

An Inclusive Fitness Model for Dispersal of Offspring

PETER D. TAYLOR

*Department of Mathematics and Statistics, Queen's University,
Kingston, Ont. K7L 3N6, Canada*

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A series of papers, Hamilton & May (1977), Motro (1982, 1983) and Frank (1986) have developed and generalized a model of dispersal of offspring to random sites in a stable environment. I present an inclusive fitness model for such dispersal behaviour, applicable in diploid or haplodiploid populations with dispersal under offspring or maternal control. This model provides an illustration of the general discussion of inclusive fitness models found in Taylor (1988*a, b*). In particular, it provides a good example of the way in which relatedness coefficients can depend, not only on the genetic structure of the population, but on the mechanism of control of the behaviour under study.

1. Introduction

The dispersal of offspring from their natal territory is a widespread phenomenon in both plants and animals. A not unreasonable view of the evolutionary advantage of such behaviour is the "grass is greener" idea, which says that those offspring which disperse must have, on the whole, a better chance of establishing themselves as breeders than if they had stayed at home and competed with their siblings and cousins. But just where does the advantage come from? Is it that they might find a better or an emptier patch of ground? For example, consider the following population-wide behaviour. Suppose half of every brood disperses, and the remainder stay at home. Those that disperse have only a 50% chance of finding a breeding patch, and those that do find such a patch face competition that is just as stiff as that faced by their siblings who remained at home. Could such behaviour be evolutionarily stable?

One guesses at first that the answer should be no, but a remarkable paper by Hamilton & May (1977) showed, with a simple game theoretic argument, that the answer could well be yes. This was for an asexual population, but they also obtained a similar result for a diploid sexual population. Motro (1982, 1983) extended this work with explicit genetic models, and Frank (1986*c*) obtained the same results using Price's (1970) formula for gene frequency change. My purpose is to extend Frank's results with an inclusive fitness model and at the same time illustrate a general approach developed in Taylor (1988*a, b*).

To be more precise, Frank (1986*c*) considered a diploid model with mating before dispersal, and derived the ESS dispersal rate d^* as a function of the cost of dispersal c and the relatedness R between mated females on the same patch. I extend his work by calculating R for various cases (mating before and after dispersal, diploid

and haplodiploid genetics, and maternal and offspring control) and obtain the ESS dispersal rate d^* in terms of c and the number N of breeding females on each patch.

For the assistance of the reader I will summarize the main variables that are used in the paper: (Their meanings will be defined more clearly in the text.)

N number of mated females breeding on a patch

d or d_i dispersal probability of individuals (of sex i)

δ differential increase in d or d_i

c cost of dispersal

$k = (1 - d)/(1 - dc)$ the probability that a random female breeding on a patch is native

x an individual chosen at random prior to dispersal

y a random patchmate of x of the same sex

z the individual controlling the dispersal behaviour of x

G_x genotypic value of x

H_x phenotypic value of x

$R = R_{x \rightarrow y}^z$ relatedness of y to x from z 's point of view

f coefficient of inbreeding

g coefficient of consanguinity between offspring born on the same patch.

LIFE HISTORY

I assume an infinite, sexually reproducing population, with diploid or haplodiploid genetics, and discrete non-overlapping generations with the following life history. Mated females gather on breeding patches, N females to a patch, and have a large number of offspring each. There are then two possible dispersal patterns. In *dispersal after mating*, the offspring mate at random on the patch, and then the new mated females disperse to a random patch with probability d and remain on their native patch with probability $1 - d$. Those that disperse incur a cost c . I will interpret c as a viability cost and assume that a proportion $1 - c$ of the dispersers survive to find another patch, but a fecundity interpretation is also possible. In *dispersal before mating*, the offspring disperse with possibly sex-dependent probabilities d_i and cost c_i , and then mating is at random on each patch amongst the natives and immigrants. In either case, the mated females on each patch then compete for the N breeding spots and the cycle begins again.

This life history has also been studied in models of sex allocation under local mate competition, by Hamilton (1967) with $d = 1$ and $c = 0$, by Bulmer (1986) and Frank (1986a) with $c = 0$, and with an inclusive fitness model by Taylor (1988a).

INCLUSIVE FITNESS

The inclusive fitness method originated with Hamilton (1964, 1970, 1972) and has since been studied and refined by many others. Using a dispersal model as an example, it proceeds as follows. We look at the population at the moment of dispersal, and consider one "mutant" individual (suppose it is a female) who has a differentially altered dispersal probability of $d + \delta$. We then calculate her fitness

(the number of offspring projected to the start of the next cycle) and the fitness of each of her patch mates (which may have been altered by her own mutant behaviour). Her *inclusive fitness increment* ΔW is her own fitness change plus the sum of the fitness changes of each of her neighbours, each of these weighted by the coefficient of relatedness of that neighbour to the mutant individual. (For an example see equation (7) below.) If some of these neighbours are of different sex, it may also be necessary to weight their fitness changes with a relative reproductive value. If the inclusive fitness increment is positive, selection should favour a change in behaviour from d to $d + \delta$. The equilibrium value of d is the one which makes this increment zero. Thus, if the number of offspring is large, at equilibrium, an individual who decides to disperse instead of remaining at home will experience no change in inclusive fitness.

For the inclusive fitness approach to provide the same condition as an exact genetic model, we need an assumption about the relationship between phenotype and genotype. Let the dispersal probability of an individual x be $d + H_x \delta$ where H_x is called the *phenotypic value* of x . Suppose the fitness of any individual depends, to first order in δ , linearly on both her own phenotype and on the phenotype of a random patchmate y (or, if you like, on the average phenotype of her patchmates). Now we relate phenotype to genotype. Suppose dispersal behaviour is controlled at a single locus at which there are two alleles, a "mutant" allele and a "normal" allele, and let the *genotypic value* G_x of an individual be the frequency of the mutant allele among her gametes. To specify the control of behaviour is to say how H_x depends on genotype. In the usual case H_x depends only on G_x , but it can be conceptually useful to have H_x depending also on the genotypes of relatives or neighbours of x . For example, in the case of maternal control of dispersal, the phenotypic value H_x of an offspring x will depend only on G_z , where z is the mother of x .

Having related H to G , the precise result (Hamilton, 1970, 1975; Charlesworth, 1980; Seger, 1981; Grafen, 1985; Taylor, 1988*a, b*) is that, under fair meiosis (Mendelian assortment of genes into offspring), the inclusive fitness increment ΔW of a mutant individual x and the change ΔQ in mutant allele frequency, as given by the covariance formula (Price, 1970), have the same sign, to first order in δ , if the relatedness coefficient used is

$$R = R_{x \rightarrow y} = \frac{\text{cov}(G_y, H_x)}{\text{cov}(G_x, H_x)} \quad (1)$$

provided the denominator of R is positive. Michod and Hamilton (1980) compare this formulation of the coefficient with a number of others that have appeared in the literature.

CALCULATION OF R

In practice, R is only easy to calculate when H_x depends linearly on genotypic value, either of x herself (this is the standard case of additive gene action), or of another "control" individual z who determines the behaviour of x . In the latter

case, $H_x = G_z$ and R is a quotient of covariances of genotypic values:

$$R = R_{x \rightarrow y}^z = \frac{\text{cov}(G_y, G_z)}{\text{cov}(G_x, G_z)} \quad (2)$$

which can be regarded as "the relatedness of y to x from the point of view of z ". If the alleles are neutral (which means $\delta = 0$), then

$$R_{x \rightarrow y}^z = \frac{f_{yz}}{f_{xz}} \quad (3)$$

(Michod & Hamilton, 1980) which is the coefficient proposed by Hamilton (1972). Here f_{ij} is the *coefficient of consanguinity* between I and J (Crow & Kimura, 1970), and is defined as the probability that random alleles from I and J , at the locus of control, are identical by descent. Of course, in practice, the alleles will not be neutral, but if selection is weak, this should very nearly hold. (See Taylor (1988*b*) for a precise theorem along these lines.) If x is diploid and controls her own behaviour so that $z = x$, (3) becomes

$$R = \frac{2f_{yx}}{1 + f_x} \quad (4)$$

which is actually the form given by Hamilton (1972). Here, f_x is the inbreeding coefficient of x .

Formula (3) provides a very intuitive expression of the relatedness of y to x . It displays R as an assessment by z of the relative quality of the gametes of y and x , where quality is measured by similarity to the gametes of z herself. The notation for R is not quite standard, and the superscript z is my own. There may be a better way of bringing the control into the notation, but I do think that for many applications of unusual control, it is important to have a notation which displays all three individuals.

In this paper we will encounter two different examples of (3). In one (dispersal before mating), x and y will be unmated offspring born on the same patch, and z will be either the mother of x (maternal control) or x herself (offspring control). In the other (dispersal after mating), x and y will be *mated* females born on the same patch and z will be the "female part" of x . The point here is that G_x and G_y in (1) measure contribution to offspring, and so if, at the time of the dispersal, x and y are mated females, the correct G must be the average genotypic value of the mated pair; on the other hand, if the female controls her own behaviour, H_x is determined only by her own genotype. An example of the calculation is given in (13) below.

2. The Inclusive Fitness Condition

DISPERSAL AFTER MATING

We suppose that mating is at random on each patch, and then each mated female disperses with probability d , incurring a cost c . After the dispersal phase, the mated

females on each patch (natives and immigrants) compete for the N mating spots. Denote by p the probability that each of these females will be a "winner", that is, will breed on the patch, and let k denote the probability that each breeding female is native to that patch. Since a proportion d of all females disperse, and are replaced by $1 - c$ as many immigrants, we have that

$$k = \frac{1 - d}{(1 - d) + (1 - c)d} = \frac{1 - d}{1 - dc}. \tag{5}$$

Now fasten attention on a patch with one mutant mated female with dispersal probability $d + \delta$. With probability δ she has the fitness (probability of breeding) $(1 - c)p$ of a dispersing female instead of the fitness p of a non-disperser. Thus the change in fitness due to her mutant behaviour is δcp . Now look at the effect of her behaviour on the fitness of her patchmates. With probability δ an extra p of these females will breed. Since each such female has probability k of being native, the fitness increment of the original female through relatives is $\delta p R k$ where R is the relatedness between two mated females born on the same patch. Her inclusive fitness increment is then

$$\Delta W = \delta p(-c + Rk) \tag{6}$$

and the condition for selection to favour an increase in d is

$$Rk > c. \tag{7}$$

Condition (6) can be interpreted as if dispersal were an altruistic act. It has the form $\Delta W = \delta(RB - C)$ where $C = cp$ is the cost of dispersal (in terms of lost probability of breeding) and $B = kp$ is the benefit to others born on the same patch. In the usual way (Hamilton, 1964, 1972) this benefit is weighted by the average relatedness of these others to the actor.

Condition (7) can be written as

$$d < \frac{R - c}{R - c^2} \tag{8}$$

the form obtained by Frank (1986c). If $N = 1$, then at equilibrium R turns out to be 1 and we get the ESS dispersal probability to be

$$d^* = \frac{1}{1 + c} \tag{9}$$

obtained by Hamilton & May (1977).

DISPERSAL BEFORE MATING

Now I fasten attention upon the offspring and suppose that each sex has its own dispersal rate d_i . Since the dispersal behaviour of members of one sex will not affect the fitness of members of the other, I can treat the sexes separately.

After dispersal and immigration, mating takes place at random on each patch, and I let p and k be defined as above. The inclusive fitness increment of a mutant female is calculated exactly as above, and is given by (6) where R is the relatedness of one female offspring to another born on the same patch. The same argument holds for male offspring, and so the condition for d_i to increase under selection is, from (7),

$$R_i k_i > c_i \quad (10)$$

where the parameters are sex-specific.

It is interesting to ask what are the factors which might make the d_i different. The first factor is certainly different costs of dispersal: if c_1 is different from c_2 then we certainly expect different rates of dispersal, and this would seem to be the main factor in most observed cases of sex-dependent dispersal rates. I propose not to pursue this question of differential costs, and for the rest of this paper will suppose that $c_1 = c_2 = c$. In this case, if the assumptions of the model are met, the only factor that could produce different ESS dispersal rates is different relatednesses R_i for the two sexes. Since this does not happen under diploidy, I conclude that in diploid populations, if the dispersal costs are the same for both sexes, we expect identical dispersal rates. But in haplodiploid populations there may well be differences in dispersal patterns due only to factors of relatedness. Since k decreases with d , we see that the effect of higher relatedness will be a higher rate of dispersal.

3. Calculation of R

To calculate the relatedness coefficients R , I assume semi-dominant gene action, and use (3), calculating the f_{ij} by assuming they are unchanged from one cycle to the next (the population is at equilibrium), and solving the resulting recursion equations. I do the calculations separately for diploidy and haplodiploidy, and, as before, I treat the cases of dispersal after mating, and dispersal before mating. In the case of dispersal after mating, the individuals are mated females who control their own dispersal, so the genotypic value G will be the average of that of the male and female genotypes, whereas the phenotypic value will be the female genotypic value (Taylor, 1988a). In the case of dispersal before mating, there will be two cases depending on whether dispersal of the offspring is controlled by the offspring themselves or by their mother. I also remark that our expression for R will generally depend on d , and so (7) and (8) will be conditions to be solved for d .

There is one easy result, worth mentioning at the beginning, and that is if there is no cost to dispersal ($c = 0$), then dispersal rates must be 1 in all cases considered here. Indeed, if d or any d_i were less than 1, then the corresponding relatedness R or R_i would exceed zero, and (7) or (10) would always hold, causing d or d_i to increase.

DIPLOID—DISPERSAL AFTER MATING

I let f denote the inbreeding coefficient of the offspring (the probability that the two alleles at the locus in question are identical by descent) and g the coefficient

of consanguinity (see (3)) between two offspring born on the same patch. The values of these coefficients for the next generation can be expressed in terms of those for this generation by the equations $f' = g$ and

$$g' = \frac{1}{N} \left[\frac{1+f+2g}{4} \right] + \frac{N-1}{N} [k^2 g]. \tag{11}$$

The two terms on the right correspond to the cases in which the offspring are sibs and not sibs. For this equation to hold, we must assume either that the number of offspring of each parent is large or, if not, that the number of offspring of each female is independent of the numbers of offspring of the other females on the patch. These two equations are solved by setting $f' = f$ and $g' = g$, and we get

$$f = g = \frac{1}{4N - 3 - 4(N-1)k^2}. \tag{12}$$

Now I calculate the relatedness R between two mated females on the same patch. I use (3) where x is a mated female, z is her female part, and y is another mated female on the same patch. The genotypic values G_x and G_y are averages of the male and female values. Then $f_{y:z} = g$ and $f_{x:z} = (1+f+2g)/4$, and so the relatedness between two mated females, born on the same patch, is

$$R = \frac{4g}{1+f+2g} = \frac{1}{N - (N-1)k^2} \tag{13}$$

obtained by Frank (1986a) for the case $c = 0$.

When we substitute this into (7) we get that selection will favour an increase in d whenever $d > d^*$ where

$$d^* = \frac{H + 1 - 2Nc}{H + 1 - 2Nc^2} \tag{14}$$

with

$$H = \sqrt{1 + 4N(N-1)c^2}.$$

This is the formula for the ESS dispersal probability of mated females in terms of the size N of a breeding patch and the cost c of dispersal. It is graphed in Fig. 1. If $c = 0$, it gives us complete dispersal $d^* = 1$, and if $c = 1$ we get $d^* = 1/2N$. (Actually, at $c = 1$, $H = 2N - 1$, and $d^* = 0/0$, so one must take a limit to resolve the expression.) It is interesting that the model predicts some dispersal even when mortality is nearly certain. At $c = 1$, of course, there are no immigrants entering a colony, and the equilibrium value of the coefficients f , g , and R is unity.

If each breeding patch is occupied by a single female, which is the case studied by Hamilton & May (1977) and Motro (1982, 1983), we have $N = 1$, and $d^* = 1/(1+c)$ which is the result obtained by Hamilton & May (1977) for a haploid population.

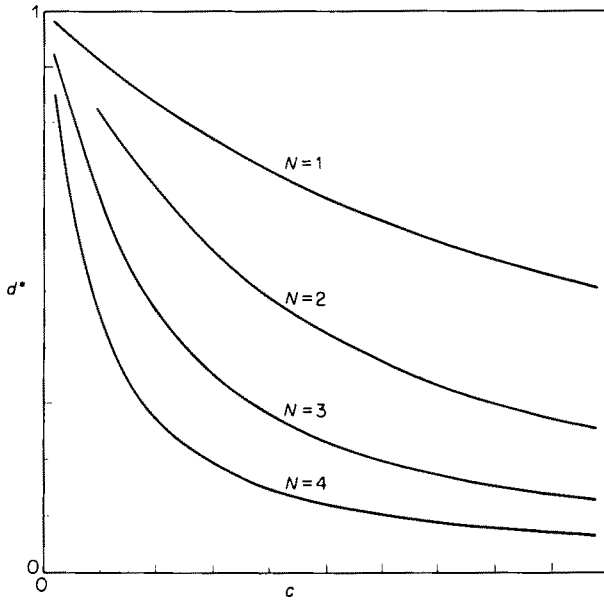


FIG. 1. ESS dispersal rate d^* of mated females against the cost c of dispersal for different values of patch size N , given by equation (14). This applies for both diploid and haplodiploid genetics. These graphs also obtain in a diploid population for dispersal of both sexes before mating with maternal control and offspring control, except under offspring control, the N values in the diagram should be halved. For example (for diploid, dispersal before mating) the above curve labelled $N = 2$, gives the $N = 2$ result for maternal control and the $N = 1$ result for offspring control.

DIPLOID—DISPERSAL BEFORE MATING

Since I am assuming the same costs for both sexes, and under diploidy the genetics are symmetric, we will have $d_1 = d_2 = d$, and hence $k_1 = k_2 = k$, and if f and g have their previous meanings, the recursion equations are $f' = k^2g$ and

$$g' = \frac{1}{N} \left[\frac{1+f+2k^2g}{4} \right] + \frac{N-1}{N} [k^2g] \tag{15}$$

which solve to give

$$g = \frac{f}{k^2} = \frac{1}{4N - (4N - 1)k^2}. \tag{16}$$

Maternal control

The phenotype of an offspring is determined by the genotype of her mother, and so we take z to be the mother of x in (3). The coefficient of consanguinity between an offspring and the mother of a patch mate, f_{xz} , is the same as that between an offspring and the father of a patch mate, and so equals g , the coefficient between two offspring. The coefficient between an offspring and her own mother, f_{xz} , is easily seen to be $(1+f+2k^2g)/4$, and so from (3),

$$R = \frac{4g}{1+f+2k^2g} = \frac{4g}{1+3f} = \frac{1}{N - (N-1)k^2} \tag{17}$$

which is the same as (13) for dispersal after mating. Thus the ESS value of d^* , for both male and female offspring, is given by (14). A mother wants the same dispersal pattern for her offspring before they have mated as the offspring would want for themselves if dispersal followed mating.

Offspring control

The phenotype of an offspring is controlled by its own genotype, so $z = x$ in (3) and the relatedness between offspring born on the same patch is then

$$R = \frac{2g}{1+f} = \frac{1}{2N - (2N - 1)k^2} \tag{18}$$

which is identical to (13) with N replaced by $2N$. Thus the ESS value of d^* , for both male and female offspring, is given by (14) with N replaced by $2N$. A female whose dispersal phase precedes mating will be less likely to disperse than one whose dispersal phase follows mating. In fact she will behave the same as a post-mating-dispersal female on a patch twice the size.

A comparison of offspring and maternal control allows us to see the effect of parent-offspring conflict over dispersal rates of offspring. In both cases the condition is (9), $Rk > c$, but R , the relatedness between patchmates, is higher under maternal control than under offspring control. Indeed, using (3), the numerator f_{xz} is the same for both cases (and equal to g) but the denominator f_{xz} is lower for maternal control, being $(1+3f)/4$ as opposed to $(1+f)/2$. Thus the mother wants a higher dispersal rate than the offspring; in fact the offspring rate coincides with the maternal rate for a patch twice the size.

HAPLODIPLOIDY—DISPERSAL AFTER MATING

Now let g_{ij} be the coefficient of consanguinity between two individuals of sex i and sex j , born on the same patch, and let f be the inbreeding coefficient of a female. Then, at equilibrium, $f = g_{12}$ and

$$g_{11} = \frac{1}{N} \left[\frac{1+f}{8} + \frac{1}{4} + \frac{g_{12}}{2} \right] + \frac{N-1}{N} k^2 \left[\frac{g_{11} + 2g_{12} + g_{22}}{4} \right]$$

$$g_{12} = \frac{1}{N} \left[\frac{1+f}{4} + \frac{g_{12}}{2} \right] + \frac{N-1}{N} k^2 \left[\frac{g_{11} + g_{12}}{2} \right]$$

$$g_{22} = \frac{1}{N} \left[\frac{1+f}{2} \right] + \frac{N-1}{N} k^2 g_{11}.$$

These equations are not hard to solve, though I will not give the solution explicitly. To calculate the relatedness between mated females, the genotypic value, which is an average of the female and male values, must now, because of the genetic asymmetry between females and males, be a *weighted* average, where the female contribution gets a relative weight of 2 (Hamilton, 1972; Pamilo & Crozier, 1982; Taylor, 1988a). This gives us

$$R = \frac{2g_{11} + g_{12}}{1+f + g_{12}} \tag{19}$$

which, unexpectedly enough, works out to be the same as (13) above. Thus the value of d^* for haplodiploidy turns out to be the same as that for diploidy, at least for dispersal of mated females, and is given by (14).

HAPLODIPLOIDY—DISPERSAL BEFORE MATING

We are assuming that the costs c_i are identical, both equal to c , but the relatednesses R_i may not be the same, and so we must allow for the possibility of different dispersal rates d_i for each sex, and thus the k_i may be different. The recursion relations are

$$g_{11} = \frac{1}{N} \left[\frac{1+f}{8} + \frac{1}{4} + \frac{\hat{g}_{12}}{2} \right] + \frac{N-1}{N} \left[\frac{\hat{g}_{11} + 2\hat{g}_{12} + \hat{g}_{22}}{4} \right]$$

$$g_{12} = \frac{1}{N} \left[\frac{1+f}{4} + \frac{\hat{g}_{12}}{2} \right] + \frac{N-1}{N} \left[\frac{\hat{g}_{11} + \hat{g}_{12}}{2} \right]$$

$$g_{22} = \frac{1}{N} \left[\frac{1+f}{2} \right] + \frac{N-1}{N} \hat{g}_{11}.$$

where $\hat{g}_{ij} = k_i k_j g_{ij}$, and f , the inbreeding coefficient of a female, equals $k_1 k_2 g_{12}$. When solved for g_{ij} in terms of N and the k_i , the expressions are quite complicated.

Maternal control

The phenotype of an offspring is determined by its mother's genotype. Suppose I am a female offspring. The coefficient f_{12} between my mother and another random female offspring is the same as the coefficient between my brother and another female offspring, which is g_{12} . And the coefficient between me and my mother is $(1+f+2k_1 k_2 g_{12})/4$, hence the relatedness between two female offspring born on the same patch is

$$R_1 = \frac{4g_{12}}{1+f+2k_1 k_2 g_{12}}. \quad (20)$$

Similarly, the coefficient between a male offspring and the mother of another male offspring is the same as the coefficient between two male offspring [a random gamete from a mother is the same as a random gamete from a random son], and this is g_{22} . Also the coefficient between a male and his own mother is $(1+f)/2$. Hence the relatedness between two males born on the same patch is

$$R_2 = \frac{2g_{22}}{1+f}. \quad (21)$$

The inclusive fitness conditions (10) give us two inequalities of quite a high order in the two unknowns k_i and appear to be analytically intractable. I have generated some solutions by computer, and these are graphed in Fig. 2. Females are seen to have a higher dispersal rate than males, and we can conclude from (10), since k decreases with d , that female patchmates are more closely related than male patchmates. It is notable that for $N \geq 2$, males should not disperse if the cost c is sufficiently

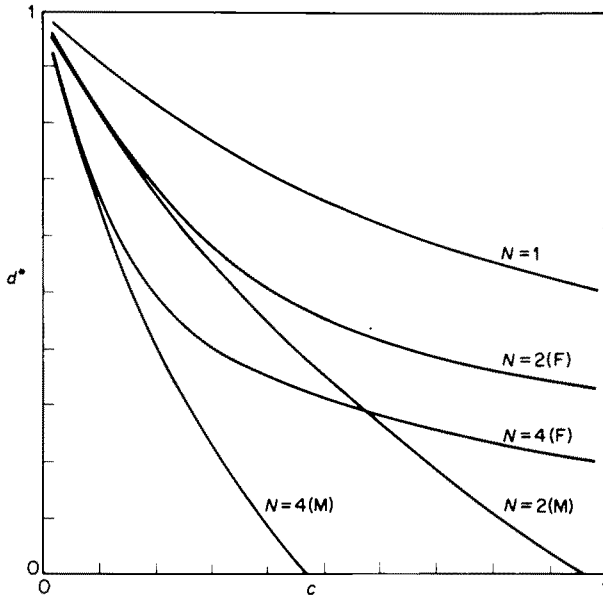


FIG. 2. ESS dispersal rates d^* for female and male offspring (before mating) under maternal control, against cost c of dispersal, for different patch sizes N , in a haplodiploid population. The curves were obtained by computer calculation from equation (10), with R values given by (20) and (21). For $N \geq 2$, the $c = 1$ intercepts are given by (A2).

large. The special case $N = 1$ turns out to be tractible: indeed, both R_i turn out to be 1 (from a mother's point of view all her daughters are equivalent and so are her sons), and (10) solves to give $d_i = 1/(1 + c)$ for both i , the same as in the diploid case.

Offspring control

The phenotype of a female is determined by her own genotype, and the relatedness between two females born on the same patch is

$$R_1 = \frac{2g_{11}}{1+f} \tag{22}$$

and similarly for the males,

$$R_2 = g_{22}. \tag{23}$$

The inclusive fitness condition (10) seems again to be analytically intractible, and some computer-generated solutions are graphed in Fig. 3. It is now the case that for all N , if the dispersal cost c is high enough, males will not disperse. Unlike the case of maternal control, I cannot obtain an explicit solution for the case $N = 1$, but I can calculate the transitional value of c above which males will not disperse: it is $c = (3 + \sqrt{3})/6$ which is approximately 0.79, as illustrated in Fig. 3.

With the intractibility of this case, one looks for special cases that can be solved, and the case $c = 1$, of certain mortality of migrants, is one of these. The mathematical method used is also quite interesting and is presented in the appendix.

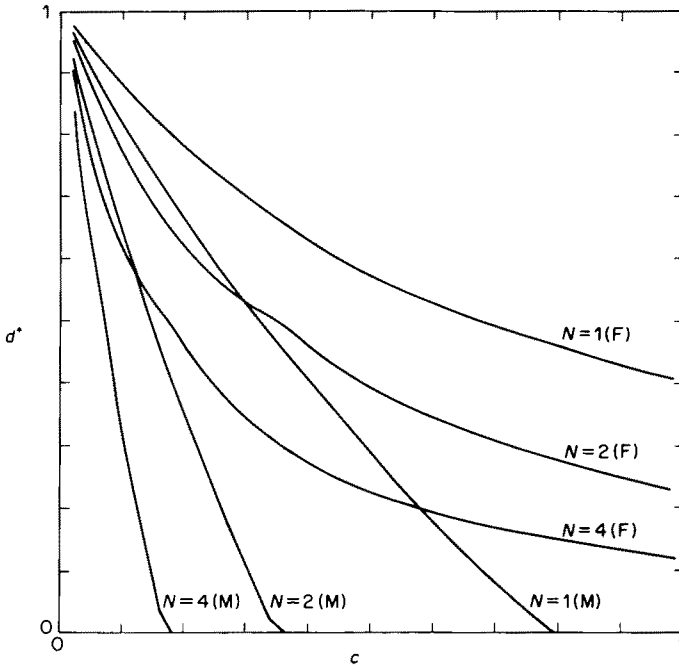


FIG. 3. ESS dispersal rates d^* for female and male offspring (before mating) under offspring control, against cost c of dispersal, for different patch sizes, N , in a haplodiploid population. The curves were obtained by computer calculation from equation (10), with R values given by (22) and (23). For all N , the $c = 1$ intercepts are given by (A3).

4. Discussion

In the population modeled here, at equilibrium, an individual who chooses to disperse will die with probability c and otherwise will establish herself on a patch on which her expected reproductive success is identical to the one she emigrated from. Why, if c is positive, would she want to disperse? The "inclusive fitness" way to answer the question is to observe that by dispersing she improves the reproductive success of all individuals of the same sex that she leaves behind, and if some of these are related to her, then she will improve the fitness of relatives, and this may compensate for her own fitness loss. It is this "altruistic" aspect of dispersal behaviour which makes inclusive fitness a particularly appropriate modeling approach. Not only do the equations of the model (7) and (10) have a simple form, but their interpretation in each instance helps us to understand the exact nature of the selective forces which encourage dispersal behaviour.

The model can be modified to fit other assumptions on genetic and mating patterns. Two interesting examples are found in the diploid models of Hamilton & May (1977) and Motro (1982, 1983). The first of these is identical to my dispersal-before-mating, offspring-control model except the male offspring are required to disperse completely, so that in these models there is no inbreeding. The condition for female dispersal rate d_1 is still given by (10), except R_1 is different from (18). In fact, in

this case,

$$R_1 = \frac{2}{4N - (N-1)k^2}. \quad (24)$$

If we put this into (10), we get the solution of Hamilton & May (1977) for the case $N = 1$, considered by them:

$$d^* = \frac{1-2c}{1-2c^2} \quad \text{for } c < 1/2, \quad (25)$$

otherwise $d^* = 0$.

In Motro's (1983) model, the breeding individuals are diploid hermaphrodites whose male gametes disperse completely, and the problem is to find the dispersal rate d of the fertilized "seeds". This can be seen to be formally equivalent to the model of Hamilton & May (1977), except that the relatedness of two seeds on the same patch is only half of the value in (24). The reason for the difference is that two seeds with the same mother had the same father in the first case, but will have different fathers in the second. The solution for $N = 1$ is

$$d^* = \frac{1-4c}{1-4c^2} \quad \text{for } c < 1/4, \quad (26)$$

as obtained by Motro (1983). Motro was under the impression that since his answer was different from that of Hamilton & May, an inclusive fitness argument would not work for his model, but we now see that what is required is to use the correct relatedness. This has been pointed out by Frank (1986c).

Comparing these outbred models with the diploid models of this paper, we see that one of the effects of outbreeding is to prohibit dispersal when the cost is high, whereas the inbred models show some positive probability of dispersal no matter how large N is or how high the cost. (However, as Figs 2 and 3 show, this is not the case for male dispersal under haplodiploidy with dispersal before mating.)

The value of this paper is not so much that it calculates optimal dispersal rates for particular models, for the models are biologically quite unrealistic, but that it demonstrates that inclusive fitness arguments can provide a simple and unified tool for analyzing a collection of related genetical models. The collection of models studied here all use the same basic ESS condition (7), but the coefficient R of relatedness between patchmates will change as the assumptions of the model concerning control and genetics are varied.

It is important to have a notation for R which reflects these complexities, and I have suggested an extension of the usual notation to include the control individual. The notation $R_{x \rightarrow y}$ of (1) is quite standard and is usually called to the relatedness of y to x (rather than x to y) to bring the terminology into line with that for regression, for when $H_x = G_x$ it is the coefficient of regression of G_y on G_x . In general, it provides the weighting given to G_y relative to G_x by the individual (or "mechanism") controlling the behaviour of x . But when this notation is used it is

important to keep in mind that the mechanism of control must be specified before the coefficient is determined. In practice, this means specifying the way in which the phenotype of x , H_x , depends on the genotype of one or more individuals. In case H_x is a function of G_z for a single individual z , I suggest that the notation $R_{x \rightarrow y}^z$ be used, and in case this function is affine (which means additivity of gene action in z), R is given by (2). I have called this the relatedness of y to x from the point of view of z , and in the absence of selection (Michod & Hamilton, 1980) it can be calculated using coefficients of consanguinity as in (3).

The best way to interpret (3) is with a "gene's eye view". A random gene in z , is trying to decide whether to make x adopt a certain behaviour which will change the fitness of both x and y , and to do this, the gene must assess the overall effect of this behaviour on the propagation of "identical by descent" copies of itself. It calculates the probabilities f_{yz} and f_{xz} that such copies will appear in gametes of y and x , respectively, and it weights the fitness changes of y and x , respectively, with these probabilities, which is the same as saying that it weights y relative to x with their quotient $R_{x \rightarrow y}^z$.

As a striking example of the effect of z on the relatedness coefficient $R_{x \rightarrow y}^z$ of y to x , observe that the relatedness of sibs of the same sex under maternal control (x and y are sibs and z is their mother) is always 1 (clear from (3)), whereas under control of one of the sibs it is typically less than one and under outbreeding is in fact one half. It is really this fact that accounts for the higher relatedness of patchmates under maternal rather than offspring control and hence produces higher rates of dispersal.

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REFERENCES

- BULMER, M. G. (1986). Sex ratio theory in geographically structured populations. *Heredity* **56**, 69-73.
- CHARLESWORTH, B. (1980). Models of kin selection. In: *Evolution of Social Behaviour: Hypotheses and Empirical Tests* (H. Markl, ed.), Weinheim, Verlag Chemie.
- CROW, J. F. & KIMURA, M. (1970). *An Introduction to Population Genetics Theory*. New York: Harper and Row. p. 68.
- FRANK, S. A. (1986a). The genetic value of sons and daughters. *Heredity* **56**, 351-354.
- FRANK, S. A. (1986b). Hierarchical selection theory and sex ratios I. General solutions for structured populations. *Theor. Pop. Biol.* **29**, 312-342.
- FRANK, S. A. (1986c). Dispersal polymorphisms in structured populations. *J. theor. Biol.* **122**, 303-309.
- GRAFEN, A. (1985). A geometric view of relatedness. *Oxford Surveys in Evolutionary Biology* **2**, 28-89.
- GRAFEN, A. (1986). Split sex ratios and the evolutionary origins of eusociality. *J. theor. Biol.* **122**, 95-121.
- HAMILTON, W. D. (1964). The genetical evolution of social behaviour, I and II. *J. theor. Biol.* **7**, 1-52.
- HAMILTON, W. D. (1967). Extraordinary sex ratios. *Science* **156**, 477-488.
- HAMILTON, W. D. (1970). Selfish and spiteful behaviour in an evolutionary model. *Nature* **228**, 1218-20.
- HAMILTON, W. D. (1972). Altruism and related phenomena, mainly in social insects. *Ann. Rev. Ecol. Syst.* **3**, 192-232.
- HAMILTON, W. D. (1975). Innate social aptitudes of man: an approach from evolutionary biology. In: *Biosocial Anthropology* (R. Fox, ed.), pp. 133-55. New York: John Wiley and Sons.
- HAMILTON, W. D. & MAY, R. M. (1977). Dispersal in stable habitats. *Nature* **269**, 578-581.

- MICHOD, R. E. & HAMILTON, W. D. (1980). Coefficients of relatedness in sociobiology. *Nature* **288**, 694-697.
- MOTRO, U. (1982). Optimal rates of dispersal II. Diploid populations. *Theor. Pop. Biol.* **21**, 412-429.
- MOTRO, U. (1983). Optimal rates of dispersal III. Parent-offspring conflict. *Theor. Pop. Biol.* **23**, 159-168.
- PAMILO, P. & CROZIER, R. H. (1982). Measuring genetic relatedness in natural populations: methodology. *Theor. Pop. Biol.* **21**, 171-193.
- PRICE, G. R. (1970). Selection and covariance. *Nature* **227**, 520-521.
- SEGER, J. (1981). Kinship and covariance. *J. theor. Biol.* **91**, 191-213.
- TAYLOR, P. D. (1988a). Inclusive fitness models with two sexes. *Theor. Pop. Biol.* (in press).
- TAYLOR, P. D. (1988b). The equivalence of genetic and inclusive fitness models in structured populations. *Theor. Pop. Biol.* (submitted).

APPENDIX

Under haplodiploidy, the calculation of R in the case of dispersal before mating turned out to be intractable. However the case $c = 1$ of certain mortality of migrants can be solved. I begin by making a general remark about this case. When $c = 1$ there may be emigrants, but there are no immigrants, so each patch is a closed finite population and at equilibrium all alleles in one patch will be identical by descent and the value of all relatedness coefficients will be 1. In this case, as long as there are enough offspring remaining to colonize the patch, it should not matter what the dispersal rate is, and so we do not expect to have an ESS dispersal rate at $c = 1$. Rather what we should be looking for is the *limiting* ESS dispersal rate as c approaches 1.

Checking this out mathematically, when $c = 1$, both k_i are equal to 1, and a glance at the recursion equations shows all g_{ij} to be equal to 1, hence both the relatedness coefficients R_i equal 1. So in fact the d_i do not appear in the inequalities (10) (both sides equal 1). To take the limit as c approaches 1, we set $c = 1 - \varepsilon$ and use the differential approximation:

$$R_i = 1 - \varepsilon R'_i \quad c/k_i = 1 - \varepsilon(c/k_i)'$$

where the prime denotes derivative with respect to c , evaluated at $c = 1$. If we calculate $(c/k_i)'$ and plug into (10) we get that the condition for d_i to increase is

$$R'_i < 1 - \frac{d_i}{1 - d_i}. \quad (\text{A1})$$

This condition is not quite as simple as it looks, because the R'_i depend on both d_j .

In the haplodiploid case, the conditions (A1) can be solved. Under maternal control, we have shown in section 3 that the case $N = 1$ gives $d_i = 1/(1 + c)$ for both i , as in diploidy, and with $c = 1$ we get $d_i = 1/2$. But for $N \geq 2$, the solution to (A1) is

$$d_1 = \frac{6N - 2}{6N^2 + 5N - 3} \quad d_2 = 0. \quad (\text{A2})$$

Asymptotically (for large N), the diploid value of $d_i = 1/2N$ for both i , is the average of d_1 and d_2 in (A2).

Under offspring control, the $c = 1$ solution is

$$d_1 = \frac{3N-1}{6N^2-N} \quad d_2 = 0 \quad (\text{A3})$$

for all N . Asymptotically, the diploid value of $d_i = 1/4N$ for both i , is the average of d_1 and d_2 in (A3).