Foraging actively can be advantageous in heterogeneous environments

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Abstract

A wealth of evidence indicates that the existence of active foragers and sit-and-wait foragers is widespread in nature. While active foragers visit foraging sites and leave them randomly, sit-and-wait foragers only do so if the benefit of leaving exceeds the cost. This dichotomy has been documented in the larval and adult stages of *Drosophila melanogaster*. For instance, when exposed to a nutrient-rich substrate, some individuals travel significantly longer distances than others. In this study, we designed an experiment to evaluate whether the distribution of food in the environment alters the foraging behavior. If some individuals acquired more food than others in a given environment, we further examined whether variation in the life history occurred among them. Our results indicated that foraging behavior is a plastic trait remarkably shaped by the distribution of food in the environment. We found that active foragers and sit-and-wait foragers increased their locomotion when food was patchy rather than clumped, but the locomotion of active foragers was higher overall. Interestingly, we found no differences in the life history between the two foraging strategies. We suggest that foraging actively should evolve faster anyway because it facilitates local adaptation via founder effect and gene flow.

Keywords: Colonization, dispersal, foraging gene, plasticity.

Introduction

A central goal of behavioral ecology is to determine how organisms exploit food in a given environment (MacArthur and Pianka, 1966). In nature, food is distributed in patches that vary in size and density over time. In response to such environmental heterogeneity, organisms can adopt varying foraging behaviors that maximize their acquisition of energy (Schoener, 1969). For instance, an active-foraging behavior is attributed to an organism that frequently abandons patches of food. By contrast, a sit-and-wait foraging behavior is attributed to an organism that rarely abandons patches of food. This behavioral dichotomy is currently known as "The Foraging-mode Paradigm"; a categorization that, albeit crude, remains useful to biologists for defining the extremes of a continuum. A seemingly tireless hummingbird that visits flowers in search of nectar, as opposed to a kingfisher that waits on a perch and swoops into the water when a fish passes by, are perfect examples to illustrate this point.

Since the early 1970s, researchers have developed mathematical models to specify which behavior is better suited for an organism to maximize energy intake in a particular environment, leading to the development of the optimal foraging theory (Schoener, 1971; Charnov, 1976). However, the initial application of the optimal foraging theory was to explain the evolution of body sizes of organisms with little emphasis on their foraging mode. This theory was later extended in models that explicitly considered foraging modes as alternative strategies (e.g., Vitt and Congdon, 1978; Janetos, 1982a). The models resulted in two main predictions: 1) Organisms should have a sim-

ple decision rule for leaving a foraging site. They should leave when the expected gain from moving surpasses the expected gain from remaining at the site. 2) If variation in foraging behavior affects the energetic benefits or costs, then growth rate, body size, and reproductive output should vary among individuals that forage differently. This expectation is supported by the idea that different behavioral strategies determine the life histories of organisms by limiting their acquisition and allocation of energy. An allocation tradeoff suggests that an increment in energy allocated to one function results in a decrement in energy allocated to other functions. Thus, an individual that acquires a surplus of energy may growth faster than one with restricted energy stores, and have both a smaller body size and greater lifetime reproductive output (Stearns et al., 1992; Roff, 2002).

Such predictions were evaluated in several elegant works fueled by the increasing interest in behavioral ecology at the time. The first empirical evidence derived from field studies of lizards (Vitt and Congdon, 1978; Vitt and Price, 1982). By comparing reproductive output among species, these researchers showed that active foragers invested less in reproduction than did sit-and-wait foragers. The explanation proposed for this pattern was that carrying a voluminous clutch while pursuing a prey increases the probability of being killed by a predator or reduces the efficiency of foraging. Interestingly, a different study on orbweaver and sheetweb weaver spiders indicated that active foragers incur lower energetic costs than do sit-and-wait foragers (Janetos, 1982b). Orbweavers decided whether to stay or leave the web based on the abundance of prey they capture in a day. By contrast, sheetweb weavers seemed to be sit-and-wait predators, staying on the web for a longer time and only leaving it at random.

Surprisingly, the sheetweb weavers pay a much higher energetic cost for constructing a new web from body reserves than do orbweavers. Importantly, these analyses might have been confounded by the evolutionary relationships among species. In comparative biology, comparisons among species based on traditional methods such as regression models cannot be used as species are part of a hierarchically structured phylogeny, and thus cannot be regarded for statistical purposes as if drawn independently from the same distribution (Felsenstein, 1985). However, any comparative analyses inevitably suffered from such limitation at the time as phylogenetic comparative methods were available only after 1985.

Around the same time, Sokolowski (1980) discovered a behavioral polymorphism in the larvae of *Drosophila melanogaster*. Quantitative genetic analyses revealed that a major gene on one of the fly's autosomes, along with minor effects from genes on the X chromosomes, influenced the foraging behavior of individuals (de Belle and Sokolowski, 1987). Genetic mapping localized the rover-sitter differences in larval foraging to a locus on chromosome-2, which was named *foraging* (*for*). Cloning of the *for* gene showed that it encodes a cGMP-dependent protein kinase (Osborne et al., 1997). Subsequent studies revealed the pleiotropic functions and complex molecular structure of *for* (Allen and Mamotte, 2017; Anreiter and Sokolowski, 2019; Vasquez et al., 2023; Sokolowski et al., 2023). The *for* gene influences the distance that fly larvae travel while foraging, with two allelic variants: rover (for^R) and sitter (for^S). Rovers travel significantly longer distances than sitters when exposed to a nutrient-rich substrate. Experiments in the laboratory indicate that the frequencies of these alleles are influenced by density-dependent selection (Sokolowski et al., 1997) and negative

frequency-dependent selection (Fitzpatrick et al., 2007). Additionally, a population genetic analysis of for revealed an east-west gradient in allele frequency driven by the seasonality of precipitation (Padilla Perez, 2024).

Although the discovery of for stimulated active research into the evolution of foraging behavior and its connection to the life history, current evidence from various studies reamins conflicting. For example, early observations under laboratory conditions suggested that rover larvae have higher survivorship and faster development than sitter larvae in nutrient-poor environments (Kaun et al., 2007). However, more recent studies indicate that fecundity does not differ between rovers and sitters under either nutritional adversity or standard conditions (Burns et al., 2012). These findings highlight the need for further investigation into the expected life history differences among organisms with varying foraging behaviors.

The well-characterized rover-sitter behavioral polymorphism of *D. melanogaster* provides an excellent opportunity to address the discrepancy described above. Accordingly, we aimed to experimentally test two long-standing predictions about the relationship between foraging behavior and the life history. First, we hypothesized that the larval foraging behavior depends on the distribution of food in the environment. In a patchy environment, we predicted that rovers would explore a larger proportion of area compared to sitters. However, this difference would become negligible if food were uniformly distributed. This prediction aligns with recent evidence suggesting that adult rovers dispersed more than sitters when the total amount of food increased with the number of patches (Edelsparre et al., 2021). Our second hypothesis was that

foraging behavior influences the energetic benefits and costs, leading to variation in the life history of the larvae. Specifically, we expected sitter larvae to grow faster than the rover larvae in a uniform environment, while the opposite pattern would be the case in a patchy environment. Additionally, we predicted that growth differences would be more pronounced when food was clumped rather than patchy. These expectations are supported by the idea that different behavioral strategies determine the life histories of organisms by limiting their acquisition and allocation of energy to growth (Reid et al., 2000; Roff, 2002; Bayne, 2004; Angilletta Jr et al., 2004).

Materials and Methods

Fly strains

We used the rover (for^R) and sitter (for^S) wildtype strains in our experiments. The rover and sitter strains were last re-isogenized in 2014, and are regularly phenotyped for the rover-sitter larval path length difference, the hallmark behavioral polymorphism described for this gene maintained in the lab. These strains share X and isogenized third chromosomes from the rover strain and differ in their second chromosomes where the foraging gene is located. The pair of wild-type second chromosomes in the rover lab strain originated from a population of flies collected in a compost bin near Toronto, Ontario, Canada (Bauer and Sokolowski, 1985). The pair of wild-type second chromosomes in the sitter strain originated from a wild-type Oregon R strain, a standard wild-type laboratory strain. Standard genetic complementation and deletion analyses showed that the wild-type lab rover and sitter strains are allelic (same gene, *foraging*,

and same effect on larval behavior) to the orchard population-derived rover and sitter strains (Pereira and Sokolowski, 1993; Sokolowski et al., 1997).

Strains were housed at 25°C, in a 12:12 hr light/dark cycle at 60% relative humidity with lights on at 7:00 AM. We reared the flies in $\sim$ 240 ml round-bottom plastic bottles, with a standard yeast-sugar-agar medium Anreiter et al. (2016). Before the beginning of each experimental trial, we transferred the flies into empty bottles and capped them with grape plates containing a small amount of dry-active yeast to stimulate reproduction. After 22 hr, we removed the grape plates from the bottles and discarded all larvae from each plate with a dissecting probe. We then incubated the eggs that remained in the grape plates for 4 hr in standard conditions as described earlier. After 4 hr in standard conditions, we picked L1 larvae of each strain from the grape plates and placed them individually in food plates (i.e., yeast-sugar-agar medium). Lastly, we collected the testing larvae about 10 hr before wandering, which generally corresponds to the L3 developmental stage (Anreiter et al., 2016).

Locomotor performance assay

We estimated the locomotion of larvae in two types of environments by computing the proportion of area covered while foraging. One environment consisted of yeast paste distributed in patches in a matrix of Drosophila agar medium, whereas the other one consisted of a single patch of the same medium. We prepared these environments in 32 $\times$ 10 mm petri dishes capped with standard lids. To make the patchy environment, we used a 12 ml insulin syringe to pour small drops of dry-active yeast mixed with water

at a 1:2 ratio (weight to volume) on the agar matrix. Patches were separated from each other by a distance of 25 mm, creating a square grid pattern whose vertices consisted of 15 patches each. We used the same method to make the uniform environment, but this time we poured the paste in such a way that a food clump formed at the center of each plate. In both environments designed, we assured that the consistency of the paste, the volume of food used (2 μl) were the same. The configuration of the food in the two environments was the only varying factor (Figure S1). After setting up the test plates, we released a single L3-stage larva into each plate capped with its lid, randomizing the combination of strain, environment, and position of release. To randomize these factors, we used the "*sample*" function available in the free software R v.4.3.2 (2023-10-31, R Core Team, 2023), which enabled us to pick a sample of a specified size ($n = 1$ in this case) from a vector of predefined elements (e.g., a vector of two characters: "rover" and "sitter"). We then transferred plates to an incubator set up at 25°C and 60% relative humidity. After a period of 1 hr, we recorded the larvae for 30 min, using a camera held 30 cm above the plates. In each trial, we recorded four plates simultaneously as indicated in Figure 2. This experiment yielded data for $n = 92$ larvae; 46 larvae of each strain were randomly divided into two groups ($n = 23$) to be tested in uniform and patchy environments. At the end of the experiments, all of the larvae were transferred back to food plates where they continued to develop. Strains were kept separately.

To analyze the video recordings, we used the free software AnimalTA v.2.2.1 (Chiara and Kim, 2023); a video-tracking software that enabled us to analyze videos recorded under the same conditions.

Growth assay

To quantify growth, we let larvae develop to the L3-stage in petri dishes capped with their lids containing the standard yeast-sugar-agar medium. We measured growth as the difference between the initial mass and the final mass of individual larvae after a 24 hr period under standard conditions. To record the initial mass of a larva, we gently washed the larva with 1 or 2 ml of water and dabbed it dry with a paper towel to avoid any confounding factors when weighing the larva. We then weighed the larvae individually using a micro-analytical balance (Mettler Toledo Model XPR6UD5 6.1 gr $\times$ 5^{-7}), and transferred them into capped plates corresponding to either one of the environments described earlier (i.e., patchy or uniform). These plates were placed in an incubator set up at 25°C and 60% relative humidity. After 24 hr, we weighed and recorded the final mass of larvae individually, following the same procedure described above. This experiment yielded data for 27 rovers, and 31 sitters in the patchy environment, and 29 rovers and 22 sitters in the uniform environment.

Data analysis

We fitted competing models to investigate the effects of strain and environment on the proportion of area visited by the larvae in the test plates. Because the mass of the larvae might affect their locomotion, we corrected for the potential effect of mass in the models. Similarly, we modeled the effects of strain and environment on the growth of the larvae. Our analyses enabled us to test the main effects and the interactions between the independent variables. To do so, we fitted Generalized Least Squares

models (GLS) to account for heterogeneity in the data, and Ordinary Least Squares models (OLS). To evaluate the models' goodness of fit, we used information-theoretic criteria such as AICc. We ranked the candidate models accordingly and selected the most likely one for inferences (lowest value of AICc).

To produce a good visualization of our results and ensure that they are fully reproducible, we carried out all the analyses in the free software for statistical computing R v.4.3.2 (2023-10-31, R Core Team, 2023).

Results

Our analyses supported a model describing the effects of strain and environment on the proportion of area covered by the larvae while foraging (Table 1). Two lines of evidence aligned almost entirely with this result. First, rovers covered larger areas than did sitters within each environment, yet the area exploited by either strain was generally larger in the patchy environment compared to that exploited in the uniform environment (Figure 1A). Second, the video-tracking experiment revealed that rovers generally traveled longer distances than did sitters, but we found no differences across environments (Figure 2)

Table 1.

Figure 1.

Although rovers traveled further and covered more area than sitters, both strains grew at similar rates. According to our analysis, a model describing only the effect of patchiness of the environment on growth was strongly supported (Table 2). Larvae of both strains grew faster in uniform environments than they did in patchy environments (Figure 1B). In either type of environment, sitters grew insignificantly faster than rovers did. In addition, they spent a longer proportion of time in food patches than rovers did (Figure 2).

Table 2.

Figure 2.

Discussion

Our results suggest that foraging behavior is a plastic trait remarkably shaped by the distribution of food in the environment, which is consistent with the findings of recent investigations (e.g., Anreiter and Sokolowski, 2019; Edelsparre et al., 2021). Based on theoretical models, we predicted that both strains would cover more area in a patchy environment compared to a uniform environment. This expectation relies on the fact that food was available over a larger area in a patchy environment; therefore, the energetic return from moving would likely surpass that of remaining in a patch. By contrast, the uniform environment only contained a single clump of food in one location. In the latter case, leaving this sole patch of food would reduce the

acquisition of energy. Following the same notion, we expected a patchy environment to cause a more pronounced difference in locomotion between strains. This predicted interaction between strain and environment was not supported by our results. These findings suggest that the relationship between patch distribution, patch density, and the locomotion of organisms is likely more complex than expected.

A key assumption underlying our predictions was that organisms behave to maximize the net energy intake during foraging. Because the rate of energetic gain or loss greatly affects fitness (Reid et al., 2000; Roff, 2002; Bayne, 2004; Angilletta Jr et al., 2004), assessing which foraging strategy yields the highest surplus energy in a given environment becomes crucial to understanding the evolution of behavior (Schoener, 1971; Charnov, 1976). Often, investigating the connection between what is being optimized (i.e., foraging behavior) and a "fitness component"—such as growth—offers the opportunity to accomplish such a task (Flatt, 2020). When testing the effects of foraging behavior on growth, we discovered that the uniform environment stimulated a faster growth in both strains than did the patchy environment. Interestingly, however, both strains grew to similar sizes in either environment even though rovers generally covered larger areas than did sitters while foraging. These observations were not entirely consistent with our predictions as we expected the rover strain to decrease the locomotor activity and grow slower in the uniform environment. Rather, our findings are consistent with previous investigations (Kaun et al., 2007; Burns et al., 2012), adding more evidence against the general belief that foraging polymorphism leads to variation in life-history traits. Because food was relatively abundant in each environment, and strains were tested individually, the density of food was not depleted at the same

rate as it would be in the presence of competitors. Thus, there may have been little incentive to minimize daily foraging time and energy by rovers. The minimization of daily energy expenditure might not be necessary when food is relatively abundant, but a highly efficient energy-expensive foraging strategy, such as pursuing the food, would become advantageous as it saves time for other critical activities (Norberg, 2021).

Based on the results of this study, the question remains which foraging strategy is better suited to maximize energy intake in a particular environment. The evidence indicates that foraging actively could be advantageous when food is either patchy or clumped. Two kinds of mathematical models provide support for this claim. As described above, an energetically-demanding but efficient strategy of searching for food enables animals to save time for other activities, such as reproduction (Norberg, 2021). In addition, eco-evolutionary models suggest that the ability of rovers to traveled longer distances while foraging influences their dispersal ("high-dispersing" strategy). In its simplest form, dispersal can be defined as any movement with potential for genetic mixing (Ronce, 2007), facilitating local adaptation via founder events, gene flow, and life history trade-offs (Hanski and Mononen, 2011). If foraging actively promotes higher dispersal, such behavior may evolve fast and lead to the colonization of new environments (Reznick and Ghalambor, 2001). Although the dispersal ability of a larva may be lower than that of an adult, previous investigations suggest that behaviors that are expressed early in life are closely integrated with a suite of life-history traits that enhance colonization ability, and often retain flexibility in expression throughout an organism's life (e.g., Roff, 1977). Such strategies are commonly described in insects that express winged dispersive and wingless nondispersive morphs (Harrison, 1980;

Roff, 1986; Zera and Denno, 1997). In other animals, such as birds, highly dispersive behaviors are often associated with aggressive behaviors that can enhance survival and competitive ability in a novel environment (Dingemanse et al., 2003; Duckworth and Badyaev, 2007).

Taken together, our study implemented a simple yet elegant way to test some of the long-standing predictions of the so-called "foraging-mode paradigm". We suggest that foraging behavior is a highly plastic trait molded by the distribution of food in the environment. Our findings support the notion that animals maximize their energy intake by adjusting their locomotion according to environmental heterogeneity. In wild populations of *D. melanogaster*, this could mean that rovers would influence the rate of population spread to a higher extent than would sitters. As such, foraging actively could have important implications for colonization or range expansion to novel habitats through the subsequent evolution of life-history traits. Although the interpretation of our results are limited to the larvae of *D. melanogaster*, evidence of correlated evolution of foraging behavior in larvae and adults enables us to make predictions at both developmental stages (Pereira and Sokolowski, 1993; Hughson et al., 2018; Sokolowski, 1980). It is important to point out that fitness should be measured over entire life cycles. Thus, the possibility exists that the appropriate time intervals for maximizing the benefits of foraging behavior is over a longer period than the one considered in our study.

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Data Accessibility Statement

A fully reproducible workflow of the data analyses, including R scripts and additional supporting material, is available in the following repositories: Github `https://dylan-padilla.github.io/foraging-experiments/`. A dryad link will be available upon acceptance: .

Conflict of interest

The authors have declared no competing interests.

Author Contributions

DP: Conceptualization, data curation, and formal analysis. Writing – original draft, writing – review and editing. MA and JV: Conceptualization, Supervision, Writing – original draft, writing – review and editing. The authors agreed to be held accountable for the work performed herein.

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Tables with captions

Table 1: Parameters estimated by the most likely model describing the effects of strain and environment on the proportion of area covered by the larvae.

	Df	Sum.Sq	Mean.Sq	F.value	Pr(>F)
strain	1	0.222	0.222	26.778	<0.001
environment	1	0.100	0.100	12.028	0.001
Residuals	89	0.739	0.008		

Table 2: Parameters estimated by the most likely model describing the effect of environment on larval growth.

	Value	Std.Error	t-value	p-value
(Intercept)	1.713e-04	1.479e-05	1.158e+01	1.334e-20
environment	1.574e-04	3.102e-05	5.075e+00	1.644e-06

Figures with captions

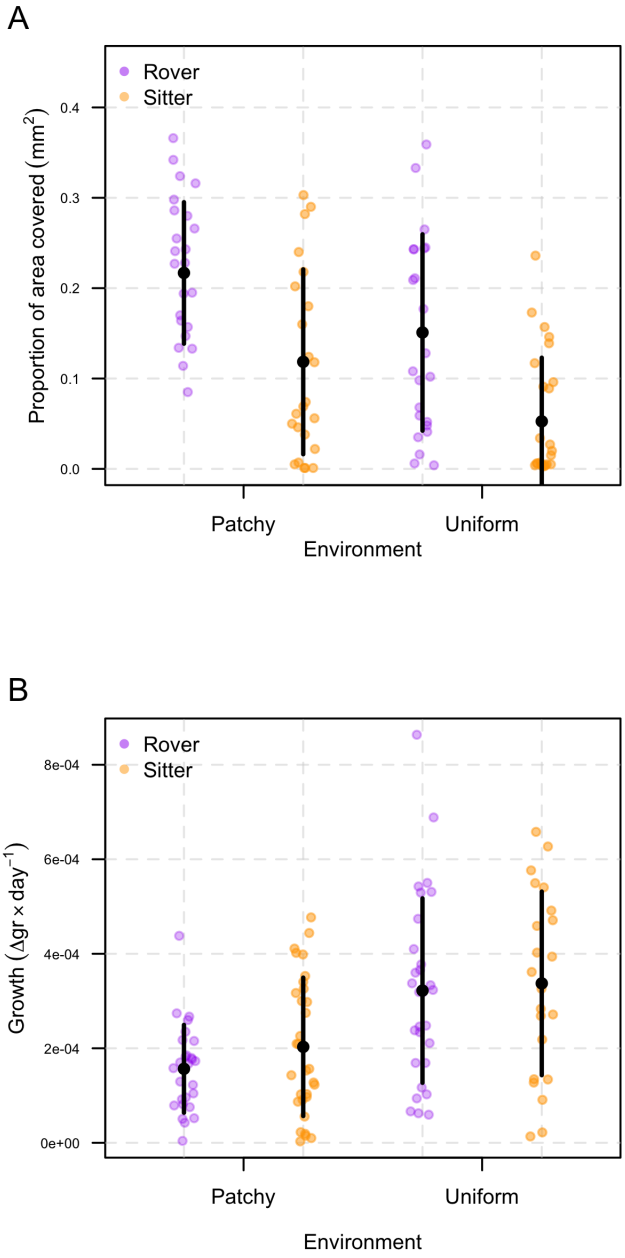

Figure 1: Statistical comparisons among the predictors involved in the experimental design of the study. A) Effects of strain and environment on the locomotor activity of the larvae. B) Effects of strain and environment on larval growth. Black dots represent the estimated means and the bars the standard deviation.

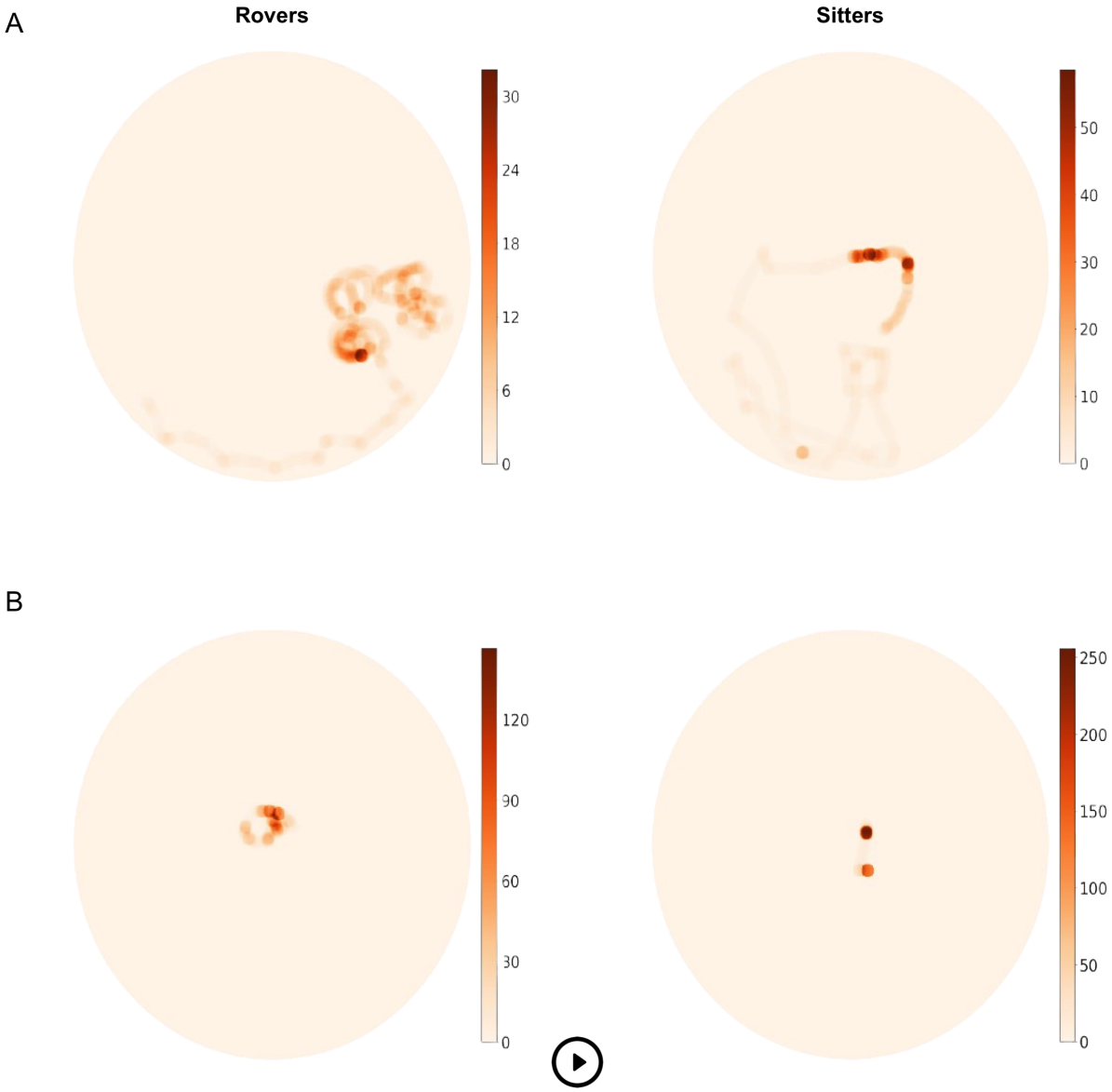

Figure 2: Animated visualization of the distance traveled by the larvae together with the proportion of time spent at specific sites of the test plates. A darker coloration indicates a longer proportion of time spent at a site (s). A) Patchy environment. B) Uniform environment. ***For the best visualization, readers should view this illustration in Adobe Reader 9 or a later version:*** *http://www.adobe.com/products/reader/*.

Supplementary material

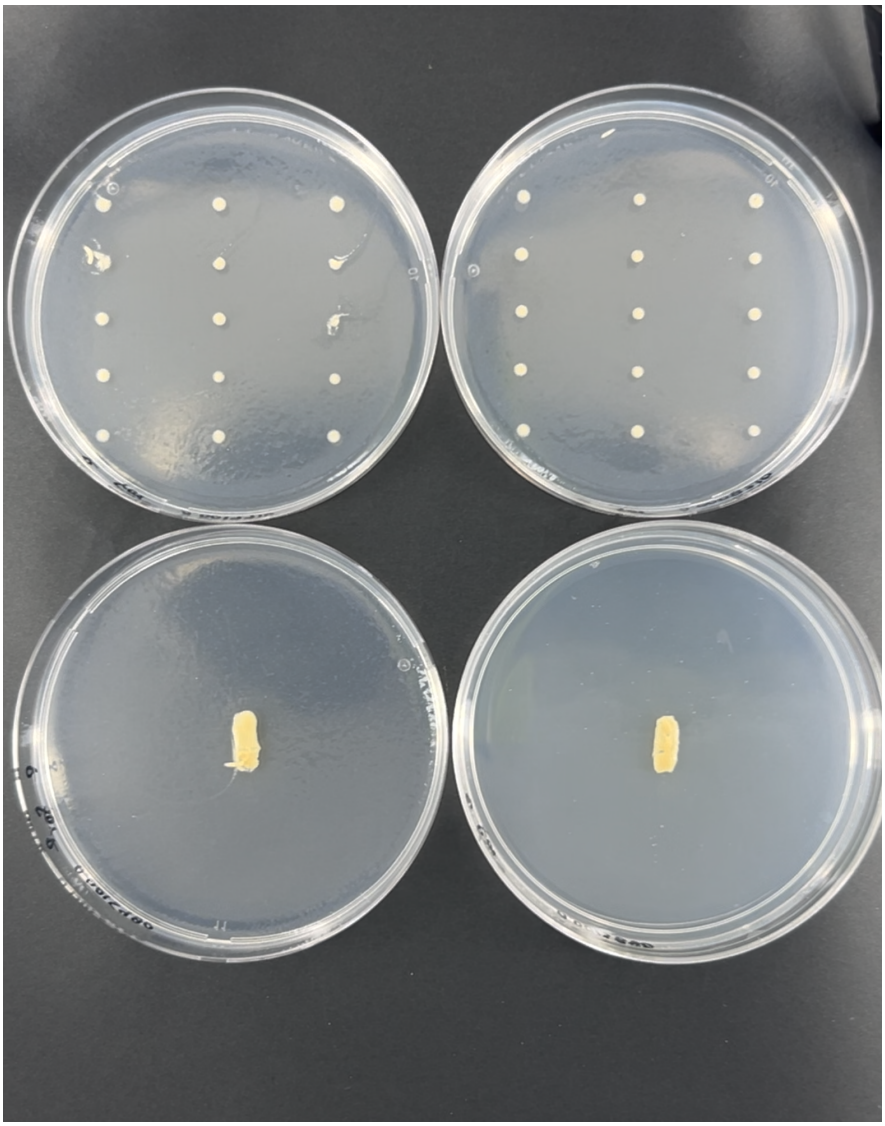

Figure S1: Visualization of the experimental design implemented in this study.