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DIURNAL VARIATION IN THE PREDATORY BEHAVIOR OF THE GRASSLAND ROBBER FLY, *PROCTACANTHELLA LEUCOPOGON* (WILLISTON) (DIPTERA: ASILIDAE)

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Diurnal variability in robber fly foraging activity is most commonly studied using a transect-census approach (Lavigne and Holland, 1969; Lavigne and Dennis, 1975; Dennis and Lavigne, 1975, 1976a, 1976b; Hespenheide and Rubke, 1977; Scarbrough and Norden, 1977, is an exception). The usual procedure involves walking a transect throughout the day and counting the number of actively foraging individuals or the number of individuals in different microhabitats. When applied to asilids of the arid western United States, this method often reveals a 4 stage activity pattern for clear, relatively windless days (Lavigne and Holland, 1969; Lavigne and Dennis, 1975; Dennis and Lavigne, 1975, 1976a, 1976b). As outlined by Lavigne and Holland (1969), the 4 stages are: (1) an early morning warm-up, (2) a mid-morning foraging peak, (3) late morning to mid-afternoon heat avoidance with low foraging activity, and (4) a late afternoon increase in foraging activity.

Despite a general recognition of this pattern, the actual hourly variation in flight activity (both foraging and relocation) has never been measured for an arid grassland robber fly species. Consequently, precise statements regarding the actual degree of foraging rate variability cannot be made, e.g. is the peak foraging rate of mid-morning double, triple, etc. the minimum foraging rate of mid-afternoon? The present study was thus undertaken to provide a quantitative assessment of diurnal flight activity for the grassland species *Proctacanthella leucopogon* (Williston). The results of a short-term mark-recapture study are also presented.

Proctacanthella leucopogon is a medium sized asilid (12–15 mm) of the grasslands of western United States and northern Mexico (Wilcox, 1965). In Colorado, adults are active from late June to early September (Rogers and Lavigne, 1972). Rogers and Lavigne (1972), Lavigne and Dennis (1980), and Shelly and Pearson (1980) all recorded Homoptera (primarily Cicadellidae), Diptera, and Hymenoptera as the major dietary components. Recently, Lavigne and Dennis (1980) described the foraging and courtship behavior of this species. Their observations of diurnal activity, however, are largely qualitative. The data presented here together with recent prey rec-

ognition tests (Shelly and Pearson, 1980) complement their observations through a more quantitative interpretation of foraging behavior.

Materials and Methods

The foraging observations and mark-recapture study were conducted from 25 July to 6 August 1978, in Sulphur Springs Valley, Cochise Co., Arizona, 8 km southeast of Wilcox, Arizona (elev. 1273 m). The study site was a shallow gully (approximately 100 m long and 6–11 m wide) in a moderately used pasture. The predominant plant species were *Distichlis stricta* (Rybd.), *Prosopis velutina* Woot., *Suaeda torreyana* S. Wats, and *Atriplex griffithsii* (Strandl.).

Data on foraging were collected between 07:00 and 17:00 on sunny days when winds were light. Observations were confined to females since (1) females were more abundant and hence more easily located than males and (2) potential complications arising from sexual differences were eliminated. An individual was observed until lost from view or until 10 minutes elapsed. The observations included: (1) number of foraging flights, (2) number of relocation flights, (3) capture success (number of successful captures/number of foraging flights), and (4) time spent perched in the sun on the ground, in the shade on the ground and on vegetation above the ground. In addition, visual estimates were made of distance for both foraging and relocation flights.

In most cases, the potential prey that elicited a foraging flight could be seen. However, even when the prey was not apparent, foraging and relocation flights were easily distinguished. A foraging flight was typified by a rapid, straight flight to an aerial point followed by a similar return to the ground. In addition, foraging flights were usually made at angles approaching vertical. In contrast, relocation flights were slower, less direct, and usually low and parallel to the ground.

Data for all individuals observed during a given hour (07:00–08:00, 08:00–09:00, etc.) were combined, and both foraging and relocation activity were expressed as flights per minute of observation time. Perch selection was expressed as the percentage of the total observation time for a given hour spent in each of the 3 perch categories. In these analyses, data for 12:00–13:00 and 13:00–14:00 were combined and treated as 1 time period since few data were collected in either of these hours alone.

The mark-recapture study was conducted during a 3 day period following completion of the foraging observations. Ten sections were established within the gully varying from 8.5 m to 10.0 m in length and from 6.25 m to 11.9 m in width; these latter values reflect variation in gully width. For its entire length the gully was bordered on either side by approximately 2–3 m of bare ground. The western end of the gully opened onto a dry pond bed,

Table 1. Perching positions of female *P. leucopogon* throughout the day. Ground surface temperatures were recorded on July 30, 1978, at the start of each observation period.

Time	Minutes of observation	Ground surface temperature (°C)		% time on ground		% time on vegetation
		Sun	Shade	Sun	Shade	
07:00–08:00	56	24	23	99	1	0
08:00–09:00	88	31	25	99	1	0
09:00–10:00	83	38	32	83	17	0
10:00–11:00	68	41	32	78	20	2
11:00–12:00	102	44	36	17	69	14
12:00–14:00	53	48	41	18	70	2
14:00–15:00	61	47	42	2	92	6
15:00–16:00	58	47	40	12	85	3
16:00–17:00	33	48	41	63	36	1

while at the eastern end several mesquite bushes (*Prosopis*) separated the study gully from another gully which ran perpendicular to it.

The flies were marked by gluing numbered, circular bee tags (Poalith-Zeichenplattcheb, Graze™) directly onto the center of the mesothorax. The tag did not appear to inhibit flight. In the field, new individuals were marked and previously marked individuals were identified during both the morning (09:00–11:00) and afternoon (13:00–15:00). The location of each fly was marked by a spike bearing a number corresponding to that fly's tag number. The exact position of each spike was obtained by triangulation. Most marked flies were later identified without capture thus disturbing them as little as possible. Minimum travel distances (straight lines) between captures/observations were then calculated for all marked individuals seen more than once.

Results

Although *P. leucopogon* females perched almost exclusively on the ground, whether they did so in sun or shade appears to be highly dependent upon the time of day and hence the ground surface temperature (Table 1). From 07:00 to 11:00 the ground temperature in the sun increased from 24°C to 44°C, and the flies spent the great majority of this time perched in the sun. However, from 10:00–11:00 to 11:00–12:00 the percent time spent in the sun and in the shade changed from 78% time in sun and 20% time in shade to 17% time in sun and 69% time in shade. Individuals remained in the shade until late day when the ground surface temperature dropped from 48°C (16:00) to 42°C (17:00). Perching on vegetation was not observed to any significant degree until the 11:00–12:00 period when 14% of the time was spent perched on vegetation. Little vegetation perching occurred in the

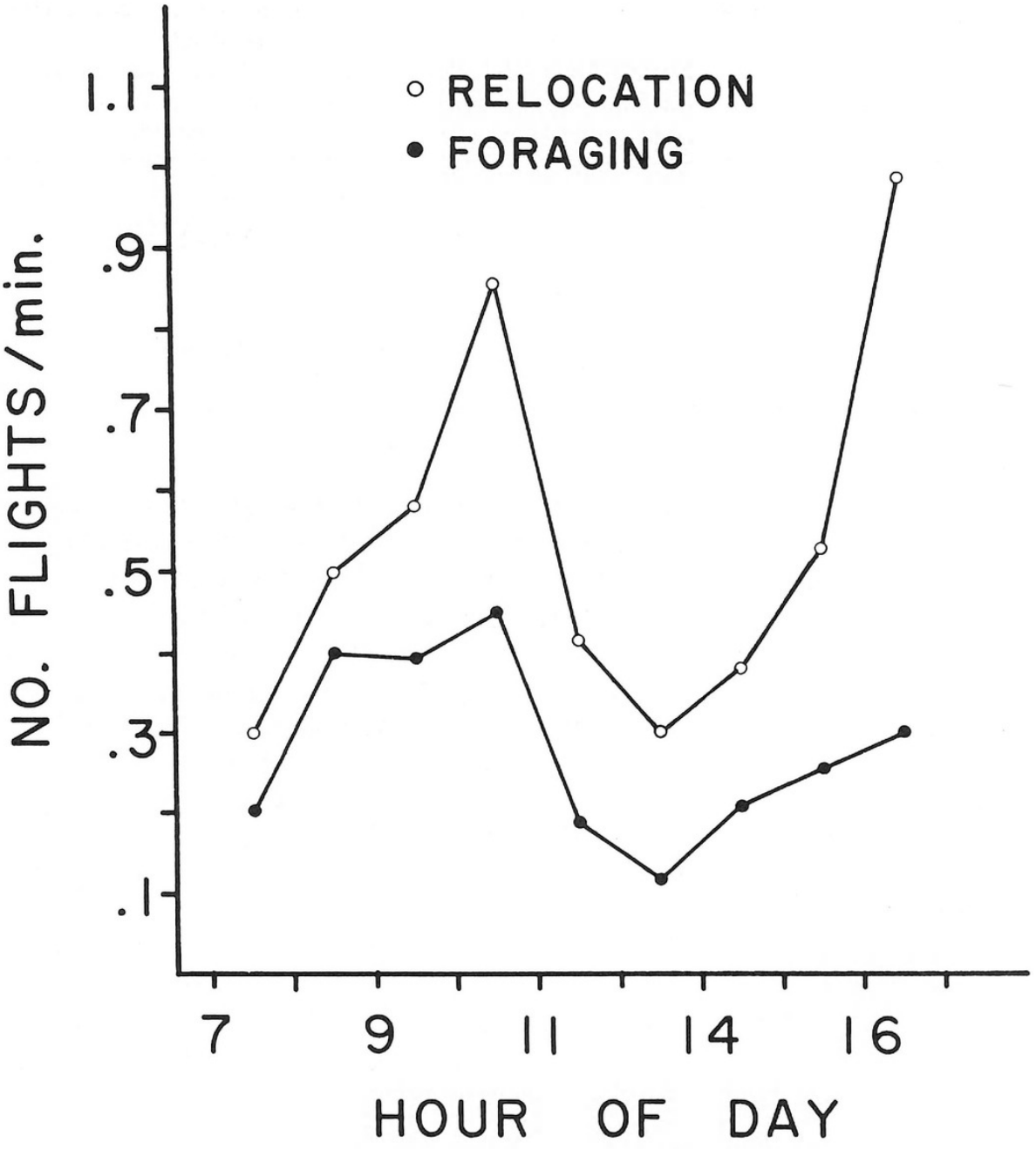

Fig. 1. Foraging and relocation flight activity throughout the day for female *P. leucopogon*. Total observation times for each-hour are given in Table 1.

afternoon although this behavior was slightly more common than in early to mid-morning.

Flight activity showed a similar dependence upon temperature (Fig. 1). Low foraging flight activity between 07:00 and 08:00 was followed by a foraging peak from 08:00 to 11:00 when 0.39 to 0.45 foraging flights/minute were made. As the temperature increased to 45°–49°C by mid-day, foraging flights/minute declined to 0.12 for the 12:00–14:00 period. From 14:00 to

Table 2. Mean minimum distance traveled by marked *P. leucopogon* females as a function of daylight hours since last capture. Standard deviation is given in parentheses.

Daylight hours since last capture	No. of observations	Mean minimum distance traveled (m)
2	15	9.0 (7.7)
7	4	18.8 (12.5)
11	7	17.1 (7.9)
24	1	28.8
	3	5.4 (1.6)
28	3	28.1 (8.3)
	3	1.5 (0.1)

17:00, however, foraging flight frequency increased, although it never reached the peak morning levels. Relocation flight behavior exhibited a similar hourly trend (Fig. 1). Unlike the morning plateau of foraging flight frquency, however, the frequency of relocation flights continued to increase and peaked during the 10:00–11:00 period. Similarly, in late afternoon relocation activity increased dramatically rather than leveling off as did foraging flight activity.

Based on visual estimates, individual foraging flights ranged from 5 cm to approximately 1.8 m with the majority being between 10 cm and 60 cm. Foraging flights were rarely more than 60 cm above ground. Capture success (number successful captures/number foraging flights) was 6%. Relocation flights ranged from 5 cm to approximately 1.2 m with the majority being between 30 cm and 90 cm.

In the mark-recapture study, the majority (67%) of the 64 females marked were not recaptured (or re-sighted) again. Fourteen individuals were recaptured once, 5 individuals were recaptured twice, 1 individual was recaptured 3 times, and another individual was recaptured 4 times. The mean distances traveled between captures for individuals recaptured once and twice were 15.4 m (SD 12.9) and 14.4 m (SD 10.6), respectively. For the individual recaptured 3 times, the minimum distances traveled between capture sites were 2.0 m, 16.1 m, and 18.0 m, and for the individual recaptured 4 times, the corresponding distances were 5.0 m, 5.5 m, 9.8 m, and 11.7 m.

The high mobility of *P. leucopogon* females is also demonstrated in a plot of minimum distance traveled as a function of daylight hours since last capture or sighting (Table 2). Following marking in the morning, the 15 females recaptured in the afternoon of the same day had traveled an average of 9.0 m. Seven and 11 daylight hours after the previous capture, females traveled an average of 18.8 m and 17.1 m, respectively. Further relations between distance travelled and hours since last capture were obscured by apparent movement of individuals in and out of the study site. For example,

after 28 daylight hours, 3 females had moved a minimum of 23 m, but 3 females were found within 3 m of their marking site (Table 2). Similarly, after 24 hours, 1 female had traveled 28.8 m, whereas 3 females were found between 4.1 m and 6.9 m of their marking site (Table 2).

Discussion

Compared to the transect-census approach, measurement of actual flight activity more precisely describes diurnal variability of robber fly behavior. During the present study period, female *P. leucopogon* exhibited 4 behavioral stages:

1. Early morning warm-up period (07:00–08:00). Females perched in the sun almost exclusively (99% observation time) but exhibited relatively low foraging and relocation rates (47% and 31% of peak rates, respectively).
2. Mid-morning foraging period (08:00–11:00). Within this period, females perched in the sun at least 78% observation time for any 1 hour and exhibited the peak foraging rate for the day and a very high relocation rate (89% of the peak rate).
3. Mid-day shade seeking period (11:00–16:00). Within this period, females perched in the shade a minimum of 63% observation time for any 1 hour and exhibited the lowest foraging and relocation rates for the day (27% and 30% of peak rates, respectively).
4. Late afternoon foraging period (16:00–17:00). Females perched in the sun 63% observation time and exhibited a relatively high foraging rate (67% of the peak rate) and peak relocation rate of the day.

Shade seeking behavior is apparently a thermoregulatory response to excessively high ground surface temperatures. The critical temperature range prompting such behavior was approximately 43°–45°C. The dramatic late morning decrease in sun perching occurred when the ground surface temperature in the sun exceeded 44°C at 11:00. Conversely, the late afternoon increase in sun perching occurred when the ground surface temperature in the sun dropped from 46°C to 42°C from 16:00 to 17:00.

Although shade seeking appears to be a thermoregulatory response, it is less clear whether or not the lowered foraging rate from shaded perches also results from thermoregulatory constraints. Two lines of indirect evidence, however, suggest that high mid-day temperatures do not limit foraging flight frequency. First, ground surface temperatures in the shade ranged from 36°–42°C during the shade seeking period. Thus, for the majority of the mid-day period ground surface temperatures in the shade were not appreciably higher than the ground surface temperatures in the sun during the mid-morning period of peak foraging activity. Second, as shown for a neotropical

robber fly (Shelly, in prep.), foraging rate in asilids may be strongly correlated with the encounter rate of potential prey items. For western grasslands, Lavigne and Holland (1969) and Hespenheide and Rubke (1977) have both suggested that prey availability decreases during the hot mid-day hours. Consequently, the low mid-day foraging rate of *P. leucopogon* may simply reflect this reduced encounter rate.

The present observations agree in large part with those of Lavigne and Dennis (1980) for a population of *P. leucopogon* in Mexico. In the Mexican population, individuals were described as "sluggish" in the early morning when the ground surface temperature was less than 29.5°C. As temperature increased, individuals foraged actively until seeking shade when the ground surface temperature in the sun exceeded 45.5°–47.5°C. Although slightly higher, this estimate is similar to the corresponding estimate of 43°–45°C for the present observations. Perhaps the major difference between the 2 populations involves the frequency with which individuals perch on vegetation to avoid high ground temperatures. Lavigne and Dennis (1980) report perching upon vegetation as an intermediate step between sun and shade perching, whereas in the present study the shift from sun to shade perching was direct. In Arizona, individuals rarely perched on vegetation (maximum value: 14% observation time for 11:00–12:00).

Regarding the mark-recapture study, 2 results indicate that *P. leucopogon* females forage over considerable areas. First, the majority of the individuals marked were not recaptured. Second, those recaptured had traveled relatively large distances. Two hours after being marked, recaptured females had traveled an average of 9.0 m, and after 7 and 11 daylight hours the corresponding values were 18.8 m and 17.1 m, respectively. Rather than reflecting a small home range, the small travel distances noted for several individuals after 24 and 28 daylight hours probably indicate that these individuals left the study site soon after being marked only to re-enter at approximately the same location. Support for this interpretation comes from the fact that these individuals were all recaptured only once and not repeatedly as would be expected if their movements were confined to a small area. Thus, whereas male *P. leucopogon* may set up territories (Lavigne and Dennis, 1980), *P. leucopogon* females do not appear to exhibit strong site fidelity.

Summary

Fluctuations in ambient temperature impose severe constraints upon the foraging activity of female *Proctacanthella leucopogon.* The diurnal activity rhythm consisted of 4 periods: (1) an early morning warming up period, (2) a mid-morning peak in foraging flight frequency, (3) a late morning to late afternoon shade seeking period, and (4) a late afternoon increase in foraging activity. Peak foraging and relocation rates were 0.45 flights/minute and 0.97 flights/minute, respectively. The mid-day shade seeking behavior reduced

foraging and relocation activity to 29% and 31% of peak levels, respectively. A preliminary mark-recapture study showed that 2 hours after being marked females had traveled an average distance of 9 m and showed no indication of territoriality.

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Literature Cited

Dennis, D. S., and R. J. Lavigne. 1975. Comparative behavior of Wyoming robber flies. II (Diptera: Asilidae). Univ. Wyo. Agric. Exp. Stn. Sci. Monogr., 30:1–68.

———, and ———. 1976a. Ethology of *Leptogaster parvoclava* in Wyoming (Diptera: Asilidae). Proc. Entomol. Soc. Wash., 78:208–222.

———, and ———. 1976b. Ethology of *Efferia varipes* with comments on species coexistence (Diptera: Asilidae). J. Kans. Entomol. Soc., 49:48–62.

Hespenheide, H. A., and M. A. Rubke. 1977. Prey, predatory behavior, and the daily cycle of *Holopogon wilcoxi* Martin. Pan-Pac. Entomol., 53:277–285.

Lavigne, R. J., and D. S. Dennis. 1975. Ethology of *Efferia frewingi* (Diptera: Asilidae). Ann. Entomol. Soc. Am., 68:992–996.

———, and ———. 1980. Ethology of *Proctacanthella leucopogon* in Mexico (Diptera: Asilidae). Proc. Entomol. Soc. Wash., 82:260–268.

———, and F. R. Holland. 1969. Comparative behavior of eleven species of Wyoming robber flies (Diptera: Asilidae). Univ. Wyo. Agric. Exp. Stn. Sci. Monogr., 18:1–61.

Rogers, L. E., and R. J. Lavigne. 1972. Asilidae of the Pawnee National Grasslands, in northeastern Colorado. Univ. Wyo. Agric. Exp. Stn. Sci. Monogr., 25:1–35.

Scarbrough, A. G., and A. Norden. 1977. Ethology of *Cerotainia albipilosa* Curran (Diptera: Asilidae) in Maryland: Diurnal activity rhythm and seasonal distribution. Proc. Entomol. Soc. Wash., 79:538–554.

Shelly, T. E., and D. L. Pearson. 1980. Predatory behavior of *Proctacanthella leucopogon* (Diptera: Asilidae): Prey recognition and prey records. Environ. Entomol., 9:7–9.

Wilcox, J. 1965. *Proctacanthella* Bromley (Diptera: Asilidae). J. Kans. Entomol. Soc., 38: 106–110.

Footnote

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