



A general ploidy model for the evolution of helping in viscous populations

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ABSTRACT

There is growing interest in understanding how kin selection drives the evolution of social behaviours in viscous populations. A key result, that has inspired much work on this topic, is the exact cancellation of the genetic relatedness and kin competition effects of dispersal in the simplest models of population viscosity, such that a reduction in the rate of dispersal neither promotes nor inhibits the evolution of helping behaviour. This theoretical result has been demonstrated for populations characterised by haploid, diploid and haplodiploid modes of inheritance. Here we develop a model of general ploidy that recovers these three scenarios as special cases and allows examination of scenarios that have not been considered previously. Specifically, we: clarify the importance of the implicit assumption of monandry in previous models; show that the cancellation result obtains in some models of ploidy but not in others; and reveal that the cancellation result obtains for different reasons in different models of ploidy. The cancellation result therefore hinges upon a population's genetic system as well as its demography.

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1. Introduction

Recent years have seen much interest in the role for demography to mediate social evolution. Of particular interest has been the evolution of helping behaviour in viscous populations. Hamilton (1964, 1971) suggested that indiscriminate helping could be favoured in populations that are characterised by low rates of dispersal, such that individuals tend to be closely related to their neighbours. However, low dispersal also leads to localised competition for resources among kin, and this can reduce selection for helping (Hamilton, 1971; Grafen, 1984; Queller, 1992; Frank, 1998; West et al., 2002). Indeed, Taylor (1992a) showed that – in the simplest scenario of an infinite, inelastic island model (Wright, 1931) – the effects of genetic relatedness and kin competition exactly cancel, such that there is no net impact of the rate of dispersal upon the evolution of helping.

This surprising result has stimulated a great deal of theoretical work, exploring which alterations to the basic model assumptions bring about a decoupling of genetic relatedness and kin competition, such that population viscosity may promote the evolution of helping (reviewed by Lehmann and Rousset, 2010). These include factors such as elastic/unsaturated populations (Taylor, 1992b; Alizon and Taylor, 2008), overlapping generations (Taylor and Irwin, 2000; Irwin and Taylor, 2001), dispersal-dependent behaviour (Perrin and Lehmann,

2001; El Mouden and Gardner, 2008), budding dispersal (Gardner and West, 2006; Lehmann et al., 2006), sex-biased dispersal (Johnstone and Cant, 2008; Gardner, 2010), birth–death versus death–birth demographies (Grafen and Archetti, 2008), reproductive skew (Pen and West, unpublished; Johnstone, 2008) and resource heterogeneity (Rodrigues and Gardner, 2012). Some of these theoretical predictions have been empirically tested using experimental evolution methods (Kümmerli et al., 2009).

Taylor's (1992a) original analysis considered three separate models, concerning haploid, diploid and haplodiploid modes of inheritance. Here, we develop a model of general ploidy (cf. Grafen, 1986, 2006a) that recovers each of these three scenarios as special cases, and allows examination of scenarios not considered by Taylor (1992a). We also relax Taylor's (1992a) implicit assumption of monandry, allowing females to mate with potentially multiple males. This allows an assessment of the robustness of Taylor's (1992a) cancellation result to variation in model assumptions, and helps to illuminate the genetical and demographic reasons for cancellation, both in his original models and also more generally.

2. Model and analysis

2.1. Model

We assume a population comprising an infinite number of patches, in which adult females each produce a large number of offspring. The probability that two randomly chosen juveniles

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that are born in the same patch are maternal siblings is denoted by α , and the probability that two randomly chosen maternal siblings are also paternal siblings is denoted by β . The number of genomes inherited by a juvenile female from her mother is denoted by κ , and the number of genomes she inherits from her father is denoted by λ (Fig. 1). The number of genomes inherited by a juvenile male from his mother is denoted by μ , and the number of genomes he inherits from his father is denoted by ν (Fig. 1).

We allow breeding females to divert resources from maternal care to communal care – i.e. helping behaviour – thereby improving the survival of random juveniles in her patch whilst reducing the survival of her own offspring. Formally, we denote a focal juvenile's probability of survival by $S(x,y)$, where x is the investment into helping made by that juvenile's mother, and y is the average investment into helping made by breeding females in the juvenile's patch. And we define $-c \equiv \partial S / \partial x$, representing the cost of helping for the actor, and $b \equiv \partial S / \partial y$, representing the benefit of helping for the recipient.

Following social interaction, adult females die, and all juveniles surviving to adulthood mate at random within their patch. After mating, the males die and the females either disperse with probability d to another patch or else remain with probability $1-d$ in their natal patch. Following dispersal, females compete within patches for breeding opportunities, returning the population to the beginning of the lifecycle. Model notation is summarised in Table 1.

Taylor's (1992a) model is recovered by setting $\alpha = 1/n$ (that is, there are n breeding females per patch, each having the same fecundity; our model keeps the number of breeding females

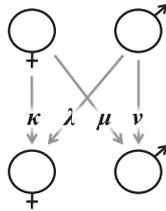


Fig. 1. A general model of ploidy. Daughters inherit κ genomes from their mother and λ genomes from their father, and sons inherit μ genomes from their mother and ν genomes from their father. Hence, females are $(\kappa + \lambda)$ -ploid whilst males are $(\mu + \nu)$ -ploid.

implicit, and allows for any degree of reproductive skew) and $\beta = 1$ (that is, monandry; our model allows females to mate with potentially multiple males). Moreover, Taylor's (1992a) haploidy model is recovered by setting $\kappa = 1$, $\lambda = 0$, $\mu = 0$ and $\nu = 0$; his diploidy model is recovered by setting $\kappa = 1$, $\lambda = 1$, $\mu = 1$ and $\nu = 1$; and his haplodiploidy model is recovered by setting $\kappa = 1$, $\lambda = 1$, $\mu = 1$ and $\nu = 0$.

2.2. Evolution of helping

We determine how natural selection operates upon indiscriminate helping behaviour, using the neighbour modulated fitness approach of Taylor and Frank (1996; see also Taylor, 1996; Frank, 1997, 1998; Rousset, 2004; Taylor et al., 2007). This yields a condition for natural selection to favour helping:

$$-c(c_f p_d + c_m p_s) + b(c_f p_f + c_m p_m) - (1-d)^2 (b-c)(c_f p_f + c_m p_m) > 0, \quad (1)$$

where c_f and c_m are the class reproductive values (Fisher, 1930; Taylor, 1996; Grafen, 2006a) of females and males, respectively; and p_d , p_s , p_f and p_m are the coefficients of consanguinity (Bulmer, 1994) between an adult female and her daughter, her son, a random juvenile female from her patch, and a random juvenile male from her patch, respectively (see Appendix for details).

Inequality (1) yields a simple inclusive fitness interpretation (Hamilton 1964, 1970). First, helping reduces the survival of the actor's offspring by an amount c , and the actor values her offspring by an amount $c_f p_d + c_m p_s$. Second, helping increases the survival of random juveniles on the actor's patch by an amount b , and the actor values these juveniles by an amount $c_f p_f + c_m p_m$. Third, to the extent that competition is local—i.e. $(1-d)^2$, the probability that two females competing for breeding opportunities within a patch are both native to that patch (Frank, 1998; Gardner and West, 2006)—the net increase $b-c$ in the survival of local juveniles leads to a competitive displacement of juveniles who were born on the actor's patch, and the actor values them by an amount $c_f p_f + c_m p_m$.

Inequality (1) may be rearranged to the form $c/b < A$, where A defines the potential for helping (cf. Gardner, 2010), i.e. the value that an adult female places on the survival of a random juvenile in her patch, relative to the value that she places on the

Table 1
A summary of model notation.

Symbol	Definition
α	Probability that two random juvenile patch mates are maternal siblings
β	Probability that two random maternal siblings are paternal siblings
κ	Number genomes in daughter that came from mother
λ	Number of genomes in daughter that came from father
μ	Number of genomes in son that came from mother
ν	Number of genomes in son that came from father
d	Rate of dispersal
S	Probability of juvenile survival
x	Helping strategy of focal juvenile's mother
y	Average helping strategy among breeding females in focal juvenile's patch
z	Average helping strategy among breeding females in population
b	Survival benefit of helping
c	Survival cost of helping
m	Male
f	Female
d	Focal female's daughter
s	Focal female's son
f	Random juvenile female in focal female's patch
m	Random juvenile male in focal female's patch
c_x	Class reproductive value of class $X \in \{m, f\}$
p_Y	Consanguinity of focal female to social partner $Y \in \{d, s, f, m\}$
A	Potential for helping

survival of one of her own offspring, chosen at random. This is

$$A = \frac{(c_f p_f + c_m p_m) - (1-d)^2 (c_f p_f + c_m p_m)}{(c_f p_d + c_m p_s) - (1-d)^2 (c_f p_f + c_m p_m)} \quad (2)$$

The class reproductive values and consanguinities – and hence, the potential for helping – can be expressed exclusively in terms of model parameters (i.e. α , β , κ , λ , μ , ν and d ; see Appendix for details). Unfortunately, the general expression for the potential for helping is too complicated to reproduce here.

3. Results

3.1. Recovery of Taylor's (1992a) results

We recover Taylor's (1992a) models by making the appropriate substitutions in our general model. Taylor's (1992a) haploidy model is recovered by making the substitutions $\kappa=1$, $\lambda=0$, $\mu=0$ and $\nu=0$. Here, we find that the potential for helping is $A=\alpha$. Recalling that $\alpha=1/n$ in Taylor's (1992a) model, this is exactly equivalent to his condition $b/c > n$ for the evolution of helping (see Rousset (2004, pp. 112–116) for discussion of how this result relates to Hamilton's rule of kin selection). Importantly, the potential for helping is not mediated by the rate of dispersal ($dA/dd=0$ for all $0 \leq d \leq 1$), and is equal to the probability that two random juveniles sharing the same patch are maternal siblings. We recover Taylor's (1992a) diploidy model by making the substitutions $\kappa=1$, $\lambda=1$, $\mu=1$, $\nu=1$ and $\beta=1$, and we recover his haplodiploidy model by making the substitutions $\kappa=1$, $\lambda=1$, $\mu=1$, $\nu=0$ and $\beta=1$. In both cases, we find that $A=\alpha$, i.e. the potential for helping is independent of the rate of dispersal.

3.2. The importance of monandry

Taylor (1992a) made an implicit assumption of monandry ($\beta=1$) in his models of diploidy and haplodiploidy. We find that the potential for helping is not, in general, independent of the probability β that maternal siblings are also paternal siblings, and hence there is an impact of female mate fidelity upon the potential for helping. Moreover, we find that relaxing the assumption of strict monandry in Taylor's (1992a) models of diploidy and haplodiploidy leads to the breakdown of the cancellation result. That is, if females mate with more than one male ($\beta < 1$), the potential for helping is not generally independent of the rate of dispersal (Fig. 2). In particular, we find that the potential for helping increases with the degree of monandry ($dA/d\beta > 0$), and that the potential for helping increases with the rate of dispersal when females are polyandrous ($dA/dd > 0$ when $\beta < 1$).

Why does polyandry ($\beta < 1$) lead to the breakdown of Taylor's (1992a) cancellation result? This is most easily understood by considering Taylor's (1992a, p. 355) diploidy analysis, and noting that his derivation of the cancellation result explicitly hinges upon the relatedness of two random juveniles on the same patch being equal to the relatedness of a mother to a random juvenile on her patch. Since the relatedness of two random juveniles is equal to the average of the relatedness between the first juvenile and the mother of the second juvenile and the relatedness between the first juvenile and the father of the second juvenile, the cancellation result requires that the relatedness between a mother and a random juvenile is equal to the relatedness between a father and a random juvenile. This is the case if all of a female's offspring are due to the same father, but need not hold more generally. For example, if there is full dispersal ($d=1$), a single breeding female per patch ($\alpha=1$), and every one of a female's offspring has a different father ($\beta=0$), then the breeding female is

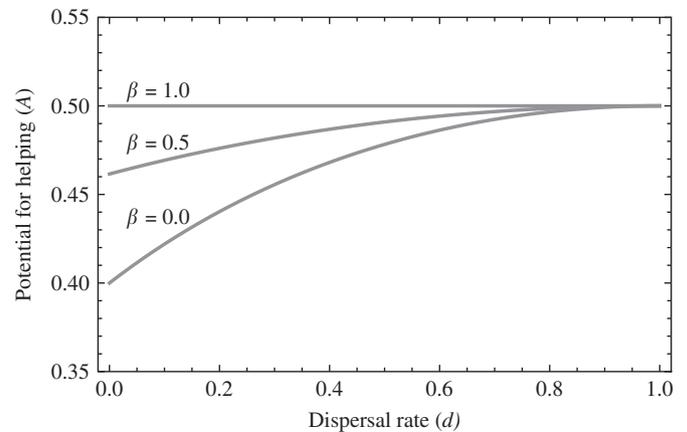


Fig. 2. The implicit assumption of monandry underlies Taylor's cancellation result. The potential for helping (A) is shown as a function of the probability that maternal siblings are also paternal siblings (β) and the rate of dispersal (d) under diploidy. There is no net impact of dispersal rate upon the potential for helping under monandry ($dA/dd=0$ when $\beta=1$). Polyandry reduces the potential for helping ($dA/d\beta > 0$) and leads the potential for helping to increase with the rate of dispersal ($dA/dd > 0$ when $\beta < 1$). Here we assume $\alpha=0.5$.

closely related to all of the offspring born in the patch but each of her mates is related to only one of these offspring.

3.3. The importance of ploidy

Having shown that polyandry ($\beta < 1$) may lead to the failure of Taylor's (1992a) cancellation result, we now proceed on the assumption of monandry ($\beta=1$). We find that, whilst the cancellation result does obtain in certain scenarios (including the haploidy, diploidy and haplodiploidy scenarios considered by Taylor), it does not obtain in every scenario. The general solution for A is too complicated to be useful in explaining when and why the potential for helping is independent of the rate dispersal. However, we are able to make some observations.

First, we observe that the cancellation result obtains in every scenario with sexually-symmetrical inheritance (i.e. $\kappa=\lambda=\mu=\nu$). In such scenarios, we have $p_d=p_s=p_o$ and $p_f=p_m=p_p$, and substituting these consanguinities into expression (2) obtains $A=(R-(1-d)^2R)/(1-(1-d)^2R)$, where $R=p_p/p_o$ is the value an adult female places upon a random juvenile in her patch relative to the value she places upon her own offspring. Noting that $R=\alpha+(1-\alpha)r$ (where r is the value an adult female places upon a random non-descendant juvenile relative to her own offspring) and $r=(1-d)^2R$ (owing to the assumption of monandry; $\beta=1$), we obtain $A=\alpha$. Thus, sexually-symmetrical inheritance is sufficient for the cancellation result to obtain.

Second, we observe that the cancellation result also occurs in some scenarios with sexually-asymmetric inheritance. This is illustrated by the haplodiploidy scenario ($\kappa=\lambda=\mu=1$, $\nu=0$), in which we have $A=\alpha$ despite sexually-asymmetric inheritance. Here, we find that artificially varying the class reproductive values away from their proper values of $c_f=2/3$ and $c_m=1/3$ causes the potential for helping to both vary and also cease to be independent of the rate of dispersal. This is in contrast to the sexually-symmetric inheritance models, in which artificially varying the values of c_f and c_m does not impact upon the potential for helping. This means that the cancellation result of Taylor (1992a) occurs for different reasons in different scenarios, and that sexually-symmetrical inheritance is not necessary for the cancellation result to obtain.

Third, we observe that the cancellation result does not hold in any scenario in which genes flow from males to females but not from females to males (i.e. $\lambda > 0$ and $\mu=0$); and hence, for the model to be biologically feasible, $\nu > 0$). In such scenarios, although females may

reproduce and contribute genes to their daughters, they have no long-term reproductive value. That is, they are the ‘living dead’, and we term them ‘zombies’. Substituting the class reproductive values $c_f=0$ and $c_m=1$ into Eq. (2) obtains a potential for helping of $A=(p_m-(1-d)^2p_m)/(p_s-(1-d)^2p_m)$. Since all of a male’s genes come from his father, the consanguinity of mother and son p_s is equal to the consanguinity of a female to her mating partner, which is the consanguinity of a juvenile female and a juvenile male who are born on the same patch, or p_{fm} . And the consanguinity of an adult female to a juvenile male in her patch is $p_m=\alpha p_s+(1-\alpha)(1-d)^2p_{fm}$. That is: with probability α the juvenile male is her son, in which case they have consanguinity p_s ; and with probability $1-\alpha$ the juvenile male is not her son, but with probability $(1-d)^2$ his father was born on her patch, in which case they have consanguinity p_{fm} . Making these substitutions, we obtain $A=[1-(1-(1-d)^2)(1-\alpha)]/[2-\alpha-(1-(1-d)^2)(1-\alpha)]$, which does depend upon the rate of dispersal (Fig. 3). Thus, the existence of zombie females is sufficient for the cancellation result to fail.

A more systematic exploration of ploidy scenarios is pursued in Table 2. Since there is an infinite number of possible scenarios, we restrict our attention to those in which an individual receives either zero or one genome from either parent (that is, $\kappa=0$ or 1, $\lambda=0$ or 1, $\mu=0$ or 1, $\nu=0$ or 1 and $\beta=1$). This binary model defines $2^4=16$ different scenarios, of which 10 are feasible for analysis

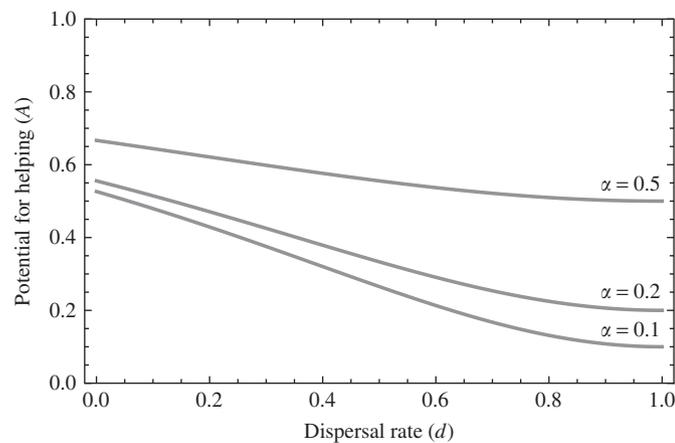


Fig. 3. Population viscosity promotes helping in zombies. In scenarios where females have zero reproductive value (e.g. scenarios 6 and 14 in Table 2), the potential for helping (A) decreases as the rate of dispersal (d) increases. Here we assume $\alpha=0.1, 0.2$ and 0.5 , and $\beta=1$.

Table 2
Results for the binary model of ploidy.

#	κ	λ	μ	ν	Potential for helping (A)	Notes
1	0	0	0	0	–	Unfeasible—females have no genes
2	0	0	0	1	–	Unfeasible—females have no genes
3	0	0	1	0	–	Unfeasible—females have no genes
4	0	0	1	1	–	Unfeasible—females have no genes
5	0	1	0	0	–	Unfeasible—females have paternal genes but males have no genes
6	0	1	0	1	$\frac{1-(1-(1-d)^2)(1-\alpha)}{2-\alpha-(1-(1-d)^2)(1-\alpha)}$	Zombie females—no cancellation
7	0	1	1	0	α	Cancellation, independent of c_f & c_m
8	0	1	1	1	α	Cancellation requires $c_f=1/3$ & $c_m=2/3$
9	1	0	0	0	α	Taylor’s haploidy model—cancellation, independent of c_f & c_m
10	1	0	0	1	α	Cancellation, independent of c_f & c_m
11	1	0	1	0	α	Cancellation, independent of c_f & c_m
12	1	0	1	1	α	Cancellation requires $c_f=1$ & $c_m=0$
13	1	1	0	0	–	Unfeasible—females have paternal genes but males have no genes
14	1	1	0	1	$\frac{1-(1-(1-d)^2)(1-\alpha)}{2-\alpha-(1-(1-d)^2)(1-\alpha)}$	Zombie females—no cancellation
15	1	1	1	0	α	Taylor’s haplodiploidy model—cancellation requires $c_f=2/3$ & $c_m=1/3$
16	1	1	1	1	α	Taylor’s diploidy model—cancellation, independent of c_f & c_m

(Table 2). The remaining 6 scenarios either make biologically impossible assumptions (such as scenario 5, in which $\kappa=0, \lambda=1, \mu=0$ and $\nu=0$; that is, males carry no genes but make genetic contributions to daughters) or else contradict the analysis (such as scenario 1, in which $\kappa=0, \lambda=0, \mu=0$ and $\nu=0$; that is, there is no genetic material in the population, such that helping cannot evolve by natural selection). We find that the cancellation result obtains in 8 of the 10 feasible scenarios (scenarios 7–12 and 15 & 16) but that the potential for helping is mediated by the rate of dispersal in 2 of the feasible scenarios (scenarios 6 and 14). Both of the scenarios in which the cancellation result does not obtain involve zombie females.

4. Discussion

We have generalised Taylor’s (1992a) model of indiscriminate helping in inelastic viscous populations, in order to determine the consequences of relaxing his implicit and explicit assumptions of the genetic system. We have shown that Taylor’s (1992a) implicit assumption of monandry (each female mates with a single male) is key to his surprising cancellation result, whereby the potential for helping is independent of the rate of dispersal. In particular, polyandry leads to a lower potential for helping over all, and a high potential for helping in populations characterised by a higher rate of dispersal. We have also shown that, even maintaining the assumption of monandry, Taylor’s (1992a) cancellation result is not robust to changes in assumptions about ploidy. In particular, in 20% of the specific ploidy scenarios that we have considered, the potential for helping is dependent upon the rate of dispersal, with a lower potential for helping in populations characterised by a higher rate of dispersal. That is, population viscosity can promote the evolution of helping.

A complete understanding of the impact of ploidy upon Taylor’s (1992a) cancellation result has been impeded by the complexity of our general results. However, we have made four general observations. First, sexually-symmetrical inheritance (i.e. $\kappa=\lambda=\mu=\nu$) is sufficient for the cancellation result to obtain (assuming monandry). An illustration is provided by Taylor’s (1992a) model of diploidy, and here we have proven the principle more generally. Second, sexually-symmetrical inheritance is not necessary for the cancellation result to obtain. An illustration is provided by Taylor’s (1992a) model of haplodiploidy (i.e. $\kappa=\lambda=\mu=1$ and $\nu=0$).

Third, scenarios in which males contribute genomes to their daughters but females do not contribute genomes to their sons do not exhibit the cancellation result. Such scenarios are rather odd from a biological perspective. However, they may not be totally

unknown in the real world. Gardner and Ross (2011) consider a model of the scale insect *Icerya purchasi*, in which females are diploid and receive one genome from their mother and one genome from their father, and dwarf males (that are reduced to infectious tissues living within the bodies of their female hosts) are haploid and receive their genome from their father. This model – representing the endpoint of evolution of this bizarre reproductive system – is similar to that of scenario 14 in Table 2, albeit corresponding to the trivial case of only one adult female per patch. In the absence of regular males, *I. purchasi* females are the ‘living dead’: they are fertile, and produce daughters, but they have zero long-term reproductive value (Gardner and Ross, 2011).

Fourth, when Taylor’s (1992a) cancellation result does occur, it appears that it does so for different reasons in different scenarios. In the diploidy scenario, the cancellation result obtains prior to the computation of class reproductive values, whereas in the haplodiploidy scenario, the cancellation result obtains only when the class reproductive values have been set to their proper values (i.e. $c_f=2/3$ and $c_m=1/3$). Hence, class reproductive value enters into the explanation of the cancellation result in haplodiploids, but does not enter into the explanation of the cancellation result in diploids, or indeed in any other sexually-symmetrical system of genetic inheritance.

More generally, the present analysis illustrates Eddington’s (1928, p. 267) point that “contemplation in natural science of a wider domain than the actual leads to a far better understanding of the actual”. By considering genetic systems that might not exist, we have recovered a better understanding of the reasons for Taylor’s (1992a) cancellation result as it relates to those genetic systems that do exist in nature. Moreover, this approach provides a means of gauging the depth of a theoretical result. Our analysis suggests that the cancellation result is not particularly robust and is not fundamental. Rather, it may be no more than coincidence that the cancellation result obtains in the three models of genetic inheritance (haploidy, diploidy and haplodiploidy) that are most familiar to students of social evolution.

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Appendix A

A.1. Evolution of helping

The expected fitness – i.e. number of surviving offspring – of a juvenile female is given by the product of the probability that she survives to adulthood and her expected breeding success given that she survives. This is

$$w_f = S(x,y) \left((1-d) \frac{K}{(1-d)S(y,y) + dS(z,z)} + d \frac{K}{S(z,z)} \right), \quad (A1)$$

where x is the helping strategy of her mother; y is the average helping strategy of breeding females in her patch; z is the average helping strategy of breeding females in the whole population; and K is a constant (Gardner, 2010). The average fitness taken over all juvenile females in the population is therefore $\bar{w}_f = K$. Hence, the fitness of the focal juvenile female, expressed relative to the average for her class, is $W_f = w_f/\bar{w}_f$, or

$$W_f = S(x,y) \left(\frac{1-d}{(1-d)S(y,y) + dS(z,z)} + \frac{d}{S(z,z)} \right). \quad (A2)$$

The expected fitness of a juvenile male is given by the product of the probability that he survives to adulthood, his expected mating success, and the expected breeding success of his mates. This is

$$w_m = S(x,y) \frac{1-s}{s} \left((1-d) \frac{K}{(1-d)S(y,y) + dS(z,z)} + d \frac{K}{S(z,z)} \right), \quad (A3)$$

where s is the sex ratio (i.e. proportion of juveniles that are male). The average fitness taken over all juvenile males in the population is therefore $\bar{w}_m = ((1-s)/s)K$. Hence, the fitness of the focal juvenile male, expressed relative to the average for his class, is $W_m = w_m/\bar{w}_m$, or

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

We consider a locus that controls helping and, choosing a gene at random from this locus from a focal individual, we denote its genic value by g . Natural selection favours an increase in the frequency of an allele if individuals carrying that allele are, on average, fitter than individuals carrying different alleles: that is, if $dW/dg > 0$. In a class structured population, this average is done using class reproductive values as weights, so we have $W = c_f W_f + c_m W_m$ (Price, 1970; Taylor, 1996; Frank, 1997, 1998; Rousset, 2004; Taylor et al., 2007). Hence, the condition for natural selection to favour helping is

$$c_f \frac{dW_f}{dg_f} + c_m \frac{dW_m}{dg_m} > 0. \quad (A5)$$

We assume vanishing genetic and phenotypic variation, so all derivatives may be evaluated at the population average (i.e. $x=y=z$; Taylor and Frank, 1996).

There are two routes by which a juvenile female’s helping gene is associated with her fitness. First, it is associated with her mother’s genetic value G , which is associated with her mother’s helping phenotype x , which is a factor impacting upon her fitness W_f . Second, it is associated with the genetic value of a random adult female in her patch G' , which is associated with that adult female’s helping phenotype y , which is a factor impacting upon her fitness W_f . Thus, we have

$$\frac{dW_f}{dg_f} = \frac{\partial W_f}{\partial x} \frac{dx}{dG} \frac{dG}{dg_f} + \frac{\partial W_f}{\partial y} \frac{dy}{dG'} \frac{dG'}{dg_f}, \quad (A6)$$

where from Eq. (A2), $\partial W_f/\partial x = -c/S(z,z)$ and $\partial W_f/\partial y = (b - (1-d)^2(b-c))/S(z,z)$; $dG/dg_f = p_d$ is the consanguinity of mother and daughter; $dG'/dg_f = p_f$ is the consanguinity of an adult female and a juvenile female in the same patch; and $dx/dG = dy/dG' = \gamma$ is the genotype-phenotype map.

Similarly, the association between a juvenile male’s gene and his fitness is

$$\frac{dW_m}{dg_m} = \frac{\partial W_m}{\partial x} \frac{dx}{dG} \frac{dG}{dg_m} + \frac{\partial W_m}{\partial y} \frac{dy}{dG'} \frac{dG'}{dg_m}, \quad (A7)$$

where from Eq. (A2), $\partial W_m/\partial x = -c/S(z,z)$ and $\partial W_m/\partial y = (b - (1-d)^2(b-c))/S(z,z)$; $dG/dg_m = p_s$ is the consanguinity of mother and son; and $dG'/dg_m = p_m$ is the consanguinity of an adult female and a juvenile male in the same patch. Making these substitutions yields inequality (1) of the main text.

A.2. Class reproductive value

A class’s reproductive value describes probability that a gene chosen at random from a distant future generation of the population derives from an individual of this class in the present generation (Fisher, 1930; Grafen, 2006a). The class reproductive

values in our model satisfy:

$$(c_f \quad c_m) = (c_f \quad c_m) \begin{pmatrix} \phi_{f \leftarrow f} & \phi_{f \leftarrow m} \\ \phi_{m \leftarrow f} & \phi_{m \leftarrow m} \end{pmatrix}, \quad (\text{A8})$$

where $\phi_{f \leftarrow f} = \kappa / (\kappa + \lambda)$ is the fraction of a daughter's genes that derive from her mother; $\phi_{f \leftarrow m} = \lambda / (\kappa + \lambda)$ is the fraction of a daughter's genes that derive from her father; $\phi_{m \leftarrow f} = \mu / (\mu + \nu)$ is the fraction of a son's genes that derive from his mother; and $\phi_{m \leftarrow m} = \nu / (\mu + \nu)$ is the fraction of a son's genes that derive from his father (Taylor, 1996; Grafen, 2006a). Solving Eq. (A8) obtains

$$c_f = \frac{\kappa\mu + \lambda\mu}{\kappa\mu + \lambda\nu + 2\lambda\mu}, \quad (\text{A9})$$

and

$$c_m = \frac{\lambda\mu + \lambda\nu}{\kappa\mu + \lambda\nu + 2\lambda\mu}. \quad (\text{A10})$$

Note that $c_f = \phi_{m \leftarrow f} / (\phi_{m \leftarrow f} + \phi_{f \leftarrow m})$ and $c_m = \phi_{f \leftarrow m} / (\phi_{m \leftarrow f} + \phi_{f \leftarrow m})$. That is, the probability that a gene drawn at random from a distant future generation traces its ancestry to a member of a given sex in the present generation is equal to the proportion of the between-sex gene flow that flows out of that sex.

A.3. Consanguinity

Coefficients of consanguinity describe the probability that a gene chosen at random from a focal individual – in this case, an adult female – is identical by descent with a gene chosen at random from the same locus in another individual of given 'role' (e.g. the focal individual's daughter; Bulmer, 1994; Grafen, 2006b).

Inequality (1) of the main text reveals that the action of natural selection depends upon the values of four coefficients of consanguinity: p_d , p_s , p_f and p_m . These depend upon model parameters and other coefficients of consanguinity. For example, the consanguinity of mother and daughter p_d is equal to the probability that a randomly chosen gene from the daughter is maternal in origin $\kappa / (\kappa + \lambda)$ times the probability that any two genes picked at random (with replacement) from her mother are identical by descent p , plus the probability that the daughter's gene is paternal in origin $\lambda / (\kappa + \lambda)$ times the probability that a gene picked at random from her mother and father are identical by descent p_{fm} . Thus, we may write the following closed system of equations:

$$p = \frac{1}{\kappa + \lambda} + \frac{\kappa(\kappa - 1)}{(\kappa + \lambda)^2} p + \frac{\lambda(\lambda - 1)}{(\kappa + \lambda)^2} q + \frac{2\kappa\lambda}{(\kappa + \lambda)^2} p_{fm} \quad (\text{A11})$$

$$q = \frac{1}{\mu + \nu} + \frac{\mu(\mu - 1)}{(\mu + \nu)^2} p + \frac{\nu(\nu - 1)}{(\mu + \nu)^2} q + \frac{2\mu\nu}{(\mu + \nu)^2} p_{fm} \quad (\text{A12})$$

$$p_d = \frac{\kappa}{\kappa + \lambda} p + \frac{\lambda}{\kappa + \lambda} p_{fm} \quad (\text{A13})$$

$$p_s = \frac{\mu}{\mu + \nu} p + \frac{\nu}{\mu + \nu} p_{fm} \quad (\text{A14})$$

$$p_f = \alpha p_d + (1 - \alpha)(1 - d)^2 \left(\frac{\kappa}{\kappa + \lambda} p_{ff} + \frac{\lambda}{\kappa + \lambda} p_{fm} \right) \quad (\text{A15})$$

$$p_m = \alpha p_s + (1 - \alpha)(1 - d)^2 \left(\frac{\mu}{\mu + \nu} p_{ff} + \frac{\nu}{\mu + \nu} p_{fm} \right) \quad (\text{A16})$$

$$p_{ff} = \frac{\kappa^2}{(\kappa + \lambda)^2} (\alpha p + (1 - \alpha)(1 - d)^2 p_{ff}) + \frac{\lambda^2}{(\kappa + \lambda)^2} (\alpha \beta q + (\alpha(1 - \beta) + (1 - \alpha)(1 - d)^2) p_{mm}) + \frac{2\kappa\lambda}{(\kappa + \lambda)^2} (\alpha + (1 - \alpha)(1 - d)^2) p_{fm} \quad (\text{A17})$$

$$p_{mm} = \frac{\mu^2}{(\mu + \nu)^2} (\alpha p + (1 - \alpha)(1 - d)^2 p_{ff}) + \frac{\nu^2}{(\mu + \nu)^2} (\alpha \beta q + (\alpha(1 - \beta) + (1 - \alpha)(1 - d)^2) p_{mm}) + \frac{2\mu\nu}{(\mu + \nu)^2} (\alpha + (1 - \alpha)(1 - d)^2) p_{fm} \quad (\text{A18})$$

$$p_{fm} = \frac{\kappa}{\kappa + \lambda} \frac{\mu}{\mu + \nu} (\alpha p + (1 - \alpha)(1 - d)^2 p_{ff}) + \frac{\lambda}{\kappa + \lambda} \frac{\nu}{\mu + \nu} (\alpha \beta q + (\alpha(1 - \beta) + (1 - \alpha)(1 - d)^2) p_{mm}) + \left(\frac{\kappa}{\kappa + \lambda} \frac{\nu}{\mu + \nu} + \frac{\lambda}{\kappa + \lambda} \frac{\mu}{\mu + \nu} \right) (\alpha + (1 - \alpha)(1 - d)^2) p_{fm}, \quad (\text{A19})$$

where p is the consanguinity of a female to herself; q is the consanguinity of a male to himself; p_d is the consanguinity of mother and daughter; p_s is the consanguinity of mother and son; p_f is the consanguinity of an adult female and a random juvenile female on her patch; p_m is the consanguinity of an adult female and a random juvenile male on her patch; p_{ff} is the consanguinity of two juvenile females born on the same patch; p_{mm} is the consanguinity of two juvenile males born on the same patch; and p_{fm} is the consanguinity of a juvenile female and a juvenile male born on the same patch, i.e. the consanguinity of mating partners.

Eqs. (A11)–(A19) can be simultaneously solved to yield all consanguinities exclusively in terms of model parameters (i.e. α , β , κ , λ , μ , ν and d). Unfortunately, the general solutions are too complicated to reproduce here.

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