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DISPERSAL OF LARVAE OF THE TENEBRIONID BEETLE, *ZOPHOBAS RUGIPES*, IN RELATION TO WEIGHT AND CROWDING¹

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Abstract. When larvae of the tenebrionid beetle, *Zophobas rugipes*, were allowed to disperse among 26 equivalent chambers in a circular dispersarium, distribution patterns were found to be a function of larval weight and number of larvae in the apparatus (N). Small larvae (\bar{x} wt \approx 250 mg) were significantly aggregated while large mature larvae (\approx 1000 mg) were highly overdispersed. Medium larvae were intermediate, being overdispersed when N was 26 and showing some aggregation within general overdispersion when N was 52. Larval distributions did not deviate significantly from randomness when N was 13, indicating weak interactions at low density. The increasing tendency to overdisperse with increasing larval weight correlates with the parallel increasing tendency to pupate. Since metamorphosis of *Zophobas rugipes* larvae is known to be inhibited by crowding, this weight-related overdispersal probably allows pupation by mature larvae by causing them to leave regions of high population density.

Key words: Dispersal; metamorphosis; population density; Tenebrionidae; *Zophobas rugipes*.

INTRODUCTION

The tendency of animals to distribute themselves in space to allow optimal utilization of resources is a fundamental adaptation and has been well studied. The resource may be food, nesting sites, and others, and the distribution response may be aggregation, random distribution or overdispersal. Among insects, dispersal patterns have been documented for factors such as food and reproduction. The dispersal of the flour beetles, *Tribolium confusum* and *T. castaneum* has been described both in time (Ogden 1970, Hågstrum and Leach 1973) and space (Naylor 1959, 1961, 1965; Ghent 1966), as well as in relation to population density. King and Dawson (1972, 1973) have studied habitat selection in populations of flour beetles. Many other reports relate to the population studies, but most involve adult insects and thus do not deal with the effects of population density and spacing on metamorphosis. Woolever and Pipa (1970) found that larval wax moths, *Galleria mellonella*, need a minimum amount of space in order to pupate, but they did not determine the effects of population density *per se*. Tschinkel and Willson (1971) reported that mature larvae of the tenebrionid beetle, *Zophobas rugipes*, and several other species as well, fail to undergo metamorphosis under crowded conditions. The inhibitory factor is the mechanical

stimulation resulting from larval contacts, and such stimulation prevents the formation of the prepupa so that inhibited larvae continue to move about actively and can disperse. Obviously larvae must pupate to complete the life cycle, and since pupation is prevented by the presence of other larvae, we postulated that mature *Zophobas* larvae must seek solitude by repelling one another and therefore overdispersing. Furthermore, we postulated that the tendency to overdisperse would increase with larval weight. We report here the results of testing these hypotheses using an apparatus similar in principle to that used by Naylor (1959, 1961). Naylor allowed adult tenebrionid flour beetles (*Tribolium*) to distribute themselves among a fixed number of equivalent vials filled with flour and found that, while the quality of the dispersal depended upon the population density, males tended to aggregate at all densities and females to distribute uniformly. Larvae showed a sporadic density-dependent tendency to leave the flour (Naylor 1965). In our apparatus, the preference of larvae of *Zophobas rugipes* for small spaces was exploited and larvae were allowed to choose among a fixed number of empty chambers.

MATERIALS AND METHODS

Construction of the dispersarium

A flat ring (inside diameter = 31 cm; outside diameter = 55 cm) was cut from a sheet of 18-mm-thick Plexiglas.TM Twenty-six circular 4-cm-diam

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holes were cut in the ring at equal intervals and connected with the inner rim by grooves (1 cm × 0.6 cm wide) on the underside of the ring. A circular piece of 0.32 cm Plexiglas™ equal to the outside diameter was fastened to the bottom of the ring and another served as the top. Brown paper lined the floor of the apparatus and was changed between experiments, and the top was fastened with knurled nuts after the larvae were placed into the center. Larvae could enter each chamber only from the central arena. Chambers were about the same size as pupal chambers which larvae excavate in soil (4 cm × 2 cm).

The experiments were carried out under dim red illumination (15-W bulb 91.4 cm above the apparatus) at a temperature between 25°C and 27°C.

Three sizes of larvae were selected from mass cultures and weighed individually to the nearest milligram: small larvae, ≈ 250 mg, medium larvae, ≈ 500 mg, and large larvae, ≈ 1,000 mg. Standard deviations for experiments were mostly < 40 mg and the actual \bar{x} weights and standard deviations of the size groups were: 237 ± 16 mg; 547 ± 53 mg; 928 ± 83 mg. Experiments were conducted one at a time over a 6-mo period without food or water at three larval densities (N) for each of the three weight groups. These densities were 13, 26, and 52 larvae in the dispersarium, giving chamber:larva ratios of 2, 1, and 0.5 respectively. There were thus nine combinations of larval density and weight. Each combination was tested twice (replicates 1 and 2) in the dispersarium, giving a total of 18 experiments, run sequentially, with each lasting 5–12 days depending upon whether larvae continued to move or settled down to pupate. In addition, a second series of experiments was run (small and large larvae only) in which each chamber received a small amount of bran. Each combination was replicated once for a total of six experiments carried out in this series.

The chambers were individually numbered and the number of larvae in each and in the central arena was observed at least three times daily for the duration of each experiment, but the analyses were carried out only on the first observation (between 0800 and 0900) of each day. The order in which the experiments were done was determined by the availability of larvae of the appropriate weight.

At the end of each experiment, the number and position of larvae undergoing metamorphosis (usually pharate pupae) were noted. Other data consisted of experimental day, chamber and central arena occupancy, number of larvae in the experiment (N), and \bar{x} weight of the larvae.

Analysis of data

Two types of indices were calculated to assess the extent of deviation of the observed occupancy pat-

terns from those expected on the basis of chance. In the first, the expected number of chambers with k larvae, $E(m_k)$, was compared with the observed number of chambers with k larvae, m_k . The expected number of chambers with 0, 1, 2, . . . larvae was calculated by the formula

$$E(m_k) = n(r/k) (1/n)^k (1 - 1/n)^{r-k}$$

where m_k = the number of chambers occupied by exactly k larvae, n = the number of chambers, r = the total number of larvae in the chambers. Feller (1957) gives this formula as an answer to the "birthday problem." The expected values for $r = 1, 2, 3, \dots, 52$ and $k = 0, 1, 2, \dots, 8$ were computed. A chi-squared value was calculated for the difference between the observed and expected numbers of chambers with 0, 1 or 2 and more larvae. In addition the total chi-square for the three levels of occupancy was calculated for each experimental day, as well as a mean chi-square over all days of each experiment.

The second estimate of dispersal was based on the Poisson approximation to the distribution of the number of chambers with 0, 1, 2, . . . larvae. Feller (1957:94) shows that $E(m_k)$ can be approximated by

$$E(m^k) = n e^{-\lambda} \lambda^k / k!$$

where n , k are as defined above and $\lambda = r/n$. This suggests as a second estimate of dispersal the ratio of the sample variance (s^2) to the sample mean (\bar{x}) of the number of larvae per chamber, the well-known coefficient of dispersion ($= s^2/\bar{x}$). For a Poisson (i.e., random) distribution this value should be close to 1.00. Values > 1.00 indicate that the larvae are more clumped than expected by chance and values < 1.00 indicate overdispersion or repulsion. Coefficients of dispersion were calculated for each experimental day and their means over all days of each experiment (mean coefficient of dispersion).

Analysis of variance of the coefficients of dispersion was carried out using the factors: time (first, middle and last days of each experiment), mean larval weight, larval density in the dispersarium (N), replicate, and combinations of these. In addition, analysis of variance of the mean coefficients of dispersion (averaged over experimental days) was carried out using the last three factors listed above.

RESULTS

When larvae were placed in the central arena of the dispersarium, their typical response was immediate rapid locomotion toward the perimeters so that within 1–5 min all but a few larvae had left the arena and were in the chambers. There followed a period lasting from one to several days during which individual larvae occasionally left chambers, moved

through the arena (usually along the outer perimeter), and re-entered other chambers. Such movement was more common among smaller larvae and among larger larvae when these were present at high density. In the larger larvae, after about a day had elapsed, intrusion of a wandering larva into an occupied chamber often resulted in attack by the resident. During the first 2-4 days, about half of the larger larvae occupying chambers lay in the entrance tunnel to the chamber, perhaps facilitating defense. As these larvae transformed into pharate pupae (usually by day 5 to day 7) they withdrew into the chamber, ceased locomotion and curled into the quiescent pharate pupal state. Molting to the pupa usually takes from 10 to 15 days at 27°C, but most experiments were terminated before this time.

The principle by which the dispersarium probably operates is the provision of a limited number of preferred sites among which the larvae must distribute themselves. Lack of interaction among larvae would result in random distribution patterns, attraction would result in aggregation (underdispersion), and repulsion in even distribution (overdispersion). For experiments in which the number of larvae did not exceed the number of chambers, the mean proportion of larvae found in the chambers is 89.2% ($\pm 5.0 s$). Obviously, the larvae have a strong preference for the chambers over the arena, perhaps in response to thigmotactic stimuli. When the number of larvae exceeded the number of chambers ($N = 52$), the mean occupancy drops significantly to 75.3% ($\pm 9.8\% s$), mostly as a result of the repulsive interactions among larger larvae.

In general, the experiments show that the dispersal of *Zophobas rugipes* larvae is strongly dependent upon larval weight and density (N), and that small larvae are underdispersed while large larvae are strongly overdispersed. The dispersal pattern within each weight group is itself a function of density. The mean chi-square indicates that all but one (small larvae) of the dispersal patterns are significantly nonrandom when $N = 26$ or 52. The chi-squared value does not indicate whether the nonrandomness is the result of over or underdispersion and this information is given by the mean coefficient of dispersion (Fig. 1). The lines of significance marked on Fig. 1 have associated probabilities that are too large, since they are based on a coefficient of dispersion value for 1 day whereas the graphed index is the average of several days' results. Since there is (statistical) dependence from day to day, it is not possible to calculate the exact significance level associated with the observed mean coefficient of dispersion. However, the analysis is conservative and underestimates the significance of the results.

The patterns for $N = 13$ do not deviate significantly

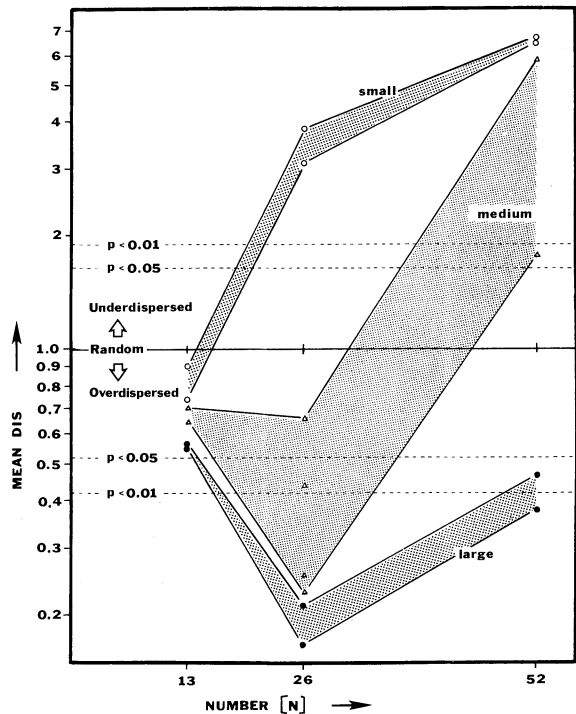


FIG. 1. The mean coefficient of dispersion (DIS) as a function of the number of larvae (N) in the 26-chambered dispersarium and larval size (small, medium, large). Small larvae underdisperse, large larvae overdisperse and medium larvae are intermediate. Shaded and bounded areas indicate the range of experimental results, not confidence intervals. The lines of significance marked on the graph are conservative, i.e., indicated probabilities are too large.

from randomness (Fig. 1). There is some tendency for overdispersion and this is especially marked for large larvae. Small larvae are generally aggregated, significantly so for $N = 26$ and 52. Medium larvae are nearly randomly distributed for $N = 13$, but are random-to-overdispersed for $N = 26$ and change to aggregated at $N = 52$. Apparently medium weight larvae are changing in their dispersal characteristics, giving rise to the observed large variation in the coefficient of dispersion at any one density and perhaps also to the density-dependent qualitative difference.

Large larvae are consistently and strongly overdispersed when the number of larvae equals or exceeds the number of chambers ($N = 26$ or 52). In these experiments, the uniformity of distribution was especially obvious when N was 26, resulting in a single larva in each of 25 or 26 chambers with an occasional one in the arena. When there were 52 large larvae in the dispersarium, the majority of the chambers still contained only a single larva, the difference remaining in the arena. Mean chamber

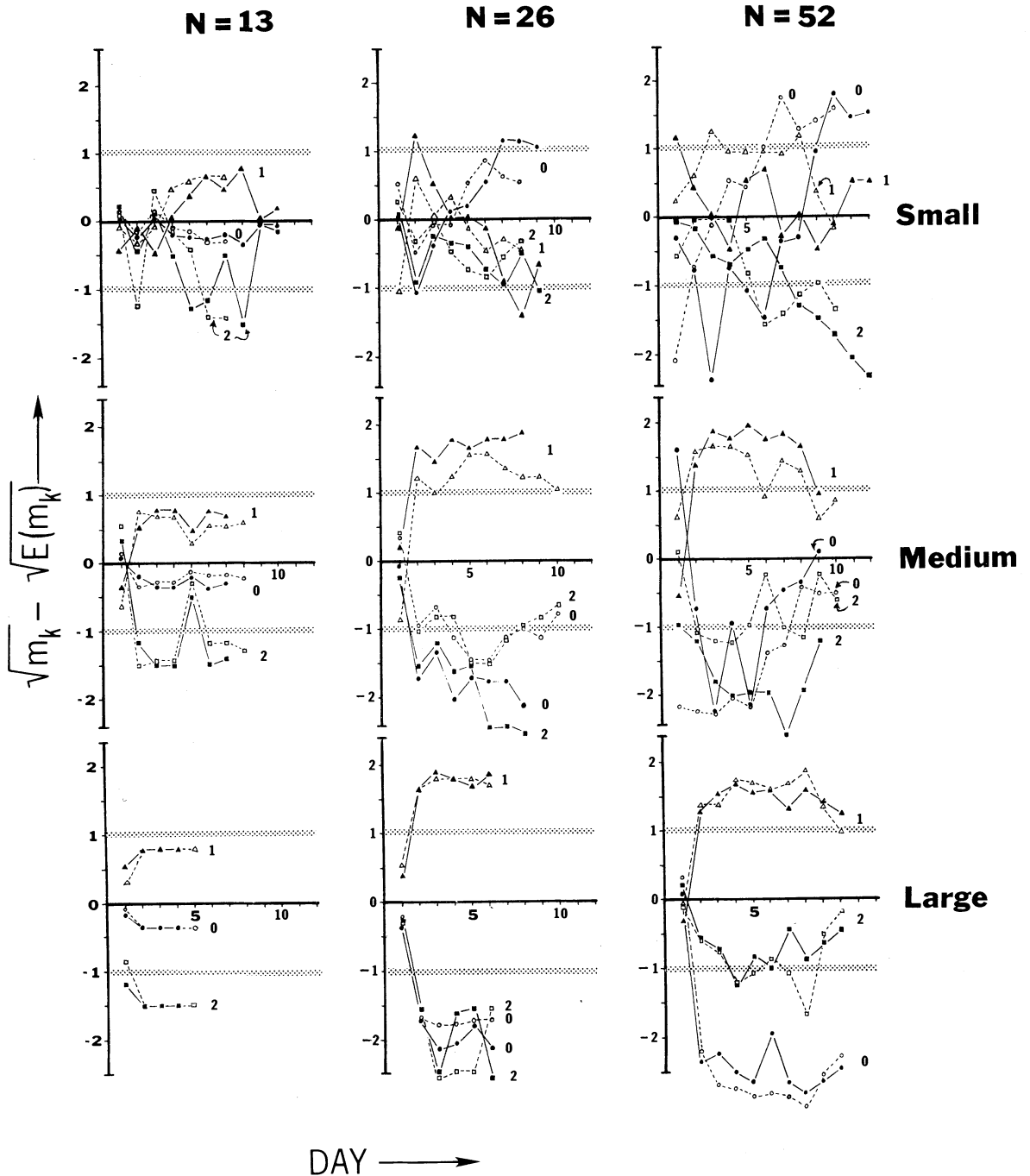


FIG. 2. Daily progress of dispersal for three levels of density and three of larval size. The deviation of the observed number of chambers of 26 with k larvae (m_k) from the number expected on the basis of random assortment, $E(m_k)$, is plotted as the difference in their square roots in order to make the difference independent of N . Replicate 1 is plotted with solid lines and closed symbols, replicate 2 with dotted lines and open symbols. Circles denote the difference for empty chambers ($k = 0$), triangles the difference for chambers with 1 larvae ($k = 1$), and squares the difference for chambers with 2 or more larvae ($k = 2$). These values of k are also given near the end of each line or pair of lines. The shaded lines at $+1.0$ and -1.0 given the approx. 95% confidence limits for random distribution.

occupancy in these experiments was only 62%. Apparent aggressive interactions between larvae were frequent in these experiments, the larvae approaching one another with open mandibles, biting one another and thrashing violently from side to side. It appeared that larvae occupying chambers defended these against intruders and often stationed themselves facing or actually in the entrance. Such interactions were not seen among small larvae and were rare among medium larvae.

The layout of the data suggested a split-plot design (Armitage 1973:253) and the appropriate analysis of variance indicated a significant interaction for Weight \times Density (N) ($p < 0.05$) as well as Weight \times Day of Experiment ($p < 0.01$). In addition, the main effects of Density, Weight and Time are significant ($p < 0.01$), assuming a fixed-effect analysis of variance model. The observed differences in the coefficient of dispersion are thus due to weight of the larvae and its interaction with density and time during the experiment. The effect of weight on coefficient of dispersion itself depends upon the density of the larvae in the dispersarium.

When the experiments were repeated with a small amount of bran (food) in each dispersarium chamber, the results were similar for the large larvae, but the small larvae were significantly less aggregated at medium and high densities. Medium larvae were not tested due to a shortage of larvae.

The nature of the larval dispersal becomes especially clear when the deviations from the "expected" random pattern are considered as the experiment progresses. Figure 2 shows these deviations for each day of each experiment. The data are plotted as the difference in the square roots of the observed and expected numbers of chambers with k larvae, where k is 0, 1, 2-or-greater. This form of plot makes the size of the deviations approximately independent of the sample size (N) and allows direct visual comparison among the three densities. Positive values of this difference indicate that there are more chambers with that number of larvae than would be expected on a random basis. The approximate 95% confidence intervals for random distribution are marked on the graphs. Note that the values of $[m_k]^{1/2} - [E(m_k)]^{1/2}$ for the three levels of k are not independent of one another.

Small larvae at $N = 13$ show no significant deviation from the randomly expected pattern and fluctuate from day to day, though there is some trend to overdispersion (an excess of chambers with 1 larva). Experiments with 26 small larvae begin similarly, but end with the larvae aggregated (an excess of chambers without larvae and a deficit with 1 and 2 or more). While the mean coefficient of dispersion for these two replicates indicates no sig-

nificance, the daily chi-squared values indicate that the larvae are highly aggregated for the last 3 days of replicate 2 and somewhat so for replicate 1. This trend toward aggregation as the experiment progresses is very marked when $N = 52$ and the initial deficit of empty chambers gives way to a large excess by the end of the experiment. Aggregation in these two experiments is obvious and in each replicate, there was at least one chamber with from 8 to 33 larvae in it. Such cases give rise to the deficit in the number of chambers with two or more larvae.

In all experiments with medium and large larvae, the dispersal patterns are established within 2 or 3 days and remain fairly stable thereafter. The gross daily fluctuations observed among small larvae are absent. The distributions are consistently overdispersed, and while not significantly so when $N = 13$, they are when $N = 26$ or 52. The pattern is stable for medium larvae when $N = 26$, and there is a decline from overdispersion after about 5 or 6 days when $N = 52$. There is even a hint of this in one of the replicates when $N = 26$. Such changes in pattern are not apparent for large larvae where the excess of chambers with one larva is particularly stable. When $N = 52$ there is an especially large deficit of empty chambers probably as a result of the larval preference for chambers over arena combined with the mutual repulsion which gives rise to overdispersion. There is a decline in this overdispersion toward the end of the experiment. By this time, the original occupants of the chambers are quiescent prepupae and can no longer exclude other larvae from their chambers.

The data for medium larvae at $N = 52$ in Fig. 1 and Fig. 2 seem to be in contradiction. Figure 1 indicates aggregation under these conditions while Fig. 2 indicates overdispersion (excess of chambers with one larva). This apparent contradiction results from the fact that in each of these two experiments, there was one chamber which contained a large number of larvae while the remainder of the larvae were more evenly dispersed. (Larvae in the arena form the pool from which this excess is drawn.) This gives rise to a large variance and coefficient of dispersion, but since only one chamber contains a large number of larvae, the $[m_k]^{1/2} - [E(m_k)]^{1/2}$ index indicates overdispersion. Obviously, the results of these two analyses complement one another and give a more complete picture of the dispersal pattern.

These dispersal patterns parallel changes in the larvae's tendency to undergo metamorphosis as reflected in the proportion of the larvae which pupate. Pupation in mature larval *Zophobas rugipes* is inhibited in relation to crowding (Tschinkel and Willson 1971), but the tendency to pupate at all develops gradually in the life of a larva. At the end of each

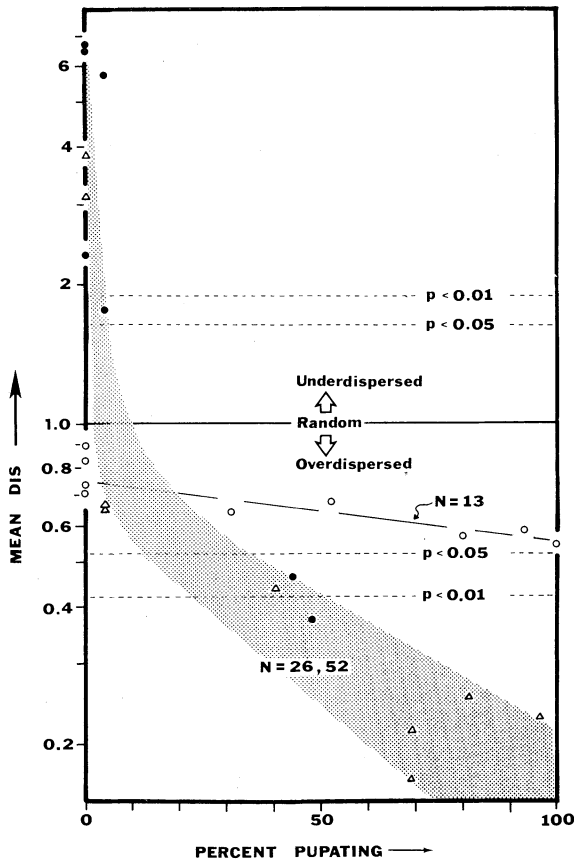


FIG. 3. The mean coefficient dispersion (DIS) as a function of the percentage of larvae pupating after the experiment. Shaded region gives the approx. relationship (not a confidence interval) when larval density is 26 (triangles) or 52 (closed circles). When N is 13 (open circles) the percentage pupating shows a slight relationship to the mean coefficient of dispersion, but none of these distributions was significantly nonrandom. Levels of significance are indicated.

experiment, the number of larvae in the prepupal stage was scored. While the experiments were too short to allow pupal molt, these pre-pupae all molted to pupae within a few days after the end of the experiments. The proportion of larvae pupating after the experiment shows a strong relationship to the coefficient of dispersion (Fig. 3), changing from underdispersed when the percentage pupating is small (small larvae) to overdispersed when the proportion is large (large and some medium larvae). The overdispersion is a reflection of the need of pupation-ready larvae for isolation.

Pupation-readiness is itself primarily a function of larval weight (Table 1) as well as density. No small larvae pupated, but a substantial fraction of medium and large ones did. The suppressive effect of high density ($N = 52$) on pupation is greater for

TABLE 1. The proportion of larvae pupating in relation to the larval size and number of larvae in the dispersarium

Nominal mean weight (mg)	Number in dispersarium		
	13	26	52
250	0	0	0
500	0.42	0.66	0.04
1000	0.89	0.69	0.46

medium larvae than for large, and for both sizes, the pupation rate when $N = 13$ is probably a reasonable estimate of the "inherent" tendency of each size group to pupate. The fact that this is higher for $N = 26$ for medium larvae is probably a reflection of the high variability of this group. The effect of larval population density on the proportion pupating has been described by Tschinkel and Willson (1971).

DISCUSSION

The overdispersion of large larvae correlates clearly with increasing pupation-readiness, itself a result of increasing weight and age. When larvae are confined at various densities, the inhibition of pupation increases with increasing crowding (Tschinkel and Willson 1971) and it has been postulated that this effect evolved in response to cannibalism of the quiescent pre-pupal and pupal stages by the larvae. When pre-pupae or pupae were added to 100-mm petri dishes containing 15 active larvae in an excess of bran, more than 75% of the pre-pupae or pupae were cannibalized before they completed the pupal or adult molt. Lower larval densities resulted in lower rates of cannibalism (W. R. Tschinkel, *personal observation*). Six cases of cannibalism were also observed in the dispersarium experiments. Clearly, pre-pupae or pupa in the presence of active larvae have greatly reduced chances of survival.

King and Dawson (1972, 1973) reported that large larvae of *Tribolium* select certain habitats for pupation so that neither larvae nor pupae occur uniformly in a heterogeneous environment. They suggested, on circumstantial evidence, that the selection of warmer pupation sites was in response to cannibalism of the pupal stage, exposure to cannibalism being shortened by the elevated temperature. In the case of *Zophobas*, evidence that pupation-site selection evolved in response to cannibalism is more compelling, for overdispersion of large larvae is almost certainly an aspect of pupation-site selection. The overdispersion reported in this study probably evolved in response to cannibalism, since by shunning other larvae, pupation-ready larvae come to rest in

areas where they are unlikely to be cannibalized or disturbed during the process of metamorphosis, thus increasing their fitness. It is significant that while small larvae tended to move about a great deal for the entire duration of the experiment, there was very little movement of larvae from chamber to chamber among large larvae. Sometimes the occupancy established on the second day was maintained throughout the experiment.

Little is known of the life habits of *Z. rugipes* under natural conditions. The larvae have been collected twice by one of us (WRT) from the guano deposits of fruit bats, and another species of the genus has been reported from a compost pile (Floyd Werner, *personal communication*). Recently, *Zophobas* sp. has been collected in guano deposits in a Peruvian Oilbird cave in which both adults and larvae were extremely abundant (W. W. Baker, *personal communication*). If these cases are indeed typical of the life habits of the species, the laboratory findings on dispersal and inhibition of metamorphosis can be interpreted as follows: The species is a general feeder (as are many tenebrionids) and exploits discrete and localized deposits of organic matter such as bat guano, compost, bran, etc. The tendency of small larvae that are unready for pupation to aggregate allows the exploitation of such localized food sources at moderate to high densities of larvae. However, the general feeding habits give a propensity toward cannibalism, especially of animals near pupal or adult molt. In order to escape this cannibalism, pupation-ready larvae are repelled by contact with other larvae and such contact inhibits metamorphosis. Not until a larva has come to rest in a place where it remains undisturbed for a minimum (3–5 days) period will it undergo metamorphosis. In the field, this probably means a cell excavated in the soil away from the food mass. It is interesting to note that almost no pupae were collected from the Costa Rican guano deposits, though larvae were quite abundant in the guano and adults on its surface and on the walls of the cave. It seems likely that pupation took place elsewhere, removed from the seething guano deposit.

The larvae do not react to one another at low densities, implying that a minimum probability of contact must exist before over or underdispersal results. At low densities, the risk of cannibalism would be low and the advantage of overdispersal would be diminished. There is therefore no significant correlation between dispersal index and the pupation-readiness of a population of larvae at low density.

The density-dependent tendency for *T. confusum* larvae to leave the flour (Naylor 1965) may be similar to the dispersal of mature *Zophobas* larvae. The

tendency of any given species of tenebrionid larva to overdispersal might be expected to be directly related to the degree of inhibition of pupation brought about by crowding which, in turn, might be related to the tendency toward cannibalism. In *Tribolium* larvae, the ability to pupate under crowded conditions would thus be in concert with the slight tendency to overdispersal, while the strong overdispersal of *Zophobas* larvae complements the strong inhibition of pupation by crowding.

Observations of the behavior of *Zophobas* larvae during dispersal suggests that spacing results from tactile and aggressive interactions, but this has not yet been specifically tested, and olfactory cues cannot be ruled out.

The biological meaning and cause of aggregation of small larvae is not clear. The extreme aggregation always appeared after several days and may be due to some environmental inhomogeneity which is accentuated by aggregation. For example, chamber humidity would rise with increasing occupancy, and a gradually increasing dehydration of the larvae during the experiment would increase their tendency to seek out these humid chambers, further increasing their humidity. Since larvae can probably derive some metabolic water from food, the presence of bran during an experiment would be expected to have the observed depressing effect on aggregation. Similarly, addition of bran to experiments with medium and large larvae would be expected to increase overdispersal (i.e., decrease aggregation) or have no effect. This has been observed in large larvae (medium larvae were not tested).

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