



Kin Competition, the Cost of Inbreeding and the Evolution of Dispersal

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Dispersal is often presented as a mechanism to avoid competition among relatives and inbreeding depression. However, the formal analysis of the effects of both these factors on the evolution of dispersal has only been conducted in few studies with strong restrictive assumptions. In this paper, I first derive the evolutionary stable dispersal rate as a function of three parameters: (1) the cost of dispersal, c , (2) the coefficient of relatedness among randomly chosen offspring, R , and (3) the cost of inbreeding, δ . In a second step, relatedness is used as a dynamical variable for the derivation of the evolutionarily stable dispersal rate. Finally, in a third step, relatedness and the cost of inbreeding are assumed to be dynamical variables. This allows to analyse the more realistic situation where dispersal, relatedness and the cost of inbreeding are coevolving simultaneously. Several subcases are considered depending on the genetic determinism (haploid or diploid), the control of the dispersal strategy (parent or offspring control of dispersal) and the plasticity of dispersal with sexes (with or without sex-specific dispersal rates). This analysis clarifies the role of the cost of inbreeding and kin competition on the evolution of dispersal (in particular on the evolution of sex-biased dispersal rates) and leads to quantitative and testable predictions.

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Introduction

Species are frequently distributed into numerous semi-isolated local populations. Such metapopulation structure may affect both population genetics and population dynamics of species. In particular, if the migration rate is low, individuals from the same populations are very likely to be more related than individuals from different populations. High relatedness within populations has two major consequences. First, it increases the level of kin competition between individuals within populations. Second, since mating takes place between related individuals, organisms may suffer more from inbreeding depression. Under

these two selective pressures, one would expect that some mechanisms evolve to avoid kin competition and inbreeding depression. For example, dispersal can be viewed as an altruistic trait that allows to avoid competition between related individuals within patches (Hamilton and May 1977, Motro, 1982a, b; Frank, 1986; Taylor, 1988; Gandon and Michalakis, 1999). In the same way, it has been shown that higher dispersal rates could also be selected for to avoid inbreeding depression (Bengtsson, 1978; Waser *et al.*, 1986, Motro, 1991; Perrin & Mazalov, 1999). The question of the evolution of dispersal as a mechanism to avoid inbreeding depression has stimulated many investigations (e.g. Packer, 1979; Lambin, 1994; Jacquot & Vessey, 1995; Dobson *et al.*, 1997). Many of these experiments provide strong

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evidence for an effect of inbreeding depression on the evolution of dispersal and, more specifically, on the evolution of sex-biased dispersal rates. However, since dispersal results from multiple causes (Dobson, 1982; Dobson & Jones, 1985), it remains unclear what is the relative importance of inbreeding depression among several other factors on the observed patterns of dispersal behaviours (Moore & Ali, 1984; Dobson & Jones, 1985; Packer, 1985; Liberg & von Schantz, 1985; Moore, 1993; Wolff, 1993; for reviews see Pusey, 1987; Pusey & Wolf, 1996). In this context, it is of paramount importance to formalize the effects of several factors acting simultaneously on the evolution of dispersal. However, the evolution of inbreeding avoidance has only been modelled under several simplifying and unrealistic assumptions (Bengtsson, 1978; May, 1979; Smith, 1979; Waser *et al.*, 1986; Motro, 1991; Perrin & Mazalov, 1999). This is probably due to the intrinsic complexity of this question since dispersal, relatedness and inbreeding depression are interconnected variables. To my knowledge, Motro (1991) is the only one who formalized both the effects of inbreeding depression and kin competition on the evolution of dispersal. His model has, however, two major restrictive assumptions: (1) each site can support only one breeding pair and (2) organisms are haploid.

In this paper, I present a general kin selection model of the evolution of dispersal that relaxes both these points and other simplifying assumptions. In particular, this model allows to study the effects of several factors: (1) the cost of dispersal; (2) kin competition; (3) the cost of inbreeding; (4) the population size; (5) the ploidy level; and (6) maternal vs. offspring control of dispersal. However, adding such realism greatly complexifies the original models on the evolution of dispersal. For the sake of simplicity, the following analysis is based on a three-step argument (Fig. 1). First, I assume that both relatedness and the cost of inbreeding are fixed parameters and derive the evolutionarily stable (ES) dispersal rates for males and females. Second, I derive relatedness as a function of several other parameters (including dispersal itself and the cost of inbreeding) and study the coevolution between dispersal and relatedness. Third, I assume that

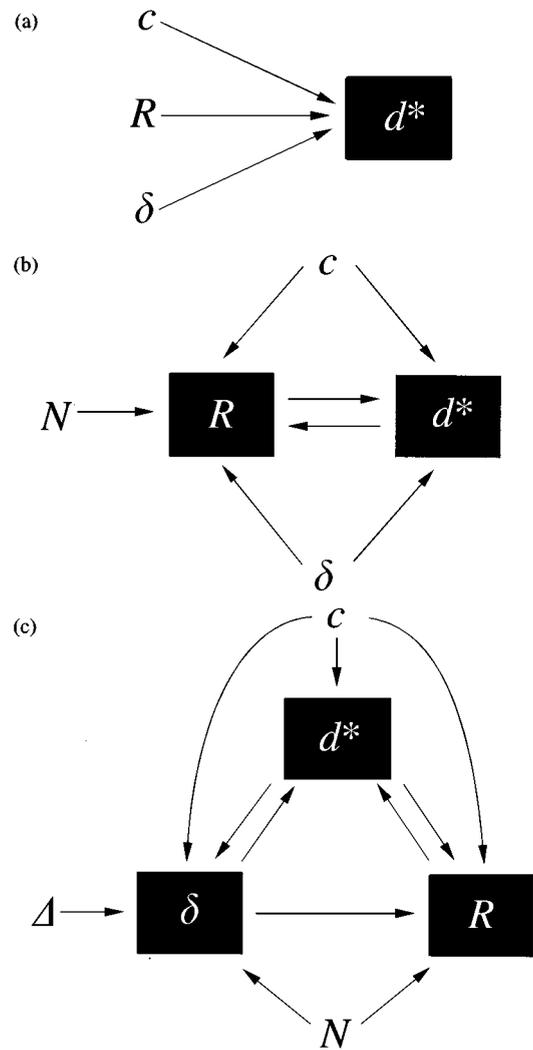


FIG. 1. Direct and indirect effects of various parameters on the evolutionarily stable dispersal rate, d^* . In (a) relatedness, R , and inbreeding depression, δ , are used as a fixed parameters. In (b) relatedness is a dynamical variable and coevolves with dispersal. In (c) both relatedness and inbreeding depression are dynamical variables that depend on various parameters (c : cost of dispersal, N : population size, Δ : number of lethal equivalents).

the cost of inbreeding depends on the level of inbreeding and on the genetic load (i.e. number of lethal equivalents). This allows to analyse the evolution of dispersal when both relatedness and the cost of inbreeding are dynamical variables. For each step, different subcases are considered depending on the ability of the organism to have sex-specific dispersal rates. This analysis determines what are the factors that may lead to the evolution of sex-biased dispersal rates.

General Life Cycle

The model is based on the following assumptions. (1) Individuals are distributed in an infinite number of populations each containing N breeding pairs (N males and N females). (2) Each breeding pair has the same expected number of offspring, n (n is assumed to be very large). The sex ratio within the progeny is 1:1. (3) After reproduction, a proportion d_m and d_f of the offspring (male and female, respectively) disperse and eventually reach another population. (4) Dispersal rates can either be under the control of the offspring or under the control of the mother. (5) Dispersing progeny incur a cost of dispersal, c ($0 \leq c \leq 1$). (6) After dispersal the parents die (i.e. generations are discrete and non-overlapping). (7) Breeding pairs are constituted randomly among all the male (and female) offspring. Following Motro (1991), I assume that the cost of inbreeding, δ ($0 \leq \delta \leq 1$), occurs before (or during) competition for space between these different breeding pairs. A pair formed by philopatric individuals is less likely to succeed (i.e. to settle and to reproduce in the population) than any other breeding pair (when at least one parent is an immigrant). This all-or-nothing response case is different from the common definition of inbreeding depression (e.g. a cost on the fecundity of inbred females). However, this assumption greatly simplifies the algebra since all the different breeding pairs have the same expected number of offspring [assumption (2)]. Such a cost of inbreeding could best be interpreted as an inbreeding avoidance parameter (because it acts before

fitness of an individual, i , randomly chosen in the population j requires the incorporation of the effects of the behaviour of its neighbours. In this respect, I assume: $d_m[ij]$ and $d_f[ij]$ are the male and female dispersal rates of the focal individual, i ; $d_m[j]$ and $d_f[j]$ are the average male and female dispersal rates in the population j ; and d_m and d_f are male and female dispersal rates averaged over the whole metapopulation. Another complication emerges from the fact that different sexes can interact. Taylor & Frank (1996) showed that in such class-structured population (here the classes are the different sexes) the total fitness, W , is:

$$W = c_m W_m + c_f W_f, \tag{1}$$

where W_m and W_f are the fitness (i.e. reproductive success) of males and females, respectively; c_m and c_f are the reproductive values of males and females. Since we consider only haploid and diploid cases we have $c_m = c_f = 1/2$ (Price, 1970).

Let me first derive male fitness:

$$W_m = W_{mp} + W_{md}, \tag{2}$$

where W_{mp} and W_{md} are the expected number of offspring produced by philopatric and dispersed individuals, respectively.

$$W_{mp} = np_{mp}, \tag{3}$$

where p_{mp} is the probability that a pair formed with a philopatric male, competing in a j -type population, will successfully settle and reproduce in this population:

$$p_{mp} = \frac{(1 - d_m[ij])((1 - c)d_f + (1 - \delta)(1 - d_f[j]))}{n((1 - d_m[j] + (1 - c)d_m)(1 - d_f[j] + (1 - c)d_f) - \delta(1 - d_m[j])(1 - d_f[j]))}. \tag{4}$$

mating). I will come back to the importance of the distinction between different definitions of the cost of inbreeding in the discussion. (8) After competition each population is filled with N breeding pairs.

3. Inclusive Fitness

As first pointed out by Hamilton (1964, 1970), in spatially structured populations, the inclusive

Equations (3) and (4) point out that the cost of inbreeding has an effect on a given breeding pair if, and only if, both the male and the female are philopatric. Indeed, under the infinite island model assumption, an immigrant will never be related with residents and with the other immigrants. As a consequence, a disperser will never pay the cost of inbreeding and, vice versa, a philopatric individual will not suffer from inbreeding depression if it breeds with an

immigrant,

$$W_{md} = np_{md}, \quad (5)$$

where p_{md} is the probability that a pair formed with a dispersed male offspring, competing in a random population, will successfully settle and reproduce in this population:

$$p_{md} = \frac{(1-c)d_m[ij](1-cd_f)}{n((1-cd_m)(1-cd_f) - \delta(1-d_m)(1-d_f))}. \quad (6)$$

Similarly, the fitness of females is obtained after replacing the subscript m by f and vice versa. Note that the expressions of male and female fitnesses do not depend on the assumption concerning the control of dispersal.

Marginal Gains in Fitness

The marginal gain in fitness (MGF) of a particular behaviour is the gain in fitness consecutive to a small change in the behaviour under study. These MGF expressions are very useful for two reasons. First, the ESS can be directly derived from calculation of MGF since a sufficient condition for a strategy to be ES is the equilibration of MGF from opposite behaviours (e.g. philopatry and dispersal). Note, however, that the equilibration of MGF is not a necessary condition of evolutionarily stability since, as will be shown later, some strategies can be ES even if the MGF are not equal. Second, the MGF formulation allows a simple cost-benefit analysis of the problem under study. This analysis has proven to be successful in explaining rather counter-intuitive results (see e.g. Gandon & Michalakis, 1999).

Following Motro (1991), two different cases will be considered. First, the dispersal strategies of males and females will be assumed to evolve independently, each behaviour being under the control of a specific autosomal locus. Second, I consider the case where there are no sex-specific dispersal rates.

SEX-SPECIFIC DISPERSAL RATES

In the following, I will assume that male and female dispersal rates are determined by their

respective genotypic values, x_m and x_f , at two autosomal and unlinked loci, X_m and X_f which have sex-specific expressions. For example, in males, the locus X_m is switched on and the locus X_f is switched off. Even with free recombination, some linkage disequilibrium may emerge between these two loci. However, since the ESS analysis considers only small variations in the mutant strategy, this effect will be assumed, as a first approximation, to be negligible. In this situation, selection will proceed independently on each locus and we can search for the evolutionary stable strategies sequentially. For instance, let me assume that the locus that controls the female behaviour is fixed (i.e. all the individuals have the same genotypic value, x_f^* , at the X_f locus). All the females have the same dispersal rate, d_f , and we can focus on the derivation of the ES dispersal rates of males.

Two major complexities emerge in this derivation. A first complication comes from kin selection since the fitness of a focal individual depends on the behaviour of its neighbours (which may be related to the focal individual). Second, note that, even if it can only be expressed in males, the females can also carry a mutant gene. Therefore, it is necessary to take into account the transmission of this gene through the production of both male and female offspring. The inclusive fitness analysis developed by Taylor & Frank (1996) and Frank (1997, 1998) will be used in the following to handle both complexities.

First assume the population to be monomorphic (i.e. all individuals have the same genotypic value, x_m^*), select a random allele at the X_m locus, mutate that allele, and its identical by descent copies, to a deviant value, x_m , and ask if this mutant allele increases in frequency. Frank (1997) showed that the direction of evolutionary change could be obtained with a simple maximization method. This method is based on the distinction between two kinds of individuals: actors and recipients. Actors are the individuals whose behaviour may be altered by a deviant genotypic value (in the present case only males are potential actors). Recipients are the individuals whose fitness depend on the behaviour of actors (here, both males and females are potential recipients). If the average effect of a particular genotype does not change between parent and offspring, the

direction of selection is given by the sign of [eqn (13) in Frank, 1997]:

$$\frac{dW}{dx_m} = \sum_s c_s \left[\frac{\partial W_s}{\partial d_m[ij]} \frac{dd_m[ij]}{dx_m[ij]} \tau_{s1} + \frac{\partial W_s}{\partial d_m[j]} \frac{dd_m[j]}{dx_m[j]} \tau_{s2} \right], \quad (7)$$

where x_m is a deviant genotypic value of the actor; the subscript s indicates the sex ($s = m, f$) where $\tau_{s1} = dx'_s/dx_m[ij]$ and $\tau_{s2} = dx'_s/dx_m[j]$ are the slopes of the transmitted genotypic values of the recipients in each sex, x'_s , on the genotypic value of their respective controlling classes $x_m[ij]$ and $x_m[j]$ (remember that in the present case only male dispersal evolves) respectively.

The first term in the brackets of eqn (7) is the effect of the actor on itself while the second term is the effect of the actor on its neighbours, the recipients. Since the recipients can be either male or female these effects are taken for both sexes and weighted by the reproductive value of each sex.

Since individual phenotypes are controlled by their own genotypic value the slopes of individual phenotypes on actors genotypes are all equal to one: $dd_m[ij]/dx_m[ij] = dd_m[j]/dx_m[j] = 1$. As a consequence, the male part of eqn (7) reduces to:

$$\frac{dW_m}{dx_m} = \frac{\partial W_m}{\partial d_m[ij]} \tau_{m1} + \frac{\partial W_m}{\partial d_m[j]} \tau_{m2}. \quad (8)$$

Since females cannot be actors (i.e. do not express the deviant male phenotype), the female part of eqn (7) depends only on $d_m[j]$, hence

$$\frac{dW_f}{dx_m} = \frac{\partial W_f}{\partial d_m[j]} \tau_{f2}. \quad (9)$$

At this stage, it is useful to divide both eqns (8) and (9) by τ_{m1} , which yields

$$G_m = \frac{\partial W_m}{\partial d_m[ij]} + \frac{\partial W_m}{\partial d_m[j]} R_{mm}, \quad (10)$$

$$G_f = \frac{\partial W_f}{\partial d_m[j]} R_{mf}, \quad (11)$$

where G_m and G_f are the MGF from males and females, respectively.

$R_{mm} = \tau_{m2}/\tau_{m1}$ and $R_{mf} = \tau_{f2}/\tau_{m1}$ will be called the coefficients of relatedness between male offspring and between male and female offspring (see the appendix on the calculation of relatedness for a discussion of these definitions).

The evolutionarily stable male dispersal rate, d_m^* , can be derived from the following condition:

$$G_m + G_f = 0, \quad (12)$$

where all the derivatives are evaluated at $d_m[ij] = d_m[j] = d_m^*$.

This formulation is not very useful to understand the processes involved in the evolution of male dispersal but it can be rearranged to let emerge the MGF from philopatry and from dispersal:

$$G_m = G_{md} - G_{mp}, \quad (13)$$

$$G_f = G_{fd} - G_{fp}, \quad (14)$$

with

$$G_{md} = \frac{\partial W_{md}}{\partial d_m[ij]} + \frac{\partial W_{md}}{\partial d_m[j]} R_{mm}, \quad (15)$$

$$G_{mp} = \frac{\partial W_{mp}}{\partial d_m[ij]} + \frac{\partial W_{mp}}{\partial d_m[j]} R_{mm}, \quad (16)$$

$$G_{fd} = \frac{\partial W_{fd}}{\partial d_m[j]} R_{mf}, \quad (17)$$

$$G_{fp} = \frac{\partial W_{fp}}{\partial d_m[j]} R_{mf}. \quad (18)$$

This leads to the following condition for evolutionarily stability:

$$G_d = G_p, \quad (19)$$

where

$$G_d = G_{md} + G_{fd}, \quad (20)$$

$$G_p = G_{mp} + G_{fp}, \quad (21)$$

are the MGF from dispersal and from philopatry, respectively. These MGF can be evaluated at $d_m[ij] = d_m[j] = d_m^*$, which yields

$$G_p = P_p(1 + kR_{mf} - (k_m R_{mm} + k_f R_{mf})), \quad (22)$$

$$G_d = P_d(1 - c), \quad (23)$$

where

$$P_p = \frac{(1 - cd_f) - \delta(1 - d_f)}{(1 - cd_m)(1 - cd_f) - \delta(1 - d_m)(1 - d_f)}, \quad (24)$$

$$P_d = \frac{1 - cd_f}{(1 - cd_m)(1 - cd_f) - \delta(1 - d_m)(1 - d_f)}, \quad (25)$$

$$k = \frac{(1 - d_f)(1 - \delta)}{(1 - cd_f) - \delta(1 - d_f)}, \quad (26)$$

$$k_m = \frac{(1 - d_m)(1 - cd_f - \delta(1 - d_f))}{(1 - cd_m)(1 - cd_f) - \delta(1 - d_m)(1 - d_f)}, \quad (27)$$

$$k_f = \frac{(1 - d_f)(1 - cd_m - \delta(1 - d_m))}{(1 - cd_m)(1 - cd_f) - \delta(1 - d_m)(1 - d_f)}. \quad (28)$$

k is the probability that a female in a randomly chosen breeding pair is philopatric; k_m and k_f are the probabilities that a randomly chosen breeding pair is composed with at least one philopatric male or female, respectively.

A similar formulation of MGF for female dispersal rate can be easily obtained after replacing the subscript m by f and vice versa.

The expressions of G_p and G_d are very useful to understand the balance between the effects of c , R and δ . Not surprisingly, G_d is a decreasing function of the cost of dispersal. The expression of G_p is more complex because, contrarily to dispersers, philopatric individuals may pay the cost of inbreeding and compete against relatives. However, this expression can be clarified through a cost-benefit analysis of the philopatric behaviour.

(1) *Cost of philopatry*: if a breeding pair succeeds in settling in the population it will take the

place of another breeding pair which may be composed with a related male, a related female or both. The occurrence of kin competition is expressed by the last two terms on the right-hand side of G_p : $-k_m R_{mm} - k_f R_{mf}$.

(2) *Benefit of philopatry*: the benefit of philopatry ($1 + kR_{mf}$) depends on the relatedness between the mates. If male and female are highly related, the male will gain an inclusive benefit from mating with a philopatric female since it will carry the same genes.

In other words, there is an ambiguity in the between-sexes relation. High relatedness between sexes select against philopatry through kin competition but the opportunity to mate with a relative may, on the other hand, select for philopatry. Therefore, the between-sexes relation is characterized by both competition (between-breeding pairs) and cooperation (within-breeding pair). Note that in the absence of inbreeding depression, there is an exact balance between these two components ($k_f = k$). At the other extreme, when $\delta = 0$, the between-sexes relation acts only through kin competition since there is no inclusive benefit to mate with a philopatric female.

NO SEX-SPECIFIC DISPERSAL RATE

Let me now assume that male and female dispersal rates are identical and determined by their genotypic value at a single autosomous locus. This leads to the same condition for evolutionary stability given above [eqn (19)] except that, in this case, $d_m = d_f = d$.

Evolutionarily Stable Dispersal Rate

The expressions of MGF from philopatry and from dispersal can be used to derive the ES dispersal rates as a function of the cost of dispersal, c , the cost of inbreeding, δ , and relatedness coefficients, R_{mm} and R_{mf} . Since we consider only haploid and diploid cases we have (see the appendix) $R_{mm} = R_{mf} = R$, where R is the relatedness among randomly chosen offspring. Therefore, the evolutionarily stable dispersal rates depend only on three parameters: c , R and δ .

I will first study the case when there is no sex-specific dispersal rates. In a second step, I will

study the coevolution between male and female dispersal rates, focusing on the evolution of sex-biased dispersal rates.

NO SEX-SPECIFIC DISPERSAL RATE

There is no simple analytic expression of d^* as a function of c , R and δ . However, it is worth pointing out four interesting extreme cases.

(1) When $\delta = 0$: not surprisingly (see Frank, 1986), the ES dispersal rate is

$$d^* = (R - c)/(R - c^2) \text{ when } R > c$$

$$\text{and } d^* = 0 \text{ when } R \leq c. \quad (29)$$

(2) When $\delta = 1$:

$$d^* = \frac{3(1 + c) - 2R - \sqrt{(1 + c)^2 + 4R(1 - 3c + R)}}{2(1 + c)^2 - 4R}. \quad (30)$$

(3) When $R = 0$:

$$d^* = (\delta - c)/(\delta - c^2) \text{ when } \delta > c$$

$$\text{and } d^* = 0 \text{ when } \delta \leq c. \quad (31)$$

Note the similarity between eqns (29) and (31).

(4) When $R = \delta = c$: the ES dispersal rate reduces to

$$d^* = \frac{1 - \sqrt{1 - R}}{R}. \quad (32)$$

For other parameter values, the ES dispersal rate is derived through numerical simulations (Fig. 2). The main effects are summarized in Table 1 and below:

- (1) *Cost of inbreeding*: d^* always increases with higher δ .
- (2) *Relatedness*: d^* always increases with higher R .
- (3) *Cost of dispersal*: d^* generally decreases with higher c . However, when both R and δ are very high, d^* can increase with very high cost of dispersal. Indeed, higher cost of dispersal

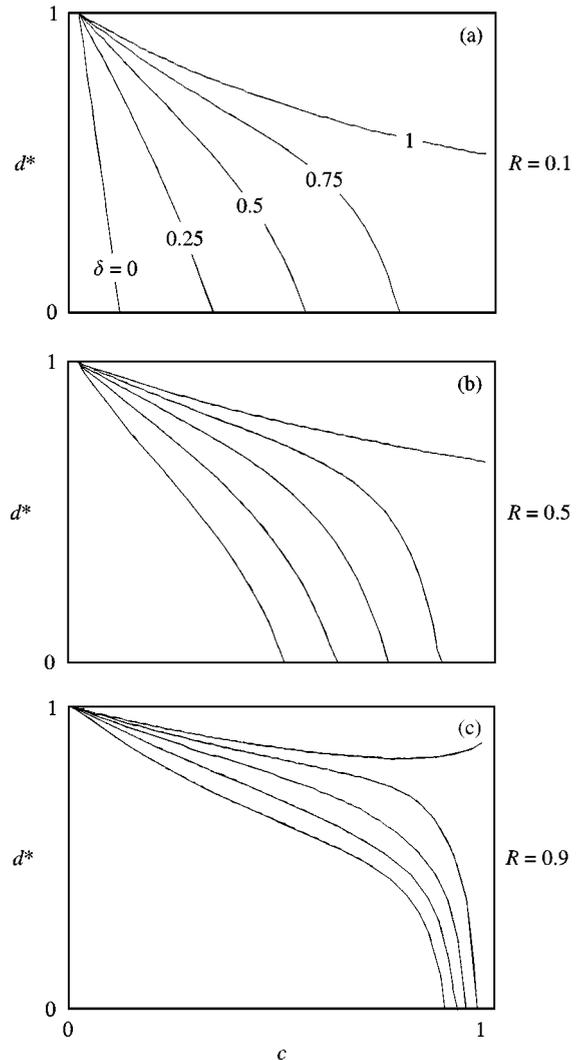


FIG. 2. Evolutionarily stable dispersal rate, d^* , versus the cost of dispersal, c , when relatedness, R , is used as a fixed parameter: in (a) $R = 0.1$, in (b) $R = 0.5$ and in (c) $R = 0.9$. On each panel five different levels of inbreeding depression, δ , are considered ($\delta = 0, 0.25, 0.5, 0.75, 1$).

increases the probability to compete (k_m and k_f) and to mate (k) with relatives. As a consequence, when R and δ are very high, G_p can decrease with higher cost of dispersal because the intensity of kin competition increases with higher c . Eventually, very high values of c lead to $G_p < G_d$ which indicates a selection for higher dispersal rates.

SEX-SPECIFIC DISPERSAL RATES

When sex-specific dispersal rates can evolve it is possible to derive the evolutionary stable dispersal rates of each sex as a function of the

TABLE 1.

Main effects of the increase of various parameters on the unbiased dispersal strategy and on its stability. These effects are presented for the three steps of the analysis. In the first step (I), relatedness, R , and inbreeding depression, δ , are fixed parameters [Fig. 1(a)]. In the second step (II), relatedness is a dynamical variable [Fig. 1(b)] that depends on several parameters including the population size, N , and the control of dispersal (maternal or offspring control). In the last step (III), inbreeding depression is a dynamical variable [Fig. 1(c)] that depends on the genetic load of the species. The arrows show the qualitative effect of an increase of a given parameter. An arrow in brackets indicates that the parameter may, in certain cases, have the opposite effect. A \sim indicates that the effect of a given parameter is negligible. A white dot indicates that a given factor is no longer a parameter at a given step of the analysis (e.g. R is a dynamical variable in steps II and III). A black dot indicates that a parameter is not yet included at this step of the analysis (e.g. Δ is only included in the last step of the analysis).

Parameter	Effect on the unbiased dispersed rate			Effect on the stability of the unbiased dispersal rate		
	I	II	III	I	II	III
R	\nearrow	\circ	\circ	\nearrow	\circ	\circ
δ	\nearrow	\nearrow	\circ	\searrow	\searrow	\circ
c	\searrow (\nearrow)	\searrow	\searrow	\nearrow	\nearrow	\nearrow
N	\bullet	\searrow	\searrow	\bullet	\searrow	\sim
Maternal versus offspring control	\bullet	\nearrow	\nearrow	\bullet	\nearrow	\nearrow
Δ	\bullet	\bullet	\nearrow	\bullet	\bullet	\searrow

behaviour of the opposite sex: $d_m^*[d_f]$ and $d_f^*[d_m]$. The intersection points between these two functions give the evolutionarily stable strategies (d_m^* , d_f^*) since at these points neither male nor female mutants can invade and spread. Note, however, these intersections points are not the only possible evolutionarily stable strategies (Motro, 1994). In certain cases, some sex-biased strategies may be evolutionarily stable although there is no equilibration of the MGF [see for example Fig. 3(b)].

Evolutionarily stability characterizes the ability to resist invasion by mutants but it does not indicate if evolution can lead to these equilibria. The attainability of each equilibrium (d_m^* , d_f^*) can be further checked by studying if a population fixed at a strategy (d_m , d_f) in the neighbourhood of the equilibrium can always be invaded by mutants with strategies closer to the ESSs. If this condition is fulfilled, the equilibrium (d_m^* , d_f^*) is

continuously stable (Eshel 1983, Motro 1994). The condition for continuous stability is [eqn (1) in Motro 1994]

$$\left. \frac{d d_m^*[d_f]}{d d_f} \right|_{d_f=d_f^*} \times \left. \frac{d d_f^*[d_m]}{d d_m} \right|_{d_m=d_m^*} \leq 1. \quad (33)$$

In this section, I study the effects of c , R and δ on the evolution of sex-biased dispersal rates. In other words, I show under which conditions (1) unbiased dispersal rates are not continuously stable and (2) sex-biased dispersal strategies are continuously stable.

Since males and females are playing a symmetrical game, the two ESS functions $d_m^*[d_f]$ and $d_f^*[d_m]$ are exactly identical. As a consequence, they always cross on the diagonal (Figs 3, 4 and 7) and this intersection point gives the evolutionarily stable unbiased dispersal rate.

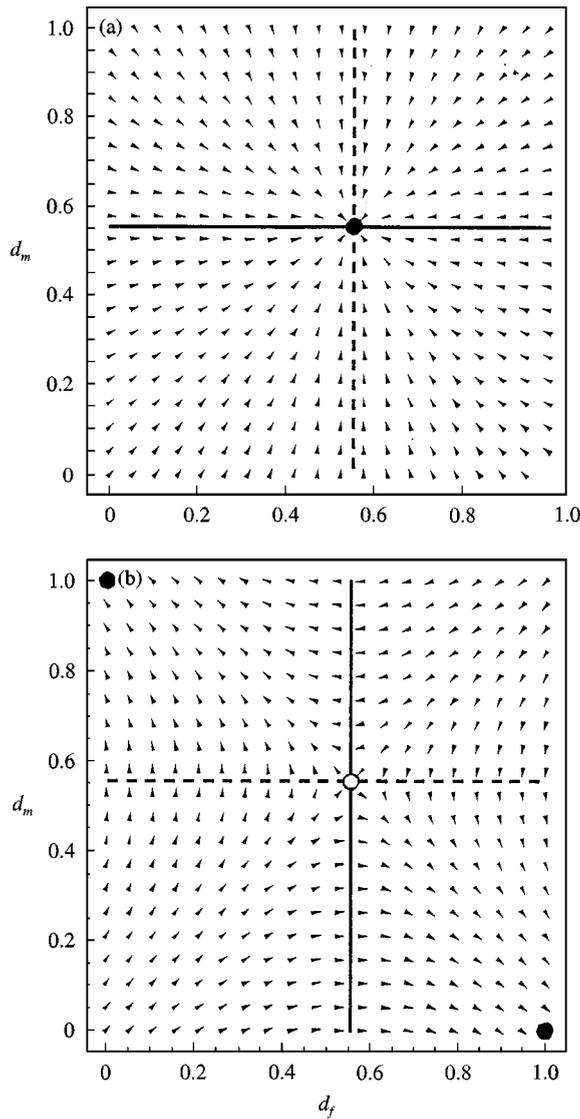


FIG. 3. Evolution of biased dispersal rates. The bold line indicates the evolutionarily stable dispersal rate of the male, d_m^* , as a function of female dispersal rate, d_f . The dashed line indicates the evolutionarily stable dispersal rate of the female, d_f^* , as a function of male dispersal rate, d_m . The arrows indicate the direction of selection for male and female dispersal. In (a) $\delta = 0$, $R = 0.4$ and $c = 0.2$. There is only one evolutionarily stable strategy (black dot) where male and female have the same dispersal rate. In (b) $\delta = 0.4$, $R = 0$ and $c = 0.2$. In this case there are two symmetrical evolutionarily stable dispersal strategies (black dots) where one sex always disperses and the other always stays at home. There is a third unbiased dispersal strategy which is an unstable equilibrium (white dot).

Unfortunately, there is no simple and general condition on c , R and δ for this equilibrium to be continuously stable. This stability can be checked numerically but, first, I present simple extreme cases.

Let me first study the case where $\delta = 0$. The resolution of eqn (19) yields the evolutionarily stable dispersal rate for males: $d_m^*(R - c)/(R - c^2)$. This expression indicates that the evolutionarily stable dispersal rate does not depend on the female strategy. In this situation the use of eqn (33) indicates that the unbiased strategy ($d_m^* = d_f^* = (R - c)/(R - c^2)$) is always stable [Fig. 3(a)].

Let me now assume that $R = 0$ (where c and δ can take any value). The derivation of the evolutionarily stable strategy of the male yields

$$d_m^* = \begin{cases} 1 & \text{if } d_f < \frac{\delta - c}{\delta - c^2}, \\ 0 & \text{if } d_f > \frac{\delta - c}{\delta - c^2}. \end{cases} \quad (34a)$$

$$d_f^* = \begin{cases} 1 & \text{if } d_m < \frac{\delta - c}{\delta - c^2}, \\ 0 & \text{if } d_m > \frac{\delta - c}{\delta - c^2}. \end{cases} \quad (34b)$$

In this case the unbiased dispersal strategy [i.e. $d_m^* = d_f^* = (\delta - c)/(\delta - c^2)$] is always unstable since

$$\left. \frac{dd_m^*[d_f]}{dd_f} \right|_{d_f=d_f^*} = \left. \frac{dd_f^*[d_m]}{dd_m} \right|_{d_m=d_m^*} = -\infty$$

[Fig. 3(b)].

In this case, there are two symmetric and biased evolutionarily stable strategies: ($d_m^* = 1$, $d_f^* = 0$) and ($d_m^* = 0$, $d_f^* = 1$). The attainability of each of these strategies is determined by the starting point or, in other words, by the history of the species. If the initial conditions are biased toward one sex (i.e. if the initial point is above or below the diagonal) the bias will remain in the same direction [see Fig. 3(b)]. These results are consistent with the model of Perrin & Mazalov (1999) in which the authors studied the evolution of sex-biased dispersal rate in the absence of kin competition.

An interesting case occurs when $c = R = \delta$. In this situation, there are no evolutionarily stable strategies since the best reply function of the male and the female overlap each other [Fig. 4(b)]. This yields a set of strategies that are all equally fit. Again, in this situation, the outcome of the evolution of dispersal rates depends on the initial conditions. Here, the only prediction that can be made is a negative correlation between male and female dispersal rates.

In the general case where $R > 0$ and $\delta > 0$, there is no simple analytic condition for the

stability of the unbiased strategy. However, numerical simulations indicate that lower relatedness, lower costs of dispersal and higher cost of inbreeding tend to destabilize the unbiased strategy (see Fig. 4 and Table 1).

Relatedness as a Dynamical Variable

In a second step, let me consider that relatedness is not a fixed parameter but a dynamical variable that depends on several other parameters including dispersal and the cost of inbreeding [Fig. 1(b)]. I first derive analytic expressions of relatedness and, second, I study the evolution of dispersal when relatedness is used as a dynamical variable.

THE CALCULATION OF RELATEDNESS

Different subcases are analysed (see the appendix):

(1) *Ploidy level*: although the probability of identity between two randomly chosen individuals from the same population depends on the ploidy level the derivation of relatedness for haploid and diploid organisms lead to the same result (i.e. no effect of the ploidy level on relatedness). This result seems counterintuitive but the absence of effects of the ploidy level has already been noted for other measures of population genetic structure (e.g. Ronfort *et al.*, 1998).

(2) *Control of dispersal*: under offspring control of dispersal, relatedness tends to be lower than if the mother controls natal dispersal [eqns (A.5) and (A.6) in the appendix].

In the Appendix, I derive the following expressions for relatedness under offspring (R_O) or maternal (R_M) control of dispersal:

$$R_O = \frac{1}{2N - k_1 - ((N - 1)/2)(2k_1 + k_2)^2}, \quad (35)$$

$$R_M = \frac{2}{2N - ((N - 1)/2)(2k_1 + k_2)^2}, \quad (36)$$

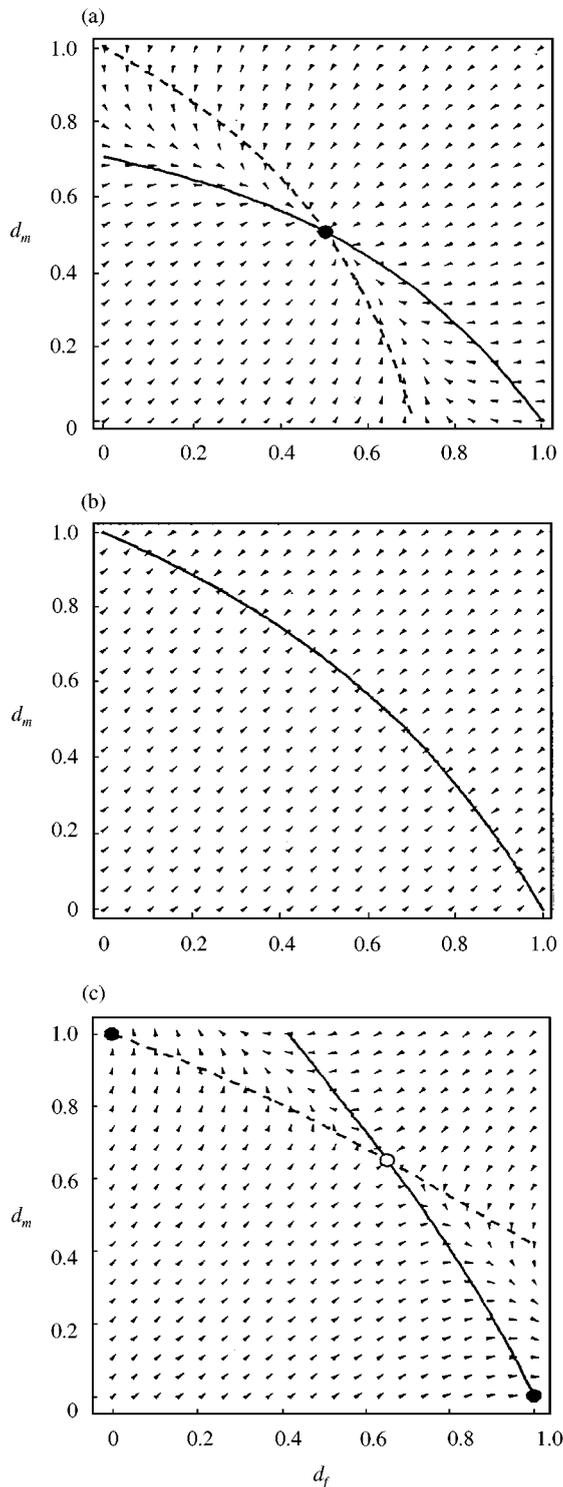


FIG. 4. Evolution of biased dispersal rates. As in Fig. 3. In (a) $\delta = 0.4$ and $R = c = 0.5$. There is only one evolutionarily stable strategy (black dot) where male and female have the same dispersal rate. In (b) $\delta = R = c = 0.5$. Here the best reply function of male and female dispersal rates coincide and define a set of strategy with equal fitness. There is no evolutionarily stable strategy. In (c) $\delta = 0.6$ and $R = c = 0.5$. In this case there are two symmetrical evolutionarily stable dispersal strategies (black dot) where one sex always disperses and the other always stays at home. There is a third unbiased dispersal strategy which is evolutionarily stable but not continuously stable (white dot).

where k_1 is the probability that the parents of a given offspring are both philopatric, while k_2 is the probability that one, and only one, parent is philopatric (see the appendix).

COEVOLUTION OF DISPERSAL AND RELATEDNESS

We already know from the above analysis the effects of higher c , R and δ on the evolution of dispersal rates. However, when relatedness is co-evolving with male and female dispersal several feedbacks emerge [see Fig. 1(b)] and some parameter may have direct and indirect effects on the evolution of dispersal rates. For example, higher costs of dispersal may affect the evolution of dispersal directly but also indirectly through its effect on relatedness. In this situation, there is, generally, no simple analytic expression for evolutionary stable dispersal rates but the effect of each parameter can be studied through numerical analysis.

No sex-specific dispersal rates

I will first consider the case where there is no sex-specific dispersal rate. Now, three parameters may affect the evolution of dispersal: the cost of inbreeding, δ , the cost of dispersal, c , and the size of the populations, N . The main effects of these parameters are presented in Fig. 5 and summarized below (see also Table 1).

(1) *Cost of inbreeding*: the ES dispersal rate always increases with higher δ .

(2) *Population size*: when $N = 1$ and when offspring control dispersal the results are identical to the analytic expression proposed by Motro [eqn (5) in Motro, 1991]. For higher population sizes, relatedness decreases and, consequently, dispersal is selected against (Figs 5 and 6).

(3) *Cost of dispersal*: the ES dispersal rate is always a decreasing function of the cost of dispersal (Fig. 5). Indeed, contrary to the case observed in the previous subsection, R and δ cannot be simultaneously very high because high level of inbreeding depression decreases relatedness.

(4) *Ploidy level*: since the ploidy level does not affect the value of relatedness, the evolutionarily stable dispersal rate is identical in the haploid and in the diploid case. This result was already noted by Motro (1982a, b).

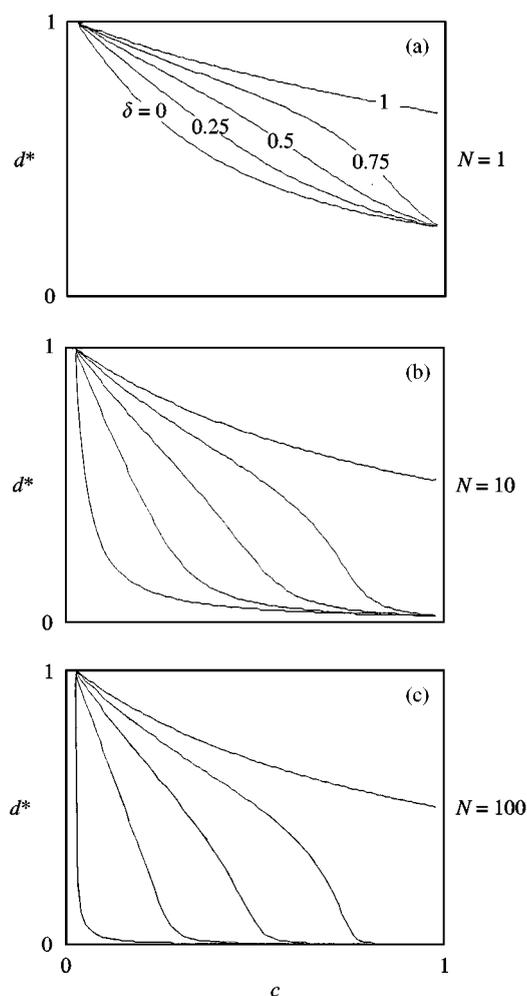


FIG. 5. Evolutionarily stable dispersal rate, d^* , versus the cost of dispersal, c , when relatedness, R , is used as a dynamical variable. In this situation relatedness depends on several parameters including the size of populations, N : in (a) $N = 1$, in (b) $N = 10$ and in (c) $N = 100$. On each panel five different levels of inbreeding depression, δ , are considered ($\delta = 0, 0.25, 0.5, 0.75, 1$).

(5) *Control of dispersal*: under parental control of dispersal, as already noted by several authors (Hamilton & May, 1977, Motro, 1983, Taylor, 1988), higher dispersal rates are selected for (Fig. 6). This effect is due to a higher coefficient of relatedness under parental than under offspring control [see eqns (35) and (36)]. A more intuitive explanation follows from the fact that the cost of dispersal is not directly paid by the mother but by the offspring. As a consequence, a mother prefers that her progeny will be more altruistic toward each other (i.e. have higher dispersal rates) than the offspring are willing to be.

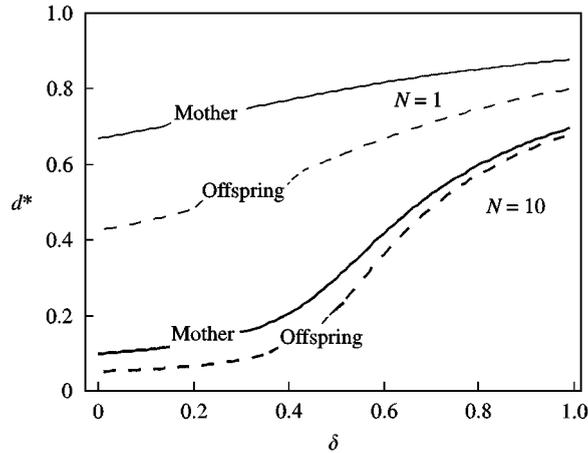


FIG. 6. Evolutionarily stable dispersal rate, d^* , versus inbreeding depression, δ , when relatedness, R , is used as a dynamical variable. The population size is $N = 1$ (in light) or $N = 10$ (in bold). The dispersal behaviour can either be under parental (full line) or offspring (dashed line) control. Other parameter values: $c = 0.5$.

Sex-specific dispersal rates

There can be one, three or five ESSs. If there is only one ESS (the unbiased strategy), it is always continuously stable. If there are three ESSs (one unbiased and two symmetrically biased strategies) only the unbiased strategies are continuously stable. Finally, if there are five ESSs (one unbiased, two intermediate biased strategies and two extremely biased strategies), the two intermediate biased strategies are never continuously stable.

The effects of the parameters of the model on the stability of the unbiased dispersal strategy are summarized below and in Table 1.

(1) *Cost of inbreeding*: higher δ destabilizes the unbiased dispersal rate.

(2) *Population size*: when $N = 1$ we end up with the same results as Motro (1991). As an example, Fig. 7 represents the special case where $c = 0.6$ and $\delta = 0.58$ (Motro, 1991, p. 114) and where five ESSs exist. As pointed out by Motro (1994), when there are five ESSs, two of these strategies are not continuously stable. In this situation, the evolution of biased or unbiased strategies depends on the initial conditions. For larger population sizes (i.e. $N > 1$), relatedness decreases [see eqns (35) and (36)] and this results in a lower stability of the unbiased dispersal rate.

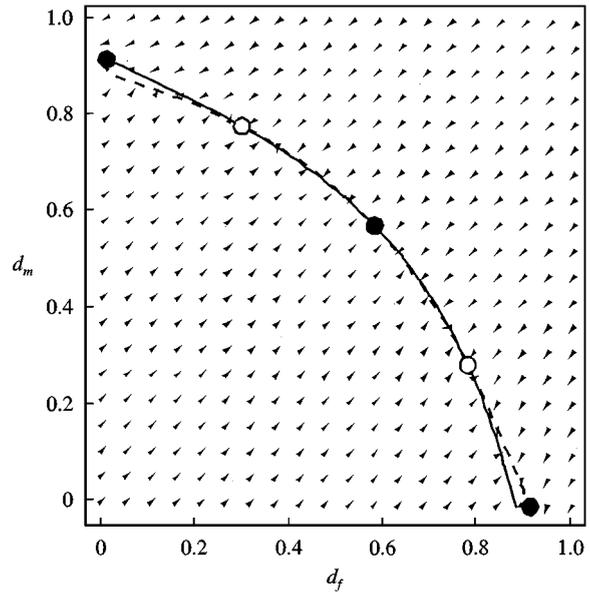


FIG. 7. Evolution of biased dispersal rates when relatedness is used as a dynamical variable. As in Fig. 3. Here I assume haploidy, offspring control of dispersal and I consider the case where inbreeding depression acts before reproduction with $\delta = 0.58$, $c = 0.6$ and $N = 1$. In this case there are five evolutionarily stable strategies but only three are continuously stable (black dot): the unbiased strategy and two biased strategies. The two other biased strategies (white dots) are not continuously stable.

(3) *Cost of dispersal*: higher cost of dispersal stabilizes the unbiased dispersal strategy.

(4) *Control of dispersal*: under maternal control of dispersal, relatedness tends to be higher and, therefore, the unbiased dispersal rate is more stable than under offspring control.

The Cost of Inbreeding as a Dynamical Variable

I now relax the assumption that the cost of inbreeding is a fixed parameter. The cost of inbreeding is due to inbreeding depression resulting from the expression of the hidden genetic load. Such a cost is likely to depend on the relatedness between the parents. Note that since diploidy is a necessary condition for the existence of some inbreeding depression, I will now restrict my analysis to the diploid case.

In a first step, I derive an analytic expression of inbreeding depression as a function of several parameters including identity coefficients and the total genetic load. In a second step, this expression is used to study the evolution of dispersal

when inbreeding depression and relatedness are used as dynamical variables [Fig. 1(c)].

THE CALCULATION OF INBREEDING DEPRESSION

In diploid organisms the genetic load (the accumulation of deleterious alleles in the genome) can be explained by the masking of deleterious recessive alleles (*dominance hypothesis*) or by the higher fitness of heterozygous individuals (*overdominance hypothesis*). The genetic load is known to depend on several demographic and genetic parameters including the mutation rate, the dominance of deleterious alleles and the effective size of the population (Lande & Schemske, 1985). However, for the sake of simplicity, I assume in the following that the genetic load is a fixed parameter that does not depend on the other factors of the model. Clearly, this assumption should be relaxed in future investigations (see the discussion section).

The expression of the hidden genetic load through mating between related individuals results in inbreeding depression. In particular, it has been shown (for both the dominance and the overdominance models of inbreeding depression) that, assuming independence and multiplicative interactions among loci, the logarithm of fitness should decline linearly with the degree of inbreeding in the progeny. For example, Morton *et al.* (1956) showed that the fitness of the progeny, S , could depend in the following way on the genetic load:

$$S = e^{-(A+\Delta F)}, \quad (37)$$

where A indicates the effects of the environment and genetics in a random-mating population and Δ is the rate at which fitness declines with a change in inbreeding, F (F is the inbreeding coefficient, the probability that a given offspring receives two genes identical by descent). In other words, Δ is the genetic load of the organism and is the average number of lethal alleles per gamete or the number of "lethal equivalents" (Morton *et al.*, 1956; Crow & Kimura, 1970).

In the above model of the evolution of dispersal, inbreeding depression, δ , measures the ratio in breeding success between philopatric and dispersed individuals. The formulation of the relative fitness loss due to inbreeding depression

leads to $1 - \delta = (1 - S_p)/(1 - S_d)$, where $1 - S_p$ and $1 - S_d$ are the fitness losses due to the expression of the genetic load in crosses between philopatric and in breeding pairs with at least one disperser, respectively. Using eqn (37) yields

$$\delta = 1 - e^{-\Delta F}, \quad (38)$$

where F is the coefficient of inbreeding in the offspring of a breeding pair formed by philopatric individuals which yields

$$F = g, \quad (39)$$

where g is the probability of identity between the parents (see the appendix: diploid case).

COEVOLUTION OF DISPERSAL, RELATEDNESS AND INBREEDING DEPRESSION

When relatedness and the cost of inbreeding are coevolving with male and female dispersal rates, a complex network of feedbacks [see Fig. 1(c)] emerges. As a consequence, because of the multiplicity of indirect effects, it is really difficult to get intuitive predictions concerning the effects of the different parameters of the model. For example, higher costs of dispersal may affect the evolution of dispersal directly but also indirectly through the effect of c on both relatedness and the cost of inbreeding. In the following, I present an analysis (based on numerical simulations) of the effect of each parameter (N , c and Δ) on the evolution of dispersal rates. Although Δ could potentially be very high, Ralls *et al.* (1988) found that the maximal estimated number of lethal equivalents (per gamete) in captive mammalian populations was 15 for the Wied's red-nosed rat (*Wiedomys pyrrhorhinos*) and that most of the variation was lying between 0 and 5. In the following (see Fig. 8) I will study the effect of Δ in the range 0–20.

No sex-specific dispersal rates

The effects of the different parameters are summarized below (see also Table 1):

(1) *Genetic load*: not surprisingly, higher Δ selects for higher dispersal rates (Fig. 8). However, note that for certain parameter values there is hardly any effect of the number of lethal

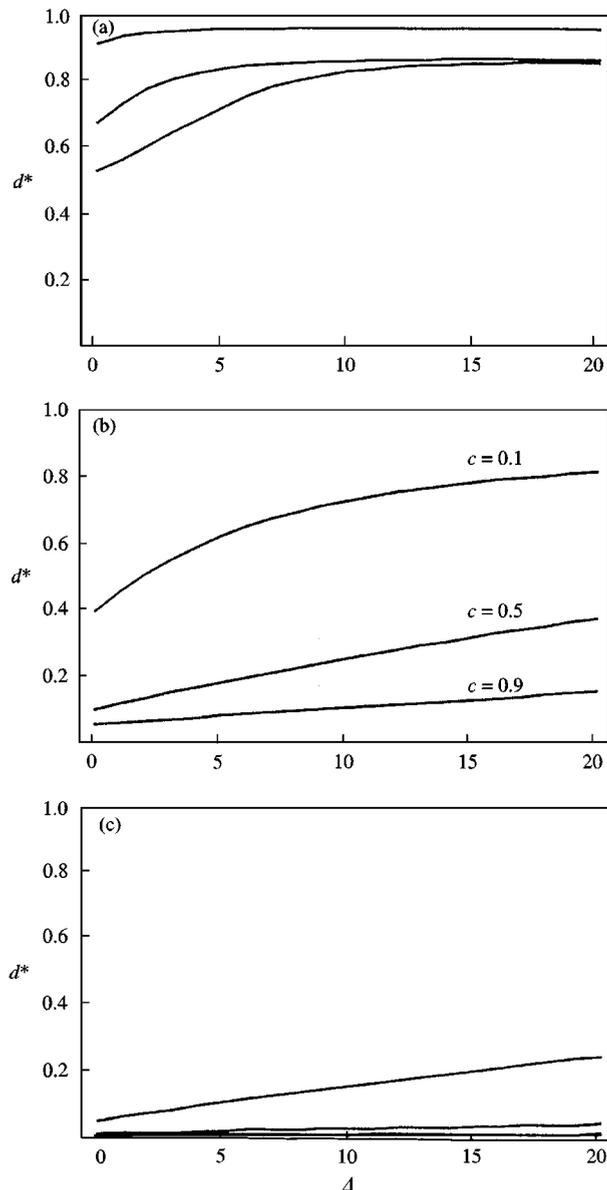


FIG. 8. Evolutionarily stable dispersal rate, d^* , versus the number of lethal equivalents, Δ , when both relatedness, R , and inbreeding depression, δ , are used as dynamical variables. In (a) $N = 1$, in (b) $N = 10$ and in (c) $N = 100$. For each panel three different values of the cost of dispersal are considered ($c = 0.1, 0.5$ and 0.9). Note d^* increases with higher cost of dispersal when $N = 1$ and when Δ is high (e.g. $\Delta > 10$).

equivalents. In particular, when the population sizes are very large the F value is always very low and, there is hardly no cost of inbreeding (i.e. δ is very low) even for large values of the number of lethal equivalents.

(2) *Population size*: higher population sizes decrease the ES dispersal rate (Fig. 8). This effect is

enhanced when δ is a dynamical variable since higher population size has mainly two effects. First, it decreases relatedness and, second, it decreases the cost of inbreeding depression, δ , since F decreases with higher population sizes.

(3) *Cost of dispersal*: higher cost of dispersal always selects against dispersal.

(4) *Control of dispersal*: again, because of higher relatedness, under maternal control the evolutionarily stable dispersal rate is higher than under offspring control.

Sex-specific dispersal rates

Similarly, four factors may affect the evolution of biased dispersal rates (Table 1):

(1) *Control of dispersal*: under maternal control relatedness is higher and, as a consequence, the unbiased dispersal rate tends to be more stable.

(2) *Cost of dispersal*: When the cost of inbreeding is coevolving with relatedness and dispersal the effect of the cost of dispersal on the stability of the unbiased strategy is much reduced. Indeed, higher cost of dispersal has several direct and indirect effects that balance each other because they act in different directions. First, there is a direct effect that stabilises the unbiased dispersal strategy. Second, higher cost of dispersal increases the probability of identity between individuals. This increases the level of relatedness which also stabilises the unbiased dispersal strategy. Third, higher probability of identity increases the cost of inbreeding. Since higher cost of inbreeding tends to select for biased dispersal strategy the last effect of higher cost of dispersal acts in opposite directions as the first two effects. This counteracts the stabilising effect of the cost of dispersal but, however, numerical results indicate that higher cost of dispersal always selects for unbiased dispersal strategies.

(3) *Population size*: As for the cost of dispersal, higher population size has two indirect effects that act in opposite directions. Larger populations decrease the probability of identity between individuals. This increases the level of relatedness and the cost of inbreeding. These two effects have opposite consequences on the stability of the unbiased dispersal rate. Numerical results show that these two forces balance each other. As a consequence, there is almost no effect of the

population size on the stability of the unbiased dispersal rate.

(4) *Genetic load*: higher Δ increases the cost of inbreeding and selects for biased dispersal rates. Under offspring control the threshold value of Δ beyond which there is selection for biased dispersal rate lies between 2 and 7 (depending on the cost of dispersal). Under maternal control the threshold of Δ lies between 4 and 10 (depending on the cost of dispersal). Again, note that these threshold values depend very weakly on the size of the populations.

Discussion

In this paper, I investigate the effects of kin competition and the cost of inbreeding on the evolution of dispersal. I relax some important assumptions of the previous models (population size, ploidy level) and, for heuristic reasons, I adopt a three-step approach that clarifies the effects of kin competition and the cost of inbreeding. In the first step, I derive the evolutionarily stable dispersal rate when relatedness and the cost of inbreeding are fixed parameters [Fig. 1(a)]. Second, I study the coevolution of dispersal with relatedness when the cost of inbreeding is a fixed parameter [Fig. 1(b)]. Finally, I study the coevolution between dispersal, relatedness and the cost of inbreeding [Fig. 1(c)]. For each step, two subcases are studied depending on the ability of the organisms to adopt sex-specific dispersal rates.

NO SEX-SPECIFIC DISPERSAL

Not surprisingly, in the absence of sex-specific dispersal rates, higher cost of inbreeding (higher Δ) and higher relatedness (lower N) always select for dispersal. Higher cost of dispersal generally selects against dispersal. However, for certain parameter values (high δ and high R), I found that the evolutionarily stable dispersal can increase with higher cost of dispersal. Since, in the present model, the cost of inbreeding and relatedness cannot be high simultaneously (R is a decreasing function of δ), this counterintuitive result vanishes when relatedness and the cost of inbreeding are dynamical variables.

Beyond these intuitive results, the model presented in this paper provides a useful analysis of

the interaction between the effects of kin selection and the cost of inbreeding. This analysis is clarified by the use of marginal gains in fitness from philopatry and dispersal.

SEX-SPECIFIC DISPERSAL

As already shown by Motro (1991, 1994), higher cost of inbreeding and lower cost of dispersal destabilize the unbiased dispersal rate and select for sex-biased dispersal strategies. The present work further shows that higher relatedness tends to prevent the evolution of sex-biased strategies. However, the last step of the above analysis (when both relatedness and the cost of inbreeding are dynamical variables) assumes that R and δ are linked variables (R is a decreasing function of δ). In this situation, the analysis of the stability of the unbiased dispersal rate requires numerical investigations. These investigations reveal that there exists a threshold value for the genetic load beyond which there is selection for sex-biased dispersal strategies. This threshold value increases with maternal control of dispersal and with higher cost of dispersal but hardly depends on the size of the population. It is worth pointing out that sex-biased dispersal rates can be selected for reasonable values of the genetic load. For example, under offspring control of dispersal with $N = 10$ and $c = 0.1$, the threshold value of the genetic load is $\Delta \sim 2.1$. This result indicates that inbreeding depression may be an important factor in the evolution of sex-biased dispersal rates. However, it is also important to point out that the absence of ES sex-specific dispersal rates does not imply that the cost of inbreeding is a minor factor in the evolution of dispersal. Indeed, in certain cases, the genetic load can be very high while the unbiased strategy is stable (e.g. $\Delta = 9$, $N = 10$, $c = 0.9$ and maternal control of dispersal).

In the present model, males and females play the same game. They both compete for space and mate and have the same cost of dispersal. Therefore, the evolution of biased dispersal rates always lead to two symmetrical strategies. The only factor that determines the direction of the sex bias is the initial condition (usually if $d_m > d_f$ at the beginning the bias will remain in the same direction). This could potentially explain the

systematic difference between mammals and birds in the direction of the sex bias (i.e. in mammals it is usually males which disperse more than females and this is the reverse in birds). If mammals and birds had ancestors with dispersal strategies biased in opposite direction these differences could remain through time and speciation events since initial conditions determine the evolutionary outcome [see the discussion in Perrin & Mazalov (1999) on the historical constraints on the evolutionary process]. However, other factors are known to lead to a systematic bias in dispersal toward one sex. For example, Taylor (1988) showed that haplodiploidy or differences in cost of dispersal could lead to such bias. Greenwood (1980) pointed out that the difference between mammals and birds could also be explained by different types of mating systems. The present study does not explore these effects and the importance of these alternative explanations remains to be investigated.

CONCLUDING REMARKS AND PERSPECTIVES

This work provides a general framework to study the evolution of sex-specific dispersal rates that could be easily modified to include more realistic assumptions and to address other questions.

Let me first discuss the assumptions concerning the cost of inbreeding. Following Motro (1991), I assumed that the cost of inbreeding was paid before reproduction. Indeed, the model assumes that inbred mating pairs (i.e. formed by two philopatric individuals) are less likely to reproduce than any other mating pair. This assumption differs from classical definition of inbreeding depression in which the cost of inbreeding is paid by the offspring. But relaxing this assumption implies that the mating pairs will have different fecundity. Finite population sizes will induce a variance in the proportion of inbred mating pairs per population and, as a consequence, the average number of offspring produced will vary from one population to another. This will induce a between-population variation in the probability of recruitment and affect both the expression of the direct fitness function and the derivation of relatedness in complicated ways. The analysis of such model remains to be done.

Another important perspective to the present work is to consider the genetic load, Δ , as a dynamical variable too. Indeed, the genetic load can decrease through the expression and the purge of deleterious recessive genes. Such expression depends on the occurrence of mating between relatives (i.e. biparental inbreeding) and, as a consequence, on various life history traits of the organism including selfing rate and dispersal rate. The coevolution between self-fertilization and inbreeding depression has attracted a lot of attention (for reviews see Holsinger, 1991; Waller, 1993; Waser, 1993b; Uyenoyama *et al.*, 1993; Ronfort & Couvet, 1995) but a similar analysis remains to be carried out for the evolution of dispersal.

In this paper, I assume that immigrants have a higher fitness than philopatric individuals. This might not always be true if one wants to consider the effects of outbreeding depression (Price & Waser, 1979; Shields, 1982; Waser, 1993a; Schierup & Christiansen, 1996) due to the coadaptation of genes within the individual on a particular habitat. Such complications would introduce an extra cost of dispersal that would depend on the distribution of the genetic variation in a spatially variable environment. Several other simplifying assumptions should be relaxed to test the robustness of the results of the present model. In particular, the potential effects of biased sex ratios and of multiple matings on the evolution of dispersal has not been explored yet. Finally, I assume throughout this paper that juvenile dispersal is the only mechanism to avoid inbreeding depression and kin competition. It might be interesting to study the evolution, and the coevolution with dispersal strategies, of other traits that allow to avoid inbreeding depression and kin competition (e.g. kin recognition, delayed maturation, biased sex ratio, etc.).

In a more general perspective, this work aims at clarifying the relation between inbreeding and social evolution. Michod (1993, p. 96) wrote: "There are two perspectives concerning the relationship of inbreeding to social behaviour. The first is the view that social structure creates conditions conducive to inbreeding. The emphasis is then on the concomitant costs of inbreeding depression ... and the evolution of mechanisms,

such as juvenile dispersal and kin recognition, by which these costs can be avoided. The second perspective concerns the implications of the population and relatedness structures created by inbreeding for the evolution of social behavior". Both perspectives are included in the present work and similar approaches could be used to study the effects of inbreeding and inbreeding depression on the evolution of other altruistic traits.

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APPENDIX

Calculation of Relatedness

The evolutionarily stable dispersal rate of the males depends on the coefficients of relatedness between males, R_{mm} , and between males and females, R_{mf} (similar coefficients are needed when we consider the evolution of female dispersal). These two coefficients can be expressed as a ratio between two other relatedness coefficients:

$$R_{mm} = \frac{\tau_{m2}}{\tau_{m1}},$$

$$R_{mf} = \frac{\tau_{f2}}{\tau_{m1}},$$

where each of these τ is a slope of the genotypic value transmitted by the recipient to the next generation on the genotypic value of the actor. In the present situation, only males can be actors but three different kinds of individuals can be recipients:

(1) *The recipient is the actor itself*: this yields

$$\begin{aligned} \tau_{m1} &= \frac{dx'_m[ij]}{dx_m[ij]} \\ &= \frac{Cov(x'_m[ij], x_m[ij])}{Var(x_m[ij])} \\ &= fc_1, \end{aligned}$$

where fc_1 is the probability of identity between the actor genotype and its transmitted genotypic value. The subscript, c , is for the control of the behaviour. $c = M$ if the mother controls dispersal and $c = O$ if the offspring controls its own behaviour.

(2) *The recipient is a randomly chosen male*:

$$\begin{aligned} \tau_{m2} &= \frac{dx'_m[j]}{dx_m[j]} \\ &= \frac{Cov(x'_m[j], x_m[j])}{Var(x_m[j])} \\ &= fc_2, \end{aligned}$$

where fc_2 is the probability of identity between the actor genotype and the transmitted genotypic value of its male recipient.

(3) *The recipient is a randomly chosen female*:

$$\begin{aligned} \tau_{f2} &= \frac{dx'_f[j]}{dx_m[j]} \\ &= \frac{Cov(x'_f[j], x_m[j])}{Var(x_m[j])} \\ &= fc_3, \end{aligned}$$

where fc_3 is the probability of identity between the actor genotype and the transmitted genotypic value of its female recipient.

Now, two subcases will be considered depending on the control of dispersal. If the mother controls the dispersal behaviour of its offspring:

- f_{M1} is the probability of identity between a son and its mother
- f_{M2} is the probability of identity between a mother and a randomly chosen male offspring.
- f_{M3} is the probability of identity between a mother and a randomly chosen female offspring.

If the male offspring controls its own dispersal behaviour:

- f_{O1} is the probability of identity between a son and its transmitted genotypic value (i.e. his own genotypic value).
- f_{O2} is the probability of identity between two randomly chosen male offspring.
- f_{O3} is the probability of identity between randomly chosen male and female offspring.

I limit my derivation to haploid and diploid cases, hence $f_{C2} = f_{C3}$. As a consequence, the two coefficients of relatedness reduces to a single one: $R_{mm} = R_{mf} = f_{C2}/f_{C1}$. Besides, note that the probability of identity between a mother and a randomly chosen offspring is equal to the probability of identity between two randomly chosen offspring, g . Therefore, $f_{M2} = f_{O2} = g$ which yields the following definition of relatedness:

$$R_M = \frac{g}{f_{M1}},$$

$$R_O = \frac{g}{f_{O1}},$$

where R_M and R_O are the relatedness coefficients under parent or offspring control of dispersal.

In the following, different cases will be considered depending on whether organisms are haploid or diploid and if it is the mother or the offspring that control the dispersal.

HAPLOID ORGANISMS

The probability of identity by descent, g , between two randomly chosen individuals in the same population can be derived from the following recurrence equation:

$$g' = \frac{1}{N} \left(\frac{1 + k_1 g}{2} \right) + \frac{N-1}{N} \left(k_1^2 g + 2k_1 k_2 \frac{g}{2} + k_2^2 \frac{g}{4} \right),$$

where the prime indicates the value of g in the next generation. X is the probability that two randomly chosen offspring have the same parents and is derived in appendix B.

$$k_1 = \frac{(1 - d_m)(1 - d_f)(1 - \delta)}{(1 - cd_m)(1 - cd_f) - \delta(1 - d_m)(1 - d_f)},$$

$$k_2 = \frac{(1 - d_m)(1 - c)d_f + (1 - d_f)(1 - c)d_m}{(1 - cd_m)(1 - cd_f) - \delta(1 - d_m)(1 - d_f)},$$

where k_1 is the probability that the parents of a given offspring are both philopatric, while k_2 is the probability that one, and only one, parent is philopatric.

The first term on the right-hand side of the recurrence equation of g is the probability of identity by descent between two offspring of the same mother. The second term is the probability of identity by descent between two offspring issued from different mothers.

At equilibrium it yields

$$\hat{g} = \frac{1}{2N - k_1 - ((N - 1)/2)(2k_1 + k_2)^2}$$

Under offspring control, $R_O = \hat{g}/f_{O1}$, where f_{O1} is the probability of identity between the actor and its transmitted genotypic value. If the actor is an offspring, the transmitted genotypic value is equal to the actor genotypic value hence $f_{O1} = 1$ and

$$R_O = \hat{g}. \tag{A.1}$$

Under parental control, $R_M = \hat{g}/f_{M1}$, where f_{M1} is the probability of identity between a mother and

its offspring which yields $f_{M1}(1 + k_1\hat{g})/2$ and

$$R_M = \frac{2\hat{g}}{1 + k_1\hat{g}}. \quad (\text{A.2})$$

DIPLOID ORGANISMS

Similarly, for diploid organisms

$$g' = \frac{1}{N} \left(\frac{1 + f + 2k_1g}{4} \right) + \frac{N-1}{N} \left(k_1^2g + 2k_1k_2\frac{g}{2} + k_2^2\frac{g}{4} \right),$$

$$f' = k_1g,$$

where f is the probability of identity by descent of two homologous genes in the same individual (i.e. coefficient of inbreeding).

At equilibrium this yields

$$\hat{g} = \frac{1}{4N - 3k_1 - (N-1)(2k_1 + k_2)^2},$$

$$\hat{f} = \frac{k_1}{4N - 3k_1 - (N-1)(2k_1 + k_2)^2}.$$

Offspring control yields

$$R_O = \frac{2\hat{g}}{1 + \hat{f}}. \quad (\text{A.3})$$

Maternal control yields

$$R_M = \frac{4\hat{g}}{1 + \hat{f} + 2k_1\hat{g}}. \quad (\text{A.4})$$

Quite surprisingly, haploid and diploid cases give the same solution for relatedness (i.e. $A1 = A3$ and $A2 = A4$). Therefore, only two different situations will be considered:

(1) Under offspring control;

$$R_O = \frac{1}{2N - k_1 - ((N-1)/2)(2k_1 + k_2)^2}. \quad (\text{A.5})$$

Under parental control,

$$R_M = \frac{2}{2N - ((N-1)/2)(2k_1 + k_2)^2}. \quad (\text{A.6})$$