

## Birth–death symmetry in the evolution of a social trait

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### Abstract

Studies of the evolution of a social trait often make ecological assumptions (of population structure, life history), and thus a trait can be studied many different times with different assumptions. Here, I consider a Moran model of continuous reproduction and use an inclusive fitness analysis to investigate the relationships between fecundity or survival selection and birth–death (BD) or death–birth (DB) demography on the evolution of a social trait. A simple symmetry obtains: fecundity (respectively survival) effects under BD behave the same as survival (respectively fecundity) effects under DB. When these results are specialized to a homogeneous population, greatly simplified conditions for a positive inclusive fitness effect are obtained in both a finite and an infinite population. The results are established using the elegant formalism of mathematical group theory and are illustrated with an example of a finite population arranged in a cycle with asymmetric offspring dispersal.

### Introduction

Given a population housed in a fixed physical structure (e.g. a configuration of breeding sites with some notion of proximity), it is known that different demographic assumptions (life-history variation, birth and death protocols, dispersal patterns) can have significant effects on the evolution of a social trait. Assumptions found in recent theoretical work, to be discussed in more detail later, have focused on two distinctions – first whether social interactions primarily affect fecundity or survival, and second whether death is primarily driven by the birth rate or birth is primarily occasioned by death. Of course, both alternatives generally operate together, but insights can be had by looking at their effects separately. As an example, Ohtsuki *et al.* (2006) used a model of continuous reproduction, with fecundity effects of social interaction, and compared the evolution of cooperation (fecundity benefit  $b$  to a neighbour at cost  $c$ ) under a birth–death (BD) and a death–birth (DB) protocol. These terms are defined below but essentially birth causes death in the first and death allows birth in the

second. They showed that under DB, costly altruism could evolve on a graph provided  $b/c > k$ , where  $k$  was the average degree of the graph (number of edges incident at a node), and in view of Hamilton's (1964) classic rule  $br > c$ , they conjectured a relationship between relatedness  $r$  and  $1/k$ . However, under a BD protocol, no such evolution was possible. A theoretical result of Taylor *et al.* (2007b) subsequently confirmed the condition  $b/c > k$  for large homogeneous graphs for the DB protocol and confirmed that under BD no amount of benefit could overcome the cost of an altruistic interaction.

My purpose here is first to attempt to better understand the relationship between these two fundamental dichotomies, fecundity vs. survival selection and BD vs. DB protocols, and I begin by pointing to a simple symmetry between them. Second, I derive a significant simplification of the inclusive fitness expressions in a homogeneous population and illustrate the results in a population structured as a five-cycle. The results are established using the formalism of mathematical group theory developed in Taylor, Lillcrap and Cownden (unpublished work). Finally I attempt to draw some general conclusions.

For the most part I draw on two central strands of investigation, first the huge literature on the formulation of inclusive fitness models (Hamilton, 1964) in structured populations, and second the study of the interaction

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between the immediate fitness effects of a social trait and the competitive effects that derive from the population structure (Taylor, 1992a,b; Queller, 1994; West *et al.*, 2002; Taylor *et al.*, 2007a; Grafen & Archetti, 2008).

### The Moran model – fecundity and survival vs. BD and DB

Increasingly, studies of the evolution of behaviour are set in a structured population. Although this means that the results obtained are particular to a certain structure, these so-called closed models gain a measure of reliability in the sense that critical parameters such as relatedness between interactants can be derived from the demographic assumptions rather than given *ad hoc* values. Gardner & West (2006) provide a more extended comparison of these two modelling approaches. Here, I use a simple graph structure, the nodes  $i$  representing breeding sites and the arcs between nodes bearing the dispersal probabilities  $d(i, j)$  defined as the neutral (no selection) probability an offspring born at node  $i$  displaces the breeder at node  $j$  (the effects of selection on these will be made precise below). I assume that these are symmetric and I include only successful offspring in the count. Thus:

$$d(i, j) = d(j, i) \quad (1)$$

$$\sum_j d(i, j) = 1 \quad (2)$$

I work with a haploid asexual population and use a Moran model of continuous reproduction. The individual fitness effects  $w_i$  at node  $i$  will be taken to be the difference between fecundity and mortality, and these will be determined in different ways under the two different demographic protocols, BD and DB (Ohtsuki & Nowak, 2006). Under BD, births drive the process and death results from the pressure generated by birth. Under DB, deaths drive the process and birth results from the openings generated by death.

I let baseline fecundity and survival both be 1, but suppose that there might be incremental changes  $F_i$  and  $S_i$  at node  $i$ . Following West & Gardner (2010), I call these increments ‘primary’ and use the term ‘secondary’ for all subsequent competitive effects these increments might have on other breeders. In terms of these, I take the node  $i$  fitness  $w_i$  to be the difference between the birth rate and death rate specified as follows:

$$\text{BD: } w_i = (1 + F_i) - \sum_j (1 + F_j) \frac{d(j, i)(1 - S_i)}{\sum_k d(j, k)(1 - S_k)} \quad (3)$$

$$\text{DB: } w_i = \sum_j (1 - S_j) \frac{d(i, j)(1 + F_i)}{\sum_k d(k, j)(1 + F_k)} - (1 - S_i) \quad (4)$$

Under BD, breeder  $i$  gives birth at rate  $1 + F_i$  and dies when replaced by an offspring. In this process, an offspring born at node  $j$  replaces the node  $i$  breeder with

relative probability  $d(j, i)(1 - S_i)$ , the product of the dispersal rate and the node  $i$  mortality. Under DB, breeder  $i$  dies at rate  $1 - S_i$  and attempts to gain an offspring whenever a neighbouring node is vacated by the death of the breeder. More precisely, a breeder death at node  $j$  will be replaced by an offspring born at node  $i$  with relative probability  $d(i, j)(1 + F_i)$ , the product of the dispersal rate and the node  $i$  fecundity. Note that in the neutral population ( $F_j = S_j = 0$ ), birth rates and death rates are both 1 under both processes.

I now take  $F_i$  and  $S_i$  to be close to zero and ignore terms of order higher than 1. This provides a simplification of the fitness expressions. To first order in the increments  $F_i$  and  $S_i$ , the fitness effects  $w_i$  can be written:

$$\text{BD: } w_i = F_i + S_i - \sum_j d(j, i)F_j - \sum_{j,k} d(j, i)d(j, k)S_k. \quad (5)$$

$$\text{DB: } w_i = F_i + S_i - \sum_j d(i, j)S_j - \sum_{j,k} d(i, j)d(k, j)F_k. \quad (6)$$

In both eqns 5 and 6, the first two terms,  $F_i + S_i$ , represent the primary effect on  $i$ , whereas the next two terms represent the secondary competitive effects on  $i$  of primary increments to other breeders  $j$  and  $k$ . Under BD, these secondary effects are on survival, and under DB, they are on fecundity.

### Intuitive analysis of the DB equation

An intuition for the  $w_i$  expressions can be had from eqn 6. It is best to consider the primary increments  $F_j$  and  $S_j$  separately and I begin with the  $S_j$  (setting all  $F_j = 0$ ). The second term  $S_i$  represents the primary effect of increased survival to  $i$ . The third term  $-\sum_j d(i, j)S_j$  represents the secondary effect on the fecundity of  $i$  of increased survival to all individuals  $j$ , as under DB,  $i$  produces an offspring only when a neighbour  $j$  dies, and in that case,  $d(i, j)$  provides the probability the spot will be won by  $i$ .

Now consider the  $F_j$  (setting all  $S_j = 0$ ). Again the first term  $F_i$  represents the primary effect of increased fecundity to  $i$ . To realize this fecundity increase of course, someone has to die, but this occurs at a fixed rate of one per breeder per unit time. The fourth term  $-\sum_{j,k} d(i, j)d(k, j)F_k$  represents the secondary effect on the fecundity of  $i$  of increased fecundity to all individuals  $k$ . Such an increase will cause the death of neighbour  $j$  of  $k$  with probability  $d(k, j)$ , and in this case, the spot will be won by  $i$  with probability  $d(i, j)$ .

Now I observe that there is a striking symmetry between the two fitness expressions in (5) and (6) – they are obtained from each other by interchanging  $F$  and  $S$ , and switching the arguments of  $d$ . Thus, the analysis above of the DB eqn 6 carries directly over to the BD eqn 5 with the corresponding changes. I note that the purpose of my assumption (1) of symmetric dispersal rates was to obtain this BD–DB symmetry.

My purpose is to use eqns 5 and 6 to track the evolution of a behavioural trait. I will assume that this trait is caused by an allele segregating at a particular locus and its behavioural effects will cause a selective change in its frequency. I will use an inclusive fitness approach (Hamilton, 1964) to track this change in frequency. It is known (Rousset, 2004; Taylor *et al.*, 2007a) that if selection is weak (small selective effects of the increments  $F$  and  $S$ ) and fitness effects are additive, the sign of the inclusive fitness effect will give the direction of frequency change of the allele. These effects are tabulated in Table 1.

It turns out that in populations with a high level of internal symmetry, or homogeneity, the Table 1 expressions can be greatly simplified. We look at that now.

**Application to homogeneous populations**

The term ‘homogeneous’ is used with many different meanings. Here, I will use it in the sense of Taylor *et al.* (2007b), that the population ‘look the same’ from each node where what is being observed are the dispersal probabilities and the frequencies of interaction. Formally, an *isomorphism* of the node set is a bijection  $T$  with the property that for every pair of nodes  $i$  and  $j$ ,

$$d(T(i), T(j)) = d(i, j) \tag{7}$$

and node  $T(i)$  interacts with node  $T(j)$  in the same way that node  $i$  interacts with node  $j$ . Given this, a population is *homogeneous* if for every pair of nodes  $i$  and  $j$ , there is an isomorphism  $T$  such that  $T(i) = j$ .

Many of the population structures studied in the literature have enough internal symmetry to make them homogeneous. Examples include island models, cycles and lattice or stepping-stone structures. We can mix these examples to produce more complex homogeneous populations such as an island model whose demes are finite cycles. Examples are found in Taylor *et al.* (2007b).

Now we let  $R(i, j)$  denote the average relatedness between the breeders at nodes  $i$  and  $j$  calculated in the

neutral population. If selection is weak, and these neutral coefficients are used in the analysis, the inclusive fitness effect will be correct to first order in the fitness effects (Rousset, 2004; Taylor *et al.*, 2007a). At equilibrium, the  $R(i, j)$  are determined as the solutions to a system of recursive equations involving only the dispersal probabilities  $d(h, k)$  (Appendix) and it follows from eqn 7 that an isomorphism  $T$  will also preserve the relatedness coefficients (Michod & Hamilton, 1980):

$$R(T(i), T(j)) = R(i, j). \tag{8}$$

P. Taylor, T. Lillicrap and D. Cownden (unpublished work) provide an elegant formalism for the study of homogeneous populations using mathematical group theory (Fig. 1). They conjecture that every homogeneous population can be structured as a mathematical group (certainly there are no known counterexamples) and thus these methods seem to be always available for establishing results that depend on homogeneity. Many of the arguments are simpler if one can assume that the underlying group is abelian (multiplication is commutative:  $ij = ji$ ) and I make that assumption in the proof of the proposition below, although the proposition holds without this assumption [the question of the abelian assumption is of little biological interest as all ‘standard’ homogeneous structures can be represented as abelian groups. But see Fig. 1c for an example of a homogeneous structured population with six nodes which requires a nonabelian group]. Another assumption that is often (but not always) needed is that dispersal be symmetric (eqn 1) and that turns out to be necessary for the following proposition to hold.

**Proposition**

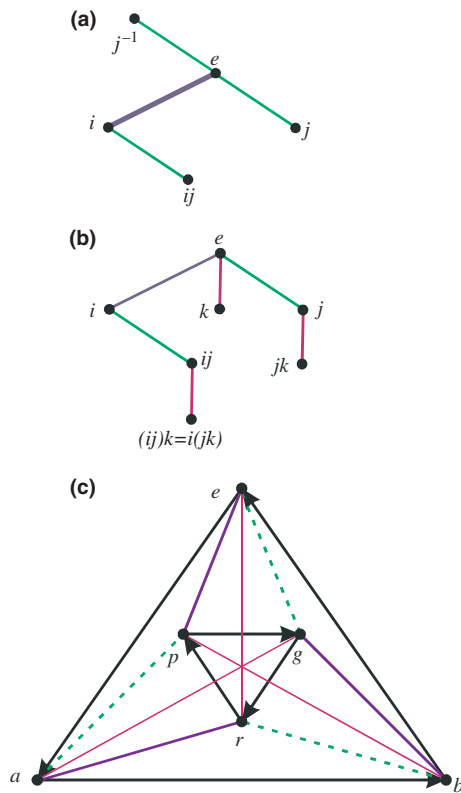
Suppose we have a finite or infinite homogeneous population structured as an abelian group under a Moran process with either a BD or a DB demography and with

**Table 1** Inclusive fitness analysis of a single primary effect of focal behaviour on breeder  $j$ .

Fitness increment	Primary effect on $j$	Competitive effect on $i$	Inclusive fitness effect
<i>BD</i>			
Fecundity	$F_j$	$-d(j, i)F_j$	$[R_j - \sum_i R_i d(j, i)]F_j$
Survival	$S_j$	$-\sum_k d(k, i)d(k, j)S_j$	$[R_j - \sum_i \sum_k R_i d(k, i)d(k, j)]S_j$
<i>DB</i>			
Survival	$S_j$	$-d(i, j)S_j$	$[R_j - \sum_i R_i d(i, j)]S_j$
Fecundity	$F_j$	$-\sum_k d(i, k)d(j, k)F_j$	$[R_j - \sum_i \sum_k R_i d(i, k)d(j, k)]F_j$

BD, birth–death; DB, death–birth.

Here we are supposing that the behaviour of a focal actor has a primary fitness effect on the fecundity or the survival of a single breeder  $j$ . Then the calculation of the inclusive fitness effect of this behaviour includes this primary effect (col. 2), along with any secondary competitive effects on other breeders  $i$  (col 3). Under BD, these competitive effects are on survival, whereas under DB they will be on fecundity (see eqns 3 and 4). In the inclusive fitness calculation (col. 4) these effects on  $i$  are weighted by the focal relatedness (either  $R_j$  or  $R_i$ ) to the affected breeder. Note that I use here the simpler notation  $R_j = R(e, j)$ . Again I remark on the striking ‘anti-symmetry’ between the inclusive fitness effects under BD and DB. These expressions for  $W_1$  apply to both a finite and an infinite population.



**Fig. 1** Mathematical groups. A group  $G$  is a set of elements  $i$  with a binary operation (which we represent multiplicatively) which satisfies the following three axioms: 1. There is an *identity* element  $e$  with the property  $ei = ie = i$  for all  $i$ . 2. Every element  $i$  has an *inverse* (denoted  $i^{-1}$ ) such that  $ii^{-1} = i^{-1}i = e$ . 3. The operation is *associative*:  $i(jk) = (ij)k$  for all  $i, j$  and  $k$ . The group is *abelian* if multiplication is commutative  $ij = ji$ . Now the wonderful thing about groups is that we have a natural set of bijections that can serve as our isomorphisms, and these are the group multiplications. Indeed, given two elements  $j$  and  $k$  of the group, multiplication on the left by  $i = kj^{-1}$  is a bijection  $T$  of the group that maps  $j$  into  $k$ . Indeed,  $T(j) = ij = (kj^{-1})j = k(j^{-1}j) = ke = k$ . Thus, if our breeding sites are the elements of a group, we can use these left multiplications as a natural transitive set of maps preserving our two critical relationships – offspring dispersal and fecundity effects:  $d(j, k) = d(ij, ik)$  and  $ij$  interacts with  $ik$  in the same way that  $j$  interacts with  $k$ . All homogeneous populations that have appeared in the literature (island models, cycles, and lattice or stepping-stone structures) can be represented as groups. Details on the representation of a homogeneous population as a group can be found in (P. Taylor, T. Lillicrap and D. Cownden, unpublished work). (a)  $ij$  is the node that looks the same from  $i$  as  $j$  looks from  $e$ . (b) Illustration of associativity. (c) For the reader’s curiosity, the smallest nonabelian group is depicted. It is isomorphic to the group  $S_3$  of all permutations on three objects. Multiplication proceeds by following the appropriate edges. Thus,  $ag = p$  because if we follow the green (dotted) edge from  $a$  we get to  $p$ . On the other hand,  $ga = r$  because the arrow leaving  $g$  leads to  $r$ .

symmetric offspring dispersal. Suppose a focal actor at node  $e$  gives a primary fitness increment, either of fecundity or survival, to breeder  $j$  (who is allowed to be

**Table 2** Inclusive fitness effect of a fitness increment from focal actor  $e$  to breeder  $j$  – the case of a homogeneous population.

Fitness increment	Inclusive fitness effect increment to focal $j = e$	Inclusive fitness effect increment to neighbour $j \neq e$
<i>Infinite population</i>		
BD		
Fecundity $F_j$	$KF_e$	Zero
Survival $S_j$	$K(1 + d(e, e))S_e$	$Kd(e, j)S_j$
DB		
Survival $S_j$	$KS_e$	Zero
Fecundity $F_j$	$K(1 + d(e, e))F_e$	$Kd(e, j)F_j$
<i>Finite population</i>		
BD		
Fecundity $F_j$	$\frac{K}{N-1}[N-1]F_e$	$-\frac{K}{N-1}F_j$
Survival $S_j$	$\frac{K}{N-1}[N(1 + d(e, e)) - 2]S_e$	$\frac{K}{N-1}[Nd(e, j) - 2]S_j$
DB		
Survival $S_j$	$\frac{K}{N-1}[N-1]S_e$	$-\frac{K}{N-1}S_j$
Fecundity $F_j$	$\frac{K}{N-1}[N-2 + Nd(e, e)]F_e$	$\frac{K}{N-1}[Nd(e, j) - 2]F_j$

BD, birth–death; DB, death–birth.

This specializes the inclusive fitness effects tabulated in the last column of Table 1 to the case of a homogeneous (group-structured) population. The key technical result is eqn A4 of the Appendix which assumes symmetric dispersal rates and an abelian group. Here, the focal actor is breeder  $e$  and we obtain different expressions for the case of a focal ( $j = e$ ) and nonfocal ( $j \neq e$ ) recipient. Note that every entry has the same common positive multiplier  $K = 1 - \sum_i R_i d(e, i)$  where  $R_i$  is focal relatedness to  $i$ . In our application to altruistic behaviour, we take  $F_e = -c$  and  $F_j = b$ .

the actor). Then the inclusive fitness effect in each of  $2^3 = 8$  cases is tabulated in Table 2.

The proof of this proposition is found in the Appendix. Table 2 presents the inclusive fitness effect of an interaction with a primary fitness effect on the focal actor  $e$  and a single recipient  $j \neq e$  for both a BD and a DB demography with primary effects on either fecundity or survival in a finite or an infinite population. The homogeneity of the population provides a remarkable simplification of the general expressions for  $W_1$  found in Table 1. In particular, the summations of Table 1, which capture the secondary competitive effects of the single interaction, disappear leaving only a residue of the primary effect. In particular, to obtain the sign of  $W_1$ , no calculations of relatedness are required. A noteworthy observation is that for fecundity effects under BD and for survival effects under DB, the inclusive fitness effect of a fitness increment to breeder  $j \neq e$  is independent of  $j$ . Otherwise, for survival effects under BD and for fecundity effects under DB,  $W_1$  depends only on  $d(e, j)$ , the probability that a focal offspring displaces breeder  $j$ .

For a finite population, a good check on the entries of Table 2 is available. If everyone in the population is given the same primary increment, the inclusive fitness effect should be zero. For example for row 6 (survival increment in BD), if all the  $S_j$  are set equal to  $S$ , the sum of the  $j = e$  entry and  $N - 1$  times the  $j \neq e$  entry should be zero. That is we should have:



$$\frac{K}{N-1} \left[ N(1 + d(e, e)) - 2 + N \sum_{j \neq e} d(e, j) - 2(N-1) \right] S = 0$$

and this can be verified to hold.

**Altruistic behaviour**

What does Table 2 tell us in terms of how to go about helping your neighbour? The first thing to decide is whether we are operating with a BD or a DB protocol. Fundamentally, this is a question of what ‘drives’ the life history. The driver is fecundity if mortality tends to come about through offspring pressure for establishment. The driver is mortality if offspring can only obtain a foothold when a breeder runs out of steam. In the first case (BD), the offspring call the shots; in the second (DB), the ‘old guard’ are in charge. Of course, in reality both forces will be at work and we can expect to have some mixture of the two. But let’s suppose we can identify the dominant driver.

For the remainder of this section, I assume we have a BD demography, noting that Table 2 allows us to translate all BD results to a DB demography. Suppose the focal actor *e* gives a breeder *j* ≠ *e* a primary fitness benefit *b* at cost *c*, each of these measured in either fecundity or survival. The interaction is termed *altruism* if both *b* and *c* are positive and is called *spiteful* if *c* is positive but *b* is negative. From Table 2, we deduce the condition for a positive inclusive fitness effect:

**Infinite population**

Fecundity selection :  $0 > c$  (9)

Survival selection :  $d(e, j)b > [1 + d(e, e)]c$  (10)

**Finite population**

Fecundity selection :  $-b > (N - 1)c$  (11)

Survival selection :  $[Nd(e, j) - 2]b > [N(1 + d(e, e)) - 2]c$  (12)

For a finite population, these results have been obtained by Taylor *et al.* (2007b) and by Grafen & Archetti (2008) (except instead of BD survival selection they worked with DB fecundity selection). Under fecundity selection, altruism can never be selected, and in fact in a finite population, spite can be selected if the harm inflicted on *j* exceeds *N* - 1 times the cost. It is worth noting that the conditions in this case are independent of *j* - no matter who receives the ‘gift’, the inclusive fitness effect is the same. Under survival selection, altruism can be selected in an infinite population if *b* is large enough. Notice that it helps if *d(e, j)* is large. One should be more likely to be altruistic the greater is the probability that ones offspring settle at node *j*.

The results summarized earlier assume that *b* and *c* are measured in the same units, both fecundity or both survival. In practice, they could be different - one could deliver food to a neighbour, increasing her fecundity, but at a survival cost. In fact, one might even have a choice. The food could be taken from ones own supply, thus reducing fecundity, or gathered with an additional foraging excursion, reducing survival. Although it is generally problematic to compare fecundity and survival costs, we might ask, all things being equal, which would be better. In an infinite population, the answer from Table 2 seems clear enough: the benefit should definitely be in survival and, all things being equal, the cost should be in fecundity - although it should be pointed out that if *d(e, e)* = 0 (offspring never displace the parent), there is no cost difference between the two. The condition is:

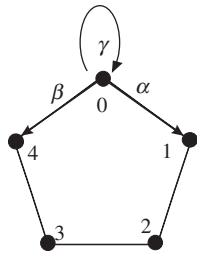
Infinite population, fecundity cost, survival benefit:

$$d(e, j)b > c \tag{13}$$

In a finite population, a fecundity gift can never be selected, but a survival gift *can* be favoured if *d(e, j)*, the probability that a focal offspring inhabits node *j* exceeds 2/*N*. Looking at costs (which need to be kept small), the survival cost has the smaller coefficient when *d(e, e)* < 1/*N*, that is, focal offspring are less likely to displace their parent than to displace a random breeder. Given this, we might conclude that in finite populations, altruism is more likely to be seen when the interaction affects the survival of both parties. In this case, we might see protection offered to others at an increased risk to self.

I have been focusing on altruism, but possibilities also exist for the evolution of *spiteful* behaviour (*S* and *F* negative), but from Table 2, this could only give us a positive inclusive fitness effect in a finite population and *N* better not be too large (Hamilton, 1970; Gardner & West, 2004). Consider a fecundity selection under BD. Equation 11 tells us that if I can cause at least *c* units of harm to every other individual in the population at cost *c*, I will have *W<sub>I</sub>* ≥ 0. That’s no surprise of course as with exactly *c* units of harm; everyone in the population has the same primary fitness change. Of greater interest is survival selection (eqn 12). Suppose my offspring never displace me and I chose another recipient *j* whom my offspring also never displace. In that case, the Table 2 condition for *W<sub>I</sub>* > 0 is (N - 2)*S<sub>e</sub>* - 2*S<sub>j</sub>* > 0. With *S<sub>e</sub>* = -*c* and *S<sub>j</sub>* = -*b*, the condition becomes 2*b* > (N - 2)*c*. In a population of size 6, the harm caused, *b*, has to be at least twice the cost, *c*.

This analysis has assumed a BD demography, and I have pointed out that, by interchanging *F* and *S*, they can be translated to death–birth. But in both cases, it’s not birth or death *per se* that are significant, but rather what I have called the ‘driving’ mode of the demography, the other being the ‘reactive’ mode. For the evolution of altruism, the general conclusion I have drawn is that, all



**Fig. 2** A five-cycle with asymmetric dispersal. The dispersal rates are shown only for breeder 0, but the other breeders follow the same pattern, dispersal  $\alpha$  to the clockwise neighbour,  $\beta$  to the counter-clockwise neighbour and  $\gamma$  to self.

things being equal, in an infinite population, the benefit should be set in the reactive mode of the life history and the cost in the driving mode, whereas in a finite population, both benefit and cost should be set in the reactive mode.

**Example. Altruism to a neighbour in a five-cycle with asymmetric dispersal**

I consider a finite population with  $N = 5$  breeders arranged in a cycle with offspring dispersal  $\alpha$  to the immediate clockwise neighbour,  $\beta$  to the counter-clockwise neighbour, and  $\gamma = 1 - \alpha - \beta$  to remain home. Dispersal is symmetric if  $\alpha = \beta$ . The population is illustrated in Fig. 2. To obtain the group structure, number the nodes from 0 to 4, clockwise and then the group operation is addition modulo 5, e.g.  $2 + 4 = 6 = 1$  (cast out 5). Essentially, we have the rotation group generated by the clockwise rotation through one-fifth of a revolution. This group is clearly abelian. I will investigate a Moran process with a BD demography.

I study an altruistic or spiteful trait whereby a breeder gives primary fitness increment  $b$  to her clockwise neighbour at fitness cost  $c$ , where fitness might measure either fecundity or survival effects. In Table 3, the primary and secondary effects are tabulated for both fecundity selection and survival selection.

Now let  $R_i$  denote the relatedness coefficient between breeders 0 and  $i$ . Then, the inclusive fitness effects are:

$$\text{Fecundity selection : } W_1 = (-c + \gamma c - \beta b)R_0 + (b + \alpha c - \gamma b)R_1 + (-ab)R_2 + \beta c R_4$$

$$\begin{aligned} \text{Survival selection : } W_1 &= [-c + (\alpha^2 + \beta^2 + \gamma^2)c \\ &- \gamma(\alpha + \beta)b]R_0 + [b + \gamma(\alpha + \beta)c - (\alpha^2 + \beta^2 + \gamma^2)b]R_1 \\ &+ [\alpha\beta c - \gamma(\alpha + \beta)b]R_2 + [\alpha\beta c - \alpha\beta b]R_3 \\ &+ [\gamma(\alpha + \beta)c - \alpha\beta b]R_4 \end{aligned}$$

A standard recursive argument (Taylor *et al.* manuscript) gives the relatedness coefficients:

**Table 3** Selection in five-cycle: Moran process BD.

Breeder	Primary effect	Secondary effect
	Fecundity	Survival
0	$-c$	$\gamma c - \beta b$
1	$b$	$\alpha c - \gamma b$
2	$0$	$-\alpha b$
3	$0$	$0$
4	$0$	$\beta c$
	Survival	Survival
0	$-c$	$(\alpha^2 + \beta^2 + \gamma^2)c - \gamma(\alpha + \beta)b$
1	$b$	$\gamma(\alpha + \beta)c - (\alpha^2 + \beta^2 + \gamma^2)b$
2	$0$	$\alpha\beta c - \gamma(\alpha + \beta)b$
3	$0$	$\alpha\beta c - \alpha\beta b$
4	$0$	$\gamma(\alpha + \beta)c - \alpha\beta b$

BD, birth–death.

This provides the fitness effects of an interaction in the five-cycle depicted in Fig. 2 with a BD demography. The actor is breeder 0 and the recipient is breeder 1. The primary effect can be of either fecundity or survival but in both cases the secondary effects will be on survival. The secondary survival effects can be intuitively derived. For example, consider the case of a primary fecundity loss of  $c$  to breeder 0 (top half of the Table). Under the BD process, mortality is caused by offspring production, so this reduced fecundity rate will be experienced by breeders 1, 4 and 0 in proportion to  $\alpha$ ,  $\beta$  and  $\gamma$  giving them a survival boost of  $\alpha c$ ,  $\beta c$  and  $\gamma c$ , and these appear in col. 3. Secondly, consider the case of a primary survival loss of  $c$  to breeder 0 (bottom half of the Table). The effect of this is that a fraction  $\beta c$  of breeder 1’s offspring will colonize node 0 who would otherwise disperse normally to nodes 0, 1 and 2. These will provide survival benefits to breeders 2, 0 and 1 in proportion to  $\alpha$ ,  $\beta$  and  $\gamma$ , giving survival effects of  $\alpha\beta c$ ,  $\beta\beta c$  and  $\gamma\beta c$  and these appear in col. 3.

$$R_0 = 1, \quad R_1 = R_4 = 0, \quad R_2 = R_3 = -1/2.$$

If these are put into the equations above, with  $\gamma = 1 - \alpha - \beta$ , we obtain:

$$\text{Fecundity selection : } W_1 = (\alpha/2 - \beta)b - (\alpha + \beta)c.$$

$$\begin{aligned} \text{Survival selection : } W_1 &= \frac{b}{2}(\alpha^2 + 3\alpha\beta + \beta^2 - \alpha - \beta) \\ &- c(2\alpha^2 + \alpha\beta + 2\beta^2 - 2\alpha - 2\beta) \end{aligned}$$

For the case of symmetric dispersal ( $\alpha = \beta$ ) this becomes:

$$\text{Fecundity selection : } W_1 = \frac{\alpha}{2}(-b - 4c)$$

$$\text{Survival selection : } W_1 = \frac{\alpha}{2}[(5\alpha - 2)b - (8 - 10\alpha)c].$$

Now compare these with the Table 2 results for a finite population under BD with  $N = 5$ . We set  $F_e = S_e = -c$  and  $F_j = S_j = b$ . We obtain:

$$\text{Fecundity selection : } W_1 = \frac{K}{4}(4(-c) - b)$$

$$\begin{aligned} \text{Survival selection : } W_I &= \frac{K}{4}((3 + 5\gamma)(-c) + (5\alpha - 2)b) \\ &= \frac{K}{4}((10\alpha - 8)c + (5\alpha - 2)b), \end{aligned}$$

and these are the same expression up to a multiple. With fecundity increments, altruism is never selected, but with increments to survival, altruism will be selected if  $\alpha > 0.4$ . For example, for  $\alpha = 1/2$ , the condition is:  $b > 6c$ . This example also shows that the assumption of symmetric dispersal is necessary for the proposition to hold.

## Discussion

Many of the population models that have appeared in the literature have a structure that is homogeneous or nearly so. The reason is simple – we need some form of structural regularity to perform the allele-frequency analysis, for example, to obtain tractable recursive equations for the relatedness coefficients. It turns out that the same regularity can also deliver significant simplifications to our expression for the inclusive fitness effects. The reason for this is that in a structured population of constant size, interactions with primary fitness effects will have a multitude of secondary effects because of alterations in the competitive landscape. The ‘map’ of these effects will follow the same dispersal patterns that are encoded in the relatedness recursions and under homogeneity, these recursion in effect provide the simplifications.

These simplifications are well illustrated in a comparison of Tables 1 and 2. The summations in Table 1 cover a wide network of secondary effects, each of which makes a contribution to  $W_I$ . But in Table 2, none of these are to be found; only fragments of the two primary effects belonging to the two interactants remain. Somehow, there has been a significant cancellation of the secondary competitive effects. The example of the five-cycle well illustrates the power of the proposition. Considerable analysis is needed to track and record the many secondary effects found in Table 3, and in addition to these, there is the calculation of the relatedness coefficients that I have omitted. But the outcome of all this is easily found from Table 2. The example does illustrate, however, that without symmetric dispersal, the result will not hold.

The first computer analyses of behavioural interaction in a spatially structured population seem to have appeared in 1992. Nowak & May (1992) and Wilson *et al.* (1992) both explored cooperation on a lattice and pointed to the significant effect of the spatial structure on the outcome. Wilson *et al.* made what I believe is the first observation of the zero in the top right-hand corner of Table 2, and this led to the original analyses of Taylor (1992a,b). Since that time a huge body of literature has arisen studying evolutionary games on graphs (see Ohtsuki *et al.*, 2007 for quite a good summary of the

development in this area), and of course most spatial structures can be represented as graphs and most social behaviours that are commonly studied can be represented by one or more two-player games.

Most of the early work on graphs (Nowak & May, 1992, 1993; Nowak *et al.*, 1994) used fecundity selection along with a variety of demographic systems (including BD and DB). The first discussion of the relationship between fecundity-selection and viability-selection seems to be found in Nakamaru *et al.* (1997, 1998), work that was extended by Nakamaru & Iwasa (2005). They worked with the Prisoner’s Dilemma in a lattice model using a version of a DB demography. In agreement with the results of the analysis here, they find fecundity selection (which they call score-dependent fertility) to be more favourable to the evolution of cooperation. The results obtained here of course suggest that they would have found an analogous result with BD demography favouring viability-selection.

Ohtsuki & Nowak (2006) provide an intuitive explanation for the difference between these two selection regimes in terms of a comparison between the ‘scale of interaction’ and the ‘scale of competition’, an idea that goes back to Queller’s (1994) ‘economic neighbourhood’. The idea can be illustrated with a comparison of fecundity selection in a BD and a DB demography. If I give a fecundity gift to my neighbour, then under BD I experience a direct decrease in my survival rate. However, under DB, my survival rate is unchanged, rather I experience decreased success in competing for a site vacated by my neighbour’s neighbour. In the first case, my economic neighbourhood is my interaction neighbourhood; in the second case, it is the interaction neighbourhood of my interaction neighbourhood. The difference between these is clearly exhibited in eqns 5 and 6 – in (5), the competitive  $F$ -term is linear in the dispersal rates  $d$ ; whereas in (6), the competitive  $F$ -term is quadratic in  $d$ . Of course (and this is the point of the paper) exactly the same point can be made with a comparison of fecundity- and viability-selection under BD using eqn 5 with the observation that whereas the competitive  $F$ -term is linear in  $d$ , the competitive  $S$ -term is quadratic. Grafen & Archetti (2008) provide a detailed analysis of this scale of competition phenomenon in terms of ‘circles of compensation’.

These conclusions are interesting but appear to be quite special as they require the assumption of homogeneity. However, there are reasons to believe that they might apply, in a qualitative sense, much more widely. In any inclusive fitness analysis, we work with a focal actor and a recipient and treat these as in some sense ‘generic’, that is, we assume that the relationship between them is mirrored in many other instances in the population, and indeed our calculation of the relatedness between them is an average of the allelic configurations at all these instances. Thus, we work with populations that have a

large amount of ‘approximate’ homogeneity, and it is reasonable to assume that results that require strict homogeneity would apply to a large extent to these. A good example of this is found in the simulation studies of Ohtsuki *et al.* (2006). They looked at a large number of graphs with variable degree  $k$  but found their result  $b/c > k$  to be quite robust with the use of the average value of  $k$ .

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## Appendix

Taylor *et al.* (submitted) provide an elegant way to handle the isomorphisms of a homogeneous population using mathematical group theory (Fig. 1). Essentially, they put a product operation on the set of nodes in the following way. Take a random node and label it  $e$ . It will serve as an ‘identity’ node. Now take another node  $i$ . The homogeneity property is that the population should look the same from  $i$  as it does from  $e$ . In particular, for any node  $j$ , there should be a node that looks the same from  $i$  as  $j$  looks from  $e$ . We call that node  $ij$ , and this in fact defines the multiplication operation on the node set. *The product node  $ij$  is the node that a breeder at  $i$  ‘sees’ if it thinks it is located at  $e$  looking at  $j$ .* For all of the homogeneous population structures that I have encountered in the theoretical literature (e.g. island models, cycles, and lattice or stepping-stone structures), this operation satisfies the axioms of a group. In fact in all these examples, the group is abelian, that is, the product operation is commutative:  $ij = ji$  (but see Fig. 1b).

In terms of this product operation, the homogeneity condition that the dispersal probabilities and thus the relatedness coefficients are invariant under left multiplication would be written:

$$d(j, k) = d(ij, ik) \quad (\text{A1})$$

$$R(j, k) = R(ij, ik) \quad (\text{A2})$$

In addition, breeders  $ij$  and  $ik$  should interact in the same way as breeders  $j$  and  $k$ .

I assume that the population is homogeneous, structured as an abelian group with symmetric dispersal, with a Moran demography with either a BD or a DB protocol. My objective is to derive the 16 expressions in Table 2.

*Infinite population.* I begin with the case of an infinite population, so that the relatedness between a pair of nodes chosen at random will be zero. I make the assumption that some dispersal to each node is from a random node; it follows that we can ignore mutation (assuming that it has small rate) and the analysis is simplified.

I begin with the recursive equation for the relatedness coefficients  $R$ . If  $k$  is a node distinct from the identity node  $e$ , then at equilibrium:



$$R(e, k) = \frac{1}{2} \left[ \sum_j R(j, k) d(j, e) + \sum_j R(e, j) d(j, k) \right] \quad (k \neq e) \quad (A3)$$

As the alleles are neutral and the population is homogeneous, the two nodes,  $e$  and  $k$ , will have equal probability ( $1/2$ ) to be the one most recently replaced. If this was  $e$ , the breeder came from  $j$  with probability  $d(j, e)$ , and we obtain the first term in the square bracket of (A3); if this was  $k$ , the breeder came from  $j$  with probability  $d(j, k)$ , and we obtain the second term in the square bracket.

However, I now show that the two terms in the square bracket are equal. The left-hand term is:

$$\begin{aligned} & \sum_j R(j, k) d(j, e) \\ &= \sum_j R(e, j^{-1}k) d(j, e) \\ & \quad \text{(invariance under left multiplication A2)} \\ &= \sum_i R(e, i) d(ki^{-1}, e) \quad (i = j^{-1}k, \text{ so that } j = ki^{-1}) \\ &= \sum_i R(e, i) d(i^{-1}k, e) \\ & \quad \text{(commutativity of multiplication)} \\ &= \sum_i R(e, i) d(k, i) \\ & \quad \text{(invariance under left multiplication A1)} \end{aligned}$$

and the symmetry of  $d$  gives us the right-hand term of (A3). Thus, (A3) can be written:

$$R_k = \sum_j R_j d(j, k) \quad (k \neq e) \quad (A4)$$

where I have adopted the simpler notation of Table 1:  $R(e, j) = R_j$ .

I now move to the proposition. I provide the proof for the BD demography, and the DB results will follow from the symmetry exhibited in Table 1. Begin with a fecundity gift of  $F_j$  from the actor  $e$  to breeder  $j$ . From Table 1, row 1, the inclusive fitness effect is  $[R_j - \sum_i R_i d(j, i)] F_j$ . For  $j \neq e$ , eqn A4 tells us that this is zero. For  $j = e$ , the expression in the square brackets is  $1 - \sum_i R_i d(e, i)$  and this is what, in Table 2, we have called  $K$ . This gives us row 1 of Table 2.

Now consider a survival gift of  $S_j$ . Table 1, row 2, gives us the inclusive fitness effect:

$$\left[ R_j - \sum_i \sum_k R_i d(k, i) d(k, j) \right] S_j \quad (A5)$$

The expression in the square brackets can be written:

$$\begin{aligned} & R_j - \sum_k \left[ \sum_i R_i d(k, i) \right] d(k, j) \\ &= R_j - \sum_{k \neq e} \left[ \sum_i R_i d(k, i) \right] d(k, j) - \sum_i R_i d(e, i) d(e, j) \\ &= R_j - \sum_{k \neq e} R_k d(k, j) - \sum_i R_i d(e, i) d(e, j) \\ & \quad \text{[using eqn A4]} \end{aligned}$$

$$= R_j - \sum_k R_k d(k, j) + R_e d(e, j) - \sum_i R_i d(e, i) d(e, j) \quad (A6)$$

For  $j \neq e$ , eqns A4 and 1 tell us that the first two terms give us zero, leaving us with:

$$\begin{aligned} &= R_e d(e, j) - \sum_i R_i d(e, i) d(e, j) \\ &= \left[ 1 - \sum_i R_i d(e, i) \right] d(e, j) = K d(e, j). \end{aligned}$$

For  $j = e$ , eqn A6 is:

$$\begin{aligned} &= 1 - \sum_k R_k d(k, e) + d(e, e) - \sum_i R_i d(e, i) d(e, e) \\ &= \left[ 1 - \sum_k R_k d(k, e) \right] (1 + d(e, e)) = K(1 + d(e, e)). \end{aligned}$$

This gives us row 2 of Table 2.

Note finally that  $K = 1 - \sum_i R_i d(e, i)$  is positive as the second term is  $< 1$  being a weighted average relatedness of the focal breeder to all breeders, where the weights are the dispersal rates of a focal offspring.

*Finite population.* In a finite population of  $N$  breeding sites, we must take mutation into account or the recursive equations for relatedness will give us equilibrium coefficients that equal 1. This is most naturally done working with the coefficients of consanguinity  $G(i, j)$  being the probability that the genes at sites  $i$  and  $j$  are identical by descent. Then, the relatedness coefficients are calculated as

$$R(i, j) = \frac{G(i, j) - \bar{G}}{1 - \bar{G}}, \quad (A7)$$

where  $\bar{G}$  is the population-wide average of the  $G(i, j)$ . I assume that the mutation rate  $\mu$  is small relative to  $1/N$ , and work to first order in  $\mu$ . Thus, I set  $G(i, j) = 1 - \mu g(i, j)$  and to first order in  $\mu$ , relatedness is:

$$R(i, j) = \frac{\bar{g} - g(i, j)}{\bar{g}}. \quad (A8)$$

The argument now follows the infinite population analysis. The  $G$ -analogue of (A3) is

$$G(e, k) = \frac{1}{2} \left[ \sum_j G(j, k) d(j, e) + \sum_j G(e, j) d(j, k) \right] (1 - \mu) \quad (k \neq e),$$

where the  $1 - \mu$  term is the probability that there was no mutation in the most recent replacement. To first order in  $\mu$  this is:

$$g(e, k) = \frac{1}{2} \left[ \sum_j g(j, k) d(j, e) + \sum_j g(e, j) d(j, k) \right] + 1$$

Write this as:

$$\begin{aligned} & \bar{g} - g(e, k) = \\ & \frac{1}{2} \left[ \sum_j (\bar{g} - g(j, k)) d(j, e) + \sum_j (\bar{g} - g(e, j)) d(j, k) \right] - 1 \end{aligned}$$

and divide by  $\bar{g}$ :

$$R(e, k) = \frac{1}{2} \left[ \sum_j R_j d(j, k) + \sum_j R(e, j) d(j, k) \right] - \frac{1}{\bar{g}}$$

Following the infinite population argument to eqn A4, we write this as:

$$R_k = \sum_j R_j d(j, k) - \frac{1}{\bar{g}} \quad (k \neq e) \tag{A9}$$

Now we rewrite the last term by summing (A9) over all  $k \neq e$ . As the sum over all  $k$  of  $R_k$  is zero and the sum over all  $k$  of  $d(j, k)$  is one, the sum of (A9) is:

$$-R_e = \sum_j R_j (1 - d(j, e)) - \frac{N-1}{\bar{g}} \tag{A10}$$

$$-1 = \sum_j R_j d(j, e) - \frac{N-1}{\bar{g}}$$

$$\frac{N-1}{\bar{g}} = K$$

(see Table 1)

$$\frac{1}{\bar{g}} = \frac{K}{N-1}$$

And we write (A9) as:

$$R_k = \sum_j R_j d(j, k) - \frac{K}{N-1} \quad (k \neq e) \tag{A11}$$

I now move to the proposition. Again I provide the BD proof, leaving the DB results to follow from the symmetry. Begin with a fecundity gift of  $F_j$  from the actor  $e$  to breeder  $j$ . From Table 1, row 1, the inclusive fitness effect is  $[R_j - \sum_i R_i d(j, i)] F_j$ . For  $j \neq e$ , eqn A11 tells us that this is  $-\frac{KF_j}{N-1}$ . For  $j = e$ , the expression in the square brackets is  $1 - \sum_i R_i d(e, i)$  and this is what, in Table 2, I have called  $K$ . This gives us row 5 of Table 2.

Now consider a survival gift of  $S_j$ . Table 1, row 2, gives us the inclusive fitness effect:

$$\left[ R_j - \sum_i \sum_k R_i d(k, i) d(k, j) \right] S_j \tag{A12}$$

The expression in the square brackets can be written as:

$$\begin{aligned} R_j - \sum_{k \neq e} \left[ \sum_i R_i d(k, i) \right] d(k, j) - \sum_i R_i d(e, i) d(e, j) \\ = R_j - \sum_{k \neq e} \left[ R_k + \frac{K}{N-1} \right] d(k, j) - \sum_i R_i d(e, i) d(e, j) \\ \text{[using eqn A11]} \\ = R_j - \sum_k R_k d(k, j) + R_e d(e, j) - \frac{K}{N-1} (1 - d(e, j)) \\ - (1 - K) d(e, j) \\ = R_j - \sum_k R_k d(k, j) - \frac{K}{N-1} (1 - d(e, j)) + K d(e, j) \\ R_j - \sum_k R_k d(k, j) - \frac{K}{N-1} (1 - Nd(e, j)) \end{aligned} \tag{A13}$$

For  $j \neq e$ , using (A11), this is

$$-\frac{K}{N-1} (2 - Nd(e, j)).$$

For  $j = e$ , (A13) is

$$\begin{aligned} 1 - \sum_k R_k d(k, e) - \frac{K}{N-1} (1 - Nd(e, e)) \\ = K - \frac{K}{N-1} (1 - Nd(e, e)) \\ = \frac{K}{N-1} (N - 2 + Nd(e, e)) \end{aligned}$$

This gives us row 6 of Table 2.

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