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DISPERSAL RATES UNDER VARIABLE PATCH DENSITY

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Many species of animals live in discrete groups. This type of population structure is central to studies of behavior, because it engenders interactions among related individuals and a need for dispersal. Several models of subdivided populations in which dispersal rates evolve have been developed (Hamilton and May 1977; Motro 1982, 1983; Frank 1986; Taylor 1988*a*). These authors have concluded that evolutionarily stable dispersal rates depend on interactions among relatives, the costs and benefits of dispersal, and who controls dispersal behavior.

In the above studies, the patches that groups inhabit are assumed to be identical with regard to the resources available for breeding. For natural populations, this assumption is unrealistic. Our purpose is to present an inclusive-fitness model for the evolution of dispersal rates in which patches are allowed to vary in size (total available resources) and density (number of offspring per resource unit) and offspring can assess and respond to variation in patch density and average relatedness to fellow patch mates. An important result of the modeling is that, under certain circumstances, a constant number of offspring are expected to remain in their native patch ("home"), and the rest should disperse. We present data from a laboratory study of wing dimorphism in a colonial thrips supporting this "constant non-disperser" principle.

THE MODEL

The biology of colonial, wing-dimorphic thrips is the inspiration for this model, but the model applies to any species that satisfies its fairly general assumptions. We suppose that the environment comprises a large number of patches, each containing a number of breeding females. Each female produces a large number of offspring, which mature in the patch. At maturity, the male offspring disperse with probability d_m to a random patch, incurring a cost c_m of dispersal. We interpret the cost in terms of viability, though a fertility interpretation is also possible. After this migration phase, mating takes place in each patch, at random between the

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(native) female offspring and the males (both native and immigrant). In our calculations of relatedness, we assume that each female is singly inseminated. After mating, the females disperse with probability d_f to attempt to colonize new patches. The establishment of these new patches is offset by a per-generation mortality μ of existing patches, such that the total number of patches remains constant. The remaining females compete to breed in the patch, and, if the patch survives, then the cycle is repeated.

Note that male and female dispersal play different roles in this model. Male dispersal precedes mating and enhances genetic input into established patches, whereas female dispersal follows mating and enhances the colonization of new patches. This pattern of mating and dispersal has important implications in our choice of relatedness coefficients. To evaluate the reproductive success of a dispersing male against that of a male patch mate, we use the standard coefficient of relatedness. However, to evaluate the reproductive success of a dispersing female against that of a female patch mate, we must also take account of the two mates involved. We therefore use the relatedness between mated females with female control (Taylor 1988*b*, eqs. 4.9 and 5.2, where x and y are mated females and u is the "female part" of x). Male dispersal keeps the patches from approaching a completely inbred state; at equilibrium, the level of inbreeding and the relatedness between patch mates is determined by the male dispersal rate.

The purpose of the model is to calculate the evolutionarily stable values of the dispersal rates, d_f and d_m . We use an inclusive-fitness argument that equates the fitnesses of dispersing and non-dispersing individuals. To compare these fitnesses, we use the *reproductive value* of an individual, which is a measure of the expected number of genes projected into a distant future generation. We use b_i to denote the reproductive value of a non-dispersing offspring of sex i ($i = m$, male; $i = f$, female) and v_i to denote the reproductive value of a dispersing sex- i offspring. The units we choose for reproductive value are the next-generation breeding females (or mates of breeding females) in established patches. Thus, for a non-dispersing female, b_f measures the probability that her offspring will breed successfully in her native patch; and for a dispersing female, v_f measures the probability that she will ultimately establish a patch multiplied by her genetic representation in the breeders in that patch. Both of the v_i incorporate the cost of dispersal, but the male cost, c_m , is the only one that we explicitly name.

In our model, patches are allowed to vary in three ways: *patch size* (the total reproductive resource of the patch), *patch density* (the number of competing offspring of each sex per resource unit), and the average *patch relatedness* between patch mates of the same sex. We think that the latter two factors are the most likely cues for dispersal behavior, and, in the model, we assume that offspring may assess and respond to one or both of these. For each sex- i offspring, we let T_i denote the density of its native patch measured in the number of sex- i offspring per unit of reproductive resource. For a male, we let R_m denote his average relatedness to male offspring native to the same patch; and for a mated female, we let R_f denote her average relatedness to mated females native to the same patch (the native patch of a mated female is the native patch of the female herself). The T_i and R_i are regarded as random variables over the population of

sex-*i* offspring, and our objective is to see how evolutionarily stable dispersal rates depend on these variables. The reproductive values b_i and v_i depend on these variables and on other quantities such as rates of dispersal and male immigration. We begin by formulating general conditions of evolutionary equilibrium. We then suppose that patches are uniform in density and relatedness and calculate how the equilibrium dispersal rates depend on the number of breeding females per patch (N), the cost of male dispersal (c_m), and patch mortality (μ). We then look at the effect, on the dispersal rates, of variation among patches in patch density T_i and relatedness R_i .

Our model uses an inclusive-fitness argument (Hamilton 1964, 1970, 1972). Under certain conditions, the main one being weak selection, such arguments have been shown to give the same equilibrium results as one-locus genetic models (Hamilton 1970; Charlesworth 1980; Seger 1981; Grafen 1985; Taylor 1988*b*, 1989), though stability conditions may not be simple to check.

Calculation of Equilibrium Dispersal Rates

We begin with general equations that compare average reproductive values of dispersing and non-dispersing individuals. Since the number of patches is constant and since all new patches are established by dispersing females, we argue that, in any generation, the proportion of total female reproductive value that lies in dispersing females must be the patch mortality, μ , leaving $1 - \mu$ in non-dispersers, such that

$$E_f(d_f v_f) / E_f[b_f(1 - d_f)] = \mu / (1 - \mu); \quad (1)$$

and for males, we suppose that a dispersing male is in the same position as a non-dispersing male once he has paid the cost $1 - c_m$, such that

$$E_m(v_m) = (1 - c_m)E_m(b_m), \quad (2)$$

where the E_i are expectations over the sex-*i* subpopulation.

Now we formulate the conditions for evolutionary equilibrium of the dispersal rate, which are that the inclusive fitnesses of a disperser and a non-disperser must be equal. We consider different cases depending on whether individuals can assess and respond to patch density T_i and average patch relatedness R_i . For each case, individuals with the same assessment of their environment are said to belong to the same *selective class*, and we assume that selection acts to give them a common optimal dispersal rate.

We first consider females. The inclusive fitness of a non-dispersing mated female is her breeding probability, b_f . By contrast, a dispersing mated female has direct fitness v_f , and, assuming that the number of offspring is large, her act of dispersal allows one extra female to breed in her patch with probability b_f . This component of her fitness must be weighted by her average relatedness R_f to mated females native to the same patch. Thus, the inclusive fitness of a dispersing mated female is $v_f + R_f b_f$.

At equilibrium, the expected inclusive fitnesses of a dispersing and a non-dispersing mated female over each selective class must be equal, such that

$$\hat{E}_f(v_f) = \hat{E}_f[b_f(1 - R_f)], \quad (3)$$

where \hat{E} denotes expectation over a selective class. More precisely, for each selective class, selection favors an increase in dispersal rate d_f if a dispersing mated female has higher inclusive fitness, which means that

$$\hat{E}_f(v_f) > \hat{E}_f[b_f(1 - R_f)]. \quad (4)$$

The argument for males is similar, except that, because of male immigration, the extra male replacing the dispersing male is native to the home patch only with some probability k_m . As a result, the inclusive fitness of the dispersing male is $v_m + R_m k_m b_m$, where R_m is his average relatedness to males native to the same patch. The equilibrium condition for male dispersal is

$$\hat{E}_m(v_m) = \hat{E}_m[b_m(1 - R_m k_m)]; \quad (5)$$

or, more precisely, selection favors an increase in the male dispersal rate, d_m , if

$$\hat{E}_m(v_m) > \hat{E}_m[b_m(1 - R_m k_m)]. \quad (6)$$

We see that dispersal can be thought of as a type of altruistic behavior. For both sexes, dispersing offspring accept a lower fitness (v_i instead of b_i) to allow a relative an increased probability of breeding.

Uniform Patches

If patches are uniform in size, density, and relatedness, then all random variables are constant, and the expectations can be removed from equations (1)–(6). Eliminating v_i/b_i from these equations yields the equilibrium equations

$$d_f = \mu / (1 - R_f + R_f \mu) \quad (7)$$

and

$$R_m k_m = c_m, \quad (8)$$

where equation (7) has been solved explicitly for d_f . Selection favors an increase in the dispersal rates d_f and d_m , respectively, if

$$d_f < \mu / (1 - R_f + R_f \mu) \quad (9)$$

and

$$R_m k_m > c_m. \quad (10)$$

Equation (8) (which was first obtained in Taylor 1988a) is solved by noting that the average number of immigrants per patch is $d_m(1 - c_m)$; hence, the probability that a breeding male is native is

$$k_m = \frac{1 - d_m}{1 - d_m + d_m(1 - c_m)} = \frac{1 - d_m}{1 - c_m d_m}. \quad (11)$$

If equation (11) is inserted into equation (8), we can formally solve for d_m . However, this is not an explicit solution because the relatednesses, R_i , depend on d_m (but not on d_f) in a fairly complicated way. To find the R_i , we must solve a set of recursions for the change in coefficients of consanguinity from one generation to the next (in terms of d_m) and find the R_i from these coefficients. At this point,

the genetic system and the mechanisms of genetic control must be specified. For a haplodiploid genetic system, with offspring control of dispersal, the equations belong to a case of dispersal before mating (explained in Taylor 1988a, p. 372) with $k_f = 1$. When these are solved, the relatedness between males is given as

$$R_m = g_{mm} \quad (12)$$

(Taylor 1988a, eq. 23), and the relatedness between mated females is

$$R_f = (2g_{ff} + F)/(1 + 2F) \quad (13)$$

(Taylor 1988a, eq. 19), where g_{ii} is the coefficient of consanguinity between two sex- i individuals native to the same patch, and F , the inbreeding coefficient, is the probability that uniting gametes are identical by descent. Equations (7) and (8) are then solved numerically; some sample results are plotted in figure 1. As expected, the equilibrium dispersal rates (d_i) decrease with the number of breeding females per patch (N), the male dispersal rate (d_m) decreases with the cost of dispersal, and the female dispersal rate (d_f) increases with patch mortality (μ).

By our inclusive-fitness analysis, the equilibria calculated from equations (7) and (8) are seen to be stable. Indeed, if the female dispersal rate, d_f , falls below its equilibrium value, then inequality (9) holds, favoring an increase in d_f . If the male dispersal rate, d_m , falls below its equilibrium, then, because both male relatedness (R_m) and the probability that a male is native (k_m) are decreasing functions of d_m , inequality (10) holds, favoring an increase in d_m . However, the question of the genetic stability of the equilibrium is more complicated than this (see Taylor 1989).

Variation in Relatedness and Patch Density

We now suppose that there is variation in the average relatedness, R_i , among sex- i offspring from the same patch and in the patch density T_i , the number of sex- i offspring in the patch per unit of available reproductive resource.

No response to variation in relatedness and patch density.—We first observe that this variation per se has an effect on the equilibrium dispersal rates even if individuals are unable to respond to it. Thus, if individuals cannot respond to variation in patch density and relatedness, then the dispersal rates, d_i , are uniform, such that d_f can be taken out of the expectation in equation (1), and equations (1) and (2) provide equations in $E(v_i)/E(b_i)$. Because all sex- i individuals are of the same selective class, the expectations in equations (3)–(6) are over the whole sex- i population and \hat{E} is equivalent to E . But equations (3)–(6) cannot be solved for $E(v_i)/E(b_i)$ without a knowledge of the correlations between the reproductive values, b_i , and the average relatednesses R_f and $R_m k_m$ of a sex- i offspring to the next generation of breeders in its native patch. Only if these correlations are zero can equations (1)–(6) be solved, as in the uniform-patch case, to yield equations (7) and (8). For example, if these correlations were negative, as might be the case if patch density were negatively correlated with the b_i and positively correlated with relatednesses R_i , then the effect would be to lower the equilibrium dispersal rates below the values obtained above in the case of uniform patches.

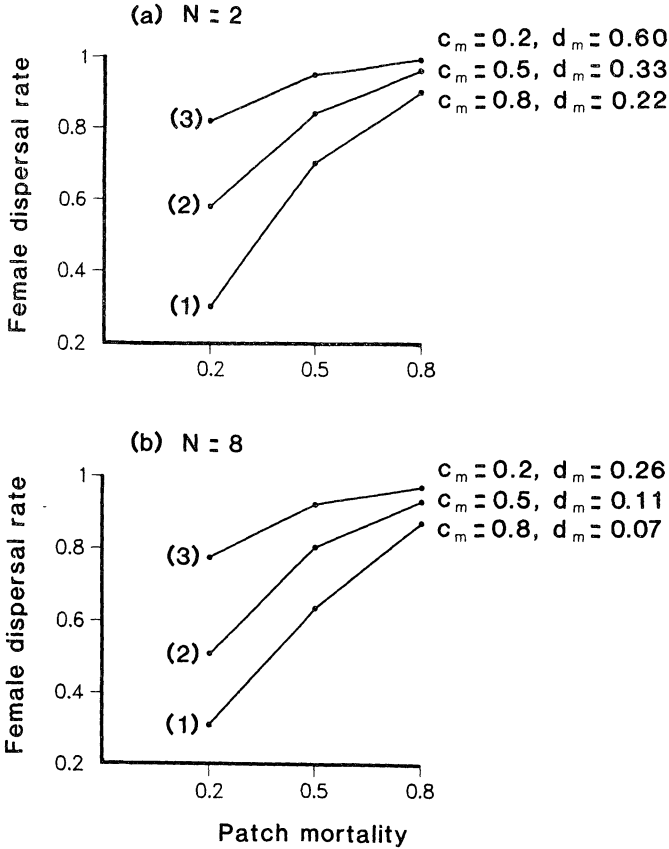


FIG. 1.—The effects of variation in per-generation patch mortality, μ , and male dispersal cost, c_m , on female dispersal rate, d_f , where N is the number of breeding females in each patch. For each plot of d_f against μ , different lines correspond to different costs of male dispersal, c_m . *a*, Female relatedness, R_f , (1) 0.60, (2) 0.82, (3) 0.95; male relatedness, R_m , (1) 0.44, (2) 0.62, (3) 0.85. *b*, R_f , (1) 0.44, (2) 0.76, (3) 0.93; R_m , (1) 0.44, (2) 0.53, (3) 0.81. The male dispersal rate, d_m , and the relatednesses R_i were determined by equation (8); d_f was found from equation (7). The effect of increasing c_m is to decrease d_m , which in turn increases the equilibrium relatedness coefficients, thereby increasing the female dispersal rate, d_f .

Response to variation in relatedness and patch density.—We assume that offspring can respond to the variation in relatedness and patch density, and we examine the effect that this might have on equilibrium dispersal rates. Since the selective class of an individual is determined by his native patch, the expected reproductive value of a disperser, $\hat{E}_i(v_i)$, must be independent of his selective class; thus, from equations (3)–(6), selection acts to render the expected values of

$$b_f(1 - R_f) \quad (14)$$

and

$$b_m(1 - R_m k_m) \quad (15)$$

the same for different selective classes. Instead of focusing on the dispersal rates, d_i , it is useful to look at the number of non-dispersers per unit of reproductive resource, S_i . Moreover, let I_m denote the number of male immigrants to the patch, again per unit of reproductive resource. Then b_f , the reproductive value of a mated female non-disperser, is proportional to $1/S_f$, and b_m , the reproductive value of a male non-disperser, is proportional to $1/(S_m + I_m)$. We therefore conclude from conditions (14) and (15) that selection adjusts the S_i such that the expected values of

$$(1 - R_f)/S_f \quad (16)$$

and

$$(1 - R_m k_m)/(S_m + I_m) \quad (17)$$

are the same over different selective classes, where k_m , the probability that a breeding male is native, is

$$k_m = S_m/(S_m + I_m). \quad (18)$$

Condition (16) implicitly provides the direct response of S_f to variation in R_f , and conditions (17) and (18) implicitly provide the direct response of S_m to variation in R_m and I_m . The signs of these responses are determined from the signs of the partial derivatives of conditions (16) and (17) with respect to the S_i , the R_i , and I_m . The results are that condition (16) decreases in both S_f and R_f and that condition (17) decreases in S_m and R_m . The dependence of condition (17) on male immigration rate, I_m , is more complicated: it increases in I_m if $R_m k_m$ exceeds $1/2$ and decreases otherwise. We note that $R_m k_m$ can be interpreted as the average relatedness of a male offspring to the next generation of male breeders in his native patch. If the male immigration rate is small, this is expected to exceed $1/2$.

It follows from this analysis of signs that, at evolutionary equilibrium, selective classes with relatively high values of relatedness between sex- i offspring must have reduced values of S_i , the number of sex- i offspring remaining at home. Moreover, selective classes with relatively high levels of male immigration, I_m , must have increased values of S_i when $R_m k_m$ exceeds $1/2$ and must have decreased values of S_i otherwise.

These results allow us to determine the direct response of dispersal rate to variation in relatedness and the indirect response of dispersal rate to variation in patch density when this co-varies with either relatedness or male immigration rate. As expected, high relatedness promotes dispersal: the above results provide a direct negative response of S_i , the number of non-dispersers, to average relatedness. If relatedness is low, then small variations in R_i have little effect. However, at least for condition (16), the case of female dispersal, if R_f is close to 1—as it may often be—then small variations in R_f could have a large effect on S_f . For example, an increase in R_f from 0.90 to 0.95 would reduce the number of females staying in the native patch by half.

The effects on dispersal rates of variation in patch density, T_i , depend on how patch density co-varies with relatednesses R_i and male immigration rate, I_m . Suppose first that relatedness and male immigration rate are independent of patch

density. For the relatednesses, this case is expected when variation in offspring density is a transient phenomenon arising through variation in female fecundity or resource density. For male immigration rate, this may occur if dispersal is passive or if males have difficulty locating patches and tend to settle on the first patch that they encounter. It follows from conditions (16) and (17) that selection must provide the same target value of S_i for patches of different density; thus, the average patch density is not correlated with the mean number of offspring staying at home. We state this as an important principle.

The "constant non-disperser" principle.—If the relatednesses R_i and the male immigration rate (I_m) are independent of patch density, then dispersal rates (d_i) in patches of different density (T_i) are such that S_i , the mean number of offspring of each sex staying at home per unit of reproductive resource, is constant.

Now relax these independence assumptions and suppose first that relatedness depends on patch density. From the above relatedness results, if relatedness R_i and patch density T_i are positively correlated, then offspring should respond to high density with reduced values of S_i ; and if relatedness and patch density are negatively correlated, then the response should be opposite. For an example of a positive correlation between relatedness and patch density, suppose that variation in patch density T_i often persists over several generations and that high-density patches have low rates of male immigration and therefore high relatedness.

Second, suppose that male immigration rate, I_m , depends on patch density T_m . From our analysis of condition (17) and equation (18), we conclude that if I_m and T_m are positively correlated, then offspring should respond to high density with increased values of S_m (decreased male dispersal) when $R_m k_m$ exceeds $\frac{1}{2}$. Conversely, if I_m and T_m are negatively correlated, then offspring should respond to high density with decreased values of S_m (increased male dispersal) when $R_m k_m$ exceeds $\frac{1}{2}$. If $R_m k_m$ is less than $\frac{1}{2}$, then the opposite responses are expected. Both positive and negative correlations between male immigration rate, I_m , and patch density T_m are plausible biologically. For example, if potential immigrants are sensitive to patch density and tend to pass up high-density patches, then T_m and I_m would be negatively correlated. Alternatively, we could imagine a positive correlation if the patch population was slow to respond to a sudden local fluctuation in conditions. For example, a sudden increase in the reproductive resource of a patch might create a temporary low density and a temporary low immigration rate, recalling that both of these quantities are measured per unit of reproductive resource. If so, such fluctuations would promote a positive correlation between T_m and I_m .

By the constant-non-disperser principle, if female fecundity is high, if relatednesses R_i and male immigration rate (I_m) are independent of patch density, and if offspring can assess and respond to variation in patch density, then the number of offspring of each sex that stay, per unit of reproductive resource, is constant among patches of different offspring density. Moreover, if offspring can assess and respond to variation in relatedness, then the number of offspring staying in the native patch should decrease with increasing relatedness. Tests of these predictions of the model require a species that satisfies its conditions and that allows for an accurate measurement of dispersal rates.

A TEST OF THE CONSTANT-NON-DISPERSER PRINCIPLE

The species *Hoplothrips karnyi*, a haplodiploid, colonial thrips that lives under bark and feeds on shelf fungi, appears to meet the conditions of the constant-non-disperser (CND) principle and the criterion that dispersal rates be measurable (for information about this and other thrips, see Crespi 1986, 1987, 1988*a,b*). First, since either sex of *H. karnyi* may be winged or wingless, dispersal rates can be measured as the proportion of wingedness among colony offspring. Second, because colonies may persist for many generations, they may approach the equilibrium dispersal situation assumed by the model. Third, the role of male dispersers in this thrips is certainly to seek other established colonies. By contrast, female dispersers probably attempt to found new colonies rather than joining established ones; among field-collected colonies most breeding females are wingless, whereas most pupae and recently eclosed females are winged (Crespi, pers. obs.). Fourth, because thrips are minute insects with fringed wings, they have weak flight abilities, and dispersers probably settle into the first patch that they encounter. Thus, the assumption that relatednesses R_i and male immigration rate, I_m , are independent of patch density is plausible and perhaps even likely. Fifth, colonies of *H. karnyi* show the type of patch variation assumed by the model: colonies vary widely in size and density, and reproduction is restricted to periods when the shelf fungi are moist and growing. Thus, when conditions are good, colonies flourish and produce hundreds of offspring, whereas in poor times colonies contain a relatively small number of nonbreeding adults. Finally, since colonies occasionally may be extinguished by prolonged drought, the pattern of colony mortality assumed by the model may be biologically plausible. The primary uncertainties with regard to the model assumptions are whether mating normally occurs before or after dispersal and whether winged females ever join established colonies.

The study of *H. karnyi* described below was designed to investigate the relationships of foundress number and foundress colony of origin (a presumed indicator of foundress relatedness) with offspring wing morph (macropterous [winged] or brachypterous [wingless]), offspring number, and offspring sex ratio, among laboratory colonies allowed to reproduce for one generation. The data on sex ratios will be discussed elsewhere.

Experimental Methods

The thrips used in this study came originally from two field-collected colonies: colony W, collected October 31, 1986, from a beech (*Fagus grandifolia*) log infested with *Polystictus versicolor* fungus at Warren Woods State Park (Berrien Co.), Michigan; and colony D, collected December 27, 1986, from a black oak log infested with *P. versicolor* at Warren Dunes State Park (Berrien Co.), Michigan, 8 km from colony W. The colonies were maintained separately on pieces of fungus-infested wood in an incubator at 20°C at a photoperiod of 16 h light and 8 h darkness.

On February 16, 1987, several dozen winged females that had molted to adulthood within the last 2 to 7 days were removed from each of the two colonies and

put into petri dishes 9 cm in diameter, each containing several dozen winged males. These two groups of males and females were put under a bright light for 6 h. Under these circumstances, which were intended to simulate dispersal, winged males and females mated readily and often attempted to fly. After mating, the winged females were removed and put, singly or in groups of two (as described below), into sealed petri dishes 9 cm in diameter. Each dish contained one piece of beech wood that was 5 cm in diameter by 0.3–0.4 mm thick and infested with *P. versicolor* fungus cut from the same log.

The colonies were founded with the following combinations of females: one female from colony D, designated 1D ($n = 16$ colonies), one female from colony W (1W, $n = 16$), two females from colony D (2D, $n = 16$), two females from colony W (2W, $n = 16$), and two females, one each from colonies D and W (1D1W, $n = 26$). Three days later, one winged male from colony W was added to each new colony. These males were added to ensure that all females were inseminated, because previous studies showed that some females apparently remain uninseminated even after they have been observed mating during the simulated dispersal. Thus, with this experimental design, females probably mated before dispersal, and mating was commonly observed in the incipient colonies after dispersal.

The colonies were kept at 20°C at a photoperiod of 16 h light and 8 h darkness, and the thrips were allowed to reproduce until all the offspring had reached the pupal stage, 8–10 wk after colony initiation. A new piece of wood was added to each colony after the eggs had begun hatching. Several colonies that became heavily infested with other species of fungi were discarded. After molting to adulthood, the offspring were sexed and their wing morphs were recorded.

In this experiment, patch size was held constant, because colonies inhabited similar pieces of fungus-infested wood. However, patch density varied because of small differences in female fecundity and variation in the number of foundresses (one or two). Relatedness is assumed to vary between the co-founded colonies with foundresses from the same or different colonies of origin, although the magnitude of this difference is unknown.

Variation in Offspring Number, Density, and Wing Morph

The average total number of adult offspring produced in colonies with two foundresses (mean \pm SD, 113 ± 41 , $n = 53$ colonies) was nearly twice that of single-foundress colonies (66 ± 31 , $n = 31$; $t = 5.5$, $P < 0.001$). This variation in offspring number and density with foundress number was caused entirely by variation in the number of winged male and winged female offspring: as predicted by the CND principle, the number of wingless male and wingless female offspring remained constant among colonies with one and two foundresses (table 1). This test of the CND principle is depicted more generally in figure 2. For both males and females, the number of winged individuals increased with total offspring number, but the number of wingless individuals remained approximately the same.

A higher proportion of males and females developed wings in co-founded colonies than in singly founded colonies (see the table). This tendency for off-

TABLE 1
 NUMBERS AND PROPORTIONS OF WINGLESS AND WINGED *HOPLOTHRIPS KARNYI*
 OFFSPRING BY COLONY TYPE

COLONY TYPE	<i>n</i>	WINGLESS		WINGED		PROPORTION WINGED	
		Males	Females	Males	Females	Males	Females
1D	16	10.9 ± 3.5	10.4 ± 8.5	4.3 ± 2.9	50.3 ± 32.2	.28 ± .16	.76 ± .22
1W	15	9.8 ± 5.4	14.7 ± 7.2	4.4 ± 4.7	27.2 ± 23.1	.26 ± .24	.53 ± .32
2D	14	15.0 ± 13.0	8.0 ± 7.6	11.1 ± 8.3	94.9 ± 42.1	.42 ± .29	.88 ± .20
2W	14	11.4 ± 5.9	12.1 ± 9.1	15.1 ± 10.4	71.4 ± 41.7	.54 ± .18	.81 ± .18
1D1W	25	10.4 ± 9.9	9.9 ± 12.9	11.3 ± 8.0	74.5 ± 32.9	.53 ± .25	.87 ± .14
<i>F</i> ratio		0.87	1.00	6.33***	8.38***	5.70***	7.68***

NOTE.—Colony types 1D and 1W were each founded by one female, colony types 2D and 2W were founded by two females from the same natal colony, and colony type 1D1W was founded by two females, one each from different natal colonies. *n* stands for the number of colonies of each type. Values are the mean number of individuals for each colony type and the proportion of each sex that became winged in each colony type, ± 1 SD. Because the proportion winged for each experimental category is an average calculated from within-colony values, it may differ from the proportion winged as determined from average numbers of each sex and wing morph.

*** *P* < 0.001.

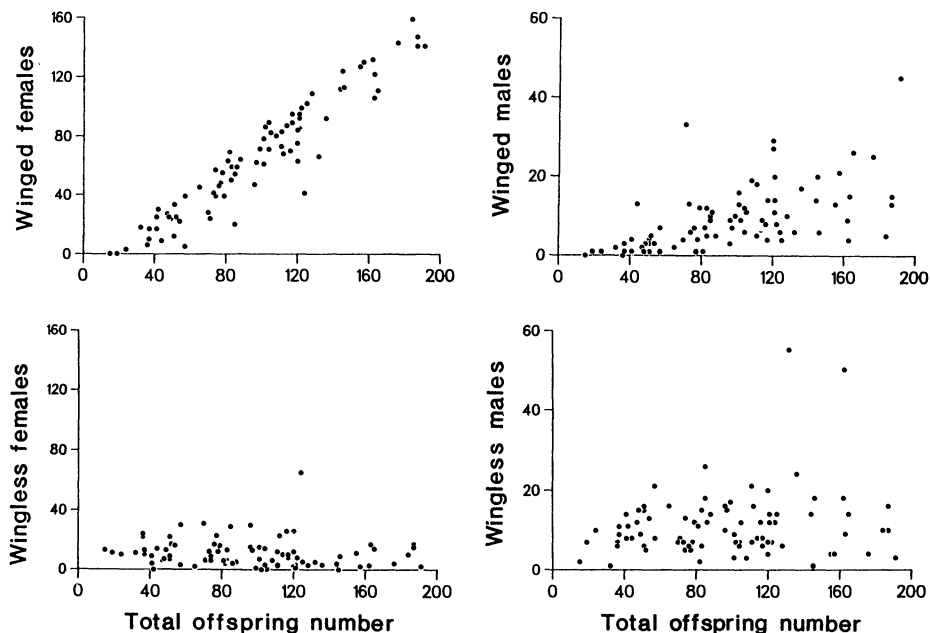


FIG. 2.—A test of the constant-non-disperser principle using the colonial thrips *Hoplothrips karnyi*: the number of individuals of each sex and wing morph versus the total number of offspring in the colony (a measure of offspring density). For comparison between wing morphs, the range of the y-axis is kept identical within each sex.

spring to become winged in co-founded colonies suggests that, as in many other insects (Harrison 1980; Roff 1986), developing offspring use high population density as a cue to become winged. Total offspring number, the indicator of population density in these colonies, was positively correlated with the proportion of females that developed wings in colony types 1D (product-moment correlation, $r = 0.66$, $n = 16$ colonies, $P < 0.01$), 1W ($r = 0.82$, $n = 15$, $P < 0.001$), 2D ($r = 0.69$, $n = 14$, $P < 0.01$), and 2W ($r = 0.54$, $n = 14$, $P < 0.05$), but not in 1D1W ($r = 0.20$, $n = 25$, $P > 0.20$). The proportion of male wingedness was correlated with offspring number in colony types 2D ($r = 0.57$, $P < 0.05$) and 2W ($r = 0.69$, $P < 0.01$), but not significantly so in 1D ($r = 0.49$, $P > 0.05$), 1W ($r = 0.50$, $P > 0.05$), or 1D1W ($r = 0.10$, $P > 0.20$).

For each of the five colony types, a much higher proportion of females than males became winged (paired t -tests, $t > 3.9$, $P < 0.02$ for each colony type; see also table 1). Pooling the data from all colonies, the average proportion of males that became winged in a colony was 0.42 ± 0.26 and the average proportion of females with wings was 0.78 ± 0.24 (paired t -test, $t = 13.4$, $n = 84$, $P < 0.001$).

Variation in Relatedness

If relatedness varies among colonies and offspring can detect and respond to the variation, then a higher proportion of offspring should develop wings where relatedness is higher. In this experiment, however, there was no difference in the proportion of wingedness between colonies with co-foundresses from the same natal colony (males, 0.48 ± 0.24 ; females, 0.85 ± 0.19 ; $n = 28$ for each) and colonies with co-foundresses from different colonies (males, 0.53 ± 0.25 , $n = 25$, $t = 0.8$, $P > 0.05$; females, 0.87 ± 0.14 , $n = 25$, $t = 0.6$, $P > 0.05$).

DISCUSSION

One objective of the mathematical model is to calculate equilibrium dispersal rates in a geographically structured population in which male and female dispersal serve different functions: for male dispersal, to secure matings in other established patches; for female dispersal, to establish new patches. The other objective is to determine how dispersal rates are expected to vary among patches, where relatedness and patch density are not uniform and where offspring can assess and respond to these two aspects of the environment.

For uniform patch size, comparing figures 1a and 1b shows, as expected, that dispersal rates are smaller for large patch size, and this is certainly an effect of lower relatedness within patches. In addition, male dispersal rate increases with decreasing cost, c_m , and female dispersal rate increases with increasing patch mortality, μ . We note that if c_m is greater than zero, there will always be some male dispersal; and if patch mortality, μ , is less than one, there will always be female dispersal. This observation of dispersal behavior even when there is a cost was first discussed by Hamilton and May (1977) with a game-theoretic model.

It is interesting to compare male and female dispersal rates but difficult to make the comparison meaningful, because male and female dispersers are in different

situations with regard to life stage and attendant costs, benefits, and relatedness. One idea is to use the ratios v_i/b_i that measure the relative individual (as opposed to inclusive) fitnesses of a dispersing and a non-dispersing individual. From equations (3)–(6), in the case of uniform patches, these ratios equal $1 - R'_i$, where $R'_f = R_f$ and $R'_m = R_m k_m$ can both be interpreted as the average relatedness between two sex- i individuals (mated females and males) in direct competition for breeding and mating opportunities, respectively. From equation (8), we find that $R'_m = c_m$; thus, the R'_i can be compared from the data in figure 1. We see that v_f/b_f is approximately half the size of v_m/b_m . A dispersing female gives up approximately twice as much as a dispersing male. Of course, a mated female is more closely related to her competitors than is a male, and three factors are at work here: first, the asymmetrical genetics of haplodiploidy lead to increased relatedness among females; second, mated females will be even more closely related than the females themselves if they are related to the two mates; and third, a male's competitors include not only fellow natives but also a certain number of unrelated immigrants.

The response of dispersal rates to variation among patches can be determined from conditions (16) and (17), which demonstrate that the equilibrium values of the number of sex- i offspring staying at home (S_i) are determined, in the first instance, by average sex- i patch relatedness, R_i , and male immigration rate, I_m . The response of S_i to variation in relatedness is negative, as expected: higher relatedness among patch mates increases the threshold for any altruistic behavior, and in particular for dispersal. Second, for males, the response of S_m to the male immigration rate is positive, provided that $R_m k_m$, the average relatedness of offspring to next-generation breeders in the native patch, is high enough (i.e., greater than $1/2$). The response of S_i to any other variable that the offspring can assess and respond to can be determined if we know how this variable correlates with relatedness and male immigration rate.

An important result of the analysis of variation in patch density is that if R_i and I_m are constant among patches, or at least independent of patch offspring density, then the average density of the offspring of each sex remaining at home is constant among patches of different initial offspring density, where "density" means the number of individuals per unit of reproductive resource. We call this the constant-non-disperser (CND) principle, because it predicts that a constant density of offspring that develop in a patch should remain there, and the rest should disperse. If patches are all the same size (in reproductive resources), as for our experimental data, then the CND principle predicts a constant number of offspring staying at home.

The CND principle calls to mind the "constant-male hypothesis" in sex allocation under variable parental investment and local mate competition among males, discussed by Yamaguchi (1985) and Frank (1987). There is an interesting parallel here, because in models of local mate competition a female-biased sex ratio can be considered an altruistic strategy whose cost (the cost of deviating from the Fisherian ratio) is compensated for by increased fitness for the male offspring of relatives (Taylor and Bulmer 1980; Wilson and Colwell 1981). Thus, the constant male effect can be interpreted as a constant level of the "selfish" strategy under

certain types of variation. In our model, the non-dispersing strategy is the selfish one, and this is the strategy that selection adjusts to a constant level.

The CND principle appears to be supported by the data from the colonial thrips *Hoplothrips karnyi*, which shows a constancy of numbers of wingless males and wingless females over a wide variation in total offspring number and density. For both sexes, the positive correlation between offspring number and the proportion of winged thrips is consistent with the hypothesis that natural selection has adjusted the wing-morph-determination pattern to yield such constancy of non-dispersers, with density as the cue. Similar effects of density on the number and proportion of non-dispersers should be found in other species that meet the assumptions of the CND principle.

In the absence of quantitative information about relatedness variation within and among the *H. karnyi* colonies studied here, we hesitate to interpret the similarities in the proportion of wingedness between co-founded colonies with foundresses from the same and different natal colonies. For example, within-colony relatedness may vary little in nature, in which case there would be little or no selection for this form of kin recognition. Strong tests of the dependence of dispersal rates on relatedness levels in this and other species require direct measurement of relatedness using molecular markers. We note, however, that the high proportion of wingedness among females compared with males is consistent with the expected higher relatedness among colony members of this sex (because thrips are haplodiploid), though an explanation in terms of sex differences in costs and benefits is also possible.

SUMMARY

This paper presents an inclusive-fitness model for the evolution of dispersal rates in subdivided populations where patches vary in the density of resources available for breeding and relatedness among patch mates of the same sex. If male and female relatednesses and male immigration rate are independent of patch density, then the model predicts that the mean number of non-dispersers per unit of reproductive resource remains constant among patches. Experimental data from the colonial, wing-polymorphic thrips of the species *Hoplothrips karnyi* support this prediction of the “constant-non-disperser” principle.

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