No place like home: competition, dispersal and complex adaptation

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Abstract

In many groups of organisms the location of settling is determined by competition, and fitter individuals tend to settle closer to their natal territory than less fit ones. In this work we study the implications of this phenomenon to the problem of adaptation and speciation on a rugged adaptive landscape. One consequence of fitness-associated dispersal (FAD) is that individuals with high fitness are more likely to experience inbreeding, especially with other fit individuals. Another consequence is that when dispersal is costly, the less fit individuals are more likely to pay the cost. When a rare and advantageous allelic combination appears, FAD may increase its chances to spread in the population. In a two-locus two-alleles model with negative epistasis, we find that FAD significantly shortens the waiting time for an adaptive peak shift in comparison with random dispersal.

Introduction

An important question in evolutionary biology is the evolution of complex traits, determined by more than one locus (Wright, 1931). In such cases gene combinations, rather than individual genes, are the relevant contributors to the fitness of the organism. When advantageous combinations (peaks) are separated by disadvantageous intermediates (valleys), natural selection tends to lead the population to a nearby peak. The question is how can a population evolve from one local peak to a higher one, crossing a less fit valley.

Wright (1931, 1982) suggested an answer in terms of a 'shifting balance' process, according to which there is subdivision of the population into small demes, with a low rate of dispersal between them. In each small deme, as long as dispersal is not too frequent, random drift can move the population away from its local peak (phase 1). If it drifted far enough, selection would take it to a higher peak (phase 2), from which migration can spread the advantageous combination into the population (phase 3). Whereas each of the stages has a reasonable parameter range for which it is feasible (Crow et al., 1990; Kondra-

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shov, 1992; Barton & Rouhani, 1993), the optimal dispersal rates for drift in the single deme and for the whole collection of demes differ significantly. Drift is most effective with low dispersal rate, whereas spreading occurs most readily with high dispersal rates. Only a limited range of intermediate dispersal rates allows the occurrence of both phases (Wade & Goodnight, 1991; Moore & Tonsor, 1994; Peck et al., 2000). Dispersal in nature varies greatly, however, and appears to fall out of that range quite often (see for example Coyne et al., 1997 and references therein).

The above models of the shifting balance process share an implicit assumption: that all individuals have the same probability to disperse. In contrast, In this work we study the evolutionary implications of the question 'Who disperses?', in the context of adaptive peak shifts. Although the mechanisms motivating an animal to leave its group (habitat, social unit, etc.) are not entirely clear, the dispersing individuals rarely constitute a random sample from the group. An overlooked aspect of non-random dispersal is likely to be nonrandom mating among those individuals that manage to remain close to their birthplace. We show here that in quite plausible and apparently common situations, nonrandom dispersal may enhance adaptive peak shifts. The effect appears to be more drastic than the classic shifting balance process, and occurs for a wider parameter range.

In many groups of organisms competition plays an important role in determining whether an individual disperses or stays in the vicinity of its natal territory. In many cases, less successful individuals are more likely to disperse than dominant ones (Gaines & McClenaghan, 1980; Greenwood, 1980; Baird & Birney, 1982; Adler *et al.*, 1984; Mech, 1987; Anderson, 1989; Hanski *et al.*, 1991; White & Harris, 1994; Gese *et al.*, 1996; Dobson *et al.*, 1998; Altwegg *et al.*, 2000; Clobert *et al.*, 2001; Serrano *et al.*, 2001), and when dispersing, tend to settle farther away (Alonso *et al.*, 1998; Forero *et al.*, 2002). We term this phenomenon fitness-associated dispersal (FAD). FAD may result from inability to acquire resources, including territory, because of competition (Murray, 1967; Lidicker, 1975), inability to find mates (Dobson, 1982), or even from active interference by the dominant individuals (Christian, 1970). When mating is most likely to occur within groups, those individuals staying in their natal territory are more likely to find mates among their kin. Inbreeding, in that case, is fitness-associated: more successful individuals disperse less, and experience a higher degree of inbreeding. To the extent that fitness is genetically determined, individuals carrying advantageous combinations of alleles tend to inbreed more than individuals carrying less advantageous combinations. This may considerably increase the survival probability of a new and advantageous combination of alleles.

As long as the individuals carrying the new advantageous combination have to compete mainly with genetically inferior group-members, they are not likely to disperse. Mating within a group with high levels of inbreeding significantly decreases the probability that recombination would destroy rare advantageous combination, much like low migration rate in phase 1 of the shifting balance process. However, when their group is saturated by their likes, the dispersal rate of individuals carrying the advantageous combination would approach the normal, sometimes high, rate of dispersal. As a result, their chance to take over other groups increases, similarly to the effect of high migration rate at phase 3 of the shifting balance process.

If dispersal is somewhat costly, FAD has an additional effect: it increases the effectiveness of natural selection. The less fit individuals are more likely to pay the cost of dispersal, and thus experience even stronger selection. As a result, deleterious alleles are more efficiently eliminated under FAD than under uniform dispersal (UD) resulting in a higher average fitness for the FAD population at mutation selection balance. It would have a more complex effect on adaptive peak shifts: On the one hand, beneficial combinations would appear less frequently. But on the other, once a beneficial mutation appears, it would have a higher chance to spread in the population.

In this work we study the effect of FAD on the probability of adaptive peak shifts in a two-locus two-alleles model. Throughout the parameter range considered, we find that FAD enhances the occurrence of complex adaptation.

The model

The same general framework will serve as a basis for analytical treatment, and later for stochastic simulations. We consider a haploid population of hermaphrodite individuals with discrete generations. The population is divided into N groups of K adult individuals each, and mating occurs exclusively between the members of the same group. The number of newborn offspring (per parent) has a Poisson distribution with expectation λ. The lifetime of an individual is divided into three phases: juvenile, young, and adult. All adults die at the end of their first reproduction season. Density-independent viability selection takes place at the juvenile phase, before dispersal and mating. The viability is genetically determined by two loci with negative epistasis, with two alleles each. The viabilities of the double mutant AB, the intermediates (Ab or aB), and the wild type ab are 1, $1 - s$, and $1 - \theta s$, respectively, where $0 < s, \theta < 1$. We further assume, for simplicity, that $(1 - s) \lambda > 1$, and that the number of all surviving individuals at that point is at least NK. The recombination rate between the loci is r, and bi-directional mutation at rate μ occurs at both loci.

Adult death and dispersal occur after juvenile selection. The carrying capacity of each group for young residents is a fixed proportion of the number of adults in the group, cK (where $0 \leq c \leq 1$). If the number of the youngsters in the group after juvenile selection is larger than cK, the surplus youngsters have to disperse. Under random dispersal the dispersing young individuals are randomly chosen from the group. FAD assumes that the young individuals compete to stay in the natal territory, and the most fit young individuals are the most likely to stay. At the end of each generation each group accepts new individuals at random from the dispersing pool until the group has K members. Individuals in the dispersing pool that have not been accepted to any group die without reproducing. Denote by ω_i the viability of individual i, and by ω the average viability of the juveniles at a given generation. The expected number of surviving juveniles that are forced to disperse is at least $NK(\lambda \omega - c)$, and is always positive under the above assumptions. Denote by d the cost of dispersal, i.e. the probability that a dispersing individual would die during the transition or would not find a place in a new group. It is easy to see that d increases with λ. For moderately large group size K, it follows from either high λ or low c that the expected number of surviving juveniles in a group, $\lambda \omega K$, is considerably larger than the quota cK of places reserved for local juveniles. In that case the total number of empty places after dispersal would be close to $NK(1 - c)$, and considerably smaller than the number of dispersing individuals that is close to $NK(\lambda \omega - c)$. Thus we get

$$d \cong 1 - \frac{1-c}{\lambda\omega - c} = \frac{\lambda\omega - 1}{\lambda\omega - c} \qquad (1)$$

Taking m_i to be the probability of individual i to disperse, the fitness of individual i, defined as its overall probability to reach maturity is

$$f_i = \omega_i(1 - m_i \cdot d) \qquad (2)$$

Independent of the dispersal rule, the average fitness in a large population is

$$\bar{f} = \frac{1}{\lambda}$$

since the expected number of newborn offspring at a certain generation is λNK, and only NK of them would be included in the next year adult population.

In the case of random dispersal m_i is equal for all individuals, and the risk of dispersal does not have any effect on the relative fitness. In the case of FAD, on the contrary, the probability m_i that individual i would disperse decreases with its quality. That is, dispersal occurs more frequently among low quality individuals. As d increases with λ, so does the intensity of selection against inferior genotypes. For example, the relative fitness of a rare AB in a large group population that is close to fixation on ab would tend to λ as the frequency of ab tends to 1. Denoting by m_w the probability of the worst individual in the group (i.e. the one with the worst genotype) to disperse, the relative fitness of a rare Ab in that population would tend to

$$\lambda(1-s)(1 - m_w d) = \lambda(1-s)\left(1 - m_w\frac{\lambda\omega - 1}{\lambda\omega - c}\right)$$
$$\xrightarrow{m_w \to 1} \lambda(1-s)\frac{1-c}{\lambda\omega - c} \qquad (3)$$

as the frequency of ab tends to 1. Although the relative fitness of AB increases with λ, the relative fitness of Ab decreases with it for $c < 1$.

The increase in the power of natural selection leads to more efficient elimination of deleterious alleles. Denoting the relative decrease in fitness of a single mutant in a wild type population by

$$s_r = 1 - \frac{1-s}{1 - \theta_s},$$

the frequency of each of the rare alleles would be μ/s_r at mutation-selection balance under UD. Under FAD this frequency decreases to

$$p(b) = p(a) \cong \frac{\mu}{s_r + m_w d - s_r m_w d} \qquad (4)$$

In unimodal fitness landscapes, or in multimodal landscapes where the population occupies the higher peak, increased selection directly increases average population fitness at equilibrium. In the context of adaptive peak shifts this has two contrasting results: whereas the selection in favour of a double mutant allows it to spread more easily once it appears, the selection against the single mutants delays the appearance of double mutants.

The amount of delay in appearance of the double mutant can be described by the ratio between $\tilde{\tau}$, the expected waiting time for appearance under FAD, and τ, the expected waiting time under UD. As we consider waiting times in two populations with the same size and the same mutation rate, the ratio is determined by the selection parameters, the cost of dispersal, and the rate of recombination. The expected delay in appearance of the double mutant can be bounded from above (see Hadany, 2003, eqn 6) by

$$\frac{E(\tilde{\tau})}{E(\tau)} \leq \left(\frac{s_r + d - s_r d}{s_r}\right)^2 \qquad (5)$$

The effect of FAD on adaptive peak shifts therefore has two features: fitness associated inbreeding and an increase in the power of natural selection. Much like the case of Fitness Associated Recombination (Hadany & Beker, 2003a), we expect the first feature to increase the probability of adaptive peak shifts. As in other cases of increased selection (Hadany, 2003), we expect the second feature to result in less frequent appearance of beneficial combinations, but higher probability of take-over. In order to separate the two effects we shall consider two different cases in the simulations: the more realistic model of costly dispersal, described above, and a case of cost-free dispersal. In the latter case each generation exactly NK juveniles survive to fill the NK places available for the next generation. The simulations also allowed us to examine parameter values for which the analytical approximation would have become inaccurate.

Materials and methods

Computer simulations were used to study the occurrence of adaptive peak shifts in a subdivided population with and without FAD. The total waiting time for adaptive peak shift can be extremely long, so we decomposed this parameter into two: the waiting time for the appearance of a double mutant, and the frequency of takeover when starting with a single double mutant. We compare the effect of FAD on these two parameters.

At each run, the population is initialized close to mutation selection balance around the lower adaptive peak ab. The expected allele frequencies are determined by the mutation rate $\mu = 0.0001$ and by the selection parameters of the specific run. The actual number of individuals with a certain genotype is drawn from a poisson distribution with expectation equal to the expected frequency of that genotype. The simulation is run until a double mutant first appears. From that point on, the probability of fixation is estimated based on 5000 repeats, each starting from the same one-double-mutant state, and ending when the double mutants either go extinct or become more than 90% of the population.

Under costly dispersal, an offspring generation is constructed from a parent generation in the following manner: For each group the number of newborn offspring is drawn from a Poisson distribution with expectation $K \cdot \lambda$. For each of these offspring two (different) parents are chosen at random from the group, and crossover occurs at probability r. At each locus of the newborn, bidirectional mutation occurs at rate $\mu = 0.0001$. The probability of survival of a newborn offspring is determined by its genotype. For a surviving offspring it is first checked whether the number of young offspring in that group has already reached the carrying capacity, cK. If not, the offspring stays at home. If the carrying capacity has been reached, someone has to leave. Under random dispersal the last to be born is the first to leave and join the dispersing pool. Under FAD the dispersal tendency of an individual is determined by its fitness, whereby the less fit individuals have higher dispersal tendencies. A dispersing offspring is chosen at random, with probability proportional to its relative dispersal tendency and joins the dispersing pool. After all newborns have gone through selection, and all young have settled or dispersed, each group randomly accepts individuals from the pool until it has K members.

To simulate the case of cost-free dispersal, a different simulation is constructed. Each generation, exactly $N \cdot K$ young offspring (that survive juvenile selection) are generated. For each offspring, two parents are chosen at random from a random group. Mating, recombination, selection, dispersal and acceptance of individuals occur as described above, but as the number of offspring is identical to the number of vacant places, nobody is left out. This allows us to isolate the effect of Fitness Associated Inbreeding from that of selection.

In order to study the effect of FAD on the overall waiting time for a peak shift more directly, we also used simulations with much higher mutation rates ($\mu = 0.005$). In each of these runs the population was initialized at mutation-selection balance near ab, and the run was stopped only when the frequency of AB was higher than 90%, thus measuring both the waiting time for double mutants and the takeover probability in a single long run.

Results

The waiting time for a double mutant was estimated from 500 simulation runs for each parameter combination, and the probability of fixation was estimated from 5000 trials in each run, altogether $2.5 \cdot 10^6$ trials. Whenever the estimated takeover probability was zero at that point, we performed an additional set of $2.5 \cdot 10^6$ trials. In all simulations we used the number of groups $N = 50$, and the number of individuals in each group $K = 20$, so the overall population size was $N \cdot K = 1000$. We studied two values of the selection parameter: $s = 0.4$ and $s = 0.04$. In order to study the effect of FAD, we compared the estimated probability of AB takeover and the waiting time for the appearance of AB under three dispersal rules: 'Perfect' FAD, where the individuals are ranked according to their fitness and the cK fittest individuals in each group stay at home, noisy FAD, where the tendency of an individual to disperse is negatively correlated with its fitness, and random dispersal. The runs presented here used the values $m_{AB} = 0.1$, $m_{ab} = 0.3$, $m_{Ab} = m_{aB} = 0.9$ in the case of noisy FAD. Other values of dispersal tendencies yielded qualitatively similar results. We studied each of these under either costly dispersal with

$$\lambda = \frac{1.1}{1 - \theta \cdot s}$$

(i.e. on average 10% surplus offspring after selection for a pure ab group) or cost-free dispersal. In all the simulations, FAD increased the estimated takeover probability in comparison with random dispersal (Fig. 1a, c, 2a, c, 3a and b). The effect was more notable with costly dispersal (Fig. 1c, 2c, 3b and 4c), probably because of the increased relative advantage of the double mutants. With costly dispersal, FAD also resulted in a slightly increased waiting time for the appearance of the double mutant (insignificant difference in Fig. 1d and 2d; significant difference between perfect FAD and UD ($P < 0.01$) in Fig. 4d). However, this effect was always outweighed by the effect on takeover probability: the overall estimated waiting time for fixation under FAD was shorter than under random dispersal in the entire parameter range studied.

The effect of r

In an infinite panmictic population, fixation of AB is globally stable if $(1 - r) > (1 - \theta s)$. That is, if the advantage of the superior combination AB is larger than the destructive effect of recombination even when AB is rare, AB would eventually take over the population. In terms of average population fitness, there is a nondecreasing path from the lower 'peak' to the higher one when $r \leq 0.2$ under strong selection (Figs 1–3), and for $r \leq 0.02$ under weak selection (Fig. 4), although a 'valley' exists between the two adaptive peaks in the individual fitness landscape, independently of r. As r increases the probability of takeover decreases both with FAD and without it, but not at the same rate. With UD the frequency of takeover was much more sensitive to the decrease in c than with FAD, especially with perfect FAD (Fig. 1a and c) and costly dispersal (Fig. 1c). An increase in r also allows the appearance of double mutants at higher rates, but this effect was much weaker than the first in all the range studied (Fig. 1b and d).

The effect of the carrying capacity

The carrying capacity parameter, c, is somewhat complementary to dispersal – individuals which cannot stay near home must disperse. The effect of c on takeover
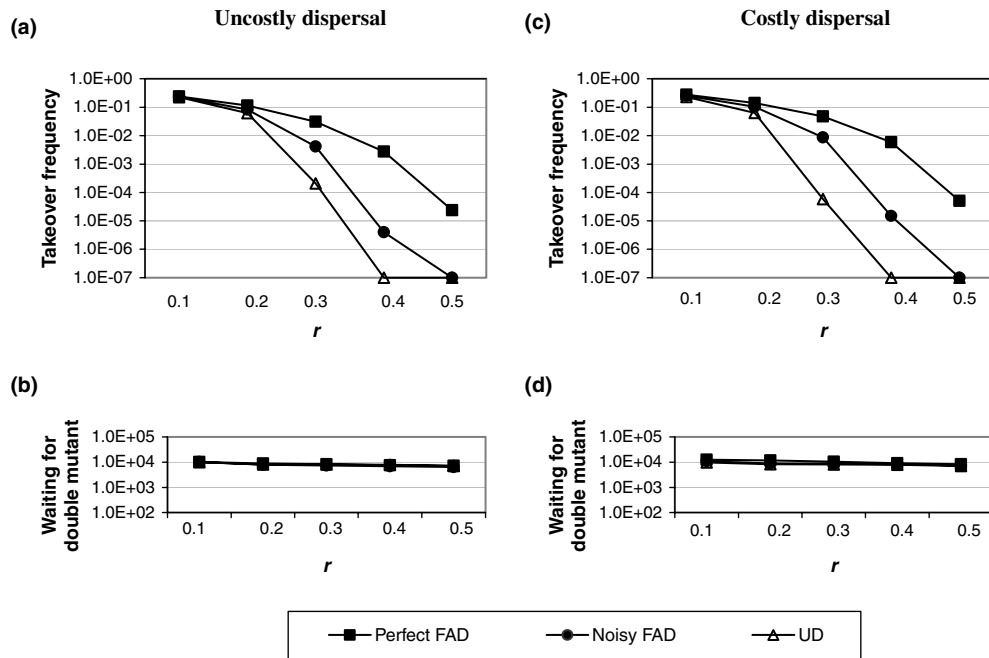
Fig. 1 Takeover frequency and waiting time for a double mutant as a function of recombination rate for cost-free (a, b) and costly (c, d) dispersal. In each graph we compare perfect fitness-associated dispersal (FAD) (where the less-fit individuals in the group disperse), noisy FAD (where the less fit individuals have higher chance to disperse), and uniform dispersal. FAD results in a significant increase in takeover frequency, and has almost no effect on the waiting time for a double mutant. The scale is logarithmic, and 10^{-7} is plotted in the cases where no takeover was observed in $5 \cdot 10^{6}$ trials. $c = 0.8$, $N = 50$, $K = 20$, $s = 0.4$, $\theta = 0.5$, $\mu = 0.0001$ and $\lambda = 1.1/(1-\theta s)$ in the case of costly dispersal.

frequency has several components: at the level of the single group, any increase in dispersal renders drift within the group less likely. After one group has shifted, some dispersal is necessary for inter-group spread. Yet low values of c make the mutant group less stable. When dispersal is costly the effect of c is more complicated – selection against the single mutants increases with c for low and intermediate values of c but weakens when c approaches 1, whereas the full advantage of rare double mutants is obtained at low levels of c.

In our model the observed effect of c on the frequency of takeover depended on the selection parameters. Under strong selection the frequency of takeover increased with c, with and without dispersal cost (Figs 2 and 3). Under weak selection a more complex pattern was observed, and both the frequency of takeover and the waiting time were not monotonous in c (Fig. 4). However, the effect of FAD was consistent throughout the parameter range: takeover frequency was always higher under FAD than under UD. This effect was stronger than the effect of FAD on the appearance of double mutants, which was always below the theoretical bound of eqn 5. The overall effect was again more notable with costly dispersal and with perfect FAD.

The fact that for most of the parameter range studied (Fig. 1–3 and 4a) the maximal takeover frequency was obtained for $c = 1$ might seem to contradict the results of

the shifting balance process (Moore & Tonsor, 1994). Note, however, that in our model $c = 1$ does not mean complete isolation between groups. Rather, it means that a resident offspring always has priority in its own natal group over a stranger, but if the number of surviving offspring in a group is smaller than the fixed group size K because of stochastic fluctuations, strangers can be accepted until the number of members equals K. For example, when $K = 20$, $c = 1$, $s = 0.4$, and $\theta = 0.5$ the probability that a pure ab group would accept at least one migrant is 0.306. (Under the same conditions, the probability that a pure AB group would accept migrants is 0.0575.) That amount of dispersal might already be higher than the optimal dispersal rate for the shifting balance.

Discussion

Fitness-associated dispersal (Murray, 1967; Christian, 1970; Ruxton & Rohani, 1999) is a condition whereby individuals with high fitness disperse less than individuals with lower fitness. That can be understood intuitively if dispersal has some cost, and thus the nondispersing individuals are chosen by competition, either direct (Christian, 1970) or indirect (Lidicker, 1975; Dobson, 1982). FAD was demonstrated in various groups of organisms (see for example Gaines & McClenaghan,
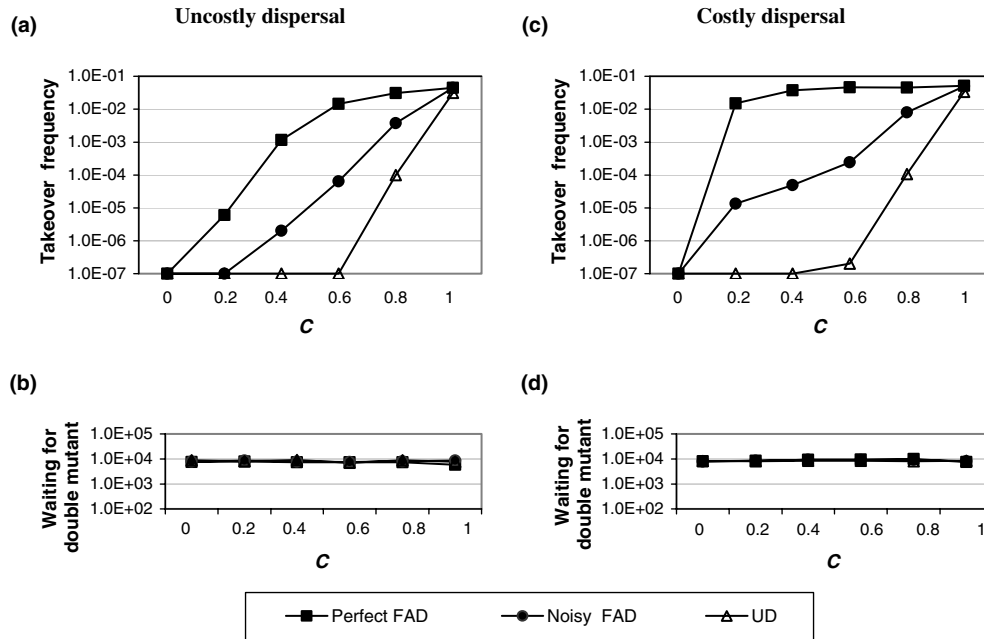
(a) Uncostly dispersal

(c) Costly dispersal

(b)

(d)

Perfect FAD — Noisy FAD — UD

Fig. 2 Takeover frequency and waiting time for a double mutant as a function of the carrying capacity parameter, c, for cost-free (a, b) and costly (c, d) dispersal. In each graph we compare perfect fitness-associated dispersal (FAD) (where the less-fit individuals in the group disperse), noisy FAD (where the less fit individuals have higher chance to disperse), and uniform dispersal. FAD results in a significant increase in takeover frequency, and has almost no effect on the waiting time for double mutant. The scale is logarithmic, and 10^{-7} is plotted in the cases where no takeover was observed in $5 \cdot 10^6$ trials. Recombination rate $r = 0.3$, $N = 50$, $K = 20$, $s = 0.4$, $\theta = 0.5$, $\mu = 0.0001$ and $\lambda = 1.1/(1-\theta s)$ in the case of costly dispersal.
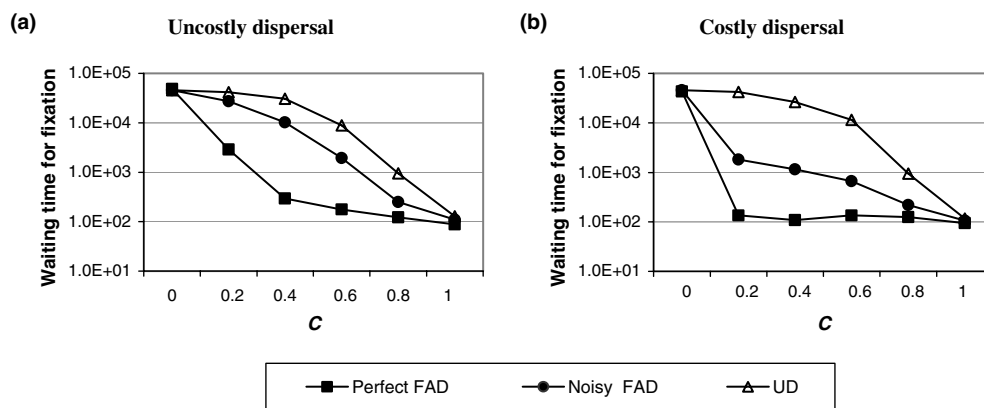
(a) Uncostly dispersal

(b) Costly dispersal

Perfect FAD — Noisy FAD — UD

Fig. 3 Overall waiting time for fixation as a function of the carrying capacity parameter, c, for cost-free (a) and costly (b) dispersal. These results were obtained at high mutation rates, allowing peak shifts to occur at reasonable rates under all models. Fitness-associated dispersal always results in a shorter waiting time for a peak shift. Recombination rate $r = 0.3$, $N = 50$, $K = 20$, $s = 0.4$, $\theta = 0.5$, $\mu = 0.005$, and $\lambda = 1.1/(1-\theta s)$ in the case of costly dispersal.

1980; Adler *et al.*, 1984; Mech, 1987; Arcese, 1989; Hanski *et al.*, 1991; Tucker *et al.*, 1998). In this work we studied the implications of FAD on the problem of adaptation on rugged adaptive landscapes (Wright, 1931). The process has at least two main consequences on population dynamics. First, the fitter individuals are more likely to experience inbreeding, especially with other fit individuals. Secondly, the efficiency of natural selection is increased. In the rare case of appearance of a new and advantageous allelic combination, FAD may enable it to spread even when the intermediates are less fit, and even when the average dispersal rate in the population is high.
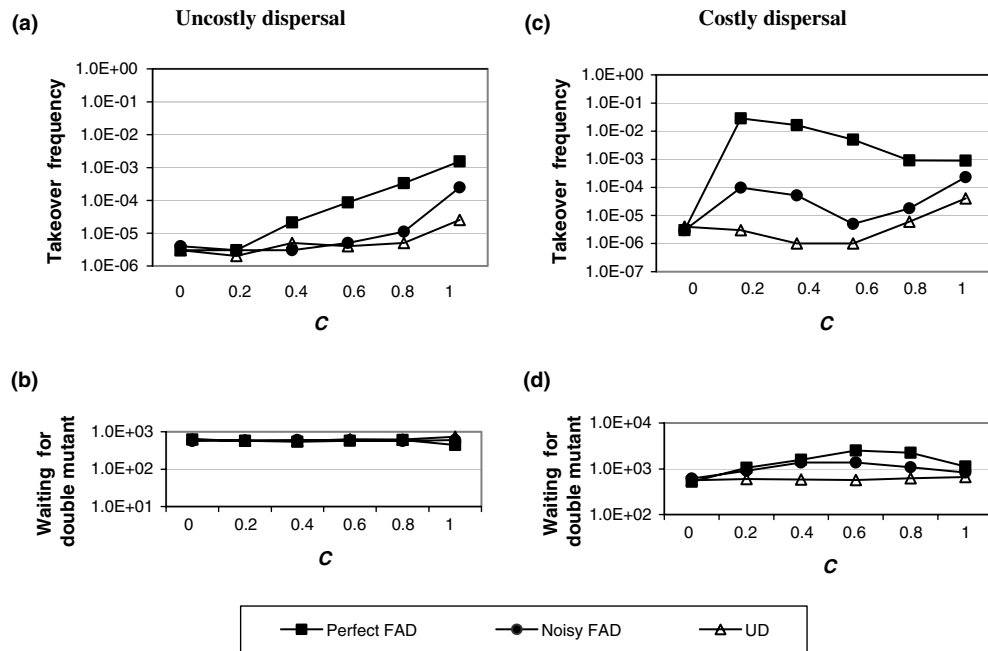
Fig. 4 Weak selection: takeover frequency and waiting time for a double mutant as a function of the carrying capacity parameter, *c*, for cost-free (a, b) and costly (c, d) dispersal. In each graph we compare perfect fitness-associated dispersal (FAD) (where the less-fit individuals in the group disperse), noisy FAD (where the less fit individuals have higher chance to disperse), and uniform dispersal. In the absence of cost, FAD results in a significant increase in takeover frequency, and has almost no effect on the waiting time for double mutant. When dispersal is costly, FAD results in a very large increase in takeover frequency, and in a small increase in waiting time. The scale is logarithmic. Recombination rate $r = 0.1$, $N = 50$, $K = 20$, $s = 0.04$, $\theta = 0.5$, $\mu = 0.0001$ and $\lambda = 1.1/(1-\theta s)$ in the case of costly dispersal.

We considered here a specific population structure of groups of equal size, where mating occurs only within each group, and dispersal at constant frequency occurs between groups. Fitness is determined by two loci with negative epistasis, and the most viable individuals are assumed to also be the most successful in terms of competition within the group. For that model we demonstrated that FAD significantly increases the probability of a peak shift, and allows its occurrence in a wider parameter range, in comparison with random dispersal.

Note that FAD is not a simple case of assortative mating for fitness (Rice, 1998). In the whole population the phenotype of high fitness, even when genetically determined, may well be a result of different genes or gene combinations. The best individuals within a family, on the contrary, have a much higher chance to be successful because of the very same genetic combination. As a result, inbreeding of the most successful individuals in a family is likely to be similar to assortative mating between individuals of the most fit *genotype* (Wright, 1921; Williams & Sarkar, 1994). Unlike the latter phenomenon, FAD does not require specific identification of that genotype apart from its effect on the fitness. Moreover, under FAD the less fit individuals do not have a high probability of mating

with individuals of the same genotype. They are thus more likely to meet low-fitness individuals with a different genetic background, possibly leading to the appearance of new good combinations.

Adaptive peak shifts are not the only result of FAD. Similarly to Fitness-Associated Recombination (Hadany & Beker, 2003b), we would expect FAD to lead to higher average fitness in unimodal fitness landscapes as well as epistatic ones. This would result partly from fitness-associated inbreeding (leading to a positive disequilibrium between advantageous fitness alleles) and partly from elimination of harmful alleles (as their carriers tend to die more often during dispersal). The latter effect is even more pronounced when selection has a relative component: a structured population would then result in a decreased efficiency of selection, since less fit individuals often compete with other not-so-fit individuals of the same family. With FAD, less fit individuals mix well in the whole population and experience stronger selection, even when the dispersal process itself is not costly. In addition, association with fitness might be important when considering the evolution of migration rates, for reasons similar to those discussed in Hadany & Beker (2003b) in the context of recombination: an allele for FAD is more likely to get seperated by outcrossing from harmful alleles than from

advantageous ones, and is thus likely to have 'good neighbours'. As a result, FAD might evolve more easily than UD.

The results presented here suggest that the effect of migration on evolution, and especially on the evolution of complex traits, might be more complex than previously assumed. Whereas uniform migration at high rates often limits adaptation, more realistic modelling should take into account the variation in migration rates, and the fact that certain individuals tend to disperse more often than others. When dispersal is negatively associated with fitness, deleterious alleles are more efficiently eliminated, whereas complex traits can evolve more easily, and under a wider parameter range.

Acknowledgements

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