Dispersal and Inbreeding Avoidance

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ABSTRACT: Using a game-theoretical approach, we investigate the dispersal patterns expected if inbreeding avoidance were the only reason for dispersal. The evolutionary outcome is always complete philopatry by one sex. The rate of dispersal by the other sex depends on patch size and mating system, as well as inbreeding and dispersal costs. If such costs are sex independent, then two stable equilibria coexist (male or female philopatry), with symmetric domains of attraction. Which sex disperses is determined entirely by history, genetic drift, and gene flow. An asymmetry in costs makes one domain of attraction extend at the expense of the other. In such a case, the dispersing sex might also be, paradoxically, the one that incurs the higher dispersal costs. As asymmetry increases, one equilibrium eventually disappears, which may result in a sudden evolutionary shift in the identity of the dispersing sex. Our results underline the necessity to control for phylogenetic relationships (e.g., through the use of independent-comparisons methods) when investigating empirical trends in dispersal. Our model also makes quantitative predictions on the rate of dispersal by the dispersing sex and suggests that inbreeding avoidance may only rarely be the sole reason for dispersal.

Keywords: sex-biased dispersal, mating systems, polygyny, evolutionarily stable strategy.

Dispersal—in particular, natal dispersal—is a frequent feature of animal life cycles. Since long-distance movements through unknown environments are bound to bear both mortality risks and energetic costs, the prevalence of dispersal must be maintained by some selective forces. Among the potential ultimate causes are the avoidance of kin competition (Hamilton and May 1977), metapopulation dynamics (extinction and colonization processes; Olivieri et al. 1995), and inbreeding avoidance (Bengtsson

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1978; Parker 1979, 1983; Waser et al. 1986). The latter possibility is supported by the frequency of sex biases in dispersal patterns: members of one sex usually disperse more frequently and/or further than those of the opposite sex, with the obvious consequence that coancestry among potential mates is reduced.

Which sex disperses more, however, varies among taxonomic groups. It has long been noticed that dispersal tends to be female biased in birds, while it is usually male biased in mammals (Greenwood and Harvey 1982). The reason for this difference may lie in their contrasting breeding systems, as suggested by Greenwood's (1980, 1983) resource-competition hypothesis. In the monogamous system that characterizes many bird species, the male takes a significant responsibility in acquiring and defending the territory and in feeding the young and therefore benefits more from philopatry through his acquaintance with local resources. By contrast, in the polygynous systems observed in many mammals, males take no or little part in parental investment. Females have more to gain from territory acquisition and defense, and the female sex, therefore, is the one that benefits more from philopatry.

Greenwood's hypothesis, however, rests on verbal arguments and has not been formalized yet to allow quantitative predictions. Formalization is often desirable not only because it permits a check of the arguments' logical consistency but also because unexpected side consequences of assumptions may be revealed. Breeding systems, for instance, may affect dispersal patterns, not only through the above-mentioned asymmetries in the benefits of philopatry but also through direct effects on coancestry. Indeed, polygyny is expected to increase coancestry within patches and thereby enhance the risk of inbreeding depression. How should both effects combine to influence sex-specific dispersal patterns? Here we propose a mathematical model to quantify this and thereby delineate the expected consequences of mating systems (polygyny level) on dispersal patterns.

Assumptions and Outline of the Model

We consider an island-population model with an infinite number of demes, each comprising n breeding sites (n

corresponds to both the number of breeding opportunities and the number of breeding females and will be referred to hereafter as patch size). Dispersal occurs before reproduction, at a rate m_M in males and m_F in females; is random with respect to which patch is reached; and incurs a cost, expressed as a survival value $s < 1$. After dispersal, members of the territorial sex x compete for breeding opportunities, with immigrants suffering from some penalty: the parameter $a_x \leq 1$ allows us to express the possibly lower competitive value of an immigrant relative to that of a local individual. Greenwood's hypothesis can thus be thought of as an increase in dispersal costs for the territorial sex.

Partners then mate at random within their patch, which results in some fecundity depression if mating turns out to occur among relatives. The system of mating is expressed through a polygyny parameter, Φ, measuring the probability that two females within one patch mate with the same male. Thus, $\Phi = 0$ in the case of strict monogamy and tends to 1 for complete polygyny (all females within a patch being mated to one single male).

Coancestry among patch mates, θ, is defined as the probability that two genes, randomly sampled from two individuals within a deme, are identical by descent. We first express it here below as a function of patch size, n, polygyny level, Φ, and dispersal patterns (m_M, m_F). We then calculate the optimal dispersal probability for each sex under different polygyny levels, taking into account both the effect of polygyny on coancestry and its possible link with asymmetries in the benefits of philopatry (the resource-competition hypothesis).

Our assumptions are obviously simplified. In many species of birds and mammals, there is sexual asymmetry in dispersal distance, but often both sexes disperse at least one territory from their natal territory, while our formalization considers only rates of dispersal, not distances. The main reason is analytical tractability: in a stepping-stone or isolation-by-distance model, dispersal distances would interact with coancestry in a complex manner. However, the point must also be made that the difference between rate and distance is partly a question of scale and convenience: field studies often consider as philopatric any individual dispersing only one home range (e.g., Favre et al. 1997), or even up to 10 home ranges (e.g., Shields 1983). Furthermore, as argued in "Discussion," the main predictions from the present model are unlikely to be challenged qualitatively by introducing isolation by distance.

Coancestry and Inbreeding

The recurrence equations to calculate the dynamics of coancestry within patches are provided in appendix A. The equilibrium value is given by

$$\hat{\theta} = \frac{1 + (n-1)\Phi/2}{4n - 3k_F k_M - (n-1)\Phi k_F(k_F + 5k_M/2) - (n-1)(1-\Phi)(k_F + k_M)^2},$$

(1)

where $k_M = (1 - m_M)/(1 - m_M + sa_M m_M)$ represents the probability that a breeding male is philopatric and $k_F = (1 - m_F)/(1 - m_F + sa_F m_F)$ is the equivalent probability for a female. From equation (1), coancestry decreases monotonically as patch size, n, increases, but the effect is important only for $n < 10$ (fig. 1). This figure furthermore shows the drastic effect of polygyny on coancestry. Finally, coancestry also increases as philopatry increases, though not linearly, as shown by figure 2: a small change in dispersal has a larger effect on $\hat{\theta}$ at low dispersal value.

This parameter, $\hat{\theta}$, actually measures coancestry among offspring born within a patch, that is, after reproduction but before dispersal, when individuals have to take their dispersal decision. The coancestry value after dispersal is obtained by multiplying this value by $k_M k_F$. Note that the resulting product also measures the inbreeding coefficient of offspring from the next generation:

$$F = k_M k_F \hat{\theta}.$$

(2)

This equation reduces to Wright's migration-drift equilibrium (e.g., Hartl and Clark 1989, eq. [6.23]) in the case
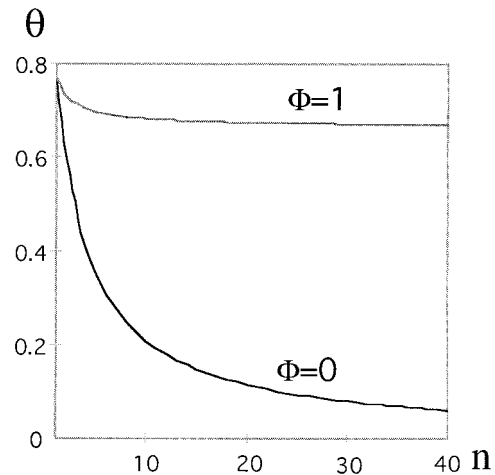

Figure 1: Coancestry $\hat{\theta}$ within patches decreases first rapidly as patch size n increases, then levels off. For any patch size, coancestry value is higher in polygynous systems ($\Phi = 1$) than in monogamous ones ($\Phi = 0$). In the example illustrated, $k_M = k_F = 0.95$.
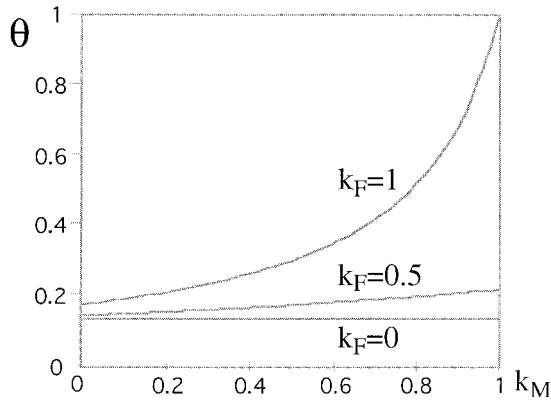
Figure 2: Coancestry increases with philopatry, but not linearly so: changes are more rapid at low dispersal values. In this example, $\Phi = 1$ and $n = 10$.

of monogamy ($\Phi = 0$, $N = 2n$) with equal dispersal ($\bar{m}_M = \bar{m}_F = \bar{m}$) at no cost ($s = a_M = a_F = 1$):

$$F = \frac{\bar{m}^2}{2N - (2N - 1)\bar{m}^2},$$

where overbars signal the complement to unity.

Equilibrium Dispersal Rates

As made explicit in equation (2), inbreeding risk increases with coancestry $\hat{\theta}$, and the best way to reduce F for a given $\hat{\theta}$ is to reduce philopatry. But dispersal also incurs costs, so that complete dispersal may not be the best strategy. What is the optimal trade-off? Since the benefits an individual gains from dispersal depends on what others are doing, an evolutionarily stable strategy (ESS) approach is required. A necessary condition for a stable equilibrium is that no mutant strategy can invade it. A mutation arising in a population fixed for the equilibrium strategy can persist only if it codes for the same dispersal probability as the established type. Technically, we first find the condition for a mutation μ_F in a $\{m_M, m_F\}$ population to maximize fitness, then we set $\mu_F = m_F$. The procedure for males is identical.

Fitness of Mutants

A female bearing the mutation will leave her natal patch with probability μ_F and stay in it with probability $\bar{\mu}_F =$

$1 - \mu_F$. If she leaves, she will reach another patch with probability s ($s < 1$ expresses a cost to dispersal) and will compete there for n breeding opportunities among $nb(1 - m_F + sm_F)$ other females (where b is the average number of daughters per female). Being an immigrant, she will suffer like all other immigrant females from a penalty ($a_F \le 1$) in this competition. Finally, winning a reproductive opportunity will translate into an amount of fecundity, b_θ, itself a negative function of coancestry θ among mates (this function expresses a cost of inbreeding). Under our infinite-island-model assumptions, coancestry among patches is 0, and so is the inbreeding coefficient of offspring whose parents stem from different patches. Thus, the fecundity of a disperser that succeeds in reproducing takes the maximal feasible value, b_0. The fitness of a dispersing female can therefore be written $(sna_F b_0)/[nb(1 - m_F + sa_F m_F)]$.

If, however, this female mutant stays home, she will benefit from the resident advantage when competing for breeding sites and, in case of success, will produce either b_0 daughters if her partner turns out to be an immigrant or b_θ if her partner is also of local origin. Thus, the total fitness of a mutant female is

$$W_{\mu F} = \mu_F \frac{sna_F b_0}{nb(1 - m_F + sa_F m_F)}$$
$$+ \bar{\mu}_F \frac{n(b_\theta k_M + b_0 \bar{k}_M)}{nb(1 - m_F + sa_F m_F)}. \quad (3a)$$

Similarly, the fitness of a mutant male in a $\{m_M, m_F\}$ population is given by

$$W_{\mu M} = \mu_M \frac{sna_M b_0}{nb(1 - m_M + sa_M m_M)}$$
$$+ \bar{\mu}_M \frac{n(b_\theta k_F + b_0 \bar{k}_F)}{nb(1 - m_M + sa_M m_M)}, \quad (3b)$$

where $a_M \le 1$ allows us to express the possible disadvantage of immigrant males in the competition over breeding opportunities.

One-Player ESSs

As evident from equations (3a) and (3b), female fitness depends on male behavior, and vice versa. Since b_0 exceeds b_θ, an increase in female dispersal increases the term, weighting $\bar{\mu}_M$ in the right-hand side of equation (3b) and thereby constitutes an incentive for males to stay home.

Formally, the selective pressure on male dispersal probability is given by

$$\frac{dW}{d\mu_M} = \frac{sa_M b_0 - \{b_\theta k_F + b_0 \bar{k}_F\}}{b(1 - m_M + sa_M m_M)}.$$ (4)

As long as this term is positive, a mutant that disperses with a higher probability than the common type is selected for. This also means that any randomly chosen male within such a population gets a higher fitness by dispersing. When the term becomes negative, a mutant dispersing with a lower probability is selected for, which also means that any given male is better off staying home. The selective pressure vanishes with the derivative. At this equilibrium, a male's fitness is not affected by whether or not he disperses, a characteristic of Ideal Free Distributions (e.g., Fretwell and Lucas 1970; Doncaster et al. 1997). The condition for an inner ESS in male dispersal ($dW/d\mu_M = 0$) is then

$$c_M = ik_F,$$ (5a)

where $c_M = 1 - sa_M$ is the cost of female dispersal, and $i = 1 - (b_\theta/b_0)$ is the cost of inbreeding. This receives the intuitive interpretation that, at balanced equilibrium, dispersal costs match the net costs of inbreeding depression (i.e., fitness cost per inbred mating times the probability of such a mating). Symmetrically, the condition for an inner ESS in female dispersal ($dW/d\mu_F = 0$) is

$$c_F = ik_M,$$ (5b)

where $c_F = 1 - sa_F$ is the cost of female dispersal.

Equations (5a) and (5b) can be used to investigate the conditions for inner evolutionarily stable (ES) sex-specific dispersal. A first observation is that in the absence of any costs to dispersal ($c_M = c_F = 0$), the terms in the right-hand side of equations (5a) and (5b) must also vanish, which implies complete dispersal (see a similar conclusion from Frank 1986 and Taylor 1988, obtained from a competition-avoidance argument).

If there are costs to dispersal ($c_x > 0$), then the right-hand side of equations (5a) and (5b) must also be positive. This implies some fecundity depression for matings among patch mates, so that coancestry within patches must exceed that among patches. Dispersal is not random, and some philopatry occurs. The question is, What are the equilibrium coancestry and philopatry values? The exact value obviously depends on the amount of inbreeding depression; that is, on the way b_θ varies with θ. For the purpose of illustration, let's assume a simple linear relation:

$$i = \gamma\theta.$$ (6)

Empirical data suggest that fecundity of full-sib matings is reduced by one-quarter to one-half (Bengtsson 1978; Keller 1998), which would imply a γ value between 1 and 2. Using equation (6) in equation (1), and then in (5a), allows us to calculate the male equilibrium dispersal as a response to a given female dispersal:

$$4n - 3k_M^* k_F - (n - 1)\Phi k_F\left(\frac{5k_M^*}{2} + k_F\right)$$
$$- (n - 1)(1 - \Phi)(k_M^* + k_F)^2$$ (7a)
$$= \frac{k_F\gamma[1 + (n - 1)\Phi/2]}{c_M}.$$

This is illustrated in figure 3*A*, with k_M^* as a function of k_F. As expected, the relationship is negative, which may receive the following intuitive interpretation: if for some reason female dispersal increases, the right-hand side of (5a) decreases, so that the equality does not hold true any more. From equation (4), this induces a selective pressure for diminished male dispersal. As males progressively disperse less, coancestry within patches increases, so that i increases. The new equilibrium is reached when ik_F again matches male dispersal costs.

A similar approach can be made for females, which leads to the following condition for female equilibrium dispersal:

$$4n - 3k_F^* k_M - (n - 1)\Phi k_F^*\left(\frac{5k_M}{2} + k_F^*\right)$$
$$- (n - 1)(1 - \Phi)(k_M + k_F^*)^2$$ (7b)
$$= \frac{k_M\gamma[1 + (n - 1)\Phi/2]}{c_F}$$

and allows us to draw the optimal female response to any given male-dispersal value (fig. 3*B*).

Two-Players ESS

It would seem intuitive to consider the meeting of conditions (7a) and (7b) (i.e., the crossing of these two curves in fig. 3*C*) as the global equilibrium (e.g., Maynard-Smith 1977; Grafen and Sibly 1978). This joint condition is given by
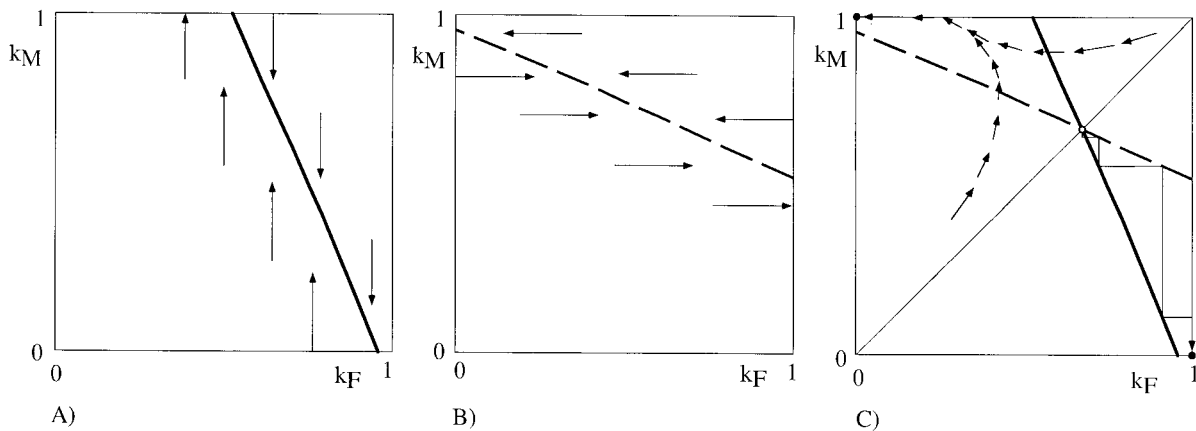
Figure 3: *A*, Male optimal philopatry decreases as female philopatry increases. On the right of the optimal response curve, male dispersal is selected for (*down arrows*), while on the left, philopatry is selected for (*up arrows*). In the example illustrated, $n = 10$, $\Phi = 0$, $c_M = c_F = 0.05$, and $\gamma = 1$. *B*, Female optimal philopatry decreases as male philopatry increases. Same parameter values as in *A*. *C*, The two best-response curves cross on the diagonal because dispersal costs are symmetrical ($c_M = c_F$). This equilibrium (*open circle*) is, however, unstable. Any slight perturbation will make the system run away toward a border equilibrium (*solid circles*), either to the right (complete female philopatry) or to the top (complete male philopatry). With the parameter values used, both equilibrium solutions are corner; that is, they involve complete philopatry by one sex and complete dispersal by the other. Further explanations in "Equilibrium Dispersal Rates."

$$k_M c_M = k_F c_F. \tag{8}$$

If the costs of dispersal are the same for both sexes ($c_M = c_F$), then the two curves (7a) and (7b) cross on the diagonal, which would result in the same equilibrium dispersal for both sexes. In case of asymmetry in dispersal costs ($c_M \neq c_F$), then the curves cross outside of the diagonal, which would result in one sex dispersing more than the other. Since these c_x can take a priori any value, it would seem that any combination of m_M and m_F is a possible candidate for an ESS.

This, however, is not the case, and it turns out that all inner equilibria are unstable. This claim may seem paradoxical, since we just showed the two curves to represent two single-sex ESSs. The point lies in the fact that, while the intersection point indeed meets the δ-stability condition (sensu Taylor 1989), which renders it immune against point mutations, it does not meet the *m*-stability condition (Taylor 1989), which would allow a population near the equilibrium to converge on it (Motro 1994; Eshel et al. 1997). Intersection points are therefore not continuously stable (or convergence stable; Christiansen 1991). A departure by one sex from such an equilibrium would indeed be counterselected, but only at the condition that dispersal by the other sex stays constant. Whereas, in fact, a departure by one sex will induce a still higher selective pressure for the other sex to diverge in the opposite di-

rection, with the result that the whole system will move away toward a different border equilibrium.

This can be understood as follows: assume an inner equilibrium such that both conditions (5a) and (5b) are met and suppose a perturbation (genetic drift, gene flow) such that male dispersal increases slightly in the population. This will have the consequence of decreasing both k_M and i in the right-hand side of (5b). In order to restore the equality, females will have to increase i (through increased k_F) at a value higher than the original one (in order to compensate also for the smaller k_M). As a consequence, the right-hand side of (5a) will exceed the left-hand side, which will now select for a higher dispersal rate in males. Thus, any slight initial disturbance will lead to an overreaction from the opposite sex and progressively induce a runaway process out of the original equilibrium.

Graphically, this process arises from the way the two curves in figure 3*C* cross in the $k_M - k_F$ space. The optimal-response curve of males crosses that of females from above. We show analytically in appendix B that this occurs for any positive γ value. It implies that the response induced in sex x by an initial change in sex y indeed exceeds the initial change. The broken arrow leading to the bottom right corner in figure 3*C* shows the trajectory of the game if sexes were allowed to play in turn. A slight initial decrease in male philopatry will induce a larger increase in female philopatry, which will in turn select for a further decrease in male philopatry, and so on, until a border

equilibrium is reached. The upper left portion of the graph displays more realistic trajectories, in which sexes are allowed to play simultaneously.

It turns out, therefore, that the only continuously stable strategies (CSS) are border. Two of them are possible: one at the top border (all males philopatric, and female dispersal between 0 and 1) and one at the right border (all females philopatric, and male dispersal comprised between 0 and 1). The top border solution is characterized by conditions

$$\begin{cases} c_F = i \\ c_M \geq ik_F \end{cases}$$

while at the right border solution, the following holds:

$$\begin{cases} c_M = i \\ c_F \geq ik_M \end{cases}$$

Thus, for the dispersing sex, the costs of dispersing exactly match inbreeding costs, while for the philopatric sex, the costs of dispersal exceed inbreeding costs.

In the symmetric game ($c_M = c_F$), these two equilibria have symmetric domains of attraction. Which one is eventually reached depends on initial conditions, random genetic drift, and gene inflow from other patches. The arrival of highly dispersing males from neighboring demes may shift a population into the domain of attraction of male-biased dispersal, but once a whole metapopulation is fixed for dispersal by a given sex, it is unlikely to change unless a strong asymmetry in dispersal costs evolves (see next paragraph). This leaves an important role for phylogenetic inertia in deciding which sex disperses.

The effect of asymmetry in dispersal costs is to make the curves cross closer to the border (fig. 4*A*), which introduces an asymmetry in the two domains of attraction. The one corresponding to dispersal from the sex with lowest costs is enhanced at the expense of the other. If asymmetry is large enough, then this last equilibrium may totally disappear (the curves do not cross any more), and only one solution remains. This opens the possibility for a sudden evolutionary shift in sex-specific dispersal patterns.

Monogamy versus Polygamy

What are now the effects of mating systems? Figure 4*B* shows optimal-dispersal curves for both sexes in the case of complete polygyny ($\Phi = 1$). As the comparison with figure 4*A* makes clear, the main direct effect of polygyny
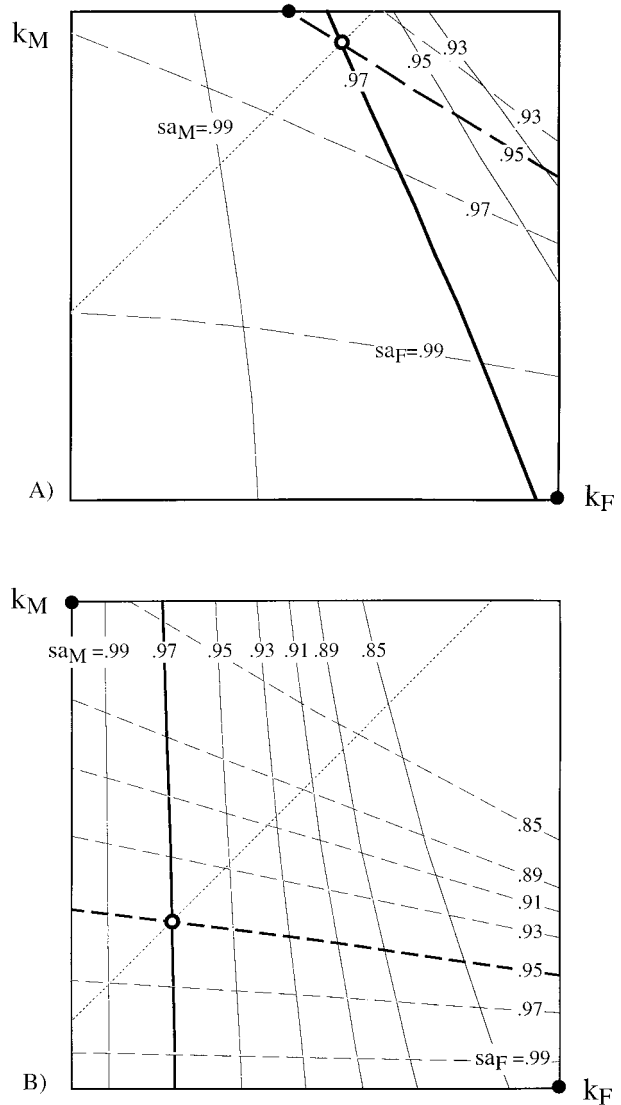

Figure 4: *A*, Male (*solid lines*) and female (*dashed lines*) best-response curves for different values of dispersal costs in a monogamous system ($\Phi = 0$). When costs differ among sexes, the lines cross outside of the diagonal. The bold lines illustrate a case with lower dispersal costs for males than for females ($c_M < c_F$). One equilibrium (*bottom right*) involves complete male dispersal (and complete female philopatry), while the other (*upper border*) involves only partial female dispersal (and complete male philopatry). As the curves cross closer to the top than to the right border equilibrium, the latter has a larger domain of attraction and has thereby a larger probability to be realized. The thin, punctuated straight line separates these two domains. *B*, Same figure in the case of complete polygyny ($\Phi = 1$). The curves are steeper and, for the same dispersal costs, closer to the left bottom corner. As a result, the domains of attraction show less asymmetry, and dispersal is typically higher for the dispersing sex. In this case, for instance, the top border solution would involve complete female dispersal, even though their dispersal costs are identical to *A*. Further comments in "Monogamy versus Polygamy."

is, for a given cost, to shift isoclines toward the bottom-left corner in such a way that the dispersing sex disperses more. This arises because polygyny increases coancestry and, thereby, the risk of inbreeding (eq. [1]). However, polygyny per se does not affect the probability that one sex in particular will disperse.

It should also be noted that the slopes are steeper (app. B), which means that individuals are more sensitive to the other sex's strategy. As for asymmetry, the same result arises as under monogamy, that is, a change in the domains of attraction of the two equilibria. But because the slopes are steeper, a double equilibrium coexists for a larger range of asymmetries.

Now the question arises of a possible link between breeding systems and asymmetry. This is the sense of Greenwood's resource competition hypothesis: in avian monogamous systems, males take the responsibility for acquiring the pair's territory, which is easier if they remain philopatric ($a_M < 1$). Since dispersal has no consequence on female mating opportunities ($a_F = 1$), we get $a_M < a_F$ so that the curves cross closer to the right border, increasing the domain of attraction of the top border equilibrium and, thereby, the probability that males will be the philopatric sex. Reciprocally, in systems where females are responsible for territory acquisition (many mammalian species), $a_M > a_F$, which increases the probability that females will be the philopatric sex. This result corroborates Greenwood's verbal argument, but with two important differences. First, the bias predicted is not in the proportion of dispersal by one sex but in the probability that one sex, rather than the other, will be the dispersing one. Thus, the bias is formally expressed in probabilistic terms. Second, our analysis shows a very important role for phylogenetic constraints: once an ancestral form has shifted toward a male-biased dispersal, its daughter species might be locked in this strategy, even if male dispersal costs exceed female dispersal costs. This point urges for the use of phylogenetic analyses and independent-comparison methods (e.g., Harvey and Pagel 1991) when testing empirical patterns.

Resource competition is not the only possible reason for a link between mating systems and sex bias in dispersal. Other asymmetries may arise. While in monogamous systems both sexes are normally choosy, in polygynous systems only the female usually is (because paternal investment is negligible). If inbreeding cost is low, and mating with a relative does not forfeit other mating opportunities for males, then all individuals should prefer relative mates over nonrelatives (Parker 1979, 1983; Waser et al. 1986). This induces a selection for both male and female philopatry. If, however, inbreeding costs are important and/or mating with a relative forfeits other mating opportunities, then females should prefer immigrant males over

locally born. This may confer significant advantages to dispersing males, boosting a_M to values exceeding 1. As a result, a_M will exceed a_F, and this inequality will increase the probability that males will be the dispersing sex. The important point here is that a strong male-biased dispersal in polygynous species does not need to stem from a resource competition situation but may also result, for example, from the sex asymmetry in choosiness that characterizes polygynous systems.

Discussion

As pointed out in the introduction, the modeling of optimal dispersal patterns has been conducted along three main lines. In the first one (metapopulation dynamics), the selective pressure for dispersal stems from the risk of local extinction combined with the regular arising of new empty patches (e.g., Cohen and Levin 1991; Olivieri et al. 1995; Holt and McPeek 1996). In such models, coancestry, sex, and mating systems are largely irrelevant.

In the second line, the avoidance of competition among relatives is the reason for dispersing (Hamilton and May 1977; Motro 1982*a*, 1982*b*, 1983; Frank 1986; Taylor 1988), so that coancestry plays here a central role. In Frank's (1986) and Taylor's (1988) models, for instance, the optimal dispersal fraction is $(r - c)/(r - c^2)$, where r is relatedness within patches and c is the cost of dispersal. Dispersal should thus be complete (for both sexes) in absence of costs and decrease as costs increase. But relatedness does not matter here because of inbreeding risk but instead because of potential competition among relatives. By moving, an individual improves settling opportunities for relatives, and thereby its inclusive fitness.

The third line explicitly addresses inbreeding as a potential cause. Bengtsson (1978) assumes a population with complete philopatry by females and complete dispersal by males and searches conditions for a mutant philopatric male to succeed. The main result is that the decrease in dispersal costs induced by philopatry must largely exceed the increase in inbreeding in order for philopatry to be favored. For instance, a male will be selected to stay and mate with his sister only if $c > 3i/2$, where $c = 1 - s$ is dispersal cost and i is inbreeding cost. The coefficient (3/2) weighting i comes from the fact that half of the male's genes are shared by his sister. In the case of strong inbreeding depression, he loses not only his genes but also his sister's. This inclusive fitness argument also suggests a strong selection against inbreeding and in favor of dispersal.

An implicit assumption in Bengtsson's model is that by mating with a sister, the male looses a chance of mating

with a nonrelative. Parker (1979, 1983) and Waser et al. (1986) propose that while this assumption is certainly correct in monogamous systems, it does not need to be so in most polygynous systems. Because paternal investment is negligible, a male accepting an incest does not forfeit other mating opportunities. This greatly enlarges the scope for inbreeding tolerance, since polygynous males would then be expected to tolerate inbreeding even in the absence of dispersal costs. Waser et al. (1986) also make the argument that, since the threshold for inbreeding rejection is lower in females (because for them an incestuous mating does forfeit other mating opportunities), they should be the dispersing sex in polygynous species. The fact that this prediction opposes empirical evidence is taken as an argument against the role of inbreeding avoidance in molding dispersal patterns (it should be noted, however, that our suggestion above opposes this argument; in polygynous systems, a female preference for immigrant males should induce important incentives for males to disperse).

The models by Bengtsson (1978), Parker (1979, 1983), and Waser et al. (1986) search the initial condition for a philopatric mutant to spread in an originally outbred population, but do not derive the ESS. As we have shown, however, the equilibrium value for any one sex strongly depends on what the other sex is doing. In this sense, the work by Motro (1991, 1994) is more relevant to our present study. Considering first that sexes often differ in dispersal patterns, this author asks whether such differences are to be expected even if both sexes are completely symmetrical with respect to their costs of dispersal.

His approach differs from ours in that it simultaneously includes both competition with relatives and inbreeding risk as potential causes for dispersal, uses an explicit genetic model for an haploid population, and assumes a single breeding pair per patch.

If both sexes are constrained to have the same dispersal, then a single equilibrium dispersal value exists that, unsurprisingly, increases with inbreeding costs and decreases as dispersal costs increase. If sexes are allowed to differ in their optimal strategy, then, as in our case, the male's best response is a negative function of female dispersal, and vice versa. When inbreeding costs are low, the only ESS is a balanced one and is continuously stable (Motro 1994). When inbreeding costs are high, the balanced ESS is no longer a CSS, and two boundaries CSSs are found. When dispersal bears high costs, these CSSs are characterized by the absolute sedentariness of one sex, and a positive dispersal strategy for the other. And when dispersal bears little costs, these additional CSSs involve complete dispersal by one sex and partial dispersal by the other.

From our analysis, by contrast, the inner solutions are always excluded because they turn out to be unstable. Furthermore, the bottom and left border do not appear within the range of possible solutions. This difference from Motro's model arises from the kin-competition features he introduced in his model, while we consider the effects of inbreeding avoidance only. Our analysis therefore shows that, if inbreeding avoidance were the only reason for dispersal, then the range of possible solutions would actually be restricted to the top and right border, implying complete philopatry by one sex and some dispersal by the other. A corollary is that inbreeding by itself is insufficient to account for situations where both sexes disperse (even at quite different rates). When such situations arise in the field (which is actually common), then inbreeding avoidance cannot be the only selective pressure. As a matter of fact, we want to reiterate that our present model consciously avoids incorporating other forces such as kin competition or kin selection that likely coexist with inbreeding in the real world and are bound to substantially affect dispersal patterns. This will be achieved in another article (Perrin and Mazalov 2000).

A second main result is the important role played by historical and phylogenetic components. Which sex disperses in a given population is likely to be influenced by initial conditions, genetic drift, and gene flow from neighboring populations. And once a whole metapopulation (species) is locked into one equilibrium, this strongly constrains the evolution of daughter species. A species in which males suffer from higher dispersal costs may nevertheless present a male-biased dispersal, simply because the particular form of the adaptive landscape evidenced here prevents it from reaching the higher adaptive peak (female dispersal). As a result, related species are likely to display related dispersal patterns, not because of similar mating patterns, but only because they inherited it from a common ancestor. As pointed out above, this nonindependence of data urges for the use of independent-comparison methods accounting for phylogenetic structures when investigating empirical patterns (e.g., Harvey and Pagel 1991). In particular, the often-cited dichotomy between birds and mammals should be played down.

Third, our analysis suggests that mating systems have no effect per se on which sex disperses but only insofar as they correlate with asymmetries in costs. These asymmetries may stem from differential competition for resources (Greenwood's hypothesis) as well as for mates (sex differences in choosiness in polygynous systems). If asymmetries are large enough, then one of the two border CSSs may disappear (and with it, phylogenetic inertia).

Finally, our approach provides a few quantitative predictions. The one most open to empirical check is that dispersal costs must exactly match inbreeding costs in the dispersing sex but exceed them in the philopatric sex. This prediction is likely to be robust with respect to our assumption of an infinite-island model and zero coancestry

between patches. In a stepping-stone or isolation-by-distance model, coancestry (and therefore the risk of inbreeding depression) would progressively decrease with distance. Our expectation in this case is that dispersing individuals would stop moving as soon as the marginal costs of dispersal meet its marginal gains in terms of decreased inbreeding. Significant discrepancies from this prediction would constitute an argument against the role of inbreeding avoidance as an important cause for dispersal.

APPENDIX A

Recurrence Equations to Calculate the Evolution of Coancestry among Randomly Chosen Offspring

From our model's assumptions, every single female mates with only one male, and two randomly chosen females within a patch choose the same male with probability Φ. Thus, three outcomes are possible with respect to the coancestry between two randomly chosen offspring (tables A1–A3).

Table A1: With probability $1/n$, these offspring share the same mother (and therefore are full-sibs since they also share the same father), which results in the following transition values for θ

Origin of parents	Probability	θ_{t+1}
Both parents local	$k_M k_F$	$(1/4)\{2[(1 + F_t)/2] + 2\theta_t\}$
Only mother local	$\bar{k}_M k_F$	$(1/4)\{2[(1 + F_t)/2]\}$
Only father local	$k_M \bar{k}_F$	$(1/4)\{2[(1 + F_t)/2]\}$
Both parents immigrants	$\bar{k}_M \bar{k}_F$	$(1/4)\{2[(1 + F_t)/2]\}$

Note: F_t is the inbreeding coefficient of the parental generation.

Table A2: With probability $[(n - 1)/n]\Phi$, they share the same father but not the same mother, which results in the following transition values for θ

Origin of parents	Probability	θ_{t+1}
All parents local	$k_M k_F^2$	$(1/4)\{[(1 + F_t)/2] + 3\theta_t\}$
One mother immigrant	$2k_M k_F \bar{k}_F$	$(1/4)\{[(1 + F_t)/2] + \theta_t\}$
Two mothers immigrant	$k_M \bar{k}_F^2$	$(1/4)[(1 + F_t)/2]$
Father immigrant	$\bar{k}_M k_F^2$	$(1/4)\{[(1 + F_t)/2] + \theta_t\}$
One mother local	$2\bar{k}_M k_F \bar{k}_F$	$(1/4)[(1 + F_t)/2]$
All parents immigrant	$\bar{k}_M \bar{k}_F^2$	$(1/4)[(1 + F_t)/2]$

Table A3: With probability $[(n-1)/n](1-\Phi)$, these offspring share no parents, which will translate into the following transitions

Origin of parents	Probability	θ_{t+1}
All parents local	$k_M^2 k_F^2$	$(1/4)(4\theta_t)$
One mother immigrant	$2k_M^2 k_F \bar{k}_F$	$(1/4)(2\theta_t)$
One father immigrant	$2k_F^2 k_M \bar{k}_M$	$(1/4)(2\theta_t)$
Both mothers immigrant	$k_M^2 \bar{k}_F^2$	$(1/4)(\theta_t)$
Both fathers immigrant	$\bar{k}_M^2 k_F^2$	$(1/4)(\theta_t)$
One mother and one father local	$4\bar{k}_M k_M k_F \bar{k}_F$	$(1/8)(\theta_t)$
One father local	$2k_F^2 k_M \bar{k}_M$	0
One mother local	$2\bar{k}_M^2 k_F \bar{k}_F$	0
All immigrants	$\bar{k}_M^2 \bar{k}_F^2$	0

From this set of relations, the transition equation for the whole population can be written down by weighting the specific transitions (right columns) by their corresponding probabilities. The equilibrium value is found by substituting $F_t = k_F k_M \theta_t$ and then setting $\theta_{t+1} = \theta_t = \hat{\theta}$. After a few rearrangements and simplifications, we get

$$\hat{\theta} = \frac{1 + (n-1)\Phi/2}{4n - 3k_F k_M - (n-1)\Phi k_F(k_F + 5k_M/2) - (n-1)(1-\Phi)(k_M k_F)^2}.$$

APPENDIX B

Proof that k_M^* Crosses k_F^* from Above

Differentiating both sides of (7a) gives

$$\frac{dk_M^*}{dk_F} = -\frac{3k_M^* + (n-1)\Phi[(5/2)k_M^* + k_F] + (n-1)\Phi k_F + 2(n-1)(1-\Phi)(k_M^* + k_F) + \gamma\frac{1+(n-1)\Phi/2}{c_M}}{3k_F + (5/2)(n-1)\Phi k_F + 2(n-1)(1-\Phi)(k_M^* + k_F)}, \qquad \text{(B1)}$$

while doing the same for (7b) provides

$$\frac{dk_M}{dk_F^*} = -\frac{3k_M + (n-1)\Phi[(5/2)k_M + k_F^*] + (n-1)\Phi k_F^* + 2(n-1)(1-\Phi)(k_M + k_F^*)}{3k_F^* + (5/2)(n-1)\Phi k_F^* + 2(n-1)(1-\Phi)(k_M + k_F^*) + \gamma\frac{1+(n-1)\Phi/2}{c_F}}. \qquad \text{(B2)}$$

At the crossing of the curves, $k_M = k_M^*$ and $k_F = k_F^*$, so that the right-hand side of (B1) and (B2) differ only by the term $\gamma\{[1 + (n-1)\Phi/2]/c\}$, which is added to the numerator of (B1) but to the denominator of (B2). Thus, for any positive γ, the right-hand side of equation (B1) is larger in absolute terms, which means that the slope of k_M^* versus k_F is steeper than that of k_M versus k_F^*. In other words, the k_M^* curve crosses the k_F^* curve from above (fig. 3C).

For the same reason, an increase in Φ (polygyny level) will make the k_M^*-versus-k_F slope (B1) steeper and that of k_M-versus-k_F^* (B2) shallower (fig. 4).

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