

FORAGING, MATING, AND THERMOREGULATORY  
BEHAVIOR OF *CYRTOPOGON WILLISTONI* CURRAN  
(DIPTERA: ASILIDAE)

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ABSTRACT

The robber fly *Cyrtopogon willistoni* Curran was studied in SW Montana, where it was an opportunistic predator of relatively small insects from 25 families in 7 orders. The most common prey were Diptera (44%) and Homoptera (21%), with Cicadellidae, Bibionidae, and Formicidae comprising 44% of the prey. The elaborate courtship behavior of males included audible airborne visual displays that made use of silvery-white combs of hairs on the males' foretarsi. While perching, the flies exhibited both lateral and dorsal basking postures, and were apparently capable of strong flight only when direct sunlight was available. I compare the foraging and courtship behaviors of *C. willistoni* to those of other *Cyrtopogon*, and their thermal responses to those of other robber flies in the same habitat.

INTRODUCTION

The robber flies of genus *Cyrtopogon* occur throughout North America (Wilcox and Martin, 1936), where they appear to be generalist predators (Bullington and Lavigne, 1992; Lavigne, 1970). Males of this genus in particular, and of the subfamily Dasypogoninae in general, exhibit elaborate courtship displays not evident in other subfamilies of Asilidae (Alcock, 1977). Here, I describe the foraging, courtship, and thermoregulatory behaviors of *Cyrtopogon willistoni* Curran, a species previously subject to a brief report by Lavigne and Holland (1969). *Cyrtopogon willistoni* is a relatively

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stout asilid, 11-15 mm in length, with a shiny black body surface. The four distal segments of the males' foretarsi have a dense comb of silvery-white hairs that appear to play a role in courtship. Although most *Cyrtopogon* live within or near coniferous forests, the *C. willistoni* studied in Montana inhabited mesic slopes of gullies on grassland.

#### MATERIALS AND METHODS

I made most of my observations 15 km south of Three Forks, Gallatin Co., Montana (45°45'N, 111°35'W; 1300 m altitude) during May and June of 1989 through 1994. However, in June 1990, I also obtained several prey records at the Red Bluffs Research Ranch, 2.5 km ENE of Norris, Madison Co., Montana. Predator head widths were determined to the nearest 0.1 mm using a micrometer accurate to 0.05 mm. Prey sizes are reported as the product of body length (not including antennae or ovipositors) and maximum width (not including appendages). In most cases, a fly could be approached and observed within several meters without apparently disturbing it.

When a perched fly was located, I used methods described in O'Neill, Kemp, and Johnson (1990) to record: 1) soil surface temperature ( $T_S$ ) of the nearest unshaded patch of bare soil > 5 cm in diameter, 2) air temperature at the exact location of the perched fly's thorax ( $T_{TH}$ ) ( $T_{TH}$  is an important variable because the air temperature will affect the rate of convective heat loss, and body temperature is a function of the relative magnitudes of radiative heat gain and convective heat loss), 3) perch height, 4) the orientation of the longitudinal axis relative to the ground, as either approximately parallel to the soil surface (horizontal) or at an angle of 30–90° to the surface (oblique/vertical), and 5) the orientation (relative to the position of the sun) of the fly's longitudinal axis in the horizontal plane. For the latter, an angle of 0° indicates that a fly was facing the position on the horizon above which the sun was located, while at 180° a fly oriented directly away from the sun. A fly with an approximately 180° orientation relative to the sun and with an oblique or vertical orientation relative to the soil surface was considered to be in a "dorsal basking" orientation. A fly perched at an angle of 90° or 270° on a horizontal surface (i.e., oriented perpendicular to the direction of the sun) was considered

to be in a "lateral basking" orientation. When data sets were bimodal, as in the case of angles clustered around either 90° or 270°, the data were divided into two subsets and analyzed separately. Data on angles of orientation were analyzed as described in Batschelet (1981) and O'Neill et al. (1990). To examine the orientation of longitudinal axis in the horizontal plane, I used Rayleigh's test and the V-test, for which significance indicates that the null hypothesis of uniform or random distribution of perch direction is rejected; for the V-test, significance further indicates that the observed values are clustered around some hypothesized angle (Batschelet, 1981).

Temperatures were measured with copper/constantan thermocouples and a Cole-Parmer Digi-Sense<sup>R</sup> thermometer. Air and soil surface temperatures were measured with the tip of the probe temporarily shaded from direct solar radiation. I used  $T_S$  as a general measure of environmental temperature, because it is relatively stable over short periods of time and is correlated with the intensity of solar radiation on clear days (O'Neill et al., 1990).

## RESULTS AND DISCUSSION

### Habitat and Seasonal Activity

At the site south of Three Forks, *C. willistoni* was primarily restricted to mesic north-facing slopes of a 1.3 km long gully that ran from SW to NE down to the Madison River. The robber flies were active primarily in expanses of herbaceous vegetation in which lupine (*Lupinus* sp.) predominated, but could also be found on snowberry shrubs (*Symphoricarpos* sp.). I did not find *Cyrtopogon willistoni* on the south-facing slopes, on level portions of the drier areas on grasses and Yucca (*Yucca glauca* Nutt.), nor on the north rim and narrower segments of the gully where there were small trees (primarily *Prunus* sp.). *Cyrtopogon willistoni* shared the mesic habitat with a smaller robber fly, *Dicolonus sparsipilosum* Back, which appeared to prefer the lower levels of the vegetation. Three larger species, *Machimus occidentalis* Hine, *Efferia staminea* (Williston), and *Stenopogon inquinatus* Loew were active in both mesic and xeric areas during the latter half of the seasonal activity of *C. willistoni*, which typically lasted from late May to late June. At the Red Bluff site, *C. willistoni* was observed on

herbaceous vegetation (including *Geranium* sp.) in a narrow mesic zone bordering a small seasonal stream.

Adults *Cyrtopogon willistoni* are ambush predators that leave their perches 4–70 cm high (mean = 24.3, SE = 1.4, N = 103) on vegetation to pursue airborne prey. The flies sometimes took circuitous routes while pursuing prey for distances of up to 50 cm away from the perch and as high as 20 cm above it. The single prey not taken in mid-air was a cicadellid leafhopper that flew into a perched male who immediately subdued it. After most prey captures, the flies immediately returned to a perch, sometimes the same one from which they took off. Occasionally, however, a fly first hovered in place while manipulating the prey with its legs. Two of these potential prey were released (or escaped).

The 120 prey of *C. willistoni* included insects from 7 orders and 25 families: EPHEMEROPTERA Ephemerellidae (5), Baetidae (1), Heptageniidae (1); HOMOPTERA Aphididae (1), Cicadellidae (23), Delphacidae (1); HEMIPTERA Miridae (13); COLEOPTERA Curculionidae (1); LEPIDOPTERA Tortricidae (2); DIPTERA Anthomyiidae (4), Asilidae (2, both male *D. sparsipilosum*), Bibionidae (16), Bombyliidae (3), Chironomidae (1), Dolichopodidae (2), Empididae (5), Muscidae (4), Sarcophagidae (4), Sepsidae (7), Syrphidae (4), Tachinidae (2); and HYMENOPTERA Braconidae (1), Ichneumonidae (2), Proctotrupidae (1), Formicidae (14).

Prey records varied among years, although this may have been due to small sample sizes. For example, all of the Ephemeroptera were taken in 1989 and 88% of the bibionids were from 1994. Like five other species of Asilidae at the same site (O'Neill, 1994), *C. willistoni* took the alate ants, 93% of which were males, during mating swarms of *Formica subpolita* Mayr. Prey were always smaller than the predator and varied widely in size, from minute Sepsidae and Aphididae to the relatively large alate ants. There was a significant correlation between prey size and predator size among female *C. willistoni* ( $r_S = 0.41$ , N = 63, P < 0.001), but not among males ( $r_S = 0.17$ , N = 49, P = 0.20).

The foraging mode of the flies I observed differed from what Lavigne and Holland (1969) reported for a population of *C. willistoni* along an intermittent stream in Wyoming. There, they primarily foraged from perches on soil or rocks, and commonly subdued

prey only after both predator and prey fell to the ground following initial contact in mid-air. In a smaller sample, they reported a narrower range of prey types (17 insects from 7 families, all Diptera and Hymenoptera). Calliphoridae was the only family on their list that did not occur in the prey of the Montana population. A wide diet breadth, similar to that found for *C. willistoni* in my study, was reported for *C. montanus* James (6 orders of prey; Bullington and Lavigne 1992), *C. auratus* Cole (7 orders, 29 families), and *C. glarealis* Melander (6 orders, 19 families) (Lavigne, 1970). The three most common families of *C. willistoni* prey in Montana, Cicadellidae, Bibionidae, and Formicidae, are quite different in size and behavior suggesting that the flies display the flexibility in prey use that is typical of many asilids (O'Neill, 1992a, b).

### Courtship and Mating

Males commonly flew slowly through the topmost vegetation, frequently pausing and turning towards plants or an insect perched on a leaf. Males initiated courtship, but not prey pursuit, during these flights. Copulation was always preceded by prolonged courtship of a perched female, during which a male alternated between hovering near the female and perching next to her on the same plant. While hovering 5–10 cm above and to the side of a female, the male repeatedly darted ~0.5 cm towards her while rapidly waving his legs forwards and vibrating them. During one continuous hover that lasted 5 min and 13 s, a male flashed his front legs over 30 times. When flashing, the pitch of wing buzzing, which is audible to humans from at least 5 m, increased and there was a distinct flash from the light reflecting off a dense comb of silvery-white hairs on the four distal segments of his foretarsi. The time between flashes varied from 6–15 s (mean 9.4 s, SE = 0.4, N = 31 in observations of 8 males). Often (9% of 22 courtships), two males simultaneously courted a single female. Females usually remained still during the males' displays, but some reacted by flying away (sometimes followed by the male) or by flying directly at the male in an apparent attempt to drive him off. One female darted at a male eight times before he terminated courtship.

Upon landing next to a female, the male remained motionless or tried to mount her from behind. Females usually rejected these mating attempts, either passively (N = 8) or by striking at the male

with her abdomen. When successful at coupling, the male always immediately dismounted and faced away from the female until copulation ended. He maintained the end-to-end position even when the female took flight and towed him behind her. I observed eight matings, including three from the initiation to the end of copulation that had a mean duration of 13.2 min (range = 10.6–16.1).

Males sometimes courted feeding females ( $N = 10$ ), and females sometimes captured prey while being courted ( $N = 3$ ); one male initiated copulation with a female that continued feeding. Males also directed “courtship” to other perched insects, including four sarcophagid flies, a syrphid fly, a moth, and seven conspecific males, all approximately the same size and color of the females. On three occasions, males vigorously “courted” shrivelled, desiccated flower heads that resembled perched females, because they were black and had dried bracts that protruded laterally.

The courtship displays of males of different species of *Cyrtopogon* exhibit commonalities, but also a great deal of diversity in form and elaboration. Of the six species studied, only *C. willistoni* males (in both Montana and Wyoming) include an aerial display in their courtship, although such displays occur in other genera of Dasyopogoninae (Alcock, 1977). In the other five species of *Cyrtopogon*, the display occurs on a substrate with the male approaching the female from the front in *C. auratus* and *C. glarealis* (Lavigne, 1970), from behind in *C. vanduzeei* Wil. and Mart. (Powell, 1969) and *C. montanus* (Bullington and Lavigne, 1992), and from the side in *C. marginalis* Loew (Lavalley, 1970). All but *C. vanduzeei* and *C. montanus* are reported to exhibit conspicuous movements of the foretarsi, which are silvery-white or yellow in many species (Wilcox and Martin, 1936). Males of some species touch the female during courtship displays, with *C. marginalis* and *C. vanduzeei* exhibiting a prolonged repetitive tactile display. As in *C. willistoni*, males of *C. glarealis* and *C. montanus* sometimes directed “courtship” at non-females. All *Cyrtopogon* apparently mate in an end-to-end position.

### Thermoregulation

Flies perched where air temperatures ( $T_{TH}$ ) ranged from 12–30°C, with the  $T_{TH}$  being correlated with  $T_S$  ( $r_S = 0.61$ ,  $N = 103$ ,  $P < 0.001$ ). When perching at times when the sun was not

obscured and  $T_S$  was  $\leq 25^\circ\text{C}$ , the flies apparently oriented themselves to maximize the amount of direct solar radiation intercepted. The particular orientation adopted was contingent on the orientation of the surface on which they were perched. On horizontal plant surfaces, the flies oriented so that their longitudinal axes were approximately perpendicular to the direction of the sun (i.e., either  $90$  or  $270^\circ$ ; Table 1). When landing on oblique/vertical surfaces, they oriented at approximately  $180^\circ$  to the direction of the sun, thus maximally exposing their dorsal surfaces; such exposure is enhanced by the fact that the perched flies held their wings in V-shaped array, so that the surface of the abdomen was unshaded. Observed angles of orientation did not differ from angles hypothesized to maximize exposure to direct solar radiation. In combined data for all flies perched when  $T_S$  was  $\leq 25^\circ\text{C}$ , the observed orientation deviated by  $\leq 15^\circ$  from expected in 69% of the observations, with only 4% of the flies deviating by  $> 30^\circ$  ( $N = 86$ ). When  $T_S$  was  $> 25^\circ$ , the flies did not display a directional bias on either type of surface.

The flies were highly dependent on direct solar radiation in order to undertake foraging and courtship. On 4 June, 1994, when clouds intermittently obscured the sun over a period of 4 h, I counted the number of *C. willistoni* seen flying, including those flushed as I walked through the area. During 15 sunny intervals totalling 200 min, I saw 105 flies (0.53/min), including 11 with prey and 16 males that were courting females. In contrast, just 3

Table 1. Orientation of the longitudinal axis with respect to the sun (horizontal plane) as a function of soil surface temperature ( $T_S$ ).

$T_S^A$	Angle of surface on which flies perched	Rayleigh's	Hypothesized angle <sup>B</sup>	Observed	V-test	
		Test Probability		mean ( $\pm$ SD) angle	N	Probability <sup>C</sup>
$\leq 25^\circ\text{C}$	horizontal	$P < 0.001$	$90^\circ$	$91.3 \pm 16.6$	20	$P < 0.001$
	oblique/vertical	$P < 0.001$	$270^\circ$	$267.3 \pm 17.8$	13	$P < 0.001$
$> 25^\circ\text{C}$	horizontal	$P < 0.001$	$180^\circ$	$179.7 \pm 19.4$	53	$P < 0.001$
	oblique/vertical	$P > 0.20$	–		8	–
	oblique/vertical	$P > 0.50$	–		7	–

<sup>A</sup>in nearest unshaded area; <sup>B</sup>angle hypothesized only if Rayleigh's test significant, indicating that there was a significant bias in the angle of orientation; <sup>C</sup>significance indicates that angle clustered around the hypothesized angle.

flies (0.08/min) were seen during 14 cloudy intervals totalling 40 min; all three were observed in the first minute after the sun was obscured and none had prey. I may have seen fewer flies during cloudy periods simply because they were inactive. Those flies seen during cloudy intervals appeared incapable of strong flight. When prodded with grass stems, they did not fly off (the usual behavior during sunny intervals), but simply rotated on their perches to face the stem ( $N = 1$ ) or just dropped off the plant ( $N = 2$ ). These responses are typical of robber flies at cooler times of day (Lavigne and Holland 1969). Several of these flies flew away after I warmed them in my hand. Some flies apparently also hid during cloudy periods. One feeding female that I was watching just as a cloud obscured the sun immediately moved to the underside of the leaf.

Because *C. willistoni* perched on vegetation well above the soil surface, they never experienced  $T_{TH}$  as high as those apparently preferred by other species of Asilidae in the drier portions of the same habitat. During cooler times of day, other species of robber flies at this site raise their body temperatures by hunting from perches on insolated soil surfaces, where the boundary layer provides a relatively warm, non-windy environment allowing the flies to bask while minimizing convective heat loss (O'Neill and Kemp, 1990, 1992; O'Neill et al., 1990). Late in morning, *Machimus occidentalis* (O'Neill and Kemp, 1992), *Stenopogon inquinatus* (O'Neill and Kemp, 1990), and *Efferia staminea* (O'Neill et al., 1990) adopt perch locations where the  $T_{TH}$  averages 31 to 34°C. Because *Cyrtopogon willistoni* always experienced  $T_{TH}$  below that range, either they occupy a habitat with suboptimal microclimate or they are adapted to these lower temperatures. The latter explanation seems more likely because *C. willistoni* became active each day before the other species and apparently ceased orienting to the sun when  $T_S$  was greater than 25°C.

O'Neill et al. (1990) demonstrated that orientation by robber flies of the genus *Efferia* had a significant effect on body temperature and that the temperature attained was highly correlated with the intensity of solar radiation. Like other species (O'Neill and Kemp, 1992; O'Neill et al., 1990), *C. willistoni* were probably able to raise body temperatures above ambient by orienting to maximize their exposure to insolation. Unlike the other species, however,

which exhibited only lateral basking, *C. willistoni* also displayed dorsal basking. Perhaps dorsal and lateral basking are equally effective in *C. willistoni* because the ratio of the area of the lateral profile to dorsal profile of the thorax of *C. willistoni* is 1:1 (mean ratio of lateral to dorsal profile = 1.04, SE = 0.03, N = 6,  $\chi^2 = 3.37$ , P = 0.65, 5 d.f.). In contrast, the thoraces of *Machimus*, *Stenopogon*, and *Efferia* have lateral profiles that are 20–30% greater in area than their dorsal profiles. Thus, for these species, lateral basking is probably more effective than dorsal basking. In addition, lateral basking allows the flies of these other species to stay within the boundary layer near the soil surface. While the orientations of perched *C. willistoni* may also be constrained by a need to maximize visibility of passing insects, the orientations adopted are consistent with the hypothesis that they are basking to raise body temperatures. Basking was shown to have a significant effect on the body temperatures of other species of robber flies (O'Neill and Kemp, 1992; O'Neill et al., 1990) and may be enhanced by black coloration in *C. willistoni*, which perhaps evolved because of its effect on thermoregulation. Furthermore, after perched flies rotated their bodies when potential prey passed, they rotated back to their original basking orientation. Their reaction to clouds obscuring the sun also supports the hypothesis that the flies depend on direct insolation to raise body temperature.

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#### LITERATURE CITED

- Alcock, J. 1977. The courtship behavior of *Heteropogon stonei* (Diptera: Asilidae). J. Kans. Entomol. Soc. 50:238–243.
- Batschelet, E. 1981. *Circular Statistics in Biology*. Academic Press: New York.
- Bullington, S.W., and R.J. Lavigne. 1992. Ethology of *Cyrtopogon montanus wilcoxi* James (Diptera: Asilidae) in Wyoming. Proc. Entomol. Soc. Wash. 94:123–131.

- Lavigne, R.J. 1970. Courtship and predatory behavior of *Cyrtopogon auratus* and *C. glarealis* (Diptera: Asilidae). J. Kans. Entomol. Soc. 43:163-171.
- Lavigne, R.J., and F.R. Holland. 1969. Comparative behavior of eleven species of Wyoming robber flies (Diptera: Asilidae). Univ. Wyoming Agric. Exp. Sta. Sci. Mono. 18:1-61.
- O'Neill, K.M. 1992a. Patch-specific foraging by the robber fly *Megaphorus willis-toni*. Environ. Entomol. 21:1333-1340
- \_\_\_\_\_ 1992b. Temporal and spatial dynamics of predation in a robber fly population (Diptera: Asilidae, *Efferia staminea*). Can. J. Zool. 70:1546-1552.
- \_\_\_\_\_ 1994. The male mating strategy of the ant *Formica subpolita* Mayr (Hymenoptera: Formicidae): Swarming, mating, and predation risk. Psyche 101:93-108.
- O'Neill, K.M., and W.P. Kemp. 1990. Behavioral responses of the robber fly *Stenopogon inquinatus* (Diptera: Asilidae) to variation in the thermal environment. Environ. Entomol. 19:459-464.
- \_\_\_\_\_ 1992. Behavioral thermoregulation in two species of robber flies (Diptera: Asilidae, *Machimus*) occupying different grassland microhabitats. J. Therm. Biol. 17:323-331.
- O'Neill, K.M.; W.P. Kemp, and K.A. Johnson. 1990. Behavioural thermoregulation in three species of robber flies (Diptera, Asilidae: *Efferia*). Anim. Behav. 39:181-191.
- Powell, J.A. 1969. Prey hunting and courtship behavior of *Cyrtopogon vanduzeei* Wil. and Mart. Pan-Pac. Entomol. 45:67.
- Wilcox, J.H., and C.H. Martin. 1936. A review of the genus *Cyrtopogon* Loew in North America (Diptera-Asilidae). Entomologica Americana 16:1-95.



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