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# Sex Differences in Dispersal and the Evolution of Helping and Harming

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abstract: In this article, we explore the impact of sex-biased dispersal on local relatedness and on selection for helping and harming behavior among males and females. We show that in a patch-structured population, when there is a marked sex bias in dispersal, selection will almost always favor harming behavior among individuals of the sex more prone to dispersal. This result holds regardless of the effects of mating skew or overlapping generations. Selection may well also favor helping behavior among individuals of the philopatric sex, particularly if there is generational overlap, but this is less likely to occur if individuals of the philopatric sex compete more intensely for fewer breeding opportunities. In this last case, if generational overlap is low and mating skew pronounced, the result may be selection for harming behavior among both males and females. In general, the rate of dispersal and the level of relatedness among individuals of one sex do not reliably predict their level of helping or harming behavior; selection on either males or females depends on the dispersal of both sexes.

*Keywords:* kin selection, kin competition, dispersal, helping, sex differences.

The theory of kin selection suggests that selection can favor altruistic actions, which are beneficial to others but costly to the actor, when these actions are directed preferentially toward relatives (Hamilton 1964*a*, 1964*b*). This might involve active kin discrimination on the part of the altruist. Alternatively, and more controversially, indiscriminate altruism might be favored if limited dispersal leads to high levels of local relatedness in a population (Hamilton 1964*a*, 1964*b*). Such constraints on dispersal ensure that individuals will interact mainly with relatives, without any need for active discrimination on their part.

The idea of indiscriminate altruism based on local relatedness has been controversial, because limited dispersal also leads to local competition among relatives. This reduces the payoff to helping kin, because any fecundity benefits conferred on one relative are likely to reduce the fitness of other competing relatives and that of the helper itself (Hamilton 1975; Queller 1992; Taylor 1992*a*, 1992*b*; Wilson et al. 1992; West et al. 2002). Indeed, the first explicit models of this issue showed that in simple structured populations with nonoverlapping generations, indiscriminate helping (behavior that confers fecundity gains on others at a cost to the fecundity of the actor) will never be favored, regardless of the level of dispersal (Taylor 1992*a*, 1992*b*; Wilson et al. 1992). However, subsequent work has shown that when the demographic assumptions of the original models are altered, limited dispersal can favor local helping (van Baalen and Rand 1998; Mitteldorf and Wilson 2000; Taylor and Irwin 2000; Irwin and Taylor 2001; Le Galliard et al. 2003; Gardner and West 2006; Lehmann et al. 2006*b*; Lehmann 2007). Perhaps the simplest such alteration in a patch-structured model is the introduction of overlapping generations (Taylor and Irwin 2000; Irwin and Taylor 2001); others include patch elasticity (Taylor 1992*a*; Lehmann et al. 2006*b*) and budding dispersal (Gardner and West 2006; Lehmann et al. 2006*b*). Helping may also be favored when benefits persist over time (Lehmann 2007).

Curiously, most existing models of local helping have paid little attention to the issue of sex differences in such behavior. Taylor (1992*b*, p. 302) showed that, in a population arrayed on a homogeneous, inelastic lattice, if "dispersal patterns are sex specific, selection may … act on fitness donations made to neighbours" but concluded that "the direction of this selection is not clear, and further work should be done on this question." The only further

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work of this kind of which we are aware, however, is that of Kawata (1998), who presents simulation results suggesting that male-biased dispersal in a lattice-structured population can promote helping (albeit only to a slight extent). Analyses of patch-structured populations have generally either focused on the simple case of an asexual population (Taylor 1992*a*; Taylor and Irwin 2000; Irwin and Taylor 2001; Gardner and West 2006) or, if they allow for sexual reproduction, assumed either that males die immediately after mating in their natal patch (Taylor 1992*a*) or that male and female dispersal rates are identical (Lehmann et al. 2006*b*; Lehmann 2007 shows that transgenerational helping can be favored given sex differences in dispersal but does not otherwise explore the effects of such differences). Only Gardner et al. (2007*b*) consider the impact of sex-biased dispersal in a model tailored to one particular biological context, the production of a sterile solider caste in polyembryonic wasps.

In this article, we extend the patch-structured model of Taylor (1992*a*) to allow for sex differences in dispersal and determine the resulting patterns of sex-specific local relatedness and of sex-specific selection on helping and harming behavior. To increase the generality of our analysis, we also explore how sex-biased dispersal interacts with overlapping generations and with mating skew to influence selection on females and males. Our approach is similar to that adopted in previous studies (Taylor 1992*a*; Taylor and Irwin 2000; Gardner and West 2006; Lehmann et al. 2006*b*): we specify rates of dispersal and, from these, derive the equilibrium levels of relatedness among males and females in a patch. Then, on the basis of the coefficients of relatedness we have derived, we can determine the inclusive fitness consequences of helping or harming behaviors that entail a fecundity cost for the actor but also affect (positively or negatively) the fecundity of other local breeders (taking into account the effect of such actions on the intensity of kin competition).

Our chief motivation in developing these models has been their relevance to vertebrate societies (including, potentially, those of ancestral humans). Local helping is potentially important in social vertebrates (e.g., cooperatively breeding birds and mammals, including primates) because there are usually restrictions on dispersal in these species as a result of shortages in suitable breeding habitats (Brown 1969, 1987; Emlen 1982; Koenig et al. 1992; Hatchwell and Komdeur 2000), predation risks outside the group (Brown 1987; Waser et al. 1994), or group defense against immigrants (Gaston 1978; Higashi and Yamamura 1993; Cant et al. 2001). Moreover, in vertebrate societies, both males and females often have the opportunity to influence the fitness of others, and they often differ markedly in their level of dispersal. Indeed, there exists a large literature (both theoretical and empirical) documenting such differences and attempting to explain their evolution in an adaptive manner (Greenwood 1980; Greenwood and Harvey 1983; Motro 1983, 1991; Liberg and von Schantz 1985; Pusey and Packer 1987; Clutton-Brock 1989; Waser et al. 1994; Clarke et al. 1997; Perrin and Mazalov 1999; Kokko and Ekman 2002; Wild and Taylor 2004; for a recent review, see Handley and Perrin 2007). We might therefore expect selection to favor sex differences in the degree of local helping (Cockburn 1998; Clutton-Brock et al. 2002).

We use the terms "helping" and "harming" to refer to actions that entail a fecundity cost for the actor and confer fecundity gains or losses on others (see Lehmann et al. 2006*a*). It is important to distinguish between helping and harming, on the one hand, and altruism and spite, on the other hand, because the latter concepts are defined in terms of an action's impact on the fitness of the actor and recipients rather than on their fecundity. Harming behavior that reduces the fecundity of other local breeders at a cost to that of the actor may, for instance, ultimately increase the actor's direct fitness by reducing the level of competition experienced by its offspring, in which case the behavior is selfish rather than spiteful (Lehmann et al. 2006*a*). Since fitness effects are not externally specified but emerge from the analysis, we will initially classify behavior as only helping or harming (although we later show that when favored, helping as we have defined it is always altruistic, and harming as we have defined it always selfish).

## The Model

We focus, to begin with, on a haploid, sexually reproducing, "infinite-island" population (Wright 1931) with nonoverlapping generations. Since the diploid case yields precisely the same results if one assumes additive genic effects, we focus on the haploid case for ease of presentation (we assume that gametes are produced clonally and pair to form diploid zygotes, which then undergo meiosis to form a new generation of haploid individuals; for a similar approach, see, e.g., Gardner et al. 2007*a*). The population comprises an infinitely large number of patches. Each patch is occupied by $n_{\mathrm{f}}$ female and $n_{\mathrm{m}}$ male breeders. In each generation, breeders mate at random within a patch to produce a large number of offspring, with a primary sex ratio of $1 - a$ females to $a$ males, and then die. A fraction $d_{\mathrm{f}}$ of the newly produced female offspring on each patch then disperse, as do a fraction $d_{\mathrm{m}}$ of the males. Of these dispersing young, a fraction $1 - k$ succeed in finding a new patch; each is equally likely to arrive (independent of the others) at any patch in the population. For simplicity, we use the composite parameters $h_{\mathrm{f}}$ $(= (1 - d_{\mathrm{f}})/(1 - kd_{\mathrm{f}}))$ and $h_{\mathrm{m}}$ $(= (1 - d_{\mathrm{m}})/(1 - kd_{\mathrm{m}}))$, which give the probabilities that a breeding female and a breeding male are native to their patch. Finally, the offspring on a patch, both native and immigrant, compete on an equal basis with others of their sex for the breeding positions available. Those who fail to obtain a position die. As detailed below, we focus on the evolution of helping and harming behavior expressed either by adult female or by adult male breeders after dispersal. Whether expressed by females or males, helping behavior increases the fecundity of other local breeders of the same sex and their mates, while harming behavior reduces the fecundity of other local breeders of the same sex and their mates (in either case, at a cost to the fecundity of the actor).

To explore the interaction between sex differences in dispersal and overlapping generations, we can extend the above model to allow for survival of adults across multiple breeding attempts. In this extended version of the model, reproduction is followed by mortality as before, but the probability of death for each adult female is $m_f$ and for each adult male is $m_m$, where both parameters may be <1. Following the dispersal phase (as before), offspring on a patch compete solely for those breeding positions that have become available as a result of the death of an adult of their own sex (so that surviving adults cannot be displaced by a newly born individual).

The analysis of this kind of patch-structured model usually proceeds in two steps (e.g., Taylor 1992*a*; Taylor and Irwin 2000; Gardner and West 2006; Lehmann et al. 2006*b*). One step is to calculate the equilibrium value of relatedness between two classes of individual on a patch, in terms of the other parameters in the model (such as $n$, $d$, $k$, etc.). In our analysis, we focus on the average relatedness among two newly born, randomly chosen offspring of either sex, which we denote $r$. Once we have obtained an expression for $r$, we can write expressions for the relatedness between other classes of individual on the patch (e.g., between two randomly chosen males or between a male and a female), all expressed in terms of $r$. The other step is to calculate the consequences of actions by one party that increase or decrease the reproductive output of other occupants of the patch, taking into account the knock-on effect of these social actions on the level of competition for breeding vacancies on the patch (i.e., the level of kin competition). Putting these two steps together and employing Hamilton's rule, we can find conditions for the spread of alleles that have social effects in limited-dispersal groups.

### *Relatedness*

Consider, first, the nonoverlapping generation case. Let $r$ denote the average relatedness among two randomly chosen offspring (of either sex) newly born on the same patch, equivalent in our case to the probability that both carry gene copies at any given (autosomal) locus that are identical by descent. On the basis of our assumptions above, the equivalent value in the next generation, denoted $r'$, is given by

$$r' = \frac{1}{4}\left(\frac{1}{n_f} + \frac{n_f - 1}{n_f} h_f^2 r\right) + \frac{1}{2} h_f h_m r + \frac{1}{4}\left(\frac{1}{n_m} + \frac{n_m - 1}{n_m} h_m^2 r\right).$$

The derivation of this expression (which is equivalent to the more general eq. [4] of Berg et al. 1998, given equal probabilities of sampling males and females) is straightforward: with probability 1/4, the two randomly chosen offspring both inherited their gene copies maternally; with probability 1/2, one inherited its gene copy from its mother and the other from its father; with probability 1/4, both inherited paternally. If both inherited maternally, then with probability $1/n_f$, they share the same mother, in which case the gene copies are identical by descent. With probability $(n_f - 1)/n_f$, they had different mothers, in which case the probability of identity is $h_f^2 r$, the probability that both mothers were born locally, multiplied by their mean relatedness in this case (note that if either mother was born nonlocally, the expected relatedness between the two is 0, given our infinite-island assumption). If one offspring inherited its gene copy from its mother and the other from its father, the probability of identity is $h_f h_m r$, the probability that both parents were born locally, multiplied by their mean relatedness in this case. Finally, if both offspring inherited paternally, then with probability $1/n_m$, they share the same father, in which case the gene copies are identical. With probability $(n_m - 1)/n_m$, they had different fathers, in which case the probability of identity is $h_m^2 r$, the probability that both fathers were born locally, multiplied by their mean relatedness in this case (for similar calculations of relatedness given sex-biased dispersal, see, e.g., Perrin and Mazalov 1999; Wild and Taylor 2004; Wild 2006). We note that the above calculation is valid whether breeders mate promiscuously (such that each individual offspring is equally likely to be derived from any one of the male breeders and from any one of the female breeders on the patch and that the probabilities of descent from any particular male or female are independent for different offspring) or whether, if $n_f = n_m = n$, they mate monogamously (such that males and females pair at random, and each offspring is then equally likely to be derived from any one of the $n$ breeding pairs).

Setting $r'$ equal to $r$, we can solve for the equilibrium relatedness among offspring newly born on the same patch:

$$r = \frac{n_{\mathrm{f}} + n_{\mathrm{m}}}{[4 - (h_{\mathrm{m}} + h_{\mathrm{f}})^2]n_{\mathrm{f}}n_{\mathrm{m}} + h_{\mathrm{f}}^2 n_{\mathrm{m}} + h_{\mathrm{m}}^2 n_{\mathrm{f}}}.$$

The average relatedness values between two adult breeders on the same patch, denoted $r_{\mathrm{ff}}$, $r_{\mathrm{fm}}$, or $r_{\mathrm{mm}}$—both female, one male and one female, and both male, respectively—are then given by

$$r_{\mathrm{ff}} = h_{\mathrm{f}}^2 r,$$

$$r_{\mathrm{fm}} = h_{\mathrm{f}} h_{\mathrm{m}} r,$$

$$r_{\mathrm{mm}} = h_{\mathrm{m}}^2 r.$$

In the case of overlapping generations, it is simpler to write recursions for $r_{\mathrm{ff}}$, $r_{\mathrm{fm}}$, and $r_{\mathrm{mm}}$ directly rather than expressing these values in terms of $r$. We then have

$$r'_{\mathrm{ff}} = (1 - m_{\mathrm{f}})^2 r_{\mathrm{ff}} + 2m_{\mathrm{f}}(1 - m_{\mathrm{f}})h_{\mathrm{f}}\left\{\frac{1}{2}\left[\frac{1}{n_{\mathrm{f}}} + \left(\frac{n_{\mathrm{f}} - 1}{n_{\mathrm{f}}}\right)r_{\mathrm{ff}}\right] + \left(\frac{1}{2}\right)r_{\mathrm{fm}}\right\}$$

$$+ m_{\mathrm{f}}^2 h_{\mathrm{f}}^2\left\{\frac{1}{4}\left[\frac{1}{n_{\mathrm{f}}} + \left(\frac{n_{\mathrm{f}} - 1}{n_{\mathrm{f}}}\right)r_{\mathrm{ff}}\right] + \left(\frac{1}{2}\right)r_{\mathrm{fm}} + \frac{1}{4}\left[\frac{1}{n_{\mathrm{m}}} + \left(\frac{n_{\mathrm{m}} - 1}{n_{\mathrm{m}}}\right)r_{\mathrm{mm}}\right]\right\},$$

$$r'_{\mathrm{fm}} = (1 - m_{\mathrm{f}})(1 - m_{\mathrm{m}})r_{\mathrm{fm}}$$

$$+ m_{\mathrm{f}}(1 - m_{\mathrm{m}})h_{\mathrm{f}}\left\{\frac{1}{2}\left[\frac{1}{n_{\mathrm{m}}} + \left(\frac{n_{\mathrm{m}} - 1}{n_{\mathrm{m}}}\right)r_{\mathrm{mm}}\right] + \left(\frac{1}{2}\right)r_{\mathrm{fm}}\right\}$$

$$+ (1 - m_{\mathrm{f}})m_{\mathrm{m}}h_{\mathrm{m}}\left\{\frac{1}{2}\left[\frac{1}{n_{\mathrm{f}}} + \left(\frac{n_{\mathrm{f}} - 1}{n_{\mathrm{f}}}\right)r_{\mathrm{ff}}\right] + \left(\frac{1}{2}\right)r_{\mathrm{fm}}\right\}$$

$$+ m_{\mathrm{f}}m_{\mathrm{m}}h_{\mathrm{f}}h_{\mathrm{m}}\left\{\frac{1}{4}\left[\frac{1}{n_{\mathrm{f}}} + \left(\frac{n_{\mathrm{f}} - 1}{n_{\mathrm{f}}}\right)r_{\mathrm{ff}}\right] + \left(\frac{1}{2}\right)r_{\mathrm{fm}} + \frac{1}{4}\left[\frac{1}{n_{\mathrm{m}}} + \left(\frac{n_{\mathrm{m}} - 1}{n_{\mathrm{m}}}\right)r_{\mathrm{mm}}\right]\right\},$$

$$r'_{\mathrm{mm}} = (1 - m_{\mathrm{m}})^2 r_{\mathrm{mm}}$$

$$+ 2m_{\mathrm{m}}(1 - m_{\mathrm{m}})h_{\mathrm{m}}\left\{\frac{1}{2}\left[\frac{1}{n_{\mathrm{m}}} + \left(\frac{n_{\mathrm{m}} - 1}{n_{\mathrm{m}}}\right)r_{\mathrm{mm}}\right] + \left(\frac{1}{2}\right)r_{\mathrm{fm}}\right\}$$

$$+ m_{\mathrm{m}}^2 h_{\mathrm{m}}^2\left\{\frac{1}{4}\left[\frac{1}{n_{\mathrm{f}}} + \left(\frac{n_{\mathrm{f}} - 1}{n_{\mathrm{f}}}\right)r_{\mathrm{ff}}\right] + \left(\frac{1}{2}\right)r_{\mathrm{fm}} + \frac{1}{4}\left[\frac{1}{n_{\mathrm{m}}} + \left(\frac{n_{\mathrm{m}} - 1}{n_{\mathrm{m}}}\right)r_{\mathrm{mm}}\right]\right\}.$$

The derivation of these expressions is again straightforward; consider, for instance, the expression for $r'_{\mathrm{ff}}$. With probability $(1 - m_{\mathrm{f}})^2$, two randomly chosen females on a patch are both adult survivors from the previous time step, in which case their expected relatedness is simply equal to the expected relatedness among randomly chosen pairs of females on a patch in the previous time step. With probability $2m_{\mathrm{f}}(1 - m_{\mathrm{f}})$, one female is a survivor and the other a newly born individual. In this case, the two may be related only if the younger was born on the patch, with probability $h_{\mathrm{f}}$. If this is the case, then with probability 1/2, the younger individual inherited its gene copy maternally and with probability 1/2 paternally. If inheritance was from the mother, then with probability $1/n_{\mathrm{f}}$, the younger female is the daughter of the older, and the probability that their gene copies are identical by descent is 1; with probability $(n_{\mathrm{f}} - 1)/n_{\mathrm{f}}$), the younger female is the daughter of another female who was present on the patch in the previous time step, and the probability that her gene copy is identical by descent to that of the focal older female is $r_{\mathrm{ff}}$. If inheritance was from the father, then the probability that the younger female's gene copy is identical by descent to that of the older female is simply $r_{\mathrm{fm}}$. Last, with probability $(1 - m_{\mathrm{f}})^2$, both randomly chosen females are newly born, in which case the expected relatedness between them can be calculated as in the case of nonoverlapping generations. The equilibrium relatedness values are easily obtained from these recursions, but since the expressions are lengthy, we do not give them here.

### *Kin Selection*

Now consider an action taken by an adult breeder that entails an immediate reduction in its fecundity (and that of its mate or mates) of magnitude $c$ (>0) relative to the baseline fecundity of 1 but confers an immediate gain of $b$ on other local breeders and their mates (where $|b|$ and $c$ are $\ll 1$). It does not affect our analysis whether this benefit is conferred on a single, randomly chosen other individual (and its mate or mates) or whether it is divided equally among the other breeders. If $b$ is positive, we will speak of helping behavior, while if $b$ is negative, we will speak of harming behavior. We treat actions taken by females and by males in the same way, assuming that both influence the total number of young produced in a patch; males, in other words, do not simply compete over paternity of offspring produced by females but are assumed to contribute materially to production of young. These immediate losses and gains will further impact the fitness of locally produced offspring (those of both the actor and others) through competition for breeding vacancies.

In the case of nonoverlapping generations ($m_{\mathrm{f}} = m_{\mathrm{m}} = 1$), a simple inclusive fitness argument (Taylor 1992*a*) yields an effective cost to the actor (in terms of surviving young) of

$$C_{\mathrm{f}} = c + (b - c)\left(\frac{h_{\mathrm{f}}^2 + h_{\mathrm{m}}^2}{2}\right)\frac{1}{n_{\mathrm{f}}} \quad \text{or}$$

$$C_{\mathrm{m}} = c + (b - c)\left(\frac{h_{\mathrm{f}}^2 + h_{\mathrm{m}}^2}{2}\right)\frac{1}{n_{\mathrm{m}}}$$

for a female and for a male, respectively (note that these effective cost and benefit terms are first-order approximations, appropriate for small $b$ and $c$). The first term in each expression represents the immediate fecundity cost of the action to the actor; the second term reflects the cost due to increased kin competition. The action yields a net increase of $b-c$ in the number of offspring born on the patch, and these additional offspring may "displace" the actor's young from potential breeding spots. Such displacement occurs only if the additional offspring remain on the natal patch, which occurs with probability $h_{\rm f}$ for a female offspring and $h_{\rm m}$ for a male offspring. If the additional offspring does remain on the natal patch, then assuming that the actor is female, the probability that the additional offspring displaces one of the actor's offspring is equal to $h_{\rm f}/n_{\rm f}$ for a female offspring and $h_{\rm m}/n_{\rm f}$ for a male offspring (the equivalent probabilities are $h_{\rm m}/n_{\rm m}$ and $h_{\rm f}/n_{\rm m}$ in the case of a male actor). Averaging across both sexes (which are weighted equally, since production of sons and production of daughters contribute equally to fitness), the net impact of kin competition is as specified above.

Similarly, the action confers an effective benefit on other local breeders of the same sex of

$$B_{\rm ff} = b-(b-c)\left(\frac{h_{\rm f}^2+h_{\rm m}^2}{2}\right)\left(\frac{n_{\rm f}-1}{n_{\rm f}}\right) \quad \text{or}$$

$$B_{\rm mm} = b-(b-c)\left(\frac{h_{\rm f}^2+h_{\rm m}^2}{2}\right)\left(\frac{n_{\rm m}-1}{n_{\rm m}}\right).$$

In addition, since changes in the fecundity of local females entail a change in the number of young produced by local males and vice versa, the action confers an effective benefit on local breeders of the opposite sex of

$$B_{\rm fm} = (b-c)\left[1-\left(\frac{h_{\rm f}^2+h_{\rm m}^2}{2}\right)\right]$$

(note that this benefit is the same regardless of the sex of the actor). The action in question will thus be favored by selection, provided that

$$B_{\rm ff}r_{\rm ff}+B_{\rm fm}r_{\rm fm}-C_{\rm f}>0 \quad \text{or}$$

$$B_{\rm mm}r_{\rm mm}+B_{\rm fm}r_{\rm fm}-C_{\rm m}>0,$$

depending on the sex of the actor.

The above condition is unaffected by changes in the population sex ratio $a$ or by sex differences in mortality in the case of overlapping generations. The greater the fraction of offspring that belong to one sex, say males, the lower the value of each relative to offspring of the opposite sex, since offspring of the more abundant sex must then compete more intensely for breeding spots. Consequently, the mean fitness gains through production of sons and production of daughters remain the same regardless of the value of $a$. Similarly, the lower the mortality of adults of one sex, say males, the greater the expected life span and hence the reproductive value of an offspring of that sex that succeeds in obtaining a breeding spot, but the lower the expected number of breeding spots available for offspring of that sex to compete over and hence the lower the chances of success. Again, the result is that the mean fitness obtained through production of sons and daughters remains the same regardless of the values of $m_{\rm f}$ and $m_{\rm m}$. The result is that the condition for helping or harming to be favored by selection remains unchanged. A more rigorous and extended argument to this effect (using the direct fitness method of Taylor and Frank 1996) is given in the appendix in the online edition of the *American Naturalist.*

We note that, as previously stated, helping behavior when favored must always represent a form of altruism. Consider, for instance, helping among females (the argument for helping among males is precisely equivalent). Helping implies positive values of $b$ and $c$, yielding $C_{\rm f}>0$, so that the act always entails a fitness cost for the actor. This means that helping can be favored only if $B_{\rm ff}r_{\rm ff}+B_{\rm fm}r_{\rm fm}>0$, that is, if the act confers a net fitness benefit on others in the local patch (summing across both females and males), in which case it can be described as altruistic. Conversely, harming behavior when favored must always (in our model) represent a form of selfishness. Consider, for instance, harming among females (the argument for harming among males is precisely equivalent). Harming implies a negative value of $b$ and a positive value of $c$, yielding $B_{\rm ff}-C_{\rm ff}<0$ and $B_{\rm fm}<0$, so that the act always entails a reduction in net productivity of the patch. This means that harming can be favored only if $B_{\rm ff}r_{\rm ff}-C_{\rm f}>0$ and hence (given that $B_{\rm ff}-C_{\rm ff}<0$) only if $C_{\rm f}<0$. This means that the act must yield a fitness benefit to the actor and can therefore be described as selfish.

### *Basic Results*

We focus first on the case in which $m_{\rm f}=m_{\rm m}=1$ and $n_{\rm f}=n_{\rm m}=n$, that is, nonoverlapping generations and no mating skew. Under these circumstances, when $h_{\rm f}=h_{\rm m}=h$, implying that the effective dispersal rate is identical for both sexes, the condition for selection to favor the act in question reduces to

$$c<0,$$

regardless of the value of $h$. Whatever the frequency of dispersal, in other words, selection will favor only behavior that yields a fecundity benefit to the actor, regardless of any impact (positive or negative) on the fecundity of other local breeders. This result is no more than a restatement of Taylor's (1992*a*) finding that limited dispersal does not alter the condition for a trait to be favored (although it may affect the classification of the behavior as selfish or altruistic; see Rousset 2004).

When there are sex differences in dispersal, however, the outcome is more interesting. Under these circumstances, an act can be favored even if $c > 0$, implying that it entails a fecundity cost to the actor. For the sex that is more prone to dispersal, such an act may be favored only if $b$ is negative, implying that the actor reduces the fecundity of other local breeders. For the sex that is less prone to dispersal, however, selection may potentially favor either harming or helping behavior, depending on the precise values of $h_f$ and $h_m$. The relevant ranges of parameter values are illustrated in figure 1. Typically, selection favors helping by the more philopatric sex when individuals of the less philopatric sex do not all disperse. When the sex bias in dispersal is extreme, however, such that one sex very rarely disperses and the other almost always does, selection can favor harming behavior in both. Formally, the boundary between the regions in which selection favors helping versus harming in females (or, exchanging the subscripts f and m, in males) satisfies the equation

$$\frac{n-1}{4n}(h_f^4 - h_m^4) = h_m(h_f - h_m).$$

In addition, for either sex, whether selection potentially promotes helping or harming behavior, an act for which $c > 0$ will be favored only if the ratio of $c$ to the magnitude of $b$ is sufficiently small, implying that the fecundity cost to the actor must not be too large compared with the fecundity benefit or harm conferred on the recipient. For an action performed by a female, the relevant condition is

$$\frac{c}{|b|} < \left| \frac{(h_m - h_f)[4nh_m - (n-1)(h_f + h_m)(h_f^2 + h_m^2)]}{n^2[8 - 2(h_f + h_m)^2] - 2n(h_f - h_m)^2 - (n-1)(h_f^4 + h_m^4)} \right|$$

(the equivalent condition for an action performed by a male may be obtained by exchanging the subscripts f and m in the above expression). Selection for harming behavior by members of the sex more prone to dispersal is stronger (i.e., possible for larger values of $c/|b|$) than selection for helping (or harming) behavior by members of the sex less prone to dispersal.

### *Effects of Mating Skew*

Because we specify independently the number of breeding females and males in each patch, our model easily lends itself to the investigation of mating skew. When $n_f > n_m$, the number of female breeders is greater than the number of males, leading to effective polygyny; under these circumstances (assuming a 1 : 1 primary sex ratio), competition for breeding status is more intense among males. By contrast, when $n_f < n_m$, the number of female breeders is less than the number of males, leading to effective polyandry; under these circumstances (assuming a 1 : 1 primary sex ratio), competition for breeding status is more intense among females.

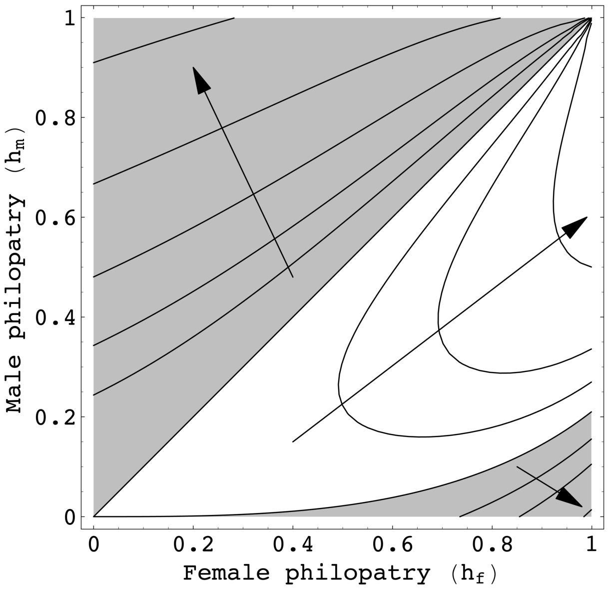

**Figure 1:** Selection for helping and harming by females as a function of female and male philopatry ($h_f$ and $h_m$) for the case of nonoverlapping generations ($m_f = m_m = 1$) and equal numbers of female and male breeders per patch (here $n_f = n_m = 3$). Shaded areas are those regions of parameter space in which selection potentially favors harming by females; the unshaded area is that region in which selection potentially favors helping. Contour lines within each region depict the strength of selection, measured as the critical ratio of the magnitude of $c$ (the cost of the act in question to the actor) to that of $b$ (the impact of the act on its recipient) below which helping or harming will be favored. Arrows indicate the directions in which selection increases in strength.

For the simple case of nonoverlapping generations ($m_f = m_m = 1$) and no sex difference in dispersal ($h_f = h_m = h < 1$), we find that selection will favor helping behavior among the less competitive sex and harming behavior among the more competitive. For either sex, in addition, the act in question (for which $c > 0$) will again be favored only if the ratio of $c$ to the magnitude of $b$ is sufficiently small. For an action performed by a female, the relevant condition is

$$\frac{c}{|b|} < \left| \frac{h^2(n_f - n_m)}{h^2(n_f - n_m) + 2n_f n_m} \right|$$

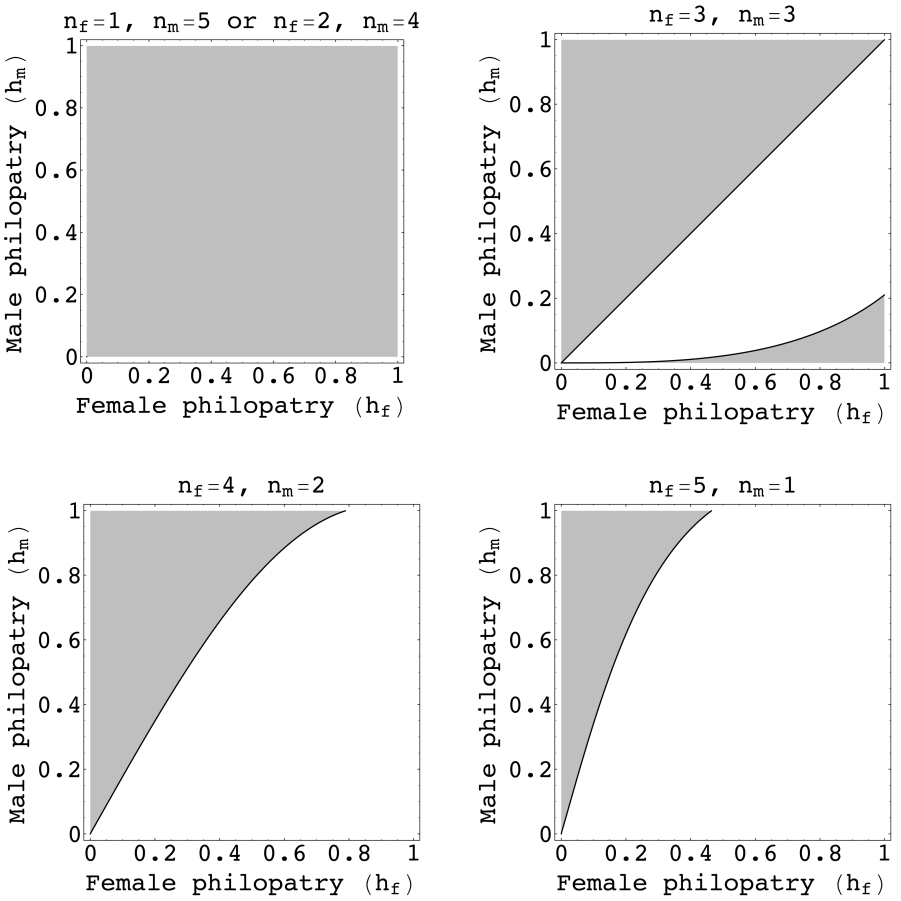

**Figure 2:** Selection for helping and harming by females as a function of female and male philopatry ($h_f$ and $h_m$) for different numbers of female and male breeders per patch ($n_f$ and $n_m$); we assume here that the total number of breeders of both sexes is always six, as in the case of figure 1 (which corresponds to the top right panel). Shaded areas are those regions of parameter space in which selection potentially favors harming by females; unshaded areas are those regions in which selection potentially favors helping. As the top left panel reveals, when competition for breeding spots is more intense among females ($n_f = 1$ and $n_m = 5$, or $n_f = 2$ and $n_m = 4$), selection always has the potential to favor harming and never helping among females, regardless of the pattern of dispersal. In all cases, $m_f = m_m = 1$.

(the equivalent condition for an action performed by a male may be obtained by exchanging the subscripts f and m in the above expression). Selection for helping among the less competitive sex and selection for harming among the more competitive sex are thus both stronger when the difference in intensity of competition is more pronounced and when dispersal rates are low. Selection for helping among the less competitive sex is slightly weaker than selection for harming among the more competitive sex, but the difference is not pronounced.

We can also investigate the interaction between sex differences in dispersal and sex differences in the number of breeders per patch (allowing, simultaneously, for differences between $h_f$ and $h_m$ and between $n_f$ and $n_m$). In this more general case, we will not give precise formulas for the conditions under which helping and harming behavior are favored because, while these are easy to derive, the resulting expressions are lengthy and consequently hard for the reader to interpret. Instead, we simply summarize the qualitative pattern of results, which is also illustrated in figure 2.

When the sex that is less prone to dispersal is also less competitive (e.g., when there is female philopatry and polygyny), the effects of mating skew reinforce those of sex-biased dispersal, and the result is strong selection for helping among the philopatric, less competitive sex and for harming among the dispersing, more competitive sex. By contrast, when the sex that is less prone to dispersal is more competitive (e.g., when there is male philopatry and polygyny), the effects of mating skew oppose those of sex-biased dispersal. In "Basic Results," we observed that selection for helping behavior in the sex less prone to dispersal is weaker than selection for harming behavior in the sex more prone to dispersal. This means that the effect of mating skew can outweigh the former but not the latter. Consequently, when the sex that is less prone to dispersal is also more competitive, the result is typically selection for harming among both females and males.

### *Effects of Overlapping Generations*

Finally, we can explore the effects of overlapping generations by considering values of $m_f$ and $m_m$ that are <1. When there is no sex bias in dispersal ($h_f = h_m = h$), no mating skew ($n_f = n_m = n$), and no sex differences in survival ($m_f = m_m = m$), our analysis simply replicates earlier studies of overlapping generations (Taylor and Irwin 2000). In a structured population ($h < 1$), adult survival across multiple breeding attempts favors helping behavior, provided that the fecundity cost to the actor is sufficiently small relative to the fecundity benefit conferred:

$$\frac{c}{b} < \left| \frac{2h(1-m)}{(2-m)n + h[m(n-2)+2]} \right|.$$

This effect is stronger the higher the probability of survival and the lower the rate of dispersal.

Allowing for sex differences in dispersal ($h_f \neq h_m$) and for mating skew ($n_f \neq n_m$), overlapping generations still tend to reinforce selection for helping behavior in the more philopatric and/or the less competitive sex and to oppose selection for harming in the less philopatric and/or the more competitive sex (once again, we will not give explicit formulas in the general case but simply summarize the qualitative pattern of results). The effects of generational overlap typically outweigh those of mating skew, thus potentially favoring (in the absence of a marked sex bias in dispersal) local helping among both males and females, even when breeders of one sex are more numerous than breeders of the other. But if there is a marked sex bias in dispersal, then even a substantial generational overlap will not outweigh selection for harming among the less philopatric sex (see fig. 3).

What of the effects of sex differences in survival? These are less dramatic than the effects of sex differences in dispersal or in the number of breeders per patch. Survival of either males or females tends to promote helping behavior among both sexes but does so more strongly in the sex that experiences lower mortality.

### *Summary of Results*

To summarize these patterns, when there is a marked sex bias in dispersal, selection will almost always favor harming behavior among individuals of the sex more prone to dispersal, regardless of the effects of mating skew or overlapping generations. Selection may well also favor helping behavior among individuals of the philopatric sex, particularly if there is generational overlap, but this is less likely to occur if individuals of the philopatric sex compete more intensely for fewer breeding spots. In this last case, if generational overlap is low and mating skew pronounced, the result may be selection for harming behavior among both males and females.

## Discussion

Increasing constraints on dispersal, of the kind often faced by social vertebrates, lead to both elevated relatedness and elevated competition among group members. Taylor (1992*a*, 1992*b*) showed that in the simplest case (i.e., nonoverlapping generations, no mating skew), these two effects cancel each other out, with the consequence that variation between populations in the level of dispersal should have no effect on the evolution of helping behavior. Within a population, by contrast, our analysis reveals that differences between males and females in the level of local relatedness are not canceled out by differences in the intensity of kin competition. Where males tend to disperse and females tend to remain on their natal patch, for example, males will be less closely related to other breeders (and hence offspring) on the patch in which they find themselves than will females. Both male and female parents, however, will produce dispersing sons and nondispersing daughters, and so their collective offspring will on average experience the same level of kin competition. Consequently, selection is thus more likely to favor harming among the dispersing sex and helping among the philopatric sex.

The prediction that helping should be favored among the more philopatric sex agrees with observations of both cooperatively breeding birds and mammals. In birds, males tend to be the philopatric sex and also provide more help (Cockburn 1998). In mammals, the reverse is true: females tend to remain in their natal territory and also provide more help (Russell 2004). It has been suggested that these patterns reflect the fact that the more philopatric sex stands to gain greater direct benefits by helping to raise further group members, especially where increasing group size results in elevated fitness (Clutton-Brock et al. 2002; Russell 2004). Even without these "group augmentation" effects, however, our model suggests that helping will be favored among the philopatric sex because they are more

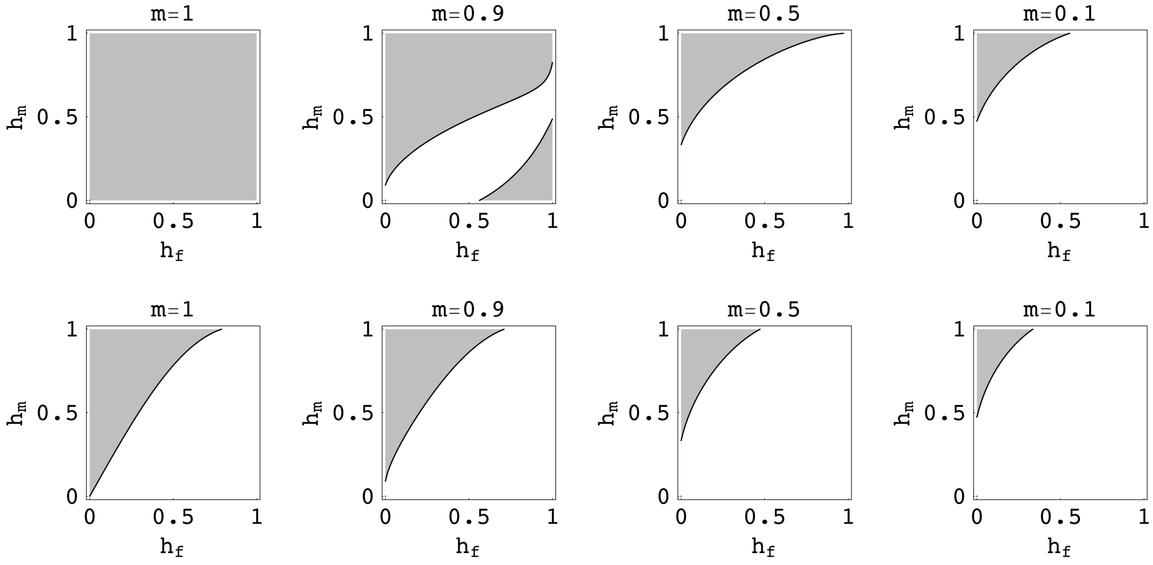

**Figure 3:** Selection for helping and harming by females as a function of female and male philopatry ($h_f$ and $h_m$) for different numbers of female and male breeders per patch ($n_f$ and $n_m$) and for different mortalities (assumed equal for males and females, $m_f = m_m = m$). In the top row, females experience more intense competition for breeding spots ($n_f = 2$, $n_m = 4$), while in the bottom row, males experience more intense competition ($n_f = 4$, $n_m = 2$). Along each row, mortality decreases from left to right (for successive panels, $m = 1$, 0.9, 0.5, and 0.1), so the left-hand side corresponds to nonoverlapping generations and the right-hand side to the greatest generational overlap. Shaded areas are those regions of parameter space in which selection potentially favors harming by females; unshaded areas are those regions in which selection potentially favors helping.

closely related to the offspring they help to raise but suffer the same average level of kin competition as the dispersing sex. The dispersing sex, for their part, are not simply neutral to the reproductive efforts of other group members but are selected to inflict direct costs on other breeders, even at an expense to their own direct fitness. We predict, therefore, that selfish or aggressive acts that reduce group productivity should be more frequent among members of the dispersing sex (typically female birds or male mammals).

But what of the more puzzling result that, when there is an extreme disparity in dispersal between the sexes, selection may actually favor harming behavior among both males and females? Related offspring that are born on the same patch compete only if they happen to remain in their natal area. The intensity of kin competition in a simple model without sex differences thus depends on $h^2$, the square of the probability that any one offspring is native to the patch in which it competes. For instance, if the probability that an offspring is native to the patch on which it competes is equal to 1/2, then the probability that two offspring born on the same patch end up competing is equal to 1/4. Suppose, however, that males disperse while females do not, that is, that $h_f = 1$ and $h_m = 0$. The overall probability that a randomly chosen offspring is competing on its native patch is in this case still equal to 1/2 (assuming a 1 : 1 primary sex ratio), but since offspring compete only with others of their own sex, the probability of competition is equal to $(h_m^2 + h_f^2)/2$, or, in this case, to 1/2 rather than to 1/4. Because individuals of the sex that is less likely to disperse compete with rivals who are also less likely to disperse, kin competition is intensified when there are sex differences in dispersal. Local relatedness is not, however, enhanced to the same extent by sex differences in dispersal, because males and females share genes with locals of both sexes (even if they compete only with rivals of their own sex). A marked sex difference in dispersal can thus favor harming even among individuals of the nondispersing sex, because it may intensify kin competition to the point that this outweighs even the higher local relatedness that they experience.

### *Sex-Specific Local Relatedness and Social Behavior*

The effects of sex-biased dispersal lead to some surprising conclusions about the relationship between sex-specific local relatedness and sex-specific social behavior. An increase in male dispersal, for instance, typically causes both a decrease in relatedness among male breeders on a patch and a decrease in selection for male helping (or increase in selection for male harming). Variation across populations or species in male dispersal should therefore tend to give rise to a positive correlation between relatedness among males and intermale cooperation and helping (or, equivalently, to a negative correlation between relatedness among males and intermale aggression and harming). By contrast, an increase in female dispersal typically causes a decrease in relatedness among male breeders on a patch but can also cause an increase in selection for male helping (or decrease in selection for male harming). Variation across populations or species in female dispersal can therefore give rise to a negative correlation between relatedness among males and intermale cooperation and helping (or, equivalently, to a positive correlation between relatedness among males and intermale aggression and harming). The net result is that one cannot hope to predict levels of intermale cooperation or aggression (across species) based simply on male-male relatedness. The expected effect of relatedness may be completely reversed, depending on the relative degree of variation among species in male and in female dispersal rates.

The above reversal is illustrated in figure 4, which shows the best-fit linear relationship between intermale relatedness and selection for helping or harming across 20 hypothetical "species" that were assigned random rates of female and male dispersal. In the top left panel, male dispersal rates were drawn from a distribution with standard deviation approximately twice that of the distribution from which female dispersal rates were drawn, so that male dispersal rates vary more strongly than do female dispersal rates. In the top right panel, the distributions of dispersal rates were exchanged, so that female dispersal rates vary more strongly than do male dispersal rates. As the figure reveals, when male dispersal varies more, the result is a positive relationship between relatedness and selection on males for helping rather than harming (positive values on the vertical axis indicate selection for helping, negative values indicate selection for harming); by contrast, when female dispersal varies more, the result is a weakly negative relationship. The bottom panels show the distribution of the slope of the best-fit lines when this procedure is repeated many times and confirm that the pattern illustrated in the top panels has not arisen simply by chance.

### *Interaction between Demographic Factors*

In addition to the effects of sex differences in dispersal, we have also explored sex differences in competition and

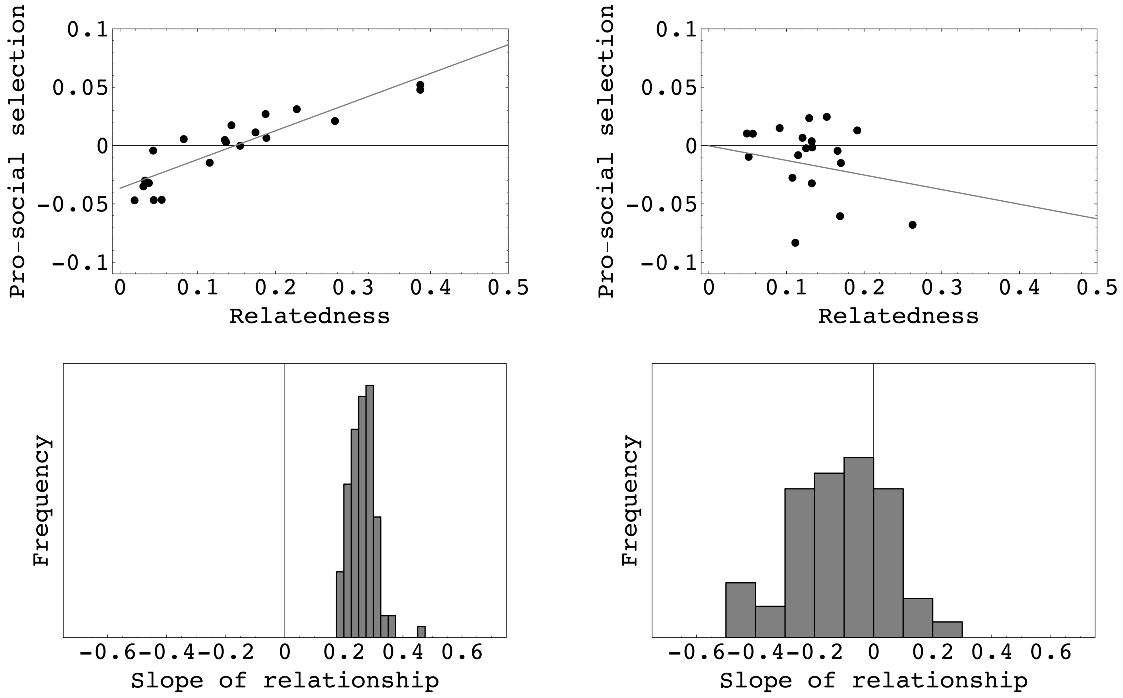

**Figure 4:** Top row shows the best-fit linear relationship between male-male relatedness and selection for helping or harming among males (measured as the magnitude of the ratio of $c:b$, below which such behavior is favored, with positive values denoting selection for helping and negative values selection for harming), in each case across 20 putative "species" that were assigned levels of male and female philopatry at random. The bottom panels show the distribution of the slope of the best-fit line when this procedure was repeated 100 times. In the left-hand column, values of $h_f$ were drawn from a beta distribution with 0.077 SD and values of $h_m$ from a beta distribution with 0.201 SD, while in the right-hand column, the reverse was true (means of all distributions were 0.667). In all cases, $n_f = n_m = 3$ and $m_f = m_m = 1$.

breeder number and in survival. Of most interest, perhaps, is the interaction between these effects. Sex-biased dispersal tends to favor harming among the dispersing sex (and helping among the philopatric sex), while mating skew tends to favor harming among the more competitive sex (and helping among the less competitive sex). When it is the less competitive sex that stays put, the two effects simply reinforce one another, but when it is the more competitive sex that remains and the less competitive sex that disperses, the result can be selection for harming among both females and males. One would therefore predict that (all other things being equal) among polygynous species, local helping and cooperation are more likely to evolve in those with male-biased dispersal than in those with female-biased dispersal. In the latter case, cooperation is less probable because it is the more competitive sex (males) that stays put and that can potentially form cooperative kin groups.

### *The Role of Males*

We have assumed in our analysis that males and females play similar roles, in the sense that both contribute materially to the production of offspring. The exchange of helping and harming behavior among individuals of either sex can thus impact the number of offspring produced in a patch. By contrast, previous analyses have often assumed that females are demographically dominant, that is, that males do not contribute to offspring production but merely compete over paternity of young raised by females (e.g., Taylor 1992*a*). Under the latter circumstance, helping can never be favored among males, because a male who assists another to gain paternity does so only at a cost to the paternity of other local males (who are, on average, just as closely related to the actor as is the recipient of his help). This outcome is similar to the case of polygyny discussed above but is more extreme. When males do not contribute materially to offspring production, for instance, female-biased dispersal will always lead to selection for harming among both sexes. We have allowed for a male contribution to production of young because, in many cases, males do assist materially with offspring care (or provide the female with direct benefits such as protection) and because there is a greater need for analysis of this more complex situation.

### *Coevolution of Helping, Dispersal, and Sex Ratios*

In this article, we have focused on the evolution of sex differences in helping and harming behavior, given specified rates of male and female dispersal. We have not considered how sex-specific dispersal rates (and, in conjunction, the sex ratio) should evolve (for analysis of this issue, see Leturque and Rousset 2004; Wild and Taylor 2004). Is it meaningful to examine the evolution of social behavior in isolation in this way, treating dispersal as a fixed parameter rather than a coevolving trait? We are concerned with the evolution of nondiscriminatory helping and harming, that is, with behaviors that impact the fitness of any or all other local breeders, regardless of their relatedness to the actor. Because individuals will therefore suffer the same costs or receive the same benefits regardless of whether they remain in their natal patch among relatives or whether they disperse, the level of helping or harming by individuals of either sex will not affect the evolutionarily stable rates of dispersal. Of course, these rates may evolve in response to changes in the mortality risk associated with migration, the cost of inbreeding, and many other factors discussed in the literature on dispersal (Motro 1983, 1991; Waser et al. 1994; Perrin and Mazalov 1999; Kokko and Ekman 2002). But, given our focus on the evolution of helping and harming, it is not necessary to specify the factors responsible for the evolution of sex differences in dispersal; we can simply treat them as givens and explore their implications for selection on indiscriminate social behavior.

Turning to the sex ratio, it is clear that sex differences in dispersal and in the levels of helping and harming behavior may select for changes in the proportion of male offspring produced (e.g., Wild [2006] explores the influence of sex-specific helping on the evolution of sex ratios). As we have shown, changes in the sex ratio do not directly affect selection for indiscriminate helping and harming. Nevertheless, if the sex ratio alters, this may select for changes in sex-specific dispersal rates, which could in turn influence selection for social behavior. In principle, therefore, if the primary sex ratio were evolutionarily labile, one would need to consider simultaneously the coevolution of all three behaviors (local helping and harming, sex allocation, and dispersal) in a single model. We are primarily concerned, however, with social behavior of vertebrates, among which there is little evidence for adaptive flexibility in the primary sex ratio, especially at the population level (Cockburn et al. 2002; Krackow 2002; West and Sheldon 2002). In this case, we argue that it is not necessary to consider such coevolutionary interactions between traits. There is evidence in a minority of species that individual females can adjust the sex ratio among their offspring to take advantage of individual differences in territory or mate quality (Cameron 2004; Sheldon and West 2004). It would be very interesting to consider the evolution of such flexible tactics within the context of our model, but this is certainly beyond the scope of our present analysis.

### *Kin Discrimination*

Although indiscriminate helping and harming do not impact selection for dispersal or philopatry, preferential helping of more related individuals (or harming of less related competitors) does favor philopatry, because individuals that disperse away from their relatives will enjoy less help and/or incur greater harm. Lehmann and Perrin (2002) have explored the coevolution of dispersal and discriminatory helping (directed preferentially toward natives rather than immigrants) but did not consider sex differences in dispersal or helping behavior. It would therefore be interesting to extend this model to allow for discriminatory helping (in conjunction with sex differences in dispersal), but this is once again beyond the scope of our present analysis. It may seem that, particularly among birds and mammals, our failure to address the possibility of kin discrimination is rather limiting (although evidence for active kin-directed helping in such societies is mixed; see Clutton-Brock et al. 2000 and references therein). We point out, however, that many individual decisions (e.g., to breed or not and how many offspring to produce if breeding) are likely to affect the fitness of all other local breeders, regardless of their relatedness to the actor, and thus constitute (in our terms) helping or harming. Help and harm are not restricted to direct assistance or aggression directed at particular individuals but encompass all behavior that impacts the fitness of others in the same patch. Consequently, whenever individuals in a patch compete over resources, we argue that kin selection is likely to impact most aspects of life history, and it is therefore important to determine its effects as we have done here.

## *Conclusion*

When the sexes differ in either their rate of dispersal or the number of breeding individuals per patch, the result is that kin selection affects males and females very differently. Indeed, it may well favor helping behavior among members of one sex and harming among the other. Kin selection and kin competition are thus very unlikely to "cancel out" when there are differences between the sexes. Moreover, under these circumstances, social behavior among individuals of either sex is likely to be influenced by the rates of dispersal and levels of mating competition among individuals of the other sex. In general, then, one cannot consider selection on males or on females in isolation.

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