

Notes on the Biology of *Efferia wilcoxi* (Bromley) (Diptera: Asilidae)

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Abstract.—*Efferia wilcoxi* was studied intensively in late May 1985, east of Portal, Cochise County, Arizona. Censuses showed flies to be more active in the late morning and to take prey at similar proportions through the day. Females appeared to outnumber males. Reproductive activities observed included searching flights by males during which they buzzed their wings, two copulations, and oviposition behavior by females; these are each similar to patterns described by Dennis et al. (1986) for other species of *Efferia*. Cicadellidae were the most frequent prey, but chalcidoid Hymenoptera, small flies, and Hemiptera (Heteroptera) were also relatively frequent. Striking differences in proportions of prey types in different years suggest the flies feed opportunistically. Cannibalism was observed.

The recent review of the ethology of the genus *Efferia* by Dennis et al. (1986) points out that only about 10% of the species in that large genus have been studied in any detail for their behavior and ecology. *Efferia wilcoxi* (Bromley) is a relatively common if somewhat local species active in the spring in the vicinity of the Chiricahua Mountains of southeastern Arizona and is unusual in being one of the smallest members of the genus (Wilcox, 1966). Because it is an extreme form, it is of special interest to compare its ecology and behavior with that known for more typical species. During the spring of 1985 I located a small population of *Efferia wilcoxi* about 3 km east of Portal, Arizona, and spent several days observing it in some detail. These and previous observations are reported here as part of an ongoing study of the Asilidae of Cave Creek Canyon and vicinity (Hespenheide and Rubke, 1977; Hespenheide et al., in prep.; Weeks and Hespenheide, 1985; and Hespenheide, unpubl.).

STUDY SITE AND METHODS

Efferia wilcoxi was studied intensively during the period of 18–28 May 1985 at a site 1370 m (4500 ft) in elevation along the Portal Road about 3 km ESE of Portal, Cochise County, Arizona. The species is locally common in areas of sparse plant cover in the vicinity of Portal at the mouth of Cave Creek Canyon and on the plains that slope gently down to the San Simon River valley, as well as upcanyon in open areas at least as high as the Sunny Flat Campground of the National Forest Service (1550 m). The study site east of Portal is fairly heavily grazed and the dominant plants are the shrubs *Prosopis juliflora* (Sw.) DC. and *Ephedra trifurca* Torr., the perennials *Gutierrezia microcephala* (DC.) Gray and *Isocoma tenuisecta* Greene, as well as the annuals *Baileya pleniradiata* Harv. and

Gray, *Eriastrum diffusum* (Gray) Mason, *Centaurea melitensis* L., *Erodium cicutarium* (L.) L'Her., *Solanum* sp., and *Eriogonum* sp. *Baileya* was in flower during the study period; other plants in the vicinity include *Acacia constricta* Benth. and a variety of annual grasses and herbs.

Flies were observed and counted over a census trail of about 150 m which paralleled the Portal Road; about $\frac{3}{4}$ of the route was on the shoulder of the road, and the rest on a slight incline oblique to it. A total of 33 censuses were made between 0700 and 1700 hr PDT between 20 and 28 May. Flies were counted and note was made of sex, whether or not the fly was feeding on a prey item, and any reproductive behavior. An attempt was made to collect each prey item by trapping the fly under a plastic shell vial, holding the fly until it released the prey, and then releasing the fly. A total of 54 prey items were collected in this manner. An additional 7 flies with prey were collected at this site in a community study 1–9 June 1975 (T. W. Sherry, S. J. Wright, and M. Lucszak, unpubl.). Other asilids in the census area during late May and early June, at least in some years, include *Ablautus flavipes*, *Cerotainiops abdominalis*, *Efferia argyrogaster*, *Ospriocerus abdominalis*, *Promachus giganteus*, *Stenopogon duncani*, and *Stichopogon fragilis*. Of these, only *Efferia argyrogaster* and *Stenopogon duncani* were frequent, and both were in much lower density than *E. wilcoxi*.

RESULTS AND DISCUSSION

Diurnal activity and behavior.—Figure 1 shows the results of counts along the census trail. The overall average of flies per census at 6.5, activity was greater than average in the morning between 0800 hr and noon, and lower than average in the afternoon. *Efferia wilcoxi* typically occurs in open, somewhat rocky areas and forages from the ground, small rocks, or from leaves or bits of dead vegetation within 2–3 cm of the ground. As with most desert Asilidae, the flies thermoregulate behaviorally. Although posture was not consistently recorded in the censuses, flies are often appressed to a sunny rock surface early in the morning, whereas in the late morning and early afternoon they move into shade or up on vegetation (at least 4–17% of flies recorded between 1000 and 1600 hr). Interestingly, females outnumbered males over all censuses by 169 to 103, or about 1.64:1, even though males were often more visible, especially in their searching behavior (below). Whether this female-biased sex ratio is a true reflection of the population sex ratio, or due to microhabitat, phenological patterns or sampling artefact is unknown.

Reproductive behavior of males consisted most obviously of a distinctive searching behavior of short “hopping” flights of a few cm each from perch to perch. The flight was conspicuously noisy (“buzzy”) and often attracted my attention before the fly was seen. Similar behavior has been reported by Lavigne and Dennis (1985) for *E. triton* (O.S.), but not for any other *Efferia* species (Dennis et al., 1986). Except for the buzzing searching flights, there is no courtship per se, and males were observed four times simply to pounce on a female: one of these was successful, two were unsuccessful, and in the other case (at 1010 hr) the male killed and fed on the female. Such cannibalism is well known on the genus (Dennis et al., 1986). Male searching behavior occurred through most of the day, and unsuccessful attempts were made at 1342 and 1532 hr. The successful copulation occurred at 1633 hr and the male assumed a male-over-female position also typical

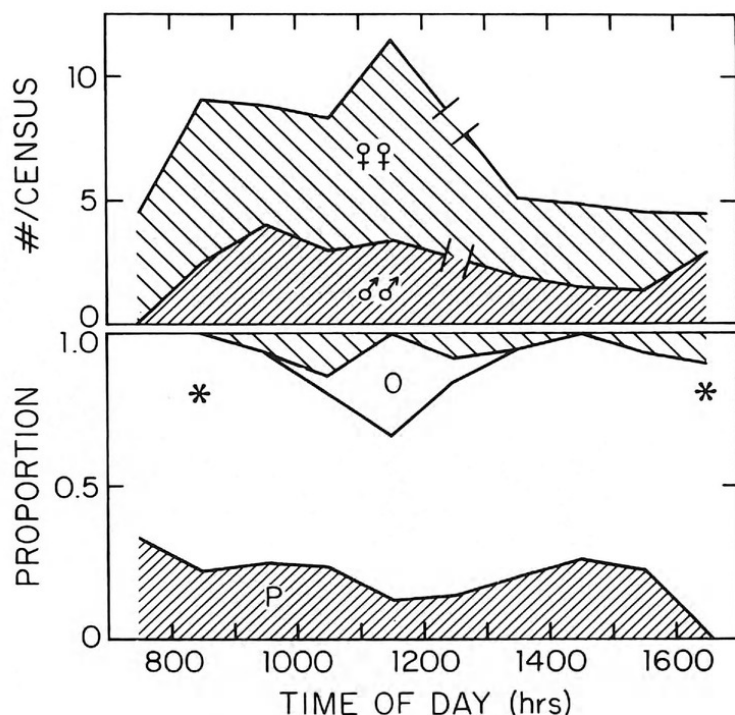


Figure 1. Diurnal pattern of activity of *Efferia wilcoxi* (Bromley) near Portal, Arizona. The upper portion of the figure gives the average number of flies per census during 1-hr periods; proportion of males indicated by shading (no complete censuses taken between 1200 and 1300 hr). The lower portion of the figure gives proportion of flies in various activities; upper shaded area = searching males, "O" = ovipositing females, lower shaded area ("P") = flies with prey items; asterisks indicate times of observed copulations.

of the genus (Fig. 2). The copulation lasted 113 sec and the male was observed to stroke the abdomen of the female with his posterior legs. The male disengaged after the female fluttered her wings. One other copulating pair was discovered in progress at 0833 hr about 15 cm above the ground in a *Gutierrezia* bush. In both copulations the female was without prey. Bimodal periods of mating were noted in all three species of *Efferia* studied by Lavigne and Dennis (1985).

Oviposition or pre-oviposition probing behavior was observed in females 15 times during this study and on several occasions in previous years (Fig. 3). Of 18 different recorded sites, 11 were in dead and 7 in live plants or parts thereof. Species of plants included *Gutierrezia* (3 times), *Baileya* (6 times), *Erodium cicutarium* (once), a mustard (Cruciferae; twice), and others not identified. The average of eight recorded pre-oviposition probing heights was 8.6 cm. An egg laid in the inflorescence of a dead annual, perhaps an *Eriogonum* species, on 1 June 1979 1 mi E of Portal measured 0.35 by 0.95 mm.

Prey.—Although reproductive activities were unevenly distributed, the proportion of flies counted with prey was relatively constant throughout the day with slightly higher proportions during the morning and lower proportions at midday and in late afternoon (Fig. 1).

Among all prey recovered, four orders were represented (Table 1): Homoptera, Hymenoptera, Diptera, and Heteroptera. Homoptera consisted entirely of cicadellids, and included the following species: *Aceratagallia bigeloviae* (Baker)—4, *A. uhleri* (Van Duzee)—1, *A. nanella* Oman or near—16, *A. sp.*—3, and *Macropsis*



Figure 2. Copulating pair of *Efferia wilcoxi*.

sp.—1. Hymenoptera were comprised of chalcidoids except for two small bees. Diptera included the following taxa: Agromyzidae—3; Cecidomyiidae—2; Bombyliidae, *Glabellula* sp.—1, *Mythicomylia* sp.—1; Chloropidae—4. Heteroptera included primarily Lygaeidae, except for two small Miridae and one Reduviidae.

Interestingly, of the 7 prey recorded in the 1975 study, 6 were Heteroptera, whereas cicadellids dominated the 1985 samples (25 of 61 prey). This suggests that prey “preference” and diet breadth (whether stenophagic or euryphagic) are influenced by availability and are not invariant characteristics of a species. This is supported by the data of Lavigne and Dennis (1985) and Dennis et al. (1986) for the prey of *E. cressoni* in Mexico and Wyoming, respectively. In the Wyoming population flies accounted for 72% of all prey and Homoptera for 11%, whereas in Mexico the two groups of prey were both about 36%. This phenomenon might be called “ecological euryphagy” by analogy with the “ecological monophagy” of herbivorous insects (Smiley, 1978). In both cases diet breadth is determined by ecological factors external to the insect which interact with some idealized diet preference. Studies of actual preference in a behavioral sense will have to compare diets with availability.

As with most robber flies, females are larger than males, both in total length (10.3 mm vs. 9.2 mm; $n = 16$ and 9, respectively) and in terms of wing length (6.2 mm vs. 5.7 mm). Males, however, take on average somewhat larger prey



Figure 3. Ovipositing female of *Efferia wilcoxi*.

than females (for males, \bar{x} = 2.49 mm, n = 14; for females, \bar{x} = 2.36 mm, n = 44), although sample sizes are not especially large. Table 1 gives sizes of prey and shows that mean sizes differ among taxa as has been shown for other asilids (e.g., Hespenheide and Rubke, 1977; Weeks and Hespenheide, 1985).

Comparative ethology. —Dennis et al. (1986) summarize the behavioral ecology of 18 *Efferia* species in their table 1. The observations on *E. wilcoxi* from this study are reviewed in the order of presentation in their table for comparison, as follows: *E. wilcoxi* forages from the soil, usually from perches on small rocks, to

Table 1. Prey of *Efferia wilcoxi* (Bromley) near Portal, Arizona.

Taxon	<i>n</i>	Frequency	Size (mm)			
			Mean	±	SD	Range
Homoptera	25	41.0	2.58	0.46		1.65–4.0
Hymenoptera	15	24.6	1.89	1.11		1.1–4.55
Diptera	11	18.0	1.70 ¹	0.19		1.4–2.1
Hemiptera	10	16.4	3.58 ²	1.26		2.45–6.4
Total	61					

¹ One specimen not measured because of damage.

² Two specimens not measured because of damage.

capture prey from the air. Prey is immobilized in the air; the method of its manipulation was not recorded. Diet is either stenophagic (1975) or euryphagic (1985), apparently depending on prey availability; cannibalism was observed. Courtship behavior of males consisted of "hopping" searching flights during which the wings were buzzed. Copulatory position was male over female, and the male was observed to stroke the female's abdomen; the one complete copulation observed lasted 2 min. Females oviposited in leaves and inflorescences of annual plants; duration of oviposition and clutch sizes were not recorded. One egg measured 0.35 by 0.95 mm. Although smaller than most other *Efferia*, *E. wilcoxi* is not especially unusual compared to the other species of the genus reviewed by Dennis et al. (1986). The minor elaboration of the searching flights of males, in which the wings are buzzed, occurs only in the one other large species *E. triton*. Despite its small size *E. wilcoxi* appears typical of members of the genus studied to date.

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