

## The influence of the ability to disperse on generation length and population size in the flour beetle, *Tribolium castaneum*

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**Abstract.** 1. In *Tribolium castaneum* Herbst, in which dispersal is genetically determined, it is possible to select for strains that are characterized by high and low dispersal. High dispersal (HD) beetles are better adapted than low dispersal (LD) beetles for colonization, as can be seen from differences that exist between the two groups with regard to several life-history parameters.

2. Comparisons were made between the dynamics of seventy-two HD and seventy-two LD populations. Generation length in HD populations was significantly shorter than in LD populations. After 9½ weeks, in open treatments (from which dispersal away from the set was allowed), HD populations had more beetles than LD populations, whereas in closed treatments (from which dispersal away from the set was not allowed) the opposite was true.

3. These findings may explain the maintenance of the genetic variability of dispersal behaviour in natural populations of *T. castaneum*.

**Key words.** *Tribolium castaneum*, dispersal, generation length, population size.

### Introduction

Variability for dispersal characterizes natural populations of many insect species (Harrison, 1980). According to Dingle (1984), dispersal is one component of a more general 'dispersal syndrome', which is an adaptation to life in shifting environments. Changes in demography, aimed at increasing the likelihood of survival of dispersing individuals, are other components of this syndrome.

Empirical studies on the relationship between habitat stability, dispersal and life-history parameters are best conducted in the field. What is

the proportion of dispersers and non-dispersers in populations that differ in the stability of their habitat? Is this difference, if it exists, associated with variation in life-history parameters?

However, a major difficulty in performing such studies in nature is related to the inability to distinguish between dispersers and non-dispersers, before they disperse. A reasonable substitute is a study in the laboratory, in which changes in the stability of the habitat can be monitored, and populations that are known a priori to differ in their tendency to disperse are compared.

The flour beetle *Tribolium castaneum* Herbst (Coleoptera: Tenebrionidae) is suitable for such a study. Its rate of dispersal was shown to be determined genetically (Ogden, 1970; Ritte & Lavie, 1977; Riddle & Dawson, 1983), and differences in several life-history traits have been found between dispersers and non-dispersers (Lavie & Ritte, 1978; Zirkle *et al.*, 1988). This

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paper followed the dynamics of *T. castaneum* populations that were established from lines that were selected for high and low rates of dispersal (Ritte & Lavie, 1977), and were kept under different regimes of environmental conditions. If differences in demographic parameters between disperser and non-disperser populations are found, they may be responsible for the maintenance of variability of dispersal in natural populations of *T. castaneum*.

## Material and Methods

**Beetles.** The individuals belonged to a strain that was derived from wild beetles, collected in a grain storage site in Rehovot, Israel. Originally, this strain was used to determine differences in the tendency to disperse among members of a natural population of *T. castaneum*. Dispersal was measured in an apparatus similar to that of Prus (1963), in which dispersers move along a string, usually placed in a narrow tubing, from their present vial that contains food, into another, empty vial. The rates of dispersal were studied in groups of siblings, and different families had different rates (Ritte & Agur, 1977).

Selection produced two lines that differed significantly in their rate of dispersal; one line had a high rate (and was called high dispersal, or HD, line), and the other had a low rate (and was called low dispersal, or LD, line). Crosses between the lines indicated that this difference had a genetic basis, and that a single, sex-linked gene was involved (Ritte & Lavie, 1977). Since the two lines differed also in several life-history parameters, it was suggested that the primary function of dispersal in *T. castaneum* was colonization (Lavie & Ritte, 1978).

Half of the beetles used in the present study were derived from the HD line, the other half from the LD line.

**Environmental conditions.** The experiment was carried out in a dark controlled environment incubator, with high (~100%) humidity and a temperature of  $29 \pm 1^\circ\text{C}$ .

The medium was composed of wheat flour, supplemented for every 100 g with 5 g brewers yeast. The mixing of flour and yeast was done in an electric mixer for at least 2 h. Before use the medium was sterilized by heating to  $60^\circ\text{C}$  for at least 24 h. The dishes used for maintaining the beetles were similarly sterilized before each run.

**The experiment.** Each population was kept in a dispersal set, a circle of eight small jars that

contained media, and were connected by 30 cm long dispersal tubes. Half of the dispersal sets were closed, and in them the beetles could move only among the eight jars. In the open sets each dispersal tube had an opening to a side branch that led to an empty small glass bottle. Beetles that arrived at these bottles were removed from the population.

Another difference between dispersal sets involved the media. In half of them (50% of the closed sets and 50% of the open sets), the media were renewed every other week. The eggs, larvae, pupae and adults were removed from each jar, and returned to it after it had received the fresh medium. The other half contained deteriorating media – here the various developmental stages were also removed every other week, but were returned to the old medium.

For each combination of conditions (open versus closed dispersal sets; renewed versus deteriorating media) eighteen sets of paired populations were conducted. Each set included one LD and one HD population that were run under identical conditions.

To initiate each population, fourteen adult beetles (seven males and seven females) were introduced into jar 1. These beetles were derived from a group of pupae that had been collected 2 weeks earlier from the HD or LD line, and separated according to sex.

Population sizes (the number of adult beetles in all jars) were determined, for each population, twice a week. The number of counts for each population was twenty (9½ weeks). At each count the jars were disconnected from the dispersal tubes, and the adults in each jar were counted. The dispersal tubes were reconnected at least 2 h after the reintroduction of the adults into the jars.

In the open dispersal sets the beetles in the empty glass bottles were also counted, and then discarded.

The present paper is limited to life-history parameters in which significant differences were found between HD and LD populations.

## Results

### (a) Generation length

The limitation of counts to twice a week, which was done in order to minimize disturbances, made it difficult to find differences between all HD and LD populations with regard

**Table 1.** The number of adult beetles found in each comparison of an HD population with a corresponding LD population (HD/LD), at the twentieth (last) count. Fifteen comparisons were made in each combination of dispersal set and type of medium.

| Type of medium | Type of dispersal set |          |
|----------------|-----------------------|----------|
|                | Closed                | Open     |
| Renewed        | 468/727               | 508/420  |
|                | 2*/377                | 252/82   |
|                | 480/574               | 236/168  |
|                | 490/988               | 474/100  |
|                | 800/1030              | 581/68   |
|                | 896/994               | 601/449  |
|                | 379/399               | 251/137  |
|                | 326/686               | 527/352  |
|                | 674/634               | 464/305  |
|                | 517/556               | 562/353  |
|                | 1501/1837             | 484/881  |
|                | 721/814               | 475/433  |
|                | 656/1217              | 745/391  |
|                | 1211/950              | 591/730  |
|                | 1435/1677             | 1114/722 |
| Deteriorating  | 350/668               | 169/284  |
|                | 317/377               | 70/30    |
|                | 431/636               | 37/272   |
|                | 636/750               | 250/177  |
|                | 512/686               | 205/141  |
|                | 918/1208              | 280/83   |
|                | 291/210               | 30/25    |
|                | 475/613               | 219/3*   |
|                | 427/932               | 60/63    |
|                | 640/830               | 94/41    |
|                | 1086/1034             | 519/418  |
|                | 340/226               | 180/95   |
|                | 622/754               | 365/465  |
|                | 498/817               | 582/174  |
|                | 592/926               | 532/544  |

\* Because of an error, the fourteen individuals from which this population was established were all of the same sex.

to the time of first appearance of the second generation. In twenty-six of the thirty-five comparisons between HD and LD populations (in closed dispersal sets), adult beetles from the second generation first appeared, in both populations, in count 9. However, in the nine comparisons in which a difference could be detected, it was always in the same direction – generation length in HD populations was shorter than in the corresponding LD populations.

Lavie & Ritte (1978) and Wu (1979) described a negative correlation between the tendency to

disperse and developmental time. Our results, which are in accordance with this correlation, indicate a shorter generation for HD populations. This difference is significant ( $P=0.002$  in a one-tailed sign test).

(b) *Population sizes at the end of the study*

At the twentieth count (9½ weeks after its establishment), each population was composed of adults from three generations: some or all of the original fourteen founders (first generation), the descendants of these founders (second generation), and their offspring (third generation). The size of each HD population was compared to the size of the corresponding LD population (Table 1).

A two-way analysis of variance indicated a highly significant effect on population size of the type of dispersal set (closed versus open), whereas neither the effect of the type of medium (renewed versus deteriorating), nor the interaction type of medium × type of dispersal set were significant (Table 2). Moreover, for both

**Table 2.** An analysis of variance, for testing the effects of type of medium and type of dispersal set on the difference in final size between matching pairs of HD and LD populations.

| Source of variation   | df | SS      | MS      | F <sub>s</sub>         |
|-----------------------|----|---------|---------|------------------------|
| Type of medium        | 1  | 21056   | 21056   | 0.5653 <sup>ns</sup>   |
| Type of dispersal set | 1  | 1200203 | 1200203 | 32.2233 <sup>***</sup> |
| Interaction           | 1  | 58282   | 58282   | 1.5648 <sup>ns</sup>   |
| Error                 | 56 | 2085803 | 37246   |                        |
| Total                 | 59 | 3365344 |         |                        |

\*\*\* $P<0.001$ . ns = non-significant.

**Table 3.** The mean (± standard error) of the difference in final size between matching pairs of HD and LD populations, for the different combinations of type of dispersal set and type of medium. The sample in each combination included fifteen paired populations.

| Type of medium | Type of dispersal set |              |
|----------------|-----------------------|--------------|
|                | Closed                | Open         |
| Renewed        | -193.60±56.10         | 151.60±57.44 |
| Deteriorating  | -168.73±44.21         | 51.80±39.13  |

types of medium, in closed dispersal sets the mean size of LD populations was larger than that of HD populations, while the reverse was true in open dispersal sets (Table 3).

### Discussion

The objectives of dispersal in *Tribolium* involve evacuation of old habitats, after the conditions in them had deteriorated, on one hand, and colonization of new habitats on the other hand. Selection should thus produce complex adaptations that include both the ability to disperse and the ability to colonize (Dingle, 1985).

For colonization, the most important life-history characteristic is rapid population growth (MacArthur & Wilson, 1967; Safriel & Ritte, 1980; Dingle, 1986), to shorten the period in which the freshly established population can undergo random extinction. Lewontin (1965) showed that a decrease in developmental times is far more effective than an increase in fecundity.

Lavie & Ritte (1978) found that, in *T. castaneum*, HD beetles developed more rapidly, produced more eggs during the first 4 days of reproduction, and produced a higher proportion of fertile eggs than LD beetles, suggesting the existence of a dispersal syndrome. It should be remembered, however, that the difference between members of HD and LD populations is not in the actual act of dispersal, which eventually they all do (as was described by Ziegler, 1976), but in the conditions that trigger it. In natural populations, which tend to occupy temporary habitats, the variability of dispersal behaviour is more continuous, and the association between dispersal and life-history attributes leads to a more efficient utilization of the environment.

In newly established populations, HD beetles have the selective advantage. As population density increases, and environmental conditions deteriorate, the advantage is transferred to non-dispersers. Being less sensitive to the deterioration of the environment (closed dispersal sets in Table 3), they can continue to reproduce in less favourable conditions. This can explain the genetic variability with respect to the tendency to disperse that exists in natural populations of *T. castaneum*.

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