

Predation on the Cactophilic Fly, *Drosophila starmeri*, in the Columnar Cactus, *Pilosocereus lanuginosus*¹

A. Escalante and M. Benado²

Departamento de Estudios Ambientales, Universidad Simón Bolívar,
P.O. Box 89000, Caracas 1086-A, Venezuela

ABSTRACT

The cactophilic fly, *Drosophila starmeri*, exploits the necroses of the columnar cactus *Pilosocereus lanuginosus* in Venezuela. The fly is the most abundant Diptera in the tissues of the cactus, and it is a food for other arthropods. We show that ants (*Pseudomyrmex* sp., *Zacryptocera* sp.) and Staphylinid coleoptera prey upon *D. starmeri* and potentially regulate *D. starmeri*'s population in the wild.

CACTOPHILIC *DROSOPHILA* breed in and feed on fermenting cactus tissues ("rot pockets"). Several studies have analyzed factors such as chemicals, microflora, and interspecific competition that affect host affiliation, distribution, and fitness of the flies (Barker & Starmer 1982; Benado & Montero, in press; Ruiz & Heed 1988). However, less is known about the interactions of the flies with other arthropods associated with the fermenting substrate.

Our data show that the cactophilic fly *Drosophila starmeri* Wasserman, Koepfer, and Ward exploits the columnar cactus *Pilosocereus lanuginosus* (L.) Byley and Rowley. Our rearing records also indicate that *D. starmeri* is the most abundant Diptera, and one of the most abundant taxa, that emerge from the rot pockets. This suggests that the fly may be an important trophic source for other organisms. The only predators previously implicated in regulating populations of *Drosophila* are parasitic wasps (Brncic 1983, Carton *et al.* 1986). In this paper we analyze predation of *D. starmeri* by other insects that share the same general microhabitat. We give evidence that *D. starmeri* is preyed upon by Staphylinid coleoptera and by ants. The null hypothesis is that the fly's population size is not affected by predation.

MATERIALS AND METHODS

Field experiments and sampling were carried out between May and July 1987 at the Simón Bolívar University Campus in Camurí Grande, 5 km east of Naiguatá Beach, at sea level, where an abundant population of *P. lanuginosus* can be found. Laboratory experiments were performed in the same period at the Simón Bolívar University Campus in Sartenejas, Caracas, at 1200 m elevation.

"Natural" substrates were found already fermenting

in the field. The samples were wrapped separately in paper, and taken to the laboratory. Each rot pocket was cut open lengthwise and the kinds and numbers of organisms that were present were recorded. Afterwards, the two halves were stuck together and put into one gallon glass flasks where flies and other organisms were allowed to emerge. Two kinds of natural substrates were found: those with ant nests of the genera *Pseudomyrmex* or *Zacryptocera* present within the necroses but without other arthropods (Table 1); and those without ants, where other organisms were abundant. The latter were considered controls to which artificially-induced fermentations were compared (see below).

"Artificial" substrates were made on cacti at the field site by cutting off the top 10 cm of the cactus stem. Next, a 1.5 cm diameter borer was used to remove a central core section of 5 cm from the lower stem portion. A fermented slurry (see below) of cactus tissue was inserted into the hole, and the core section was replaced. Finally, the top of the stem was stuck back on to the stem and secured with a band of aluminum foil. The slurry was prepared by grinding natural substrates in a Waring blender and freezing the resulting suspension at -6°C, to kill larval and adult arthropods and other macroorganisms. The slurry was used after thawing.

Artificially fermented substrates were then treated like the natural ones. They were opened, and the organisms present were recorded. Next, the substrates were divided into two sets. One set was put into the flasks without further treatments, and the organisms were allowed to emerge. This series was compared to the natural substrates without ants, to make sure that the induced fermentation was comparable to the natural one. We detected no differences in the taxa present in either kind of substrate.

The second set consisted of artificial substrates from which all the predators were removed (Richards & Davies 1977; see Table 2). The rot pockets were cut open as before, and a vacuum pump was used to eliminate pred-

¹ Received 22 June 1988, revision accepted 16 November 1988.

² Author to whom correspondence should be sent.

TABLE 1. Substrate weights and *D. starmeri* emergences under predation.

Substrate	Predator	N	Weight* (g)	Emergences* (flies)	Yield* (flies/g)
Artificial	none	12	395.0 ± 43.7	202.8 ± 63.5	0.50 ± 0.12
Artificial	Staphylinid 1	6	397.9 ± 46.6	64.5 ± 20.8	0.16 ± 0.04
Natural	<i>Zacryptocera</i>	5	417.1 ± 44.7	33.8 ± 14.7	0.08 ± 0.03
Natural	<i>Pseudomyrmex</i>	3	340.0 ± 21.8	0.3 ± 0.6	0.00 ± 0.00

N: sample size. *: mean ± SE.

ators. This last set was further divided into two series. One series was put without further treatments into the flasks, and the organisms were allowed to emerge. The other series consisted of substrates to which 2–3 adult "Staphylinid 1" predators were added. Afterwards these samples were also put into the flasks, and the organisms were allowed to emerge. This particular predator was chosen for its easy handling, large size, and high activity.

Ants from the genus *Pseudomyrmex* are exclusively carnivorous (Janzen 1967) whereas those from the genus *Zacryptocera* are facultatively so (K. Jaffé, pers. comm.). However, we considered that predation was occurring in the necroses where either of the species was found.

Predation was observed directly for Staphylinid 1 predators (see Results). The effect of predation upon the fly's population size was tested by comparing the emergences of the artificial substrates without predators, the emergences of the artificial substrates with the predators added, and the emergences of the natural substrates with ants. To test for the effect of predation, it was necessary to adjust the fly emergences for the weights of the samples. First, both variates were log-transformed, and then the following ANCOVA model was adjusted to the data: $\log(\text{emergence}) = \text{constant} + \log(\text{substrate weight}) + \text{predation} + \text{error}$, where weight is the concomitant variable. For the statistical tests, substrates with *Pseudomyrmex*

were not included, since they yielded almost no flies (Table 1).

Larvae, pupae and adults of the Staphylinid 1 predator, as well as ant nests and all the other organisms listed in Table 2, have been preserved and deposited in the collection of the Universidad Simón Bolívar, Sartenejas, Caracas.

RESULTS

A total of 136 samples were processed. Predators were in all rot pockets (Table 2). Ants, but not other predators, were present in eight pockets (Table 1). "Staphylinid 1" and other predators were in 120 pockets. In the other eight "Staphylinid 1" was absent, and other predators excepting ants were present. We found no ants in artificial substrates, and the two ant species were never found together in the natural necroses.

The "Staphylinid 1" predator completed its life cycle within the rot pockets. Its adult and larval stages preyed upon *D. starmeri*'s larvae, actively burrowing into the fermenting substrate both in the field and in the laboratory. In a few cases they were observed preying upon adult flies.

Drosophila yields under different predators ranged from 0.50 ± 0.12 flies/g tissue (controls) to 0.00 ± 0.00 (*Pseudomyrmex*) (Table 1). Both substrate weight and predation had significant effects on the emergences (Table 3). It follows that predation affects *D. starmeri*'s population size, as measured by the emergences.

DISCUSSION

There is disagreement concerning the roles of competition and other factors, such as natural enemies, in structuring phytophagous insect communities. In a careful

TABLE 2. Predators found in the fermenting tissues of *P. la-nuginosus*. Sample size: 136 necroses. References for insects are Janzen (1967) and Richards and Davies (1977).

Predator	Size (cm)	% rot pockets present
Hysteridae 1	>1.0	79.4
Hysteridae 2	>1.0	83.1
Hysteridae 3	<0.5	89.0
Hemiptera 1	<0.5	72.1
Hemiptera 2	<0.5	53.7
Staphylinidae 1	>1.5	88.2
Staphylinidae 2	<0.5	75.0
Staphylinidae 3	<0.5	47.8
<i>Pseudomyrmex</i>	—	2.2
<i>Zacryptocera</i>	—	3.7
Pseudoscorpion	<0.5	59.6

TABLE 3. ANCOVA of effects of substrate weights and of predation on *D. starmeri*'s emergences.

Source	SS	df	MS	F	P
Logweight	2.264	1	2.264	77.113	0.000
Predation	14.942	2	7.471	254.486	0.000
Error	0.558	19	0.029		

review of the evidence, Strong *et al.* (1984) concluded that detailed analyses of phytophagous populations frequently fail to detect significant interspecific competition. This is true because many populations are kept rare relative to the availability of potentially limiting resources by the impact of natural enemies, insect predators, parasitoids, etc. Hence, community processes work vertically, rather than horizontally, through the food chain. Our evidence indicates that vertical processes may be important in regulating *Drosophila* populations.

Ants clearly depress the fly's population size. Forty-eight natural substrates were collected: 17 percent of them harbored ant nests. In these, emergence of the fly was severely reduced (Table 1).

For the staphylinid predator, the evidence is not so distinct. This organism was present in 88 percent of the necroses, and it also kept *D. starmeri*'s population below the controls in the laboratory. Our experimental design, however, did not allow the flies to recolonize the necroses, as they surely do under natural conditions, nor did it allow

the predator to move from one rot pocket to the other, as was observed in the field. Without a more detailed study of these processes, it is difficult to gauge the reduction of population size in the field caused by the staphylinid predator.

Parasitic wasps are likely to regulate *Drosophila* populations. Brncic (1983) reported that the frequency of wasp-parasitized pupae of *D. flavopilosa* ranged from 0 to 64 percent. Other authors (reviewed in Carton *et al.* 1986), indicate infestation by wasps up to 80 percent.

Our data indicate that non-parasitoid predators occur very frequently in the insect community associated with rot pockets (Table 2), and they are as likely to be a limiting factor for *D. starmeri* as wasps are for other species.

ACKNOWLEDGMENTS

This study was funded by CONICIT grant S1-1206. We thank P. Berry, G. Benado, and an anonymous reviewer whose comments improved the manuscript.

LITERATURE CITED

- BARKER, J. S. F., AND W. T. STARMER. 1982. (Eds.) Ecological genetics and evolution. The cactus-yeast-*Drosophila* model. Academic Press, New York.
- BENADO, M., AND C. MONTERO. Competition between the cactophilic species *Drosophila starmeri* and *D. uniseta*. Rev. Chil. Hist. Nat. In press.
- BRNCIC, D. 1983. Ecology of flower-breeding *Drosophila*. In M. Ashburner, H. L. Carson, and J. N. T. Thompson, Jr. (Eds.). The genetics and biology of *Drosophila*, Vol. 3d, pp. 333-382. Academic Press, London.
- CARTON, Y., M. BOULETREAU, J. J. M. VAN ALPHEN, AND J. C. VAN LENTEREN. 1986. The *Drosophila* parasitic wasps. In M. Ashburner, H. L. Carson, and J. N. T. Thompson, Jr. (Eds.). The genetics and biology of *Drosophila*, Vol. 3e, pp. 348-394. Academic Press, London.
- JANZEN, D. 1967. Interaction of the Bull's-horn Acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea*) in eastern Mexico. Univ. Kansas Sci. Bull. 67: 315-558.
- RICHARDS, O. W., AND R. G. DAVIES. 1977. IMMS' general textbook of entomology. 10th ed. Vol. 2. Classification and biology. Wiley, London.
- RUIZ, A., AND W. HEED. 1988. Host-plant specificity in the cactophilic *Drosophila mulleri* complex. J. Anim. Ecol. 57:237-249.
- STRONG, D. R., J. L. LAWTON, AND T. R. SOUTHWOOD. 1984. Insects on plants. Harvard Univ. Press, Cambridge, Massachusetts.