Reproductive effort in viscous populations

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Abstract

I study a kin selection model of reproductive effort, the allocation of resources to fecundity versus survival, in a patch-structured population. Breeding females remain in the same patch for life. Offspring have costly partial long-distance dispersal and compete for breeding sites becoming vacant upon the death of previous occupants. The main result is that the evolutionarily stable reproductive effort decreases as offspring dispersal rate increases. The result can be understood like this: in a well-mixed population with global competition neither adults nor juveniles compete with relatives, but in a patch-structured population with dispersal restricted to the juvenile phase, juveniles experience relatively less competition with relatives than adults, making juveniles relatively more valuable. Since this asymmetry between adults and juveniles decreases with the dispersal rate, so does the evolutionarily stable level of allocation to fecundity.

Lower genetic exchange through dispersal between neighborhoods leads to more 'viscous' populations (Hamilton 1964; Taylor 1992; Queller 1994) and a higher degree of relatedness between locally interacting individuals. Thus, in viscous populations competition for breeding space or resources tends to be more often between relatives than in non-viscous populations. Will this affect the outcome of natural selection on the division of resources between survival and reproduction by an iteroparous organism?

I study this question here for the following scenario: a population consists of a large number of patches with N breeding sites or territories per patch. The sites are occupied by haploid asexually reproducing females, each producing f surviving offspring per reproductive season. A fraction d of the offspring engage in long-distance dispersal, with cost $0 \leq c \leq 1$. The cost may be due to mortality while migrating, or result from patch natives being dominant in competition for breeding sites. Subsequent to reproduction, females survive with probability S, and if they do they keep their breeding site. Surviving offspring compete for the $(1 - S)N$ sites that become vacant in the patch. Offspring that fail to obtain a site perish. Breeding females face the decision how much effort to invest in their current reproductive attempt versus alternative actions that may affect their expected future reproductive output. Total investment or reproductive effort E determines a female's survival $S = S(E)$, and the number of surviving offspring $f = f(E)$. I assume that survival of a mother and her offspring is not directly affected by the neighbors' effort. This assumption would be violated when, say, neighbors share a common limited resource pool and higher effort by one's neighbors reduces the amount of resources available to oneself. Rather, reproductive effort of neighbors has an effect only through the number of competing offspring produced as a result of that effort.

Will selection favor an increase, decrease or no change in reproductive effort as population viscosity (determined by d) increases? The correct answer is an increase. The intuition behind this result may be stated as follows: in a well-mixed panmictic population neither adults nor juveniles compete with relatives, whereas in a patch-structured population with dispersal restricted to the juvenile phase, juveniles are less likely to compete with relatives than adults. This makes juveniles relatively more valuable. This asymmetry in kin competition between adults and juveniles decreases

as the tendency for juveniles to disperse increases, hence allocation to fecundity by adults decreases with juvenile dispersal.

The model

I assume that all females in the population are identical in the sense that for a given reproductive effort E they all have the same expected survival $S(E)$ and fecundity $f(E)$, independently of age or any other "state" variable. As a result, genes affecting reproductive effort are in demographic equilibrium (randomly distributed with respect to state) within the span of one season. A female's direct fitness (as opposed to inclusive fitness; see Frank 1997) is therefore the number of her direct descendents (including herself) that obtain a breeding site in the next season. The direct fitness of a female can be written as the sum of three fitness components. The first component is the probability she will keep her own site which is given by her survival probability $S(E)$. The second fitness component is the expected number of breeding sites obtained by her non-dispersing offspring. This is given by the number of non-dispersing offspring, $(1 - d)f(E)$, multiplied by the expected number of empty breeding sites per competing offspring. The expected number of empty sites in the focal patch is given by $(1 - \bar{S})N$, where $\bar{S}$ denotes the average survival of breeding females in the focal patch. The total number of competing offspring in the focal patch is given by the total number of non-dispersing offspring produced in the focal patch, $N(1 - d)\bar{f}$, where $\bar{f}$ denotes the average fecundity of females in the focal patch, plus the expected number of offspring dispersed from elsewhere, $N(1 - c)df^*$, where f^* denotes the population average fecundity. The number of empty breeding sites per competing offspring is therefore given by the quotient

$$p(\bar{E}, E^*) = \frac{1 - \bar{S}}{(1 - d)\bar{f} + (1 - c)df^*} \ . \tag{1}$$

Note that N has canceled out of this expression. The second fitness component can now be written as $(1 - d)f(E)p(\bar{E}, E^*)$. The third fitness component, the number of breeding sites obtained by a female's dispersing offspring, is given by the number of dispersing offspring she produces, $df(E)$, multiplied by the probability that a dispersing offspring reaches a random patch, $(1 - c)$, multiplied by the ex-

pected number of empty breeding sites per offspring in a random patch, $p(E^*, E^*)$: $(1 - c)df(E)p(E^*, E^*)$. Summing the three fitness components, we get the following expression for the direct fitness of a female with reproductive effort E in a patch with average reproductive effort $\bar{E}$ in a population with average reproductive effort E^*:

$$W(E, \bar{E}, E^*) = S + \frac{(1 - d)f}{(1 - d)\bar{f} + (1 - c)df^*}(1 - \bar{S}) + \frac{(1 - c)df}{(1 - cd)f^*}(1 - S^*) \,. \quad (2)$$

I assume that $\bar{S} = S(\bar{E})$, $S^* = S(E^*)$, $\bar{f} = f(\bar{E})$ and $f^* = f(E^*)$. This is a good approximation as long as within-patch and between-patch variance in reproductive effort is small: $E[g(x)] \approx g(\bar{x}) + \frac{1}{2}\text{Var}(x)g''(\bar{x})$, a prime denoting differentiation. This assumption is consistent with the usual assumptions of an ESS analysis, in which the evolutionary stability of a monomorphic population is assessed by repeatedly introducing rare mutants with behavior deviating slightly from the monomorphic population behavior.

The equilibrium condition

Let R be the relatedness between a breeding female and all breeding females (including herself) in the same patch. The direct fitness equilibrium condition (Taylor and Frank 1996; Frank 1997) for an evolutionarily stable reproductive effort E^* is given by

$$\left(\frac{\partial W}{\partial E} + R\frac{\partial W}{\partial \bar{E}}\right)_{E = \bar{E} = E^*} = 0 \,. \quad (3)$$

This condition expresses the notion that a small change in a female's reproductive effort affects her fitness via two pathways. The first partial derivative measures the effect of a change in a female's own reproductive effort on her fitness. It is given by

$$\frac{\partial W}{\partial E} = S' + (1 - S)\frac{f'}{f} \quad (4)$$

In a panmictic population (with $R = 0$), the evolutionarily stable reproductive effort is a root of this equation. In a viscous population, however, a change in a female's reproductive effort will be accompanied by a correlated change in the reproductive effort of other females in the patch. Local interactions cause the change in reproductive effort of other females in the patch to affect the fitness of the focal female. This

is measured by the second term in (3):

$$R\frac{\partial W}{\partial \bar{E}} = -Rh\left(S' + h(1-S)\frac{f'}{f}\right),$$ (5)

where

$$h = \frac{1-d}{1-cd}$$ (6)

represents the probability that an individual in the patch was born there. The equilibrium condition (3) as a whole can now be written as

$$\left(S' + (1-S)\frac{f'}{f}\right) = Rh\left(S' + h(1-S)\frac{f'}{f}\right).$$ (7)

Main result: informal proof

The equilibrium condition (7) contains information about how the evolutionarily stable reproductive effort E^* covaries with the other life history parameters in the model. I am specifically interested in the relationship between E^* and the offspring dispersal rate d. In this section I present an informal analysis, relying on visual inspection of the equilibrium condition and an educated guess. The next section contains a more formal analysis.

Note from (7) that both sides must be negative. Since $0 < h < 1$ and fecundity increases with effort ($f' > 0$), the factor between parentheses on the right is smaller than the left-hand side. Because $0 < Rh < 1$ it follows that both sides of (7) are negative. In particular, $\partial W/\partial E < 0$. From this we can conclude that the evolutionarily stable reproductive effort in a viscous population is larger than in a panmictic population, because in a panmictic population we must have $\partial W/\partial E = 0$ and $\partial^2 W/\partial E^2 < 0$. Since a viscous population approaches a panmictic population as the dispersal rate increases, it seems safe to conjecture

Main result. *The evolutionarily stable reproductive effort decreases with offspring dispersal rate.*

The reason why the stable reproductive effort is higher in a viscous population than in a panmictic population is because in a viscous population offspring are relatively more valuable. This can be seen by writing the equilibrium condition (7) in a slightly different way:

$$(1 - Rh)\frac{S'}{1 - S} + (1 - Rh^2)\frac{f'}{f} = 0 \ . \tag{8}$$

The factor $1/(1 - S)$ can be interpreted as the reproductive value of a surviving female relative to a reproductive value $1/f$ of a surviving offspring. The first term in (8) is then seen to represent the marginal cost of reproduction $S'/(1 - S)$ in units of female's reproductive value times the weighing factor $(1 - Rh)$. Similarly, the second term in (8) represents the marginal benefit of reproduction f'/f in units of offspring reproductive value times a different weighing factor, $(1 - Rh^2)$. The offspring's weighing factor is larger than the female's weighing factor because the probability of being native to the patch $h < 1$. Hence, in a viscous population $(R > 0)$, offspring have a relatively higher value than in a panmictic population $(R = 0)$. The weighing factors can be interpreted as probabilities of *not* competing with individuals carrying identical genes at the effort-determining locus. Rh is the probability that genes in a random offspring competing for a given female's breeding site are identical by descent to the female's genes. Hence, $1 - Rh$ is the probability that this is not so. Likewise, $1 - Rh^2$ is the probability that genes in two offspring competing for the same site are not identical by descent.

Main result: formal proof

The informal analysis in the last section may have yielded some intuitition as to why reproductive effort in a viscous population is likely to be higher than in a panmictic population, but it remains to be shown that reproductive effort decreases in a monotone fashion with the dispersal rate. That is, it remains to be shown that $\mathrm{d}E^*/\mathrm{d}d < 0$. The sign of $\mathrm{d}E^*/\mathrm{d}d$ can be calculated by implicitly differentiating the equilibrium condition (7) with respect to d. Writing $G(E^*, d)$ for the left-hand side of (7), we obtain

$$\frac{\mathrm{d}E^*}{\mathrm{d}d} = -\frac{\partial G/\partial d}{\partial G/\partial E^*} \ . \tag{9}$$

In order for E^* to be convergence stable (Taylor 1996), the denominator of the right-hand side must be negative. Convergence stability means that in a population close to E^*, selection favors those mutants that are even closer to E^*. Hence, assuming that E^* is convergence stable, the sign of dE^*/dd must equal the sign of $\partial G/\partial d$. Since the first term between parentheses in (7) is independent of d, the sign of $\partial G/\partial d$ equals the sign of

$$
\begin{aligned}
&-\frac{\partial}{\partial d}Rh\left(S' + h(1-S)\frac{f'}{f}\right)\\
&= -\frac{\partial R}{\partial d}h\left(S' + h(1-S)\frac{f'}{f}\right) - R\frac{dh}{dd}\left(S' + 2h(1-S)\frac{f'}{f}\right)
\end{aligned}
\tag{10}
$$

>From the equilibrium condition (7) we get that

$$
S' = -(1-S)\frac{f'}{f}\frac{1-Rh^2}{1-Rh} \; .
\tag{11}
$$

Plugging into (10), dividing by the positive factor $(1-S)f'/f$ and multiplying by $1-Rh$ yields

$$
h(1-h)\frac{\partial R}{\partial d} + R\left(1 - 2h + Rh^2\right)\frac{dh}{dd} \; .
\tag{12}
$$

It is difficult to see what the sign of this expression is without an exact expression for $\partial R/\partial d$. In the appendix it shown that

$$
R = \frac{1}{N - (N-1)h^{\frac{h(1-S)+2S}{1+S}}} \; ,
\tag{13}
$$

and we get

$$
\frac{\partial R}{\partial d} = 2\frac{dh}{dd}R^2(N-1)\frac{h(1-S)+S}{1+S} \; .
\tag{14}
$$

Substitution in (12) yields the greatly simplified expression

$$
\frac{dh}{dd}\left(\frac{1-h}{1+(N-1)(1-h)}\right)^2 \; ,
\tag{15}
$$

hence dE^*/dd has the same sign as

$$
\frac{dh}{dd} = -\frac{1-c}{(1-cd)^2} < 0 \; ,
\tag{16}
$$

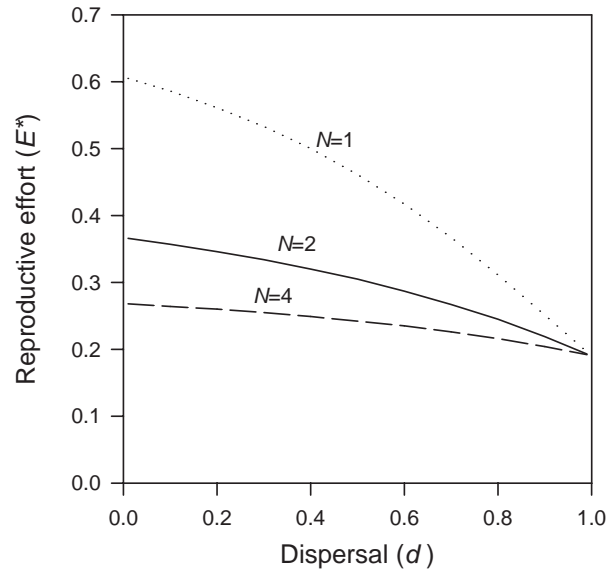which completes the proof of the main result.

Figure 1: Optimal reproductive effort in relation to dispersal rate for several patch sizes N. Functions and parameters: adult survival $S(E) = 0.9(1 - E)^{1/2}$; offspring survival $f(E) = E^{1/2}$; cost of dispersal $c = 0.5$.

Example and simulation results

Figure 1 depicts a specific example of the relationship between optimal reproductive effort and dispersal rate. Optimal reproductive effort decreases with dispersal rate, but the relationship becomes weaker quite quickly as patch size increases. In order to check the analytical results, I implemented the patch-structured population in an individual-based computer simulation model, where reproductive effort was coded for by a single haploid locus. The simulated population consisted of 500 patches, genes mutating to slightly different 'values' with a rate of 10^{-3} per generation. Relatedness was estimated as the least squares linear regression coefficient between genetic values of two random females drawn with replacement from each patch. Figure 2 shows that the analytical predictions of relatedness and reproductive effort closely match the
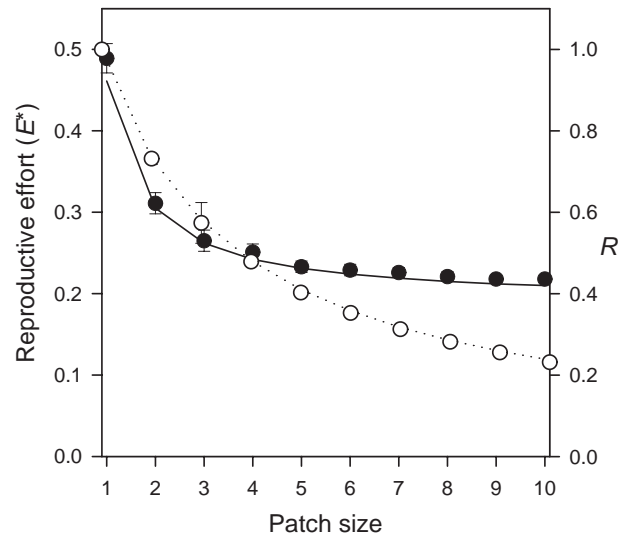
Figure 2: Optimal reproductive effort (solid line) and local relatedness (dashed line) in relation to patch size N, predicted by analytical model. Adult and offspring survival and cost of dispersal as in figure 1, dispersal $d = 0.5$. Dots represent outcomes of simulation model, error bars representing standard deviations over 10 simulations; solid dots reproductive effort, open dots relatedness.

averages of 10 simulation runs after 5000 generations.

Discussion

I have shown here that in a patch-structured population, given a trade-off between survival and fecundity, the optimal allocation of resources to fecundity decreases with offspring dispersal rate. The kin selection approach adopted here clarifies the nature of the selective forces that affect reproductive effort in a geographically structured population. If a proportion of the offspring engages in long-distance dispersal to a random patch, the rest remaining at the native patch, then two related offspring are less likely to compete for the same breeding site as an offspring and a related

adult. Hence, lower adult survival reduces local competition between relatives more strongly than the increase in local competition caused by higher offspring survival. Since reproductive effort has opposite effects on adult and offspring survival, higher local relatedness selects for higher reproductive effort.

The problem studied here resembles that of sex allocation in a patch-structured population with differential dispersal between the sexes (Bulmer and Taylor 1980). Compared to optimal sex allocation in a population with global competition, the optimal sex allocation in a patch-structured population is more biased towards the most dispersing sex because this tends to reduce local competition between relatives. In the model of this paper, offspring are analogous to the most dispersing sex and breeding females analogous to the least dispersing sex. Clearly, both examples are special cases of the general expectation that when competition is partially local, an individual should allocate relatively fewer resources to the type of offspring (a surviving female can be regarded as a kind of offspring of herself) with the higher amount of local competition.

Ronce and Olivieri (1997) recently published a paper on the evolution of reproductive effort in a metapopulation. The biology and population structure in their models matches my model exactly, except that they included the possibility of local extinctions and ecological succession. By means of analytical ESS models they conclude that, contrary to the results presented here, if all breeding sites in a patch are always occupied, then dispersal has no effect on the evolutionary stable reproductive effort. The reason for the discrepancy seems to be that their analytical models ignore the effect of local relatedness, or equivalently, assume effectively infinitely large patches. By means of a simulation model, Ronce and Olivieri conclude that their analytical models tend to underestimate the stable level of reproductive effort and in their simulations reproductive effort decreases with dispersal rate, consistent with my results. But as I have shown here, as long as subpopulations are not too large, a negative relationship between dispersal rate and reproductive effort does not necessarily require 'local demographic disequilibrium' due to local extinctions or ecological succession, but may also be attributed to variation in the degree of local relatedness. It might be interesting to combine the kin selection approach adopted here with the extinction/succession approach of Ronce and Olivieri to investigate the relative importance

of the different processes for optimal reproductive effort.

An important assumption in the model presented here is that surviving adults always keep their breeding site. In other words, density dependence is assumed to affect juveniles only. This is a common assumption in models of life history evolution (e.g. Charnov 1993), but it may affect the outcome of the analysis (Mylius and Diekmann 1995). The assumption seems reasonable for most plant species, but for animals its validity is probably less general.

Is there any empirical evidence that could be used to test the predictions of the model? A potential problem is that many confounding variables might affect selection on both dispersal and reproductive effort. This could lead to spurious correlations between the two traits. For example, in populations inhabiting highly disturbed areas with high mortality rates, there may be selection for higher fecundity and a higher dispersal rate at the same time. A comparison between populations in disturbed and undisturbed areas would reveal a positive correlation between reproductive effort and dispersal, contradicting the prediction of this paper. This is in fact found in many plant species (see Ronce and Olivieri 1997 and refs therein), although there are also studies on plants that support the prediction (Venable and Levin 1983). A better way to test the logic of my results might be to use laboratory metapopulations of, say, Drosophilids, with known genetic variation for fecundity, where dispersal patterns are under full control of the experimenter.

Acknowledgments

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Appendix. Calculation of relatedness

The relatedness between an "actor" performing an action and a "recipient" affected by the action is usually defined as the regression coefficient of recipient phenotype on actor genotype (Michod and Hamilton 1980). The coefficient may be non-zero due to common genealogy, but also due to external factors such as a shared environment (Frank 1997). However, for the present purpose I exclude the latter possibility.

Recall that R actually measures the average relatedness between a female and all other females in the patch, *including herself.* However, I find it easier to work with the relatedness between *different* females, denoted by R_d. First I derive R_d and then compute R as

$$R = \frac{1}{N} + \frac{N-1}{N} R_d \; . \tag{A1}$$

The first term on the right is the probability that by drawing two females at random and with replacement from the same patch, the same female is drawn twice, weighed by a relatedness of unity. The second term on the right is the probability that two different females are drawn, weighed by an average relatedness of R_d, which is a solution of the recurrence relation

$$R_d = S^2 R_d + 2S(1-S)h\left(\frac{1}{N} + \frac{N-1}{N} R_d\right) + (1-S)^2 h^2 \left(\frac{1}{N} + \frac{N-1}{N} R_d\right) \; . \tag{A2}$$

The first term on the right is the probability that two random females are both surviving breeders from the previous season, weighed by their relatedness. The second term represents the probability $2S(1-S)$ that a surviving breeder and a surviving offspring are drawn, multiplied by the probability h that the offspring is native to the patch, multiplied by the probability that the offspring is either an offspring of the survivor (probability $1/N$, relatedness 1) or not (probability $1 - 1/N$, relatedness R_d). The final term is the probability $(1-S)^2$ that two surviving offspring are drawn, times the probability h^2 that both are native to the patch, times the probability that they are sibs (probability $1/N$, relatedness 1) or not (probability $1 - 1/N$, relatedness R_d). The calculations yield

$$R = \frac{1}{N - (N-1)h\frac{h(1-S)+2S}{1+S}} \; . \tag{A3}$$