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AVOIDING INBREEDING AND SIBLING COMPETITION:
THE EVOLUTION OF SEXUAL DIMORPHISM FOR DISPERSAL

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Abstract.—Natal dispersal can reduce sibling competition and the risk of inbreeding, but it may also confer a personal cost on the disperser. A simple gene-frequencies model is presented, which takes into consideration the effects of both competition and inbreeding avoidance on the evolution of dispersal. The evolutionarily stable strategies of dispersal are obtained, and the possibility of sexual dimorphism with regard to dispersal behavior is analyzed. If the cost of inbreeding is low, both sexes adopt the same dispersal strategy, whereas if the cost of inbreeding is high enough, we can expect to find sexual dimorphism with respect to dispersal behavior (even if both sexes have the same costs and benefits associated with dispersal).

By dispersing from their natal site, offspring decrease the probability of future encounters with each other, thus reducing sibling competition (Hamilton and May 1977; Motro 1982*a*, 1982*b*, 1983; Moore and Ali 1984; Frank 1986; Taylor 1988; Cohen and Motro 1989) and also decreasing the risk of possible inbreeding (Bengtsson 1978; May 1979; Greenwood 1980; Shields 1982). Whether its main function is to reduce sibling competition or to avoid inbreeding, dispersal presents an evolutionary problem, since it imposes a personal cost on the individuals that disperse, whereas its possible benefits are shared by all siblings. Hence, it is clearly more advantageous for an individual if its siblings disperse; the individual thus enjoys the benefits of dispersal without paying the cost. Since such an argument applies to all other siblings as well, it seems that natural selection always favors absolute sedentariness. Theoretical models, however, demonstrate that a mixed strategy of dispersal, characterized by a positive probability of choosing to disperse, is evolutionarily stable and that dispersal can evolve even in the absence of parental manipulation. As the cost of dispersal increases, compared with the possible damage resulting from competition (Hamilton and May 1977; Motro 1983; Frank 1986; Taylor 1988) or from inbreeding (Bengtsson 1978), the evolutionarily stable dispersal tendency decreases.

Many species exhibit sexual differences in their dispersal behavior, and it is not uncommon to find cases in which only one of the sexes disperses. Indeed, the a priori assumption in several models (Hamilton and May 1977; Bengtsson 1978) is that only one sex can disperse, while the other always remains sessile.

I attempt here to reconsider that assumption by trying to identify conditions under which evolutionary stability will result in the dispersal of both sexes and conditions under which evolutionary stability will result in the dispersal of only one sex (and the sedentariness of the other). I present a model that takes into consideration both the effects of sibling competition and of inbreeding avoidance.

Clearly, a possible mechanism allowing for sexual dimorphism is sex linkage (i.e., haplodiploidy of the relevant genetic locus). In a sibling-competition model, Taylor (1988) demonstrated that sex linkage indeed results in different evolutionarily stable dispersal strategies for males and for females: if both sexes have the same dispersal cost, the evolutionarily stable dispersal rate for the heterogametic sex (the "males") should be smaller than the evolutionarily stable rate for the "females" (and if the cost is high enough, "males" should always stay at home). This, however, cannot explain the opposite phenomena found in many species: generally, among mammals, the male disperses; among birds, the female does. (There are, of course, exceptions to these rules; for a review, see Greenwood 1980.) If both sexes have the same dispersal costs and benefits, is haplodiploidy then the only possible mechanism that can explain sexual dimorphism in dispersal behavior? In other words, can we expect to find sexual differences in dispersal behavior if both sexes are completely *symmetrical* with regard to their dispersal genetics?

THE MODEL

The model deals with a dispersal strategy whereby the decision of whether to disperse or to remain at the natal place is made by the offspring itself. The assumptions of the model are as follows.

1. Consider a population of sexually reproducing haploid organisms. The environment is divided into an infinite number of living sites, each occupied by a single breeding pair, a male and a female. Each pair has the same expected number of descendants, and the sex ratio within the progeny is 1:1.

2. Each descendant either remains at its natal site (with probability $1 - x$, $0 \leq x \leq 1$) or leaves its natal site and disperses (with probability x) in an attempt to establish itself at another living site. The number x is genetically determined (by a single locus), and the decision of whether to disperse or to stay at home is made according to the genotype of the descendant. Progeny that leave their natal site are uniformly dispersed over the entire range of the population.

3. Generations are discrete and nonoverlapping. After reproduction, the preceding generation is eliminated, and each living site is reoccupied by a single pair.

4. The succeeding pair of a site is chosen from among all pairs of young individuals present at that site. These individuals are either the undispersed descendants of the former occupants, or immigrants, the descendants of pairs that occupied other living sites in the preceding generation. Sibs, however, are less likely to form a breeding pair. The probability that a given pair of sibs becomes the succeeding pair at a site is only a fraction $1 - \sigma$ ($0 \leq \sigma \leq 1$) of that probability for any given pair of nonsibs at that same site. The parameter σ can be interpreted

either as a "cost" of inbreeding or simply as an inbreeding-avoidance parameter, with $\sigma = 1$ indicating a complete incest taboo.

5. Because of the risks of dispersal, such as the possibility of not reaching a living site, the probability of a disperser's attaining the state of competition at a living site is only a fraction β ($0 < \beta \leq 1$) of that probability for a nondisperser. The smaller β is, the more stringent are the environmental conditions endured by the dispersing young. The parameter $c = 1 - \beta$ can be interpreted as the cost of dispersal.

In order to find the evolutionarily stable dispersal strategies, we consider the locus that determines the dispersal rate to have two alleles: a (the wild type), determining a probability of dispersal x , and A (a mutant), determining a probability of dispersal $\xi \neq x$. Let u , v , and w ($u + v + w = 1$) be the frequencies of the three types of breeding pairs $A \times A$, $A \times a$, and $a \times a$ (respectively), and let $p = u + \frac{1}{2}v$ and $q = w + \frac{1}{2}v$ denote the frequencies of the alleles A and a . The next-generation frequencies for the three types of breeding pairs are

$$(u', v', w') = (u, v, w) \begin{bmatrix} P_{11} & P_{12} & P_{13} \\ P_{21} & P_{22} & P_{23} \\ P_{31} & P_{32} & P_{33} \end{bmatrix}, \quad (1)$$

where, assuming a large number of competing young per living site,

$$\begin{aligned} P_{11} &= \frac{(1 - \xi + \beta p \xi)^2 - \sigma(1 - \xi)^2}{(1 - \xi + \beta p \xi + \beta q x)^2 - \sigma(1 - \xi)^2}, \\ P_{12} &= \frac{2(1 - \xi + \beta p \xi)\beta q x}{(1 - \xi + \beta p \xi + \beta q x)^2 - \sigma(1 - \xi)^2}, \\ P_{13} &= \frac{(\beta q x)^2}{(1 - \xi + \beta p \xi + \beta q x)^2 - \sigma(1 - \xi)^2}, \\ P_{21} &= \frac{[\frac{1}{2}(1 - \xi) + \beta p \xi]^2 - \frac{1}{4}\sigma(1 - \xi)^2}{[\frac{1}{2}(1 - \xi) + \frac{1}{2}(1 - x) + \beta p \xi + \beta q x]^2 - \frac{1}{4}\sigma[(1 - \xi) + (1 - x)]^2}, \\ P_{22} &= \frac{2[\frac{1}{2}(1 - \xi) + \beta p \xi][\frac{1}{2}(1 - x) + \beta q x] - \frac{1}{2}\sigma(1 - \xi)(1 - x)}{[\frac{1}{2}(1 - \xi) + \frac{1}{2}(1 - x) + \beta p \xi + \beta q x]^2 - \frac{1}{4}\sigma[(1 - \xi) + (1 - x)]^2}, \\ P_{23} &= \frac{[\frac{1}{2}(1 - x) + \beta q x]^2 - \frac{1}{4}\sigma(1 - x)^2}{[\frac{1}{2}(1 - \xi) + \frac{1}{2}(1 - x) + \beta p \xi + \beta q x]^2 - \frac{1}{4}\sigma[(1 - \xi) + (1 - x)]^2}, \\ P_{31} &= \frac{(\beta p \xi)^2}{(1 - x + \beta p \xi + \beta q x)^2 - \sigma(1 - x)^2}, \\ P_{32} &= \frac{2(1 - x + \beta q x)\beta p \xi}{(1 - x + \beta p \xi + \beta q x)^2 - \sigma(1 - x)^2}, \\ P_{33} &= \frac{(1 - x + \beta q x)^2 - \sigma(1 - x)^2}{(1 - x + \beta p \xi + \beta q x)^2 - \sigma(1 - x)^2}. \end{aligned} \quad (2)$$

Consider the determinant

$$\begin{vmatrix} \partial u' / \partial u - 1 & \partial u' / \partial v \\ \partial v' / \partial u & \partial v' / \partial v - 1 \end{vmatrix}, \tag{3}$$

where the derivatives are taken at $(u, v, w) = (0, 0, 1)$, with $w = 1 - u - v$. The value of this determinant is a function of ξ and x and is denoted by $f(\xi, x)$. (Note that $f(x, x) = 0$.) The strategy x is an evolutionarily stable strategy (ESS) if for all $\xi \neq x$, $f(\xi, x) < 0$. Thus, the ESS is the solution of the equation

$$\partial f(\xi, x) / \partial \xi |_{\xi=x} = 0. \tag{4}$$

After some algebra, we obtain the quadratic equation in x :

$$2[(1 - \beta)(2 - \beta) - 2\sigma]x^2 - [5(1 - \sigma) - 4\beta]x + (1 - \sigma) = 0,$$

whose solution is the ESS,

$$x^* = \begin{cases} \frac{5(1 - \sigma) - 4\beta - \Delta^{1/2}}{4[(1 - \beta)(2 - \beta) - 2\sigma]} & \text{if } \sigma \neq \frac{1}{2}(1 - \beta)(2 - \beta) \\ \frac{3 - \beta}{7 - 5\beta} & \text{if } \sigma = \frac{1}{2}(1 - \beta)(2 - \beta) \end{cases}, \tag{5}$$

where $\Delta = [3(1 - \sigma) - 4\beta]^2 + 8\beta(1 - \beta)(1 - \sigma)$.

Not surprisingly, the ESS, x^* , is an increasing function of β and an increasing function of σ . Thus, the evolutionarily stable dispersal probability is a decreasing function of the cost of dispersal but an increasing function of the cost of inbreeding.

If there is no cost associated with inbreeding and the only cause for dispersal is to reduce sibling competition (i.e., if $\sigma = 0$), the ESS is

$$x^* = \frac{5 - 4\beta - [1 + 8(1 - \beta)^2]^{1/2}}{4(1 - \beta)(2 - \beta)}, \tag{6}$$

which is the same result obtained by Taylor in his ‘‘diploid–dispersal before mating’’ model with offspring control (1988, p. 371).

If $\sigma = 1$ (i.e., the incest taboo is complete), the ESS is

$$x^* = 2/(3 - \beta). \tag{7}$$

The situation may be different, however, if each sex can display a distinct dispersal behavior. The consequences of this possibility are studied in the next section.

SEX-SPECIFIC DISPERSAL

Suppose that each sex can have its own specific dispersal strategy. A simple genetic pattern allowing for such sexual difference is, for example, the existence of two distinct autosomal loci responsible for the dispersal behavior, only one of

which is activated in each individual, according to its own sex. For simplicity, I assume that these loci are unlinked.

Suppose that the population is fixed on a particular male strategy y and a particular female strategy x , and consider the fate of a mutation at the female-strategy locus, which determines a female dispersal strategy $\xi \neq x$. The transition probabilities (2) become

$$\begin{aligned}
 P_{11} &= \frac{(1 - \xi + \beta p \xi)(1 - y + \beta p y) - \sigma(1 - \xi)(1 - y)}{(1 - \xi + \beta p \xi + \beta q x)(1 - y + \beta y) - \sigma(1 - \xi)(1 - y)}, \\
 P_{12} &= \frac{(1 - \xi + \beta p \xi)\beta q y + (1 - y + \beta p y)\beta q x}{(1 - \xi + \beta p \xi + \beta q x)(1 - y + \beta y) - \sigma(1 - \xi)(1 - y)}, \\
 P_{13} &= \frac{\beta^2 q^2 x y}{(1 - \xi + \beta p \xi + \beta q x)(1 - y + \beta y) - \sigma(1 - \xi)(1 - y)}, \\
 P_{21} &= \frac{[\frac{1}{2}(1 - \xi) + \beta p \xi][\frac{1}{2}(1 - y) + \beta p y] - \frac{1}{4}\sigma(1 - \xi)(1 - y)}{[\frac{1}{2}(1 - \xi) + \frac{1}{2}(1 - x) + \beta p \xi + \beta q x](1 - y + \beta y) - \frac{1}{2}\sigma[(1 - \xi) + (1 - x)](1 - y)}, \\
 P_{22} &= \frac{[\frac{1}{2}(1 - \xi) + \beta p \xi][\frac{1}{2}(1 - y) + \beta q y] + [\frac{1}{2}(1 - x) + \beta q x][\frac{1}{2}(1 - y) + \beta p y] - \frac{1}{4}\sigma[(1 - \xi) + (1 - x)](1 - y)}{[\frac{1}{2}(1 - \xi) + \frac{1}{2}(1 - x) + \beta p \xi + \beta q x](1 - y + \beta y) - \frac{1}{2}\sigma[(1 - \xi) + (1 - x)](1 - y)}, \\
 P_{23} &= \frac{[\frac{1}{2}(1 - x) + \beta q x][\frac{1}{2}(1 - y) + \beta q y] - \frac{1}{4}\sigma(1 - x)(1 - y)}{[\frac{1}{2}(1 - \xi) + \frac{1}{2}(1 - x) + \beta p \xi + \beta q x](1 - y + \beta y) - \frac{1}{2}\sigma[(1 - \xi) + (1 - x)](1 - y)}, \\
 P_{31} &= \frac{\beta^2 p^2 \xi y}{(1 - x + \beta p \xi + \beta q x)(1 - y + \beta y) - \sigma(1 - x)(1 - y)}, \\
 P_{32} &= \frac{(1 - x + \beta q x)\beta p y + (1 - y + \beta q y)\beta p \xi}{(1 - x + \beta p \xi + \beta q x)(1 - y + \beta y) - \sigma(1 - x)(1 - y)}, \\
 P_{33} &= \frac{(1 - x + \beta q x)(1 - y + \beta q y) - \sigma(1 - x)(1 - y)}{(1 - x + \beta p \xi + \beta q x)(1 - y + \beta y) - \sigma(1 - x)(1 - y)}. \tag{8}
 \end{aligned}$$

Consider again the determinant (3) of the preceding section. Its value is a function of ξ and x , but now it has y as a parameter and is denoted by $f(\xi, x; y)$. For any given y , the female strategy x is an ESS if for all $\xi \neq x$, $f(\xi, x; y) < 0$. Thus, the females' ESS is the solution of

$$\partial f(\xi, x; y) / \partial \xi |_{\xi=x} = 0 \tag{9}$$

and is a function of y . Let us denote this solution by $\hat{x}(y)$ and call it the females' "best reply" to y , the prevailing male strategy in the population. It can be shown that $\hat{x}(y)$ is a continuous and decreasing function of y and that

$$\hat{x}(0) = \begin{cases} \frac{1 - \sigma}{2[(1 - \beta) + 1 - 3\sigma]} & \text{if } \sigma < 1 - \beta \\ 1 & \text{if } \sigma \geq 1 - \beta \end{cases}$$

and

$$\hat{x}(1) = \begin{cases} 0 & \text{if } 1 - \beta \geq 1/2 \\ \frac{2\beta - 1}{4\beta - \beta^2 - 1} & \text{if } 1 - \beta < 1/2 \end{cases}.$$

Furthermore, if $\sigma < 1 - \beta$, then

$$\hat{x}\left(\frac{1 - \sigma}{2(1 - \beta) + 1 - 3\sigma}\right) \begin{cases} = 0 & \text{if } \sigma \geq (2 - \beta)/2(1 + \beta) \\ & ; \\ > 0 & \text{otherwise} \end{cases}$$

and if $1 - \beta < 1/2$, then

$$\hat{x}\left(\frac{2\beta - 1}{4\beta - 2\beta^2 - 1}\right) \begin{cases} = 1 & \text{if } \sigma \geq 1/(1 + 2\beta) \\ & ; \\ < 1 & \text{otherwise} \end{cases}$$

Because of symmetry, the males' best-reply function (denoted by $\hat{y}(x)$) has the same characteristics as the females' best-reply function, $\hat{x}(y)$.

Following Maynard Smith (1977) and Grafen and Sibly (1978), (x^*, y^*) is called an evolutionarily stable strategy of our game with two types of player, if a population that maintains a female strategy x^* and a male strategy y^* is stable in the face of any mutant female strategy $\xi \neq x^*$ or any mutant male strategy $\eta \neq y^*$. Hence, the two-types-of-player ESS of our model is the intersections of the best-reply curves $\hat{x}(y)$ and $\hat{y}(x)$.

There always exists an intersection point on the diagonal of the strategy space $0 \leq x \leq 1$ and $0 \leq y \leq 1$ (i.e., an ESS having $x^* = y^*$), and this value is exactly the same as the ESS of the preceding section (given by eq. [5]).

However, if the cost of dispersal is high enough (i.e., if $1 - \beta \geq 1/2$) and the cost of inbreeding is also high (i.e., $\sigma \geq (2 - \beta)/2(1 + \beta)$), two more ESSs exist. These additional ESSs are characterized by the absolute sedentariness of one sex and a positive dispersal strategy for the other. More precisely, if $1 - \beta \geq 1/2$ and $\sigma \geq 1 - \beta$, the two additional ESSs are $(x^*, y^*) = (0, 1)$ and $(x^*, y^*) = (1, 0)$. If $1 - \beta \geq 1/2$ and $1 - \beta > \sigma \geq (2 - \beta)/2(1 + \beta)$, the two additional ESSs are $(x^*, y^*) = (0, (1 - \sigma)/[2(1 - \beta) + 1 - 3\sigma])$ and $(x^*, y^*) = ((1 - \sigma)/[2(1 - \beta) + 1 - 3\sigma], 0)$. In other words, if one sex commits itself to being sedentary (e.g., by abandoning its dispersal ability), the other sex is then forced to disperse more. This situation is evolutionarily stable if the cost of dispersal and the cost of inbreeding are high enough. Then, if $\sigma \geq 1 - \beta$, it results in the complete dispersal of the nonsedentary sex; and if the cost of inbreeding is not that large (but above $(2 - \beta)/2(1 + \beta)$), it results in a positive probability of dispersal for the nonsedentary sex, smaller than 1, yet larger than the symmetrical ESS of the diagonal.

If, however, the cost of dispersal is small (i.e., if $1 - \beta < \frac{1}{2}$) but the cost of inbreeding is large enough (i.e., $\sigma \geq 1/(1 + 2\beta)$), then again two ESSs exist, in addition to the symmetrical ESS of the diagonal. These additional ESSs are characterized by the complete dispersal of one sex and a positive dispersal strategy for the other. More precisely, these two ESSs are $(x^*, y^*) = ((2\beta - 1)/(4\beta - 2\beta^2 - 1), 1)$ and $(x^*, y^*) = (1, (2\beta - 1)/(4\beta - 2\beta^2 - 1))$.

In the parameter regions $1 - \beta \geq \frac{1}{2}$ and $\sigma < (2 - \beta)/2(1 + \beta)$, and $1 - \beta < \frac{1}{2}$ and $\sigma < 1/(1 + 2\beta)$, a "boundary" ESS (i.e., an ESS for which either one sex is completely sedentary or one sex is completely committed to dispersal) does not exist, and the only ESS is the symmetrical one.

In the parameter region $1 - \beta \geq \frac{1}{2}$ and $(2 - \beta)/2(1 + \beta) \leq \sigma < 1 - \beta$, more than three ESSs can exist. For example, if $1 - \beta = 0.60$ and $\sigma = 0.58$, there are five ESSs, namely, the symmetrical ESS (0.5753, 0.5753), the boundary ESSs (0, 0.9130) and (0.9130, 0), and also (0.2900, 0.7780) and (0.7780, 0.2900). But if $1 - \beta = 0.60$ and $\sigma = 0.59$, only the symmetrical point (0.5810, 0.5810) and the two boundary points (0, 0.9535) and (0.9535, 0) are evolutionarily stable.

DISCUSSION

Natal dispersal, which helps to reduce sibling competition for the same resources and to avoid inbreeding, reflects an intrasibship conflict. It confers a cost on the disperser, since it may reduce its viability and possibly also its fertility (Bengtsson 1978), whereas the benefits are enjoyed by the dispersers and by the nondispersers as well.

This work explores the ESS for dispersal in a model that considers the effects of both sibling competition and inbreeding avoidance. It turns out that an ESS of dispersal exists, represented by a positive probability of choosing to disperse. As might have been expected, the tendency to disperse decreases as a function of the cost of dispersal but increases as a function of the cost of inbreeding.

A similar result holds if we consider dispersal a sex-influenced trait, thus allowing each sex to display its own sex-specific dispersal behavior. (Such a pattern can exist, for example, if each individual carries two distinct loci that are responsible for the dispersal behavior but only one of these is activated, according to the sex of the carrier.) If the cost of dispersal is the same for both sexes, there is a symmetrical ESS that assigns to each sex the same value as the aforementioned ESS (whereby dispersal strategies were governed by the same gene in both sexes). But this is not the only possible ESS. If, on the one hand, the cost of dispersal and the cost of inbreeding are high enough, one sex's commitment to being sedentary will then force the other sex to disperse more (and even to disperse completely), and this sexual dimorphism is evolutionarily stable. If, on the other hand, the cost of dispersal is low but the cost of inbreeding is above a certain threshold, dimorphic ESSs again exist, but in this case they reflect a complete dispersal by one sex and a reduced, yet positive, dispersal strategy for the other.

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