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Sex-biased dispersal of adults mediates the evolution of altruism among juveniles

Andy Gardner

Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, United Kingdom.

Email: andy.gardner@zoo.ox.ac.uk

Abstract – Population viscosity has been proposed as an important mechanism for the evolution of cooperation. The idea is that if individuals do not disperse far during the course of their lives, they will tend to interact with their genealogical relatives, which may give kin-selected benefits for cooperation. However, in the simplest model of population structure, the evolution of cooperation is unaffected by the rate of dispersal, owing to dispersal also mediating competition between social partners. This surprising result has generated much research interest in recent years. Here I show that dispersal does matter if there is a sex difference in dispersal rate, even when the expression of cooperation is not conditional upon the actor's dispersal status or sex. In particular, I show that cooperation among juveniles is relatively favoured when there is a small sex bias in adult dispersal in favour of the sex with the greatest variance in reproductive success, and is relatively disfavoured when this sex bias is large or in the opposite direction. This is because dispersal by individuals of each sex can have different consequences for the genetic structure of the population.

Keywords – cooperation, Hamilton's rule, inclusive fitness, kin selection, viscosity.

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Introduction

Explaining cooperation is one of the major challenges for evolutionary biology (Maynard Smith & Szathmáry 1995; Hamilton 1996; West et al. 2007a). Natural selection favours those individuals who have the greatest reproductive success relative to the population average (Darwin 1859; Fisher 1930; Price 1970). Yet, cooperation is when an individual provides a benefit for others and, all else being equal, this will tend to reduce its relative fitness (West et al. 2007a). The problem of cooperation is to explain how it can be favoured by natural selection.

Adaptive explanations for cooperation seek direct and/or indirect fitness benefits for cooperators. Cooperation is readily explained when it returns a direct fitness benefit to the actor (mutually-beneficial cooperation; West et al. 2007a,b), such as reciprocated cooperation from recipients (Trivers 1971). Alternatively, cooperation may incur a net direct fitness cost for the actor (altruistic cooperation; West et al. 2007a,b), and be favoured owing to indirect fitness benefits, which are derived from improving the reproductive success of the actor's genetic relatives (kin selection; Hamilton 1963, 1964, 1970; Maynard Smith 1964). The sum of direct and indirect fitness is "inclusive fitness", and this describes how well the individual transmits copies of its genes to future generations (Hamilton 1964).

Two major mechanisms have been suggested that ensure cooperative interactions occur between genealogically-close kin, so that individuals are able to derive indirect fitness benefits from their altruism. First, kin discrimination allows individuals to adjust their behaviour conditional upon the relatedness to their social partners

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(Hamilton 1964). This mechanism has been shown to operate in a range of species, from microbes to vertebrates (e.g. Russell & Hatchwell 2001; Mehdiabadi et al. 2006). Second, indiscriminate cooperation may be favoured when individuals do not disperse far during the course of their lifetime, as many social interactions will occur among kin (Hamilton 1964, 1972). This second mechanism, termed "population viscosity" suggests a relatively general explanation for cooperation, that could be applied to all levels of biological organization, and particularly to organisms lacking the requisite capacity for kin discrimination.

Surprisingly, in the simplest model of population structure – Wright's (1931) infinite, inelastic island model – the degree of population viscosity has no impact on the evolution of cooperation. Taylor (1992a) showed that, in the context of this model, the cooperation-promoting effects of high relatedness due to high viscosity are exactly cancelled by the cooperation-inhibiting effects of intensified kin competition in such populations. This is true irrespective of whether cooperation occurs among juveniles before dispersal or among adults after dispersal. To the extent that individuals do not disperse, they will have interactions with their relatives, but these will include competitive as well as social interactions. This result has led to the emergence of a large literature on how adjustments to the basic island model can decouple the effects of relatedness and kin competition, so that viscosity could favour cooperation (reviewed by Queller 1992, West et al. 2002).

A simple extension to Taylor's (1992a) model is to allow organisms to adjust their social behaviour conditional upon their dispersal status (Perrin & Lehmann 2001; El Mouden & Gardner 2008). Non-dispersers are, on average, more related to their social

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partners than are dispersers, and hence the former can be favoured to invest in cooperative behaviour (and the latter in harming behaviour) in viscous populations (El Mouden & Gardner 2008). When dispersal status is not known directly, any cue can be used. For example, Johnstone & Cant (2008) showed that when the sexes disperse at different rates, the sex with the lower dispersal can be favoured to help while the sex with the higher dispersal can be favoured to harm.

In this article, I show that sex-biased dispersal can mediate social behaviour even in the absence of individuals responding to conditional information regarding their dispersal status. In particular, I show that the dispersal of adults mediates the evolution of altruism among juveniles, even if altruism is expressed equally in juveniles of both sexes and before dispersal occurs. This is because the dispersal of individuals of each sex can impact upon the genetic structure of the population in different ways. Altruism is relatively favoured if there is a small dispersal bias towards the sex with the greater variance in reproductive success, and is relatively disfavoured if the bias is strong or in the opposite direction. This extends the scope for population viscosity to act as a general mechanism for the evolution of cooperation in the natural world.

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Model & Analysis

I consider an infinite island model (Wright 1931), with each patch containing a large number of diploid juvenile individuals. Juveniles engage in social interaction, which mediates their survival to adulthood. Upon reaching maturity, surviving individuals either disperse to a random patch, or else remain in their natal patch. Adult females

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disperse with probability d_f, and adult males disperse with probability d_m. I assume an even sex ratio. Following dispersal, individuals engage in mating and reproduction within their patch, giving rise to the next generation of juveniles. This is Taylor's (1992a, pp355-356) model of cooperation among juveniles before dispersal, extended to include sex-biased dispersal among adults.

The expected relative fitness of a juvenile who invests an amount x into helping, while its patchmates invest an average of y and the population as a whole invests an average of z, is:

$$W = S(x,y)\left\{\frac{1}{2}\left(\frac{1-d_f}{(1-d_f)S(y,y)+d_f S(z,z)}+\frac{d_f}{S(z,z)}\right)+\frac{1}{2}\left(\frac{1-d_m}{(1-d_m)S(y,y)+d_m S(z,z)}+\frac{d_m}{S(z,z)}\right)\right\} \quad (1)$$

where S is the probability that an individual survives to maturity (see Appendix for derivation). I assume that helping incurs a personal survival cost (e.g. $\partial S(x,y)/\partial x = -c < 0$) and improves the survival of patchmates (e.g. $\partial S(x,y)/\partial y = b > 0$). Analysis of this fitness function – using the kin selection methodology of Taylor & Frank (1996; see Appendix for details) reveals that natural selection favours an increase in helping when:

$$\frac{c}{b} < \frac{r-ar}{1-ar}, \quad (2)$$

where r denotes the kin selection coefficient of relatedness between juveniles within a patch, and a denotes the proportion of competition for breeding opportunities that

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occurs between individuals deriving from the same patch ('scale of competition'; Frank 1998). Below, I provide expressions for both of these quantities in terms of the model parameters.

The amount of helping that is predicted to evolve is dependent upon the details of the survival function, *S*. However, irrespective of such details, the expression $A = (r-ar)/(1-ar)$ describes how an individual values the survival of its patchmates relative to its own survival. I term this quantity the "potential for altruism" (in the Appendix, I show that helping is always formally altruistic in this model). In general, the potential for altruism is increased with higher relatedness (r) and decreased with higher scale of competition (a) – the motivation for costly helping is that social partners may be related, but this motivation is reduced if the beneficiaries of one's helping behaviour are likely to interfere with one's own breeding success and that of one's other relatives (Figure 1). Queller (1994) has conceived A as a type of relatedness coefficient, which measures the genetic similarity of social partners relative to one's competitors.

In the Appendix, I show that the coefficient of relatedness is given by:

$$r = \frac{\alpha + \beta}{\alpha + \beta + (1-\alpha)\left(1-(1-d_f)^2\right) + (1-\beta)\left(1-(1-d_m)^2\right) + 2\left(1-(1-d_f)(1-d_m)\right)}, \quad (3)$$

where α is the probability that two juveniles chosen at random from the same patch share the same mother and β is the probability that they share the same father. The parameters α and β allow for a range of possible mating systems, including details of

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how many individuals of each sex find breeding success within a patch, and how equitably this breeding success is shared among breeders. A higher value of α indicates fewer breeding females and/or reproduction being skewed towards one or a few of the breeding females, and a higher value of β indicates fewer breeding males and/or reproduction being skewed among one or a few of the breeding males. For example, strict monogamy with n equally-fecund couples in each patch gives $\alpha = \beta = 1/n$, whereas a harem system of n equally-fecund females mated by a single male would give $\alpha = 1/n$ and $\beta = 1$. In general, higher values of α and β increase relatedness (because this increases the probability that patchmates are siblings), whereas higher values of d_f and d_m decrease relatedness (because this decreases the probability that patchmates are cousins) – as illustrated in Figure 2. Note that relatedness is not symmetrical with respect to the dispersal rates of the two sexes: the quantitative effect of dispersal upon relatedness is different for the two sexes (e.g. $\mathrm{d}r/\mathrm{d}d_f|_{df=dm=d} = -2(\alpha+\beta)(1-d)(2-\alpha)/(\alpha+\beta+(4-\alpha-\beta)(1-(1-d)^2)^2$ and $\mathrm{d}r/\mathrm{d}d_m|_{df=dm=d} = -2(\alpha+\beta)(1-d)(2-\beta)/(\alpha+\beta+(4-\alpha-\beta)(1-(1-d)^2)^2$, which are not equal if $\alpha \neq \beta$).

In the Appendix, I show that the scale of competition is given by:

$$a = \frac{(1-d_f)^2 + (1-d_m)^2}{2}, \tag{4}$$

which is a decreasing function of both male and female dispersal rates (d_f and d_m) – illustrated in Figure 3. This is because juvenile patchmates only compete for future breeding opportunities to the extent that individuals do not disperse from their natal patch. As the total reproductive success of both sexes is constrained to be equal, all

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competition is within-sex. With probability ½ the focal individual is female, and she competes with female patchmates to the extent that neither she nor they disperse, i.e. with probability $(1-d_f)^2$. With probability ½ the focal individual is male, and he competes with male patchmates to the extent that neither he nor they disperse, i.e. with probability $(1-d_m)^2$. Note that the scale of competition is symmetrical with respect to the two sexes: the quantitative effect of dispersal upon scale of competition is the same for both sexes (e.g. $\mathrm{d}a/\mathrm{d}d_f|_{df=dm=d} = \mathrm{d}a/\mathrm{d}d_m|_{df=dm=d} = -(1-d)$).

Dispersal has two opposing effects on the potential for altruism. First, increased dispersal leads to a lower relatedness (Figure 2), which acts to disfavour altruism (Figure 1). Second, increased dispersal leads to a reduced scale of competition (Figure 3), which acts to favour altruism (Figure 1). The net effect of female and male dispersal is found by substituting equations (3) and (4) into the RHS of inequality (2), to yield an expression for the potential for altruism which is given purely in terms of model parameters: d_f, d_m, α and β. This is too cumbersome to reproduce here; however, its dependence upon each of the four model parameters is illustrated graphically in Figure 4, and analytical expressions for some special cases are considered below.

It is useful to consider first the special case where there is no sex bias in dispersal ($d_f = d_m = d$). Here, relatedness is given by $r = [\alpha+\beta]/[\alpha+\beta+(4-\alpha-\beta)(1-(1-d)^2)]$ and the scale of competition is given by $a = (1-d)^2$. While both relatedness and scale of competition are dependent on the rate of dispersal, and the evolution of altruism is dependent upon relatedness and scale of competition, there is no net impact of dispersal rate upon the potential for altruism, which is given by $A = (\alpha+\beta)/4$. This

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mirrors results given by Taylor (1992a) and Johnstone & Cant (2008), who also found an unresponsiveness of helping behaviour to dispersal rate when both sexes disperse at the same rate. Here, the potential for altruism is mediated by the probabilities of maternal and paternal sibship (α & β) of juveniles within a patch, with there being no potential for altruism in the limit of zero sibship ($A = 0$ when $\alpha = \beta = 0$) and with the survival of patch mates valued at one half of one's own survival in the limit of guaranteed full sibship ($A = ½$ when $\alpha = \beta = 1$).

More generally, when the dispersal rates of females and males can be varied independently, the rate of dispersal can affect the potential for altruism (Figure 4). If the probabilities of maternal and paternal sibship are equal ($\alpha = \beta = \gamma$), the potential for altruism is maximized when there is no sex bias in dispersal, and here it is given by $A = \gamma/2$. In this scenario, any sex bias in adult dispersal always reduces the potential for altruism among juveniles (Figure 4, panels on the anti-diagonal). Altruism is most inhibited when one sex always disperses and the other sex never disperses ($d_f = 0$ & $d_m = 1$ or $d_f = 1$ & $d_m = 0$), and here the potential for altruism is reduced by one-third relative to the unbiased-dispersal scenario: $A = \gamma/3$ (i.e. 67% of $\gamma/2$).

If the probabilities of maternal and paternal sibship are not equal ($\alpha \neq \beta$), then sex-biased dispersal can also promote altruism. In general, altruism is promoted if there is a small dispersal bias in favour of the sex that has the greater variance in reproductive success (i.e. $d_f > d_m$ if $\alpha > \beta$, and $d_m > d_f$ if $\beta > \alpha$), and altruism is inhibited if this bias is large or in the opposite direction (Figure 4, panels not on the anti-diagonal). The condition for sex-biased dispersal to promote altruism (relative to the unbiased-

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dispersal case) is $d_{max} < (2/(2+|\alpha-\beta|))d_{min} + (2\,|\alpha-\beta|)/(2 + |\alpha-\beta|)$, where d_{max} and d_{min} are the dispersal rates for the more-highly and less-highly dispersing sexes, respectively. The potential for altruism is maximized in the limit of $d_{max} \rightarrow 0$ and $d_{min} = 0$: here, the potential for altruism is $A = (\alpha+\beta)/(4-|\alpha-\beta|)$, and in the extreme of $|\alpha-\beta| = 1$, this represents one third greater potential for altruism relative to the unbiased-dispersal case (i.e. 1/3 is 133% of 1/4). The potential for altruism is minimized when the 'wrong' sex always disperses and the other sex never disperses ($d_{max} = 1$ & $d_{min} = 0$): here, the potential for altruism is $A = (\alpha+\beta)/(6+|\alpha-\beta|)$, and in the extreme of $|\alpha-\beta|=1$, this is only a little more than a half as great as in the unbiased-dispersal case (i.e. 1/7 is 57% of 1/4).

Discussion

The population processes that can generate relatedness between social partners – which favours cooperation – can also lead to intensified competition for reproductive resources among social partners – which disfavours cooperation (Queller 1992; West et al. 2002). A challenge for social evolution theory is to place social interaction in its proper ecological and demographic context, in order to correctly understand the fitness costs and benefits, as well as the relatedness coefficients, relevant to a kin selection analysis. Taylor's (1992a) seminal result – that in the simplest scenario, the relatedness and competition consequences of dispersal exactly cancel so that cooperation evolves no more readily in a structured population than in a fully-mixing population – has painted a rather gloomy picture of the prospects for viscosity to explain cooperation.

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Here, I found that Taylor's (1992a) prediction breaks down when the sexes differ in their dispersal rates. The potential for juveniles to express altruism is increased, relative to the unbiased dispersal case, if there is a small dispersal bias towards the sex with the greater variance in reproductive success. This is because while the scale of competition is symmetrical with respect to the dispersal rate of both sexes, the coefficient of relatedness is not generally symmetrical with respect to the two dispersal rates, so that a slight increase in dispersal of the sex with the greatest variance in reproductive success eases competition without incurring so great a loss of relatedness. For example, if a single male mates with multiple females in each patch, then all juveniles are guaranteed to be paternal siblings – irrespective of the rate of male dispersal – whereas the probability of their being genealogically related through their mothers crucially depends upon the rate of female dispersal.

This result is similar to the prediction, made by Johnstone and Cant (2008), that sex-biased dispersal could promote sex-specific helping and harming behaviours among adults after dispersal. Their model allows individuals to respond to conditional information regarding their dispersal status (namely, their sex), by adjusting their social behaviour. This mechanism is analogous to El Mouden & Gardner's (2008) model of social behaviour conditional upon dispersal status, in which nondispersers are favoured to help while dispersers are favoured to harm their neighbours. The present analysis has made a distinction between this conditional-information effect and a more basic effect due to a sex asymmetry in the dispersal ramifications for the genetic structure of populations. I have isolated the latter effect by situating social interaction prior to dispersal, and among juveniles who do not display sex-differences

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in social behaviour. For an example of how sex differences in adult dispersal can mediate sex specific social behaviours among juveniles, see Gardner et al. (2007).

A striking difference between the predictions of the present analysis and that of Johnstone & Cant (2008) is that the latter showed costly harming could be favoured in one or both sexes whereas, in the present analysis, costly harming is never favoured among juveniles (this would require $A < 1$). However, this difference is simply due to the inflated relatedness among juvenile patch mates before dispersal, relative to the relatedness among adult patch mates after dispersal (Taylor 1992a). The two models differ in several other ways. For clarity, and in order to fully isolate the impact of sex-biased dispersal upon social behaviour of juveniles, several features of Johnstone & Cant's (2008) model have been removed from the present analysis. These include overlapping generations (see also Taylor & Irwin 2000 and Irwin & Taylor 2001), biased sex ratios, and a mortality cost of dispersal. The present analysis is more general in one respect: by describing the probabilities of maternal and paternal sibships directly, the present analysis allows for any degree of reproductive skew among breeding adults, not considered by Johnstone & Cant (2008).

The aim of the present study has been to provide a simple illustration of how sex-biased dispersal can decouple genetic relatedness and scale of competition, so that cooperation can be relatively favoured in viscous populations. The model has been developed without any particular species in mind, and the sex-biased-dispersal effect is expected to manifest at all life history stages – not just among juveniles. However, the model does generate a number of readily testable predictions for juvenile cooperation. Typically, males are the sex with the greater variance in reproductive

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success, so a simple comparative test of theory could be performed by seeing if there is any tendency for species exhibiting a small degree of male-biased dispersal to have greater cooperation among juveniles than species exhibiting a small degree of female-biased dispersal. More generally, species with extreme sex-bias in dispersal (i.e. dispersal by virtually all individuals of one sex, and virtually no individuals of the other sex) are predicted to exhibit lower levels of juvenile cooperation than otherwise similar species in which the sexes disperse at approximately equal rates. Juvenile cooperation may include striking behaviours such as collective begging (e.g. Bell 2007), as well as a simple reduction in investment into competition for limiting resources.

There is scope for future theoretical extension of the present model. Especially useful for proper testing of theory will be the development of models that are more tailored to the specific biology of particular study organisms. In addition, analogous to theory that has shown that the impact of dispersal upon sex allocation can itself mediate the evolution of dispersal rates (Leturque & Rousset 2003; Wild & Taylor 2004; Wild et al. 2006), there is an interesting possibility that juvenile social behaviour could drive the evolution of sex-biased dispersal. In general, understanding the feedback between social evolution and population demography presents a major challenge for the future.

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Appendix

Fitness function

Here I derive the fitness function given in equation (1) of the main text. It is helpful to treat fitness effects for males and females separately. If the individual is female, then her expected fitness can be written as the product of her probability of survival to adulthood and her expected breeding success conditional upon surviving. I assume that the total breeding success on a patch is independent of the number of individuals striving for a breeding position (a form of inelastic regulation; Taylor 1992b), hence a surviving female's expected reproductive success is inversely proportional to the relative number of other survivors on her patch, which is $(1-d_f)S(y,y)+d_fS(z,z)$ if she did not disperse, and $S(z,z)$ if she did disperse. Hence, her expected fitness is:

$$w_f = S(x,y)\left(\left(1-d_f\right)\frac{k}{(1-d_f)S(y,y)+d_fS(z,z)} + d_f\frac{k}{S(z,z)}\right), \tag{A1}$$

where k is a constant of proportionality. Note that I make no assumption about the number of females successfully breeding on the patch, nor how they share this reproductive success. The average fitness of all females is $\overline{w} = k$, and hence the expected fitness of the juvenile female relative to the average for her class is $W_f = w_f/\overline{w}_f$, or:

$$W_f = S(x,y)\left(\frac{1-d_f}{(1-d_f)S(y,y)+d_fS(z,z)} + \frac{d_f}{S(z,z)}\right). \tag{A2}$$

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The expected fitness of a juvenile male is given by the product of his probability of survival and his expected breeding success conditional upon his survival. His breeding success is given by his mating success and the contribution of his mating partners to the patch's next generation of juveniles. His expected mating success is simply the ratio of adult females to adult males within the patch, which is $[(1-d_f)S(y,y)+d_fS(z,z)]/[(1-d_m)S(y,y)+d_mS(z,z)]$ if he remains on his natal patch, and 1 if he dispersed to a new patch. Hence, his expected fitness can be written as:

$$\begin{aligned} w_m &= S(x,y)\left\{(1-d_m)\frac{(1-d_f)S(y,y)+d_fS(z,z)}{(1-d_m)S(y,y)+d_mS(z,z)}\frac{k}{(1-d_f)S(y,y)+d_fS(z,z)}+d_m\frac{k}{S(z,z)}\right\} \\ &= S(x,y)\left\{(1-d_m)\frac{k}{(1-d_m)S(y,y)+d_mS(z,z)}+d_m\frac{k}{S(z,z)}\right\} \end{aligned}. \quad \text{(A3)}$$

The average fitness of juvenile males is $\overline{w}_m = k$, hence the expected fitness of the juvenile male relative to the average for his class is $W_m = w_m/\overline{w}_m$, or:

$$W_m = S(x,y)\left\{(1-d_m)\frac{1}{(1-d_m)S(y,y)+d_mS(z,z)}+d_m\frac{1}{S(z,z)}\right\}. \quad \text{(A4)}$$

A gene is favoured by natural selection if it increases the average fitness of its bearers. The correct 'average' is the expected relative fitness of an individual drawn at random from a population, the probability that it is drawn from a particular class being equal to that class's reproductive value (its asymptotic genetic contribution to future generations; Fisher 1930; Price & Smith 1972; Taylor 1990, 1996). In this case, average fitness over all juveniles is $W = c_f W_f + c_m W_m$, where c_f and c_m are the class

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reproductive values of females and males respectively. For diploids, these values are given by $c_f = c_m = ½$, and substituting equations (A2) and (A4) into this definition for average fitness obtains equation (1) of the main text.

Hamilton's rule

I assume that genetic variation is segregating at a locus controlling the helping behaviour. A gene chosen at random from this locus can be assigned a genic value g, and an additive genetic "breeding" value for helping $\tilde{g}$ can be defined for an individual, by taking the average of its two genic values. Natural selection acts to increase the average genic / breeding value for the population $\bar{g}$ when larger genic values are associated with greater expected fitness. Assuming vanishing genetic variation, this gives a condition for increase $\mathrm{d}W/\mathrm{d}g > 0$. This derivative may be expanded as follows:

$$\frac{\mathrm{d}W}{\mathrm{d}g} = \frac{\partial W}{\partial x}\frac{\mathrm{d}x}{\mathrm{d}\tilde{g}}\frac{\mathrm{d}\tilde{g}}{\mathrm{d}g} + \frac{\partial W}{\partial y}\frac{\mathrm{d}y}{\mathrm{d}\tilde{g}'}\frac{\mathrm{d}\tilde{g}'}{\mathrm{d}g}, \tag{A5}$$

where $\tilde{g}'$ denotes the average breeding value of an individual's social partners, where the genotype-phenotype map $\mathrm{d}x / \mathrm{d}\tilde{g} = \mathrm{d}y / \mathrm{d}\tilde{g}'$ can be set to unity, and where all derivatives and partial derivatives are evaluated at $x=y=z$ (Taylor & Frank 1996; Frank 1997, 1998; Taylor et al. 2007). The derivatives $\mathrm{d}\tilde{g} / \mathrm{d}g$ and $\mathrm{d}\tilde{g}' / \mathrm{d}g$ are equal to the coefficients of consanguinity of an individual to itself and of an individual to its social partner, respectively. These may be denoted p and p'. Hence, equation (A5) can be re-written as:

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$$\frac{\mathrm{d}W}{\mathrm{d}g} = p\left(\frac{\partial W}{\partial x} + \frac{\partial W}{\partial y}\frac{p'}{p}\right) = p\left(-C + Br\right), \tag{A6}$$

where $-C = \partial W/\partial x$ is the direct fitness cost of increased helping, $B = \partial W/\partial y$ is the indirect fitness benefit of receiving help from neighbours, and $r = p'/p$ is the kin selection coefficient of relatedness of juvenile patch mates. Thus, the condition for increase is Hamilton's (1963, 1964, 1970) rule $-C + Br > 0$.

From equation (1), we have:

$$-C = -c / S, \text{ and} \tag{A7}$$

$$B = \left(b - \frac{(1-d_f)^2 + (1-d_m)^2}{2}\left(b - c\right)\right) / S, \tag{A8}$$

where $-c$ is the partial derivative of S with respect to its first argument, and b is the partial derivative of S with respect to its second argument, both evaluated at $x = y = z$. Hence, $B > 0$ and $C > 0$, which means that helping is formally an altruistic trait (Hamilton 1964; West et al. 2007b).

The condition for increase $-C + Br > 0$ can be rearranged into the form:

$$\frac{c}{b} < \frac{r - ar}{1 - ar}, \tag{A9}$$

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where $a = [(1-d_f)^2+(1-d_m)^2]/2$. I reproduce this condition as inequality (2) in the main text. The relatedness coefficient can be expressed in terms of model parameters by calculating its component coefficients of consanguinity (Malécot 1948; Taylor 1992a; Rousset 2004). The consanguinity of a juvenile to itself can be written as $p = (1+\phi)/2$, where ϕ is the inbredness of that juvenile (the consanguinity of its parents), and is itself given by $\phi = (1-d_f)(1-d_m)p'$, i.e. the probability that both parents were previously juveniles on same patch times the consanguinity of juvenile patchmates. The consanguinity of juvenile patchmates is in turn given by: the probability that both randomly chosen genes are maternal (1/4), times the probability that they share the same mother (α) times the consanguinity of the mother to herself (p), plus the probability that they do not share the same mother ($1-\alpha$) times the expected consanguinity of their mothers ($(1-d_f)^2p'$); plus the probability that one of the randomly chosen genes is maternal and the other is paternal (1/2), times the consanguinity of mating partners (ϕ); plus the probability that both of the genes are paternal (1/4), times the probability that they share the same father (β) times the consanguinity of the father to himself (p) plus the probability that they do not share the same father ($1-\beta$) times the expected consanguinity of their fathers ($(1-d_m)^2p'$). This gives:

$$p' = \frac{1}{4}\left(\alpha p + (1-\alpha)(1-d_f)^2 p'\right) + \frac{1}{2}\phi + \frac{1}{4}\left(\beta p + (1-\beta)(1-d_m)^2 p'\right). \qquad \text{(A10)}$$

Making the substitution $p = (1+\phi)/2$, (A10) can be solved to obtain ϕ and p' in terms of model parameters: d_f, d_m, α and β. Relatedness of a juvenile to its patchmates is

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given by the ratio of their consanguinity and the consanguinity of the juvenile to itself, i.e. $r = p'/p$ (Gardner et al. 2007), and this obtains equation (3) of the main text.

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Figure Legends

Figure 1 | Relatedness and competition mediate the evolution of altruism. The potential for altruism (A; the valuation of social partners relative to self) as a function of within-patch relatedness (r) and within-patch competition (a). The potential for altruism increases with increasing relatedness, and decreases with increasing competition.

Figure 2 | Dispersal mediates relatedness. Contour plots of the relatedness of patchmates (r) as a function of female dispersal (d_f; abscissae), male dispersal (d_m; ordinates), probability of maternal sibship of patchmates (α; columns) and probability of paternal sibship of patchmates (β; rows), on a scale from 0 (black) to 1 (white). Relatedness is a decreasing function of both female and male dispersal, and an increasing function of both maternal and paternal sibship.

Figure 3 | Dispersal mediates competition. Within-patch competition (a) as a function of female dispersal (d_f) and male dispersal (d_m). Competition decreases with increasing female and male dispersal.

Figure 4 | Sex-biased dispersal mediates the evolution of altruism. Contour plots of the potential for altruism (A) as a function of female dispersal (d_f; abscissae), male dispersal (d_m; ordinates), the probabilities of maternal sibship (α; columns) and paternal sibship (β; rows) among social partners, on a scale from 0 (black) to ½ (white). The dashed line marks $A = (\alpha+\beta)/4$, the level of altruism that is predicted under unbiased dispersal ($d_f = d_m = d$). Sex-biased dispersal may promote altruism

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(area enclosed by dashed line) or inhibit altruism (area outwith dashed line). Altruism is promoted if there is a small dispersal bias towards the sex with the greater variance in reproductive success, and altruism is inhibited if the bias is large or in the opposite direction.

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Figure 1

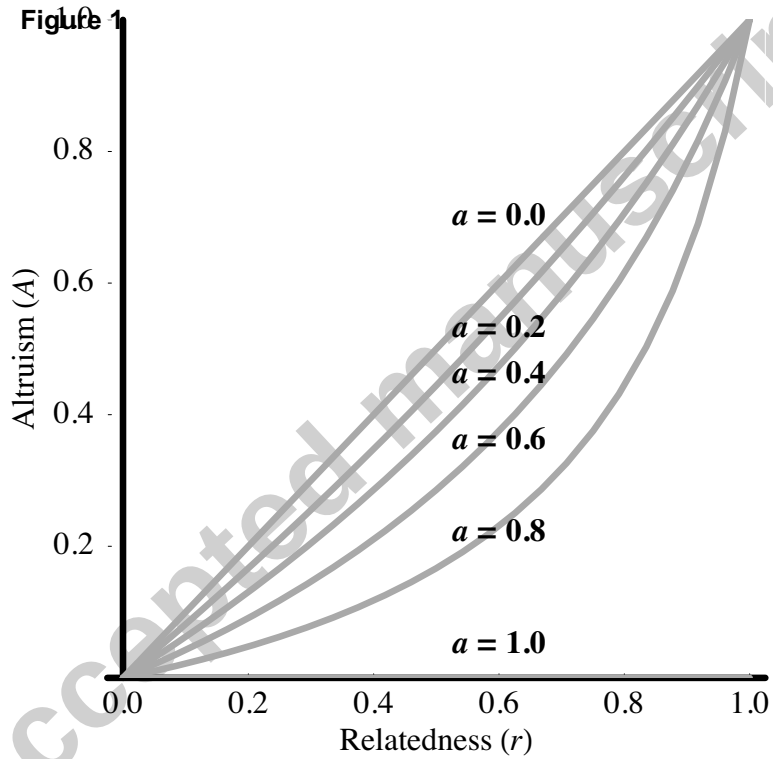

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Figure 2

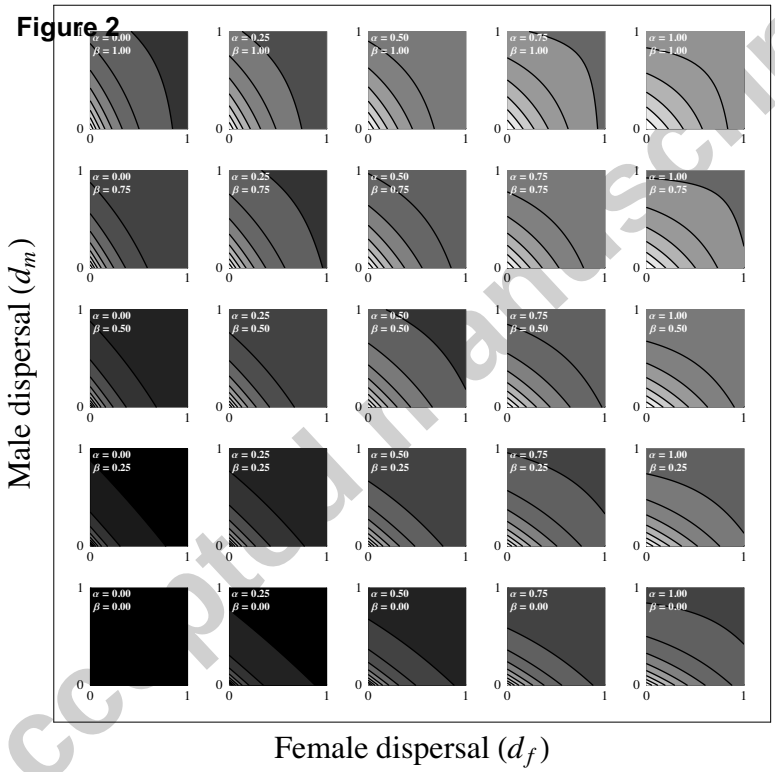

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Figure 3

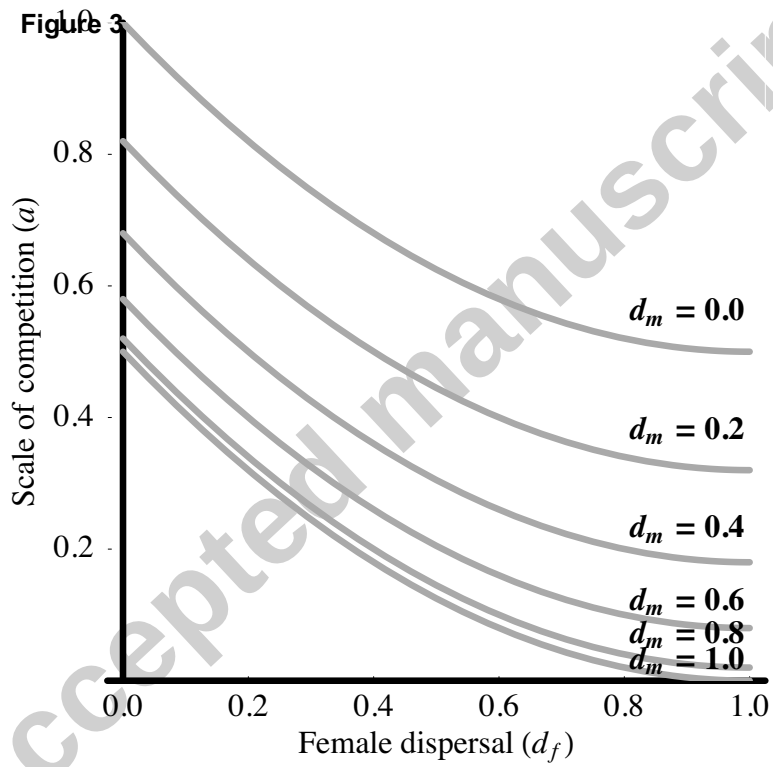

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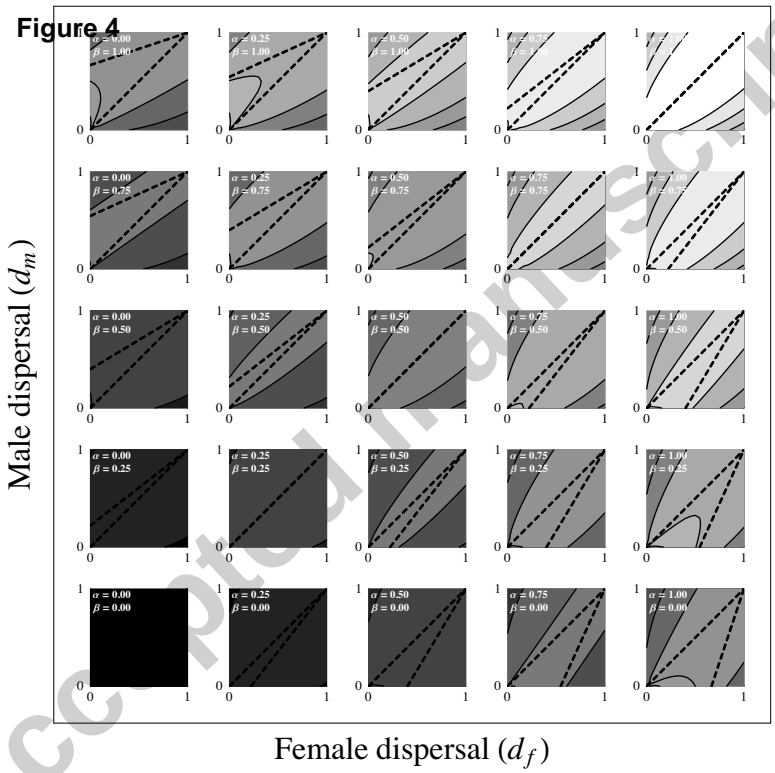
Figure 4



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