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Inbreeding Avoidance through Kin Recognition: Choosy Females Boost Male Dispersal

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ABSTRACT: Inbreeding avoidance is predicted to induce sex biases in dispersal. But which sex should disperse? In polygynous species, females pay higher costs to inbreeding and thus might be expected to disperse more, but empirical evidence consistently reveals male biases. Here, we show that theoretical expectations change drastically if females are allowed to avoid inbreeding via kin recognition. At high inbreeding loads, females should prefer immigrants over residents, thereby boosting male dispersal. At lower inbreeding loads, by contrast, inclusive fitness benefits should induce females to prefer relatives, thereby promoting male philopatry. This result points to disruptive effects of sexual selection. The inbreeding load that females are ready to accept is surprisingly high. In absence of search costs, females should prefer related partners as long as $\delta < r/(1+r)$, where r is relatedness and δ is the fecundity loss relative to an outbred mating. This amounts to fitness losses up to one-fifth for a half-sib mating and one-third for a full-sib mating, which lie in the upper range of inbreeding depression values currently reported in natural populations. The observation of active inbreeding avoidance in a polygynous species thus suggests that inbreeding depression exceeds this threshold in the species under scrutiny or that inbred matings at least partly forfeit other mating opportunities for males. Our model also shows that female choosiness should decline rapidly with search costs, stemming from, for example, reproductive delays. Species under strong time constraints on reproduction should thus be tolerant of inbreeding.

Keywords: inbreeding depression, local competition, mate choice, mating systems, sexual selection.

An obvious way to avoid the fitness costs of inbreeding is to disperse. Intuition suggests that dispersal, in that case, should be sex biased. If males disperse, females may stay home at no risk (and conversely). Theoretical models support intuition and predict strong sex biases for inbreeding-driven dispersal patterns (Motro 1991; Gandon 1999; Perrin and Mazalov 1999).

But which sex should disperse? Empirical data point to a significant role of mating patterns. Dispersal is usually female biased in birds, which are predominantly monogamous, but male biased in mammals, most of which are polygynous (Greenwood 1980, 1983). Within mammals, the male bias is strong in polygynous species, while no statistical trend emerges among the few monogamous species (Dobson 1982).

Perrin and Mazalov (2000) proposed that mating systems matter because they induce sexual asymmetries in the patterns of local competition. In polygynous systems, the two sexes do not compete for the same items; males compete for females, while females compete for resources. Because the process of transforming resource into offspring (a female task) is much more time consuming than that of fertilizing females, local mate competition among males normally exceeds local resource competition among females. This asymmetry is expected to induce a male-biased dispersal.

However, asymmetries in inbreeding costs might also play a role. In polygynous systems, inbreeding is more costly to females than to males (Parker 1979, 1983; Smith 1979). Inbred matings actually benefit males by adding a few offspring to their reproductive output without forfeiting other mating opportunities. But females incur drastic reductions in their lifetime reproductive output. Building on this argument, Waser et al. (1986) reasoned that if inbreeding avoidance was a significant cause of dispersal, then females, rather than males, should disperse. Or, put differently, the fact that males disperse in polygynous species suggests that inbreeding is unlikely to be an important force behind dispersal.

This conclusion appears rather surprising given the widespread importance of inbreeding depression in nat-

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ural populations (review in Keller and Waller 2002). The idea has emerged that this apparent paradox might be solved by introducing female choice in the equation (Pusey and Packer 1986; Keane 1990*b*; Perrin and Goudet 2001). When it comes to avoiding inbreeding, kin discrimination certainly constitutes an important alternative to dispersal (Blouin and Blouin 1988). If inbreeding load is high, females in a group might prefer immigrant over resident males, thereby inducing a selective pressure for male dispersal.

In this article, we formalize this idea and show that female mate choice through kin recognition may indeed boost male dispersal. This outcome suggests that sexually dimorphic dispersal, and particularly the strongly male-biased dispersal of many mammals, might partly result from sexual selection. Interestingly, our results also show that when inbreeding load is low, kin selection should favor female preference for related males, thus inducing sexual selection for male philopatry. Indeed, in such a case, the direct costs to females are outweighed by the inclusive fitness gained through the benefits provided to related mates. This points to contrasting effects of sexual selection, where female choice promotes male dispersal above some inbreeding depression threshold and restricts it below this threshold.

The Model

Life Cycle

We consider diploid individuals living in patches of limited size (say, N breeding spots; symbols are displayed in table A1). Patches are numerous enough that coancestry among them can be neglected (infinite-island model). The life cycle is annual, with events occurring in the following order.

Offspring first spend a juvenile period in their place of birth, where they fully develop phenotypic features. Similarity among patch mates arises from common genes and/or common environment. Before reaching maturity, males and females disperse with respective probabilities y and x (that may evolve) and survive dispersal with probability s. The proportions of resident and immigrant males in a patch after dispersal are thus $k_y = (1-y)/(1-y+ys)$ and $\tilde{k}_y = 1 - k_y$, respectively. For females, the proportions are $k_x = (1-x)/(1-x+xs)$ and $\tilde{k}_x = 1 - k_x$, respectively.

Females from the same patch then compete for the N breeding spots, while males compete for the N successful females. Females mate only once. Let us assume for the moment that inbreeding depression is strong enough that they prefer immigrants. They inspect several potential mates for fitness-indicative cues (in our case, relatedness, indicated by phenotypic similarity; see app. B in the online edition of the *American Naturalist*) and accept the first one with similarity below a threshold t (fig. 1*A*). Because immigrant females have no relatives in their breeding patch, all males (resident or immigrant) have the same probability A_{u_t} to be accepted (fig. 1*A*), so these females conduct on average $1/A_{u_t}$ trials before successfully mating. Search time is thus geometrically distributed, while male mating success is binomially distributed. If each trial bears a fitness cost, then the fecundity penalty of an average

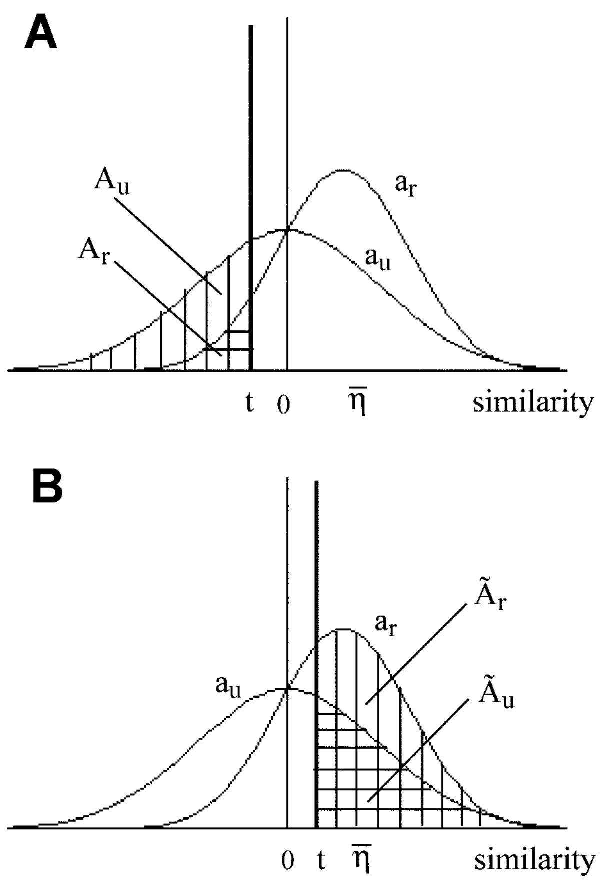

Figure 1: Distributions of similarities with immigrants a_u (*left curve*) and residents a_r (*right curve*) as estimated by a focal resident. The former distribution is centered on 0, the latter on $\bar{\eta}$, which measures the expected similarity among patch mates, owing to both common genes and common environment. The sampling variance around expectations makes distributions overlap to some extent. *A*, Immigrants are considered the desirable class and are accepted with probability A_u (*vertically striped area*), whereas residents are accepted with probability A_r (*horizontally striped area*). *B*, Residents are considered the desirable class and are accepted with probability $\tilde{A}_r$ (*vertically striped area*), while immigrants are accepted with probability $\tilde{A}_u$ (*horizontally striped area*).

search is c_s/A_{u_t}. Resident females accept immigrant partners with the same probability A_{u_t}, but they accept resident partners with the probability A_{r_t} (because of higher phenotypic similarity stemming from relatedness; fig. 1). A random male is thus accepted with probability $A_t = k_y A_{r_t} + \tilde{k}_y A_{u_t}$, so resident females conduct on average $1/A_t$ trials before successfully mating (see also Reeve 1989, p. 423). If each trial bears a fitness cost c_s, then the fecundity penalty of an average search is c_s/A_t.

During the reproductive episode that follows, finally, inbreeding decreases the baseline fecundity of a female by an amount δ, a function of the coancestry θ with her mating partner. This inbreeding depression adds to the costs incurred through mate search. The fecundity of an immigrant female is thus $m_d = 1 - (c_s/A_{u_t})$, while that of a resident is

$$m_p = \frac{k_y A_{r_t}(1-\delta) + \tilde{k}_y A_{u_t} - c_s}{A_t}.$$

Average fecundity on a patch is $m = k_x m_p + k_x m_d$.

Direct Fitness

According to the direct fitness approach (Taylor and Frank 1996; Frank 1997, 1998), the selective pressure on a gene coding for a phenotypic trait x can be written

$$\frac{dw}{d\zeta} = \sum_i p_i \sum_j r_j \frac{\partial w_i}{\partial x_j}, \tag{1}$$

where $w\zeta$ is the fitness of the gene under study, ζ is its breeding value, p_i is the frequency of its transmission through individuals of category i, w_i is the fitness of a focal individual of category i, and x_j is the phenotypic expression of trait x in individuals bearing relatedness r_j to the focal individual. In our infinite-island settings, the focal individual recognizes three levels of relatedness: 1 with self, $0 < r < 1$ with potential mates born on the same patch (the exact value has to be found through recurrence equations; see app. C in the online edition of the *American Naturalist*), and 0 with unrelated individuals born on different patches.

The evolutionarily stable strategy (ESS) is found by setting the selective pressure to 0 (eq. [1]) while equating all the x_j. According to this rule, the evolutionarily stable (ES) female dispersal is found by solving

$$\frac{\partial w_f}{\partial x_\bullet} + r\left(\frac{\partial w_f}{\partial x_j} + \frac{\partial w_m}{\partial x_j}\right) = 0\bigg|_{x_\bullet = x_j = x}, \tag{2}$$

where w_f is female fitness, w_m is male fitness, and r is relatedness among males and females born on the same patch. Female dispersal probability is written $x_\bullet$, x_j, or x depending on whether it is expressed in the focal individual, a relative, or an unrelated individual, respectively. Here, below, we first establish male and female fitness functions and then derive these functions to find the ES male dispersal (y), female dispersal (x), and female acceptance threshold (t).

Female Fitness

The part of fitness that a focal female gains through the dispersing option is calculated as the probability of successful dispersal ($x_\bullet s$) weighted by that of gaining a breeding spot ($1/m(1 - x + xs)$) times associated fecundity $m_{d\bullet} = 1 - (c_s/A_{u_t\bullet})$. The part she gains through the philopatric option is obtained as her probability of staying home ($1 - x_\bullet$) weighted by that of breeding ($1/m(1 - x_j + xs)$) times the associated fecundity

$$m_{p\bullet} = \frac{k_{y_j} A_{r_t\bullet}(1-\delta) + \tilde{k}_{y_j} A_{u_t\bullet} - c_s}{k_{y_j} A_{r_t\bullet} + \tilde{k}_{y_j} A_{u_t\bullet}}.$$

Collecting these terms provides the female fitness function

$$w_f = (1 - x_\bullet)\frac{m_{p\bullet}}{(1 - x_j + xs)m} + x_\bullet s\frac{m_{d\bullet}}{(1 - x + xs)m}. \tag{3}$$

Note that the fecundity m of the parental generation should receive a subscript j in the philopatric option. The first denominator would then read $(1 - x_j)m_j + xsm$. We derived this exact equation and found that having this subscript adds considerable complexities to the mathematical derivations, with no detectable effect on the equilibrium dispersal and only slight effect on the equilibrium threshold (see "Discussion"). We thus decided to drop it in the present derivation.

Male Fitness

Under our infinite-island assumptions, immigrant and resident males are equally related to immigrant females and thus equally preferred. The mating success of an immigrant male through the pool of immigrant females is thus $\tilde{k}_x A_{u_t}/mA_{u_t}(1 - y + ys)$ (i.e., random). His mating success through resident females, by contrast, is $k_x A_{u_t}/m[(1 - y)A_{r_t} + ysA_{u_t}]$ because resident females choose resident males with probability A_{r_t}. In both cases, the fecundity per mating is $1 - (c_s/A_{\mathrm{u}_\mathrm{t}})$.

The mating success of a resident male through immigrant females is written $\tilde{k}_x A_{\mathrm{u}_\mathrm{t}}/m(1 - y_j + ys)A_{\mathrm{u}_\mathrm{t}}$ (y_j arises because competition for females partly occurs among related males), with fecundity per mating $1 - (c_s/A_{\mathrm{u}_\mathrm{t}})$. His mating success through resident females is $k_{x_j}A_{\mathrm{r}_{\mathrm{t}j}}/m[(1 - y_j)A_{\mathrm{r}_{\mathrm{t}j}} + ysA_{\mathrm{u}_{\mathrm{t}j}}]$ because resident females do not choose relatives and immigrants with the same probability. Fecundity per mating in that case is $(1 - \delta) - (c_s/A_{\mathrm{r}_{\mathrm{t}j}})$ because of inbreeding depression. Collecting all these terms provides the male fitness function

$$
\begin{aligned}
w_\mathrm{m} = {} & (1 - y_\bullet)\left\{\frac{k_{x_j}A_{\mathrm{r}_{\mathrm{t}j}}}{m[(1 - y_j)A_{\mathrm{r}_{\mathrm{t}j}} + ysA_{\mathrm{u}_{\mathrm{t}j}}]}\left(1 - \delta - \frac{c_s}{A_{\mathrm{r}_{\mathrm{t}_j}}}\right)\right. \\
& \left. + \frac{\tilde{k}_{x_j}}{m(1 - y_j + ys)}\left(1 - \frac{c_s}{A_{\mathrm{u}_\mathrm{t}}}\right)\right\} \\
& + y_\bullet s\left\{\frac{k_x A_{\mathrm{u}_\mathrm{t}}}{m[(1 - y)A_{\mathrm{r}_\mathrm{t}} + ysA_{\mathrm{u}_\mathrm{t}}]}\right. \\
& \left. + \frac{\tilde{k}_x}{m(1 - y + ys)}\right\}\left(1 - \frac{c_s}{A_{\mathrm{u}_\mathrm{t}}}\right).
\end{aligned}
\tag{4}
$$

Note that the same comment applies as for the female fitness concerning the fecundity subscripts for the philopatric option. Note also that at equilibrium (i.e., when $x_\bullet = x_j = x$, $y_\bullet = y_j = y$, $t_\bullet = t_j = t$), we obtain $w_\mathrm{m} = w_\mathrm{f} = 1$ (the population is stable, and females obtain the same fitness returns through sons and daughters).

Analysis

ES Female Dispersal

Direct and indirect selective pressures on dispersal are obtained as partial derivatives of the fitness functions (i.e., holding other traits constant). In order to simplify notations, the results of calculations are provided for $x_\bullet = x_j = x$ (which necessarily holds true at equilibrium). The direct selective pressure equals the fitness differential of dispersing and philopatric females

$$
\frac{\partial w_\mathrm{f}}{\partial x_\bullet} = \frac{sm_\mathrm{d} - m_\mathrm{p}}{m(1 - x + xs)}. \tag{5a}
$$

The indirect selection stemming from local resource competition avoidance (realized when the breeding opportunity left behind by the focal female is taken over by a related female) is

$$
\frac{\partial w_\mathrm{f}}{\partial x_j} = \frac{k_x m_\mathrm{p}}{m(1 - x + xs)}, \tag{5b}
$$

while that stemming from the decrease in the inbreeding risk of related males (realized when this breeding opportunity is seized by an immigrant female) is

$$
\frac{\partial w_\mathrm{m}}{\partial x_j} = \frac{\tilde{k}_x k_y}{(1 - x + xs)m}\left[m_\mathrm{d} - \frac{A_\mathrm{r}}{A}\left(1 - \delta - \frac{c_s}{A_\mathrm{r}}\right)\right]. \tag{5c}
$$

Setting to 0 the sum of all selective pressures weighted by the corresponding relatedness coefficient yields the condition for the ES level of female dispersal:

$$
m_\mathrm{p} - sm_\mathrm{d} = rk_x m_\mathrm{p} + r\tilde{k}_x k_y\left[m_\mathrm{d} - \frac{A_\mathrm{r}}{A}\left(1 - \delta - \frac{c_s}{A_\mathrm{r}}\right)\right]. \tag{5d}
$$

ES Male Dispersal

Holding other traits (x and t) constant, the direct selective pressure on males is obtained as the partial derivative of equation (4) with respect to $y_\bullet$ is

$$
\begin{aligned}
\frac{\partial w_\mathrm{m}}{\partial y_\bullet} = {} & s\left\{\frac{k_x A_\mathrm{u}}{[(1 - y)A_\mathrm{r} + ysA_\mathrm{u}]m} + \frac{\tilde{k}_x}{(1 - y + ys)m}\right\}\left(1 - \frac{c_s}{A_\mathrm{u}}\right) \\
& - \left\{\frac{k_x A_r}{[(1 - y)A_\mathrm{r} + ysA_\mathrm{u}]m}\left(1 - \delta - \frac{c_s}{A_\mathrm{r}}\right) + \frac{\tilde{k}_x}{(1 - y + ys)m}\left(1 - \frac{c_s}{A_\mathrm{u}}\right)\right\}.
\end{aligned}
\tag{6a}
$$

By dispersing, a male also leaves open some mating opportunities, which will be taken over by other males. His mating share of immigrant females will go to related males with probability k_y, while that of resident females go to related males with probability $k_y A_\mathrm{r}/A$. Both terms are obtained by taking the partial derivative of equation (4) with respect to y_j:

$$\frac{\partial w_{\mathrm{m}}}{\partial y_j} = \left(\frac{k_y A_{\mathrm{r}}}{A}\right)\left\{\frac{k_x A_r}{[(1-y)A_{\mathrm{r}} + ysA_{\mathrm{u}}]m}\right\}\left(1 - \delta - \frac{c_s}{A_{\mathrm{r}}}\right)$$

$$+ \frac{k_y \tilde{k}_x}{(1 - y + ys)m}\left(1 - \frac{c_s}{A_{\mathrm{u}}}\right). \tag{6b}$$

If, however, these shares go to unrelated males, then the fitness of related females will increase insofar as some inbreeding depression is thereby avoided. This indirect pressure is obtained as the partial derivative of female fitness (eq. [3]) with respect to y_j:

$$\frac{\partial w_{\mathrm{f}}}{\partial y_j} = k_x \tilde{k}_y \left[\frac{A_{\mathrm{r}} - A_{\mathrm{u}}(1-\delta)}{A(1-y+ys)m}\right] - k_x \tilde{k}_y \left(\frac{A_{\mathrm{r}} - A_{\mathrm{u}}}{A}\right)$$

$$\times \left[\frac{k_y A_{\mathrm{r}}(1-\delta) + \tilde{k}_y A_{\mathrm{u}} - c_s}{A(1-y+ys)m}\right]. \tag{6c}$$

Combining all these terms with corresponding relatedness coefficients provides the first-order condition for male ES dispersal:

$$\frac{k_x A_{\mathrm{r}}}{A}\left(1 - \delta - \frac{c_s}{A_{\mathrm{u}}}\right) + \left[\tilde{k}_x - s\left(\frac{k_x A_{\mathrm{u}}}{A} + \tilde{k}_x\right)\right]$$

$$\times \left(1 - \frac{c_s}{A_{\mathrm{u}}}\right) = r\left(\frac{\partial w_{\mathrm{f}}}{\partial y_j} + \frac{\partial w_{\mathrm{m}}}{\partial y_j}\right)(1 - y + ys)m. \tag{6d}$$

ES Threshold

The threshold t is a trait expressed by females to discriminate resident males from immigrants. Holding other traits (x and y) constant, the direct selective pressure is obtained as the partial derivative of female fitness (eq. [3]) with respect to $t_\bullet$:

$$\frac{\partial w_{\mathrm{f}}}{\partial t_\bullet} = k_x\left\{\frac{k_y a_{\mathrm{r_t}}[(1-\delta) - m_{\mathrm{p}}] + \tilde{k}_y a_{\mathrm{u_t}}(1 - m_{\mathrm{p}}))}{A_{\mathrm{t}} m}\right\}$$

$$+ \tilde{k}_x\left(\frac{c_s a_{\mathrm{u_t}}}{mA^2_{\mathrm{u_t}}}\right), \tag{7a}$$

where $a_{\mathrm{r_t}}$ is the probability that a female perceives a similarity t with a related male and $a_{\mathrm{u_t}}$ is the corresponding value for an unrelated male (fig. 1*A*). Equation (7a) can be interpreted as follows. As t increases, females become more permissive. For a resident female, acceptance probability increases by an amount $k_y a_{\mathrm{r_t}}/A_{\mathrm{t}}$ if the potential partner is a relative (which translates into a cost if $(1 - \delta) < m_{\mathrm{p}}$; i.e., if an inbred mating provides less offspring than expectation) and by an amount $\tilde{k}_y a_{\mathrm{u_t}}/A_{\mathrm{t}}$ if the partner is an immigrant (which translates into a benefit given that $m_{\mathrm{p}} < 1$; an average mating is always less fecund than an outbred mating). For an immigrant female, being more permissive always translates into benefits because search costs then decrease (last term in the right-hand side of eq. [7a]).

Female choosiness also affects the fitness of related males. This indirect selective pressure is obtained as the partial derivative of male fitness (eqq. [5]) with respect to t_j:

$$\frac{\partial w_{\mathrm{m}}}{\partial t_j} = \frac{k_y}{m}\left\{\frac{k_x c_s a_{\mathrm{r_t}}}{A_{\mathrm{t}} A_{\mathrm{r_t}}} + \left[\frac{k_x a_{\mathrm{r_t}}}{A_{\mathrm{t}}}\right.\right.$$

$$\left.\left. - \left(\frac{k_y a_{\mathrm{r_t}} + \tilde{k}_y a_{\mathrm{u_t}}}{A_{\mathrm{t}}}\right)\frac{k_x A_{\mathrm{r_t}}}{A_{\mathrm{t}}}\right]\left(1 - \delta - \frac{c_s}{A_{\mathrm{r_t}}}\right)\right\} \tag{7b}$$

The first term in the right-hand side corresponds to the benefit stemming from decreased search costs, the second term corresponds to the benefit gained from the increased probability for the focal male to be accepted, and the third term corresponds to the cost of increased competition (increased probability that other males, related or not, are accepted).

Setting the total selective pressure to 0 leads to the first-order condition for an ES threshold:

$$a_{\mathrm{u}} \tilde{k}_y w_{\mathrm{u}} = a_{\mathrm{r}} k_y w_{\mathrm{r}}, \tag{7c}$$

where

$$w_{\mathrm{u}} = k_y A_{\mathrm{r}}[\delta(1 + r) - r] + c_s\left(1 + rk_y + \frac{\tilde{k}_x A^2}{k_x \tilde{k}_y A^2_{\mathrm{u}}}\right) \tag{7d}$$

is the relative benefit gained from accepting (rather than rejecting) an immigrant and

$$w_{\mathrm{r}} = \tilde{k}_y A_{\mathrm{u}}[\delta(1 + r) - r] - c_s(1 + rk_y) \tag{7e}$$

is the relative cost of accepting (rather than rejecting) a resident. Equation (7c) states that at equilibrium, the marginal benefits of decreasing selectivity (increased chance of mating with a immigrant weighted by the corresponding fitness benefit) exactly compensate the marginal costs (increased risk of mating with a relative times corresponding fitness cost).

Preference for Relatives and Window of Tolerance

The interpretation given here to equation (7c) assumes that both w_u and w_r are positive. However, δ might be small enough that both are negative, meaning that benefits turn into costs and vice versa. Relatives should thus be preferred over immigrants, so acceptance probabilities are to be found by integrating similarity distributions from the right (fig. 1*B*). The acceptance threshold then receives a different interpretation (being now the similarity value above which a male is accepted) and is obtained by replacing A_u with

$$\tilde{A}_u = 1 - A_u = \int_{\tau=t}^{\infty} a_{u_\tau} d\tau$$

and A_r with

$$\tilde{A}_r = 1 - A_r = \int_{\tau=t}^{\infty} a_{r_\tau} d\tau$$

in all derivations above.

A third possible outcome is that w_r and w_u have different signs. In that case, condition (7c) cannot hold true for any real t value. The solution is either $t = \infty$ (selectivity disappears, and females mate with the first partner they meet) or $t = -\infty$ (selectivity is absolute, and females do not mate at all) depending on whether w_u or w_r is positive, respectively. Though the last option obviously does not correspond to any realistic biological situation, the three others are plausible outcomes and will now be analyzed in more detail.

In absence of search costs, equation (7c) becomes either $a_u/a_r = A_u/A_r$ or $a_u/a_r = \tilde{A}_u/\tilde{A}_r$ depending on whether immigrants or relatives are preferred, respectively (the optimal t then maximizes the probability of mating with the desirable category). It can be seen from equations (7d) and (7e) that the fitness returns w_r and w_u then necessarily have the same sign, determined by the relative values of δ and $r/(1 + r)$. Namely, inbreeding should be avoided, and immigrants should be preferred, provided

$$\delta > \frac{r}{1 + r}. \tag{8}$$

If the opposite holds true, females should prefer inbreeding. In an otherwise outbred population, for instance, a female should refuse mating with a full brother only if the corresponding fitness loss exceeds one-third. For half sibs,

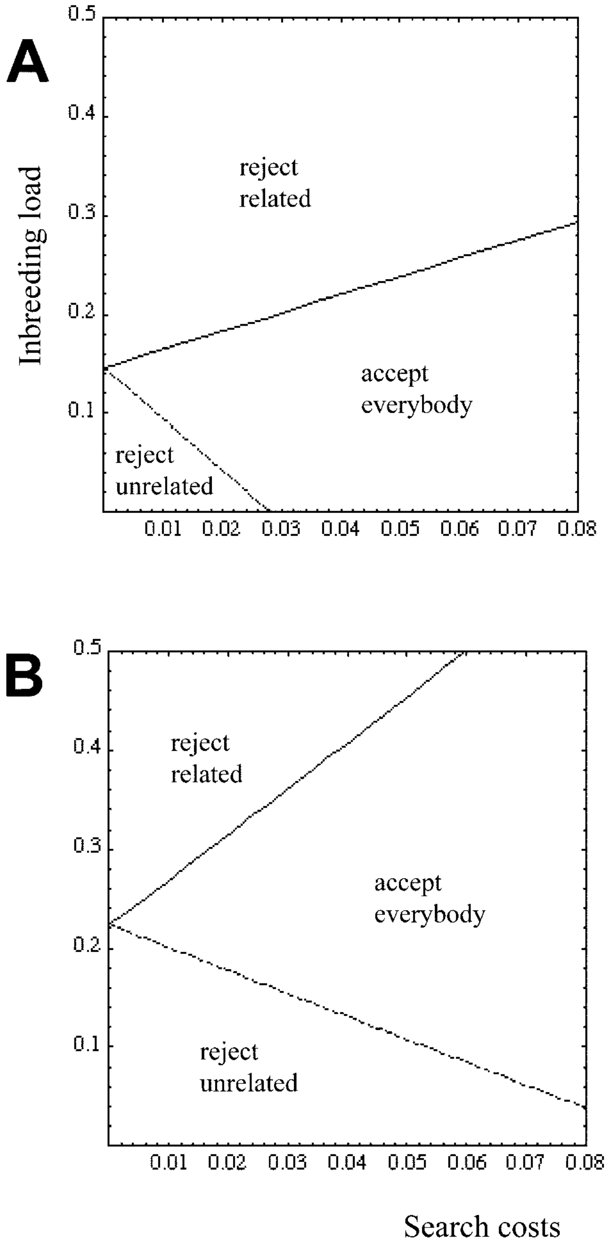

Figure 2: Inbreeding tolerance increases with search costs. Relatives are rejected above the plain line (defined by $w_r = 0$; eq. [7d]) and accepted otherwise (*below the plain line*), while unrelated are accepted above the dashed line (defined by $w_u = 0$; eq. [7e]) and rejected otherwise (*below the line*). These lines thus define an area where the focal female should accept only relatives (*bottom part of the set*), one where only nonkin should be accepted (*top part*), and a third area in between, where both kinds of partners are accepted. This last area is restricted to a single point value in absence of search costs, but a "window of tolerance" opens up as search costs increase. *A*, $n = 5$ and $k_x = k_y = 0.5$. *B*, $n = 5$ and $k_x = k_y = 0.8$.

this threshold loss amounts to $\delta = 1/5$, so a female is more likely to reject a full brother than a half brother.

In absence of costs, selectivity pays in any case, except for the single point value $\delta = r/(1 + r)$ (fig. 2). Search costs have the potential to outweigh the benefits expected from choosiness and thereby to open a wider window of tolerance. It appears from equations (7d) and (7e) that search costs enhance w_u but decrease w_r. Thus, whatever the starting conditions (preference for immigrants or residents), increasing search costs eventually leads to a domain where w_u is positive and w_r is negative (i.e., where choosiness is counterselected). Figure 2 shows how this window of tolerance opens up as searching costs increase, starting from the single point $\delta = r/(1 + r)$ when $c_s = 0$.

Numerical Simulations

We evaluated ESSs numerically (using Mathematica; Wolfram 1991) for a range of parameter values. The main goals of these simulations were to investigate the effects of inbreeding depression and discrimination ability. We did not include search costs in the simulations because their effect is to drop choosiness in such a way that the problem reduces to well-known situations. Equilibrium relatedness was obtained from recurrence equations that account for the effect of patch size, sex-specific dispersal rates, and differential reproductive output of residents versus immigrants (see app. C in the online edition of the *American Naturalist*). Inbreeding load was assumed to increase linearly with coancestry among mating partners ($\delta = \gamma\theta$). Different discrimination abilities were obtained by varying e, the proportion of environmental variance in phenotypic traits due to differences among groups (see app. A in the online edition of the *American Naturalist*), while keeping heritability to 0. The cumulative normal distribution was approximated by the logistic function (Johnston and Kotz 1970).

Strong Inbreeding Depression

In the case of high inbreeding load ($\gamma = 2$; fig. 3), the ES dispersal rate for each sex crucially depends on what members of the other sex are doing. Whenever possible, females

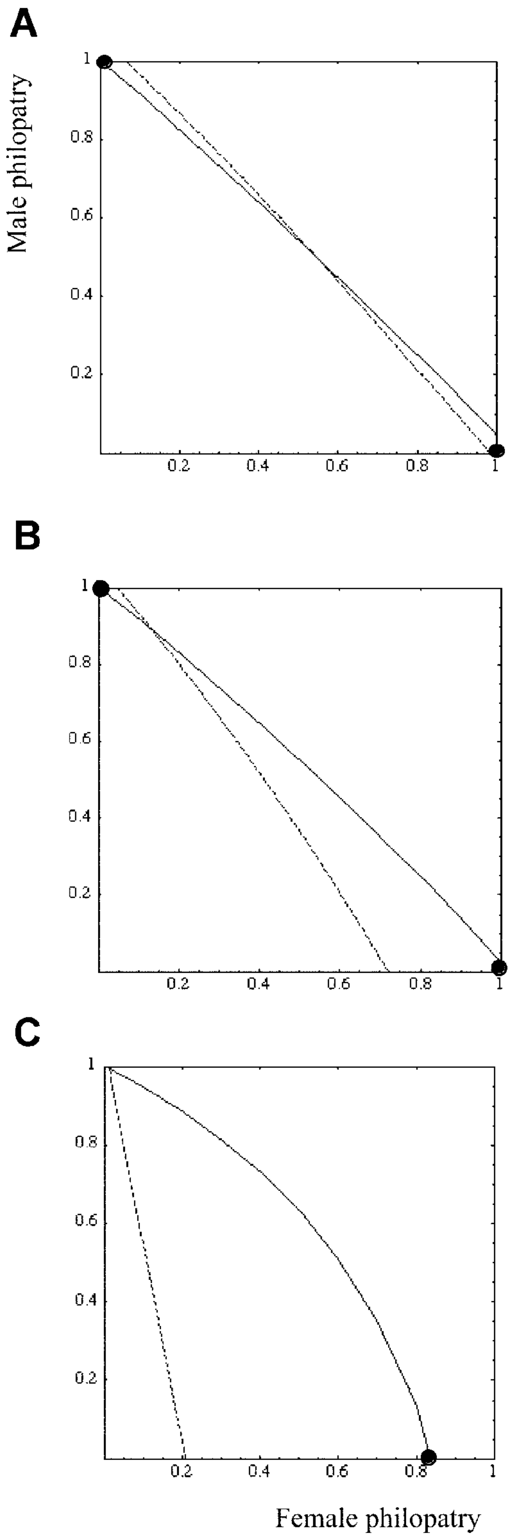

Figure 3: Best-response curves for male (*dashed line*) and female (*plain line*) philopatry when nonkin are preferred. Black dots indicate continuously stable strategies. Parameters values are set to $\gamma = 2$, $n = 10$, $s = 0.9$, and $h^2 = 0$. *A*, In absence of recognition ($e = 0$), the curves cross on the diagonal, and the two equilibriums have similar fields of attraction. *B*, Under weak recognition ($e = 0.01$), the field of attraction of the female-dispersal strategy develops at the expense of the male-dispersal strategy. *C*, With improved recognition ($e = 0.1$), the field of attraction of the female-philopatry equilibrium occupies the whole option set so that male dispersal becomes the only continuously stable strategy.

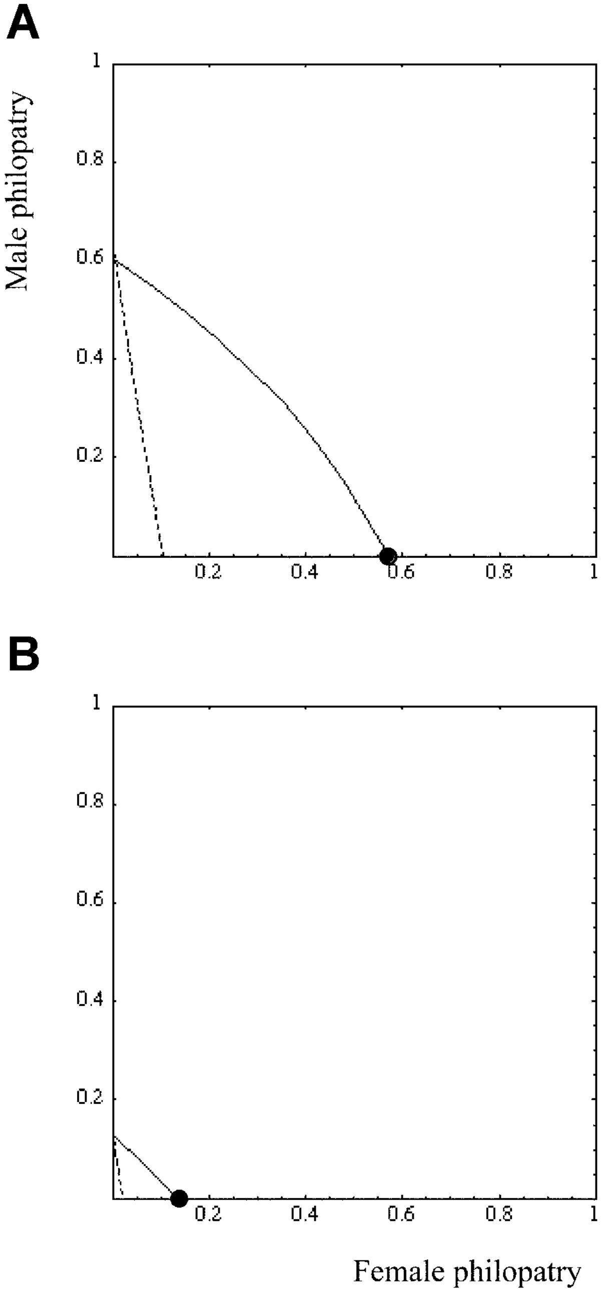

Figure 4: Same as figure 3*C* but with lower cost to dispersal. Dispersal increases in females as costs decrease. *A*, $e = 0.1$ and $s = 0.95$. *B*, $e = 0.1$ and $s = 0.99$.

should prefer immigrant males. As our results show, their ability to discriminate immigrants from among residents has contrasting effects on the ES dispersal strategies of the two sexes.

In absence of discrimination ($e = 0$; fig. 3*A*), the problem reduces to one already addressed by Motro (1991), Gandon (1999), and Perrin and Mazalov (1999). The ES dispersal curves are symmetrical and cross on the diagonal, but the inner equilibrium is unstable. Two continuously stable equilibria coexist on the borders, with similar domains of attraction. Sex bias is therefore complete at equilibrium, with only one sex dispersing, either male or female.

Adding a touch of discrimination ($e = 0.01$; fig. 3*B*) enhances male sensitivity to female behavior. The incentive for males to disperse is actually double because they are rejected by their female relatives and preferred by resident females if they disperse. This increase in sensitivity displaces the crossing of the curves away from the diagonal and decreases the domain of attraction of the male-philopatry equilibrium. The system is thus much more likely to evolve toward a male-biased dispersal.

Improving discrimination ($e = 0.1$; fig. 3*C*) further enhances male sensitivity to female dispersal. Females, by contrast, become less sensitive over most of the range of male dispersal values, owing to their better ability to pick the few immigrants for mating. Only when male philopatry is near complete should female dispersal increase (immigrant males are then so rarely met that dispersing becomes a valuable alternative). Female dispersal should be complete if all males decide to stay home. The ES curves cross on the border, so the domain of attraction of the male philopatry option vanishes. Male dispersal thus quickly becomes the only continuously stable strategy.

A decrease in dispersal costs pushes both ESS curves toward the left corner (fig. 4). As a result, the joint ESS shifts toward higher female dispersal. As costs vanish, kin competition avoidance is left unopposed, so dispersal prevails among both sexes.

No Inbreeding Depression

In absence of inbreeding load ($\gamma = 0$; fig. 5), the dispersal incentive for individuals stems mainly from competition with their same-sex relatives (competition for resources in females, competition for mates in males), which stabilizes the inner equilibrium. Whenever possible, females should prefer relatives. Their ability to discriminate immigrants from residents again has contrasting effects on the ES dispersal strategies of the two sexes.

In absence of recognition ($e = 0$; fig. 5*A*), the two curves cross on the diagonal, and the equilibrium is continuously stable (Gandon 1999; Perrin and Mazalov 2000). Both sexes disperse equally at equilibrium.

A weak discrimination ability ($e = 0.01$; fig. 5*B*) significantly reduces male dispersal. The incentive for philopatry is, again, double. Males are not only preferred by their female relatives but also rejected by resident females on foreign patches. The crossing point of the two ESSs thus shifts away from the diagonal into the domain of female-biased dispersal.

If discrimination still improves ($e = 0.1$; fig. 5*C*), male philopatry further increases, so the two curves do not cross anymore within the set of feasible solutions. The only equilibrium is boundary, with complete male philopatry and partial female dispersal.

A decrease in population size, unsurprisingly, results in higher dispersal for both sexes because of enhanced kin competition (cf., e.g., fig. 5*C* with fig. 6*A*). Interestingly, the male ESS becomes a nonmonotonic function of female philopatry (fig. 6). At high female dispersal (*left part of curve*), males have few incentives for philopatry. As female philopatry increases, males benefit more from philopatry (increased mating success). As philopatry further increases, however, kin competition among males is enhanced, which boosts dispersal. The effect of dispersal costs, finally, can be evaluated by comparing figure 6*A* with figure 6*C*. Low costs induce higher dispersal for both sexes.

Discussion

Our results show that mate choice by females in polygynous species has the potential to play a crucial role in the evolution of dispersal patterns. Its exact role, however, is expected to vary considerably with search costs, genetic load, and kin-discrimination ability.

When Female Choosiness Boosts Male Dispersal

Males usually are the dispersing sex in female defense systems (Greenwood 1980; Dobson 1982). Why is that so given that females are the sex paying the highest cost to inbreeding (and that inbreeding depression is pervasive in natural populations; Keller and Waller 2002)? Our results give a clear response to this question raised by Waser et al. (1986) and provide formalized support for a verbal argument originally proposed by Pusey and Packer (1986; see also Keane 1990*b*; Perrin and Goudet 2001). If females

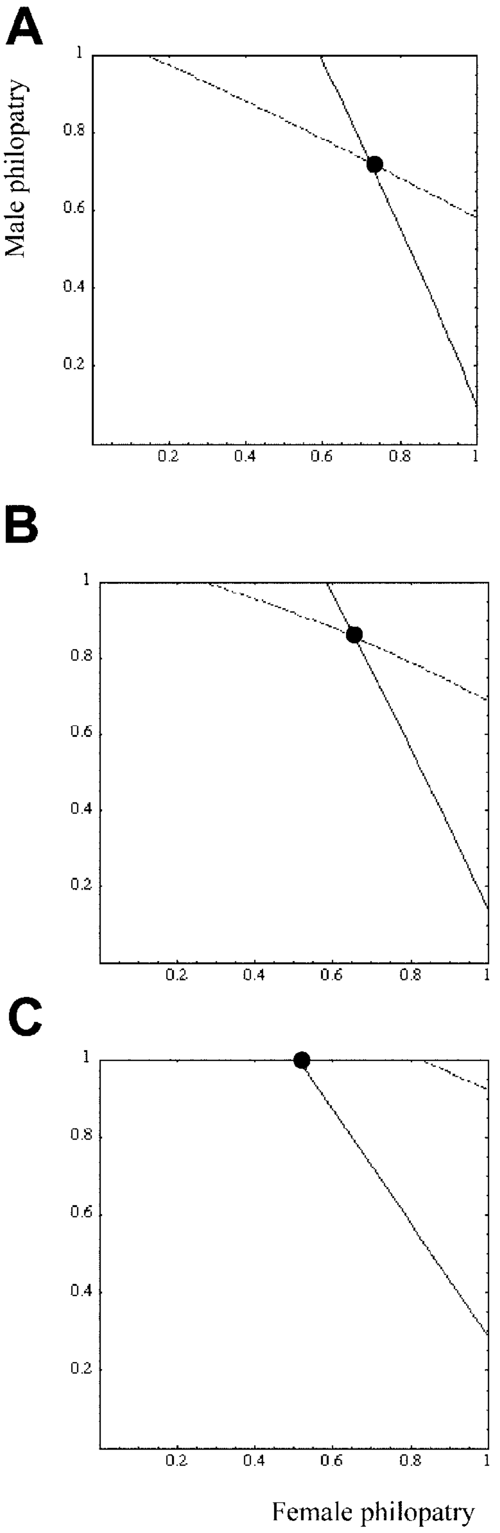

Figure 5: Same as figure 3, but kin are now preferred owing to low inbreeding load. Parameters set to $\gamma = 0$, $n = 10$, $s = 0.9$, and $h^2 = 0$. *A*, In absence of recognition ($e = 0$), the curves cross on the diagonal, defining there the only continuously stable strategy. *B*, Under weak recognition ($e = 0.01$), the equilibrium shifts toward male philopatry. *C*, With improved recognition ($e = 0.1$), male philopatry becomes complete.

can avoid inbreeding through mate choice, then males, rather than females, should be the dispersing sex.

Our assumptions and predictions are also consistent with field studies and experimental data showing not only that females can choose mates according to relatedness (e.g. Holmes and Sherman 1983) but also that rejection of related males can induce male dispersal. Packer's (1979) long-term study of olive baboons (*Papio anubis*), for instance, revealed that females prefer immigrant over resident males, with the result that emigration from local troops is strongly male biased. Cockburn et al. (1985) noted, in their study of the marsupial mouse *Antechinus* (a classic example of inbreeding-mediated, sex-biased dispersal; Harvey and Ralls 1986), that adult females evict their sons and accept unrelated males onto their breeding sites, which results in a strongly male-biased dispersal. In black-tailed prairie dogs (*Cynomys ludovicianus*), females avoid incest by kin recognition gained through direct social learning within breeding groups (Hoogland 1982, 1992). A yearling female is significantly less likely to come into estrus when her father is still in her natal coterie, and estrous females frequently refuse to copulate with close male kin but solicit copulations from unrelated males. As a result, young males depart from natal coteries before sexual maturity, and older males disperse to a new breeding coterie before their daughters reach sexual maturity. In white-footed mice (*Peromyscus leucopus*), estrous females are able to discriminate between males of different degrees of relatedness (Grau 1982) and avoid mating with close kin (Keane 1990*b*), which results in male dispersal (Keane 1990*a*).

Optimal Inbreeding

Interestingly, female white-footed mice seem to prefer mates with an intermediate degree of relatedness (Keane 1990*b*), a pattern also reported from other species of rodents (Barnard and Fitzsimons 1988) and birds (Bateson 1982; Burley et al. 1990). This outbreeding avoidance might allow preservation of coadapted gene complexes (Shields 1982; Templeton 1986), but this article raises the possibility of an alternative to this classic interpretation.

Indeed, even when inbreeding depresses their fecundity, females should not necessarily avoid it. Related males should be accepted if prospective depression lies

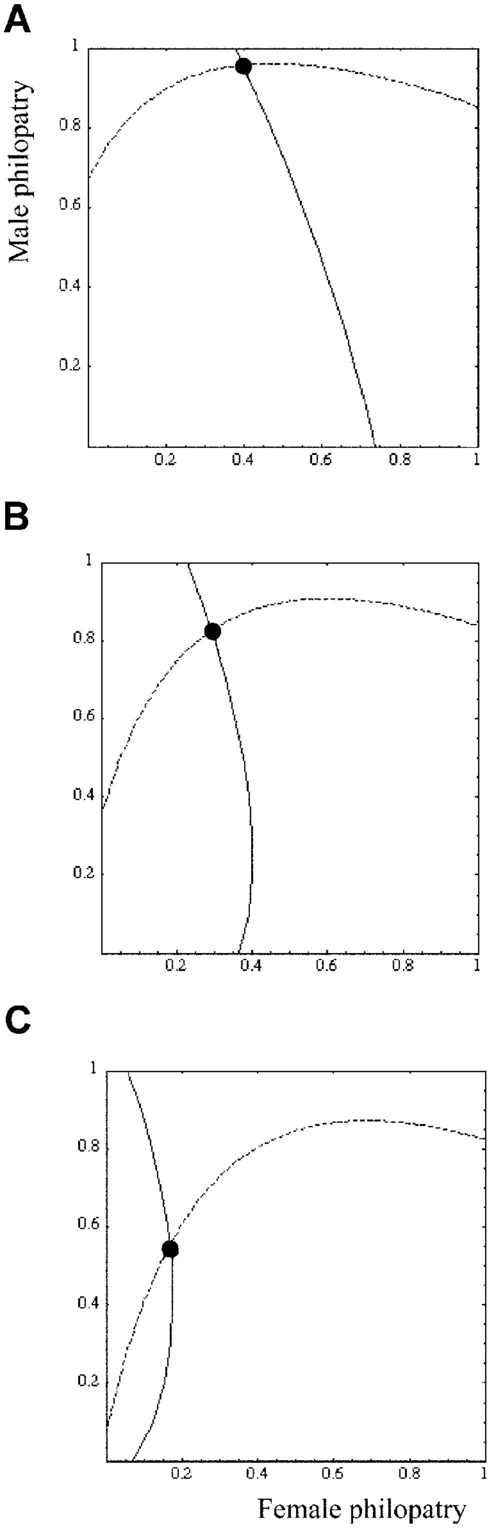

Figure 6: Same as figure 5*C* but with smaller patch size ($n = 5$) and increasing survival rate. Male best response becomes a nonmonotonic function of female philopatry because of the interplay between female preference and kin competition *A*, $e = 0.1$ and $s = 0.9$. *B*, $e = 0.1$ and $s = 0.95$. *C*, $e = 0.1$ and $s = 0.99$.

below a certain threshold determined by relatedness (in absence of search costs, the male is accepted if $\delta < r/(1 + r)$, and search costs further enhance the threshold; fig. 2). This might be thought of as an "altruistic" inbreeding because it increases the female inclusive fitness through the fecundity gains of her related partner. Inbreeding therefore bears costs (depression) but also brings inclusive benefits. An optimal inbreeding level results as a balance between inbreeding depression and kin selection. We show in appendix D in the online edition of the *American Naturalist* that in an otherwise outbred population, full brothers should be preferred as mating partners below 1.33 lethal equivalents per gamete, while completely unrelated individuals are to be preferred above two lethal equivalents. Choosing a partner of optimal relatedness, however, requires higher cognitive abilities than those underlying the simple dichotomous response envisaged in the present model.

When to Avoid Inbreeding?

The level of inbreeding depression required to satisfy condition (8) is surprisingly high. A female should avoid mating with a full brother only if her fecundity is thereby depressed by more than one-third and with a half sib if her fecundity is depressed by more than one-fifth. Empirical evidence suggests that as a rule of thumb, an increase in inbreeding by 10% leads to a reduction in fitness components of 5%–10% (Keller and Waller 2002). Accordingly, a full-sib mating is expected to incur a 15%–25% fitness depression. This expectation lies below the threshold delineated here (33%), implying that full-sib matings should be accepted in the general case.

This prediction clearly opposes empirical observations. Inbreeding avoidance mechanisms seem widespread, and close inbreeding is often avoided (Harvey and Ralls 1986; Pusey 1987; Pusey and Wolf 1996). This discrepancy might reflect higher inbreeding loads, which in some instances have been shown largely to exceed the threshold delineated here. Up to 6.3 lethal equivalents were documented in *Peromyscus leucopus* (Jimenez et al. 1994) and up to 7.5 in *Ficedula albicollis* (Kruuk et al. 2002). Furthermore, inbreeding loads currently documented may often underestimate δ (eq. [8]) because few studies are conducted in a way that is likely to reveal the full extent of depression in the wild, which will be reflected not only in adult fecundity but also in the survival and breeding success of any inbred young (e.g., Kruuk et al. 2002). This discrepancy, however, might also reflect the failure to meet one crucial assumption in the present model, namely that mating with a relative does not jeopardize other mating opportunities in males (see Waser et al. 1986). The threshold for inbreeding acceptance should obviously decrease if an inbred mating does forfeit, even partially, other reproductive opportunities. In particular, this threshold should drop to 0 under strict monogamy (assuming no search costs). Our model therefore predicts a correlation between mating system and the intensity of inbreeding avoidance. Interestingly, such a correlation has indeed been suggested among microtine rodents (Ferkin 1990). Inbreeding seems to be avoided in monogamous species such as *Microtus ochrogaster* (McGuire and Getz 1981), *Microtus pinetorum* (Schadler 1983), or *Microtus montanus* (Berger et al. 1997) but not in polygynous species such as *Microtus pennsylvanicus* (Batzli et al. 1977; Pugh and Tamarin 1988).

A Role for Mate Choice and Sexual Selection

In absence of discrimination, our results reduce to classic predictions. If, on the one hand, inbreeding is strong, then two stable equilibria coexist, with similar domains of attraction (fig. 3; Motro 1991; Gandon 1999; Perrin and Mazalov 1999). Adding discrimination in this case makes the system evolve toward complete male dispersal (fig. 3*C*). If, on the other hand, inbreeding is weak, the selective forces are dominated by kin competition, so one medium stable equilibrium remains (Gandon 1999; Perrin and Mazalov 2000). Including discrimination in that case makes the system evolve toward complete male philopatry (fig. 5).

Thus, one important outcome from this analysis is that female mate choice and discrimination put male dispersal under a form of disruptive sexual selection. Male philopatry is favored below the inbreeding-load threshold delineated by equation (8) and counterselected above this threshold. Male dispersal thereby presents the features of a secondary sexual character, which can, as morphological attributes often do, be strongly exaggerated by sexual selection, in one direction or the other, depending on which feature males should advertise.

Classical analyses of sexual selection categorize the mechanisms underlying sexual selection into either runaway processes or good-genes models (Andersson 1994). The mechanism delineated in this analysis clearly enters the second category. Good-genes models assume a viability advantage conferred by the selected males (Pen and Weissing 2000). This role is played here by the higher fecundity of choosy females in the case of inbreeding avoidance and by their inclusive benefits through related males in the case of inbreeding preference. Note, however, that the trait under sexual selection is genetic (dis)similarity, not dispersal per se. Selection on dispersal is always indirect and mediated through its correlation with genetic similarity.

Search Costs and Window of Tolerance

The main effect of search costs is to open a window of tolerance. In absence of costs, the conditions derived here behave as a threshold, so females should always reject some potential partners. The inclusion of costs creates a range of inbreeding loads for which any partner will be accepted, and this range widens as costs increase (fig. 2). This result may account for situations in which inbreeding is not avoided even when it is detrimental. Keller and Arcese (1998) developed a similar argument to explain why song sparrows (*Melospiza melodia*) do not avoid inbreeding despite a fairly large inbreeding load.

Conversely, this argument might also account for the reverse situation in which females do not mate preferentially with relatives even when inbreeding might bear inclusive benefits (e.g., Duarte et al. 2003) or when outbreeding is costly (e.g., LeBas 2002). Search costs, in the form of mortality risk, energetic losses, or time constraints, might thus select against mate choice in species that otherwise present all the cognitive abilities required for kin recognition.

Model Assumptions and Limitations

Our model relies on a series of simplifying assumptions that potentially limit the scope of our conclusions. However, we expect these simplifications to have only quantitative, and not qualitative, consequences (though delineating these consequences remains interesting).

As already mentioned, dropping the subscript j for the fecundity of the philopatric option in the fitness equations (eqq. [3], [4]) has only limited effects on the results. We derived the full model (not shown here) and found that the main effect of adding the subscript was to enhance slightly the critical inbreeding load (δ) for which females should switch to inbreeding avoidance and the more so when dispersal is low. Females thus become more likely to accept relatives. At the limit (i.e., when dispersal vanishes) and in absence of search costs, the critical δ tends to 1.

Discrimination in our model is unconditional in the sense that females always express choosiness both as residents and as immigrants. A plastic expression of discrimination might actually be favored because discrimination is always costly for immigrant females (as soon as search bears costs). Allowing for plasticity would select for a higher threshold, expressed in resident females only, and better discrimination. This would impose a still stronger selective pressure on male dispersal.

Note also that discrimination in our model is mediated by phenotype-matching kin recognition because these settings allow easy modulation of the quality of discrimination through a simple parameter shift. There is only scant evidence (e.g., Potts et al. 1991) for this sort of mechanisms in vertebrates, which more commonly rely on associative cues. Our results, however, would also apply to other discrimination mechanisms, be they perfect (corresponding to our situation where $e = 1$) or not ($e < 1$). In particular, the abrupt reversal of expectations predicted here would also occur under familiarity-based recognition because potential mates would still be accepted below a presumed level of relatedness and rejected above.

Finally, our infinite-island assumptions are certainly unrealistic because gene flow often decreases with distance among real populations and dispersal neighborhoods are limited in size. Owing to the ensuing isolation by distance, immigrant individuals might show a positive coancestry with the residents of the patch they are entering. The point remains, however, that resident females would still be less related to immigrant than to resident males, so the patterns predicted here should remain qualitatively similar. Introducing isolation by distance in evolutionary models usually adds significant mathematical complexity, with only weak quantitative consequences in terms of predicted outcomes (e.g., Gandon and Rousset 1999; Irwin and Taylor 2001).

Acknowledgments

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APPENDIX A

Table A1: Symbols used in the model

Symbol	Definition
N	Number of breeding females per patch
x	Female dispersal probability
y	Male dispersal probability
s	Survival probability during dispersal
$k_x = \tilde{x}/(\tilde{x} + sx)$	Probability that a breeding female was born locally
$k_y = \tilde{y}/(\tilde{y} + sy)$	Probability that a mating male was born locally
δ	Inbreeding depression
e	Proportion of the environmental variance in phenotypic traits due to differences among groups
h^2	Heritability of a trait (proportion of phenotypic variance that is additive genetic)
$\bar{\eta} = rh^2 + (1 - h^2)e$	Expectation of phenotypic similarity among patch mates
n	Number of indicator traits scanned during the kin-recognition process
t	Similarity threshold for mate acceptance
a_{r_τ}	Probability that a female perceives similarity τ to a related male. Perceived similarity may range from $-\infty$ to $+\infty$, though its expectation ($\bar{\eta}$) ranges from 0 to 1 (fig. 1)
a_{u_τ}	Probability that a female perceives similarity τ to an unrelated male (fig. 1)
$A_{\mathrm{r}_\mathrm{t}} \equiv \int_{\tau=t}^{-\infty} a_{\mathrm{r}\tau} d\tau$	Probability of accepting a related mate when nonkin are preferred
$A_{\mathrm{u}_\mathrm{t}} \equiv \int_{\tau=t}^{-\infty} a_{\mathrm{u}\tau} d\tau$	Probability of accepting an unrelated mate when nonkin are preferred
$\tilde{A}_{\mathrm{r}_\mathrm{t}} \equiv \int_{\infty}^{\tau=t} a_{\mathrm{r}\tau} d\tau$	Probability of accepting a related mate when kin are preferred
$\tilde{A}_{\mathrm{u}_\mathrm{t}} \equiv \int_{\infty}^{\tau=t} a_{\mathrm{u}\tau} d\tau$	Probability of accepting an unrelated mate when kin are preferred
m_p	Average progeny of a breeding philopatric female
m_d	Average progeny of a breeding dispersing female
m_r	Average fecundity of a mating among residents
$m = k_x m_\mathrm{p} + \tilde{k}_x m_\mathrm{d}$	Average fecundity per female in the whole metapopulation
θ	Average coancestry among individuals born on the same patch (probability that alleles sampled from two individuals are identical by descent)
F	Average inbreeding (probability that an individual bears two alleles identical by descent)
$r = 2\theta/(1 + F)$	Average relatedness among individuals born on the same patch
ϕ	Level of polygyny, probability that two females have mated with the same male
P_i	Probability that two offspring share a same parent of sex i

Note: Traits have subscript bullet when expressed in the focal individual. Subscript j designates average value of the trait in individuals from the same patch as the focal individual (and bearing with it relatedness r), and absence of subscript denotes the average value for the whole metapopulation. Tilde denotes the complement to unity (e.g., $\tilde{x} \equiv 1 - x$).

Literature Cited

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, N.J.

Barnard, C. J., and J. Fitzsimons. 1988. Kin recognition and mate choice in mice: the effects of kinship, familiarity and interference on intersexual selection. Animal Behaviour 36:1078–1090.

Bateson, P. 1982. Preference for cousins in Japanese quail. Nature 295:236–237.

Batzli, G. O., L. L. Getz, and S. S. Hurley. 1977. Suppression of growth and reproduction of microtine rodents by social factors. Journal of Mammalogy 58:583–591.

Berger, P. J., N. C. Negus, and M. Day. 1997. Recognition of kin and avoidance of inbreeding in the montane vole, *Microtus montanus*. Journal of Mammalogy 78:1182–1186.

Blouin, S. F., and M. Blouin. 1988. Inbreeding avoidance behaviors. Trends in Ecology & Evolution 3:230–233.

Burley, N., C. Minor, and C. Strachan. 1990. Social preference of zebra finches for siblings, cousins and nonkin. Animal Behaviour 39:775–784.

Cockburn, A., M. P. Scott, and D. J. Scotts. 1985. Inbreeding avoidance and male-biased natal dispersal in *Antechinus* ssp. (Marsupialia: Dasyuridae). Animal Behaviour 33:908–915.

Dobson, F. S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. Animal Behaviour 30:1183–1192.

Duarte, L. C., C. Bouteiller, P. Fontanillas, E. Petit, and N. Perrin. 2003. Inbreeding in the greater white-toothed shrew, *Crocidura russula*. Evolution 57:638–645.

Ferkin, M. H. 1990. Kin recognition and social behavior in microtine rodents. Pages 11–24 *in* R. Tamarin, R. S. Ostfeld, S. R. Pugh, and G. Bujalska, eds. Social systems and population cycles in voles. Birkhäuser, Boston.

Frank, S. A. 1997. Multivariate analysis of correlated selection and kin selection, with an ESS maximization method. Journal of Theoretical Biology 189:307–316.

———. 1998. Foundations of social evolution. Princeton University Press, Princeton, N.J.

Gandon, S. 1999. Kin competition, the cost of inbreeding, and the evolution of dispersal. Journal of Theoretical Biology 200:345–364.

Gandon, S., and F. Rousset. 1999. Evolution of stepping-stone dispersal rates. Proceedings of the Royal Society of London B, Biological Sciences 266:2507–2513.

Grau, H. J. 1982. Kin recognition in white-footed deermice (*Peromyscus leucopus*). Animal Behaviour 30:497–505.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28: 1140–1162.

———. 1983. Mating systems and the evolutionary consequences of dispersal. Pages 116–131 *in* I. R. Swingland and P. J. Greenwood, eds. The ecology of animal movement. Clarendon, Oxford.

Harvey, P. H., and K. Ralls. 1986. Do animals avoid incest? Nature 320:575–576.

Holmes, W. G., and P. W. Sherman. 1983. Kin recognition in animals. American Scientist 71:46–55.

Hoogland, J. L. 1982. Prairie dogs avoid extreme inbreeding. Science 215:1639–1641.

———. 1992. Level of inbreeding among prairie dogs. American Naturalist 139:591–602.

Irwin, A. J., and P. D. Taylor. 2001. Evolution of altruism in stepping-stone populations with overlapping generations. Theoretical Population Biology 60:315–325.

Jimenez, J. A., K. A. Hughes, G. Alaks, L. Graham, and R. C. Lacy. 1994. An experimental study of inbreeding depression in a natural habitat. Science 266:271–273.

Johnson, N. L., and S. Kotz. 1970. Continuous univariate distributions. Houghton Mifflin, Boston.

Keane, B. 1990*a*. Dispersal and inbreeding avoidance in the white-footed mouse, *Peromyscus leucopus*. Animal Behaviour 40:143–152.

———. 1990*b*. The effect of relatedness on reproductive success and mate choice in the white-footed mouse, *Peromyscus leucopus*. Animal Behaviour 39:264–273.

Keller, L. F., and P. Arcese. 1998. No evidence for inbreeding avoidance in a natural population of song sparrows (*Melospiza melodia*). American Naturalist 152:380–392.

Keller, L. F., and D. M. Waller. 2002. Inbreeding effects in wild populations. Trends in Ecology & Evolution 17: 230–241.

Kruuk, L. E. B., B. C. Sheldon, and J. Merila. 2002. Severe inbreeding depression in collared flycatchers (*Ficedula albicollis*). Proceedings of the Royal Society of London B, Biological Sciences 269:1581–1589.

LeBas, N. 2002. Mate choice, genetic incompatibility, and outbreeding in the ornate dragon lizard, *Ctenophorus ornatus*. Evolution 56:371–377.

Lehmann, L., and N. Perrin. 2002. Altruism, dispersal and phenotype-matching kin recognition. American Naturalist 159:451–468.

McGuire, M. R., and L. L. Getz 1981. Incest taboo between sibling *Microtus ochrogaster*. Journal of Mammalogy 62: 213–215.

Motro, U. 1991. Avoiding inbreeding and sibling competition: the evolution of sexual dimorphism for dispersal. American Naturalist 137:108–115.

Nagylaki, T. 1995. The inbreeding effective population number in dioecious populations. Genetics 139:473–485.

Packer, C. 1979. Inter-troop transfer and inbreeding avoidance in *Papio anubis*. Animal Behaviour 27:1–36.

Parker, G. A. 1979. Sexual selection and sexual conflict. Pages 123–166 *in* M. S. Blum and N. A. Blum, eds. Sexual selection and reproductive competition in insects. Academic Press, New York.

———. 1983. Mate quality and mating decisions. Pages 141–164 *in* P. Bateson, ed. Mate choice. Cambridge University Press, Cambridge.

Pen, I., and J. Weissing. 2000. Sex allocation and sexual selection: an ESS analysis. Selection 1:111–121.

Perrin, N., and J. Goudet. 2001. Inbreeding, kinship, and the evolution of natal dispersal. Pages 123–142 *in* J. Clobert, A. Danchin, A. A. Dhondt, and J. Nichols, eds. Dispersal. Oxford University Press, Oxford.

Perrin, N., and V. Mazalov. 1999. Dispersal and inbreeding avoidance. American Naturalist 154:282–292.

———. 2000. Local competition, inbreeding, and the evolution of sex-biased dispersal. American Naturalist 155: 116–127.

Potts, W. K., C. J. Manning, and E. K. Wakeland. 1991. Mating patterns in semi-natural populations of mice influenced by MHC genotype. Nature 352:619–621.

Pugh, S. H., and R. H. Tamarin. 1988. Inbreeding in a population of meadow voles, *Microtus pennsylvanicus*. Canadian Journal of Zoology 66:1831–1834.

Pusey, A. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends in Ecology & Evolution 2:295–299.

Pusey, A., and C. Packer 1986. Dispersal and philopatry. Pages 250–266 *in* B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker, eds. Primate societies. University of Chicago Press, Chicago.

Pusey, A., and M. Wolf. 1996. Inbreeding avoidance in animals. Trends in Ecology & Evolution 11:201–206.

Reeve, H. K. 1989. The evolution of conspecific acceptance thresholds. American Naturalist 133:407–435.

Schadler, M. H. 1983. Male siblings inhibit reproductive activity in female pine voles, *Microtus pinetorum*. Biology of Reproduction 28:1137–1139.

Schields, W. M. 1982. Philopatry, inbreeding, and the evolution of sex. University of New York Press, Albany.

Smith, R. H. 1979. On selection for inbreeding in polygynous animals. Heredity 43:205–211.

Taylor, P. D., and S. A. Frank. 1996. How to make a kin selection model. Journal of Theoretical Biology 180:27–37.

Templeton, A. R. 1986. Coadaptation and outbreeding depression. Pages 105–116 *in* M. E. Soulé, ed. Conservation biology. Sinauer, Sunderland, Mass.

Wang, J. 1997. Effective size and *F*-statistics of subdivided populations. II. Dioecious species. Genetics 146:1465–1474.

Waser, P. M., S. N. Austad, and B. Keane. 1986. When should animals tolerate inbreeding? American Naturalist 128:529–537.

Wolfram, S. 1991. Mathematica: a system for doing mathematics by computer. 2d ed. Addison-Wesley, Redwood City, Calif.

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Our treatment of phenotype-matching kin recognition is identical to that of Lehmann and Perrin (2002), to which we refer for further details. Phenotype matching relies on the similarity between the focal individual and potential partners with respect to a series (say, n) of uncorrelated recognition traits. These traits have both environmental and genetic components (the latter assumed additive only for simplicity), and they are normally distributed and standardized for the analysis. From the point of view of a focal individual, the maximum likelihood estimate of its similarity with a partner is given by the coefficient of regression η of the phenotype of this partner on its own phenotype. The expectation of η is obtained as

$$\bar{\eta} = rh^2 + e(1 - h^2), \qquad \text{(B1)}$$

where r measures the relatedness of the focal individual to its patch mates (equal to the proportion of genetic variance due to among-patches differences), h^2 is the heritability of the traits (proportion of phenotypic variance which is additive genetic), and e is the proportion of environmental variance due to among-patches differences. The sampling variance of η around this expectation is obtained as

$$\sigma_\eta^2 = \frac{1 - \bar{\eta}^2}{n}. \qquad \text{(B2)}$$

Figure 1*A* illustrates the normal distribution of perceived similarities with both unrelated (a_u) and related (a_r) partners. A threshold (t) allows us to separate these two sets of potential mates, mating being accepted only if recipients are less similar (fig. 1*A*) or more similar (fig. 1*B*) than t is to the focal individual.

Appendix CDynamics of Relatedness

Go to

General Equations

The recurrence equation for inbreeding is obtained by noting that the inbreeding coefficient of an offspring equals the coancestry among its parents. Under our infinite-island assumptions, inbreeding accrues only insofar as both parents of a random offspring were resident:

$$F_{t+1} = k_x k_y \frac{A_r}{A} \frac{m_r}{m} \theta_t, \qquad \text{(C1)}$$

where $k_x k_y$ measures the probability that a random male and a random female are both resident, A_r/A is the probability that a resident female mates with a resident male, m_r/m is the relative fecundity of a mating among residents ($m_r = 1 - \delta - (c_s/A_r)$), and θ_t is their coancestry.

Our recurrence equation for coancestry (probability that two alleles randomly taken from different offspring are identical by descent [IBD]) is derived along the lines proposed by Wang (1997) for the general structure and Nagylaki (1995) for the specific relationships. First, with probability of one-fourth, both alleles were inherited along the paternal lines. If the offspring share the same father, then IBD probability is $(1 + F_t)/2$. If fathers differ, then IBD probability equals their coancestry. Under infinite-island assumptions, this means θ_t if both fathers were born locally and 0 otherwise. Thus, paternal descent ensures a coancestry of

$$\frac{1}{4}\left(P_{\mathrm{m}}\frac{1+F_t}{2} + Q_{\mathrm{m_{pp}}}\theta_t\right), \qquad \text{(C2a)}$$

where P_{m} is the probability that two random offspring share the same father and $Q_{\mathrm{m\ pp}}$ is the probability that their fathers differed but were both resident.

Second, with probability of one-fourth, both alleles were inherited from mothers. Using the same reasoning, maternal descent ensures a coancestry of

$$\frac{1}{4}\left(P_{\mathrm{f}}\frac{1+F_t}{2} + Q_{\mathrm{f_{pp}}}\theta_t\right), \qquad \text{(C2b)}$$

where P_{f} is the probability that two random offspring share the same mother and $Q_{\mathrm{f\ pp}}$ is the probability that their mothers differed but were both resident.

Finally, with probability of one-half, these alleles were inherited, one from a mother and one from a father. The IBD probability in that case equals the expected coancestry among these parents, $Q_{\mathrm{fm\ pp}}\,\theta_t$, where $Q_{\mathrm{fm\ pp}}$ measures the probability that both paternal and maternal alleles stem from resident parents.

Collecting all these terms provides the recurrence equation for coancestry

$$\theta_{t+1} = \frac{1}{4}\left[(P_{\mathrm{m}} + P_{\mathrm{f}})\left(\frac{1+F_t}{2}\right) + (Q_{\mathrm{m_{pp}}} + Q_{\mathrm{f_{pp}}} + 2Q_{\mathrm{fm_{pp}}})\theta_t\right]. \qquad \text{(C3)}$$

Because $r = 2\theta/(1 + F)$, dividing both sides by $(1 + F_t)/2$ provides the corresponding equation for relatedness. At equilibrium ($r_{t+1} = r_t = r$), we thus obtain

$$r = \frac{P_{\mathrm{m}} + P_{\mathrm{f}}}{4 - Q_{\mathrm{m_{pp}}} - Q_{\mathrm{f_{pp}}} - 2Q_{\mathrm{fm_{pp}}}}. \qquad \text{(C4)}$$

Specific Relationships

Maternal Genes.

The probability that two offspring share the same mother is given by

$$P_{\mathrm{f}} = P_{\mathrm{f_p}} + P_{\mathrm{f_d}}, \qquad \text{(C5a)}$$

where

$$P_{\mathrm{f_d}} = N\tilde{k}_x \frac{\sigma_{\mathrm{d}}^2 + m_{\mathrm{d}}(m_{\mathrm{d}} - 1)}{Nm(Nm - 1)} \qquad \text{(C5b)}$$

is the probability that two random offspring share the same immigrant mother and

$$P_{\mathrm{f_p}} = Nk_x \frac{\sigma_{\mathrm{p}}^2 + m_{\mathrm{p}}(m_{\mathrm{p}} - 1)}{Nm(Nm - 1)} \qquad \text{(C5c)}$$

is the corresponding probability for a resident mother. From the multinomial distribution of reproductive success, the variances in the progeny of immigrant and resident mothers are

$\sigma_{\mathrm{d}}^2 = m_{\mathrm{d}}[1 - (m_{\mathrm{d}}/N_{\mathrm{m}})]$ and $\sigma_{\mathrm{p}}^2 = m_{\mathrm{p}}[1 - (m_{\mathrm{p}}/N_{\mathrm{m}})]$, respectively. Substituting these

values into equations (C5) provides $P_{\mathrm{f_d}} = \tilde{k}_x m_{\mathrm{d}}^2/Nm^2$, $P_{\mathrm{f_p}} = k_x m_{\mathrm{p}}^2/Nm^2$, and

$P_{\mathrm{f}} = (k_x m_{\mathrm{p}}^2 + \tilde{k}_x m_{\mathrm{d}}^2)/Nm^2$.

The complementary probability that two offspring have different mothers is given by

$$Q_{\mathrm{f}} = Q_{\mathrm{f_{pp}}} + Q_{\mathrm{f_{dd}}} + Q_{\mathrm{f_{pd}}}, \qquad \text{(C6a)}$$

where

$$Q_{\mathrm{f_{pp}}} = \frac{k_x N(k_x N - 1)(m_{\mathrm{p}}^2 + \rho_{\mathrm{pp}})}{Nm(Nm - 1)} \qquad \text{(C6b)}$$

corresponds to the case when both mothers are resident,

$$Q_{\mathrm{f_{dd}}} = \frac{\tilde{k}_x N(\tilde{k}_x N - 1)(m_{\mathrm{d}}^2 + \rho_{\mathrm{dd}})}{Nm(Nm - 1)} \qquad \text{(C6c)}$$

corresponds to the case when both are immigrant, and

$$Q_{\mathrm{f_{pd}}} = 2\frac{k_x \tilde{k}_x N^2(m_{\mathrm{d}} m_{\mathrm{p}} + \rho_{\mathrm{dp}})}{Nm(Nm - 1)} \qquad \text{(C6d)}$$

corresponds to the case when one is immigrant while the other is resident. Note that equation (C6b) corrects the mistaken equation (B4b) in Lehmann and Perrin (2002). In all cases, ρ_{ij} is the covariance in offspring number for females from class *i* and *j*. From the multinomial distribution of reproductive success, the covariances in the progeny of two immigrants, two residents, and one resident and one immigrant mother are

$\rho_{\mathrm{dd}} = -mN(m_{\mathrm{d}}/m_N)(m_{\mathrm{d}}/m_N)$, $\rho_{\mathrm{pp}} = -mN(m_{\mathrm{p}}/m_N)(m_{\mathrm{p}}/m_N)$, and

$\rho_{\mathrm{dp}} = -mN(m_{\mathrm{d}}/m_N)(m_{\mathrm{p}}/m_N)$, respectively. Substituting these values into equations (C6) provides: $Q_{\mathrm{f}_{\mathrm{pp}}} = [k_x(k_xN-1)m_{\mathrm{p}}^2]/Nm^2$, $Q_{\mathrm{f}_{\mathrm{dd}}} = [\tilde{k}_x(\tilde{k}_xN-1)m_{\mathrm{d}}^2]/Nm^2$, and $Q_{\mathrm{f}_{\mathrm{pd}}} = 2(k_xm_{\mathrm{p}}\tilde{k}_xm_{\mathrm{d}}/m^2)$.

Paternal Genes.

Owing to our assumption that females mate only once, two offspring from the same mother necessarily share the same father. Besides this, owing to polygyny, two offspring with different mothers may nevertheless share the same father. We thus obtain

$$P_{\mathrm{m}} = P_{\mathrm{f}} + \sum_{ij=\mathrm{p,d}} Q_{\mathrm{f}ij}\phi_{ij}, \qquad \text{(C7)}$$

where φ_{ij} is the probability that two females of classes *i* and *j*, respectively, have mated with the same male. This can be decomposed as: $\phi_{ij} = \phi_{ij_{\mathrm{p}}} + \phi_{ij_{\mathrm{d}}}$ (i.e., the probabilities that two females of classes *i* and *j* have been fertilized by the same resident or dispersing male, respectively). Namely, $\phi_{\mathrm{dd}_{\mathrm{p}}} = k_y/N$, $\phi_{\mathrm{dd}_{\mathrm{d}}} = \tilde{k}_y/N$, $\phi_{\mathrm{pd}_{\mathrm{p}}} = (k_y/N)(A_{\mathrm{p}}/A)$, $\phi_{\mathrm{pd}_{\mathrm{d}}} = (\tilde{k}_y/N)(A_{\mathrm{d}}/A)$, $\phi_{\mathrm{pp}_{\mathrm{p}}} = (k_y/N)(A_{\mathrm{p}}/A)^2$, and $\phi_{\mathrm{pp}_{\mathrm{d}}} = (\tilde{k}_y/N)(A_{\mathrm{d}}/A)^2$.

The probability that two offspring have different but resident fathers is given by $Q_{\mathrm{m}_{\mathrm{pp}}} = Q_{\mathrm{f}_{\mathrm{pp}}}\phi_{\mathrm{pp}_{\mathrm{pp}}} + Q_{\mathrm{f}_{\mathrm{pd}}}\phi_{\mathrm{pd}_{\mathrm{pp}}} + Q_{\mathrm{f}_{\mathrm{dd}}}\phi_{\mathrm{dd}_{\mathrm{pp}}}$, where $\phi_{\mathrm{pp}_{\mathrm{pp}}} = (Nk_yA_{\mathrm{p}}/NA)[(Nk_y-1)A_{\mathrm{p}}/NA]$ is the probability that two resident females have been fertilized by two different resident males, $\phi_{\mathrm{pd}_{\mathrm{pp}}}\ (Nk_yA_{\mathrm{p}}/NA)[(Nk_y-1)/N]$ is the probability that a resident female and an immigrant female have been fertilized by two different philopatric males, and $\phi_{\mathrm{dd}_{\mathrm{pp}}} = (Nk_y/N)[(Nk_y-1)/N]$ is the probability that two immigrant females have been fertilized by two distinct resident males.

Finally, the probability that the mother of a random offspring and the father of another random offspring were both resident is given by

$$Q_{\mathrm{fm}_{\mathrm{pp}}} = \left(\frac{k_xm_{\mathrm{p}}}{m}\right)\left(\frac{k_yA_{\mathrm{p}}}{A}\frac{k_xm_{\mathrm{p}}}{m} + \frac{k_y\tilde{k}_xm_{\mathrm{d}}}{m}\right).$$

Appendix DOptimal Inbreeding

Go to

Mating with a relative (instead of an unrelated male) bears direct costs to a female because her fecundity thereby decreases from 1 to $1 - \delta$. But it also provides benefits to the related male, whose fecundity is increased by the same amount $(1 - \delta)$. The ensuing inclusive benefits may thus counterbalance the direct costs. The optimal inbreeding problem, therefore, is one of choosing a male whose relatedness maximizes $(1 + r)(1 - \delta)$. In particular, a related male should be preferred over an unrelated whenever $(1 + r)(1 - \delta) > 1$ (i.e., when $\delta < r/(1 + r)$).

Noting that $r = 2\theta/(1 + F)$, and assuming that inbreeding costs increase linearly with the coancestry among mating partners ($\delta = \gamma\theta$; Perrin and Goudet 2001), then the optimal-inbreeding problem becomes

$$\max_{\theta}\left(1 + \frac{2\theta}{1 + F}\right)(1 - \gamma\theta). \qquad \text{(D1a)}$$

The optimal coancestry is obtained by setting to 0 the derivative of equation (D1a) with respect to θ (while keeping *F* constant because it represents the inbreeding level of the choosing female). Hence:

$$\hat{\theta} = \frac{2 - \gamma(1 + F)}{4\gamma}. \qquad \text{(D1b)}$$

Thus, in an otherwise outbred population ($F = 0$), the optimal mate is a full brother if $\gamma = 1$, and an unrelated mate will always be preferred as soon as γ reaches 2.

One might prefer to model inbreeding depression as an exponential negative: ($\delta = 1 - e^{-\beta\theta}$) because β then directly expresses a number of lethal equivalents per gamete (Keller and Waller 2002). Under such settings, the optimal-inbreeding problem becomes

$$\max_{\theta}\left(1 + \frac{2\theta}{1 + F}\right)e^{-\beta\theta}. \qquad \text{(D2a)}$$

Hence:

$$\hat{\theta} = \frac{2 - \beta(1 + F)}{2\beta}. \qquad \text{(D2b)}$$

Thus, in an otherwise outbred population, the optimal mating partner will be a full brother for a number of lethal equivalents equal to 1.33, and unrelated partners should always be preferred as soon as β reaches 2.