

Competition between the cactophilic species *Drosophila starmeri* and *D. uniseta*

Competencia entre las especies cactófilas *Drosophila starmeri* y *D. uniseta*

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ABSTRACT

Breeding records indicate that the cactophilic species *Drosophila uniseta* outnumbers *D. starmeri* in the tissues of the columnar cactus *Stenocereus griseus*. Serial transfer experiments in a medium with *S. griseus* show that *D. uniseta* always outcompetes *D. starmeri*. Competition may be an explanation for the rearing records in nature.

Key words: *Drosophila martensis* cluster, cactus, Venezuela.

RESUMEN

Los tejidos en fermentación del cactus columnar *Stenocereus griseus* son explotados por *Drosophila uniseta* y *D. starmeri*. *D. uniseta* emerge de dichos tejidos siempre en mayor número que la otra especie. Experimentos de competencia bajo regímenes de transferencia seriada en un medio que contenía el cactus demostraron que *D. uniseta* desplazó siempre a la otra especie en el laboratorio. Se concluye que la competencia es uno de los mecanismos que puede explicar las emergencias en condiciones naturales.

Palabras claves: Enjambre *Drosophila martensis*, cactus, Venezuela.

INTRODUCTION

Drosophila uniseta Wasserman, Koepfer & Ward 1973 and *D. starmeri* Wasserman, Koepfer & Ward 1973 are cactophilic insects, that is, they breed and live upon fermenting cactus tissues ("rot pockets"). The flies belong to the *D. martensis* cluster of the *D. repleta* group of the subgenus *Drosophila*, a taxon endemic to Venezuela and Colombia (Wasserman & Koepfer 1979, Wasserman *et al.* 1983). Both species exploit the columnar cactus *Stenocereus griseus* (Gibson & Horak 1978), and our rearing records indicate that this cactus is the only host for *D. uniseta*, that it breeds very few individuals of *D. starmeri*, that the *Drosophila* species are sympatric throughout Venezuela (Benado *et al.* submit.), and that the flies show little host overlap (Table 1). The experiments reported here test the hypothesis that the differential utilization of *S. griseus* by *D. uniseta* can

be explained by a competitive displacement of *D. starmeri* by *D. uniseta*.

TABLE 1

Emergence of *Drosophila uniseta* and *D. starmeri* in Venezuela (flies).

Emergencias de *Drosophila uniseta* y *D. starmeri* en Venezuela (moscas).

	Cactus spp.			Total
	<i>Stenocereus griseus</i>	Other		
Rot pockets	73	1	185	259
<i>D. uniseta</i>	3304	42	0	3346
<i>D. starmeri</i>	0	2	11746	11748

MATERIAL AND METHODS

The *D. uniseta* and *D. starmeri* strains used in the experiments were founded with flies that emerged simultaneously from the

same rot pocket of *S. griseus* collected in Prudencio, W. Venezuela (Benado *et al.* 1984). The strains were allowed to compete under a serial-transfer regime (Benado *et al.* 1976, Mueller & Ayala 1981, Mueller 1985) in 100 ml bottles with 20 ml of food and 1 week transfer periods. The food was prepared as follows: 237 g fermenting *S. griseus*, 237 g unfermenting *S. griseus* in 1 cm³ pieces, 8 g agar, 500 ml distilled H₂O, 4 ml propionic acid. After boiling, and just before the agar solidified, the cactus pieces and the propionic acid were added. A 20 x 30 cm piece of tissue paper was included as a substrate for the larvae and the adults.

Competition started with 20 females and 20 males at 3 different frequencies of *D. uniseta* ($p = 0.2, 0.5, 0.8$), with 4 replicates by frequency and 4 replicates by control (single-species serial-transfer experiments). The bottles were discarded after the 6th week. All the experiments were carried out at 25°C ± 1 in a Percival incubator with a 12h light/dark cycle. The single-species experiments were terminated at week 13.

None of the species survived when they were kept in a control medium without cactus.

RESULTS

Statistics for the competition experiments are given in Table 2. In all the cases, *D. uniseta* outcompeted *D. starmeri*. The trajectories of some of the replicates are depicted in Fig. 1. Data for the single species experiments are given in Table 3 and Fig. 2. Both *D. starmeri* and *D. uniseta* survived when growing alone. Moreover, a one-way ANOVA showed that non significant differences existed among the population sizes at fixation (K) and the controls' populations at week 13 ($F_{4, 15} = 0.58$).

DISCUSSION

The experiments mimic what was found in nature: most rot pockets of *S. griseus* yielded only *D. uniseta* and when both *D. uniseta* and *D. starmeri* emerged, the former outnumbered the latter (Table 1). We conclude that competitive interactions between *D. uniseta* and *D. starmeri* may be an explanation for the rearing records of *S. griseus*.

TABLE 2

Statistics for the competition experiments.

Estadísticas de los experimentos de competencia.

p=0.2 replicate	W	K
A	18	183
B	19	190
C	12	167
D	14	185
Mean	15.8 ± 1.7	181.3 ± 5.0
p=0.5		
A	10	162
B	12	181
C	11	188
D	14	163
Mean	11.8 ± 0.9	173.5 ± 6.5
p=0.8		
A	10	165
B	13	159
C	10	165
D	11	193
Mean	11.0 ± 0.7	170.5 ± 7.6

p: *D. uniseta*'s initial frequency. W: weeks to fixation of *D. uniseta*. K: population size at fixation (flies).

p: Frecuencia inicial de *D. uniseta*. W: semanas hasta la fijación de *D. uniseta*. K: moscas en la fijación.

TABLE 3

Population size at week 13 in the single-species experiments.

Tamaño poblacional en la semana 13 en los experimentos monoespecíficos.

Replicate	<i>Drosophila uniseta</i>	<i>D. starmeri</i>
A	184	180
B	163	173
C	190	176
D	180	173
Mean	179.3 ± 5.6	175.5 ± 1.7

Further insights into the mechanisms of the interactions can be gained by observing that, in serial-transfer techniques, food is never in short supply. Thus, competition for food can be ruled out. Our results, that the population sizes at fixation do not differ significantly from the controls, are consistent with this property of serial-transfer regimes.

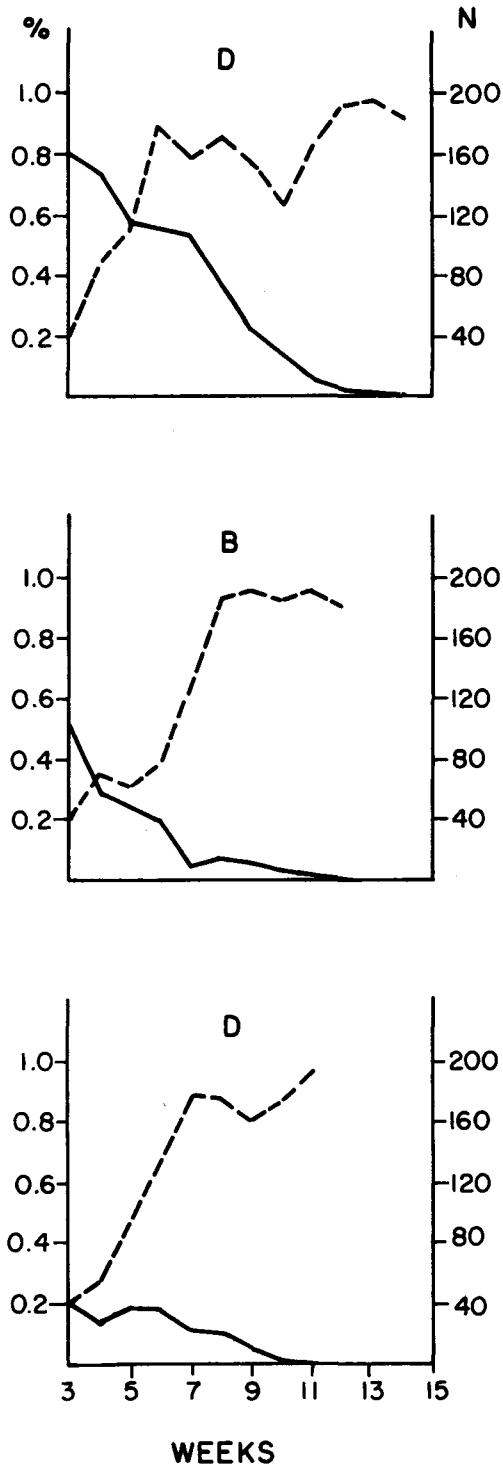


Fig. 1: Competition experiments between *Drosophila uniseti* and *D. starmeri*. % : proportion of *D. starmeri* in the culture (continuous line). N: total population size (broken line), D, B, replicates.

Experimentos de competencia entre *D. uniseti* y *D. starmeri*. % : proporción de *D. starmeri* (línea continua). N: tamaño poblacional total (línea quebrada), D, B, réplicas.

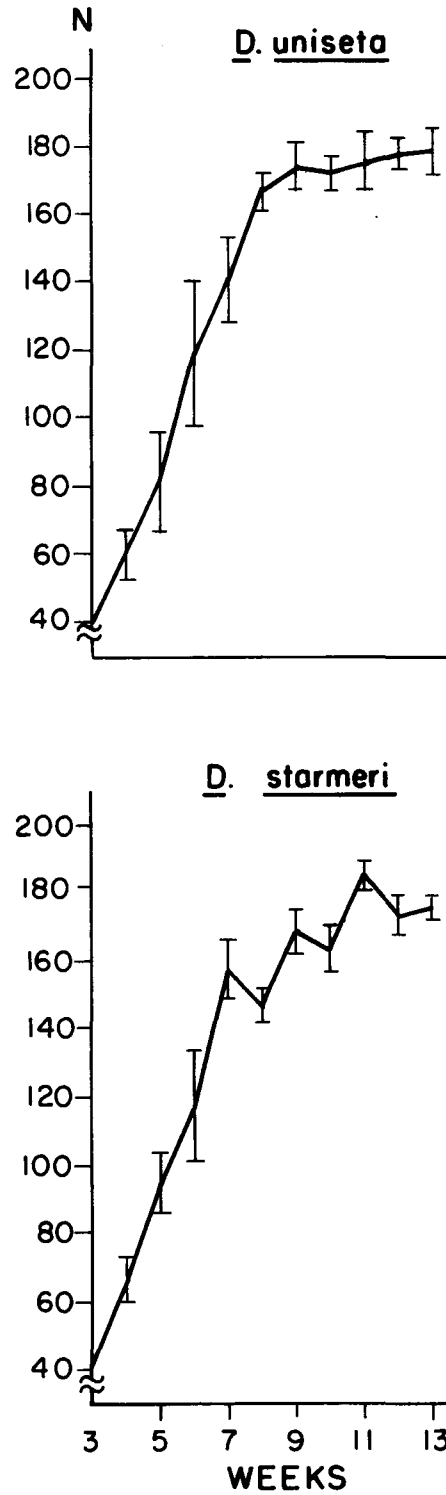


Fig. 2: Single-species experiments. N: population size. Each data point is the average (± 1 SE) of 4 replicates.

Experimentos monoespecíficos. N: tamaño poblacional. Cada punto es el promedio (± 1 EE) de 4 réplicas.

In the field, we have registered several cacti, at least 3 m tall x 40 cm diameter, that have been fermenting for 6 months, rearing flies (and other insects) continuously. We conclude that in nature food is very seldom in short supply, and that our experimental setup mimics adequately food availability under natural conditions.

An alternative hypothesis can be put forward, that larval metabolic residues of *D. uniseta* interfere with the development of *D. starmeri*. A similar hypothesis was set forth by Budnik & Brncic (1975) to explain the fact (among others) that "*D. pavani* very seldom has been found coexisting in the same breeding sites with other sympatric species like *D. melanogaster*" (notice that our rearing data are similar to these observations). Through a series of carefully designed experiments ("conditioned medium techniques") that eliminated the effect of food competition, they showed that *D. pavani* larvae are inhibited by metabolic wastes of *D. melanogaster*. Clearly, this is a mechanism that may explain the fact that the species' breeding sites do not coexist in nature.

A similar mechanism may also be operating in our system. *D. uniseta* could be lowering *D. starmeri*'s viability, and the rearing records, as well as the experimental results, reflect this.

Other mechanisms, like oviposition and habitat choice (Mueller 1985) can also explain host utilization in nature. We are currently testing the null hypothesis that *D. starmeri* does not choose substrates (cactus species) for laying eggs. The results of these tests will be critical for evaluating the experiments reported here.

It should be stressed that competitive interactions have already been considered a mechanism in explaining distribution of cactophilic flies breeding sites. Thus, Heed & Mangan (1986) considered that com-

petition of *D. mettleri* and *D. mojavensis* with the resident species *D. nigrospiracula* can be a factor in excluding the species from the tissues of the columnar cactus *Carnegiea gigantea* in the Sonoran desert.

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