

DROSOPHILA LARVAL FORAGING BEHAVIOUR: DEVELOPMENTAL STAGES

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Abstract. Two distinct developmentally related behaviour patterns can be identified in third-instar larvae of *Drosophila melanogaster*, 'foraging' behaviour and 'wandering', a pre-pupation behaviour. An age-related change in behaviour from foraging to wandering is quantified by measuring larval locomotion at the early, middle and late third instar in an environment where food is distributed in patches. Strain, moisture, food and inhomogeneities in the texture of the surface of the medium significantly influence larval locomotory behaviour.

Larval foraging behaviour can be quantified as the relative amount of feeding and locomotor behaviour performed on a food substrate during a test period (Sokolowski 1980). The number of probes with the mouth hooks ('shovels') and the number of muscular contractions passing along the body of the larva ('crawls') are discrete measures of feeding and locomotor behaviour respectively. Sewell et al. (1975), Burnet et al. (1977) and Ohnishi (1979) studied larval feeding rate in an aqueous yeast suspension. Sokolowski (1980) examined larval feeding and locomotor behaviour simultaneously, by placing a larva in a petri dish covered with a yeast paste so that when it moved it left a visible trail or path in the yeast. The length of the foraging trail during a 6-min test period was measured. This measurement was termed the 'path length' of the foraging trail. Since path length was strongly positively correlated (+0.9) with the number of crawls, path length was used to provide a rapid determination of the locomotory component of the foraging behavioural phenotype (Sokolowski 1980). Long-path-length larvae, which have high crawling scores and traverse a large area while foraging in a yeasted dish, were called 'rover' larval foragers. 'Sitter' larval foragers have relatively shorter path lengths, low crawling scores and cover a smaller area while foraging.

Many variables influence larval behaviour in the third instar, including age (Sewell et al. 1975), strain (Burnet et al. 1977; Godoy-Herrera 1977; Ohnishi 1979; Sokolowski 1980, 1982; Sokolowski & Hansell 1983a) and the type and homogeneity of the medium (Sokolowski et al. 1983). The effects of age are of particular interest, since by the end of the third instar larvae are searching for a pupation site rather than foraging. Pupation site choice and rate of development are strain-

dependent (Sameoto & Miller 1968; Markow 1979; Sokolowski & Hansell 1983b). Thus at some time in the third instar, larvae may be expected to shift from foraging-related acts to pre-pupation acts in a strain-dependent manner. Can these different acts be reliably separated by assaying for locomotory behaviour? In the present study, larvae of four strains, W_2W_3 , W_2E_3 , E_2E_3 and E_2W_3 (Sokolowski 1980) were tested at three different stages in third-instar development (3, 4 and 5 days post-hatching) in order to answer this question.

The behavioural test used by Sokolowski (1980) (larval locomotion during a 6-min period on yeast paste) reliably distinguished early third-instar larvae of different strains. The yeast paste medium has at least three characteristics important to foraging: it is homogeneous, moist and a concentrated food source. How do larvae behave when presented with a heterogeneous medium and with choices between food and non-food medium? In this paper we present data relating to these questions; we defer discussion of the effect of changing the quality of the medium with respect to moisture and consistency to another paper (Sokolowski et al., in preparation).

Methods

Strains

The four stocks isogenic for the second and third pairs of chromosomes used in this study were designated W_2W_3 , W_2E_3 , E_2E_3 and E_2W_3 . A breeding scheme that uses the presence of crossover suppressors to permit substitution of intact second or third chromosome pairs from one stock into another is described in Sokolowski (1980). The chromosome-substituted stocks were W_2E_3 and E_2W_3 . E_2W_3 had the same second chromosome pair as E_2E_3 , but differed in having

the third chromosome pair from W_2W_3 . W_2E_3 and E_2E_3 both carried recessive alleles for the gene for ebony body colour (e^{11}) on their third chromosomes.

Aging of Larvae

The following procedure was used in order to prepare culture dishes (100 larvae/dish) of accurately (± 1.75 h) aged larvae. Culture dishes were prepared by allowing approximately 200, 5- to 10-day-old flies of each strain to lay eggs on a spoon covered with cream of wheat molasses medium, seeded with a dab of yeast and autoclaved honey paste. The spoon and flies were placed inside a 0.25-litre bottle. The spoons were incubated for 20 h at $24 \pm 1^\circ\text{C}$ and approximately 60% RH, on a light cycle of 12 h light followed by 12 h of darkness (lights on at 0800 hours). The spoons were then removed from the bottles and all larvae which had hatched were cleared from the surface of the medium. Any group of larvae which hatched within 3.5 h after the spoon was cleared were ± 1.75 h in age.

Culture Dishes

One hundred freshly hatched larvae were removed from the spoon using a dissecting needle and placed in a petri dish (8.5 cm in diameter and 1.4 cm high) which contained no less than 28 g of a standard non-living brewer's yeast agar medium. This dish, which will be referred to as the culture dish, was incubated under the conditions previously described. Replicate culture dishes were prepared to enable the testing of 3-, 4- and 5-day-old (post-hatching) larvae. All behavioural tests were performed between 1400 and 1900 hours.

Paired Behavioural Testing Apparatus

The paired behavioural testing apparatus illustrated in Fig. 1 was prepared as follows. Two large (13.5 cm in diameter and 2.2 cm high) petri dishes were filled to a depth of 0.5 cm with hot Difco agar (prepared by combining 8 g of agar with 500 ml of distilled water and then boiling the solution for 5 min). The agar in the dishes was then flamed (using a Bunsen burner) to eliminate bubbles from the surface, thereby ensuring a smooth surface texture for larval locomotion. After the agar had cooled, two plugs (2.5 cm in diameter and 0.5 cm high) were placed on the agar layer in the positions indicated in Fig. 1. The apparatus on the left (C-T) contained one agar (non-nutritive) plug which will be called the C or control plug and one food plug (of a standard yeast-agar medium darkened with

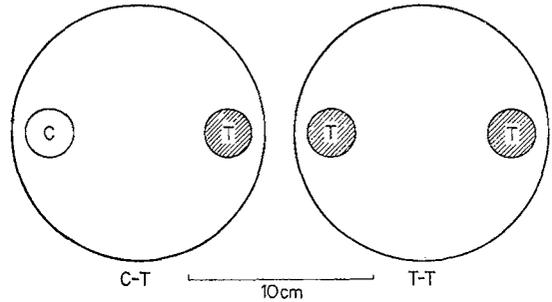


Fig. 1. The paired behavioural testing apparatus. Two plugs were placed on an agar surface. The C-T apparatus contained one agar plug (C) and one food plug (T). The T-T apparatus contained two food plugs positioned as shown.

charcoal; Sokolowski 1982) which will be called the T or treatment plug. The apparatus on the right (T-T) contained two food plugs. The plugs were cut with a sharp metal cutter and placed on the surface of the agar using a spatula.

Testing Procedure

All of the larvae were collected from each culture dish and rinsed twice in a small amount of distilled water to remove all food residue. All of the larvae removed from a single culture dish comprised the group from which a random sample of 50 larvae were chosen for the paired behavioural tests. Two sub-groups of 25 larvae were tested synchronously in the paired behavioural testing apparatus. One sub-group of larvae was placed on the centre of the control plug in the C-T apparatus using a no. 2 Reeves series paint brush. Simultaneously, the second sub-group was placed on the centre of the left treatment food plug in the T-T apparatus (see Fig. 1), after which the lids of the dishes were placed on the apparatus, marking the beginning of the experiment. One investigator observed the entire paired behavioural testing apparatus and recorded the number of larvae on each of the four plugs and the number of larvae off both plugs in C-T and T-T. This information was recorded every minute for the first 10 min of the test, and afterwards at 10-min intervals, up to 60 min. In this paper only the 'long-term' results (20-60 min) are discussed. We used the longer term data because most effects, while apparent in the short-term data, are more definitive in the longer term data. The short-term data probably reflected larval adjustment to a new environment. All behavioural tests were performed at $22 \pm 1^\circ\text{C}$, with

diffuse overhead fluorescent lights and with the apparatus placed on a black table-top.

Results

I. Tendency to Leave a Plug

At each time interval, we calculated the number of larvae that left the plug on which they were placed. Since larvae from each culture were placed on the control (non-food) plug in the C-T apparatus, and on a food plug in the T-T apparatus, the number of larvae which were off each plug at a given time formed a matched pair of observations. By averaging these values for the observations at times 20–60 min, we obtained a single pair of numbers for each culture. This (paired) observation represents the mean long-term tendency to leave a plug (Fig. 2). Each symbol represents results from one culture.

The distribution of points in Fig. 2 shows several aspects of larval behaviour. First, note that all 3-day points (triangles) are on or near the vertical axis. Few 3-day-old larvae of any strain left a food plug. The number of larvae leaving the non-food plug at day 3 was variable and strain-dependent. A two-way analysis of variance was performed. An arcsin square root transformation was performed to normalize the data (proportion of larvae off the control plug). The independent variables were: (1) 2nd chromosome

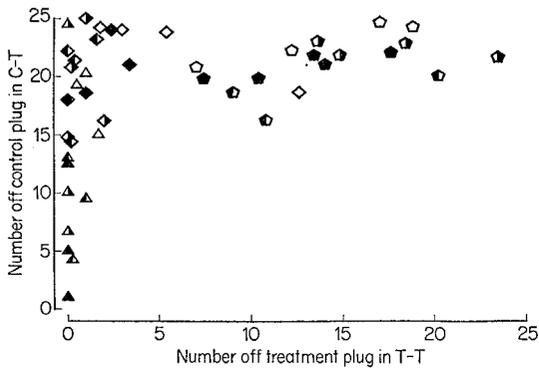


Fig. 2. The average number of larvae out of 25 which left the plug upon which they were originally placed (during 20 to 60 min). The *y*-axis shows the number having left the C plug in the C-T apparatus. The *x*-axis shows the number having left the T plug in the T-T apparatus. Triangles, diamonds and pentagons represent 3-, 4- and 5-day-old cultures respectively. A shaded left or right half of the symbol indicates the strain used had a W 2nd or 3rd chromosome. Thus, a fully shaded triangle represents a 3-day-old culture of strain W_2W_3 ; an unshaded pentagon represents 5-day-old E_2E_3 larvae. A diamond with a shaded left half and an unshaded right half represents a 4-day-old culture of W_2E_3 larvae.

and (2) 3rd chromosome. *F* values for these variables ($df=1,8$) were: (1) 5.65, $P < 0.025$, and (2) 0.61, NS, indicating that the 2nd chromosome had a significant effect on leaving non-food plugs at 3 days; the effect of the 3rd chromosome was not significant. No significant interactions between 2nd and 3rd chromosomes were found ($F=0.01$, NS). This can be seen in Fig. 2, where W_2 strains (triangles with shaded left halves) fall lower than E_2 strains.

Four-day-old larvae (diamonds in Fig. 2) showed a greater tendency to leave the non-food plug than 3-day-old larvae. Four-day-old larvae rarely left food plugs. In contrast, 5-day-old larvae often left the food plugs. No significant strain differences were found in the behaviour of 4- and 5-day-old larvae.

II. Tendency to Leave All Plugs

By calculating the mean numbers of larvae off the plugs during times 20 to 60 min for C-T and T-T, a second pair of numbers was calculated for each culture. These paired observations are plotted in Fig. 3. Three and 4-day-old larvae tended to be found on one of the plugs in both C-T and T-T arrangements. Few 3- or 4-day-old larvae stayed off all plugs. In contrast, 5-day-old larvae were more likely to be found off both plugs. This tendency was not strain-dependent. At day 5, approximately equal numbers of larvae left both plugs in the C-T and T-T arrangements. Most of these larvae were observed contacting food plugs and leaving them during the course of the experiments. As larvae did not remain on the plugs contacted, this wandering behaviour may

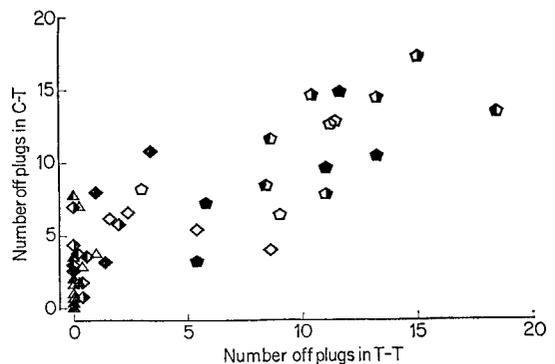


Fig. 3. The average number of larvae off both plugs, in C-T on the *y*-axis and in T-T on the *x*-axis. The triangles, diamonds and pentagons represent 3-, 4- and 5-day-old larvae respectively. Symbols of strains are depicted as in Fig. 2.

represent searching for a pupation site. In several 5-day-old cultures, some larvae were already forming puparia. Two replicates for 4-day-old E_2E_3 larvae represent the main exceptions; these same replicates are located among the 5-day points in Fig. 2.

III. Tendency to Go to Food

Three- and 4-day-old larvae frequently leave the control plugs (section I above). Are they 'wandering' regardless of the presence of food (section II above) or will they stay on food if they encounter it? In Fig. 4, we plot the mean number of larvae on the non-food plug versus the mean number on the food plug in the C-T arrangement during times 20-60 min. We conclude from Fig. 3 that almost all 3-day-old larvae were on one of the two plugs, as the triangles lie near the diagonal line (number on food plug plus number on non-food equals 25). Almost all 3-day-old larvae which left the non-food plug in the C-T arrangement found the food plug and remained on it. Three-day-old larvae with W 2nd chromosomes tended not to leave the control plug as frequently as 3-day-old larvae with E 2nd chromosomes (see Fig. 2). When W_2 larvae left the control plug, they quickly found the food plug. A greater number of 3-day-old E_2 larvae tended to leave the non-food plug than W_2 3-day-old larvae, and more E_2 larvae reached the food plug; thus they fall near the right half of the line.

Four-day-old larvae leave control plugs more readily than 3-day-old larvae. Most of the 4-day-old larvae that leave the control plug locate and remain on the food plug. All 4-day points fall in the lower right portion of the figure. Many 5-day-

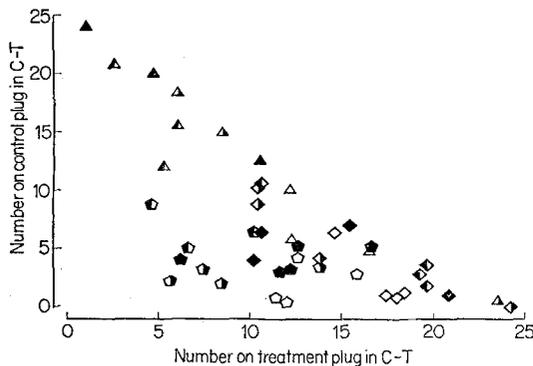


Fig. 4. The number of larvae of the different strains that were found on either the C plug or the T plug in the C-T apparatus. Symbols for strains are depicted as in Fig. 2.

old larvae leave all plugs (section II above), but of those on plugs, the majority are on food plugs. Thus, almost all 5-day-old larvae leave the non-food plug; some of those wander, others locate food and remain on the food.

Discussion

I. The Relationship Between Larval Behaviour and Age

The results indicated a simple relationship between the behaviour observed in the two parts (C-T and T-T) of the paired behavioural test apparatus. The age dependency of larval behaviour patterns can be summarized as follows. (1) Three-day-old larvae remained on food plugs. Larvae on the control plugs slowly moved to food plugs at a strain-dependent rate. (2) Four-day-old larvae tended to remain on the food plugs, but less so than 3-day-old larvae. The major difference in 4-day-old larvae (compared with 3-day-old larvae) is that they left the C plug and moved to the food plug more rapidly. (3) Five-day-old larvae left the C plug as readily as 4-day-old larvae. However, 5-day-old larvae also left the food plug.

Two distinct developmentally related behavioural patterns can be identified in third-instar larvae of all strains: 'foraging' and 'wandering'. These behaviours are performed sequentially. 'Foraging' involves remaining on the food plugs in the T-T arrangement, whereas in C-T larvae leave the non-food plug (C) and subsequently move towards and remain on the food plug (T). The frequency with which larvae leave the C plug is low at 3 days and reaches a maximum at 4 days. 'Wandering' involves leaving food plugs. As larvae get older, they tend to leave food plugs (Fig. 4). In our apparatus the second behaviour (wandering) is performed only after the first behaviour (foraging) is maximally expressed. As larvae get older the tendency to leave food plugs does not increase until the tendency to leave non-food plugs is fully displayed.

Since these behaviour patterns are expressed sequentially, we can outline a simple model which relates changes in behaviour to developmental stage (measured by larval age; Fig. 5, Table I). In this model we propose that the two behaviours are developmentally related.

We have repeated the same experiments for other strains of *D. melanogaster* ('smell blind' (*sb1*) and 'Canton-S'; Aceves-Pina & Quinn 1979; Tompkins et al. 1982). The same sequence of behaviour (as described above) is observed, although the magnitude of the effects differ in

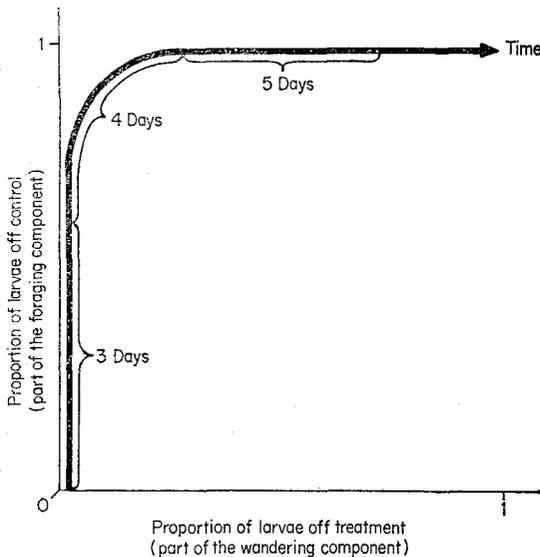


Fig. 5. The behavioural-development curve, showing the change in behaviour from foraging to wandering as time (age of the larvae) increases from 3 to 5 days.

some details (Sokolowski et al., in preparation). Thus we are encouraged to believe that this sequence of behaviours may be representative of those that will be found in most well-fed third-instar *D. melanogaster* larvae.

II. Variability in Larval Developmental Rates Between Cultures of the Same Strain

In these experiments, within-strain replicates were performed using larvae cultured in different dishes. Culture dishes identical in the density (100 larvae/dish) and chronological age (3, 4 or 5 days post-hatching) of larvae sometimes showed large variations in both larval behaviour and developmental stage. For example, the developmental

stage attained in replicate 5-day-old cultures of the same strain, as measured by the number of puparia, varied from 0 to 35%. Among the 3-day-old replicates of one strain (E_2W_3), C-plug leaving varied from 33% to 92%. Although within-strain, between-replicate variation was large, all matched pairs of observations for all replicates still fell along the behavioural-development curve shown in Figs. 2 and 5.

The sources of variation between culture dishes are unknown. Culture conditions such as temperature, light, humidity, type of medium, volume of medium, density and age of the larvae were standardized. There were, however, visible differences in the culture dishes which were most obvious in the 5-day-old replicates. The amount of larval processing of the medium differed. In some dishes the medium had been worked into a fine mixture, whereas in other dishes the medium was firm. There may have been an interaction between the rate of larval development and the condition of the medium. Initial small differences in the medium may have been amplified and expressed as larger developmental differences in the culture dishes.

The variability between replicates reinforces the importance of testing larvae in a paired behavioural testing apparatus. The matched pair of observations enabled us to control for larval development. Since larval age strongly affected the performance of the two behaviours, paired tests yielded more useful information than unpaired tests would have done. By using paired tests, most of the within-strain variability between replicates can be explained as variability in the developmental stage attained. Furthermore, the mean of all within-strain replicates is not as informative as the behavioural-development curve (Fig. 5) along which individual replicates lie.

Table I. The Relationship Between Third-instar *Drosophila melanogaster* Larval Behaviour and Age

Age (days)	Response to non-food plug	Response to food plug	Response to agar surface
3	Leave C plug slowly when contacted	Remain at food plug when contacted	Traverse surface until a plug is contacted
4	Leave C plug rapidly	Remain at food plug when contacted	Traverse surface until a plug is contacted
5	Leave C plug rapidly or pupate on plug	May leave food plug when contacted	Traverse surface until a plug is located or a pupation site is located

III. Strain-dependent Behaviour in Early 3rd-instar Larvae: the Edge Effects

Differences in the behaviour of 3-day-old larvae were strain-dependent and attributable to the second pair of chromosomes. Strains that shared E_2 chromosomes (E_2E_3 and E_2W_3) showed a higher propensity to leave a non-food (C) plug than W_2 (W_2W_3 and W_2E_3) strains. Older larvae (4 days) of all strains also left the C-plug more frequently. Could E_2 strains simply have developed faster? The observed times (in hours) to pupation, counted from 3 days post-hatching, is approximately 87 for E_2E_3 , 71 for E_2W_3 , 64 for W_2W_3 and 73 for W_2E_3 . Clearly, both E_2 and E_3 chromosomes lead to longer developmental times. The differences in developmental time in the four strains are opposite in direction to the observed behavioural effects of the E chromosomes in the present study. At 3 days, E_2E_3 and E_2W_3 were found further along the behavioural-development curve (Fig. 2). We conclude that the differences in the tendency of 3-day-old larvae to leave the C plug are primarily due to an effect of the 2nd chromosomes on behaviour rather than to differences in developmental rate.

Three-day-old larvae showed some novel behaviour patterns. Many larvae, after being placed on top of an agar plug (non-food plug) remained in contact with the side of the plug and/or burrowed beneath it. The presence of any physical inhomogeneities or 'edges' in the medium profoundly affected larval behaviour in a strain-dependent manner. This 'edge effect' is important in any experimental apparatus with punctures, holes or edges in blocks of otherwise uniform medium. For example, the preference of 3-day-old W_2 strains for remaining at edges almost completely masked other aspects of foraging behaviour in our raw data.

There is a significant effect of the 2nd chromosomes on the likelihood of leaving a C plug at 3 days. However, of those larvae which left the C plug, there was no significant strain difference in the number which reached the food plug within an hour. The strain-dependent manner in which 3-day-old larvae reached the food plug in the C-T apparatus was a function of differences in 'edge-leaving' behaviour rather than the rate of locomotion on agar.

Do any of the strain differences in the 3-day-old larvae reflect the 'rover/sitter' behaviours described by Sokolowski (1980)? The 6-min locomotory tests (Sokolowski 1980) were done in a moist nutrient-rich paste-like yeast slurry.

The present longer-term experiment was performed using an inhomogeneous environment and required that larvae traverse a smooth, firm, relatively dry, non-nutritive agar surface in order to reach a food source. The E_2 ('sitter') larvae reach the food as quickly (if not faster) than the W_2 ('rover') larvae. This implies that the 'rover/sitter' forager types described by Sokolowski (1980) do not reflect differences in general activity levels between the W_2 and E_2 strains. Rather, the expression of 'rover' and 'sitter' behaviours is dependent on there being a moist nutrient-rich test surface.

Earlier research (Sokolowski 1982) also showed a significant effect of the second chromosomes on digging behaviour. 'Rover' larvae may also be predisposed to burrow or dig into inhomogeneities in the medium (Sokolowski et al., in preparation).

IV. Food Searching by 4-day-old Larvae: Transitional Behaviour

Four-day-old larvae of all strains showed little tendency to leave food plugs. There was a radical increase in the tendency to leave non-food plugs in 4-day-old as compared to 3-day-old larvae. The significant strain differences in C-plug leaving in 3-day-old larvae were no longer evident at 4 days. Since food-leaving behaviour has not yet appeared, but the frequency of C-plug leaving has peaked, we feel that 4-day-old larvae are in a transitional state between the two behavioural patterns described (section I, above).

V. Five-day-old Larvae: Switch to 'Wandering' Behaviour

While the locomotory behaviour of 3- and 4-day-old larvae can be said to be related to foraging (since they locate and remain on food), 5-day-old larvae show a dramatic shift in their response to food. Increasing numbers leave food plugs with time and begin a 'wandering' movement around the agar surface of the C-T and T-T apparatus. As this behaviour seemed most pronounced in cultures where some puparia were found, it is reasonable to suppose that it may be related to the search for a suitable pupation site. Although pupation height is known to be under genetic control in these strains (Sokolowski & Hansell 1983b), no obvious strain differences in pre-pupation behaviour were seen in 5-day-old larvae in the present study.

Early third-instar larval foraging behaviour is affected by strain, 'edges' or inhomogeneities in the medium, surface texture and moistness, and

the presence of food. Mid-way through the third larval instar, 'food-searching' behaviour (leaving non-food plugs and staying at food plugs) peaks; strain differences are not apparent at this time. By the time larvae are 5 days old, foraging behaviour is at a minimum, and 'wandering', a non-foraging pre-pupation behaviour, is increasingly expressed. Changes in larval foraging and wandering behaviour may co-occur with known developmental events, such as ecdysone secretion or the attainment of minimum pupation weight (Bakker 1961). Further studies of third-instar larval behaviours may help to establish the relationship between genetically controlled behaviour and developmental events.

Acknowledgments

We gratefully acknowledge Krystyna Tarkowski for typing the manuscript, Sharon Bauer for technical assistance and Allen Sokolowski, Sharon Bauer and Virginia Wai-Ping for critically reading the preliminary manuscript. We thank John Ringo and an anonymous reviewer for comments. This work was supported by an NSERC University Research Fellowship to M. B. Sokolowski.

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(Received 22 March 1983; revised 31 August 1983;
MS. number: A4041)