Population regulation by dispersal under selection pressure for and against dispersal: an experimental test with beetles, *Tribolium confusum*

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ABSTRACT

Hypothesis: Dispersal outside a local population maintains population density below the possible maximum, but within a single local population selection acts against dispersal and consequently against such maintenance. Individuals that disperse exhibit lower fitness that is correlated with their smaller body size.

Organism: Laboratory populations of *Tribolium confusum* beetles.

Methods: Four confined populations with no dispersal, four with the progeny of dispersing individuals removed and four with the progeny of non-dispersing individuals removed were maintained and monitored for seven generations.

Results: Confined populations were larger than those from which dispersal was allowed. From generation three onwards, dispersal rates were significantly lower in the population in which progeny of dispersing beetles were removed than in the population in which progeny of non-dispersing beetles were removed. The differences in dispersal rates mentioned above affected population density in the native populations but not in the places to which beetles emigrated. The removal of the progeny of dispersing individuals does not eradicate dispersal altogether. Average body weights of dispersing beetles are not lower than of those of non-dispersing beetles.

Keywords: metapopulation, migration, population density, *Tribolium* laboratory populations.

INTRODUCTION

Permanent dispersal of an individual outside a local population has, for this particular population, the same effect as that individual's death. Therefore, one may expect strong selection against dispersal within a single population unless some countervailing mechanism intervenes. Yet, dispersal is common.

The tendency to disperse may well be an adaptation to temporal and spatial heterogeneity (Olivieri and Gouyon, 1997). Several theoretical concepts have been proposed to explain the evolution and maintenance of dispersal from optimum locations in which organisms were

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born, to suboptimum or hostile habitats. These are metapopulation theory (Levins, 1970; Hanski, 1999), kin selection theory (Hamilton and May, 1977), theories of despotic distribution (Fretwell, 1972), and contest competition with unequal resource partitioning (Łomnicki, 1988).

Many papers on the theory of dispersal and related phenomena have been published (for references, see Clobert *et al.*, 2001; Cadet *et al.*, 2003). On the other hand, experimental data are rather scarce (but see Friedenberg, 2003). In this paper, I shall add to that experimental literature by presenting work on laboratory populations of flour beetles.

Flour beetles of the genus *Tribolium* provide an outstanding empirical model for studying dispersal. The general biology of these insects and the ecology of their dispersal are well known. The dispersal of *Tribolium confusum* Duval and *T. castaneum* (Herbst) is density-dependent and may serve as a mechanism of population regulation (Ziegler, 1978). Regulation significantly below the level of available resources was shown for *T. castaneum* (Łomnicki, 1988), but this species is much more dispersive than *T. confusum*.

The distribution of resources in which *Tribolium* live is highly heterogeneous in both space and time, favouring dispersal. Moreover, it is relatively easy to create a system of local habitats among which migration is either allowed or prevented. Finally, because dispersal behaviour in *Tribolium* has a hereditary component (Ogden, 1970; Ritte and Lavie, 1977; Korona, 1991), selection for high or low dispersal should be possible. In the two extreme cases, the experimentalist would remove all individuals that do not disperse or all those that do.

Dispersal may regulate population density below the level of carrying capacity (or the maximum possible without dispersal) as proposed by Lidicker (1962) and discussed more extensively elsewhere (Łomnicki, 1988). However, such regulation requires high mortality during a dispersal episode; such high mortality allows dispersing individuals to colonize some of the empty local habitats but prevents them from producing a significant increase in population size in already occupied local habitats. Through their effects on population density, different dispersal rates may impose different survival times on local populations.

I designed laboratory experiments to test the following three hypotheses:

1. Confined populations maintain much higher densities in relation to the available resources than populations from which beetles may emigrate.
2. Removing dispersing individuals for several generations results in an evolutionary reduction of the tendency to disperse so that the size of unconfined populations approaches levels similar to those of confined populations.
3. Dispersing individuals will have lower body weights than non-dispersers, reflecting a lower fitness for dispersers.

The experiments mimic natural conditions, maintaining populations of beetles in which all life stages – eggs, larvae, pupae and imagines – are present. However, I did introduce one extremely unnatural factor: I removed all adult beetles in every generation, leaving only eggs, larvae and pupae to begin the next. Without such removal, one cannot observe changes between discrete generations, since imagines of this species may survive and reproduce for several months.

I also prevented emigrating individuals from returning to their native local habitats. Perhaps one may consider this also to be artificial. However, imagines of *Tribolium* beetles can move tens of metres per hour and survive several days without food, so their dispersal without return might be a common phenomenon in nature. In any case, one should consider it to be long-distance dispersal as defined by Muller-Landau *et al.* (2003). In the laboratory,

where space is limited, a set-up that does not allow return of movement is the only way to mimic long-distance dispersal.

METHODS

The flour beetles *Tribolium confusum* used in this experiment were part of the stock kept in the Laboratory of Population Ecology of the Institute of Environmental Sciences since the early 1980s, to which wild stock brought from Israel in the mid-1990s was added. They were kept in large numbers (thousands of individuals) in glass vials under standard laboratory conditions for these beetles: darkness; a medium of 95% wheat flour and 5% baker's dried yeast; temperature about 29°C; relative humidity about 70%. I kept the experimental populations under the same laboratory conditions but in a climatic chamber (KBF720, Binder GmbH, Tuttlingen, Germany) for more precise control of temperature (accuracy ± 0.1°C) and humidity (accuracy ± 1.5%). I counted beetles at the end of old and the start of new generations outside the chamber at room temperature and humidity.

I arranged three experimental series: sedentary, migratory and confined. Sedentary selected against dispersal, migratory selected for dispersal and confined did not allow dispersal. There were four replicates in each series.

In the sedentary series, four 100 ml glass beakers (diameter 50 mm, height 80 mm) and one plastic beaker (diameter 30 mm, height 70 mm) were connected by glass tubes (4 mm internal diameter) with a thread inside on which the imagines could walk in one direction from beaker A through B, C and D to E (Fig. 1). At the beginning of each generation, 10 g of old medium with eggs, larvae and pupae were placed in beaker A along with 10 g fresh medium. Beakers B and D remained empty, without medium. Ten grams of fresh medium was placed in beaker C and 5 g of fresh medium in beaker E. All these small beakers were placed in a 3000 ml glass beaker (diameter 140 mm, height 210 mm), one for each replicate.

Over a 5-week period, the eggs, larvae, and pupae placed in beaker A could become imagines. As imagines, they could migrate along the chain of beakers from A to B to C to D to E. The dispersing individuals were those that moved up the thread in the narrow tube in one beaker and fell down into the next one even if the next beaker had no nutritive medium.

In the sedentary series, all imagines were counted and removed after 6 weeks (after 5 weeks in the first and second generations). The 20 g of old medium in beaker A with eggs,
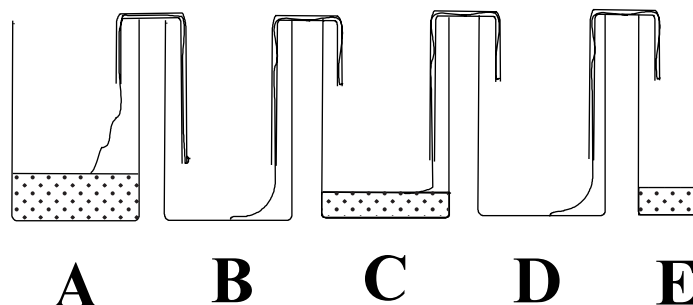

Fig. 1. Schematic representation of five beakers used to keep beetles in the migratory and sedentary series within a single generation. Imagines from beaker A may move on a thread inside a glass tube to beakers B, C, D and E. Medium is placed in beakers A, C and E only. Movement in the opposite direction is not possible.

larvae and pupae was divided into two. One half was used to initiate a new generation, while the other half was discarded. Similarly, the pupae in the old medium were counted and half were used to start the next generation. The medium in beakers C and E was also discarded, as shown in Fig. 2. Thus, only those eggs laid in native beaker A passed to the next generation.

The migratory series was maintained in exactly the same way as the sedentary series, except that I began the next generation with the entire 10 g of medium from beaker C. The old medium from beakers A and E was discarded (Fig. 2). Thus, only eggs laid by migrating beetles passed to the next generation.

In the confined series, beetles could not emigrate. I kept the entire population in a single 100 ml beaker identical to those used in the two other series. At the end of each generation, all imagines were counted and removed, and the old medium was halved. Half of the old medium, together with 10 g of fresh medium, was used to start the new generation; the other half was discarded (Fig. 2). The pupae in this series, as in the sedentary series, were also counted. Half of them were used to start the next generation.

At the end of generations 5 and 7, all living imagines of all three series of a single replicate were weighed using a Sartorius S4 microbalance (accuracy of 0.01 mg; Sartorius GmbH, Göttingen, Germany). Then I determined the sex of each weighed individual.

The designs of the experiments simulated the fate of local populations either in very temporary or in very permanent habitats. In the migratory series, the individuals that did not disperse and did not leave their progeny in beaker C were selected against. Such a
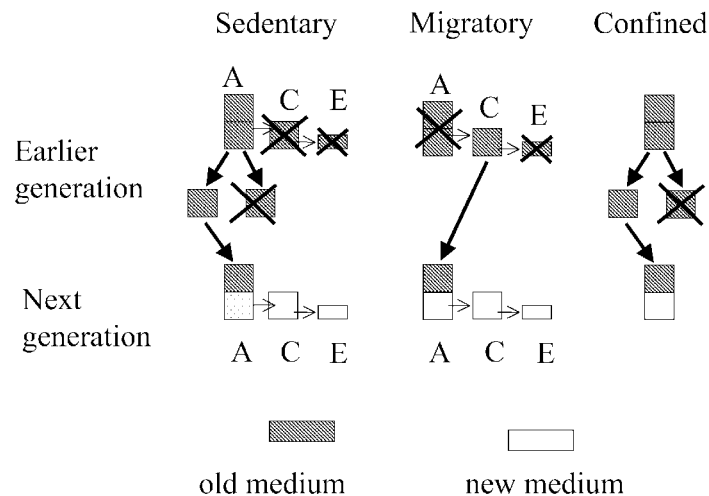

Fig. 2. Schematic representation of the three experimental series. Bold arrows show which of the media used by the former generation, together with eggs, larvae and pupae, are transferred to the next generation. Thin arrows in the migratory and sedentary series represent possible movements of imagines from beaker A through beakers C to E. In the sedentary series, only part of the progeny left in beaker A are used to form the next generation; the medium with the progeny of migrants left in C and E is discarded. In the migratory series, only the progeny left in beaker C are used to form the next generation (in beaker A); the medium from beakers A and E is discarded. Transfer of medium between generations in the confined series is the same as in the sedentary series, but with no possibility of emigration.

phenomenon would occur if extinctions of local habitats and the establishment of new ones are common, occurring in every generation. The design of the sedentary series mimicked conditions in permanent local habitats surrounded by a hostile space. In such habitats, the beetles that migrate from a local population – that is, from beaker A – are selected against.

Several features of the experimental design require additional comments. First, I did not set up a pure selection experiment, but an experiment that addressed the long-term effects of colonization and extinction on population dynamics as determined by dispersal. The selection for and against dispersal was not as strong as it might have been. Beetles leaving beaker A could deposit eggs in A before dispersing. Therefore, some eggs of migrating beetles did enter the next generation in the sedentary series, reducing selection pressure against dispersal in this series. On the other hand, in the migratory series, the beetles with a very strong tendency to disperse might have remained in beaker C only for a short time, leaving only a small number of their eggs there. Beetles with a weaker tendency to disperse might have moved only from A to C, leaving more progeny in C and attenuating the value of dispersal to fitness.

Second, I designed the experiments to simulate dispersal outside a local population, not dispersal within the immediate neighbourhood. The latter can occur among larvae as well as imagines. Therefore, I allowed only imagines to move from one beaker to another. Moreover, the experimental set-up prevented dispersers from ever returning.

Since the space in the climatic chamber was limited, I used empty beakers to simulate long-distance migration. The first beaker to which dispersers could move had no nutritive medium. A beetle that leaves a beaker with medium and moves to an empty beaker is ready for long-distance dispersal. (In contrast, a beetle moving from a medium with a high beetle density to one with a low beetle density would simply have been selecting a better immediate environment without any risk of dispersal.)

Confined beakers promote the unnaturally high densities of beetles that lead to food shortage and egg cannibalism. In nature, local habitats are not confined. To simulate natural conditions, I allowed dispersal from beaker C to beakers D and E. Thus, as in nature, dispersal (immigration and emigration) helped to regulate population sizes in beaker C. That is why I used eggs laid in beaker C, not in beaker E, to start the next generation in the migratory series.

RESULTS

I carried out the experiment for seven generations. Unfortunately, after the seventh generation, grain moths attacked the experimental populations, and this made it impossible to end it by assaying the migratory rates of different series in an identical environment.

The average number of imagines found in all beakers of the migratory and sedentary series and in the single beaker of the confined series (Fig. 3), analysed by one-way repeated-measures analysis of variance (ANOVA), varied over generations ($F_{6,54} = 4.3$, $P = 0.001$). However, there were no significant differences between the three series ($F_{2,9} = 0.27$, $P = 0.77$).

The fraction of dispersing individuals found outside beaker A (Fig. 4) did not differ in generation 1 ($F_{1,6} = 0.00001$, $P = 0.998$). But from generation 3 onwards, dispersal was greater in the migratory series than in the sedentary series and the differences were significant ($F_{2,6} = 25.6$, $P = 0.002$). At the same time, there was no significant variation between
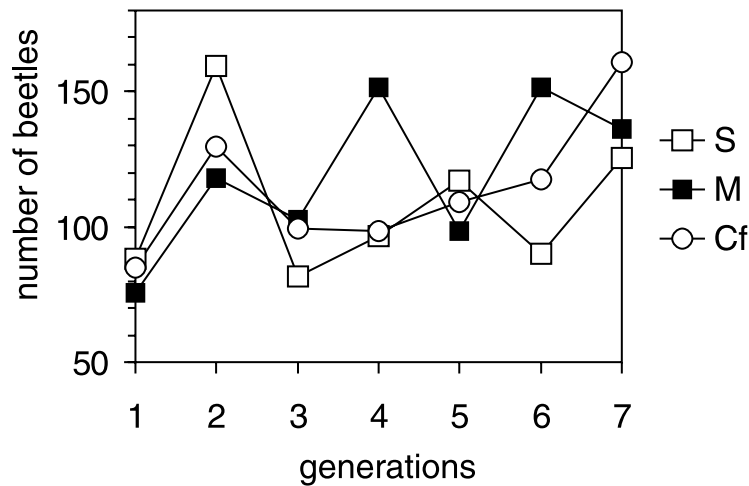
Fig. 3. Average number of imagines of all four replicates found and removed from all beakers in each generation for the migratory (M), sedentary (S) and confined (Cf) series.
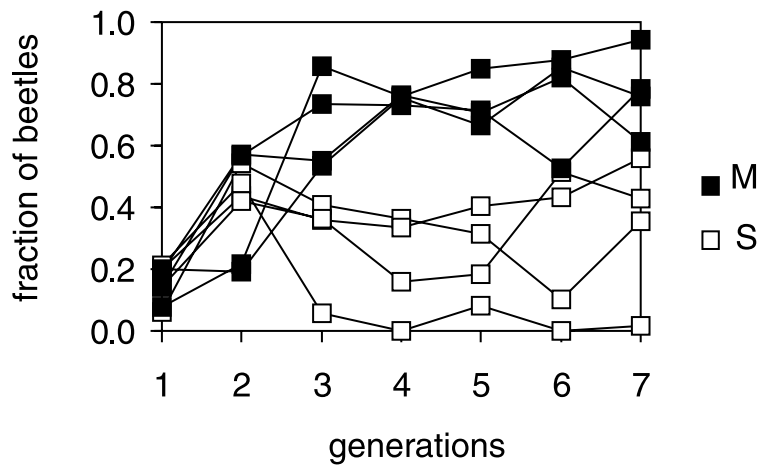

Fig. 4. Proportions of imagines that dispersed from beaker A in all four replicates of the migratory (M) and sedentary (S) series.

generations ($F_{4,24} = 0.66$, $P = 0.62$) and no significant interaction between series and generations ($F_{4,24} = 0.72$, $P = 0.59$).

The numbers of imagines found at the end of each generation in the confined series and in beakers A and C in the migratory and sedentary series are shown in Fig. 5. Since the fraction of dispersing beetles stabilized after generation 2, I performed analyses of variance for generation 1 and then for generations 3–7. In generation 1, one-way ANOVA yielded $F_{4,15} = 137.8$, $P < 0.000001$. But Tukey's *a posteriori* test showed no statistical differences in the numbers of imagines in beaker A between the migratory and sedentary series ($P = 0.261$), or in beaker C between the same two series ($P = 0.992$). However, the numbers of imagines in the confined series was higher than in beaker A of the migratory series
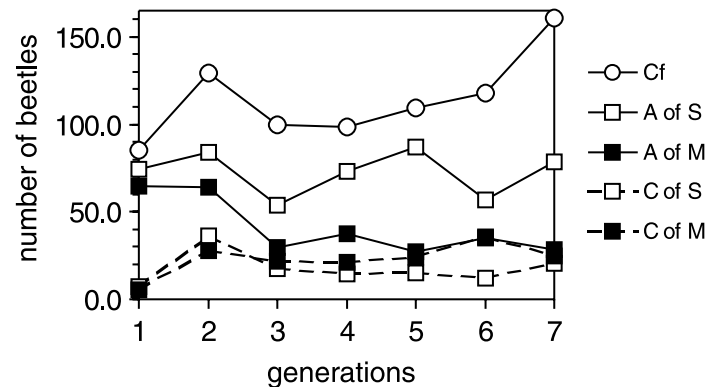
Fig. 5. Mean number of imagines of all four replicates found in beakers A and C of the migratory (A of M and C of M) and sedentary (A of S and C of S) series, compared with those in the confined series (Cf).

($P = 0.0037$). Within the migratory series, the number in beaker A was higher than in beaker C ($P = 0.00015$).

Repeated-measure ANOVA for generations 3–7 revealed significant variation among series and beakers ($F_{4,15} = 22.751$, $P < 0.000003$), but no significant variation between generations ($F_{4,60} = 2.315$, $P = 0.068$), and no interaction ($F_{16,60} = 1.789$, $P = 0.054$). Tukey's *a posteriori* test showed no significant differences within the group of three series and beakers, namely A in the migratory series and C in the migratory and sedentary series ($P > 0.722$ for all three comparisons). But the same test showed significant differences in beaker A between the migratory and sedentary series ($P = 0.0498$) and between the sedentary and confined series ($P = 0.012$).

Figure 6 presents mean body weights separately for males and females for both generations 5 and 7. Analysis of variance for males of the migratory and sedentary series showed differences between generations ($F_{1,135} = 11.121$, $P = 0.001$) and between the series ($F_{1,135} = 18.071$, $P = 0.00004$). Males of the migratory series were significantly larger than those of the sedentary and confined series. However, there were no differences between beakers A and C of the sedentary and migratory series ($F_{1,135} = 0.854$, $P = 0.36$) and no interactions between generations, series and beakers ($P > 0.24$). Planned comparisons (contrasts) of body weights of the beetles from beakers A and C of the sedentary series with the confined series showed no significant differences (comparison with beaker A: $F_{1,244} = 0.899$, $P = 0.346$; comparison with beaker C: $F_{1,244} = 0.119$, $P = 0.730$).

Analysis of variance for females of the migratory and sedentary series showed differences between generations ($F_{1,100} = 11.253$, $P = 0.001$) and between series ($F_{1,100} = 5.495$, $P = 0.021$), as well as a strong interaction between beakers A and C against series ($F_{1,100} = 6.246$, $P = 0.014$). This interaction was due to the differences in weight between the beetles found in beakers A and C of the sedentary series. Planned comparisons (contrasts) of beakers A and C of the sedentary series with the confined series showed no significant difference between the confined series and beaker C of the sedentary series ($F_{1,203} = 0.485$, $P = 0.487$), but a very significant difference between the confined series and beaker A of the sedentary series. In summary, females in beaker A fell into a size order: migratory > confined > sedentary. But regardless of the series, those in beaker C differed non-significantly in size.
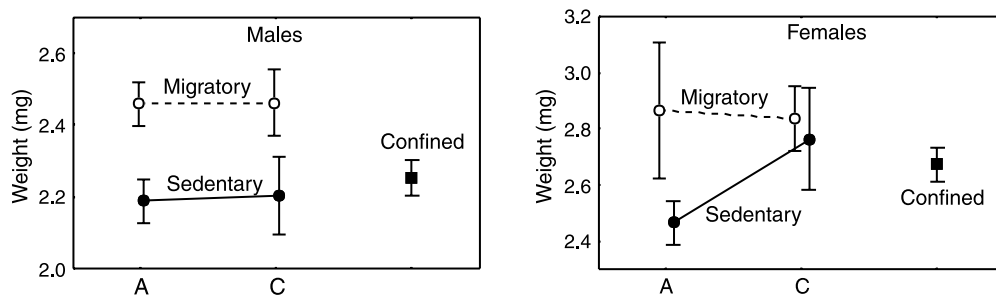
Fig. 6. Mean body weights of adult males and females, with 95% confidence intervals, for generations 5 and 7 (combined), for the three series, and for beakers A and C of the migratory and sedentary series.

DISCUSSION

The results of this study support some of the hypotheses outlined in the Introduction, but with reservations. In accord with the first hypothesis, the numbers of imagines after the third generation in unconfined populations (migratory and sedentary series) in their native beaker A were lower than in the confined series. Thus dispersal resulted in reduced population density.

Response of population size to selection regime

Selection for dispersal allowed regulation of population density much below the level of the confined population, since the number of imagines found at the end of every generation was much lower in the migratory series than in the sedentary and confined series. Let us assume that most animals which migrate outside their native local population are quickly killed by predators and adverse weather conditions, so that only a small fraction survive, enough to colonize empty habitats. That situation – like the situation in this experimental model – is a case of population regulation at a level much below the maximum possible due to the element of dispersal.

Intermediate population size in the sedentary series

The second hypothesis, that selection pressure against dispersal makes the size of the unconfined populations approach that of the confined population, received only partial support. The number of imagines in beaker A of the sedentary series was significantly higher than that in the migratory series, but not as high as that in the confined series. This does not appear to have been caused by an inadequate number of experimental generations, since it occurred in successive generations during which the proportion of migrants had already stabilized (Fig. 4). Instead, the failure of population size in the sedentary series to grow as much as that in the confined series was probably due to the incomplete selection against dispersal in the sedentary series. This incomplete selection allowed a certain amount of limited dispersal to persist.

Recall that in the sedentary series, dispersing imagines were able to lay eggs in their native beaker A and thus pass progeny of dispersers on to the next generation. However, imagines

not dispersing from their native beaker A should have layed even more eggs than dispersers, so that dispersal should have been selected against. This happened, but only for the first two generations. After a rapid increase from generation 1 to generation 3, the proportion of non-dispersing beetles in the sedentary series showed no further trend.

Additionally, the presence of dispersing beetles in the sedentary series can be explained by the higher reproduction of females moving from beaker A to beaker C. Those females that moved were significantly heavier (Fig. 6). Heavier females produce more and larger eggs (Hanzlova, 1994). Therefore, females laying eggs in beaker A and then moving to beaker C may have left behind more progeny that those remaining in beaker A.

Response of body size

The theory of despotic distribution (Fretwell, 1972) predicts that dispersing individuals are smaller and less competitive. Therefore, I expected the dispersing beetles to have lower weights. This was not the case.

The only difference between dispersing and non-dispersing beetles was among females of the sedentary series. But females that dispersed were significantly heavier rather than lighter than those that did not.

Body size changes in the different series also suggest that individuals with a higher tendency to disperse are heavier. Males from the migratory series were heavier than males from the other two series; the same was true for females in the migratory series, although not significantly so in beaker C.

Half-way dispersal

A small number of imagines moved to beaker C and remained there. I found them in beaker C at the end of every generation. Because they did not continue to beaker E, one can term them 'half-way dispersers'. However, bear in mind that these are the beetles whose progeny form the new generations in the migratory series; in fact, they are used to select for dispersal.

The number of half-way dispersers did not differ significantly between the migratory and sedentary series, and it did not change much between generation 2 and generation 7 (Fig. 5). This contrasted with beaker A, where populations in the sedentary series outnumbered those in the migratory series after generation 1.

So the overall pattern involved similar increases in half-way dispersers from generation 1 to generation 2, followed by a steady number. Meanwhile, the numbers of non-dispersers (those in A) were steady in the sedentary series, but declined for two generations in the migratory series until they reached the values typical in the C beakers. After that, the latter values were also steady despite the continued selection pressure for dispersal.

Why did dispersers stop in beaker C? Beetles (of both the migratory and sedentary series) that dispersed to beaker C and remained there may have responded behaviourally to population densities. Their tendency to disperse allowed them to leave their native beakers (A) and find a much less crowded place to stay (beaker C). If beaker C had been given time to become more crowded, these half-way dispersers might have dispersed further in search of a less crowded environment.

Perhaps it was merely by chance that, in the migratory series, the populations of imagines in beaker C declined to match those in beaker A. However, a possible explanation does

exist. There may be a population trigger point for dispersal: at a certain population size, when the average cost of moving is balanced by its average reward, beetles begin dispersing. Such a trigger point is implicit in the theory of ideal free distributions (Fretwell, 1972); there, the cost is the loss of the current habitat patch.

The explanation is as follows. Initially, beetles have an inappropriately high trigger point produced by many generations of selection in the laboratory (where populations are kept in closed glass beakers). Under such conditions, the propensity to disperse may have declined to a very low level. Given the opportunity and the need to disperse, a new, lower trigger point quickly evolved. This lower trigger point would reflect the optimal densities for this amount of medium in the habitat (when dispersal is possible). But it would have been the same in both beakers because, in the migratory series, all those that began a generation were descendants of beetles that actually dispersed to beaker C.

If the latter argument explains why population sizes in beakers A and C of the migratory series converge, it might suggest a different question. Why don't A- and C-population sizes converge in the sedentary series? However, there is no reason to expect them to.

Each sedentary generation began with a mixed stock of disperser and non-disperser progeny. At the end of a generation, most of the adults in beaker A would have been non-dispersers with a high trigger point. But those in beaker C would all have been dispersers with the newly evolved, lower trigger point. Hence, one may expect the population in a C beaker of the sedentary series to have about the same number of adults as in both A and C beakers of the migratory series. Indeed, that is what was observed.

One may attempt to explain the population densities of beetles in beakers C of both the migratory and the sedentary series in another way. Suppose beetles succeeded in finding a place with plenty of food and low population density. Because of their success, they may assess their environment to be rich and expect to find more such places. Hard to please, they would tend to emigrate from fairly low-density patches. On the other hand, if emigration results in finding a new patch with difficulty, and that patch tends to be poor and have high population density, then individuals should be rather reluctant to emigrate. Such behaviour was predicted by theoretical (Korona, 1989a) and empirical (Korona, 1989b) models of two *Tribolium confusum* females competing for a limited amount of medium. It is also predicted by the theory of giving-up-density (Brown, 1988) for all organisms.

The theory of giving-up-density has had many successes but may not apply here. It presupposes foragers that can sample enough patches to estimate the distribution of patch conditions. Thus, it may apply at a local scale and contribute to the overall behaviour of *Tribolium*. Nonetheless, it appears unsuited to explaining changes in the tendency for long-range dispersal.

Further investigations of the contribution of dispersal to population regulation should be carried out on free-living populations of *Tribolium* beetles instead of those kept for many generations in the laboratory. To provide good evidence for hereditary changes in dispersal activity, common-garden experiments would be useful. In them, beetles emerging from different experimental series would be introduced to a single environment where their dispersal tendencies would be compared. Nevertheless, even without such common-garden experiments and even without a selection regime favouring complete elimination of dispersal activity, the experiment presented here did show several things: (1) Dispersal may help to regulate population density. (2) Selection in favour of dispersal can increase the tendency to disperse and selection against it can decrease it. (3) Dispersing beetles are not smaller than non-dispersers; indeed, they may be larger.

ACKNOWLEDGEMENTS

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