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## Metapopulation extinction and genetic variation in dispersal-related traits

Olof Leimar and Ulf Norberg

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When the suitable habitat for a population is fragmented into relatively isolated patches, an individual's probability of success in interpatch migration may become low. If, in addition, the local demes inhabiting the patches experience random extinctions, the persistence of the entire metapopulation can be threatened. A reduction in migration success results in natural selection, and given genetic variation in dispersal-related traits, fragmentation may be followed by a change in dispersal behaviour and capacity, which in turn can influence the persistence of the metapopulation. Using computer simulation, we investigate the consequences of genetic variation in dispersal-related traits for the probability of extinction following fragmentation. We find that within-deme selection against dispersal can set off a critical phase, during which the patch occupancy is low and the risk of extinction high. In this manner, genetic variation can pose a threat to persistence. However, if a metapopulation recovers from the critical phase, through recolonization of empty patches by efficient dispersers, the ensuing persistence tends to be higher than would have been the case without genetic variation. The severity of a critical phase depends on factors like the rapidity of the fragmentation process and the magnitude of the drop in survival.

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It is generally recognized in conservation biology that habitat fragmentation may pose a threat to the long-term persistence of a population. One quite likely but rather little studied consequence of a fragmentation event is an episode of natural selection acting on dispersal capacity and behaviour. Our intention here is to investigate whether such selection tends to reduce the probability of extinction of a metapopulation, or if it instead makes extinction more likely.

For a population divided into demes restricted to patches of suitable habitat, and where each deme has a finite life-time because of events like random local extinctions or successional transformations, interpatch dispersal must be a component of a long-term viable life-history strategy. A number of factors are known to influence how much an organism should invest in dis-

persal (Johnson and Gaines 1990), one being the probability of success in a dispersal attempt. A high chance of success tends to favour an inclination to disperse, insofar as dispersal can be achieved without much cost, but a very low chance of success can also select for dispersal-related traits (Comins et al. 1980). When a small but nonzero chance of spreading its copies in space is a gene's only possibility for long-term representation, a heavy dispersal investment in the face of low odds is one expected evolutionary outcome, the alternative outcome being extinction.

To put this dichotomy into a conservation perspective, consider a fragmentation event where some region originally contains many suitable patches with correspondingly small interpatch distances, and then most patches are destroyed so that interpatch distances in-

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crease substantially, sharply reducing the probability of successful dispersal. If the original metapopulation contains sufficient genetic variation in dispersal-related traits, the selection imposed by the fragmentation event may, given that the population escapes extinction, produce a response in the form of greater propensity for and investment in dispersal. Although the dispersal strategy emerging in this way might not be the one maximising the long-term persistence of the population under the new, less favourable conditions (Roff 1975, Comins et al. 1980), such a response would still tend to enhance persistence. This then suggests that genetic variation in dispersal-related traits should lower the probability of extinction of a metapopulation.

However, the process of establishment of a metapopulation whose members invest more heavily in dispersal may contain a relatively brief but critical phase where most patches become empty, and the risk of extinction during this phase could be enhanced by the very same genetic variation that makes possible the evolution of higher investment in dispersal. Within a deme surviving the fragmentation event, genes for dispersal-related traits will decrease in frequency, both because individuals with stronger tendencies to disperse leave the deme and because traits enhancing the capacity to disperse, such as an efficient flying apparatus, will trade off with juvenile survival and adult reproductive potential (Roff and Fairbairn 1991). Selection for dispersal instead occurs among demes (Van Valen 1971), and its most important component may be the founding of new demes by migrants arriving in empty patches. A sequence of such founding events can produce demes where genes for enhanced investment in dispersal have become fixed or have reached a very high frequency, and these demes can then act like seeds of a new metapopulation. The process may require that most of the old demes first go extinct, opening up a supply of empty patches, but if the old demes are the main sources of migrants the process might fail, because the old demes become fewer and less able to send out migrants. This would then be the critical phase, where the metapopulation runs a high risk of extinction.

The components entering into this scenario are all well known from previous theoretical and empirical research. Following Van Valen (1971), the distinction between selection within and among demes has been one of the main themes of theories of the evolution of dispersal (e.g., Roff 1975, 1994, Järvinen and Vepsäläinen 1976, Comins et al. 1980, Levin et al. 1984, Olivieri et al. 1995). In particular, Roff (1975) found that selection on dispersal-related traits could cause a population to go extinct. There are also a number of observations showing that genetic variation in dispersal-related traits is common (Wilson 1995, Dingle 1996, Roff 1996), that members of old and new demes differ genetically in their dispersal strategies (Wallace 1953, Den Boer 1970, Stein 1977, Olivieri and Gouyon 1985),

and that adaptations for dispersal usually have a cost in reduced juvenile survival and adult reproductive potential (Roff and Fairbairn 1991). Nevertheless, the question of how genetic variation in dispersal-related traits influences the probability of extinction following a fragmentation event appears not to have been considered previously.

Here we study this problem by simulating a fragmentation event in a model metapopulation, following the approach of Roff (1975, 1994). In general, habitat fragmentation involves both a reduction in the total number of available patches and a reduction in inter-patch migration survival. Since the phenomenon of a critical phase ought to depend mainly on the latter aspect, we use the simplification of a fixed number of patches, and simulate fragmentation as a reduction in the probability of successful dispersal between these patches. We then investigate how the probability of extinction is influenced by such factors as the distribution of genotypes prior to fragmentation, the number of available patches, and the rapidity and severity of the fragmentation process. As a further simplification, we consider only a single two-allele locus, which could be regarded as a simplified description of the genetics of a wing-dimorphic insect, although our results could have relevance also in other situations, such as with quantitative inheritance of dispersal-related traits.

Our conclusion is that genetic variation in dispersal-related traits can have a strong effect on extinction probabilities. Over the very long term, the presence of genetic variation tends to be beneficial since it allows the evolution of a more persistent metapopulation, but the risk of extinction during the selective process leading to this state can be quite sensitive to the original genotypic distribution and the rate of fragmentation, varying from near certain extinction to a very high probability of continued existence.

## The model

Of previous modelling approaches, our treatment is most similar to the development by Roff (1975, 1994). Consider a metapopulation existing on a square grid of  $L \times L$  patches, each of which may support a deme. Dispersal is of the 'stepping stone' kind, from a patch to one of its four nearest neighbours. However, migrants moving out of the metapopulation, from patches on the edges of the grid, are considered to be lost; an interpretation could be that there is no suitable habitat outside of the grid. A fragmentation event is modelled by letting the probability of migration survival change from an initial fairly high value to a lower value, either abruptly or in a more gradual fashion. One could think of this as a technically simple way of mimicking a situation where some patches are destroyed, leading to an increase in the average interpatch distance.

Time is divided into discrete periods (years), and there is one generation per time period. With a certain probability  $q$  a patch may become uninhabitable during a period, and the resulting local extinctions are uncorrelated over time and between patches. For concreteness, we may think of a univoltine insect overwintering as egg or early instar larva, and with local springtime conditions varying so that with probability  $q$  all juveniles present in the patch die. When the patch stays habitable, the emerging adults are subjected to density regulation, with a maximum of  $K$  adults emerging in the patch.

There are two possible phenotypes, each characterized by a tendency to migrate, a migration survival, a juvenile survival, and a reproductive capacity. The low and high dispersal phenotypes have the respective probabilities  $M$  and  $m$  of attempting migration out of the patch before reproducing, with equal chance of leaving in each of the four possible directions, and the corresponding probabilities of migration survival are  $S$  and  $s$ . The probabilities of survival from juvenile to adult of the two types are  $V$  and  $v$ , ignoring density regulation. Given an opportunity to reproduce in a patch which stays habitable, they have the capacities of producing  $F$  and  $f$  next-year juveniles, respectively. The inequalities  $M \leq m$ ,  $S \leq s$ ,  $V \geq v$ , and  $F \geq f$  express that the high dispersal phenotype has invested in dispersal capacity, such as wing muscles, at the cost of reduced juvenile survival and/or fecundity.

An individual's phenotype is determined by the genotype at a single locus with two alleles,  $A$  and  $a$ . The genotypes  $AA$  and  $Aa$  produce the low dispersal phenotype and the genotype  $aa$  produces the high dispersal phenotype. The reason for assuming the low-dispersal allele  $A$  to be dominant is that this agrees with the observed genetics of a number of wing-dimorphic insects (Roff and Fairbairn 1991).

Mating takes place prior to dispersal. As a simplification we do not explicitly model two sexes, but rather assume that an individual's offspring are formed by the union of one of its own gametes with one from a pool of gametes produced by all adults in the deme. Although such hermaphroditism would be unrealistic for many animals, the assumption is unlikely to influence the results in any important way, and can be regarded as an approximation of a situation where the individuals considered are females, with an equal number of males being produced in a patch.

## Description of the simulation

The stochastic events in the simulation are the local patch extinctions, the individual decisions whether and in which direction to migrate, and the subsequent migration survival. In addition, the genotypic distribution among the adults emerging in a patch is drawn from an

expected genotypic distribution, thus allowing for genetic drift. However, we ignore within-patch demographic stochasticity: provided that a patch stays habitable, the number of emerging adults is given by deterministic density regulation acting on the expected production of the previous-period adults.

Consider a particular patch and time period, and let  $N^{(1)}$  be the expected number of emerging current period adults, ignoring density regulation. If the patch becomes uninhabitable or lacked reproductive adults in the previous period we have  $N^{(1)} = 0$ . In other cases we can compute  $N^{(1)}$ , as well as the expected frequencies

$$(P_{AA}^{(1)}, P_{Aa}^{(1)}, P_{aa}^{(1)}) \quad (1)$$

of the three genotypes among these adults, from the expected fecundity and clutch genotypic distribution of each of the previous-period adults, together with the genotype-specific juvenile survival.

Density regulation could take place through competition between growing juveniles, but for simplicity we may think of it as happening at the time of emergence. The number of actually emerging adults in the patch is the smallest of  $N^{(1)}$  and  $K$ ,

$$N^{(2)} = \min\{N^{(1)}, K\} \quad (2)$$

so that no more than  $K$  adults can emerge. For the simulations, the value obtained from (2) is rounded to achieve an integer number of adults.

The genotypic distribution among the emerging adults is then taken to be multinomially distributed with expected frequencies given by (1), so that the genotype of each of the  $N^{(2)}$  emerging adults is randomly assigned from the distribution (1). Splitting the emerging adults into the three genotypes, we have

$$N^{(2)} = N_{AA}^{(2)} + N_{Aa}^{(2)} + N_{aa}^{(2)}, \quad (3)$$

with the frequency of the low dispersal allele  $A$  given by

$$p_A = (N_{AA}^{(2)} + \frac{1}{2}N_{Aa}^{(2)})/N^{(2)}. \quad (4)$$

The emerging adults mate randomly within the patch. Mating is modelled so that the genotype of each offspring produced by an individual from the patch is formed by combining a random allele from the individual's own genotype with a random allele from a local gamete pool with allele frequency specified by eq. (4). The expected distribution over offspring genotypes, expressed in the form  $(P_{AA}, P_{Aa}, P_{aa})$ , in the clutches of each adult genotype is then

$$\begin{aligned} AA: & (p_A, 1 - p_A, 0) \\ Aa: & (\frac{1}{2}p_A, \frac{1}{2}, \frac{1}{2} - \frac{1}{2}p_A) \\ aa: & (0, p_A, 1 - p_A). \end{aligned} \quad (5)$$

Note that the expected genotypic distribution in the clutch of a migrant individual is determined by the allele frequency (4) in the patch of emergence.

After mating, individuals with the low and high dispersal phenotype have the probabilities  $M$  and  $m$  of leaving the patch, randomly selecting one of the four possible directions. For emigrants staying within the borders of the grid of patches, the probabilities of safely arriving in a neighbouring patch are  $S$  and  $s$ . After migration out of and into the patch is completed, it will contain  $N^{(3)}$  reproducing adults, divided into genotypes:

$$N^{(3)} = N_{AA}^{(3)} + N_{Aa}^{(3)} + N_{aa}^{(3)}.$$

Letting  $G$  denote  $AA$ ,  $Aa$ , or  $aa$ , the numbers of three genotypes are given by

$$N_G^{(3)} = N_G^{(2)} - N_G^{em} + N_G^{im},$$

where the  $N_G^{em}$  are the (binomially distributed) number of emigrants of the different genotypes, and the  $N_G^{im}$  are the number of immigrants arriving safely from neighbouring demes. The expected number of next-generation juveniles in the patch is

$$N^{(4)} = F(N_{AA}^{(3)} + N_{Aa}^{(3)}) + fN_{aa}^{(3)},$$

given that the patch stays habitable. The expected genotypic distribution among these next-period juveniles,  $(P_{AA}^{(4)}, P_{Aa}^{(4)}, P_{aa}^{(4)})$ , is obtained as the fecundity-weighted average of the distributions (5) for each of the  $N^{(3)}$  reproducing current-period adults in the patch. Note that for the immigrants into the patch, the clutch genotypic distribution is influenced by the allele frequency (4) in their patch of emergence. Taking into account juvenile survival but ignoring density regulation, we then obtain the expected number of next-period emerging adults as

$$N^{(1)}(t+1) = [V(P_{AA}^{(4)}(t) + P_{Aa}^{(4)}(t)) + vP_{aa}^{(4)}(t)]N^{(4)}(t),$$

where  $t$  denotes the current time period. The expected genotypic distribution among these next-period adults, corresponding to (1) above, is proportional to

$$(VP_{AA}^{(4)}(t), VP_{Aa}^{(4)}(t), vP_{aa}^{(4)}(t)).$$

All patches are taken to have the same probability  $q$  of local extinction and the same density regulation (2) with carrying capacity  $K$ . A fragmentation simulation with the two phenotypes, specified by  $M$ ,  $S$ ,  $V$ ,  $F$  and  $m$ ,  $s$ ,  $v$ ,  $f$ , is then performed by starting with some more or less arbitrary situation where all patches contain  $K$  reproducing adults and all three genotypes are present. After a number of time periods

with high migration survivals  $S = S_0$  and  $s = s_0$ , allowing any effects of the particular starting conditions to decay, the migration survivals are lowered to  $S_1$  and  $s_1$ , either abruptly or gradually, and the fate of the metapopulation is followed for a considerable number of time periods. The whole procedure is replicated many times, to estimate the probability of extinction and other characteristics of the metapopulation.

### Approximate condition for persistence

For the interpretation of the simulations, it will be helpful to have an approximate analytic condition for persistence of a metapopulation where all individuals use the same fixed dispersal strategy. This type of problem has been studied in some detail previously (e.g., Lande 1987), but here we will limit ourselves to a very simple approach.

Let  $\hat{m}$ ,  $\hat{s}$ ,  $\hat{v}$ , and  $\hat{f}$  be the migration probability, migration survival, juvenile survival, and reproductive capacity of the phenotype in question, and consider a situation where all patches are empty. Introduce a single reproducing adult into one of the patches away from the edges of the grid. With probability  $1 - q$  the adult's offspring will emerge the next season, whereupon the deme will have an expected life-time of  $1/q$ . Thus, the expected number  $E$  of successful emigrants from a deme formed in this manner, summed over its time of existence, is

$$E = (1 - q) \frac{1}{q} \bar{N} \hat{m} \hat{s}, \quad (6)$$

where  $\bar{N}$  is the average of number of adults before dispersal during the life-time of a deme initiated by a single reproductive individual. Instead of deriving a formula for  $\bar{N}$  we simply note that it must lie between  $\hat{v}$  and  $K$ , will be fairly close to the carrying capacity for high reproductive capacity and/or long expected life-time of the deme.

For the metapopulation to have any chance of long-term persistence, the total number of successful emigrants from such a deme must exceed one, which would lead to the condition  $E > 1$  for persistence. However, with nearest neighbour dispersal the occupied patches tend to occur in clusters, even when most patches are empty. In such a case some of the successful emigrants will arrive in already occupied patches, which does rather little to increase the persistence of the metapopulation. A somewhat more realistic condition would be  $E > 2$ , which is sufficient to maintain a relatively sparse metapopulation on a grid containing many patches, in which on average half of a deme's nearest neighbour patches are empty. With fewer patches, somewhat larger values of  $E$ , resulting in a higher proportion of

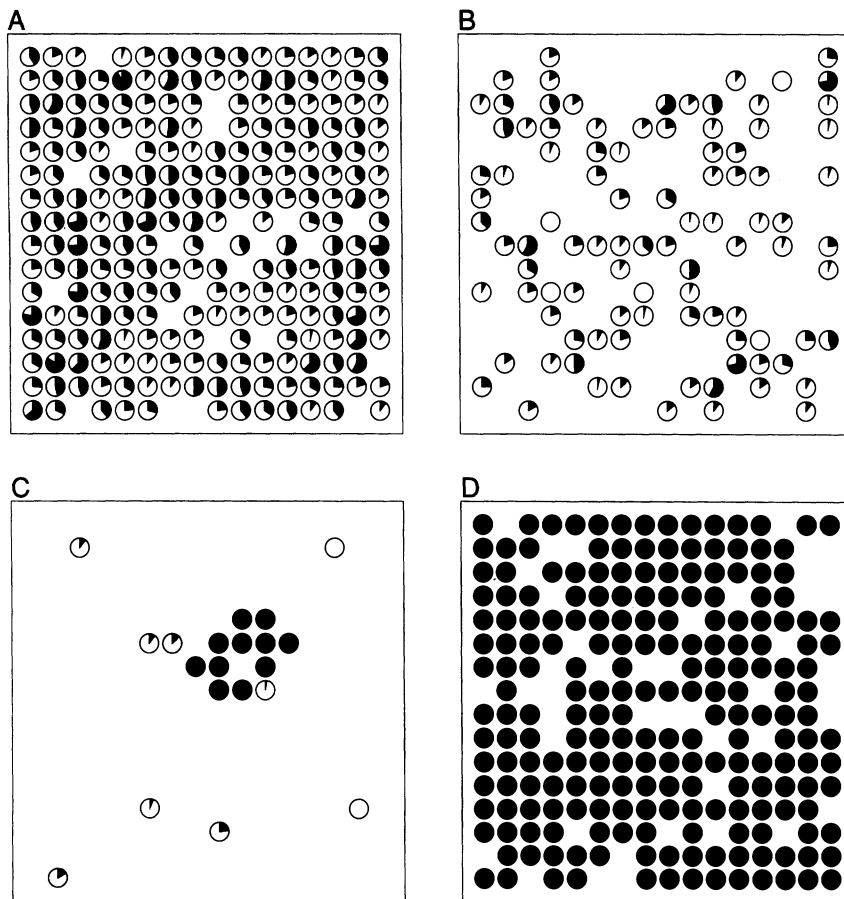


Fig. 1. A depiction of a simulated metapopulation at four points in time, before, during, and after a critical phase produced by an abrupt reduction in migration survival. At each occupied patch of the  $16 \times 16$  grid, there is a pie diagram with the white part corresponding to the local frequency  $p_A$  of the low dispersal allele. Each patch has the same carrying capacity and the same probability of becoming uninhabitable during a season. The four points in time are immediately before the reduction in migration survival (A), ten generations later (B), 35 generations later (C), and 200 generations later (D).

occupied patches, are needed for persistence. Note also that with finitely many patches eventual extinction is guaranteed regardless of dispersal strategies, for instance because all patches can simultaneously become uninhabitable, although the time until such unavoidable extinction will be extremely long except for a very low number of patches.

## Results

To concretely visualize the possible effect of a rapid fragmentation, four snapshots of the time course of a simulation on a rather large grid of patches is shown in Fig. 1. Each patch has a carrying capacity of  $K = 50$  adults and becomes uninhabitable during a season with probability  $q = 0.1$ . The two phenotypes differ in dispersal-related traits and in juvenile survival but, for simplicity, are assumed to have the same reproductive capacity. We may think of the low dispersal type as having poorly developed wings and the high dispersal type as an efficient flier. Before a reduction in migration survival, the low dispersal phenotype ( $M = 0.1$ ,  $S_0 = 0.3$ ,  $V = 0.1$ ,  $F = 50$ ) can easily maintain the metapopu-

lation on its own; a numerical computation for eq. (6) leads to  $\bar{N} = 43.0$  and thus  $E = 11.6$ . The high dispersal phenotype ( $m = 0.5$ ,  $s_0 = 0.9$ ,  $v = 0.075$ ,  $f = 50$ ), which on its own would give  $\bar{N} = 31.8$  and  $E = 128.7$ , has a 25% lower juvenile survival but is quicker at exploiting empty patches. The net effect is a statistical equilibrium where both phenotypes are present (Fig. 1A). The metapopulation average of the frequency  $p_A$  of the dominant low dispersal allele (eq. [4]) is about 61%, and about 9% of the individuals have the high dispersal genotype  $aa$ . Since empty patches are most often colonized by high dispersers, there is substantial interdeme allele frequency variation, with older demes tending to have a higher  $p_A$ .

An abrupt fragmentation event is then introduced by changing  $S$  to  $S_1 = 0$ , so that the low dispersal type no longer has any chance of success in migration, and by lowering  $s$  to  $s_1 = 0.05$ . Fig. 1B shows the situation 10 generations after this event, corresponding to the average life-time,  $1/q$ , of a deme. Because of the lower migration survival, recolonization has not kept up with local extinction, and there is also a more pronounced interdeme allele frequency variation. As more and more of the demes dominated by low dispersers go extinct,

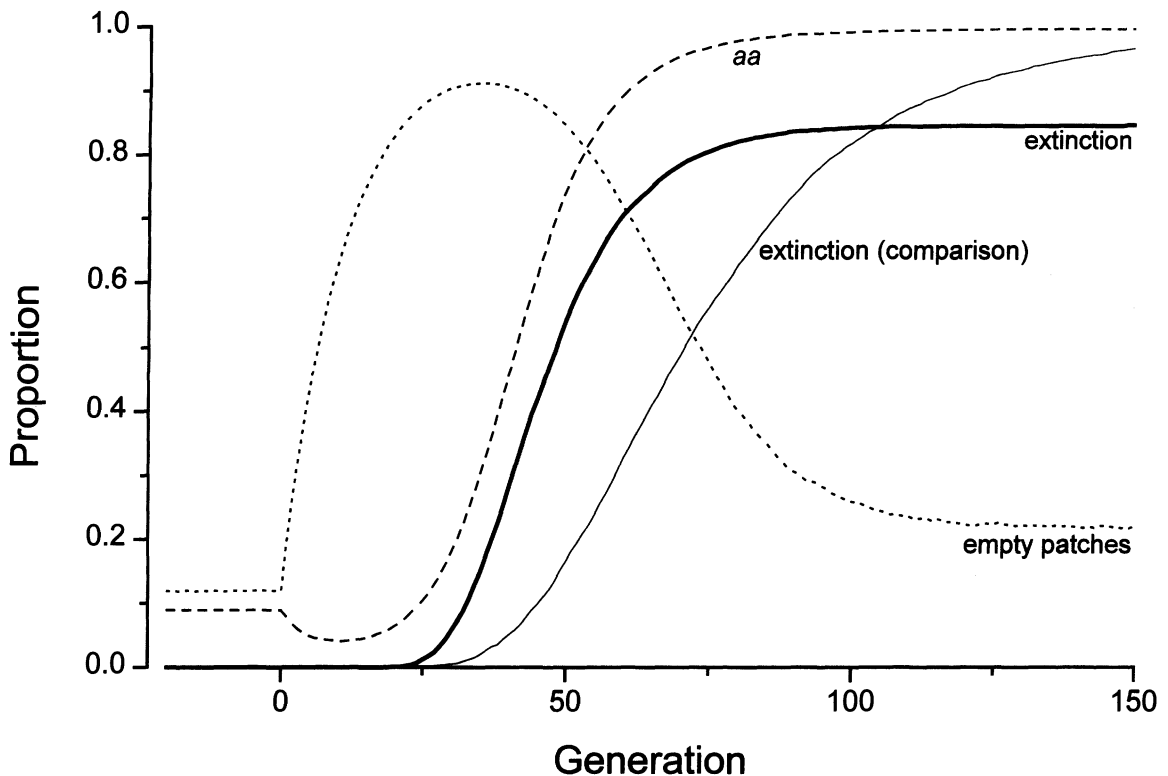


Fig. 2. The curves show the proportion of the high dispersal genotype *aa* (dashed curve), the proportion of empty patches for non-extinct metapopulations (dotted curve), and the accumulated probability of extinction (thick solid curve), following an abrupt reduction in migration survival at time zero. The additional curve (thin solid) shows the accumulated probability of extinction for a comparison metapopulation without genetic variation. The curves are the averages over 10 000 replicates. The initial migration survivals of the two phenotypes,  $S_0 = 0.3$  and  $s_0 = 0.9$ , are reduced to  $S_1 = 0$  and  $s_1 = 0.05$ . Other phenotypic parameters are  $M = 0.1$ ,  $V = 0.1$ ,  $F = 50$  and  $m = 0.5$ ,  $v = 0.075$ ,  $f = 50$ . The parameters of each of the  $7 \times 7$  patches in the grid are  $K = 50$  and  $q = 0.1$ .

small clusters of demes fixed for the high dispersal allele *a* have a chance to form, and Fig. 1C shows such a cluster at 35 generations after the fragmentation event. Even with the lowered migration survival, the high dispersal type has  $E = 7.1$  and is thus quite capable of maintaining the metapopulation. As shown in Fig. 1D, after 200 generations the high dispersal type has recolonized the grid of patches. Once the high dispersal type has gained a sufficient foothold, the metapopulation will persist essentially forever, but it may still go extinct during the critical phase illustrated in Fig. 1C. Even for the fairly large grid of  $16 \times 16$  patches in Fig. 1, there is about 31% chance of metapopulation extinction following the fragmentation event.

Extinction occurs when a region of empty patches extends to cover the entire grid. For a very large grid, a critical phase would appear as a reduction in patch occupancy, with empty regions surrounding clusters of occupied patches, although the entire metapopulation might be safe from extinction. The smaller the grid, the more likely it is that the entire grid becomes empty.

So, with the same two phenotypes as in Fig. 1 but a somewhat smaller grid of patches, the risk of extinction

becomes substantially higher. Fig. 2 shows the averages over many replicates of simulations on a  $7 \times 7$  grid. The same abrupt reduction in migration survival as in Fig. 1 has been used, and about 85% of the metapopulations go extinct during the critical phase. Following the fragmentation event, there is first a decline in the overall frequency of the high dispersal type, reflecting the within-deme selection. Lagging slightly behind this decrease, there is an increase in the proportion of empty patches and in the probability of extinction. For those metapopulations escaping extinction, there is then an increase in the frequency of the high dispersal type, followed by a recapturing of most of the empty patches, after which there will be essentially no additional extinction. Note also that the curves in Fig. 2 are the averages over many simulations with varying outcomes, and thus tend to smooth out the critical phase somewhat.

To further illustrate the influence of genetic variation, Fig. 2 also shows the probability of extinction for a comparison metapopulation without genetic variation. For the comparison case there is only one genotype, but each emerging adult is randomly determined

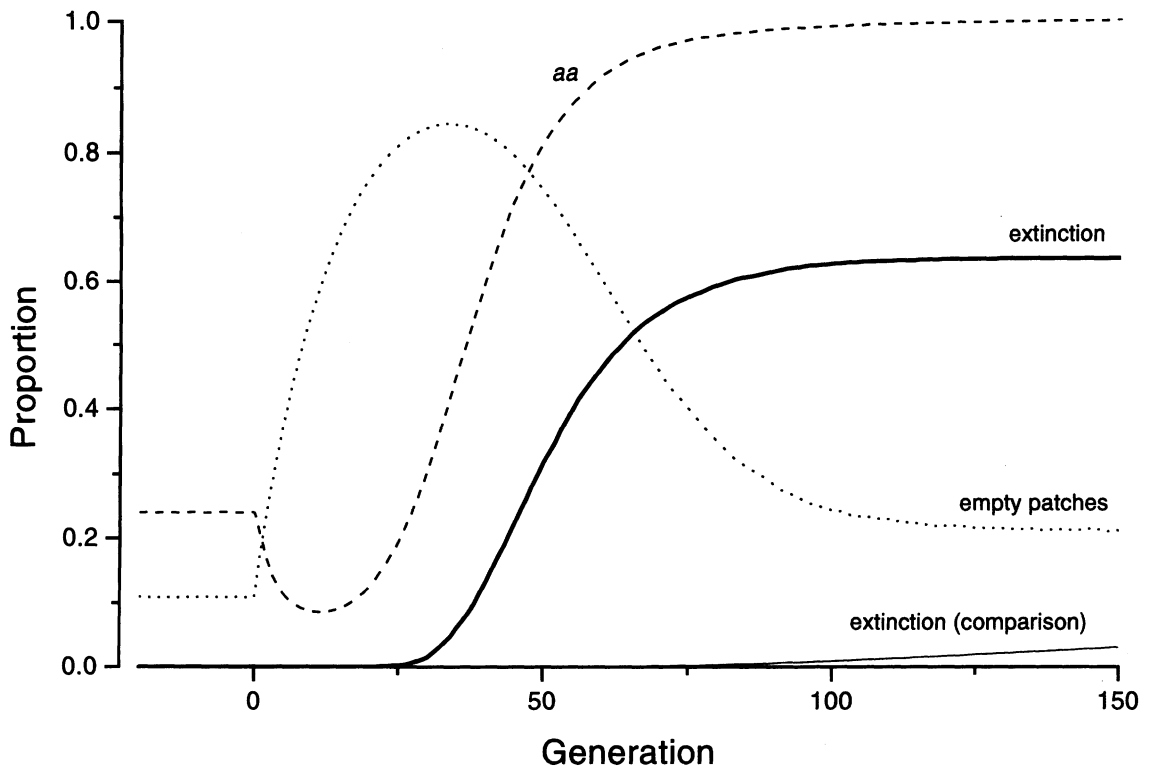


Fig. 3. Same as Fig. 2, except that the low dispersal phenotype does not attempt dispersal ( $M = 0$ ,  $V = 0.1$ ,  $F = 50$ ) and the high dispersal phenotype has a slightly better juvenile survival ( $m = 0.5$ ,  $v = 0.08$ ,  $f = 50$ ), leading to a greater equilibrium proportion of the high dispersal genotype  $aa$  for  $s_0 = 0.9$  prior to fragmentation, at which time  $s$  is reduced to  $s_1 = 0.05$ . The curve depicting the accumulated probability of extinction for the comparison metapopulation will intersect the corresponding curve for the case with genetic variation at about 1300 generations after the reduction in migration survival.

to be either a low or a high dispersal type, in a way leading to the same overall proportions of the two types as for the pre-fragmentation equilibrium with genetic determination of the dispersal strategy. After the reduction in migration survival, a comparison metapopulation is not able to maintain itself; the number of successful migrants corresponding to eq. (6) will be slightly less than one for the mixed phenotype. However, the process of extinction is more gradual, without any critical phase. Up to about 105 generations after fragmentation the comparison metapopulation has a lower probability of extinction than the one with genetic variation, after which the two extinction curves in Fig. 2 cross. The one for the comparison case approaches complete extinction, and the one for the case with genetic variation approaches 0.85. This indicates that the degree of heritability of dispersal-related traits influences both the time course and the long-term probability of extinction.

One reason for the high probability of extinction in Fig. 2 is the rather low frequency of the high dispersal type prior to fragmentation, only 9%, necessitating a large shift in genotypic frequencies following fragmentation. Changing the parameter values so that the low dispersal type no longer attempts to migrate ( $M = 0$ ),

thus making  $S$  irrelevant, and giving the high dispersal type a slightly better juvenile survival ( $v = 0.08$ ), leads to about 25% of the high dispersal genotype  $aa$  before fragmentation (Fig. 3). As shown in Fig. 3, the effect of an abrupt reduction in migration survival from  $s_0 = 0.9$  to  $s_1 = 0.05$  is somewhat milder than in Fig. 2; about 64% of the metapopulations go extinct during the critical phase. Again looking at a comparison metapopulation, having no genetic variation but the same overall frequencies of the two types as in the pre-fragmentation equilibrium with genetic variation, illustrates that genetic variation can sometimes be quite detrimental to persistence (Fig. 3). The number of successful migrants corresponding to eq. (6) for the mixed phenotype is slightly above two in this case. For a large grid this would ensure more or less unlimited persistence, but for the  $7 \times 7$  case in Fig. 3 there will be some extinction. For times after fragmentation longer than about 1300 generations, the comparison metapopulation will have a greater probability of extinction than the one with genetic variation in dispersal-related traits.

The severity of the critical phase produced by fragmentation depends on the speed of reduction in migration survival. As shown by the top curve in Fig. 4, the same total reduction in migration survival which causes

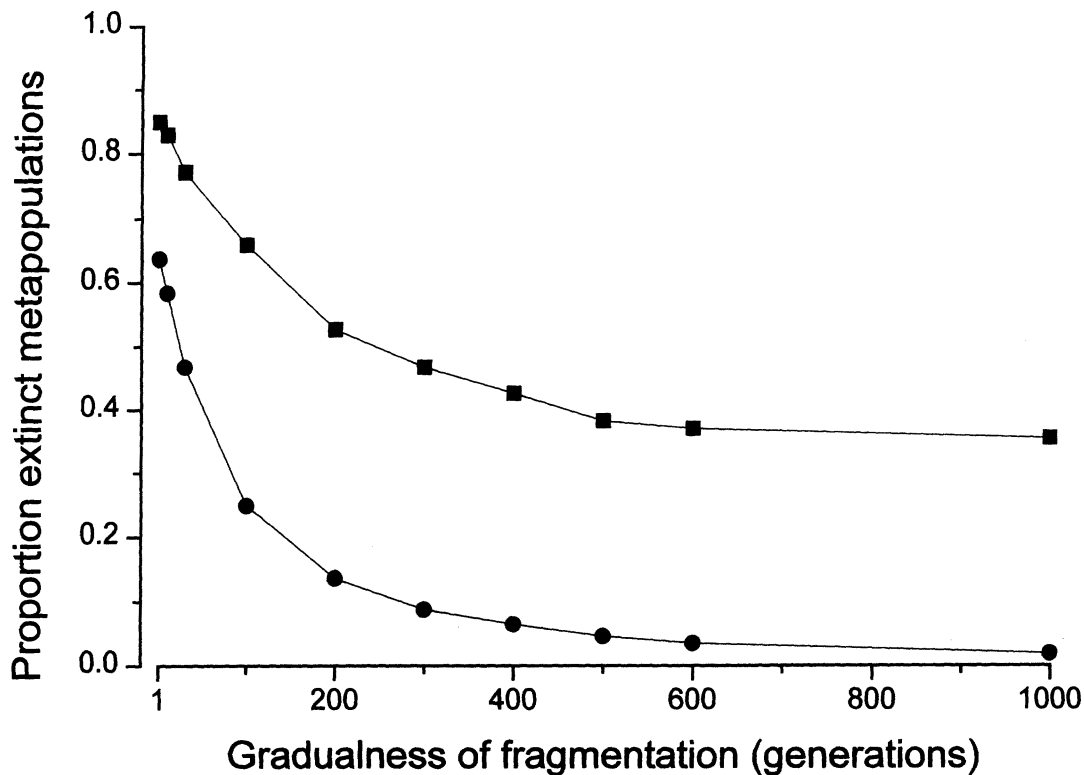


Fig. 4. Probability of the metapopulation being extinct at 300 generations after completion of a more or less gradual reduction in migration survival. The upper curve (squares) corresponds to the case in Fig. 2, and the lower curve (circles) to Fig. 3. A gradual reduction is achieved by spreading the same total reduction evenly over a number of generations. The points are based on 10 000 replicates.

85% extinction when applied abruptly, as in Fig. 2, poses less of a threat to persistence if it occurs very gradually. For the parameter values used to compute this curve, a certain fraction of the metapopulations will go extinct even in the limit of an extremely gradual fragmentation. The reason is that the metapopulations must pass through a critical stage with fairly extensive spatial fluctuations, which is most pronounced when the migration survivals reach  $S = 0.025$  and  $s = 0.12$ . For the bottom curve in Fig. 4, illustrating the effect of making the abrupt fragmentation for the case in Fig. 3 more gradual, these spatial fluctuations are less strong, and almost all metapopulations persist if the reduction in migration survival occurs at a slow enough rate. A further point to note about Fig. 4 is that for the gradualness of a fragmentation to significantly decrease the probability of extinction, the reduction in migration survival must be spread out over times about as long as the duration of the critical phase produced by an abrupt reduction.

Naturally, the magnitude of the drop in migration survival influences the probability of extinction following an abrupt fragmentation event. Fig. 5 illustrates this effect by varying the post-fragmentation migration survival  $s_1$  for the two cases corresponding to Figs 2 and 3. The values of  $s_1$  in Fig. 5 for which extinction has

become unlikely are also the ones where the low and high dispersal types both remain at appreciable frequencies in the metapopulation following fragmentation. In these cases there is still somewhat of a critical phase, in the form of an increase in the proportion of empty patches soon after fragmentation, but it is too weak to pose much of a threat to persistence.

We have assumed the low dispersal allele  $A$  to be dominant, and this is in accordance with observation for wing dimorphic insects with single-locus morph determination (Roff and Fairbairn 1991). However, it is worth noting that a critical phase of the kind shown in Fig. 1 can appear also for other patterns of genetic determination. In fact, if one instead assumes the high dispersal allele  $a$  to be dominant, the critical phase tends to become more severe. For instance, for the case shown in Fig. 3, the probability of extinction following fragmentation becomes 94% instead of 65% when the high dispersal allele is made dominant. Furthermore, extending the  $7 \times 7$  grid of this example up to  $20 \times 20$  patches still produces about 48% metapopulation extinction, showing that very large regions of patches become empty during the critical phase. The reason is that, with dominance of the high dispersal allele, successful migrants are often heterozygous, carrying the low dispersal allele along to new patches, where it tends to take

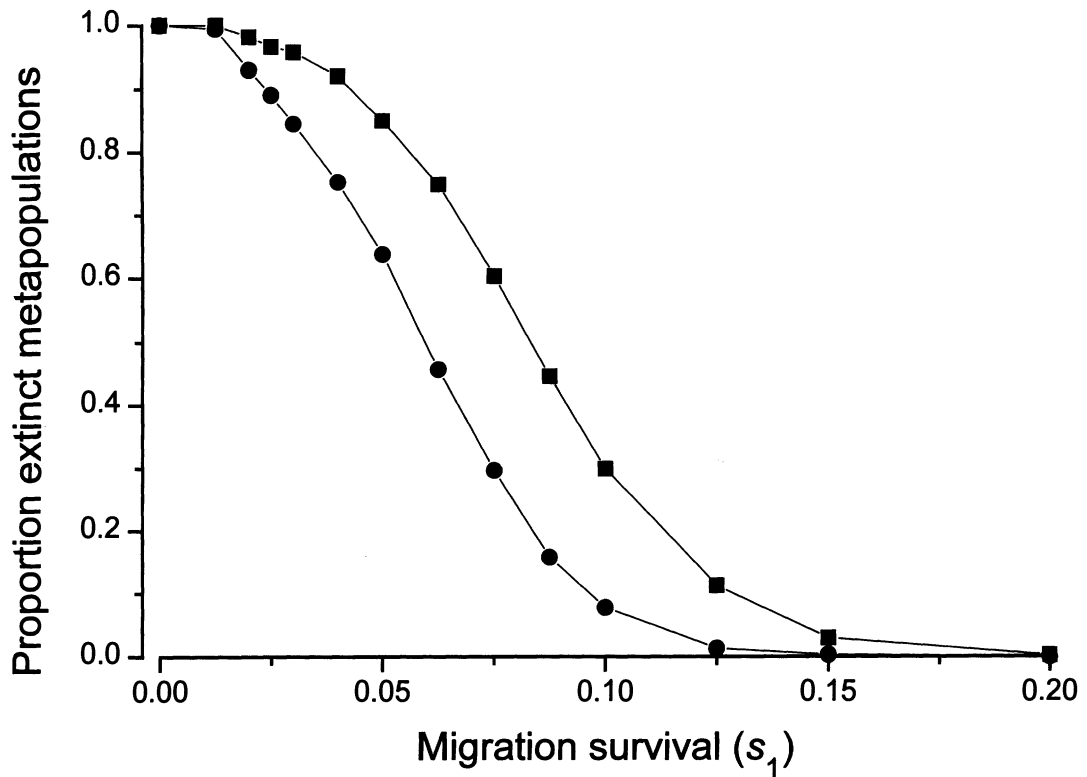


Fig. 5. Probability of the metapopulation being extinct at 300 generations after an abrupt but more or less severe reduction in migration survival  $s_1$ . The post-fragmentation migration survival of the high dispersal phenotype is on the  $x$ -axis, and the corresponding survival  $S_1$  for the low dispersal phenotype is zero in all cases. The upper curve (squares) corresponds to the case in Fig. 2, and the lower curve (circles) to Fig. 3.

over because of within-deme selection. This greatly impedes the build-up of clusters of demes fixed for the high dispersal allele, and these clusters are needed as starting points for a persistent metapopulation. A similar process is also at work when the high dispersal allele is recessive, since migrant individuals are assumed to carry along random gametes from the deme of emergence, but the degree to which migrants transport the low dispersal allele is smaller.

Our main intention is to point to a phenomenon of potential importance for conservation biology using a simple example. Nevertheless, in addition to the cases shown in the figures, we have run a considerable number of other simulations to further explore the conditions producing a critical phase. First, a lower reproductive capacity for the high dispersal type ( $f < F$ ) has a similar effect as a lower juvenile survival, but because we assumed random mating within a deme it is less strong in disfavoring the high dispersal allele. Perhaps somewhat unexpectedly, a lower probability  $q$  of local extinction can make the critical phase more severe, mainly because of a lower pre-fragmentation equilibrium proportion of the high dispersal type, but in part also because the negative within-deme selection following fragmentation can act for a longer time. Increasing the carrying capacity  $K$  of the patches re-

duces the severity of a critical phase. The entire phenomenon is dependent on low absolute numbers of successful migrants from a deme, at least when the proportion of the high dispersal type in old demes is depressed shortly after fragmentation. However, a critical phase can occur also with higher carrying capacities, but then the post-fragmentation migration survival must be quite low. For instance, using  $K = 500$ ,  $q = 0.02$  on a  $7 \times 7$  grid, and modifying the phenotypic parameters from Fig. 3 so that  $s_1 = 0.01$ , leads to about 90% extinction during the critical phase.

Finally, letting each patch have a different randomly determined carrying capacity  $K$ , varying with about a factor of five from the lowest to the highest, produces more or less the same effect as when all demes have the average  $K$ , and the same is true when the expected life-time  $1/q$  of a deme also varies in direct proportion to the carrying capacity. Thus, for a critical phase to appear, it is not necessary that all patches are identical.

## Discussion

In order to study the phenomenon of a critical phase following fragmentation with the simplest possible

model, we have limited ourselves to only two dispersal phenotypes with single-locus genetic determination. Although our assumptions may roughly correspond to the situation in some wing-dimorphic insects, in many cases wing dimorphism is a threshold trait with a quantitative genetic background (Roff and Fairbairn 1991, Roff 1996). Nevertheless, it is possible that selection as a result of fragmentation could have a similar effect on dimorphic traits with a quantitative genetic background, and the effect may well be present also for continuously distributed dispersal traits. The difference between various types of traits and mechanisms of genetic determination ought to be varying degrees of intensity of a critical phase, with high heritability tending to produce a stronger effect. Other aspects of our assumptions, such as adult rather than juvenile dispersal, may also be inessential, and a similar phenomenon could occur, for instance, in patchily distributed plant populations with seed dispersal.

A dispersal phenotype, which was treated as a unit in our simulations, in reality contains a number of potentially independent traits, such as the tendency to attempt migration and the efficiency of a flying apparatus. It is often the case that these traits show positive genetic correlations, making it reasonable to use the approximation of a single migratory syndrome (Dingle 1996). The various components of a migratory syndrome will jointly influence the course of events produced by an increased habitat fragmentation. Lower juvenile survival and lower adult reproductive capacity for more migratory phenotypes both contribute in a similar way to within-deme selection against high dispersal genes, leading to a steady decline in the frequency of such genes as a deme grows older. The departure of migratory individuals adds to the decline, but as long as migration survival stays fairly high, this part of the decline is counteracted by the arrival of migrants from neighbouring demes. When migration survival drops because of fragmentation, there is also a drop in the number of immigrants, and the resulting faster decline within demes in the frequency of genes for dispersal is essential in setting off a critical phase. In fact, genetic variation in the tendency to migrate, with no correlated variation in other life-history traits, can on its own produce a critical phase with increased probability of extinction.

It is clear from our results that genetic variation in dispersal-related traits has the potential to dramatically affect the probability of metapopulation extinction following a fragmentation event. However, the intensity of a critical phase depends on a number of factors, so the importance of the phenomenon for conservation biology is not self-evident. First, there is the matter of whether metapopulation dynamics, involving local extinction and colonization of habitat patches, captures an essential aspect of the population dynamics of many threatened organisms (Hastings and Harrison 1994,

Harrison and Hastings 1996). Another relevant issue concerns the magnitude of the influx of migrants into suitable patches. If this flux remains very high also after an increased fragmentation, extinction is not an issue, and if it drops to zero, persistence will entirely be determined by the separate local persistence of each existing deme. It is only somewhere between these two extremes, when the most efficient migrants have an appreciable chance of reaching new patches but at the same time a patch may sometimes lack immigrants during a season, that a critical phase of the kind dealt with here will be important. Nevertheless, such an intermediate situation between negligible and catastrophic fragmentation would seem to be of interest for conservation biology. Since there is often considerable genetic variation in dispersal-related traits (Wilson 1995, Dingle 1996, Roff 1996), and the expected consequence of declining frequencies of genes for dispersal with deme age has also been observed (Roff 1990), there is a definite possibility of a transient critical phase involving low patch occupancy and possible extinction following a fragmentation event. At present, the perhaps clearest evidence for metapopulation dynamics with intermediate rates of colonization comes from studies on butterflies (Thomas and Harrison 1992, Thomas et al. 1992, Hanski et al. 1994, 1995, Hanski and Thomas 1994). It is less well known whether isolation of local butterfly populations is accompanied by genetic changes in dispersal-related traits, although there are suggestive data to this effect (Dempster et al. 1976, Dempster 1991).

Assuming that a critical phase set off by fragmentation may sometimes occur in nature, two main lessons for conservation can be drawn from our results. The first is that a relatively brief phase of lowered patch occupancy can be a component of an adaptive change to new circumstances (Figs 1, 2, 3). If the original habitat is split up into a number of fairly small and mutually isolated networks of patches, each network suffers a high risk of extinction, and cannot be reached in a subsequent wave of recolonization. The second point is that the rapidity of a fragmentation process is in itself a threat to persistence (Fig. 4).

Since one aspect of micro-evolutionary change is the improvement of an organism's ability to survive and reproduce in its current circumstances, a population's supply of genetic variation in life-history traits is of potential importance for conservation biology. The main application of this perspective has been a concern with the preservation of genetic variation, both to avoid the negative consequences of inbreeding and to preserve the potential for continued adaptation. A somewhat contrasting view is that demography, where organisms are approximated as having fixed properties, is of greater immediate importance (Lande 1988). Whatever may be the relative merits of these views, our results here show that genetic variation in dispersal-related

traits can sometimes profoundly affect demography, in a way not previously considered.

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