Sex allocation and dispersal in a heterogeneous two-patch environment

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Abstract

We investigate the evolution of sex allocation and dispersal in a two-habitat environment using a game theoretic analysis. One habitat is of better quality than the other and increased habitat quality influences the competitive ability of offspring in a sex-specific manner. Unlike previous work, we allow incomplete mixing of the population during mating. We discuss three special cases involving the evolution of sex allocation under fixed levels of dispersal between habitats. In these special cases, stable sex-allocation behaviors can be both biased and unbiased. When sex-allocation behavior and dispersal rates co-evolve we identify two basic outcomes. First—when sex-specific differences in the consequences of spatial heterogeneity are large—we predict the evolution of biased sex-allocation behavior in both habitats, with dispersal by males in one direction and dispersal by females in the other direction. Second—when sex-specific differences are small—unbiased sex-allocation is predicted with no dispersal between habitats.
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1. Introduction

Models of sex allocation address the question of how best to divide a fixed investment between male and female components of fitness. In a dioecious species, sex allocation usually refers to the tradeoff between the production of sons and the production of daughters (in a brood of fixed size, a parent cannot choose to rear a son without also choosing not to rear a daughter). Alternatively, in a hermaphrodite, sex allocation might refer to the tradeoff between the production of male and female reproductive structures.

Under certain conditions, gains made through investment in male components of fitness can exceed those made through an identical investment in female components, and vice versa. In turn, such differences can lead to the evolution of biased sex allocation (e.g. Trivers and Willard, 1973; Maynard Smith, 1980; Frank, 1987).

A spatially heterogeneous environment is one way by which sex-differences in fitness gains might come to be established, provided spatial heterogeneity has different consequences for males and females. In fact, a spatially heterogeneous environment—consisting of patches of differing quality—has been a popular theoretical tool for investigating the consequences of sex-specific fitness gains for the evolution of sex allocation behavior (e.g. Charnov, 1979; Bull, 1981; Yamaguchi, 1985; Werren and Simbolotti, 1989; Ikawa et al., 1993; Wade et al., 2003).

Despite the prominence of spatial heterogeneity, many models only consider specific patterns of dispersal (Charnov, 1979; Bull, 1981; Yamaguchi, 1985; Werren and Simbolotti, 1989; Ikawa et al., 1993; Leimar, 1996; Wade et al., 2003). Furthermore, the influence of the co-evolution of dispersal has remained largely unexplored. Previous work has demonstrated that dispersal behavior that is in some sense "costly" cannot be maintained by selection in a spatially heterogeneous but temporally constant environment, under most conditions (Comins et al., 1980; Hastings, 1983; Greenwood-Lee and Taylor, 2001). However, some forms of costly dispersal can be maintained over evolutionary time when populations are class-structured; but in these cases only certain patterns of dispersal can evolve (Greenwood-Lee and Taylor, 2001).

The existence of different sexes and sex-specific dispersal provides the class structure necessary for dispersal to evolve. In turn, we expect sex-specific dispersal patterns to have important implications for adaptive sex-allocation behavior in a spatially heterogeneous environment.

In this paper, improved habitat quality results in the improved success of offspring but we assume that the extent of the improved success is sex-specific. Our main goal is to investigate how predictions about patterns of sex allocation change in a spatially heterogeneous environment when there is partial dispersal among habitat patches. For the reasons outlined above, we are particularly interested in models where sex allocation behavior and dispersal are both influenced by selection.

We build a game theoretic model and search for stable sex-allocation and dispersal behaviors. We assume that sex-allocation behavior is conditional upon local habitat quality and that dispersal behavior is conditional upon both local habitat quality and sex. Our main finding describes how environmental heterogeneity and the evolution of dispersal rates contribute to the evolution of different stable levels of sex-allocation. Our co-evolutionary approach offers insight into the practical application of competing hypotheses of sex-allocation evolution, and highlights some important features of the evolution of dispersal in a spatially heterogeneous environment.

2. Model life cycle

All notation used in the description of the model below is summarized in Table 1. We consider a dioecious species undergoing discrete, non-overlapping, and we suppose that its population is separated into two patches of habitat connected by dispersal of offspring.

As is typical of the game theoretic approach, we focus on the overall fitness of a rare "mutant" reaction norm in a population of individuals using the "resident" reaction norm.

We assume that offspring produced on one habitat (the "good" habitat) are more vigorous competitors than offspring produced in the other habitat (the "bad" habitat). Let $w_s > 1$ denote the competitive ability of a sex $s = m, f$ individual born on the good patch, measured relative to the competitive ability of a same-sex individual born on the bad patch. Male–male competition occurs for mates, whereas female–female competition occurs for breeding sites. For simplicity we consider only cases where $w_m > w_f$, i.e. where the advantage of being raised in the good habitat is more substantial for males than for females.

We assume that the habitat of quality q supports a large number of breeding sites n_q (where $q = g$ if good, and $q = b$ if bad). We assume further that n_q is constant over time, and is large enough to allow us to disregard kin selection. The way in which kin-selection operates on the evolution of sex allocation and its co-evolution with dispersal has been explored elsewhere and is well understood (Taylor, 1988, 1994, 1995; Leturque and Rousset, 2003; Wild and Taylor, 2004).

Table 1
Summary of notation used in the main text

Symbol	Explanation
det	The determinant of a matrix
d/dx	Derivative of a function of a single variable x
$\partial/\partial x$	Partial derivative with respect to variable x
$\nabla_{\mathbf{x}}$	Gradient operator $(\partial/\partial x_1, \ldots, \partial/\partial x_k)$
a_{ij}	# of class-i offspring of a class-j individual, weighted by genetic contribution
$\mathbf{A}$	$= \|a_{ij}\|_{i,j=1,\ldots,4}$, the class transition matrix
α_q	Proportion of brood that the mutant devotes to sons in habitat of quality q
β_q	Proportion of brood that the resident devotes to sons in habitat of quality q
b	Index for quantities associated with the poor quality habitat
c	Prop'n of dispersal pool that fails to reach its destination, the cost of dispersal
d_{sq}	Probability that a resident sex-s offspring disperses from habitat of quality q
δ_{sq}	Probability that a mutant sex-s offspring disperses from habitat of quality q
f	Index for quantities associated with females
F_q	Effective number of females in mating pool of type-q habitat
g	Index for quantities associated with good quality habitat
$\mathbf{G}$	Matrix of additive genetic variances and covariances (assumed to be the identity matrix)
$\mathbf{I}$	The identity matrix
i, j	Index quantities associated with class-i or j; $i, j = 1, \ldots, 4$, or $i, j = sq$
K	Brood size
m	Index for quantities associated with males
$\mathbf{m}$	Joint sex-allocation/dispersal reaction norm describing mutant behavior
M_q	Effective number of males in mating pool of type-q habitat
n_q	Large number of breeding sites available in type-q habitat
$\mathbf{p}$	Frequency distribution of mutant across classes
q	Indexes quantities associated with habitat quality, $q = g, b$
$\mathbf{r}$	Joint sex-allocation/dispersal reaction norm describing resident behavior
s	Indexes quantities associated with sex, $s = m, f$
t	"Ecological time," $t = 1$ corresponds to one generation
τ	"Evolutionary time"
w_s	Competitive weight given to sex-s offspring born in the good habitat, we assume $w_m > w_f > 1$.
W	Mutant fitness function

Fig. 1 depicts the model life cycle. A given generation is begun with the birth of offspring. Each female in the population produces K offspring, where K is very large. On average, a proportion β_q of the offspring of a resident female in a type-q habitat is devoted to sons. We denote the same proportion for a mutant female as α_q. We assume that these "sex-allocation behaviors" are under maternal control (i.e. due to maternal genotype).

Following birth, all adults die, and offspring disperse. We assume that offspring dispersal behavior is controlled by the offspring itself. A resident sex-s offspring leaves a patch of quality q (to compete on the other patch) with probability d_{sq}, independent of others in its cohort. The analogous probability for mutant is δ_{sq}. Dispersal is costly, and a proportion c of dispersing individuals
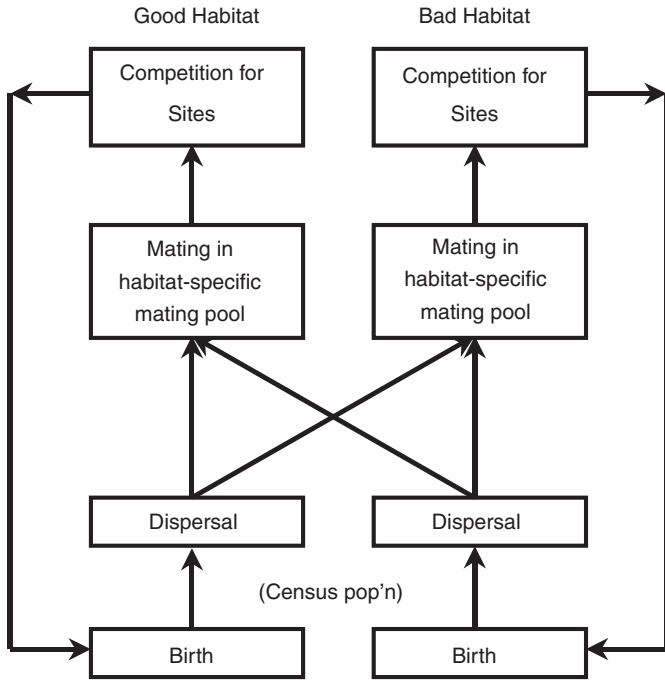
Good Habitat　　　　　Bad Habitat

Fig. 1. A schematic depicting the life cycle considered by the model.

is removed from the dispersal pool, on average. Patch-specific mating pools form immediately after dispersal.

Each female is fertilized by one male in the local mating pool. In contrast, males must compete for their mates; and males are not equally competitive in this respect. Moreover, from the perspective of a male, not all mates are equally desirable: winning a mating with a female raised in the bad habitat is not as valuable as winning a mating with one raised in the good habitat. In order to discuss the mating success of males, then, we must consider effective numbers of same-sex competitors (i.e. number of competitors weighted by competitive ability, w_m) and effective numbers of mates (i.e. number of female mates weighted by competitive ability, w_f). In short, we seek to calculate the expected effective number of matings. Let

$$M_g = K[w_m n_g \beta_g (1 - d_{mg}) + n_b \beta_b d_{mb}(1 - c)], \quad (1a)$$

$$M_b = K[n_b \beta_b (1 - d_{mb}) + w_m n_g \beta_g d_{mg}(1 - c)] \quad (1b)$$

be the effective number of males competing in the mating pools of the good and bad habitats, respectively; and let

$$F_g = K[w_f n_g (1 - \beta_g)(1 - d_{fg}) + n_b (1 - \beta_b) d_{fb}(1 - c)], \quad (2a)$$

$$F_b = K[n_b (1 - \beta_b)(1 - d_{fb}) + w_f n_g (1 - \beta_g) d_{fg}(1 - c)] \quad (2b)$$

be the effective number of receptive females in the mating pools of the good and bad habitats, respectively. It follows that a male, reared in the good habitat, but competing in the type-q habitat expects

$$w_m F_q / M_q \quad (q = g, b) \quad (3)$$

effective matings. Similarly, a male reared in the bad habitat, but competing in the type-q habitat, expects

$$F_q / M_q \quad (q = g, b) \quad (4)$$

effective matings.

After mating, fertilized females in a type-q habitat compete with one another for one of n_q breeding opportunities. Since F_q can also be interpreted as the effective number of females competing in the type-q habitat, we have that the expected reproductive success of a female raised in the good habitat but competing in the type-q habitat is

$$w_f n_q / F_q \quad (q = g, b). \quad (5)$$

Likewise, the expected reproductive success of a female raised in the bad habitat but competing in the type-q habitat is

$$n_q / F_q \quad (q = g, b). \quad (6)$$

Because the competition for breeding opportunities occurs among fertilized females, not all of the matings won by a male translate into reproductive success. To determine the reproductive success of males, then, we normalize (3) and (4) by multiplying these by n_q/F_q, respectively. That is to say, the reproductive success of a male produced in the good habitat and competing in the type-q habitat is

$$(w_m F_q / M_q)(n_q / F_q) = w_m n_q / M_q \quad (q = g, b) \quad (7)$$

and that of a male raised in the bad habitat and competing in the type-q habitat is

$$(F_q / M_q)(n_q / F_q) = n_q / M_q \quad (q = g, b). \quad (8)$$

Eqs. (5)–(8) will be used in the calculation of fitness, below.

3. Mutant fitness and evolutionary dynamics

We use the class-structured approach described in Taylor (1990), and in Taylor and Frank (1996). If a census is taken at birth (Fig. 1), individuals can be placed into one of four categories (i.e. classes): class 1 = female on the good patch; class 2 = male on the good patch; class 3 = female on the bad patch; and class 4 = male on the bad patch. When it is convenient to do so, we will use $fg = 1$, $mg = 2$, $fb = 3$, and $mb = 4$ to index classes.

To calculate mutant fitness, in general, we introduce the mutant sex-allocation/dispersal reaction norm

$$\mathbf{m} = (\alpha_g, \alpha_b, \delta_{fg}, \delta_{mg}, \delta_{fb}, \delta_{mb}) \quad (9)$$

at low frequency, to a resident population whose average behaviors are described by

$$\mathbf{r} = (\beta_g, \beta_b, d_{fg}, d_{mg}, d_{fb}, d_{mb}). \quad (10)$$

Our measure of mutant fitness, W is related to the initial rate of increase of a small subpopulation of mutants. When computing W, we will assume that (i) the resident population is at demographic equilibrium,

Table 2
Description of the transition matrix, $\mathbf{A}(\mathbf{m}, \mathbf{r}) = \|a_{ij}(\mathbf{m}, \mathbf{r})\|$

$$
\left\|
\begin{array}{cccc}
K(1-\alpha_g)(1-\delta_{fg})w_f n_g/2F_g & K(1-\beta_g)(1-\delta_{mg})w_m n_g/2M_g & K(1-\alpha_g)(1-c)\delta_{fb}n_g/2F_g & K(1-\beta_g)(1-c)\delta_{mb}n_g/2M_g \\
K\alpha_g(1-\delta_{fg})w_f n_g/2F_g & K\beta_g(1-\delta_{mg})w_m n_g/2M_g & K\alpha_g(1-c)\delta_{fb}n_g/2F_g & K\beta_g(1-c)\delta_{mb}n_g/2M_g \\
K(1-\alpha_b)(1-c)\delta_{fg}w_f n_b/2F_b & K(1-\beta_b)(1-c)\delta_{mg}w_m n_b/2M_b & K(1-\alpha_b)(1-\delta_{fb})n_b/2F_b & K(1-\beta_b)(1-\delta_{mb})n_b/2M_b \\
K\alpha_b(1-c)\delta_{fg}w_f n_b/2F_b & K\beta_b(1-c)\delta_{mg}w_m n_b/2M_b & K\alpha_b(1-\delta_{fb})n_b/2F_b & K\beta_b(1-\delta_{mb})n_b/2M_b
\end{array}
\right\|
$$

(ii) the distribution of mutants across classes is the same as that for the resident, and (iii) selection is weak. These assumptions are standard in game-theoretic analyses of class-structured populations (e.g. Taylor, 1990).

Let $a_{ij}(\mathbf{m}, \mathbf{r})$ denote the expected number of class-i offspring of a class-j mutant, weighted by genetic contribution. We determine expressions for these expectations following the model life cycle outlined above (Fig. 1). To compute $a_{11}(\mathbf{m}, \mathbf{r})$, for instance, we note that a mutant female born in the good habitat (i) does not disperse with probability $(1-\delta_{fg})$, (ii) is mated exactly once, (iii) competes successfully for $w_f n_g/F_g$ breeding opportunities in the good habitat, and (iv) expects a proportion $(1-\alpha_g)$ of her K offspring to be daughters. It follows that

$$a_{11}(m,r) = (1/2)K(1-\alpha_g)(1-\delta_{fg})w_f n_g/F_g, \tag{11}$$

where 1/2 weights the daughters by the genetic contribution of their mother.

We compute other a_{ij}'s (15 others, 16 in total, see Table 2), and summarize them with the positive matrix-valued function

$$\mathbf{A}(\mathbf{m}, \mathbf{r}) = \left\| a_{ij}(\mathbf{m}, \mathbf{r}) \right\| \quad i, j = 1, \ldots, 4. \tag{12}$$

If $\mathbf{p}(t)$ is the vector whose ith entry is the frequency of the mutant in class i at the beginning of generation t, the dynamics of the small mutant subpopulation are described by

$$\mathbf{p}(t+1) = \mathbf{A}(\mathbf{m}, \mathbf{r})\mathbf{p}(t). \tag{13}$$

Mutant fitness, then, is correctly expressed as the leading eigenvalue of $\mathbf{A}(\mathbf{m}, \mathbf{r})$ (Metz et al., 1992).

Computing the leading eigenvalue of a 4×4 matrix-valued function is often very difficult. Therefore, we opt for the alternative fitness expression based on one proposed by Courteau and Lessard (2000):

$$W(\mathbf{m}, \mathbf{r}) = -\det[\mathbf{A}(\mathbf{m}, \mathbf{r}) - \mathbf{I}], \tag{14}$$

where $\mathbf{I}$ is the 4×4 matrix identity matrix (see also Taylor and Bulmer, 1980; Maynard Smith, 1982).

Our game theoretic analysis will rely on the so-called "selection gradient" defined by the vector

$$
\begin{aligned}
\nabla_{\mathbf{m}} W(\mathbf{r}) = (&\partial W/\partial\alpha_g, \ \partial W/\partial\alpha_b, \ \partial W/\partial\delta_{fg}, \\
&\partial W/\partial\delta_{mg}, \ \partial W/\partial\delta_{fb}, \ \partial W/\partial\delta_{mb})_{\mathbf{m}=\mathbf{r}}.
\end{aligned}
\tag{15}
$$

We use (15) in the following dynamical description of the evolution of $\mathbf{r}$:

$$d\mathbf{r}/d\tau = \mathbf{G}\nabla_{\mathbf{m}} W(\mathbf{r}), \tag{16}$$

where $\tau = 1$ represents one unit of evolutionary time, and $\mathbf{G}$ is a matrix whose diagonal entries give the additive genetic variance found in the component traits, and whose off-diagonal entries give the additive genetic covariance between pairs of component traits (Abrams et al., 1993; Day and Taylor, 2003).

An "evolutionarily stable reaction norm" will be understood as an asymptotically stable equilibrium of (16) with the additional property that no rare mutant using $\mathbf{m}$ will have a rate-of-increase strictly greater than one (the "Nash condition"). For simplicity, we will assume $\mathbf{G}$ is the 6×6 identity matrix. In general, $\mathbf{G}$ will not be the identity matrix, which means that, in general, genetic constraints will yield equilibria other than those we study here (i.e. other than points at which the selection gradient vanishes).

We checked asymptotic stability of equilibria following the standard mathematical techniques from the theory of dynamical systems (e.g. Hofbauer and Sigmund, 1988; see Appendices A and B). We will deal with the Nash condition with a heuristic argument set out in Appendix A.

4. Special cases with fixed dispersal

Our purpose in this section is to connect our model with previous theoretical results. Setting $\delta_{sq} = d_{sq}$ ($s = m, f$ and $q = g, b$) in Table 2, reduces our model to one that describes the evolution of sex-allocation behavior, alone. In this reduced model, dispersal behavior is considered to be a parameter, and mutants are permitted to deviate only from the resident sex-allocation behaviors, β_g and β_b. We need only consider two of the equations from the six-dimensional system (16):

$$d\beta_q/d\tau = \partial W/\partial\alpha_q|_{\mathbf{m}=\mathbf{r}} \quad (q = g, b). \tag{17}$$

4.1. Case 1: no dispersal between habitats

When dispersal parameters are all set equal to zero $\mathbf{A}$ is a block-diagonal matrix and the model describes the evolution of sex-allocation behavior in two isolated habitats. In

this case stable sex-allocation behaviors are $\beta_g = \beta_b = 1/2$. This corresponds to Fisher's (1930) classical result for the evolution of the unbiased sex ratio.

4.2. Case 2: no dispersal by one sex

In many animal taxa one sex is often described as being more "philopatric" while the other is described as being more "dispersive" (Greenwood, 1980). We consider an extreme instance of this pattern of sex-specific dispersal in which one sex does not disperse (dispersal by the opposite sex, conditional on habitat quality, is fixed at some arbitrary level). In both cases—either $d_{mq} = 0$, or $d_{fq} = 0 (q = g, b)$—we find stable sex-allocation behaviors, $\beta_g = \beta_b = 1/2$. This result generalizes an earlier result about the evolution of unbiased sex allocation in a patchy, but otherwise homogeneous landscape (Kirkpatrick and Bull, 1987).

4.3. Case 3: all dispersal parameters equal $1/(2-c)$

Setting all dispersal parameters equal to $1/(2-c)$ yields a scenario in which the probability that an offspring competes in a type-q habitat is independent of its birthplace. This case corresponds to models studied previously by Charnov (1979) and Bull (1981), where (i) the global population is well-mixed at the time of mating,

Table 3
Summary of evolutionarily stable sex-allocation behaviors in a heterogeneous environment when the habitat on which an offspring competes is independent of its natal habitat. Note that dispersal does not evolve

	$n_b/n_g < w_f < w_m$	$w_f < n_b/n_g < w_m$	$w_f < w_m < n_b/n_g$
β_g	$[1 + n_b/w_f n_g]/2$	1	1
β_b	0	0	$[1 - w_m n_g/n_b]/2$

and (ii) all fertilized females encounter the various habitat types with the same probability (Fig. 2).

We identify three possible outcomes for the evolution of β_g and β_b in this case. As expected, each outcome has been previously identified by both Charnov (1979), and Bull (1981). Table 3 shows that habitat-dependent sex-allocation is always biased in favor of one or the other sex, and that there is always at least one habitat in which pure-sex broods are produced. The direction of sex-allocation bias in a given habitat depends on inequality relationships between the parameters w_m and w_f, and the ratio n_b/n_g (see Table 3).

5. Co-evolution of sex allocation and dispersal

5.1. Preliminaries

Analysis of the complete six-dimensional system (16) is simplified by four observations. Each observation is justified in the appendix using an argument based on reproductive value (RV) (i.e. genetic contribution to the population in the distant future).

Suppose the population has reached an evolutionarily stable state. It follows that:

1. One-way dispersal does not occur;
   a single sex does not exhibit bi-directional dispersal.
2. At this point we note either (a) patches are not connected by dispersal (i.e. "isolated"), or (b) they are connected through dispersal by males in one direction and dispersal by females in the opposite direction. The third and fourth observations, respectively, provide details about the patterns of dispersal and sex allocation we expect in a population that has reached an evolutionarily stable state.
3. If the two habitats are connected by dispersal, then it must be that males disperse from the good habitat to bad, and females disperse from the bad habitat to good. In addition, evolutionary stability requires $w_m(1-c) \geq w_f/(1-c)$.
4. If mothers in both habitats produce broods of mixed sex, and if habitats are connected by dispersal, then $w_m(1-c) = w_f/(1-c)$.

We regard the case in which $w_m(1-c) = w_f/(1-c)$ as structurally unstable, that is to say a small perturbation in the parameters leads to one of four generic scenarios
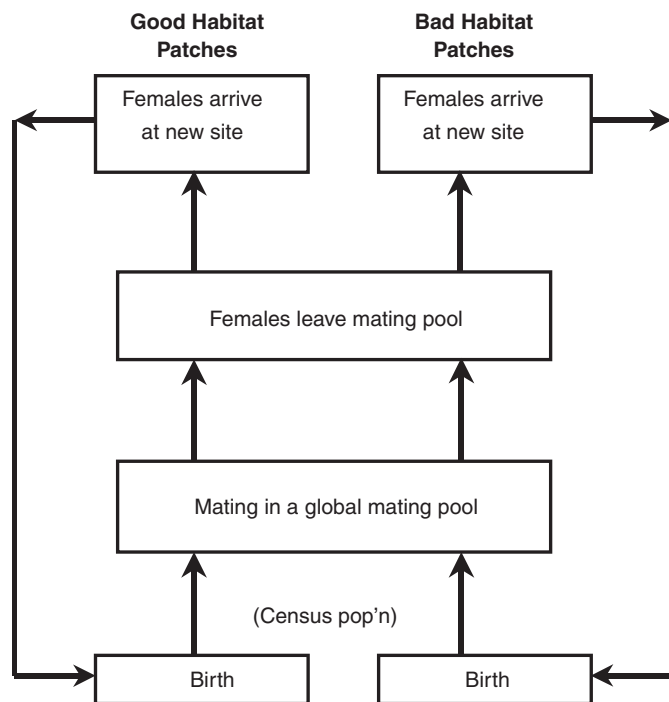

Fig. 2. A schematic depicting the life cycle considered in previous models for the evolution of sex allocation in a heterogeneous environment. In these models, we often think of the environment as being divided into many habitat patches. Some patches are of high quality (good habitat patches), others are of low quality (bad habitat patches).

outlined below. In the first three scenarios, habitats are connected by dispersal and extreme sex-allocation behaviors are found in at least one habitat (Fig. 3a–c, appendix). In the fourth scenario, when $w_m(1-c) < w_f/(1-c)$, dispersal between habitats does not occur and sex-allocation behavior is unbiased (Fig. 3d).

5.2. Evolutionarily stable behaviors

When $w_m(1-c) > w_f/(1-c)$ the co-evolution of sex allocation and dispersal results in one of Figs. 3a–c.
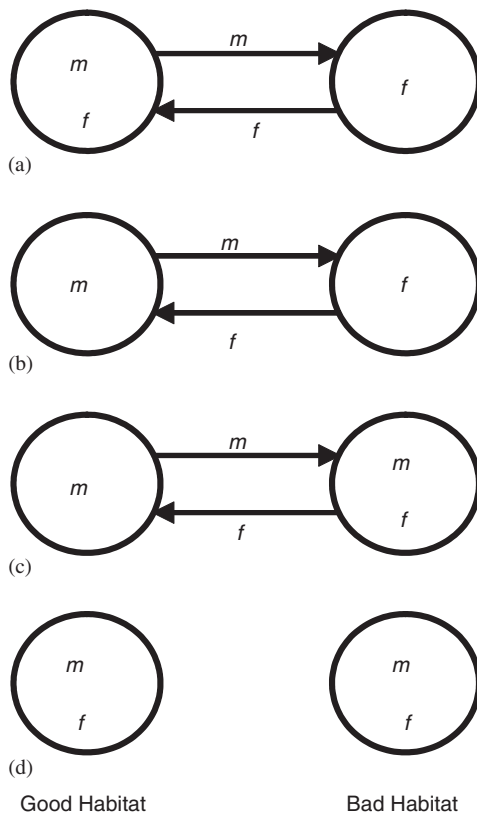

Fig. 3. A schematic depicting four generic outcomes for the co-evolution of sex-allocation behavior and dispersal. Sexes found in the broods produced in a given habitat are indicated inside a circle. The dispersive sex in a given habitat is written above the arrow indicating the direction of dispersal.

Table 4 presents expressions for the stable equilibrium sex-allocation/dispersal behaviors in each case.

There are two noteworthy features of Table 4. First, we find sex-allocation behavior almost identical to that for the models studied by Charnov (1979) and Bull (1981)—the exception being that $w_s(1-c)$ or $w_s/(1-c)$ have taken the place of $w_s, s = m, f$ (cf. Table 3). Second, we see a stable pattern of dispersal that is quite different from the dispersal pattern assumed in the model summarized by Table 3, i.e. $d_{sq} = 1/(2-c)$. Since this precise dispersal pattern cannot be recovered in the co-evolutionary model with costly dispersal, we do not, strictly speaking, regard the result presented in Table 4 as a generalization of those in Table 3.

Although the expressions $w_f/(1-c)$ and $w_m(1-c)$ might seem strange, they do have a biological interpretation. Think of same-sex competition as a lottery, with the winner being awarded either a mate, or a breeding site. For every lottery ticket given to a male (respectively, female) born in the bad habitat, w_m (respectively, w_f) are given to a same-sex competitor born in the good habitat. But, since bi-directional dispersal by one sex is not stable, w_m and w_f do not represent the true advantage enjoyed by individuals in the lottery born into a good habitat. Recall that the lottery occurs after costly dispersal and an individual who disperses must forfeit a proportion c of his/her tickets. Relative to a (philopatric) competitor in the bad habitat, a male who leaves the good habitat, has only $w_m(1-c)$ tickets in the lottery. Similarly, relative to a (dispersive) competitor from the bad habitat—namely a female who remains in the good habitat—has $w_f/(1-c)$ tickets in the lottery. In short, costly dispersal modifies the realized advantage of being born in a good habitat.

Let us now try to further develop our intuition about the results summarized by Table 4. Consider the middle column of Table 4. Why might we expect the evolution of dispersal rates equal to 1/2, when $\beta_g = 1$ and $\beta_b = 0$? The answer is not immediately clear. To be specific, suppose $n_b = 2n_g$, and $w_f/(1-c) < 2 < w_m(1-c)$. In this case, male-advantage in the good habitat is strong enough to encourage complete investment in sons here. In contrast, the corresponding female-advantage is weak enough to favor mothers in bad habitat who produce

Table 4
Summary of evolutionarily stable sex-allocation and dispersal behaviors in a heterogeneous environment when the difference between w_m and w_f is large

	$n_b/n_g < w_f/(1-c) < w_m(1-c)$ Fig. 3a	$w_f/(1-c) < n_b/n_g < w_m(1-c)$ Fig. 3b	$w_f/(1-c) < w_m(1-c) < n_b/n_g$ Fig. 3c
β_g	$[1 + n_b(1-c)/w_f n_g]/2$	1	1
β_b	0	0	$[1 - w_m(1-c)n_g/n_b]/2$
d_{fg}	0	NA	NA
d_{mg}	$n_b(1-c)/[w_f n_g + n_b(1-c)]$	$\frac{1}{2}$	$\frac{1}{2}$
d_{fb}	$\frac{1}{2}$	$\frac{1}{2}$	$w_m(1-c)n_g/[w_m(1-c)n_g + n_b]$
d_{mb}	NA	NA	0

NA = not applicable, selection cannot act on dispersal rate because it is not expressed.

only daughters. By assumption, the bad habitat provides twice as many breeding opportunities as the good habitat. Does it not stand to reason that 1/3 of females should disperse (two females settle in the bad habitat for every one female that settles in the good habitat)? If so, then does it not follow that males should disperse with probability 2/3 for a similar reason? The answer is, no. To correct this line of reasoning, we must consider RV.

The total RV of males equals the total RV of females (Fisher, 1930). Since there are twice as many females as males at birth ($n_b = 2n_g$), the RV of one son is twice that of one daughter. By assumption, there are twice as many females as males at birth; and so the RV of one son is twice that of one daughter. Even though there are twice as many breeding opportunities in the bad patch, offspring produced there (i.e. females) are only half as valuable. It follows that offspring should wish to encounter both habitats with equal frequency.

Next suppose n_b/n_g is smaller, say $n_b/n_g = 1$, but we keep $w_f/(1-c)$ and $w_m(1-c)$ unchanged. We are now in the first column of Table 4. As long as daughters are produced in the bad habitat, a smaller n_b/n_g reduces the total number of daughters born, and there is now incentive to produce daughters in the good habitat also.

Now let us consider why the dispersal rates in Table 4 are to be expected when $n_g/n_b = 1$ (first column). If sex allocation behaviors are at stable levels, then there are fewer males than females at birth. Furthermore, one daughter born in the good habitat is a better competitor than is one daughter born in the bad habitat. It follows that offspring (male or female) born in the good habitat are more valuable than the females born in the bad habitat.

The male dispersal decision in this case is relatively straightforward. Competition in the (good) habitat-specific mating pool means that there are fitness gains to be made by dispersing to the bad habitat. Nevertheless, a male expects that offspring born in the good habitat are more valuable. It follows that he chooses dispersal rate less than one half so that his offspring, should he have any, are more likely to be born in the good habitat (observe that $n_b/([w_f/(1-c)]n_g + n_b) = (n_b/n_g)/(w_f/(1-c) + n_b/n_g) < 1/2$).

The dispersal decision made by a female when $n_g/n_b = 1 < w_f/(1-c) < w_m(1-c)$ is more complicated. Following the logic used to explain male dispersal we might expect that $d_{fb} > 1/2$; so why is this not so (cf. Table 4)? Unlike male dispersal in this case, dispersal from the bad habitat puts a female at a disadvantage by placing her in proximity to superior competitors. Although the offspring produced in the good habitat have higher RV, it is less likely that a poor quality female would win a breeding opportunity here.

A description of the case in which $w_f/(1-c) < w_m(1-c) < n_b/n_g$ (last column) can be constructed in an analogous manner, and this is left to the reader.

5.3. Additional dynamic equilibria

We must acknowledge that when $w_m(1-c) < w_f/(1-c)$ there exist equilibria of (16) for which both dispersal between habitats and sex-allocation bias are maintained. For convenience we refer to these equilibria as, "additional equilibria."

We consider the "additional equilibria" to be of little biological importance. Invariably, their stability is enforced by a requirement that potential mutant invaders disperse in a direction that is opposite to that of their same-sex competitors. Although we have found that local stability of "additional equilibria" is mathematically possible, they lack the more desirable property of global stability. By the proof of Observation 2 (appendix), dispersal by the aforementioned mutant invaders is always detrimental. Interestingly, when such mutants are not forced into dispersal, the stability of each "additional equilibrium" fails.

The reader should note that we can not guarantee the global stability of the main equilibria discussed above (i.e. our stability analysis is still local). However, unlike the "additional equilibria," the global stability of our main equilibria cannot be ruled out in the same manner.

6. Discussion

6.1. Main results

This paper investigates the evolution of sex-allocation in a two-habitat environment when sex-allocation and dispersal co-evolve. Many theoretical models have considered the evolution of sex allocation when fitness gains made through the investment in one sex differ from those made through an equal investment in the other sex. However, most do not adequately model spatial heterogeneity, which is an important mechanism by which such differences in fitness gains arise. Some recent exceptions include Juillard (2000) and Leturque and Rousset (2003), but these are limited to the case where habitat quality only influences overall fecundity, i.e. $w_f = w_m$. In this paper, we assume that spatial heterogeneity has sex-specific consequences for competitive ability. Most importantly, we do not assume that the population is well mixed when mating occurs (cf. Charnov, 1979; Bull, 1981; Leimar, 1996; Wade et al., 2003).

Special cases of our model highlight the importance of mixing in a heterogeneous environment to the evolution of biased sex-allocation behavior. When dispersal between habitats is prevented, differences in competitive ability among individuals are of no consequence, and selection favors equal investment in sons and daughters in both habitats. This is the sex-allocation prediction made by Fisher (1930). Equal investment is also favored when dispersal is limited to a single sex.

By contrast, in a well-mixed population (i.e. $d_{sg} = 1/(2-c)$ for $s = m, f$ and $q = g, b$), stable sex-allocation

are precisely those presented in Charnov (1979) and Bull (1981). Biased sex-allocation behavior is expected to evolve, consistent with predictions of verbal theory (Trivers and Willard, 1973; see also Carranza, 2002).

Recent authors have noted the need for a complete co-evolutionary theory of sex allocation and dispersal (e.g. Perrin and Mazalov, 2000). The theory developed in this paper shows the value of such "co-evolutionary approaches." In particular, we demonstrate that both the sex-allocation predictions made Fisher and those made by Trivers and Willard are possible within the context of a single, unified model framework (note that, in contrast to predictions made by Trivers and Willard (1973, p. 91) themselves, biased sex-allocation behavior in this model, i.e. biased investment, is reflected in biased brood sex-ratios).

When the difference between w_m and w_f is small so that $w_f/(1-c) > w_m(1-c)$ (or c close to one), habitats become isolated and sex allocation behaviors become unbiased (a "Fisherian" prediction). When the difference in sex-specific advantages w_m and w_f are substantial so that $w_f/(1-c) < w_m(1-c)$ (or c close to zero) sex-allocation behavior will be consistent with the predictions of Charnov (1979) and Bull (1981), provided competitive advantage is discounted appropriately.

6.2. Implications for the evolutionary theory of sex-allocation

Extreme sex-allocation behavior can be found across a wide variety of taxa. Some of this extreme behavior matches the predictions of existing theory quite well. The sex-allocation behavior of parasitoid wasps in relation to host quality, for instance, shows a tight match to theory (e.g. Charnov et al., 1981; see also Ode and Hunter, 2002).

In other cases, theoretical predictions about sex-allocation behavior can be difficult to verify. Variation in the sex-allocation behaviors of birds and mammals, for instance, presents a challenge to sex-allocation theory simply because multiple interacting factors might be considered relevant (Clutton-Brock and Iason, 1986; Cockburn et al., 2002; Silk et al., 2005). Similar difficulties have arisen in the study of human sex ratios (Lazarus, 2002), and sex ratios of the eusocial hymenoptera (e.g. Boomsma and Grafen, 1990 and references therein). It is in these kind of problematic cases where the theory developed above might be best considered.

Inconsistent empirical results have lead to the reasonable attitude that problematic sex-allocation behavior need not be "fitted into the straightjacket of theory" (Cockburn et al., 2002, p. 280). Instead of relying on a single adaptive hypothesis to explain observed sex-allocation behaviors, authors might seek pluralistic explanations that reflect the biology of the taxon of study. Nevertheless, some patterns of sex-allocation can even confound this pluralistic approach (e.g. Silk et al., 2005).

Few (if any) studies of sex-allocation behavior in nature account for the co-evolution of sex-allocation with other important traits like dispersal. Including dispersal evolution in a theoretical framework could explain any problematic variety of sex-allocation behaviors as simply a consequence of disparities in habitat quality within a particular metapopulation. We must emphasize, however, that these comments are only speculative at present and more field data is required. The message we wish to convey is that careful consideration of co-evolving behaviors is important to understanding the evolution of sex-allocation behavior. A co-evolutionary approach could reduce the complexity of explanations for observed sex-allocation behavior.

Many authors have noted that life-history details, in particular, ought to be considered when making predictions about sex-allocation behavior (see note and references in West and Sheldon, 2002). Our results indicate that, in addition to life history details, predictions about sex allocation ought to account for spatial heterogeneity of the environment (e.g. extent of heterogeneity, how a particular organism experiences this heterogeneity, etc.).

6.3. Implications for the evolutionary theory of dispersal

Dispersal between habitat patches is predicted to evolve for a variety of reasons. For instance, dispersal is favored in a temporally variable habitat when the threat of local extinction looms (Comins et al., 1980). Dispersal is also advantageous when it ensures that competition between relatives or inbreeding can be avoided (Motro, 1991). In the absence of kin selection, temporal fluctuation and inbreeding depression, it is class structure (e.g. sex-structure, age-structure) of a population that becomes the main feature by which costly dispersal in a spatially heterogeneous environment can be maintained (Greenwood-Lee and Taylor, 2001). Even in the presence of class structure, only specific patterns of dispersal can be considered to be evolutionarily stable. In particular, it has been demonstrated both here and elsewhere that in a two-patch habitat selection will not favor either one-way or bi-directional dispersal by a single class (Greenwood-Lee and Taylor, 2001).

It is likely that habitats in nature vary in such a way that optimal division of resources among different class-components of fitness in one habitat patch is not optimal in another. For example, sex-allocation behavior might be strongly biased, or size-at-maturity may be noticeably smaller in one habitat than in another. The habitat-specific economics of these important life-history decisions will certainly have implications for optimal rates of dispersal. Again we stress that understanding dispersal in a broader co-evolutionary context is useful.

6.4. Limitations and extensions

There are at least four important limitations to our investigation not yet addressed. First, we have made some simplifying ecological assumptions. Most notable are the

assumptions that habitat density and quality both remain constant over time. At some ecological scales, both of these quantities are likely to fluctuate over time. We might expect, for example, that there are "good seasons" where disparities between patches are small (perhaps non-existent) and population densities unusually high. Our conclusions, of course, are limited by such assumptions; and future work might seek to understand the consequences of incorporating a more "realistic" ecology into our model.

Second, our model posits a habitat that is divided into only two patches, but such habitats are likely rare in nature. This assumption is primarily made for convenience, since one of our intentions was to understand the consequences of movement between habitats of different quality for sex-allocation behavior. In a multipatch model, where all type-q patches are identical in all respects, dispersal between habitat patches of the same quality will not occur. Individuals should be unwilling to pay a cost for no gain. Other generalizations, though, might still be interesting. For example, one might consider the case in which habitats are divided into an arbitrary number of quality levels.

Third, the relationships that determine whether or not sex-allocation bias is stable involve not only w_m and w_f, but also the cost of dispersal, c. In natural populations these costs might be difficult to ascertain (Wolff, 1994). This limits the applicability of the qualitative predictions made by our model.

Finally, we have assumed that competition between males and females is irrelevant to both the evolution of sex-allocation behavior and dispersal. Recent theory indicates that male–female competition can influence predictions about the co-evolution of these behaviors (Leturque and Rousset, 2004).

Acknowledgments

Appendix A. Co-evolution when habitats connected by dispersal

It is possible to use simple RV arguments to say a great deal about which dispersal and sex allocation configurations might be evolutionarily stable. In particular we can argue that when habitats are connected by dispersal the only possibilities are those identified in Fig. 3a–c. We will need the following notation:

- v_{sq} = RV of a sex-s individual born in the type-q habitat at the time of census in a monomorphic resident population.

- $v'_{sq1,q2}$ = RV of sex-s individual born in the type-$q1$ habitat after successful dispersal to a type-$q2$ habitat, while in a monomorphic resident population.

The row vector, $[v_{fg}, v_{mg}, v_{fb}, v_{mb}]$ is the left eigenvector of the matrix $\mathbf{A}(\mathbf{r}, \mathbf{r})$ associated with an eigenvalue of one. The conditional RVs can be defined in terms of the entries of the left eigenvector as follows:

$$v'_{fgq} = w_f[Kn_q/2F_q][(1 - \beta_q)v_{fq} + \beta_q v_{mq}], \tag{A.1}$$

$$v'_{mgq} = w_m[Kn_q/2M_q][(1 - \beta_q)v_{fq} + \beta_q v_{mq}], \tag{A.2}$$

$$v'_{fbq} = [Kn_q/2F_q][(1 - \beta_q)v_{fq} + \beta_q v_{mq}], \tag{A.3}$$

$$v'_{mbq} = [Kn_q/2M_q][(1 - \beta_q)v_{fq} + \beta_q v_{mq}]. \tag{A.4}$$

Note that always $v'_{sgq} = w_s v'_{sbq}$.

There is another connection between conditional RV and the entries of the left eigenvector when dispersal is at equilibrium. It is easy to see that complete dispersal $d_{sq} = 1$ will never occur in a two-habitat model at equilibrium. Thus, at equilibrium either dispersal is zero, in which case

$$v'_{sq1,q1} < (1 - c)v'_{sq1,q2} \tag{A.5}$$

or dispersal lies strictly between zero and one, in which case

$$v'_{sq1,q1} = (1 - c)v'_{sq1,q2}. \tag{A.6}$$

If we write

$$v_{sq1} = (1 - d_{sq1})v'_{sq1,q1} + d_{sq1}(1 - c)v'_{sq1,q2}, \tag{A.7}$$

Eqs. (A.5)–(A.7) tell us that, at equilibrium

$$v_{sq1} = v'_{sq1,q1}. \tag{A.8}$$

Argument for observation 1

The argument for observation 1 is based on one made in Greenwood-Lee and Taylor (2001), but is not identical. We will show that one-way dispersal is not stable, by showing instead that any dispersal to the bad habitat must be compensated by dispersal from the same habitat, and vice versa.

Write the transition matrix $\mathbf{A}(\mathbf{r}, \mathbf{r})$ as

$$\left\| \begin{matrix} \mathbf{A}_g & \mathbf{0} \\ \mathbf{0} & \mathbf{A}_b \end{matrix} \right\| \left\| \begin{matrix} \mathbf{D}_{gg} & \mathbf{D}_{gb} \\ \mathbf{D}_{bg} & \mathbf{D}_{bb} \end{matrix} \right\|, \tag{A.9}$$

where

$$\mathbf{A}_q = \frac{K}{2} \left\| \begin{matrix} n_q(1 - \beta_q)/F_q & n_q(1 - \beta_q)/M_q \\ n_q\beta_q/F_q & n_q\beta_q/M_q \end{matrix} \right\|, \tag{A.10}$$

$$\mathbf{D}_{gg} = \left\| \begin{matrix} w_f(1 - d_{fg}) & 0 \\ 0 & w_m(1 - d_{mg}) \end{matrix} \right\|, \tag{A.11}$$

$$\mathbf{D}_{bb} = \left\| \begin{array}{cc} 1 - d_{fb} & 0 \\ 0 & 1 - d_{mb} \end{array} \right\|, \tag{A.12}$$

$$\mathbf{D}_{bg} = \left\| \begin{array}{cc} w_f(1-c)d_{fg} & 0 \\ 0 & w_m(1-c)d_{mg} \end{array} \right\|, \tag{A.13}$$

$$\mathbf{D}_{gb} = \left\| \begin{array}{cc} (1-c)d_{fb} & 0 \\ 0 & (1-c)d_{mb} \end{array} \right\|. \tag{A.14}$$

It can be verified that there exists a column vector $\mathbf{u} = [\mathbf{u}_g, \mathbf{u}_b]^T = [u_{fg}, u_{mg}, u_{fb}, u_{mb}]^T$ such that at equilibrium in a monomorphic population $\mathbf{u} = \mathbf{A}(\mathbf{r}, \mathbf{r})\mathbf{u}$. The vector $\mathbf{u}$ gives the steady state distribution of individuals in this monomorphic, class-structured population. Using the notation introduced above, we have that

$$\mathbf{u}_b = \mathbf{A}_b[\mathbf{D}_{bg}\mathbf{u}_g + \mathbf{D}_{bb}\mathbf{u}_b]. \tag{A.15}$$

Eqs. (A.3)–(A.4) and (A.8) tell us that, at equilibrium, the row vector $\mathbf{v}_b = [v_{fb}, v_{mb}]$ is the left eigenvector of $\mathbf{A}_b$ associated with an eigenvalue of one. Left multiplication of (A.15) by $\mathbf{v}_b$ yields

$$\mathbf{v}_b\mathbf{u}_b = \mathbf{v}_b[\mathbf{D}_{bg}\mathbf{u}_g + \mathbf{D}_{bb}\mathbf{u}_b]. \tag{A.16}$$

Let the column vector $\mathbf{e}_b = [d_{fb}u_{fb}, d_{mb}u_{mb}]$ denote the number of individuals dispersing from the bad habitat, and note that

$$\mathbf{D}_{bb}\mathbf{u}_b = \mathbf{u}_b - \mathbf{e}_b. \tag{A.17}$$

Similarly, the entries of the column vector

$$\mathbf{i}_b = \mathbf{D}_{bg}\mathbf{u}_g \tag{A.18}$$

give the numbers of individuals arriving on the bad patch. Substituting (A.17) and (A.18) into (A.15) and (A.16) we get

$$\mathbf{v}_b\mathbf{i}_b = \mathbf{v}_b\mathbf{e}_b. \tag{A.19}$$

Eq. (A.19) tells us that a weighted sum of immigrants must be balanced by a weighted sum of emigrants.

Argument for observation 2

Suppose that sex-s disperses in both directions. As indicated above dispersal cannot be complete. It follows that

$$v_{sg} = v'_{sgg} \quad \text{(from A.8)}, \tag{A.20}$$

$$= (1-c)v'_{sgb} \quad \text{(from A.6)}, \tag{A.21}$$

$$= (1-c)w_sv'_{sbb} \quad \text{(from comment following A.4)}, \tag{A.22}$$

$$= (1-c)^2 w_sv'_{sbg} \quad \text{(from A.6)}, \tag{A.23}$$

$$= (1-c)^2 v'_{sgg} \quad \text{(from comment following A.4)}, \tag{A.24}$$

$$= (1-c)^2 v_{sg} \quad \text{(from A.8)}. \tag{A.25}$$

Since, both c and v_{sg} are greater than zero (A.25) yields a contradiction. We conclude that sex-s cannot disperse in both directions.

Argument for observation 3

Suppose sex-$s1$ disperses from the good habitat to the bad habitat; and suppose sex-$s2$ disperses in the opposite direction. Note that this assumption implies that sex-$s1$ is certainly produced in the good habitat, and sex-$s2$ is certainly produced in the bad habitat. It follows that

$$v'_{s1,gg} = (1-c)v'_{s1,gb} \quad \text{(from A.6)}, \tag{A.26}$$

$$= (1-c)w_{s1}v'_{s1,bb} \quad \text{(from comment following A.4)}, \tag{A.27}$$

$$= (1-c)w_{s1}v_{s1,b} \quad \text{from A.8)}, \tag{A.28}$$

$$\leqslant (1-c)w_{s1}v_{s2,b} \quad \text{(since } s2 \text{ is produced in bad habitat)}, \tag{A.29}$$

$$= (1-c)w_{s1}v'_{s2,bb} \quad \text{(from A.8)}, \tag{A.30}$$

$$= (1-c)^2 w_{s1}v'_{s2,bg} \quad \text{(from A.6)}, \tag{A.31}$$

$$= (1-c)^2 w_{s1}v'_{s2,gg}/w_{s2} \quad \text{(from comment following A.4)}, \tag{A.32}$$

$$= (1-c)^2 w_{s1}v_{s2,g}/w_{s2} \quad \text{(from A.8)}, \tag{A.33}$$

$$\leqslant (1-c)^2 w_{s1}v_{s1,g}/w_{s2} \quad \text{(since } s1 \text{ is produced in good habitat)}, \tag{A.34}$$

$$= (1-c)^2 w_{s1}v'_{s1,gg}/w_{s2} \quad \text{(from A.8)}. \tag{A.35}$$

We can summarize (A.26)–(A.35) with the inequality $v'_{s1,gg} \leqslant (1-c)^2 w_{s1}v'_{s1,gg}/w_{s2}$ which is equivalent to

$$w_{s2}/(1-c) \leqslant w_{s1}(1-c). \tag{A.36}$$

Since we assume $w_f < w_m$, (A.36) tells us that males must be sex-$s1$ and females must be sex-$s2$.

Argument for observation 4

If mixed-sex broods are produced on both habitats, and if habitats are connected by dispersal, then (A.29) and (A.34) hold as equalities. It follows that (A.36) holds as an equality.

Appendix B. Sketch of stability argument

In this appendix, we present a brief sketch of a typical stability argument. We assume that the reader is familiar with Appendix A and has convinced him/herself that (if dispersal is occurring in an evolutionarily stable state) (a) one sex disperses in one direction while the opposite sex disperses in the opposite direction; and (b) one sex is not produced in at least one of the two habitats.

Consider the situation illustrated in Fig. 3a, i.e. suppose that resident behaviors are fixed at

$$d_{fg} = 0 \quad \text{and} \quad \beta_b = 0. \tag{B.1}$$

When (B.1) is substituted into to Eq. (16), we find that the remaining four elements of the righthand side of (16) vanish when

$$\beta_g = [1 + n_b(1 - c)/w_f n_g]/2, \tag{B.2}$$

$$d_{mg} = n_b(1 - c)/[w_f n_g + n_b(1 - c)], \tag{B.3}$$

$$d_{fb} = 1/2, \tag{B.4}$$

$$d_{mb} = \text{arbitrary value}. \tag{B.5}$$

A standard linear stability analysis reveals that (B.1)–(B.5) is stable against local perturbations restricted to β_g, d_{mg} and d_{fb}. Furthermore, the projection of the selection gradient at (B.1)–(B.5) onto the β_b-axis (respectively, d_{fg}-axis) indicates that selection will maintain $\beta_b = 0$ (respectively, $d_{fg} = 0$).

Clearly, selection cannot maintain d_{mb} at any particular value, since this trait is not expressed at equilibrium ($\beta_b = 0$). The results of Appendix A, however, show that selection will "correct" any expressed perturbation in d_{mg}.

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