
Short Communication

Parasitization of Embedded and Nonembedded *Drosophila melanogaster* (Diptera: Drosophilidae) Pupae by the Parasitoid *Pachycrepoideus vindemniae* (Hymenoptera: Pteromalidae)

Yves Carton¹ and Marla B. Sokolowski²

Accepted September 9, 1992; revised June 15, 1993

KEY WORDS: *Drosophila*; parasitoid wasp; behavior; genetics.

Does genetically based variation in host behavior influence parasitization rates? We have reported that *Drosophila melanogaster* larvae show an interesting dichotomy in their pupation behavior (Wong *et al.*, 1985). Some larvae dig a tunnel prior to pupation. They pupate at the end of this tunnel and expose only a small portion of their anterior end. We call these "embedded" pupae. In contrast, other larvae pupate on the surface of the food, leaving their entire pupal case exposed. We call these "nonembedded" pupae. Does this difference in behavior result in different levels of parasitization by *Pachycrepoideus vindemniae*, a pupal parasitoid of *Drosophila*? Indeed, little is known about how genetically based variation in host behavior can influence the degree of parasitization in any parasitoid (Carton and Sokolowski, 1992).

The embedding behavioral phenotype is an excellent candidate for studies of natural selection by the wasp because (1) variation in embedding behavior has a heritable basis in *D. melanogaster*, (2) embedding behavior is modifiable by the moisture content of the food, and (3) variation in embedding behavior is found in natural populations along with the pupal parasitoid *Pachycrepoideus* (Wong *et al.*, 1985).

Here we ask whether *P. vindemniae* parasitizes embedded and nonembedded pupae at random. We used two host strains of *D. melanogaster* selected for differences in embedding behavior. Parasitoids were exposed to a dish where

¹Centre National De La Recherche Scientifique, Laboratoire de Biologie et Genetique Evolutive, 91190, Gif-Sur-Yvette, France.

²Department of Biology, York University, 4700 Keele Street, Toronto, M3J1P3 Canada.

30 larvae had been allowed to pupate. Therefore, the proportion of embedded pupae in a dish varied as a result of differences in larval pupation behavior.

We used a heterogeneous population of *D. melanogaster* from the Nasrallah oasis in Tunisia (Sokolowski and Carton, 1989). This population underwent bidirectional selection for embedding behavior. Two lines were established, which differed significantly in this behavior: The low line (L) had about 20% of the pupae embedded and the high line (H) had 60%. *P. vindemniae* was collected from the Bordeaux region of France and cultured on *D. melanogaster*. *P. vindemniae* are also found at the Nasrallah oasis in Tunisia. Flies and wasps were reared at 25°C.

To measure parasitization of embedded and nonembedded pupae by this parasitoid, 30 wandering third-instar larvae (5 days posthatch at 25°C) were placed in a test dish. The dish (75 mm in diameter and 20 mm high) contained 9 ml of a 2.5% agar solution which had 250 μ l of a yeast solution (22 g of yeast in 100 ml of water) spread on it. Three female parasitoids were then introduced into each dish and were allowed to parasitize for 4 days. Female wasps prefer to parasitize newly pupated larvae. After 20 days, pupae were examined for infestation. This procedure was repeated six times for each of the L and H strains.

After six generations of selection the means for the L and H strains differed significantly, 20.8% for the L and 58.8% for the H strain (Sign test, $P = 0.02$; $n = 6$). This rapid response to bidirectional selection implies that relatively few genes are involved in differences in embedding behavior in this population.

We chose the L and H strains for this study so that the degree of parasitization was measured over the full range of embedding. As mentioned previously, the ratio of embedded-to-nonembedded pupae differed in each dish. If the wasps were parasitizing at random, we would expect the number of parasitized and unparasitized pupae to be distributed evenly between the embedded and the nonembedded pupae. For the L strain, no difference in the percentage of parasitized embedded (38.7%) compared to nonembedded (48.9%) pupae was found, indicating that at lower embedding frequencies, the wasps were parasitizing pupae at random. However, for the H strain, the parasitoids parasitized embedded pupae 80% of the time, compared to non-embedded pupae, which were parasitized 39.7% of the time.

The data were analyzed using a multidimensional contingency table categorical analysis (Feinberg, 1970; Sokal and Rolf, 1969). Log-linear models were fit to the observed frequencies of individuals that were classified by the tendency to embed pupae (E), parasitization choice (P), strain (S), and replicate (R). The model that best fit the data was [(PER), (PRS), (PES)], where the three-way interaction (ERS) was not needed in the model (log-likelihood ratio, 15.67; $df = 10$; $P = 0.11$). This means that within a strain, there was no difference in embedding behavior among replicates. However, the number of

larvae that were embedded in the medium was dependent on the fly strain, and the proportion of larvae that were parasitized was dependent on whether or not the larva was embedded. However, the associations among these factors varied among replicates.

Is there a selective advantage to wasps that can distinguish between embedded and nonembedded pupae? Wasps that parasitize embedded pupae may have some advantage in hot, dry environments since the fly pupa and hence the wasp larva would be protected by the moderating effect of being embedded in the food. In contrast, wasps that parasitize embedded pupae under conditions of a high *Drosophila* larval density would be at a disadvantage because embedded pupae have a greater chance of being drowned by actively foraging larvae (Meuller and Sweet, 1986). Some questions for future research are (1) Is the wasp specifically able to distinguish between embedded and nonembedded pupae, and if so, what cues are used? (2) Is there genetic variation in the wasp for this ability? (3) Does the wasp show frequency-dependent selection for embedded and nonembedded pupae?

REFERENCES

- Carton, Y., and Sokolowski, M. B. (1992). Interactions between searching strategies of *Drosophila* parasitoids and the polymorphic behavior of their hosts. *J. Insect. Behav.* 5: 161-175.
- Feinberg, S. E. (1970). The analysis of multidimensional contingency tables. *Ecology* 51: 419-433.
- Meuller, L. D., and Sweet, V. F. (1986). Density dependent natural selection in *Drosophila*: Evolution of pupation height. *Evolution* 40: 1354-1356.
- Sokal, R. R., and Rohlf, F. J. (1969). *Biometry*, W. H. Freeman, San Francisco.
- Sokolowski, M. B., and Carton, Y. (1989). Microgeographic variation in *Drosophila melanogaster* larval behavior. *J. Insect Behav.* 2: 138-139.
- Wong, J. L., Sokolowski, M. B., and Kent, C. F. (1985). Prepupation behavior in *Drosophila*: Embedding. *Behav. Genet.* 15: 155-164.