$ / $r_2 > 0.5 > r_1$	$r_2 > 0.5 > r_1$ / $r_2 > 0.5 > r_1$

The dominant selective force is shown after the dispersal rates and the fitness gains (Bull 1981; Guillon et al. 2006)

DMD male Dispersal-Mating-zygote Dispersal model (Freeman et al. 1980), *C&B* Charnov and Bull (Bull 1981), *HS* Habitat Selection (Guillon et al. 2006), *SSR* Secondary Sex Ratios (Guillon et al. 2006)

dominant selective forces have opposite directions when $d_z < d_m$ and $F_m > F_f$ or when $d_z > d_m$ and $F_m < F_f$. Figure 2b shows the predicted sex ratios as a function of d_m for two values of d_z, when $g = 0.5$, $F_f = 2$, and $F_m = 2.5$. In the case of $d_z = 0.8$, the sex ratio is

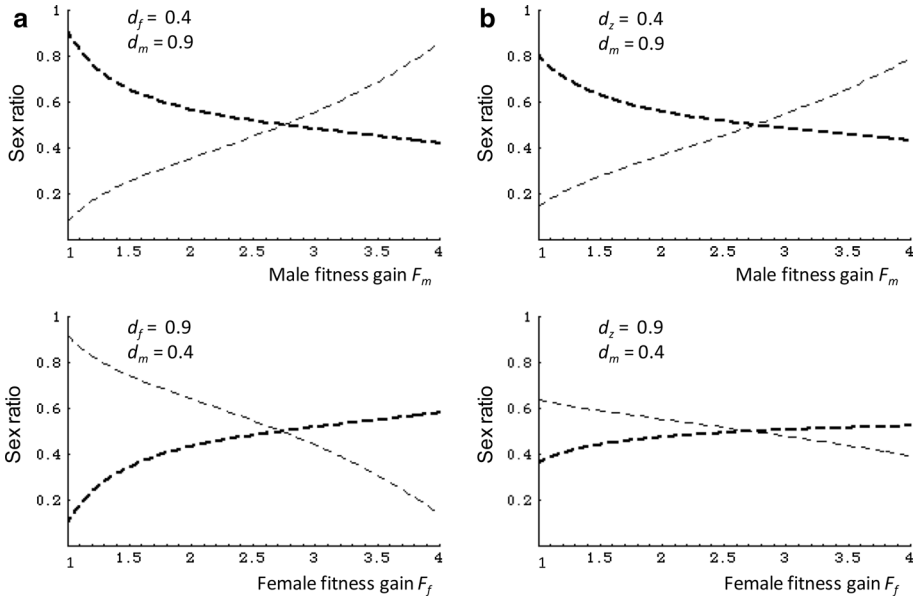

Fig. 3 Sex ratio as a function of male fitness gain (F_m, *upper row*) or female fitness gain (F_f, *lower row*) for different dispersal rates. **a** DDM model. **b** DMD model. r_1: *thin line*, r_2: *bold line. Upper row* $F_f = 2$; *lower row* $F_m = 2$. $g = 0.5$ and $c_m = c_f = c_z = 0$ throughout

always biased toward females in habitat 1 and males in habitat 2, even when $d_m > d_z$, as expected when the C&B force dominates. In the case of $d_z = 0.4$, females are produced in excess in habitat 1 only when $d_m < 0.788$. For high values of d_m, the sex ratio in habitat 1 is biased toward the more dispersing sex (males), as expected from the HS force. Again, the direction of the sex ratio bias can be reversed, depending on male and female dispersal rates, and when d_m or d_z is nil, the predicted sex ratio is always balanced ($r_1 = r_2 = ½$).

Sex-biased dispersal, when fitness gains vary

Whether the HS or C&B force dominates is also dependent on the values of the fitness gains F_m and F_f. Figure 3a shows that fitness gains are able to reverse the sex ratio

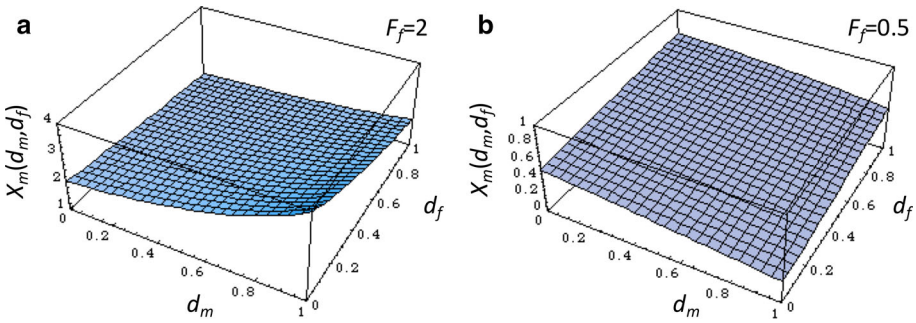

Fig. 4 Graphical representation of $X_m(d_m,d_f)$ for **a** $F_f = 2$, and **b** $F_f = 0.5$. $c_m = c_f = 0$ and $g = 0.5$ throughout. $X_m(d_m,d_f)$ is the value of F_m that gives an unbiased sex ratio ($r_1 = r_2 = 0.5$) for male and female dispersal rates d_m and d_f

expected from dispersal rates alone, in the range of values for which these selective forces have opposite directions ($d_f < d_m$ and $F_m > F_f$ or when $d_f > d_m$ and $F_m < F_f$). In the DMD model (Fig. 3b), any of the three selective forces can dominate (HS or C&B for $d_z < d_m$ and $F_m > F_f$; SSR or C&B for $d_z > d_m$ and $F_m < F_f$).

I define $X_m(d_m, d_f)$ as the value of F_m that yields a balanced sex ratio ($r_1 = r_2 = ½$) in the DDM model, for male and female dispersal rates d_m and d_f, and a given value of F_f, g, $c_m < 1$, and $c_f < 1$. Likewise, I define $Y_m(d_m, d_z)$ as the value of F_m that yields a balanced sex ratio in the DMD model, for male and zygote dispersal rates d_m and d_z, and a given value of F_f, g, $c_m < 1$, and $c_z < 1$. Computing with Mathematica (Wolfram Research Inc 2005) proves that if $c_f = c_z$ and F_f, g, and c_m are identical in the two models, then, for any a and b, $Y_m(a,b) = X_m(a,b)$. For all tested values of parameters $F_f > 1$, g, c_m, and c_f, $X_m(d_m, d_f)$ is an increasing function of d_m and a decreasing function of d_f (Fig. 4a). In contrast, for all tested values of parameters $F_f < 1$, g, c_m, and c_f, $X_m(d_m, d_f)$ is a decreasing function of d_m and an increasing function of d_f (Fig. 4b). Additional computing (Wolfram Research Inc 2005) proves that for any F_f, g, c_m, c_f and c_z:

$$\lim_{(d_m,d_f)\to(1,0)} X_m(d_m,d_f) = \lim_{(d_m,d_z)\to(1,0)} Y_m(d_m,d_z) = F_f^2,$$

$$\lim_{(d_m,d_f)\to(0,1)} X_m(d_m,d_f) = \lim_{(d_m,d_z)\to(0,1)} Y_m(d_m,d_z) = F_f^{\frac{1}{2}},$$

Consequently, Fig. 5a shows the domain of parameters F_m and F_f for which the direction of the sex ratio bias depends on dispersal rates. For both DDM and DMD models, this domain is comprised between the curves $F_m = F_f^{1/2}$ and $F_m = F_f^2$, *i.e.*, $F_f^2 > F_m > F_f^{1/2} > 1$ or $F_f^2 < F_m < F_f^{1/2} < 1$. For all other values of the parameters F_m and F_f, the direction of the sex ratio bias is always as expected from the relative values of the fitness gains (whether $F_m < F_f$ or $F_m > F_f$), as is the case when dispersal rates are equal (Fig. 5b).

When $F_m = F_f$ and $d_f = d_m$ or $d_z = d_m$, a sex-specific cost ($c_f \neq c_m$ or $c_z \neq c_m$) results in sex-biased effective dispersal rates. This yields biased sex ratios: the simple pattern observed in Fig. 5b is thus no longer true. Now consider Fig. 2a: when $d_f = 0.8$ (as in the upper panel), a cost $c_f = 0.833$ results in an effective female dispersal rate $d_e = 0.4$ (as in the lower panel), thus modifying the direction of the sex ratio bias for high values of d_m. Hence, because it affects effective dispersal rates, a sex-specific cost is also able to reverse the sex ratio bias. However, the theoretical domains shown in Fig. 5a remain unchanged, because in the presence of a given cost c, any effective dispersal rate d_e can be reached by simply adjusting the value of the corresponding dispersal rate $d = d_e/(1 - c(1 - d_e))$.

Discussion

The present study documents the influence of dispersal rates on convergence stable sex ratios when fitness gains differ for males and females. Results show that the direction of the sex ratio bias, as expected with the Charnov and Bull model in a two-patch environment, can be reversed by sex-biased dispersal. This effect derives from sex-biased dispersal alone, independently of local mate or resource competition, or local resource enhancement. The predicted sex ratio is the product of three selective forces described by Bull (1981) and Guillon et al. (2006): (1) the force that results from the competition between individuals of the same sex from different patches and leads to the production of the sex that benefits

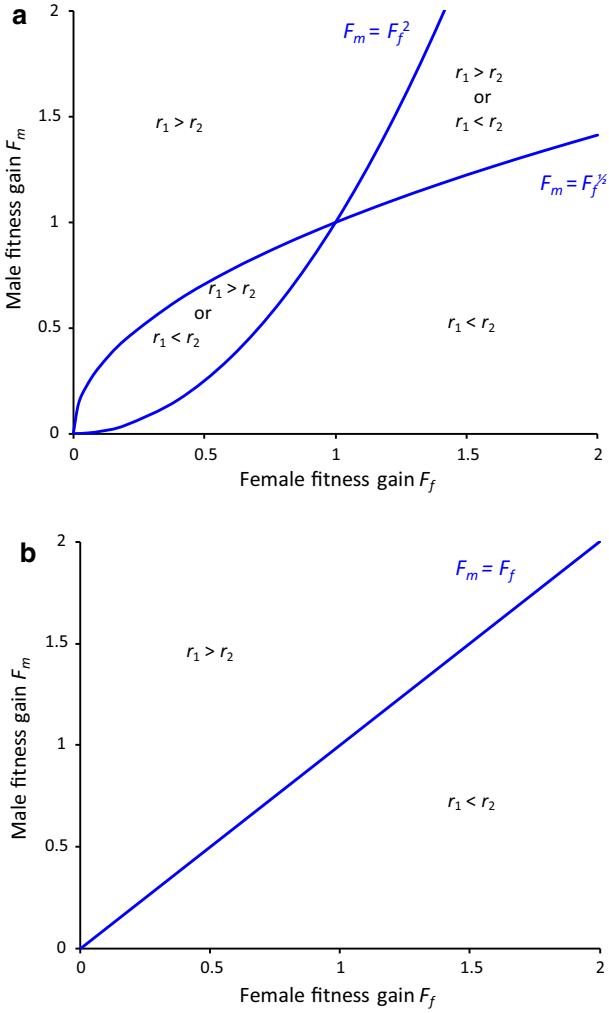

Fig. 5 Predicted direction of the sex ratio bias as a function of female fitness gain (F_f) (x-axis) and male fitness gain (F_m) (y-axis). **a** $0 < d_m \neq d_f \leq 1$ (DDM model) or $0 < d_m \neq d_z \leq 1$ (DMD model) with any value of dispersal costs. **b** $0 < d_m = d_f \leq 1$ and $c_m = c_f < 1$(DDM model) or $0 < d_m = d_z \leq 1$ and $c_m = c_z < 1$ (DMD model). Predictions in (**a**, **b**) do not depend on the value of g. When $d_m = 0$ or $d_f = 0$ or $c_m = 1$ or $c_f = 1$ (DDM model) or when $d_m = 0$ or $d_z = 0$ or $c_m = 1$ or $c_z = 1$ (DMD model), the sex ratio is predicted to be unbiased in both habitats

more (or loses less) from the quality of its native patch (C&B); (2) the force that results from asymmetrical exchanges of males and females and aims to equilibrate the secondary sex ratios after dispersal (SSR); (3) the force that results from sex-biased dispersal and provides a way to select habitat for progeny (HS). Strikingly, the two modeled life cycles (female dispersal either before or after mating; DDM and DMD, respectively) give qualitatively similar results. This observation was already made in a previous study on sex-biased dispersal (Guillon et al. 2006). However, it must be stressed that although the predictions for the two models (DDM and DMD) are qualitatively similar, they are not the same quantitatively, because of a fundamental difference in the equilibrium between HS and SSR forces in the models (Guillon et al. 2006). As a result, the C&B or HS force may dominate in the DDM model, whereas any of the three selective forces may dominate in the DMD model.

When it is not sex-biased, partial dispersal does not change the direction of the sex ratio bias predicted by the Charnov and Bull model (Fig. 5b), as already observed (Van Dooren

and Leimar 2003; Leimar et al. 2004). However, a decrease in dispersal rates as well as an increase in dispersal costs can drastically reduce the expected sex ratio bias (Fig. 1). This effect can be interpreted as follows: in the DDM or DMD model, when dispersal rates decrease or dispersal costs increase, individuals are not distributed at random among patches. After dispersal and before mating, there will be an excess of males in the habitat where they are produced and likewise an excess of females in the habitat where they are produced. To mitigate this effect, the SSR force pushes the sex ratio towards 0.5 in both habitats. Further, in the DMD model when $d_z < 1$, zygotes are not distributed at random among patches. As the zygote dispersal rate decreases or zygote dispersal cost increases, there will be an excess of zygotes in the habitat where females are produced and a deficit in the habitat where males are produced. The HS force then favors the production of some zygotes (i.e., some females) in male-producing patches and the production of fewer zygotes (i.e., fewer females) in female-producing patches. When the sex ratio remains so biased that only one sex is produced in one habitat (e.g., females), the fitness gain for the other sex (*e.g.*, males) has no effect on sex ratio in the other habitat (Fig. 1). Since males are only produced in one habitat, competition between males from the two habitats no longer occurs, so the male fitness gain has no more importance in determining male reproductive success. Overall, under partial dispersal, the balance between the three selective forces results in sex ratios biased in the direction predicted by Charnov and Bull (Fig. 5b), but less so than with total dispersal.

Van Dooren and Leimar (2003) studied the evolution of the reaction norm of sex ratio in response to habitat quality in a DDM model, when dispersal rates were equal for both sexes. They found that a non-switch-like reaction norm evolved for low dispersal rates and small differences in fitness gains between sexes. Similarly, Leimar et al. (2004) showed that evolutionary stability of a single-threshold reaction norm was favored by high dispersal rates and when habitat-specific fitness gains differed strongly between males and females. These results are in accordance with those obtained in the two-patch model (Fig. 1).

While partial dispersal was already found to favor the evolution of gradual sex ratio shifts, the present study shows that sex-biased dispersal has the same effect when the dominant selective forces push the sex ratio in opposite directions. Sex-biased dispersal may even reverse the direction of the sex ratio bias expected with the Charnov and Bull model (Figs. 2, 5). The C&B force increases with a greater difference between F_m and F_f. The reversal of the sex ratio bias is thus more readily observed in the case of a smaller difference between male and female fitness gains and a greater difference between male and female effective dispersal rates. That the reversal of the sex ratio bias is more readily observed when there is a large difference between effective dispersal rates (one close to 0, and the other close to 1) may seem rather intuitive. However, this result was unexpected because these conditions produce only slightly biased sex ratios in models without sex-specific fitness gains (Guillon et al. 2006; Guillon and Bottein 2011). Still, in the two-patch model, there is a large range of fitness gain values for which the direction of the sex ratio bias predicted by the Charnov and Bull model holds true, regardless of the dispersal rate values (Fig. 5a): when F_m is very different from F_f or when males and females do not gain fitness in the same habitat ($F_m < 1 < F_f$ or $F_m > 1 > F_f$).

Here, dispersal cost has the effect of diminishing the effective dispersal rate (except when dispersal is total). When a between-sex difference in dispersal costs yields a greater difference in effective dispersal rates (i.e., when $d_f < d_m$ and $c_f > c_m$, or when $d_f > d_m$ and $c_f < c_m$ in the DDM model), the reversal of the sex ratio bias predicted by the Charnov and Bull model is thus more readily observed. Such a combination is most likely to occur if

sex-biased dispersal evolves under the effect of sex-specific dispersal costs (Gros et al. 2008). Indeed, that dispersal cost has the sole effect of diminishing the effective dispersal rate is the consequence of the fixed dispersal rates assumed in the model. If dispersal co-evolves with sex ratio, conditional on habitat quality, dispersal rates are expected to decrease in the presence of dispersal costs (Wild et al. 2006).

In the model, sex-specific fitness gains are determined by survival rates in the two patches. However, fertility for females and competitive ability to access mating for males could also differ between patches. In this case, female fitness gain should be calculated from the multiplication of survival by fertility, and male fitness gain should be calculated from the multiplication of survival by competitive ability. The role of fitness gains in Eqs. (6) and (9) (Appendix 1) would otherwise remain unchanged (result not shown). Sex ratios would thus be the ones predicted by the present model for these modified values of fitness gains. In the present model, the C&B selective force results from survival rates that are assumed to be sex-specific ($F_i^m \neq F_i^f$). However, recent work has shown that sex-specific fitness gains may also arise from differences between the sexes in demographic life-history traits (Schindler et al. 2015; Schwanz et al. 2016). For example, in a model structured in age classes, sex-specific fitness gains may result from a non-sex-specific effect of natal habitat on interannual survival, when age at sexual maturity is not the same for males and females.

Sex determination is here supposed to occur during zygote development, as in the original Charnov and Bull model. However, the same equations apply when parents determine the sex of their offspring at conception if the sex ratio adjustment is costless (Charnov 1979; Bull 1981). Indeed, when parents can predict where the immature animal will develop after conception, natural selection could favor sex ratio control by parents (Adams et al. 1987). One may also wonder whether these results on sex ratio could be generalized to the issue of sex allocation (the relative investment in male or female offspring). This would be the case if fitness increases linearly with parental investment for both males and females (Wild and West 2007). As highlighted by Taylor (1994), there is a formal equivalence between hermaphroditic species and species with separate sexes in this type of analysis. The present results may thus be extrapolated to hermaphroditic species, provided that there is a simple (linear) trade-off between investment in male and female functions.

There is much that this study has ignored: for example, dispersal evolution and kin competition. The aim of this work, however, was to consider fixed dispersal separately from other factors known to influence sex ratio strategies. Wild et al. (2006) investigated the joint evolution of sex ratios and dispersal rates in a DDM model. They noted that setting the female or male dispersal rate to 0 yielded unbiased sex ratios, as in the present study. I show here that when $d_f = 0$, the predicted sex ratio is generally biased, provided that $d_z > 0$ (DMD model). Interestingly, when Wild et al. (2006) let dispersal evolve conditional on sex and habitat quality without dispersal cost, they found the same evolutionarily stable sex ratios as in the original Charnov and Bull model.

Wild and West (2007) examined the effect of female dispersal rate in a two-patch DDM model when $d_m = 1$, $F_m > F_f \geq 1$, with each patch supporting one individual. When both male and female dispersal rates were equal to one, the authors obtained Bull's result (1981). For $0 < d_f < 1$, the results depended on female and male fitness gains, with a greater difference between these gains yielding a sex ratio biased in the direction predicted by Bull's model (male-biased in high-quality patches and female-biased in low-quality patches). In contrast, when male and female fitness gains did not greatly differ, they found

that the sex ratio could be biased in the opposite direction. Thus, local resource competition together with sex-biased dispersal could reverse the predictions of the Charnov and Bull model. Wild and West (2007) also noted that female philopatry established an asymmetric pattern of inheritance in patch quality, as already observed (Reinhold 1998; Julliard 2000), thus favoring the production of daughters in high-quality patches.

The present study documents the effect of sex-biased dispersal without regard to kin effects, a situation expected for large population sizes. Schwanz and Robert (2014) studied the sex ratios of the tammar wallaby (*Macropus eugenii*) and observed an excess of the less dispersing sex (females) in good-quality habitats and the more dispersing sex (males) in poor-quality habitats. They coined the term "local resource inheritance" (LRI) to designate the selective force at work in their populations, which is equivalent to "habitat selection" (HS) here. The present study shows that LRI (or HS) may not be the only outcome of sex-biased dispersal, as the opposite pattern of sex ratio bias can theoretically be observed with the DMD life cycle, when the SSR force dominates (for low male dispersal rates relative to zygote dispersal rates).

In small populations, local competition for resources between related individuals (LRC) is expected to occur (Clark 1978). It is important to note that LRC and LRI make the same prediction regarding the direction of the sex ratio bias in a heterogeneous environment: it should be biased toward the more dispersing sex in poor-quality habitats and the less dispersing sex in good-quality habitats (Chapman et al. 1989; Johnson et al. 2001; Wild and West 2007; Schwanz and Robert 2014). For intermediate population sizes, it is possible that both LRI and LRC drive the evolution of sex ratios. Hence, studies showing a sex ratio biased in the direction expected under LRC could consider the possibility that LRI is also at play (Chapman et al. 1989; Hewison and Gaillard 1996; Johnson et al. 2001; Hjernquist et al. 2009). Comparing the sex ratio bias in populations of different sizes should be useful in terms of disentangling these two selective forces.

When fitness gains do not greatly differ for males and females, LRI could also explain the mixed support for the Trivers and Willard hypothesis (Cockburn et al. 2002). Indeed, several studies have provided evidence for LRI in cases when the Trivers and Willard hypothesis predicts the same (Romano et al. 2012) or opposite (Goltsman et al. 2005; Banks et al. 2008; Schwanz and Robert 2014) sex ratio bias. In particular, LRI may be important in cases where males profit more from habitat quality and are the dispersing sex, which is a common situation in mammals (Greenwood 1980; Cockburn et al. 2002; West 2009). Sex-biased dispersal could also play a role in sex ratio evolution under environmental sex determination. In reptiles, temperature-dependent sex determination sometimes induces extremely biased nest sex ratios (Bull and Charnov 1989). The standard explanation for this phenomenon invokes different fitness gains for males and females depending on incubation temperature (Charnov and Bull 1977). However, despite years of research on this issue, scarce evidence supports this hypothesis in reptiles (West 2009; but see Warner and Shine 2008; Spencer and Janzen 2014). If fitness gains do not differ much between sexes, as seems to be the case, LRI could be a relevant selective force in species showing female nest-site philopatry (Reinhold 1998; Julliard 2000; Hulin and Guillon 2007). More generally, partial dispersal and sex-biased dispersal should be considered whenever Trivers and Willard's effects are dependent on habitat quality.

Conclusions

This study highlights the effects of partial dispersal, sex-biased dispersal, and dispersal costs on the evolution of habitat-dependent sex ratios when fitness gains according to patch type differ for males and females. The results of the model show a striking resemblance for female dispersal occurring before or after mating: sex-biased dispersal rates and sex-biased dispersal costs can considerably modify the predictions of the model with total dispersal. The sex ratio bias may be opposite to that predicted under total dispersal when there is a large difference between effective dispersal rates and when fitness gains for the two sexes are not too different. Sex-specific dispersal costs alone are able to reverse the sex ratio bias regardless of whether fitness gains differ between sexes. These results indicate that the effect of sex-specific dispersal on sex ratio evolution should be considered when habitat quality affects the fitness of individuals.

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Appendix 1: Computing $W_{ji}(r^{\circ},r)$

For an easier understanding of the formulation of the model, especially how population is regulated by density, I introduce the expressions N_1 and N_2 into the equations, as the number of adults in a patch of habitats 1 and 2, respectively. However, as I suppose $N_1 = N_2$, these cancel each other out during the analysis. F_i^f and F_i^m are the probability of survival until reproduction of a female and male, respectively, developing in habitat i. In the analysis, F_i^f and F_i^m reduce to F_f and F_m, the ratio of survival in habitat 2 over survival in habitat 1 for females and males, respectively. The number of zygotes produced by any female is noted as n, with n being large enough for all patches to be saturated with zygotes.

$W_{ji}(r_i^{\circ}, r)$ is split in two terms: $W_{ji}^m(r)$ denotes the expected number of gene copies transmitted to the next generation in habitat j per gene of a male developing in habitat i, and $W_{ji}^f(r)$ denotes the expected number of gene copies transmitted to the next generation in habitat j per gene of a female developing in habitat i. Assuming additive allele effects, the probability of a focal zygote (carrying the rare allele r_i°) developing into a female in habitat i is $(r_i^{\circ} + r_i)/2$ while the probability of a focal zygote developing into a male in habitat i is $(2 - r_i^{\circ} - r_i)/2$. Thus, for all i and for all j,

$$W_{ji}(r_i^{\circ}, r) = \frac{2 - r_i^{\circ} - r_i}{2} W_{ji}^m(r) + \frac{r_i^{\circ} + r_i}{2} W_{ji}^f(r). \tag{5}$$

Consider the different ways for a gene of a female developing in habitat i to be transmitted to the next generation to an individual living in habitat j. First, the female may be fertilized in habitat 1; the zygotes resulting from this fertilization then have to grow in habitat j. Second, the female may be fertilized in habitat 2; the zygotes resulting from this fertilization then have to grow in habitat j. $W_{ji}^f(r)$ can be represented as follows:

$$W_{ji}^f(r) = \frac{1}{2} n \left(Z_{j1}(r) P_{1i}^f + Z_{j2}(r) P_{2i}^f \right), \tag{6}$$

where $P_{1i}^f$and $P_{2i}^f$are the probability that a female developing in habitat i survives and is fertilized in habitats 1 and 2, respectively, and $Z_{j1}(r)$ and $Z_{j2}(r)$ are the probability that a zygote produced in habitats 1 and 2, respectively, will develop (after competition with

other zygotes) in habitat j in the next generation. The factor ½ holds for the probability of a given gene of the female being transmitted to any zygote, while n is the number of zygotes produced by any female.

Consider females developing in habitat i. A fraction $(1 - d_f)$ of surviving females will stay locally, while a fraction d_f will disperse. Accounting for dispersal cost, a fraction $(1 - g)(1 - c_f)$ of these dispersing females will reach habitat 1, whereas a fraction $g(1 - c_f)$ will reach habitat 2. $P^f_{11} = F^f_1\ (1 - d_f + (1 - g)(1 - c_f)d_f)$ is thus the probability that a female developing in habitat 1 survives and mates in habitat 1. Likewise, $P^f_{21} = F^f_1\ g(1 - c_f)d_f$ is the probability that a female developing in habitat 1 survives and mates in habitat 2. Further, I define $P^f_{22} = F^f_2\ (1 - d_f + g(1 - c_f)d_f)$ and $P^f_{12} = F^f_2\ (1 - g)(1 - c_f)d_f$.

$\zeta_1(r)$ and $\zeta_2(r)$ are the total number of females mating in habitats 1 and 2, respectively:

$$\begin{aligned} \zeta_1(r) &= gN_2P^f_{12}r_2 + (1 - g)N_1P^f_{11}r_1, \\ \zeta_2(r) &= gN_2P^f_{22}r_2 + (1 - g)N_1P^f_{21}r_1. \end{aligned} \tag{7}$$

Then, fertilization occurs. Among zygotes produced in good habitats, a fraction $(1 - d_z)$ will stay and compete locally for access to adulthood, while a fraction d_z will disperse. Accounting for dispersal cost, a fraction $(1 - g)(1 - c_z)$ of these dispersing zygotes will reach habitat 1, whereas a fraction $g(1 - c_z)$ will reach habitat 2. $P^z_{11} = (1 - d_z) + (1 - g)(1 - c_z)d_z$ is thus the probability that a zygote produced in habitat 1 competes in habitat 1 for access to adulthood. Likewise, $P^z_{21} = g(1 - c_z)d_z$ is the probability that a zygote produced in habitat 1 competes in habitat 2 for access to adulthood. Further, I define $P^z_{22} = (1 - d_z) + g(1 - c_z)d_z$ and $P^z_{12} = (1 - g)(1 - c_z)d_z$. As each female produces n zygotes, the total number of zygotes competing after dispersal in a patch of habitat 1 is $n(\zeta_1(r)P^z_{11} + \zeta_2(r)P^z_{12})$, and the total number of zygotes competing after dispersal in a patch of habitat 2 is $n(\zeta_2(r)P^z_{22} + \zeta_1(r)P^z_{21})$. Thus, the probability $Z_{11}(r)$ that a zygote produced in habitat 1 will grow in habitat 1 in the next generation (after competition with other zygotes) can be defined as:

$$Z_{11}(r) = (1 - g)N_1 \frac{P^z_{11}}{n(P^z_{11}\zeta_1(r) + P^z_{12}\zeta_2(r))}. \tag{8}$$

Likewise, I define:

$$Z_{12}(r) = (1 - g)N_1 \frac{P^z_{12}}{n(P^z_{11}\zeta_1(r) + P^z_{12}\zeta_2(r))},$$

$$Z_{22}(r) = gN_2 \frac{P^z_{22}}{n(P^z_{21}\zeta_1(r) + P^z_{22}\zeta_2(r))}.$$

$$Z_{21}(r) = gN_2 \frac{P^z_{21}}{n(P^z_{21}\zeta_1(r) + P^z_{22}\zeta_2(r))},$$

Now consider the different ways for a gene of a male developing in habitat i to be transmitted to the next generation to an individual living in habitat j. First, the male may fertilize a female in habitat 1; the zygotes resulting from this fertilization then have to grow in habitat j. Second, the male may fertilize a female in habitat 2; the zygotes resulting from this fertilization then have to grow in habitat j. $W^m_{ji}(r)$ can be represented as follows:

$$W_{ji}^{m}(r) = \frac{1}{2} n\big(Z_{j1}(r)P_{1i}^{m}(r) + Z_{j2}(r)P_{2i}^{m}(r)\big), \tag{9}$$

where $P_{1i}^{m}(r)$ and $P_{2i}^{m}(r)$ are the probability that a male developing in habitat i will survive and fertilize a female in habitats 1 and 2, respectively, and n, $Z_{j1}(r)$ and $Z_{j2}(r)$ are as previously defined.

I will now detail the expressions of $P_{ji}^{m}(r)$'s. Consider a male developing in habitat i. A fraction $(1 - d_m)$ of surviving males will stay locally in a habitat i, and a fraction d_m will disperse. Accounting for dispersal cost, a fraction $(1 - g)(1 - c_m)$ of the dispersing males will reach habitat 1, whereas a fraction $g(1 - c_m)$ will reach habitat 2. If a male reaches a given patch of habitat j, it will compete for the fertilization of the ζ_j females with all the other males that reach this patch, $\mu_j(r)$:

$$\begin{aligned}\mu_1(r) &= gN_2F_2^m(1-r_2)(1-g)(1-c_m)d_m + (1-g)N_1F_1^m(1-r_1)(1-d_m+(1-g)(1\\ &\quad -c_m)d_m),\\ \mu_2(r) &= gN_2F_2^m(1-r_2)(1-d_m+g(1-c_m)d_m) + (1-g)N_1F_1^m(1-r_1)g(1-c_m)d_m.\end{aligned} \tag{10}$$

Thus I define:

$$\begin{aligned}P_{11}^{m}(r) &= F_1^m\frac{1-d_m+(1-g)(1-c_m)d_m}{\mu_1(r)}\zeta_1(r), \quad P_{21}^{m}(r) = F_1^m\frac{g(1-c_m)d_m}{\mu_2(r)}\zeta_2(r),\\ P_{22}^{m}(r) &= F_2^m\frac{1-d_m+g(1-c_m)d_m}{\mu_2(r)}\zeta_2(r). \quad P_{12}^{m}(r) = F_2^m\frac{(1-g)(1-c_m)d_m}{\mu_1(r)}\zeta_1(r),\end{aligned} \tag{11}$$

Appendix 2: Costly dispersal

For a costless male or female dispersal rate $d_e = (1 - c)d/(1 - cd)$, I compute the probabilities to reach
habitat 1, starting from habitat 1:

$$1 - d_e + (1-g)d_e = 1 - \frac{(1-c)d}{1-cd} + (1-g)\frac{(1-c)d}{1-cd} = \frac{1-d+(1-g)(1-c)d}{1-cd};$$

habitat 2, starting from habitat 1:

$$gd_e = \frac{g(1-c)d}{1-cd};$$

habitat 1, starting from habitat 2:

$$(1-g)d_e = \frac{(1-g)(1-c)d}{1-cd};$$

habitat 2, starting from habitat 2:

$$1 - d_e + gd_e = 1 - \frac{(1-c)d}{1-cd} + g\frac{(1-c)d}{1-cd} = \frac{1-d+g(1-c)d}{1-cd}.$$

Because W^f_{ji} (r), and W^m_{ji} (r) each include ratios of these expressions, the denominator cancels in Eqs. (6) and (9). Inspecting the numerators, it can be seen that they express the probability of reaching different habitats, with dispersal rate d and dispersal cost c. In the model, for males and females, dispersing with rate d and cost c is thus equivalent to dispersing without cost at rate $d_e = (1 - c)d/(1 - cd)$.

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