The development of larval movement patterns in *Drosophila*

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A survey in the development of larval movement patterns of *D. melanogaster* and *D. simulans* wild stocks was made. Larval movement patterns of four lines of *D. melanogaster* genetically selected for fast and slow feeding rate were also examined. The following behavioural elements were considered: locomotion, turning behaviour and number of larvae moving within a small area ("sitter" larvae). Because locomotion increases with larval age whilst turning does not substantially change between 24 to 96 hours of age, the larval movement pattern of *Drosophila* tends to be straighter as development proceeds. In the absence of food, *Drosophila* larvae increase locomotion and decrease turning. The opposite situation occurs when larvae are deposited on a nutritive substrate. However, larvae of a slow feeding line (SA) have a modified pattern of movement in the presence and in the absence of food. Orthokinesis and klinokinesis were more obvious in *D. simulans* larvae. Quantitative differences in the larval movement pattern of these two sibling species were greater on a nutritive medium. In both species the percentage of "sitter" larvae increases in the presence of food, particularly in *D. simulans*. This increase depends on larval age. Crosses between two *D. melanogaster* strains, which differ in larval turning, suggest that one pair of major additive genetic factors control this behaviour. The adaptive nature of larval movement patterns of *Drosophila* is discussed.

INTRODUCTION

The distribution in the wild of animal species depends in part on individual movement patterns of each sex (Andrewartha and Birch, 1954; Brown, 1975). The way an animal moves should be a product of natural selection to maximise fitness as a function, for instance, of a feeding strategy, search for conspecifics and avoid predators and/or parasites (Schoener, 1971; Bond, 1980). Individual movement patterns should also be considered within an ontogenic perspective. As development of *Drosophila melanogaster* proceeds it is believed that a differential activation and repression of some groups of genes occurs (review in García-Bellido, 1982). Modifications in the epigenetic relationships between genes have consequences for the development of behavioural patterns (Godoy-Herrera *et al.*, 1984). Individual differences in the development of a behaviour may represent alternative solutions to adaptate to particular ecological conditions.

Studies on the genetic control of the development of movement patterns in *Drosophila* could help to elucidate the behavioural mechanisms involved in microhabitat distributions of these species (Parsons, 1983). Besides, a study of movement patterns in *Drosophila* should help to understand how these insects perceive and orient themselves in space and how these flies adjust their activities in response to changes in the temporal and spatial distribution of resources such as food and space. The developmental processes affecting larval pattern of movement of *Drosophila* should be related to the ecological demands of each larval instar.

Very few reports have been published on the development of larval movement patterns in *Drosophila*. Green *et al.*, (1983) provided a description of the organization of larval behavioural patterns in *D. melanogaster* and *Drosophila simulans*. Godoy-Herrera *et al.*, (1984) reported that young larvae of *D. melanogaster* show a preference for moist substrate, while mature larvae prefer dry substrates on which to crawl. These authors also found that, in *D. melanogaster*, increase in larval

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locomotion with age is caused by growth in body size and changes in the genetic architecture of this behaviour. Sokolowski *et al.*, (1984) have reported that *D. melanogaster* larvae of 3 to 4 days old stay on food, but 5-day-old larvae leave food for a more dry place. These behaviours are expressed sequentially during larval development of this species.

In this paper the development of larval movement patterns of the sibling species *D. melanogaster* and *D. simulans* are described in terms of level of locomotion and number of changes in direction made by larvae while moving in the presence and in the absence of food. The goal is to understand how larval movement pattern of *Drosophila* is organised and what relation exists between this behaviour and larval feeding pattern. A genetic analysis of turning behaviour is also provided.

MATERIALS AND METHODS

Strains and egg collections

The stocks of *D. melanogaster* used in this research were the *vestigial* (*vg*) and Oregon R-C (wild type) strains and four lines kindly supplied by Dr Barrie Burnet, which had been genetically selected for fast (*FA* and *FA spa*) and slow (*SA* and *SA spa*) feeding rate. The *FA spa* and *SA spa* lines contained the mutation *sparkling* (*spa*) located on chromosome 4. A detailed description of all these lines is provided by Sewell *et al.* (1975) and Burnet *et al.*, (1977). Flies of the Quilicura strain of *D. simulans* were also used. This strain was formed with adults captured by Budnik and Brncic in Quilicura, near Santiago (see Budnik and Brncic, 1983, for details). All strains employed were kept by mass culture in half-pint bottles filled with about 50 cc of Burdick's medium (1954), at $24 \pm 1^\circ\text{C}$ with a constant regime of light.

Groups of inseminated females of *D. melanogaster* (the Oregon R-C strain) and *D. simulans* (the Quilicura strain) and of the *FA*, *FA spa*, *SA* and *SA spa* lines were left without food for a 3 hour period in half-pint bottles. After this time, a plastic spoon was introduced into each one of the bottles; each spoon was previously filled with medium spread with fresh live yeast and acetic acid. These two substances stimulate oviposition. Eggs laid by the females were collected after 3–4 h with the aid of a dissecting needle. About 50 eggs were sown in each spoon. Successive samples of larvae of 24, 48, 72 and 96 h of age were collected from the spoons. Each group of larvae was placed

in a petri dish filled with 3 per cent agar. After 5 min the larvae were again individually captured and their patterns of movement recorded as described below.

Larval movement patterns

A set of $15 \times 15 \times 2$ cm of perspex boxes were filled with 3 per cent agar. After coding, the agar was covered with a film of 2 per cent yeast suspension (see Sewell *et al.*, 1975 for details). Larvae tested were deposited onto the agar at the center of the box and covered with a lid of the same material divided into squares of 0.5 cm. The positions of the larvae were recorded by plotting the position on a drawing at interval of 30 s in a total period of 2 min. Fifty individuals from each age group (24, 48, 72 and 96 hours old) were scored.

Locomotion was measured by counting the number of squares crossed by each larva. A detailed description of this method is given by Godoy-Herrera *et al.*, (1984). Larval turning behaviour of *D. melanogaster* was measured at 48, 72 and 96 hours. *D. melanogaster* larvae of 24 hours moved slowly on agar (they moved still more slowly on agar spread with yeast) making it difficult to record turning behaviour. This was not observed for 24 hours larvae of *D. simulans*. In each drawing straight lines were traced among consecutive positions of larvae. This procedure allowed for counting and recording changes in direction and number of movements in straight line made during larval locomotion. A movement in a straight line was registered when three consecutive larval positions appeared in line.

Genetics of turning

A further set of experiments were performed to examine the hereditary basis of larval turning behaviour of *D. melanogaster*. The Oregon R-C and *vestigial* strains were used. Larvae of these two strains seem to show important differences in this behaviour (Godoy-Herrera, 1982). Larvae of 108 hours of the Oregon R-C and *vestigial* strains and of the F_1 and F_2 were individually transferred onto an agar substrate, and number of changes in direction was counted for a 3 min period. Hybrid larvae of 108 hours obtained by crossing the F_1 and the parental strains were also examined. Data for all crosses were analysed following Mather and Jinks (1971), Cavalli-Sforza and Bodmer (1971) and Stewart (1969).

Arcsin and log scales were used to transform data (Sokal and Rohlf, 1969).

RESULTS

Development of larval movement patterns in D. melanogaster and D. simulans

Table 1 shows larval locomotor behaviour in the sibling species *D. melanogaster* and *D. simulans* at 24, 48, 72 and 96 hours-of-age. Distance travelled increases with larval development. On food, larval locomotor activity in both species is lower than on agar, as measured by the means of squares crossed. Orthokinesis in 48 and 72 hours larvae of *D. simulans* is more intense than in larvae of the same age of *D. melanogaster*. Differences in locomotion between larvae of the same age of these two species are statistically significant (t values ranged from 2.655 to 4.753; $P < 0.05$; $df = 98$) either on agar or food, with the exception of larvae of 24 hours moving on food and 96 hour larvae crawling in both environments.

Some of the larvae tested to 24, 48 and 72 hours old of *D. melanogaster* and *D. simulans* moved within a surface area of about 1 cm². Larvae aged 96 hours of these two species also showed this behaviour progressing within a surface area of 2 cm². Figure 1 shows that the percentage of "sitter" larvae of *D. melanogaster* at 24, 48 and 72 hours is similar in the presence and in the absence of food (t values for the significance of differences between two percentages (Sokal and Rohlf, 1969) ranged from 0.469 to 0.963; $P > 0.05$); *D. melanogaster* larvae of 96 hours show substantial differences in "sitter" larvae in the presence and in the absence of food ($t = 2.677$; P , two tailed < 0.01). In contrast, in *D. simulans* the percentage of "sitter" larvae at 24, 48, 72 and 96 hours of age is greater on food than on agar (t values fluctuated between 2.677 and 5.208; P , two tailed < 0.01).

Figure 1 also shows that, in the absence of food, larvae of *D. melanogaster* and *D. simulans* exhibit a similar number of "sitter" individuals,

with the exception of 72 hour larvae ($t = 2.255$; P , two tailed < 0.05). However, on food, the percentage of "sitter" larvae at 24 and 48 hours of development is greater in *D. simulans* than in *D. melanogaster* (t values were, respectively, 2.955 and 3.262; P , two tailed < 0.01).

Table 2 shows the percentage of turns on agar and on food made at 24, 48, 72 and 96 hours of development by *D. simulans* and *D. melanogaster* larvae. In the same substrate *D. simulans* larvae of 24, 48, 72 and 96 hours of age exhibit a similar percentage of turns. *D. melanogaster* larvae of 48, 72 and 96 hours also show a similar percentage of turns on the same substrate. On agar and on food larvae of the same age in both species do not substantially differ in percentage of changes in direction. Larvae of these two sibling species increase the number of turns in the presence of food. Klinokinesis is more obvious in *D. simulans* larvae of 24, 48 and 72 hours of age (table 2).

Development of movement patterns in larvae selected for fast and slow feeding rate

Distance travelled by larvae of 24, 48, 72 and 96 hours of age in the fast (*FA* and *FA spa*) and slow (*SA* and *SA spa*) feeding lines is shown in table 3. *FA*, *FA spa* and *SA spa* larvae decrease locomotion on food; magnitude by which this occurs depends on strain and larval age. *SA* larvae show a similar level of locomotor behaviour in the presence and in the absence of food. *FA* larvae show lowest locomotion on food and on agar. In agar environment, differences in locomotor activity are significant, with the exception of larvae of 48 hours of the *FA* and *FA spa* strains and larvae of 72 hours of the *FA* and *SA spa* strains (t values ranged from 2.003 to 8.779; $P < 0.05$; $df = 98$). On food, t values fluctuated between 2.217 and 24.978; $P < 0.05$; $df = 98$; larvae of 24, 48, 72 and 96 hours of the *FA spa* and *SA spa* strains do not show important differences in locomotor activity on food.

Table 1 Larval locomotor activity at 24, 48, 72 and 96 hours of age in *D. simulans* (the Quilicura strain) and *D. melanogaster* (the Oregon R-C strain) on agar and food. In each experiment 50 larvae of each age group were scored

Species	Substrate	Hours of development			
		24 Mean of squares crossed	48 Mean of squares crossed	72 Mean of squares crossed	96 Mean of squares crossed
<i>D. simulans</i>	agar	2.46 ± 0.18	7.28 ± 0.39	11.28 ± 0.48	10.26 ± 0.54
	food	1.16 ± 0.14	2.08 ± 0.23	5.70 ± 0.38	6.40 ± 0.53
<i>D. melanogaster</i>	agar	3.74 ± 0.29	4.92 ± 0.31	9.54 ± 0.45	9.64 ± 0.47
	food	1.56 ± 0.19	2.93 ± 0.31	8.16 ± 0.42	5.54 ± 0.42

Figure 1 Percentage of "sitter" larvae at 24 (a), 48 (b), 72 (c) and 96 (d) hours of age in the sibling species *D. melanogaster* and *D. simulans* in the absence (open bars) and in the presence (hatched bars) of food.

Figure 2 shows the percentage of "sitter" larvae on agar, and on food, between 24 to 96 hours of development in the *FA*, *FA spa*, *SA* and *SA spa* lines. On food, percentages of "sitter" larvae of 24, 48, 72 and 96 hours of age in the *FA* line are greater than in the absence of this resource (t values for the significance of differences between two percentages ranged from 3.688 to 9.060; P , two tailed < 0.01). Something similar occurs with larvae of 24, 48 and 72 hours of the *FA spa* line

(t values fluctuated between 2.639 and 5.527; P , two tailed < 0.01), and larvae of 24 and 72 of hours of the *SA spa* line (t values were respectively, 1.995 and 5.836; P , one tailed < 0.05). Only *SA* larvae of 72 hours increase the percentage of "sitter" larvae on food ($t = 2.255$; P , one tailed < 0.01).

Figure 2 also shows that differences in percentage of "sitter" larvae between the lines are greater in the presence of food, particularly at 24, 48 and 72 hours of development. For instance, on food,

Table 2 Percentage (arcsin transformation) of turns made by *D. simulans* (the Quilicura strain) and *D. melanogaster* (the Oregon R-C strain) larvae on agar and on food at different ages. Thirty eight larvae of each age group were scored

	Agar				Food		<i>ts</i> respect to the absence of food for % of turns
Hours of development	N of turns	N of movement in straight line	% of turns	N of turns	N of movement in straight line	% of turns	
<i>D. simulans</i>							
24	118	32	62.51	142	8	76.69	3.97*
48	117	33	62.03	132	18	69.73	2.12*
72	116	34	61.55	133	17	70.36	2.42*
96	125	25	65.88	119	31	62.94	0.80
<i>D. melanogaster</i>							
48	110	40	58.89	128	22	67.45	2.30*
72	119	31	62.94	127	23	66.97	1.10
96	114	36	60.67	125	25	65.88	1.40

* $p < 0.01$.

Table 3 Larval locomotor activity at 24, 48, 72 and 96 hours of age on agar and on food in the *FA*, *FA spa*, *SA* and *SA spa* lines. In each experiment 50 larvae of each age group were scored

Strain	Substrate	Hours of development			
		24 Mean of squares crosses	48 Mean of squares crosses	72 Mean of squares crosses	96 Mean of squares crosses
<i>FA</i>	agar	1.24 ± 0.18	3.94 ± 0.21	5.72 ± 0.41	8.26 ± 0.35
	food	0.12 ± 0.05	0.34 ± 0.09	1.66 ± 0.24	3.60 ± 0.28
<i>FA spa</i>	agar	1.86 ± 0.21	3.32 ± 0.26	8.04 ± 0.45	9.56 ± 0.47
	food	0.34 ± 0.08	2.38 ± 0.26	4.74 ± 0.34	6.58 ± 0.39
<i>SA</i>	agar	3.02 ± 0.25	4.78 ± 0.32	8.54 ± 0.42	9.50 ± 0.45
	food	3.56 ± 0.30	5.96 ± 0.35	7.16 ± 0.39	10.68 ± 0.47
<i>SA spa</i>	agar	2.50 ± 0.24	6.83 ± 0.31	6.22 ± 0.39	11.78 ± 0.49
	food	0.96 ± 0.21	2.80 ± 0.28	3.88 ± 0.34	5.26 ± 0.56

FA larvae of 24, 48 and 72 hours show a percentage of "sitter" larvae greater than *FA spa*, *SA* and *SA spa* larvae (t values fluctuated between 3.537 and 10.234; P , two tailed < 0.01). In the absence of food, these differences are not statistically important, with the exception of larvae of 24 hours of the *FA* and *SA spa* lines ($t = 2.007$; P , two tailed < 0.05). These findings suggest genetic variation

between the lines for larval movement pattern associated with feeding behaviour. The results also suggest that young larvae of the *FA*, *FA spa*, *SA* and *SA spa* lines have a similar searching pattern for food.

Larval turning behaviour on agar and on food in the *FA*, *FA spa*, *SA* and *SA spa* lines is shown in table 4. Turning did not substantially alter with

Figure 2 Percentage of "sitter" larvae at 24 (a), 48 (b), 72 (c) and 96 (d) hours of age in the lines genetically selected for fast (*FA* and *FA spa*) and slow (*SA* and *SA spa*) feeding rate in the absence (open bar) and in the presence (hatched bar) of food.

Table 4 Percentage (arcsin transformation) of turning in larvae of lines genetically selected for fast (*FA* and *FA spa*) and slow (*SA* and *SA spa*) feeding rate. Turns were recorded on agar and on food at various larval ages. Thirty eight individuals of each age group were screened

Hours of development	Agar			Food			ts respect to the absence of food for % of turns
	N of turns	N of movement in straight line	% of turns	N of turns	N of movement in straight line	% of turns	
<i>FA</i>							
72	124	26	65.42	130	20	68.61	0.94
96	110	40	58.89	118	32	62.51	0.55
<i>FA spa</i>							
48	108	42	58.05	120	30	63.44	1.42
72	119	31	62.94	112	38	59.80	0.82
96	108	42	58.05	117	33	62.03	1.04
<i>SA</i>							
24	117	33	62.03	77	40	54.21	1.19
48	118	32	62.51	108	42	58.05	0.68
72	102	48	55.55	85	62	49.49	0.92
96	101	49	55.12	100	47	55.55	0.07
<i>SA spa</i>							
48	118	32	62.51	121	29	63.94	0.39
72	109	41	58.24	116	34	62.24	1.05
96	125	25	65.88	112	38	59.80	1.63

larval development in the 4 strains, though younger larvae (24 and 48 hours) of the *SA* line exhibit a percentage of turns on agar greater than those shown by older larvae of this line (72 and 96 hours). Turning behaviour of larvae of the *FA*, *FA spa* and *SA spa* lines tends to increase on food; these differences are not statistically significant (*t* test, table 4). *SA* larvae show decrease in turning behaviour on food. Larvae of the 4 lines show a similar number of turns, with the exception of *FA* and *SA* larvae of 72 hours of age which, on food, show a different turning behaviour ($t = 2.909$; *P*, two tailed < 0.05).

Genetics of turning behaviour

Table 5 shows the means of changes in direction made on agar by larvae of 108 hours of the Oregon R-C and *vestigial* strains (parentals) and F_1 , F_2 and back-crosses. Frequency distributions of turns is shown in fig. 3. On agar, the mean of changes in direction made by *vestigial* larvae is lower than for Oregon R-C larvae ($t = 23.137$; $df = 67$). Figure 3(a) confirms this result, though some superposition of frequency distributions exists. Larvae of the F_1 , F_2 and the Oregon R-C show similar turning behaviour (t ranged from 1.081 to 1.710; $df = 100$). F_1 and *vestigial* larvae differ in turning ($t = 2.043$; $df = 105$). Variance of individuals scored in F_2 generation is substantially higher than those of the parental strains and F_1 generation, suggesting

genetic segregation for turning behaviour. Movement pattern of larvae of the back-crosses shows a mean of turns comparable to that of F_1 hybrid larvae (table 5).

Following Mather and Jinks (1971) and Cavalli-Sforza and Bodmer (1971), a genetic analysis of turning behaviour was made by using the means and variances of table 5. The genetic component of phenotypic variance (log scale) was equal to 0.2811 being essentially additive in nature. Number of effective factors controlling changes in direction was 0.01672 whose corresponding anti-log is 1.036, that is one pair of factors. These

Table 5 Means of turns made on agar by larvae of 108 hour old of the Oregon R-C and *vestigial* strains (parental strains), F_1 , F_2 and back-cross. Turning behaviour was recorded for 3 min

cross	N larvae tested	Mean of turns (log scale)	Variance
parental strains			
(a) <i>vestigial</i>	30	0.590	0.111
(b) Oregon R-C	39	0.778	0.055
hybrid F_1	67	0.700	0.029
hybrid F_2	65	0.778	0.307
back-cross			
<i>vestigial</i>	70	0.705	0.307
back-cross			
Oregon R-C	69	0.679	0.026

Figure 3 Frequency distributions of number of turns made by larvae of the Oregon R-C (black circles) and *vestigial* (open circles) strains (parentals) (a); F_1 (b); and back-cross $F_1 \times \text{vestigial}$ (c), and $F_1 \times \text{Oregon R-C}$ (d). Larvae of 108 hours were scored (see Materials and Methods).

findings are in agreement with fig. 3: each back-cross produces two peaks of segregation for changes in direction, one of them is in line with that of F_1 and the other one with the corresponding parental strain. This is particularly obvious in the cross between the F_1 and the *vestigial* strain (fig. 3(c)). Besides, examination of the data by using parentals, F_1 and back-cross distributions (Stewart, 1969) gave similar results: one pair of factors seem to control turning behaviour of *D. melanogaster* larvae.

DISCUSSION

This work shows that *D. melanogaster* and *D. simulans* larvae change their foraging activities in response to changes in food availability, as shown by larval movement pattern in the presence and in the absence of this resource. These changes in larval movement pattern of *Drosophila* depend on age and are relative to individual genotype (tables 1 to 4 and figs. 1 and 2). At least two behavioural mechanisms are involved in the variations in larval movement pattern of *Drosophila*: locomotion and turning behaviour. On a non-nutritive substrate locomotion increases and turning tends to decrease. In the presence of food the

opposite situation occurs. These findings confirm those of Green *et al.* (1983).

Our results suggest that the movement pattern of *Drosophila* larvae is straighter when some ecological resource, like food, is limited. A relatively straight larval movement pattern could reflect searching orientation for a resource like food (24, 48 and 72 hour larvae) or for a dry substrate to pupariate (96 hour larvae). Breeding sites of several *Drosophila* species such as *D. melanogaster*, *D. simulans*, *D. immigrans* and *Drosophila hydei* are fallen fruit or flowers and others rotting plant materials (Carson, 1971; Heed, 1957; Parsons, 1983). On these substrates yeasts and bacteria grow and these organisms are the principal food of larvae and adults of *Drosophila* (Parsons, *op. cit.*). It is probably that these breeding sites are exposed to relatively rapid dessication which affects the growth of the yeasts and bacteria. This could lead to a patchy distribution of these organisms, and under these conditions changes in the interplay between larval orthokinesis and klinokinesis could help in the location of food sources. The results of this study are in line with those of Sokolowski and Hansell (1983) and Sokolowski *et al.* (1983) who found that *D. simulans* larvae show a stationary feeding pattern more than *D. melanogaster*, and that larvae of

both species are able to search for and locate to food sources. These behaviours are genetically controlled. Bell *et al.*, (1985) found that, in a non-nutritive medium, the movement pattern of *D. melanogaster* adult flies is straighter than in the presence of food (sucrose). These changes in searching orientation are referred to as ranging and local searching, respectively (Jander, 1975). Our results suggest that these two kinds of behaviours could also be recognised in larval behaviour repertoire of *Drosophila*.

In *D. melanogaster*, larval demand for food and space is age-related (Sewell *et al.*, 1975; Godoy-Herrera, 1986). The straighter movement pattern shown by bigger older larvae is probably adaptative because it may help larvae to cover a minimal feeding area (72 hour larvae) or explore the environment to locate a pupariation place (96 hour larvae). Movement pattern of *Drosophila* larvae could also be in connection with burrowing activity and the dispersal pattern into food. Godoy-Herrera (1977, 1986) found that older larvae of *Drosophila* go into the culture medium deeper than younger larvae.

Contrasting with *FA*, *FA spa* and *SA spa* larvae, on food, *SA* larvae do not substantially reduce locomotion. The *SA* larvae increase turning on non-nutritive substrate (tables 3 and 5 and fig. 2). These findings suggest that there is genetic variation for larval movement pattern between these four strains of *D. melanogaster*. The results also indicate that there is no a simple relation between larval feeding behaviour (Sewell *et al.*, 1975) and larval movement pattern of *Drosophila*. The way that a *Drosophila* larva moves probably represents a compromise among different selective forces for adaptation to a particular array of ecological conditions or breeding sites. It could be instructive to compare the development of larval movement patterns in *Drosophila* species living in widely different ecological conditions such as those of neotropical, tropical and desert ecology (Brncic, 1983; Carson, 1971; Heed, *et al.*, 1976).

The Oregon *R-C* and *vestigial* strains (the parental strains) are not inbred. However, given that larvae of these two strains seemed to show important differences in turning (Godoy-Herrera, 1982), it was attractive to cross them to investigate the genetic control of this behaviour. The results of the genetic analysis suggest that one pair of major additive genetic factors control turning behaviour in *D. melanogaster* larvae (table 5 and fig. 3). This is not to say that other genes cannot modify turning. Allelic segregation with additive minor effects on this behaviour could perhaps

account for superposition of the frequency distributions shown in fig. 3. An additive genetic control of larval turning behaviour of *D. melanogaster* could be related to phenotypic flexibility for this behaviour. One of the characteristics of breeding sites of many *Drosophila* species is their transient nature which include changes in microenvironmental conditions of these habitats (Carson, 1971; Heed *et al.*, 1976; Parsons, 1983).

Turning behaviour seems not change substantially with larval development (tables 2 and 4). In contrast, locomotion increases with larval age (tables 1 and 3). This increase occurs with growth in body size and genetically controlled changes in locomotion (Godoy-Herrera *et al.*, 1984). These two lines of evidence suggest that different genetic systems control these two behaviours in *D. melanogaster* larvae.

In summary, this research shows that the characteristics of larval movement patterns in *Drosophila* depend on larval age, genotype and environment in which the larva moves. Changes in the development of larval movement patterns of *Drosophila* seem to represent ontogenetic adaptations to several different environments to which the larva must adjust at different periods of its life.

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