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Rover/sitter *Drosophila melanogaster* Larval Foraging Polymorphism as a Function of Larval Development, Food-Patch Quality, and Starvation

Susanne A. Graf[1] and Marla B. Sokolowski[1, 2]

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The genetically based rover/sitter behavioral difference in Drosophila melanogaster *larval foraging is expressed throughout most of the larval instars when larvae forage on food patches of differing food quality. The amount of locomotor behavior decreases when third-instar larvae of both rover and sitter strains are starved just prior to the behavioral test. Such strain differences in locomotor behavior are maintained despite the starvation-induced decrease in locomotion found in both strains. Measurements of larval body length and width, taken at 24, 48, 72, and 96 h posthatching, reveal that rover and sitter larval growth rates do not differ. The finding that rover/sitter differences are expressed in a variety of environments and throughout the majority of the larval instars should aid in attempts to uncover selection pressures which may differentially affect the two morphs in environmentally heterogeneous natural populations.*

KEY WORDS: *Drosophila melanogaster*; larval foraging behavior; genetics; development; plasticity; patch quality.

INTRODUCTION

Understanding the relationship between an organism and its environment is crucial to erecting hypotheses of how populations change in ecological and evolutionary time. Most work on the ecology of the fruit fly *Drosophila* has concentrated on the adult stage. More recently, an interest in the larval stage, a period characterized by maximum resource use, has emerged, focusing on

[1]Department of Biology, York University, 4700 Keele Street, Toronto, Ontario, Canada M3J 1P3.
[2]To whom correspondence should be addressed.

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larval foraging behavior, development, and survivorship to adulthood (Sokolowski, 1985).

This is the first in a series of papers which addresses how *Drosophila melanogaster* larval foraging behavior may influence survivorship to adulthood. In this study we measure changes in the locomotor component of foraging behavior during larval development in environments of different food quality, using yeast as the only food stimulus. Due to the many interacting biotic and abiotic factors, it is often difficult to determine which environmental cues ellicit a certain behavior pattern. Experiments conducted in controlled laboratory environments allow the individual evaluation of potentially important factors.

The natural microhabitat of *D. melanogaster* larvae is a complex environment which is in a constant state of flux. Adult females deposit eggs on, for example, fruit, slime fluxes, and cacti (Begon, 1982). These substrates are always innoculated with some type of microorganism such as yeasts, which metabolically alter the substrates. Yeasts are saprophytic and induce fermentation when a sugar source is present, resulting in waste products of alcohol, acetaldehyde, acetic acid, CO_2, and water. Larvae are exposed to this assemblage of stimuli while foraging for food. In choice experiments some larvae display preferences for different yeasts (da Cunha *et al.*, 1951; Lindsay, 1958; Cooper, 1960; Fogleman *et al.*, 1981), alcohols (Parsons and King, 1977; McKechnie and Morgan, 1982) and sugars (Miyakawa *et al.*, 1980).

A *Drosophila* larva feeds by successive extensions and retractions of its mouth hooks and moves along the substrate by alternately extending its anterior and retracting its posterior end (crawling) (Sokolowski, 1980; Green *et al.*, 1983). The number of shovels and the number of crawls are respective measures of feeding and locomotion, which can be quantified by placing individual larvae into petri dishes, covering the bottom of each with a thin coat of yeast paste meant to simulate a food patch. This yeast paste has three characteristics which are important to larval foraging: it is homogeneous and moist and acts as a concentrated food source. Larval movement in the dish leaves a visible trail or path in the yeast, which we call the path length of the foraging trail. Larval path length and larval crawling behavior show a strong positive correlation (Sokolowski and Hansell, 1983). Larvae that have long path lengths are called rovers; those with shorter path lengths are sitters (Sokolowski, 1980). Genetic analyses have revealed that differences in these forager types are attributable to a single major gene on the left arm of the second pair of chromosomes, with the rover phenotype showing complete dominance over the sitter (Sokolowski, 1980, 1986; Bauer and Sokolowski, 1985; de Belle and Sokolowski, 1987, 1989). The rover/sitter behavioral polymorphism is found in both natural (Sokolowski, 1982a; Bauer and Sokolowski, 1984) and laboratory populations (Sokolowski, 1980). We have speculated that variation in foraging behavior may influence a larva's ability to exploit food resources (Sokolowski, 1985) and

thereby its fitness by affecting development (Robertson, 1963), the time to reach the critical weight for pupation (Bakker, 1961), and adult emergence (Ohnishi, 1979).

D. melanogaster larval behavior changes during development. First, second- and early third-instar larvae choose food (yeast) over nonfood conditions and moist over dry substrates; immediately prior to pupation, nonfood is preferred to food conditions, and dry over moist substrates (Godoy-Herrera *et al.*, 1984; Sokolowski *et al.*, 1984).

In the present study, rover and sitter larvae are tested during larval development in each of several food substrates varying in yeast concentration. Substrates are ranked according to the ratio of yeast (a nutritive substrate) and agar (a non-nutritive substrate) present in the environment. The period of larval development spans 120 h (5 days) commencing at the time of egg hatch and continuing until the time of pupation. We measure the path length of the foraging trail on each of 4 consecutive days posthatching (called 24, 48, 72, and 96 h posthatch) by exposing the larvae to yeast–agar pastes designated S-0 (no yeast), S-1, S-2, S-3, and S-4 (all yeast). Path lengths of 72-h-old larvae, which were starved for 4 h prior to testing, were also tested on these substrates. In order to compare growth rates of the two morphs, the length and width of rover and sitter larvae on each of the 4 consecutive days posthatch were measured. In essence, we investigate the phenotypic plasticity of rovers and sitters. Specifically, we ask whether the rover/sitter trait is expressed throughout larval development and if this expression is altered in patches of differing food quality.

METHODS

Strains

Two *D. melanogaster* strains which differed in larval foraging behavior, EE, exhibiting a sitter phenotype (described and called E_2E_3 by Sokolowski, 1980), and BB, exhibiting a rover phenotype [described and called B15B15 by Bauer and Sokolowski (1985)], were used. Strains were housed in 0.25-liter glass urine bottles containing 45 ml of Parker's dead yeast–agar medium at a density of about 250 flies/bottle. Bottles were incubated under standard conditions at 24°C, under 60% RH, with a 12:12 L:D cycle (with lights on from an overhead source at 0800 h).

Preparation of Yeast–Agar Pastes

Five yeast–agar pastes labeled S-0 to S-4 were used to test the effects of altering the food quality of the foraging substrates. Substrate consistency was controlled to facilitate visibility of larval trails (Sokolowski, 1980). Agar was

added to each of the pastes so that their consistency qualitatively matched that of S-4. The all-yeast paste (S-4) is the standard used in recent studies of larval path length from our laboratory. Consistencies were visually compared by tipping each dish 45° and watching the displacement of the foraging substrate. Eighty milliliters of water was used in the preparation of each substrate. Each of the five substrates contained 0, 10, 20, 30, and 40 g of yeast and 7.9, 8.9, 7.4, 3.8, and 0 g of agar, respectively.

Collection of Larvae

The procedure described by Sokolowski *et al.* (1984) for aging and collection of larvae was followed with slight modification. Two types of culture containers, each with standard medium, were darkened with fine powdered charcoal (3 g per 400 ml of medium). Charcoal increased the visibility of larvae for collection prior to testing. Plastic spoons filled with 6 ml of charcoal medium and seeded with 100 larvae were used to culture larvae to be tested at 24 and 48 h posthatch. Plastic petri dishes (150 mm in diameter and 15 mm in height) filled with 100 ml of medium and seeded with 300 larvae were used to culture larvae tested at 72 and 96 h posthatch. The different container sizes provided adequate space and food for both younger and older larvae. All experiments were conducted under uniform light conditions between 1300 and 1900 h at room temperature (23°C).

Testing of 24- and 48-h-Posthatch Larvae

On the appropriate test day, single larvae were randomly collected with the aid of a dissecting microscope and transferred to the center of a test dish containing a thin layer of one of the substrates applied with a glass rod on a petri dish spinner (de Belle and Sokolowski, 1987). Tests were run with the lids on. Due to the small size (<2 mm) of the larvae, trails were not always visible in the test dish. A dot was placed on the lid of the petri dish to indicate the position of the larva at 0, 2.5, and 5 min. At the end of the 5-min test, the dots were joined to produce the path-length measure.

Testing of 72- and 96-h-Posthatch Larvae

On the appropriate test day all larvae (300) were removed from the culture medium with a paintbrush and temporarily placed on a food plug (25 mm in diameter and 5 mm high) to minimize starvation prior to the behavioral test. Five groups of 25 larvae were randomly chosen and tested for each strain in each of the substrates. Each larva was transferred to the center of a test dish containing one of the five substrates, after which the lid was replaced. After 5 min, the visible trail left in the foraging substrate was traced onto the lid of the

dish. Another group of 72-h larvae (10 larvae/substrate) were collected and tested as above except that they were placed on an (nonnutritive) agar plug for a 4-h starvation period prior to the behavioral test. In all cases (24–96 h posthatch) the length of the foraging trail was measured from the test lid using a NUMONICS Model 1224 electronic digitizer. It was necessary to perform a natural logarithm transformation on the data prior to statistical analysis since we found a significant positive correlation between the means and the variances. This transformation also normalized the data.

Body-Size Measurements

Newly hatched larvae were gathered in groups of 100 over a 3-h period and transferred into one of two culture containers. On the day of measurement, 24 larvae per strain were randomly chosen and placed into a plexiglass tube (20 mm in inside diameter, 5 mm in height), one end of which was covered with 80-μm Nitex mesh (i.e., functioning like a sieve). This unit was lowered into 70°C water for a period of 30 s resulting in fixation of the larvae in an extended state (Godoy-Herrera *et al.*, 1984). Larval lengths and widths were measured from a microscope image projected onto a TV monitor using a computer-assisted caliper digitizing device (Sprules *et al.*, 1981). Larval lengths were measured from the apex to the base of each animal while width measures were made at the midpoint, excluding the width added by the spicules.

RESULTS

In this study we measured larval path lengths on two strains, during four posthatch periods and on five substrates. Two important patterns were observed: (1) larvae of both strains move farther as they get older, and (2) rovers show a dramatic increase in path length from 24 to 96 h posthatch, compared with the more subtle increase in sitters.

The development of the path-length phenotype for each strain separately is shown in Fig. 1. The obvious finding here is that larvae of the rover strain have longer paths than those of the sitter strain. The hours posthatch, substrate, and interaction of hours posthatch by substrate significantly affect the path-length measure for each strain (Table I). Overall, at 24, 48, and 72 h the average path lengths of sitter larvae do not vary between substrates. The greatest increase in sitter path length occurs from 72 to 96 h posthatch. In contrast, the greatest increase in path length for rovers occurs from 48 to 72 h posthatch along with a significant increase in path length from 72 to 96 h.

In general, the behavioral differences between rovers and sitters first reported by Sokolowski (1980) are maintained throughout larval development and across the different foraging substrates. When comparing the path lengths

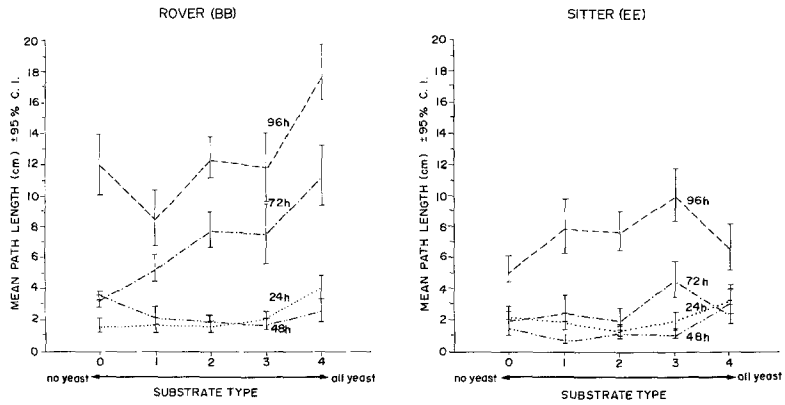

Fig. 1. Mean larval path lengths (cm) ± 95% confidence intervals (C.I.) for each of the sitter (EE) and rover (BB) strains at 24, 48, 72, and 96 h posthatch in patches of different food quality ranging from 0 (no yeast) to 4 (all yeast). In general, sitter paths are shorter than rover paths. Dotted lines are used to join all the means within an age to indicate minimal extrapolation between them.

of rover and sitter strains in each of the four (hours posthatch) by five (substrate) combinations, we find that rovers always move more than sitters and that, in 17 of these 20 comparisons, the differences were significant ($P < 0.05$). As these larvae get older, locomotor disparity between the two strains increases.

The rover/sitter trait is first expressed clearly at 48 h (second instar); its expression is greatest in third-instar larvae (72 and 96 h posthatch). At 24 h posthatch, food quality significantly affects path length, however, strain and strain by substrate interaction are not significant (Table II). By the second and third instars, strain, substrate, and the interaction of the two are all significant, indicating that the strains differ in both their path lengths and their response to different substrates. The rover response to substrates is somewhat more variable

Table I. The Effect of "Hours Posthatch" and "Foraging Substrate" on *D. melanogaster* Rover and Sitter Larval Path Lengths (ANOVA Uses the Natural Logarithm of Path Length)

Strain	Source	df	SS	*F*	*P*
EE-sitter	Hours posthatch	3	110.51	164.27	<0.0001
	Substrate	4	8.09	9.01	<0.0001
	Hours posthatch by substrate	12	16.21	6.02	<0.0001
	Error	483	108.32		
BB-rover	Hours posthatch	3	179.38	319.66	<0.0001
	Substrate	4	16.97	22.68	<0.0001
	Hours posthatch by substrate	12	17.53	7.81	<0.0001
	Error	479	89.60		

Table II. The Effect of "Strain" and "Foraging Substrate" on *D. melanogaster* Larval Path Lengths on Each of the 4 Days Posthatch (ANOVA Uses the Natural Logarithm of Path Length)

Hours posthatch	Source	df	SS	*F*	*P*
24	Strain	1	0.19	0.91	ns[a]
	Substrate	4	10.56	12.95	<0.0005
	Strain by substrate	4	1.68	2.06	ns
	Error	243	49.52		
48	Strain	1	5.49	29.98	<0.0005
	Substrate	4	9.03	12.32	<0.0005
	Strain by substrate	4	4.65	6.35	<0.0005
	Error	247	45.25		
72	Strain	1	36.46	151.54	<0.0005
	Substrate	4	12.38	12.86	<0.0005
	Strain by substrate	4	8.27	8.60	<0.0005
	Error	232	55.82		
96	Strain	1	13.26	67.25	<0.0005
	Substrate	4	4.36	5.52	<0.0005
	Strain by substrate	4	7.86	9.97	<0.0005
	Error	240	47.31		

[a] Not significant ($P > 0.05$).

than the sitter, especially at 72 h, where larval path length increases from the no-yeast to the all-yeast substrate (from S-0 to S-4).

Path Lengths of 72-h-Posthatch Starved and Nonstarved Rover and Sitter Larvae

We starved larvae for 4 h prior to the path-length test to determine whether starvation significantly affected this trait. Two unambiguous effects of starvation on path length can be seen in Fig. 2. First, starvation significantly decreases the path length in both the rover and the sitter strains, and second, starvation decreases the variability in the response to substrates in both strains. The shape of the response curves for the starved larvae are flatter than those for the nonstarved larvae. Notice that the rover/sitter path-length differences are still expressed in starved larvae. The nonstarved rover paths are significantly longer than the nonstarved sitter paths; the starved rover paths are significantly longer than the starved sitter paths (see Fig. 2).

Body-Size Measurements

As can be seen from Fig. 3, rovers and sitters have similar growth rates. Larval widths do not differ at each of the 4 days posthatch, nor do larval lengths at 24 and 96 h posthatch ($P > 0.05$).

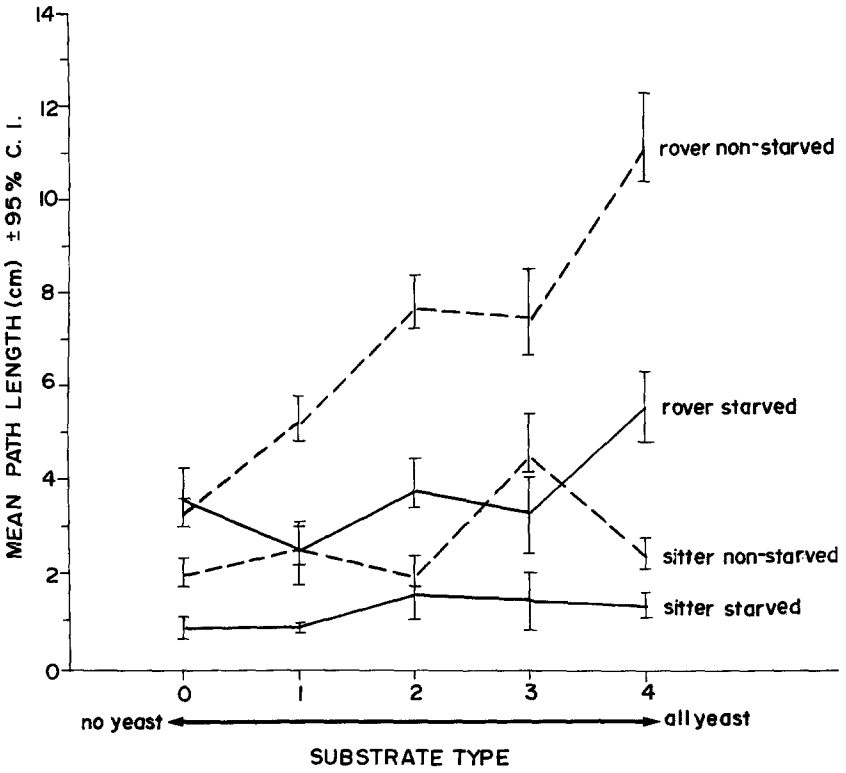

Fig. 2. Mean path length (cm) ± 95% C.I. of 72-h-posthatch rover and sitter nonstarved (dashed line) and starved (solid line) larvae in the five substrate types. Starvation decreases path length in both strains. Rover and sitter path-length differences are maintained within a treatment (nonstarved or starved).

DISCUSSION

Rover/Sitter Behavior and Larval Body Measures

Drosophila larvae move by alternately extending their anterior and retracting their posterior end. This locomotor movement, called crawling, (Sokolowski, 1980), enables them to move along the foraging substrate upon which they leave a trail (called path length). The rover and sitter strains differ in the length of these trails. Could the foraging trails of rovers be longer than sitters simply because rovers are physically longer and consequently take bigger "steps"? To answer this question, we measured rover and sitter path and body lengths during each of the four posthatch periods. We found that larvae of the rover and sitter strains grow to the same size and that rovers are never consist-

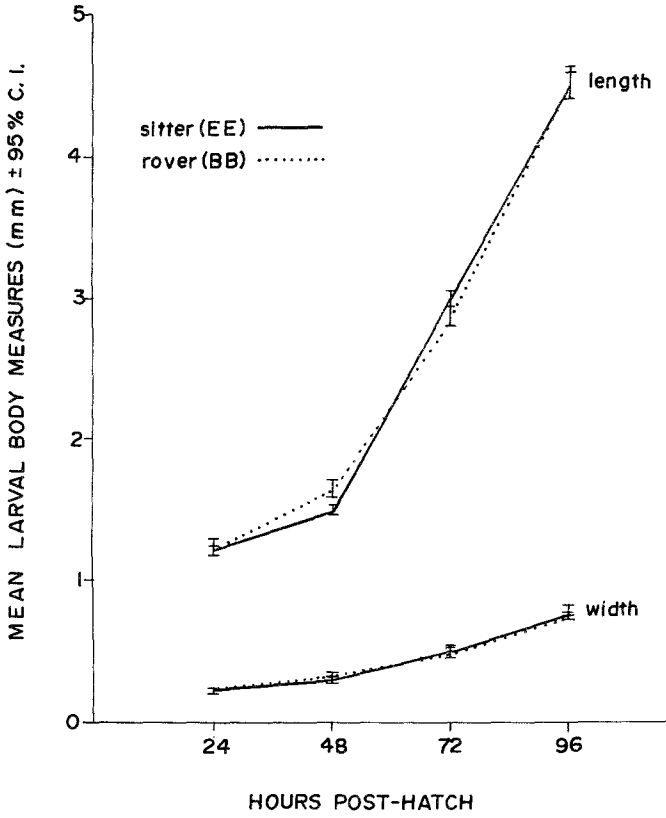

Fig. 3. Mean larval body length and width (mm) ± 95% C.I. are shown at 24, 48, 72, and 96 h posthatch for the rover and sitter strains.

ently longer or wider than sitters during development. We also found no correlation between larval body length and larval path length within a posthatch period (Sokolowski, unpublished). We conclude from this that rover/sitter behavioral differences cannot be explained on the basis of differences in larval body size. Although rovers are not taking longer steps than sitters, they are taking more steps, as shown by Sokolowski (1980), where rovers have significantly higher crawling rates than sitters.

Development of Rover/Sitter Differences

Rover/sitter differences first appear at 48 h posthatch (Fig. 1 and Table II). This difference in path length is most fully expressed at 72 and 96 h posthatch. In a previous study Bauer and Sokolowski (unpublished) used a dissecting microscope to measure the crawling rates of 24-h larvae and found higher crawl-

ing rates in rovers than sitters. In the present study no difference in the 24-h path lengths of rovers and sitters was found. This may result from the "join-the-dot" measuring technique used on 24- and 48-h larvae, compared to the direct path-length tracing technique used on the older 72- and 96-h larvae. The join-the-dot technique will tend to underestimate the path-length differences of the 24- and 48-h-old larvae. Furthermore, the depth of the substrate relative to the size of a larva at 24 h may have decreased our chance of finding a significant path-length difference between the strains at 24 h since more digging behavior may have occurred (Sokolowski, 1982b). Despite this nonsignificant path-length difference at 24 h, the results of the present study show that rover/sitter differences are expressed throughout most of the larval period.

Rover/Sitter Expression on Different Substrates

Bell and Tortorici (1987) found that when starved *Drosophila melanogaster* adult flies cease feeding on a sucrose drop, they pivot around it; this is called the "period of intensive search" and is characterized by locomotion with a high turning rate. After intensive search, the turning rate decreases and flies walk in relatively straight lines away from the drop; this is called "ranging." Nagle and Bell (1987) showed that our rover and sitter larval strains also differ in adult foraging behavior. Adults of the sitter larval strain spend more time in intensive search then do those of the rover larval strain. Rovers switch to ranging much sooner than sitters. When adult foraging behavior is measured during a fixed time interval (30 s), the paths of the sitter adult cover a much smaller area, reflecting more time spent in intensive search. In contrast, the paths of the rover adult cover a larger area and show the relatively straight-line walking patterns characteristic of ranging. Several analogies between the adult and the larval behavior patterns can be drawn. In the present study, we found that sitter larvae have shorter foraging trails than rovers. These shorter trails may reflect the greater amount of time that sitter larvae spend in intensive search compared to rover larvae, whose trails are longer and characteristic of ranging. However, a detailed examination of the larval and adult testing procedures reveals important differences between them. The larval test measures behavior of the animal *in* a patch, whereas the adult test measures behavior after the animal has fed from a patch (the sucrose drop) and is in the process of searching for a new patch. Bell and Tortorici (1987) have shown that by modifying the sucrose concentration, rover adults will vary their search pattern. When the sucrose concentration is high, rover adults spend more time in intensive search, and hence their foraging trails more closely resemble those of the sitter adult. Although we did not find this pattern in the larvae (rover paths were longest at the highest yeast concentrations), we did find that the response of rovers to the different substrates was more variable than the response of sitters, especially at 72 h. This may indicate greater phenotypic plasticity in the rover than the sitter. Bell and

Tortorici (1987) also found that when the starvation period was increased prior to testing, both strains spent more time in intensive search. In our study, the larvae of both strains also showed this pattern. Path lengths were shorter when 72-h-old larvae were starved for 4 h prior to the larval path-length test. Note, however, that starved rover larvae still had longer paths than starved sitter larvae. We tested starved 72-h-posthatch larvae since this is the time in the third instar when larvae complete a sufficient amount of foraging to pupate and emerge successfully. Therefore the degree of starvation after this time should have direct measureable consequences on the adult body size. (The relationship among foraging behavior, starvation, and adult fitness is currently under investigation.) Despite the inherent differences in the larval and adult life-history stages and the foraging test procedures, we can see similarities in the plasticity of the larval and adult rover/sitter responses to patches of different quality and to periods of starvation prior to foraging. Whether these similarities in response are due to similarities in physiological processes resulting from correlated genetic systems remains to be determined.

The picture that is emerging for the larval rover/sitter trait is that of a genetically determined behavioral difference (for review see Sokolowski, 1985) with some degree of plasticity. Rover/sitter is expressed during larval development, in food patches of varying quality, and after a period of starvation.

A number of selective pressures may differentially affect the fitness of rover and sitter larvae. First, the cost of roving and sitting may differ in patchy as compared to homogeneous environments. From a larva's perspective a fallen fruit is a heterogeneous environment, containing discontinuities in yeast, sugar, and alcohol concentrations, for example. Rovers may forage more efficiently than sitters when food is distributed in patches. To test this, we plan to alter patch size, patch quality, and interpatch distance to determine if the interplay between the "cost of locomotion" and the "characteristics of the foraging substrate" will differentially affect the fitness of rovers and sitters. Second, *Asobara tabida* Nees (Braconidae: Alysiinae), a *Drosophila* larval parasitoid which locates and parasitizes larvae with high locomotor activity (Sokolowski and Turlings, 1987), is found in our orchard field site. The present study showed that rovers move more than sitters throughout most of the larval instars and over a range of food concentrations. This implies that *Asobara tabida* should parasitize rovers more frequently than sitters. Thus the interaction between host behavior patterns and parasitoid searching mode should have important fitness consequences for the polymorphism.

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