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Inclusive Fitness in Finite Deme-structured and Stepping-stone Populations

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Very little attention has been given in the literature to the interesting question of how to handle relatedness in finite populations. The main problem is that a finite population is never really "at equilibrium" in that it represents just one realization of an infinite assemblage of possible allelic distributions. A recent paper of Rousset and Billiard (manuscript) provides coefficients which, if used in inclusive fitness models under conditions of weak selection, give us a measure of average allele frequency change where the average is taken over all such realizations. Their coefficients are expressed in terms of identity in state, and an alternative formulation (Taylor and Day, manuscript) in terms of coefficients of consanguinity permits the calculation of relatedness in simple cases from pedigree analysis. Here we implement these calculations in a finite asexual haploid population with either a deme structure or a one-dimensional stepping-stone structure and verify our results with numerical simulations in small populations. Our simulations allow us to investigate the dependence of relatedness on allele frequency, and our results here agree qualitatively with those obtained by Rousset and Billiard. Finally, we examine a model of altruism in a deme-structured population to verify numerically that our relatedness coefficients provide a correct measure of allele frequency change.

Keywords: Relatedness, inclusive fitness, finite population, deme-structured, stepping-stone, altruism

1. Introduction

In the study of the evolution of behaviour we typically want to know whether a certain behavioural trait is evolutionarily stable in the sense that it will resist invasion by an alternative "deviant" behaviour. Under certain general assumptions, the method of inclusive fitness (Hamilton, 1964) provides a powerful way to answer this question. The inclusive fitness effect of a deviant individual (the actor) is defined to be the sum of the fitness effects of the deviation, not only on the actor itself, but on all "recipients" each such recipient weighted by its relatedness to the actor. If the behaviour is genetically determined, simple assumptions on gene action (e.g. that the effects on fitness be additive and small) will allow the sign of the inclusive fitness effect to tell us whether or not the deviant behaviour will invade. To be precise, if alleles A and B code for the deviant and normal behaviour respectively, then the allele A will increase in frequency when introduced into a B population precisely when its inclusive fitness effect is positive (Michod and Hamilton, 1980; Seger, 1981; Grafen, 1985; Taylor, 1996).

To illustrate these ideas, we look at a simple example of altruistic behaviour in a haploid population. Let a deviant actor (with allele A) augment the fitness of a random neighbour by a small amount b while incurring a small cost c to its own fitness. Suppose the population has size N and the frequency of A is q. Then to calculate the increase in q in one generation due to a single deviant act, we need to know

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John Maynard Smith

It is an honour for me to be included in this volume. John is most certainly the reason I am a theoretical biologist. In 1976 I was a mathematician wanting in some way to break out into the world, not sure where. I had spent a year investigating game theory in economics and then the Canadian Math Society held a two-week biomathematics conference at Sherbrooke, Quebec. There were several lecturers, but I only remember Richard Levins and John. Especially John – he gave us an application of mathematics that worked. No need to worry anymore about the tangled assumptions of rational behaviour; this seemed to all of us to be the natural laboratory for the powerful ideas of game theory and the new treatment of stability that emerged. Not the least of the effect was his ease, his joy, his eccentric compelling authority. I was hooked. PDT.

the probability r that this random neighbour also has the allele A. Given r, the numbers of A and B alleles in the next generation will be

$$\#A: \quad qN(1-c+rb)$$
$$\#B: \quad (1-q)N + qN(1-r)b$$

and the new frequency of A is

$$q' = \frac{\#A}{\#A+\#B} = q[1-c(1-q)+b(r-p)] \quad (1.1)$$

where in the simplification we have used the fact that b and c are small to ignore terms in their squares. The change in q can be written

$$\Delta q = q' - q = q(1-q)[-c+bR] \quad (1.2)$$

where

$$R = \frac{r-q}{1-q}. \quad (1.3)$$

The term in square brackets in (1.2) is the inclusive fitness effect and R in (1.3) is the relatedness of the actor to its neighbour, and we can see that q increases in frequency when the inclusive fitness effect is positive.

From the form of (1.3) it would appear that R will depend on the allele frequency q, but this is not clear as r itself will depend on q. An important reformulation of R can be obtained with the concept of identity by descent. Two alleles are called identical by descent (IBD) if they derive from a common ancestor. Suppose we can assume that two alleles in the population are either IBD or independent (so that they each have state A with probability q independently of the state of the other). Define the *coefficient of consanguinity* (CC) between the two individuals as the probability that the two alleles in the two individuals are IBD, and let G be the CC between actor and neighbour. Then when actor and neighbour are IBD, r will equal 1, and otherwise it will be q so that

$$r = G + (1-G)\,q \quad (1.4)$$

and if we put this into (1.3) we get

$$R = G\,. \quad (1.5)$$

Since we are working to first order in the deviations b and c, we can calculate R to zeroth order in these deviations (see 1.3) and therefore G can be calculated under the assumption that b and c are zero, in which case A and B are indistinguishable. This tells us R is independent of allele frequency and usually provides a way to calculate it from pedigree analysis.

But something is not right. Suppose the "neighbour" happens to be a random individual in the population (with replacement, so that we allow the actor to interact with itself). Then $r = q$ and from (1.3) we must have $R = 0$. But in a finite population, the CC G to a random individual will certainly exceed zero (in fact it must exceed $1/N$) and this is a contradiction (Seger, 1981). What went wrong?

What does not hold is our assumption that two alleles are either IBD or independent (Rousset and Billiard, manuscript). This will typically hold in an infinite population which has attained an "equilibrium" distribution of allelic states, and in such a population (1.5) is valid and relatedness is independent of allele frequency. But in a finite population the situation is more complicated. It is worth observing that, in a finite population, r will usually depend not only on allele frequency q but on the distribution of the allele and since this will generally change from generation to generation due to random effects the calculation of r is problematic in any case.

In short, the question of how to handle relatedness in a finite population presents difficulties which have not received much attention in the literature. In section 2 we recall previous work which provides a way to circumvent these difficulties and this leads to formula (2.9) below for relatedness. In section 3 we use numerical calculation and simulation to check our relatedness calculations in a deme-structured population and in section 4 we do the same for a stepping-stone population. In section 5 we use a model of altruism in a deme-structured population to check that our relatedness coefficients really do predict allele frequency change.

2. Review of past work

Our notation is found in Table 1. We assume that we have a finite haploid population with two neutral alleles A and B, A with frequency q, and discrete non-overlapping generations. Each generation is ob-

TABLE 1
Notation

N	population size (# breeders)
d	number of demes
n	number of individuals per deme
k	probability a breeder is native
x	genotypic value of actor
y	genotypic value of recipient
u	mutation rate from B to A
v	mutation rate from A to B
$w = u + v$	contrived mutation rate for both alleles
$p = u/w$	probability contrived mutation is to A
q	population allele frequency
E_{A}	expectation over all realizations of the population
E_q	expectation over all realizations with allele frequency q
G	coefficient of consanguinity between actor and recipient
G^*	coefficient of consanguinity between random individuals in population
R	coefficient of relatedness
R_{A}	average coefficient of relatedness over all possible realizations
R_q	average coefficient of relatedness over all realizations with allele frequency q

tained by sampling individuals (alleles) from the previous generation according to a set of rules determined by the structure of the population. In each generation there is a possibility of mutation with mutation rates u from B to A and v from A to B. As generations pass, q will drift under these forces, with the force of mutation attracting q towards $p = u/(u + v)$, and the sampling of gametes attracting q towards the end-points 0 and 1.

Now if we introduce a source of weak selection, this will provide another force on the evolution of q and our objective is to understand how to make an inclusive fitness argument (Hamilton, 1964) to estimate the effect of this on q. As we have mentioned above, the problem is that this will generally depend not only on q itself but on the distribution of the allele and in any particular instance we are unlikely to know very much about this. An elegant way to get around this is to use an average measure of allele frequency change over a set of possible "realizations" of the population (Rousset and Billiard, manuscript).

To investigate this, assume that the allele A causes a slight behavioural change and let the fitness $W(X, Y)$ of a focal individual depend on its own phenotypic value X and that of a neighbour Y with whom it interacts. Let these individuals have genotypic values x and y and suppose the resulting phenotypic changes are $\mathrm{d}X = \delta x$. and $\mathrm{d}Y = \delta y$ for small δ so that fitness can be written to first order in δ:

$$W(X,Y) = W_O + \delta\left[\frac{\partial W}{\partial X}x + \frac{\partial W}{\partial Y}y\right]. \qquad (2.1)$$

Then it can be shown (Price, 1970; Rousset and Billiard, manuscript; Taylor and Day, manuscript) that the average allele frequency change taken over any class C of realizations has the form

$$\mathrm{E}_{\mathrm{c}}(\Delta q) = \delta K W_{\mathrm{I}} + w(p - \mathrm{E}_{\mathrm{c}}(q)) \qquad (2.2)$$

for some positive constant K, where w is the mutation rate, discussed below,

$$W_{\mathrm{I}} = \frac{\partial W}{\partial X} + \frac{\partial W}{\partial Y}R_{\mathrm{C}} \qquad (2.3)$$

is the *inclusive fitness effect* of the interaction over the class C, and

$$R_{\mathrm{C}} = \frac{\mathrm{E}_C \operatorname{cov}(x, y)}{\mathrm{E}_C \operatorname{cov}(x, x)} \qquad (2.4)$$

where E_{C} signals the average taken over all realizations in the class C. We call R_{C} the *average relatedness over the class C* though this is a slight abuse of terminology as it is defined not as an average, but as a quotient of averages (see Michod and Hamilton, 1980 for a definitive account of relatedness as a quotient of covariances). The covariances in (2.4) are to be calculated in a neutral population, and with this convention equation (2.2) is valid to first order in the fitness deviation δ.

Now what might be a good class of realizations to take? One obvious candidate is the set of all realizations with a fixed allele frequency q, since a result of this type would allow us to see how relatedness varies with q. In this case we would write (2.4) as

$$R_q = \frac{\mathrm{E}_q \operatorname{cov}(x, y)}{\mathrm{E}_q \operatorname{cov}(x, x)}. \qquad (2.5)$$

The dependence of R_q on q is one of the questions we are interested in here, but except for small populations, the calculation of the covariances conditional on q seems intractable. Another obvious choice is the set of all possible realizations and for this we use the subscript A:

$$R_{\mathrm{A}} = \frac{\mathrm{E}_{\mathrm{A}} \operatorname{cov}(x, y)}{\mathrm{E}_{\mathrm{A}} \operatorname{cov}(x, x)}. \qquad (2.6)$$

We can regard this as an average over all "possible" (neutral) populations or we can take a single population and track it over a large number of generations and (2.2) is the average of the changes we would get if the mutant allele were "activated" in each of these generations.

In this case, where we take our universe as the set of all possible realizations, a standard argument (Crow and Kimura, 1970) shows that when the alleles are neutral, the expected frequency of A is

$$\mathrm{E}_{\mathrm{A}}(q) = u/(u+v) = p \tag{2.7}$$

and (2.2) can be written

$$\mathrm{E}_{\mathrm{A}}(\Delta q) = \delta K W_I. \tag{2.8}$$

We conclude that at the neutral equilibrium, the inclusive fitness effect provides the direction of average initial allele frequency change due to selection where the average is taken over all realizations of the population.

What we would like to have is a formula for R_{A} in terms of coefficients of consanguinity. Rousset and Billiard (manuscript) have recently drawn attention to a number of difficulties in this objective, in particular the assumption that two alleles are either IBD or independent. However, Taylor and Day (manuscript) have shown that we can still have this desirable property if the mutation rate is reconstructed. The idea is to endow both alleles with the same mutation rate $w = u + v$, and suppose that each allele mutates to A with probability p and to B with probability $1 - p$ (so that an allele can mutate to itself). Then the effective rate at which B mutates to A is $pw = u$ and the effective rate at which A mutates to B is $(1 - p)w = v$, so that as far as the *state* of an allele is concerned, there is no distinction between the original and this new "contrived" mutation process. The difference is that under this higher mutation rate two alleles are less likely to be IBD than before because, for example, when A mutates to A, we will no longer consider the new allele to be IBD to the old. Henceforth our notion of IBD will assume this contrived rate. We further assume there is some ancestral population that is far enough back that the probability of having an IBD copy of any original allele is negligible.

What we get from this reconstruction is a rigorous argument that if two alleles in the population are not IBD then they are independent, not within any single population, but within the universe of all possible realizations of the (neutral) population. This leads to the formula:

$$R_{\mathrm{A}} = \frac{G - G^*}{1 - G^*} \tag{2.9}$$

where G is the CC between the interactants and G^* is the CC between two individuals chosen at random (with replacement) from the entire population. This formula makes sense. If, for example, I give a gift of fitness to a neighbour, this can benefit me (that is, increase the fitness of my genes and their IBD copies) only if the neighbour is more closely related to me than is a random member of the population.

Because of the importance of (2.9) for our work here, we give a sketch of its derivation. Details are found in Taylor and Day (manuscript). Let x and y be the genotype of actor and neighbour. If they are IBD then they are both A with probability p and are both B with probability $1 - p$ for a covariance of $p(1 - p)$ and if they are not IBD then they are independent with covariance 0. Thus

$$\mathrm{COV}(x, y) = Gp(1 - p). \tag{2.10}$$

Note that we are operating here within the universe of all realizations, and we use uppercase COV to emphasize that. If we apply the covariance decomposition theorem to the class of realizations, we get

$$\mathrm{COV}(x, y) = \mathrm{E}_{\mathrm{A}}\,\mathrm{cov}(x, y) + \mathrm{cov}(q, q), \tag{2.11}$$

where the first term on the right is the average within-realization covariance and the second term is the covariance of the average genotypic value between realizations, noting that x and y both have average q. If we put (2.10) and (2.11) together, we get

$$\mathrm{E}_{\mathrm{A}}\mathrm{cov}(x, y) = Gp(1 - p) - \mathrm{var}(q). \tag{2.12}$$

A special case arises when x and y are chosen independently within the population. Then $\mathrm{cov}(x, y)$ will be zero in every realization, and $\mathrm{E}_{\mathrm{A}}\mathrm{cov}(x, y) = 0$. Since in this case $G = G^*$, we have

$$\mathrm{var}(q) = G^* p(1 - p). \tag{2.13}$$

Putting (2.13) into (2.12) we get (2.9). Rousset and Billiard (manuscript) choose another path around

the IBD problem and provide a formula analogous to (2.9) in terms of identity in state.

To calculate G we need to know the population structure. In an unstructured population, the standard mechanism is to select offspring independently from one another by random sampling from the entire gamete pool. In this case a standard argument (Taylor and Day, manuscript) shows that for small mutation rates,

$$G^* = 1 - 2w(N - 1) \tag{2.14}$$

to first order in w. [This formula is often reported with $N-1$ replaced by N but this is an approximation that is reasonable only for large N. For example, if $N = 1$, there is only one individual, and (2.14) gives the correct answer $G^* = 1$. See Crow and Kimura (1970, 6.6.2) to view this approximation in action.] Here we generalize (2.14) and hence calculate R_A for two common structures, a deme or island structure and a one-dimensional stepping-stone structure.

3. Deme structure

We suppose that we have discrete non-overlapping generations in a population consisting of d demes of size n for a total size of $N = dn$. For example, the deme might be a breeding patch with n breeding sites. We suppose that in each generation a breeder has a large number of offspring and these either stay on the home site (we will call these *natives*) or disperse to a migrant pool, possibly with some cost, and from there settle on a random deme which may (with probability $1/d$) be their native site. We will call these *migrants* even if by chance they return to their native site. Then on each deme there is fair competition among all the offspring, native and migrant, for the n breeding sites. This is the *island model* of Wright (1943), studied since that time by many authors. We let k be the probability that a random breeder is a native. Here we calculate the relatedness between random individuals (with replacement) on the same deme. This is the appropriate coefficient when one of the components of an action affects equally everyone on the deme, including the actor, for example, an act of altruism in which the benefit is shared by all individuals on the deme. This example is discussed in section 4.

3.1. Calculation of average relatedness

In Appendix 1 we calculate that

$$G^* = 1 - 2w\left(N - \frac{1 - dk^2}{1 - k^2}\right) \tag{3.1}$$

and that the CC between two individuals on the same deme (with replacement) is

$$G = 1 - 2w(N - d) \tag{3.2}$$

and is independent of the migration rate. Analogous formulae have been obtained by Latter (1973) using a continuous time model instead of discrete generations. For example, in the notation of our paper, Latter's formula for G is obtained from (3.2) by setting $d = 0$. That is, the continuous analogue of (3.2) is independent of the number of demes into which a population of fixed size is subdivided (to first order in the mutation rate w).

Using (2.9) we get the average relatedness of an individual to a random individual on the same deme to be:

$$R_A = \frac{d - 1}{N - 1 - k^2(N - d)}. \tag{3.3}$$

As a check we look at a few special cases. If we set $d = 1$ the deme is the entire population and G should equal G^* and from (2.9) that makes $R_A = 0$ as expected. If $d = N$, then each deme is a single individual and we expect $G = 1$ and $R_A = 1$, as indeed they are. If we set $k = 0$ then everyone migrates and we have a panmictic population of size N, and G^* should coincide with (2.14), as indeed it does. In this case, the demes are essentially formed at random, and $R_A = (d-1)/(N-1)$. Finally if we set $k = 1$, there is no migration and each deme is an isolated population of size n. In this case we might expect $R_A = 0$ (as in the case $d = 1$) but this is not the case. Rather (3.3) gives us $R_A = 1$. The reason for this is that the relatedness in this case is being calculated with respect to the entire population. Mathematically, we see from (3.1) that G^* is not defined in case $k = 1$ (unless $d = 1$) and therefore our calculations are simply not valid in this case. Rather the value given by (3.3) for this case represents a limit as k approaches 1, and if $k < 1$, no matter how small the difference, the deme is "aware" of the rest of the population.

To check the equivalence of (3.3) and the covariance formula (2.6) we have calculated the dis-

TABLE 2

Deme structure

1	2	3	4	5	6	7	8
q	morph	frequency (simulated)	frequency (eigenvector)	var(x) = $q(1-q)$	var($\bar{x}$)	E_q var($\bar{x}$)	R_q (3.6)
0	(0,0,0)	0.501240	0.499231	0	0	0	
1/6	(1,0,0)	0.000415	0.000407	5/36	1/18	1/18	0.4
2/6	(2,0,0)	0.000092	0.000091	2/9	2/9	0.1166	0.5246
	(1,1,0)	0.000160	0.000158		1/18		
3/6	(2,1,0)	0.000172	0.000171	1/4	1/6	0.1264	0.5056
	(1,1,1)	0.000055	0.000054		0		
4/6	(2,2,0)	0.000092	0.000091	2/9	2/9	0.1166	0.5246
	(2,1,1)	0.000157	0.000158		1/18		
5/6	(2,2,1)	0.000410	0.000407	5/36	1/18	1/18	0.4
6/6	(2,2,2)	0.497208	0.499232	0	0	0	

The dependence of relatedness R_q on allele frequency q in a population of total size N=6 structured into d = 3 demes of size n = 2 with $k = p = 0.5$ and mutation rate $w = 10^{-4}$. There are a total of 10 different morphs each described by a triple which records the number of mutant alleles in each of the three demes (col. 2) and these represent 7 different possible frequencies q (col. 1). For the Monte Carlo simulations we take an arbitrary starting configuration, and then construct successive generations, creating the next-generation breeders one at a time according to the appropriate probabilistic rules of migration and mutation. After each generation is formed we identify the population morph and update the frequency distribution. After 10^9 generations these seem to be stationary, and the resulting distribution is tabulated in column 3. In column 4 we have tabulated the "theoretical" frequencies obtained from the morph frequency recursions. These recursions are linear and col. 4 is actually the dominant right eigenvector of the recursion matrix. We provide both frequency columns in order to show the close fit between the simulation and the matrix results. The variances in columns 5 and 6 can all be calculated from the allele configuration in column 2, but to get E_q var($\bar{x}$) in col. 7 for three intermediate values of q we need the relative frequencies of the two morphs and we have used the eigenvector in col. 4. Column 8 is the quotient of columns 7 and 5. The averages of columns 5 and 6 over the morph distribution col. 4 are 0.002799 and 0.001317 respectively and these have quotient $R_A = 0.4704$ (see 2.6). This agrees closely with the theoretical formula (3.3) $R_A = 8/17 = 0.4706$.

tribution of the different possible realizations by two methods – for $N = 6$ from the dominant eigenvector of the linear recursion equations and for $N = 6$ and $N = 20$ by Monte Carlo simulation. The method and parameters are provided in Table 2. For a population of size $N = 6$ with $d = 3$ demes, (3.3) predicts $R_A = 8/17 = 0.4706$ and using (2.6) we get $R_A = 0.4704$ from both the eigenvector and from the simulations. For a population of size $N = 20$ with $d = 5$ demes (3.3) predicts $R_A = 16/61 = 0.2623$ and our simulations give us $R_A = 0.2629$. These agreements are excellent.

3.2. The dependence of relatedness on allele frequency

In a deme-structured population, a standard covariance decomposition theorem allows the covariance to be written as the sum of the average within-deme covariance plus the covariance of the deme averages:

$$\operatorname{cov}(x, y) = \mathrm{E}\operatorname{cov}_{\mathrm{D}}(x, y) + \operatorname{cov}(\bar{x}, \bar{y}) \qquad (3.4)$$

where the bar denotes deme average. If x and y are chosen at random in the deme with replacement, then they are independent within the deme and $\operatorname{cov}_D(x, y) = 0$. Since, in this case, we also have $\bar{y} = \bar{x}$:

$$\operatorname{cov}(x, y) = \operatorname{cov}(\bar{x}, \bar{x}) = \operatorname{var}(\bar{x}) \qquad (3.5)$$

and the relatedness (2.5) between x and y conditional on q can be written,

$$R_q = \frac{\mathrm{E}_q \operatorname{var}(\bar{x})}{\mathrm{E}_q \operatorname{var}(x)} = \frac{\mathrm{E}_q \operatorname{var}(\bar{x})}{q(1-q)}. \qquad (3.6)$$

To calculate the numerator of (3.6) we need the re- lative frequency of the various morphs which have allele frequency q and we can obtain these from the numerical calculations described above. The method and the results for $N = 6$ are presented in Table 2. The case $N = 20$ is more instructive and the

results (Figure 1) show very little dependence of relatedness on allele frequency.

A deme structure which is different from but related to the above model is the case in which the demes play no role in reproduction (like the case $k = 0$) but are formed for the purpose of the fitness interaction by selecting n individuals at random with replacement. [This "replacement" requirement is technical but it will have little effect if the deme size is much smaller than the population size.] In this case $\bar{x}$ is an average of n independent copies of x. Hence $\mathrm{var}(\bar{x}) = \mathrm{var}(x)/n$ and $R_q = 1/n$. The special case in which the demes are of size 2 is the case of random mating with the possibility of self-fertilization and the within-deme relatedness is essentially the average relatedness between sibs among the offspring of the pairing. The interesting result is that in these cases R_q is independent of q. Putting this result together with Figure 1, we conjecture is that it is typical of deme-structured populations for relatedness to depend only weakly on allele frequency.

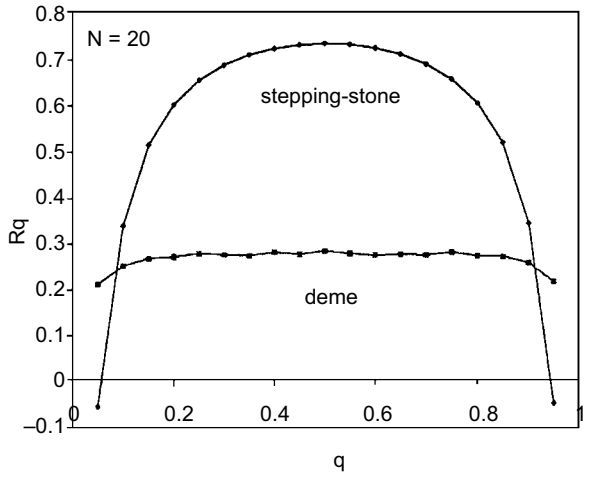

FIG. 1. Graph of frequency-specific relatedness R_q against frequency q after 10^9 iterations with $k = 0.5$, $w = 10^{-4}$, and $p = 0.5$ for both the deme-structured population ($N = 20$, $d = 5$) and the stepping-stone population ($N = 20$, $k = 0.5$). With the deme structure we obtain a very weak dependence of R_q on q, whereas the stepping-stone graph shows a strong dependence

4. Stepping-stone structure

We suppose there are N sites equally spaced around a circle of circumference 1, each occupied by a single breeder. At each site, the next generation occupant is native with probability k and comes from each adjacent site with probability $(1 – k)/2$. We are interested in the relatedness between breeders on adjacent sites. The general method here, for both finite and infinite populations has emerged from many years of work by Malécot (reviewed in 1975) and is also discussed in Kimura and Weiss (1964).

4.1. Calculation of average relatedness

The one-generation recursions for the CC between individuals j sites apart, for $1 \le j \le N/2$, involve the coefficients for $j – 1$ and $j + 1$ (with an obvious adjustment for the diametrically opposite sites at $j = [N/2]$) and hence we cannot solve for any of these without solving for them all. For general N this involves a system of $[N/2]$ equations in the same number of unknowns. We cannot find a simple general equilibrium solution for these, but we can solve them with computer algebra for small values of N. As an example the calculations for $N = 5$ are presented in Appendix 2. Here we fasten attention on the average relatedness R_A between breeders on adjacent sites. The results are, ignoring terms in the mutation rate w ,

$$\mathrm{N} = 5 \qquad R_A = -\frac{1-k}{2+6k} = -\frac{0.5}{5} = -0.1 \tag{4.1}$$

$$\mathrm{N} = 20 \qquad R_A = \frac{184083057}{293182135} = 0.6279. \tag{4.2}$$

Here the numerical values are calculated for $k = 0.5$. For $N = 20$, R_A is a quotient of polynomials in k of degree 9, and in general R_A appears to be the quotient of polynomials in k of degree just less than $N/2$. For $N = 5$, R_A is negative. This is not surprising – in a population in which the average relatedness to a random individual (with replacement) is 0, the relatedness to certain individuals other than self must be negative.

To check the equivalence of covariance formula (2.6) and (4.1, 4.2) we have calculated the distribution of the different possible realizations by two methods – for $N = 5$, from the dominant eigenvector of the linear recursion equations and for $N = 5$ and $N = 20$, by Monte Carlo simulation. The method and parameters are provided in Table 3. For $N = 5$, (2.6) gives $R_A = –0.10004$ from the eigenvector distribution and $R_A = –0.09905$ from the simulations and these are close to (4.1). For $N = 20$, our simulations give us $R_A = 0.6269$ and this is close to (4.2).

TABLE 3

Stepping-stone structure

1	2	3	4	5	6	7	8
q	configuration	frequency (simulated)	frequency (eigenvector)	cov(x, x)	cov(x, y)	E_q cov(x, y)	R_q
0	(0,0,0,0,0)	0.499288	0.499294	0	0	0	
0.2	(1,0,0,0,0)	0.000399	0.000397	0.16	–0.04	–0.04	–0.25
0.4	(1,1,0,0,0)	0.000261	0.000258	0.24	0.04	0.006838	0.02849
	(1,0,1,0,0)	0.000052	0.000051		–0.16		
0.6	(1,1,1,0,0)	0.000261	0.000258	0.24	0.04	0.006838	0.02849
	(1,1,0,1,0)	0.000052	0.000051		–0.16		
0.8	(1,1,1,1,0)	0.000399	0.000397	0.16	–0.04	–0.04	–0.25
1	(1,1,1,1,1)	0.499288	0.499294	0	0	0	

Relatedness calculation for the stepping-stone population of size $N = 5$ with $k = p = 0.5$ and mutation rate $w = 10^{-4}$. The individuals are arranged in a circle and the configuration records the relative placing of the mutant alleles. Column 3 gives the results of the Monte Carlo simulations after 10^9 generations. In column 4 we have tabulated the dominant right eigenvector of the recursion matrix, similar to Table 2. In column 6, y is taken to be adjacent to x. Column 8 is the quotient of columns 7 and 5. The covariances in columns 5 and 6 can all be calculated from the allele configuration in column 2, but to get col. 7 for two intermediate values of q we need the relative frequencies of the two morphs and for this we have used the eigenvector in col. 4. Column 8 is the quotient of columns 7 and 5. The averages of columns 5 and 6 over the morph distribution col. 4 are 2.7552×10^{-4} and -2.7562×10^{-5}, respectively, and these have quotient $R_A = -0.10004$ from (2.6). This agrees closely with the theoretical value $R_A = -0.1$ from (4.1).

4.2. The dependence of relatedness on allele frequency

The structure of the calculation for R_q is displayed in Table 3 for the case $N = 5$, and Figure 1 provides a plot of relatedness R_q against frequency q for the case $N = 20$. Unlike the deme-structured case, we find here a fairly strong dependence of relatedness on allele frequency, with R_q being significantly higher for intermediate values of q. In fact R_q nearly doubles as the frequency goes from 0.1 to 0.5. This suggests, for example, that an altruistic trait might have trouble getting started, but if it drifted to a sufficiently high frequency it might then increase further under selection, but would have trouble attaining fixation. This, of course, would encourage the formation of relatively stable polymorphisms. Similar results have been obtained by Rousset and Billiard (manuscript) in a simulation study of a one-dimensional stepping-stone population with 200 sites.

5. Altruism in a deme-structured population

Consider a population at the neutral equilibrium and endow the allele A with a small selective effect ($\delta > 0$). Then by (2.8) the average frequency $E_A(q)$ will change in the direction given by W_I. As soon as this change gets underway, (2.8) is no longer valid, but (2.2) (with C replaced by A) should remain approximately true and by setting $E_A(\Delta q) = 0$ it gives us an approximation to the new equilibrium average frequency:

$$E_A(q) = p + \delta \frac{K}{w} E\,\mathrm{cov}(x,x) W_I. \qquad (5.1)$$

An analogous equation is found in Rousset and Billiard (manuscript, eq. 9). This tells us that the average inclusive fitness W_I should be able to predict which side of p the new equilibrium will be on.

Here we employ a model of altruism in a haploid deme-structured population to give us a numerical check on this qualitative result. We assume that in each generation each A individual performs an altruistic act with fecundity cost c to the actor and benefit b distributed uniformly over the deme, both b and c assumed small. An inclusive fitness model for this is found in Taylor (1992a) for an infinite population and more generally in Rousset and Billiard (manuscript) and Taylor and Day (manuscript). An altruistic act creates b extra offspring with relatedness R to the actor and $-c$ extra offspring with relatedness 1, and these $b - c$ extra offspring remain on the natal patch with probability k and in that case displace

$b - c$ deme offspring who are native with probability k and in that case have relatedness R. The net inclusive fitness offspring count is then

$$W_I = bR - c - k^2(b - c)R$$

and the condition that this be positive can be written:

$$bR\sim > c. \tag{5.2}$$

where

$$R\sim = \frac{R - k^2R}{1 - k^2R} \tag{5.3}$$

is what might be called the "effective" relatedness and we see that it is somewhat less than R. This is an effect of what Hamilton (1964) called the "viscous" structure of the population. When population dispersal is only partial, the benefits of altruism can compete with and displace normal reproductive output and these same factors moderate the costs (Hamilton, 1964, p. 11; Wilson et al., 1992; Taylor, 1992a, b; Kelly, 1997), and the k^2 terms in (5.3) provide the necessary discounting of these benefits and costs. We see from (5.2) that the effective relatedness $R\sim$ is the threshold cost:benefit ratio c/b, in the sense that the altruistic trait is neutral if this ratio is equal to $R\sim$, and is at an advantage or disadvantage if the ratio is less than or greater than $R\sim$. Note that we can eliminate this "viscosity" by setting $k = 0$ (complete migration), and in this case $R\sim = R$ and (5.2) becomes Hamilton's (1964) classic condition $b\,R > c$.

If we replace R by the average within-deme relatedness R_A given by (3.3), then the effective relatedness (5.3) simplifies to:

$$R\sim = \frac{d - 1}{N - 1} \tag{5.4}$$

and is independent of the migration parameter k. This provides a finite population version of a general result that in a viscous inelastic infinite population the kin-selected effects of a fitness interaction are exactly counterbalanced by the competitive effects, and the natural selection acts on the trait exactly as it would in a panmictic population with random interactions – the case $k = 0$ (Wilson et al., 1992; Taylor, 1992a, b).

To model the behaviour we ran the Monte Carlo simulations described in Section 3, each generation assigning appropriate cost and benefit to each breeder according to its genotype and the average genotype in the deme, until the morph distribution became stationary. We used a fixed benefit $b = 0.1$ and variable cost c. When $bR\sim = c$, we should have $W_I = 0$ and (5.1) tells us that the equilibrium distribution should have an average allele frequency of $E_A(q) = p$ (see also 2.7), but when $bR\sim > c$ or $bR\sim < c$, the equilibrium distribution should have an average allele frequency of $E_A(q) > p$ or $E_A(q) < p$, respectively. Table 4 shows that this is indeed the case for two populations of size 6 and 20.

TABLE 4

Equilibrium allele frequency $E_A(q)$ in a finite deme-structured population with an altruistic trait

Population size N	# Demes d	$R\sim$ (from 5.3)	c b	$E_A(q)$
6	3	0.40	0.35	0.5117
			0.40	0.5000
			0.45	0.4881
20	5	0.21	0.16	0.5445
			0.21	0.4985
			0.26	0.4535

We take $p = 0.5$ so that a neutral allele should have equilibrium frequency 0.5. Other parameter values are $k = 0.5$, mutation rate $w = 10^{-4}$ and fixed benefit $b = 0.1$. Each population was run for 10^9 generations with different values of the cost c giving a c/b ratio which was below, equal to, and above the "effective" average within-deme relatedness $R\sim$. In each case the frequency responded as predicted by condition (5.1). This provides evidence that the average within-deme relatedness R_A correctly predicts allele frequency change averaged across all realizations.

6. Discussion

It needs to be emphasized that it is not at first clear exactly how relatedness should be defined in a finite population. This question was perhaps first raised by Seger (1981) and recently was analyzed by Rousset and Billiard (manuscript) and the methodology they set forward, which is to attempt to model the allele frequency change averaged over all realizations of the finite population, turns out to be very fruitful, in that the corresponding "average" relatedness coefficient can be formulated in terms of the average probability of identity in state (Rousset and Billiard, manuscript) or identity by descent (2.9).

Here we have looked at two common theoretical structures, in each case calculating the coefficients of consanguinity G from standard recursions, and then obtaining the average relatedness R_A from

(2.9). We have then used numerical simulations to run two different kinds of check. The first of these in sections 3 and 4 compares (2.9) to the covariance definition of R_A given in (2.6), and the results are presented in Tables 2 and 3. The second of these, in section 5, checks whether or not (5.1) actually predicts the direction of average allele frequency change under weak selection. For this we have looked at an altruistic trait in a deme-structured population and the results of Table 4 show that the equilibrium frequency of the allele is shifted in the expected direction from the neutral equilibrium p.

For both of these checks we need to know the equilibrium frequency with which the different possible morphs (realizations) occur and we have used two different methods to calculate these. The first uses a Monte Carlo simulation, running the population for a large number (10^9) of generations and simply recording the proportion of occurrences of each morph, and the second obtains these as the dominant eigenvalue of the linear recursion equations for the morph frequencies. These are reported in columns 3 and 4 of Tables 2 and 3.

An important difference between a deme structure and a stepping-stone structure is that the second is "spatial" whereas the first is not. In many ways this makes the stepping-stone model more realistic; however, because the genetic similarity between any pair of sites depends on the previous similarity between *every* pair of sites, calculations of relatedness are difficult or intractable. In the deme structure on the other hand, there is no local structure among demes, and the recursion equations for relatedness are typically easy to solve (Appendix 1). For small populations, perhaps with a computer algebra package, we can handle the stepping-stone recursions analytically and Appendix 2 presents the method for $N = 5$. Stepping-stone populations in 2 or 3 dimensions are harder still to analyze.

Our simulations have suggested a difference between these two population structures in the dependence of relatedness on allele frequency q. With the deme structure this is very weak, and R_q is almost constant, whereas the stepping stone structure shows a strong dependence with higher relatedness to a neighbour for intermediate frequencies (Fig. 1).

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APPENDIX 1

Coefficients of consanguinity in a deme-structured population

Define the following coefficients of consanguinity:

G = two individuals on the same deme (with replacement)

$G\#$ = two individuals from different demes.

Then

$$G^* = \frac{1}{d}G + \frac{d-1}{d}G\# \qquad \text{(A.1)}$$

and we have the recursions:

$$G = \frac{1}{n} + \frac{n-1}{n}[k^2G + (1-k^2)G^*](1-w)^2 \qquad \text{(A.2)}$$

$$G\# = [k^2G\# + (1-k^2)G^*](1-w)^2 \qquad \text{(A.3)}$$

which solve to give (3.1) and (3.2).

APPENDIX 2

Average relatedness in a stepping-stone population of size $N = 5$

Recall that k is the probability that an occupant is native. The equations are more transparent if we let $2m = (1 - k)$ be the probability that an occupant is an immigrant. In that case it came from either adjacent site with probability m. We let G_1 be the CC to a neighbour (at distance $s = \pm 1/5$) and let G_2 be the CC to either of the two "opposite" individuals (at distance $s = \pm 2/5$). Then the CC between random individuals with replacement is

$$G^* = \frac{1 + 2G_1 + 2G_2}{5}.$$

The one-generation recursions are:

$$G_1' = [(k^2 G_1) + (2m^2 G_1) + (m^2 G_2 + m^2 G_1) + \\ +(2km + 2kmG_2)][1 - w]^2,$$

$$G_2' = [(k^2 G_2) + (2m^2 G_2) + (m^2 G_1 + m^2) + \\ +(2kmG_1 + 2kmG_2)][1 - w]^2,$$

In each equation, the four terms in the round brackets catalogue the different movement types of the two offspring. In the first term, they both stay at home, in the second they both move one unit in the same direction, in the third they move in opposite directions, and in the fourth one stays at home and the other moves. The final term provides the probability that neither offspring has mutated.

The equilibrium values of the G_i are obtained by setting $G_i' = G_i$ and solving. If w=0, the solutions are clearly $G_i = 1$, so that the solutions have the form

$$G_i = 1 - g_i w + \mathrm{o}(w).$$

If we put this into above equations and set $g_i' = g_i$ we obtain the equations:

$$g_1(1 - k^2 - 3m^2) + g_2(-m^2 - 2km) = 2,$$

$$g_1(-m^2 - 2km) + g_2(1 - k^2 - 2m^2 - 2km) = 2$$

and the solution is:

$$g_1 = \frac{8 - 10m}{m(4 - 10m + 5m^2)},$$

$$g_2 = \frac{12 - 20m}{m(4 - 10m + 5m^2)}.$$

If we write $G^* = 1 - g^* w$, then

$$g^* = \frac{2g_1 + 2g_2}{5} = \frac{8 - 12m}{m(4 - 10m + 5m^2)}$$

and the relatedness between individuals at adjacent sites is

$$R_A = \frac{G_1 - G^*}{1 - G^*} = \frac{g^* - g_1}{g^*} = \frac{-m}{4 - 6m}$$

and this is (4.1).

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