THEY MOVE IN MYSTERIOUS WAYS: ABUNDANCE AND DISPERSION OF DIPTERAN FLOWER PARASITES

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Abstract. Flowers and flower buds of *Bomarea* sp. are infested with the larvae of a Dipteran parasite whose feeding destroys the flower's reproductive organs. We examined the dispersion of Diptera larvae among flowers within vines, among vines within patches, and among patches of *Bomarea* sp. Larvae dispersion was random within vines, suggesting that females oviposit independently of the presence of other eggs. Larvae were highly aggregated on some plants within patches, indicating that Diptera selectively oviposit on some vines. However, patches of individual plants were infested at similar densities throughout the landscape, suggesting that all patches are equally likely to be infested by Diptera.

INTRODUCTION

At least one plant species at Cuerici Biological Station bears hummingbird-pollinated flowers that are heavily parasitized by the larval stage of a Diptera sp. Within forest and field habitats, the Diptera larvae seemed to be present only in the umbels of a single vine species (*Bomarea* sp., Umbelliform). The dispersion of fly larvae seemed to be clumped at some spatial scales (individual vines) and regular at other spatial scales (flower pods within vines). In some other systems (e.g., fruit flies and *Heliconius* butterflies), females preferentially oviposit on sites not occupied by other eggs (Green 1986). We tested the hypothesis that the dipteran flower parasites at Cuerici choose patches, plants, and flowers non-randomly. We also explored some reasons for the parasites specificity to a single host plant species.

METHODS

Our study plant (probably *Bomarea* sp.) was a vine with multiple red-orange tubular flower heads 3 cm long, striking charcoal-blue colored anthers, and simple, alternating leaves that were ≈ 7 cm in length. We found the vine growing on the ground and shrubs in both forest and field habitats. The Diptera larvae that infested umbels were transparent and 3.5-5.0 cm long as late instars.

Research was conducted at Cuerici Biological Station on 26-27 January 1996. All flowering *Bomarea* along an ≈ 0.8 km forest path were collected and sorted based on locaion within a patch (defined as an area < 10 m in diameter containing > 1 plants). We dissected each flower and recorded flowers per vine, flower stage (open or closed), and the number, size, and stage (instar or pupa) of any Diptera. We refer to all the umbels as flowers, although 52% were nearly mature umbel buds that had not yet opened.

We tested for patterns in larval dispersion at three levels: among flowers within vines, among vines within patches, and among patches across the landscape. The distribution of larvae among flowers within vines was compared to a poisson distribution (using 3 vines that contained > 25 larvae). We tested for non-random dispersion patterns among flowers within vines by comparing the observed frequency distribution of the number of Diptera in flowers against that of a poisson distribution with the same mean. A significant P-value indicated a non-random dispersion; clumped dispersion patterns were indicated if the variance exceeded the mean (variance/mean > 1), and a regular dispersion was indicated if the mean exceeded the variance (variance/mean < 1). We used Chi-squares and nominal logistic regression (SAS 1995) to test for non-random dispersion among vines within patches (using 3 patches, each containing 3 or more vines and > 30 larvae), and among patches (using 6 patches that contained > 2 vines).

Three flower samples of three hummingbird-pollinated species, including *Bomarea* sp., were collected to measure relative moisture content (gravimetric analysis) and toughness (penetrometer). We recorded the temperatures of 3 flower buds from each of 3 species at 1715, 1845, 2020, and 0600.

Table 1. Dispersion of diptera larvae among flowers within vines.

	Number of flowers	Number of larvae	Larvae/ bud			Test for random dispersion	
			Mean	Variance	Ratioa	X^{2b}	P
Vine 1	21	30	1.43	0.94	0.66	2.20	0.90
Vine 2	46	66	1.48	1.49	1.01	0.47	0.98
Vine 3	22	44	1.82	2.07	1.14	0.23	0.99

[a] Variance/Mean
[b] df = 3

Table 2: Dispersion of diptera larvae among vines within patches.

	Vine #	Total Larvaea	Total Flowers [a]	Larvae/flower foreach vine	Test for random dispersion		
					X^2	df	P
Patch 1	3	30	57	1.42, 0.00, 0.00	33.64	2	0.005
Patch 2	3	92	70	0.50, 1.43, 1.90	7.55	2	0.025
Patch 3	4	32	35	0.57, 0.00, 2.67, 0.00	21.67	3	0.005

[a] number of plants examined

Table 4: Flower characteristics of three hummingbird pollinated plant species with similar floral morphology and habitats. Only *Bomarea* sp. flowers were infested by Diptera.

Plant	na	Mean	
		Relative Moisture Content (%)	Toughness (g)
Bomarea sp. - with larvae	3	74.3	190
Bomarea sp. - no larvae	3	69.1	190
Species B	3	71.4	135
Species C	3	66.8	58

RESULTS

We collected a total of 252 flowers (48% recently opened) on 16 vines in 6 patches. Contrary to our initial impressions, the dispersion of larvae among flowers within vines was very consistent with the null model of random dispersion (Table 1). For example, vine 1 contained 30 larvae in 21 flowers. Under a poisson distribution, the expected frequency of flowers with 0, 1, 2 and ≥ 3 larvae was 5.0, 7.2, 5.1, and 3.6, which was very similar to the observed frequencies of 3, 10, 4, and 4 (Table 1).

In contrast to the pattern within vines, larvae tended to be highly aggregated on some vines, while appearing to avoid others (Table 2). Patch 1 contained 30 larvae in 57 flowers, but the density of larvae per flower varied immensely across three vines (larvae / flower = 1.42, 0.00, 0.00; Table 2).

Table 3: Dispersion of larvae among patches.

Source	df	X^2	P
Patches	5	2.56	0.63
Vines (Patches)	4	31.25	0.0001

At the landscape level, patches were colonized at very similar densities by dipteran larvae. Across 6 patches, the ratios of larvae per flower bud were 0.53, 1.31, 0.91, 0.17, and 0.96 (Table 3).

The *Bomarea* flower had a high relative moisture content and the highest toughness of the three hummingbird-pollinated flowers with similar morphologies in the area (Table 4). Unlike the other two flower species, the temperature within the*Bomarea* was higher than ambient in every sampling period (Figure 1).

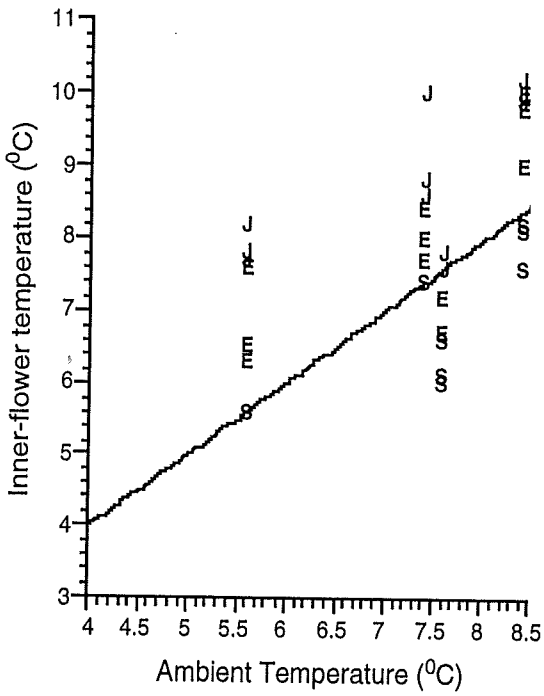

Fig. 1. Comparison of inner-flower temperatures of *Bomarea* flowers (filled circles) compared to inner-flower temperatures of two other species with similar floral morphology (open circles and open triangles). Line represents a flower temperature equal to ambient temperature.

Discussion

Location of patches, selection of vines, and dispersion among flower buds within vines may all be important in influencing the reproductive success of ovipositing Diptera adults. Across patches, Diptera densities were extremely similar, suggesting that Diptera efficiently search the entire population for suitable vines, and all patches have an equal chance of being infested. The bright conspicuous coloration of *Bomarea* sp. may be advantageous in attracting hummingbirds, but may also make *Bomarea* sp. more easily detected by flower parasites.

It may be beneficial for Diptera to expend energy to seek the most favorable vines for increased fitness. Alternatively, Diptera may not be able to distinguish between each flower's potential growth environments. Further research could distinguish between these theories by presenting the larvae with a range of flower phenotypes such as varying nitrogen content, secondary compounds, or those previously having parasitic encounters.

Larval dispersion was random among flowers within vines, indicating a lack of oviposition preference within an individual present. Larval biomass was quite high relative to the flower biomass, and larval success may be reduced in flower buds with multiple larvae. Future studies could test for intraspecific competition by looking for negative correlations between larval size and number. From the vine's perspective, random dispersion is more damaging than clumped dispersion of larvae. More flowers are affected if the same number of larvae are distributed randomly, and it only requires one larva to neuter each flower. Further research could explore the behavioral mechanisms that lead to dispersion of Diptera within and between vines.

Analysis of *Bomarea* sp. flowers suggested toughness, temperature insulation, and moisture retention may set *Bomarea* flowers apart and contribute to the development of Diptera parasites. However, several other local species had similar morphological characteristics. Secondary chemicals in the flower tissue may be another important determinant of host plant quality for the Diptera. Further, analysis of flower characteristics, as well as experimental manipulation, could lead to a better understanding of Dipteran host specificity.

Literature Cited

Green, M. 1986. Effect of guayaba density on fruit fly density. OTS **86** (3): 123-125.