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Ethology of *Proctacanthus fulviventris* Macquart, 1850 (Diptera: Asilidae) in Northeastern Florida, U.S.A.

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ABSTRACT

Proctacanthus fulviventris Macquart, 1850 (during 214 hours of observation) foraged primarily from the ground, capturing and immobilizing prey in flight. Identified prey came from two insect orders (Diptera and Hymenoptera), with Hymenoptera making up 88%. Mating occurred in the male over female position and oviposition was in the ground, typically in the shade of vegetation or a shaded depression in the ground when the sun was shining. This species exhibited a distinct daily rhythm of activity for feeding, mating, and oviposition. Grooming behavior resembled that described for other species of Asilidae. Habitats, resting behavior, and predators and parasites also are discussed.

Key words: Behavior, robber flies, prey, Diptera, Asilidae.

INTRODUCTION

The 29 described extant species of robber flies in the genus *Proctacanthus* occur in the Nearctic and Neotropical zoogeographic regions of the world (Geller-Grimm, 2013). Of these species only the ethology of *P. brevipennis* (Wiedemann, 1828) (Dennis, 2012), *P. micans* Schiner, 1867 (Dennis and Lavigne, 1975; Rogers and Lavigne, 1972), and *P. nearno* Martin, 1962 (Lavigne and Dennis, 1979) have been described in detail. Dennis (2012) listed other publications that reported only observations of habitat and/or prey for the 19 species occurring in the United States of America (U.S.A.).

This paper provides detailed information on the ethology of *P. fulviventris* Macquart, 1850 in sites in the Moses Creek Conservation Area (MCCA) in St. Augustine in northeastern Florida, U.S.A. *Proctacanthus fulviventris* is 25-30 mm in length and is a colorful species (Fig. 1). The mystax and bristles around the head are yellow, the scutellum has numerous yellow bristles and hairs, the femora are black, the tibiae are red, and usually the dorsum of abdominal segments 3 or 4-7 are red.

The St. Johns River Water Management District (District) owns and operates the MCCA. To restore, maintain, and protect natural communities and diversity, the District uses a combination of prescribed fire and mechanical (roller chopping and mowing) vegetation management in the sandhill and scrub/scrubby flatwoods communities. To facilitate access to the MCCA, the District also mows along roads and the sides or edges of roads, where most *P. fulviventris* occurred.

Fig. 1. Male *Proctacanthus fulviventris* resting on sugar sand.

MATERIALS AND METHODS

Proctacanthus fulviventris is widely distributed in Florida on sand roads and depending on location, generally occurs from May through September. Observations were made over a period of 3 years, from: 1 June through 12 October 2011; 7 May through 1 October 2012; and 1 June through 20 September 2013. The author observed a number of *P. fulviventris*, primarily on and along mowed sugar sand roads, in three vegetation communities (upland mixed forest, scrub, and scrubby flatwoods) and in a previously mowed scrub community in the MCCA. Sugar sand is a fine silt made up of ultrafine mineral sand mixed with a large percentage of organic granules. It resembles fine sugar.

The times when *P. fulviventris* was most abundant in the previously mentioned areas in the MCCA determined the periods of study. Observations during these times involved an average of eight individuals per day, each for up to 134 minutes. Total number of hours of observation equaled approximately 214.

The study began with the author sitting or standing and observing individual flies for as long as the flies were in sight, in order to collect information on their various behaviors and diurnal activities. After gathering data on their individual behavior, the author slowly walked through a study area and observed the activities of many flies. This also allowed for the collection of prey and the observation of mating pairs and ovipositing females.

Collected prey were placed in glass vials with the following information: sex of predator (if observed); date; time; and location. All prey were measured with a clear, plastic ruler to the nearest 0.5 mm. The author sent prey that he could not identify to the U.S.A. Department of Agriculture, Agricultural Research Service, Systematic Entomology Laboratory, Beltsville, Maryland, U.S.A. for identification.

Ovipositing females were observed for as long as they continued to exhibit oviposition site seeking behavior or until they moved out of sight as they flew about the habitat. When a female ceased to oviposit or the author lost visual contact, he dug up the oviposition site with a small hand shovel. Then he visually examined the soil in the laboratory and the eggs, if present, were removed. Oftentimes eggs were not found, but those that were recovered (from seven ovipositions) were placed in 95% ethyl alcohol for later examination and measurement to the nearest 0.1 mm with a 10X reticle scale measuring comparator magnifier.

Important environmental variables that determine the activities in which adult asilids engage include temperature and wind. A hand held Taylor thermometer was used to take air, surface and subsurface ground temperatures. A Dwyer Hand-Held Wind Meter was used to measure wind speed.

RESULTS AND DISCUSSION

Habitat

The mowed roads and sides of the roads in the MCCA are approximately 3-4 m and 4-6 m wide, respectively. The roads generally have little vegetation or some sparse grasses (Fig. 2). The mowed sides of the roads and mowed scrub community contain plants associated with the vegetation communities shown in Table 1. The dominant plants in these areas are 30 cm to 1 m tall saw palmetto, scrub oak, rusty lyonia, and rusty staggerbush. The road edges in each community also have the following abundant plants at various locations: upland mixed forest (fennel, bushy bluestem); scrub (gallberry, tar flower, vanillaleaf, shiny blueberry, wiregrass, bushy bluestem, broomsedge bluestem); scrubby flatwoods (Elliott's white milk pea, bushy bluestem); and mowed scrub community (tailed bracken, Elliott's white milk pea, bushy bluestem, broomsedge bluestem).

Bromley (1950) stated that *P. fulviventris* occurred in Florida, "In scrub or white sand, alighting on or close to the ground." Bromley (1928) also noted that *Proctacanthus* "…inhabit dry fields or pastures, several being restricted to dry sandy plains." Hull (1962) indicated that *Proctacanthus* are found in "…rank grassland and shrubs on the edges of woodlands in swampy country and some prefer sandy river banks."

Fig. 2. *Proctacanthus fulviventris* habitat along road consisting of sugar sand.

Table 1. Vegetation in areas in which *Proctacanthus fulviventris* was studied in the Moses Creek Conservation Area.

Vegetation Type	Mowed Edges of Road in Vegetation Community			Mowed Scrub Community
Family/Genus/Species Common Name	Upland Mixed Forest	Scrub	Scrubby Flatwoods	
Aquifoliaceae				
Ilex glabra (L.) A. Gray Gallberry	X[1]	X	-	-
Arecaceae				
Serenoa repens (W. Bartram) Small Saw palmetto	X	X	X	X
Asteraceae				
Carphephorus corymbosus (Nutt.) Torr. and A. Gray Coastalplain chaffhead (Florida paintbrush)	-	X	X	X
Carphephorus odoratissimus (J. F. Hamel) H. Hebert Vanillaleaf (Deer's tongue)	X	X	X	X
Eupatorium sp. prob. *leptophyllum* DC Fennel	X	-	-	-
Solidago sp. Goldenrod	X	-	X	X
Cactaceae				
Opuntia humifusa (Raf.) Raf Prickly pear cactus	X	X	-	X
Dennstaedtiaceae				
Pteridium aquilinum L. (Kuhn) var. *pseudocaudatum* (Clute) Clute ex. A. Heller Tailed bracken	-	-	X	X
Ericaceae				
Bejaria racemosa Vent. Tar flower	X	X	X	X
Ceratiola ericoides Michx. Florida rosemary (sand heath)	-	X	-	-
Lyonia ferruginea (Walter) Nutt. Rusty lyonia	X	X	X	X
Lyonia fruticosa (Michx.) G. S. Torr. Rusty staggerbush (Coastal plain staggerbush)	X	X	X	X
Vaccinium myrsinitas Lam. Shiny blueberry	-	X	-	-
Fabaceae				
Galactia elliottii Nutt. Elliott's (white) milkpea	X	X	X	X

Footnotes: X = present; - = not observed.

Table 1. (Continued) Vegetation in areas in which *Proctacanthus fulviventris* was studied in the Moses Creek Conservation Area.

Vegetation Type	Mowed Edges of Road in Vegetation Community			Mowed Scrub Community
Family/Genus/Species Common Name	Upland Mixed Forest	Scrub	Scrubby Flatwoods	
Fagaceae				
Quercus incana W. Bartram Bluejack oak	X	X	X	X
Quercus virginiana (P. Mill.) Live oak tree	-	-	-	X
Quercus sp. Scrub oaks	X	X	X	X
Pinaceae				
Pinus clausa(Chapm. ex Engelm.) Vasey ex Sarg. Sand pine	X	-	X	-
Pinus serotina Michx. Pond pine	-	-	-	X
Poaceae				
Andropogon glomeratus (Walter) Britton *et al*. Bushy bluestem	X	X	X	X
Andropogon virginicus L. Broomsedge bluestem	X	X	X	X
Aristida stricta Michx. Var. beyrichiana (Trin. and Rupr.) D. B. Ward Wiregrass	-	X	-	X
Other grasses	X	X	X	X
Saururaceae				
Saururus cernuus L. Lizard's tail	-	X	X	X
Zamiaceae				
Zamia integrifolia L. Florida arrowroot (Coontie)	X	X	-	X

Footnotes: X = present; - = not observed.

Resting Behavior

Proctacanthus fulviventris rested on the ground, on dead vegetation on the ground, and on the stems and leaves of live vegetation. When on the ground or dead vegetation on the ground, individuals would often turn so that one of their sides faced and was slightly elevated to the sun. They also flattened themselves against the substrate, in particular if clouds obscured the sun or the ground and air temperatures were less than 30˚C and 29˚C, respectively. When flattened on the ground some asilids spread their wings at a 45-degree angle to their bodies. Also, as the ground temperature increased to 34.5˚C and air temperature approached 31˚C, some would elevate themselves on their fore tarsi so that their bodies were at a 45-degree angle to the substrate or they would stand up on all tarsi and assume their normal foraging position. Also, a few individuals held their fore tarsi off the ground.

Proctacanthus fulviventris typically started to move from the ground onto live vegetation between 10:00 to 11:00 AM when the ground temperature reached 34-35˚C with an average of 37.5˚C and the air temperature was 33-34˚C with an average of 34.9˚C. Movement to live vegetation was complete by the time the ground temperature had reached 40-43˚C. When moving to live vegetation, a *P. fulviventris* would land on the shaded side of a leaf or vertical plant stem with its body at a 45-degree angle or parallel to the vegetation. *Proctacanthus brevipennis* shows similar behavior (Dennis, 2012).

In the afternoon, when the ground and air temperatures began to drop (to approximately 38˚C on the ground and 34˚C in the air) a few *P. fulviventris* would move back to the ground. However, the majority stayed on vegetation near the roads and presumably spent the night there.

Dennis and Lavigne (1975) observed that robber flies on the ground apparently attempt to maintain their body temperature by changing their position and flattening themselves against the ground. *Proctacanthus fulviventris* also maintains its body temperature by its position on the ground, spreading its wings at a 45 degree angle, and by resting in the shady side of vegetation. Morgan *et al*. (1985) and Morgan and Shelly (1988) indicated that foraging Neotropical and desert robber flies regulate their body temperatures by microhabitat selection and postural adjustments.

While resting and feeding, a number of asilids expelled a drop of creamy-white liquid from the anus. Rau and Rau (1916) commented on *P. milbertii* expelling a drop of brown, pasty substance whether awake or asleep. Dennis (2012) also observed *P. brevipennis* expelling drops of creamy-white liquid from their anus. According to Lehr (1958c) the expulsion of liquid from the anal opening is common in robber flies.

Foraging and Feeding Behavior

Proctacanthus fulviventris foraged primarily from the ground (roads) and sometimes from vegetation after they had moved from the roads to vegetation. When foraging from roads, they typically faced in the direction of the road. This may have been to give them a more extensive frontal view of the area as a berm/vegetation up to 30-45 cm in height on the edge of the roads would limit their vision if they landed crosswise.

When *P. fulviventris* moved to vegetation they were more likely to continue foraging when their bodies were at a 45 degree angle. When they assumed a position with their bodies parallel to the vegetation, they usually became inactive, and remained in one place for at least 2 hours unless disturbed. Lavigne *et al*. (2000) indicated that robber flies usually forage from the ground early in the morning or late in the afternoon when the ground and air temperatures are cool, and from vegetation when the ground surface is hot.

While foraging, *P*. *fulviventris* would often arrange its body at a 45-degree angle to the substrate and face the sun. This foraging attitude, or posture, presumably allowed the asilids to better see their prey because of backlighting. Other investigators have made similar observations for several species of robber flies (Dennis, 2012; Dennis *et al*., 1986; Hespenheide, 1978; Hespenheide and Rubke, 1977; Lavigne, 1970b, 1971; Lavigne and Dennis, 1985; Melin, 1923). In addition, it is assumed that the body held at a 45-degree angle allowed the asilids to better see potential prey utilizing the central ommatidia of their eyes. According to Melin (1923), the central ommatidia "…have greater intensity of vision than the outer ones." Nation (2008) commented that robber flies have higher visual acuity near the forward part of their eyes and this probably allows them to better see and capture prey.

When foraging, *P. fulviventris* frequently made investigatory flights without making contact with potential prey or other *P. fulviventris.* Flights were for distances of 20 cm to 1.5 m slightly behind, above, to the side of or in front of an individual's original foraging position and 7.5 cm to 1.5 m above the ground. Investigatory flights are common for robber flies (Dennis, 2012, 2013; Dennis and Lavigne, 1975; Dennis *et al*., 1975; Lavigne, 1964; Lavigne and Dennis, 1975; Lavigne and Holland, 1969; Melin, 1923). Parmenter (1952) and Lavigne *et al*. (2000) indicated that investigatory behavior is probably necessary because some robber flies cannot identify suitable prey except at a short distance. Lehr (1958c) noted that robber flies often cannot determine whether a flying insect is acceptable prey. However, in general robber flies are known to have excellent vision, in particular for detecting movement.

Following investigatory flights, *P. fulviventris* typically landed near their original foraging locations, although one individual moved approximately 3 m from its original position. Even if *P. fulviventris* did not make investigatory flights they changed their foraging locations after periods ranging from a few seconds to 33 minutes. Time spent at any one location varied with the individual and the weather. Asilids would either quickly move to within about 3 m of their previous location or remain in one place for up to 7 minutes, except when feeding, during inclement weather or when clouds obscured the sun. During the latter, one male remained in the same position for 33 minutes and then resumed foraging when the sun shone again. Depending on the species, robber flies either forage from one location for variable periods of time or move frequently to new locations. Hayat and Çalışkan (2003) observed that male *Dasypogon irinelae* Weinberg, 1986 remain at one location for longer periods of time than females.

Dennis and Lavigne (1975) called short flights around a foraging position without pursuing potential prey, "orientation flights." *Proctacanthus fulviventris* made orientation flights within 5 m of its foraging position and 2 m above the ground or moved to a new foraging site up to 30 m away. Lavigne (1992) observed *Colepia abludo* (Daniels, 1983) (as *Neoaratus*) making orientation flights in excess of 10 m after the asilids stayed in one location for an extended period. He presumed the long flight was in response to the lack of potential prey in the immediate vicinity or was a strategy used by males to relocate when no females had been seen. Others also have commented on robber flies moving to new foraging locations to increase the probability of finding prey (Lavigne and Holland, 1969; Hespenheide and Rubke, 1977; Scarbrough, 1979, 1981a; Scarbrough and Sraver, 1979).

Abdominal pumping of the first two to three segments was observed when one female was feeding. According to Musso (1968) and Lavigne and Holland (1969), abdominal pumping or contractions during feeding are associated with the injection of proteolytic enzymes into prey and extraction of dissolved substances. The author has observed similar pumping with *P. brevipennis* and it has been reported for a number of other species of robber flies (Dennis and Lavigne, 1975; Lavigne and Holland, 1969), but not for *P. micans* (Dennis and Lavigne, 1975) or *P. nearno* (Lavigne and Dennis, 1979).

Some *P. fulviventris* captured potential prey within 3 m of their foraging position, 3 m above the ground and released them while still in flight. A few individuals also released prey after falling to the ground or landing and then releasing prey in a hover. Dennis and Lavigne (1975) commented that some species may capture and release prey because robber flies use both visual and other stimuli to select prey.

Proctacanthus fulviventris captured all of its prey in the air when the prey were within 1 m in front of, to the side of or slightly behind, and within 1 m above the asilid's foraging position. Both *P. brevipennis* (Dennis, 2012) and *P. micans* (Dennis and Lavigne, 1975) also captured most of their prey in flight.

Height and distance that robber flies fly in a habitat has been shown to decrease when the wind is blowing (Dennis and Lavigne, 1975; Lehr, 1961). In the MCCA there often was wind gusting up to 11.3 km/hr. However, wind gusting did not appear to decrease the distances or heights that *P*. *fulviventris* flew or affect mating and ovipositing activities.

Having captured prey, an asilid would generally hold onto it with all six tarsi, often while hovering, and insert its proboscis in the dorsum of the prey's thorax with the prey's head underneath the asilid's head. This suggested that the asilid attacked prey from behind and above. A few prey were not immediately subdued and the asilids would fall to the ground and hold onto the prey until the latter stopped moving. The asilid would then generally fly to nearby vegetation to feed, often in the shade of a leaf or plant stem.

During feeding *P. fulviventris* manipulated prey up to four times in a hover above the feeding site. While hovering, some individuals buzzed their wings. The number of times that prey was manipulated did not depend on prey length. *Proctacanthus brevipennis* (Dennis, 2012), *P. micans* (Dennis and Lavigne, 1975; Rogers and Lavigne, 1972), and *P. nearno* (Lavigne and Dennis, 1979) also manipulate prey during a hover and hold larger prey against the ground or vegetation and crawl on them before reinserting their proboscises.

When *P. fulviventris* were feeding, prey hung free from the asilid's proboscis without support by the tarsi. One female used her body to hold large prey against vegetation while grasping the vegetation with all six tarsi.

As researchers have observed for other species, the time robber flies spend feeding usually depends on prey length (Dennis, 2012, 2013; Dennis and Lavigne, 1975; Lavigne and Dennis, 1975). *Proctacanthus fulviventris* fed on prey with an average length of 9.3 mm (e.g., *Prionyx sp*. and Tiphiidae) for approximately 46 minutes.

Longer prey such as *Apis mellifera and Vespula squamosa*, with an average length of 13 mm, took about 98 minutes. Length of time that *P. fulviventris* spent feeding on individual prey varied from 10 to 134 minutes, with an average of 66.5 minutes.

Male *P. fulviventris* captured prey that averaged slightly shorter than those captured by females. Mean prey length for males was 13.4 mm (n = 10) with a range from 10-23.0 mm; whereas, for females it was 14.4 mm (n = 37) with a range from 8.0 -to 26.0 mm. The overall mean prey length was 14.1 mm with a predator to prey ratio of 1.9:1.0 which indicates that *P. fulviventris* was almost twice as large as its prey. Mean predator to prey ratios of *P. micans* and *P. brevipennis* were 2.0:1.0 and 3.0:1.0, respectively (Dennis, 2012; Dennis and Lavigne, 1975). Other species of robber flies have ratios that range from 0.9:1.0 to 8.4:1.0 with a mean of 2.9:1.0 (Dennis, 1979, 2013; Dennis and Lavigne, 1975, 1976a and b, 1979; Hespenheide, 1978; Lavigne, 1979, 1984, 1992; Lavigne and Bullington, 1984, 1999; Lavigne and Dennis, 1975, 1985; Lavigne *et al*., 1983, 1993; Lavigne and Holland, 1969; Lehr, 1958c, 1971; Scarbrough, 1978, 1979, 1981a, 1982; Scarbrough and Sraver, 1979; Shelly and Pearson, 1980).

At the completion of feeding, each individual *P. fulviventris* discarded prey in one of four ways: (1) it dropped prey in flight as it moved to a new location; (2) it pushed prey off its proboscis with the fore tarsi while it was still at the feeding site; (3) it allowed prey to drop-off the proboscis at the feeding site; or (4) it dropped prey during a hover at the feeding site. *Proctacanthus brevipennis* discarded prey in flight, pushed prey off its proboscis or allowed prey to drop off its proboscis at the feeding site (Dennis, 2012); *P. nearno* allowed prey to drop-off its proboscis either at the feeding site or in flight shortly after leaving the feeding site (Lavigne and Dennis, 1979); whereas, *P. micans* usually pushed prey off its proboscis with the fore tarsi as it moved to a new location (Dennis and Lavigne, 1975).

Interfeeding times (between feedings) for *P. fulviventris* were extremely difficult to obtain because the speed, distance flown by individuals, and the height of flight in relation to that of the vegetation, made the flies hard to follow. This resulted in the recording of only one interfeeding time of 10.5 minutes.

One can calculate the theoretical number of prey an individual *P. fulviventris* could feed on in one day if we assume that: (1) it continually forages and feeds between 9:00 AM and 2:00 PM (the observed major period of foraging and feeding activity for 85.9% of individuals), and (2) it captures and feeds on prey every 77 minutes (based on the average feeding time and one interfeeding time). Thus, over a 5-hour period an individual could feed on approximately 3 to 4 prey. This is believed to be a liberal estimate because of the relatively short interfeeding time. Dennis and Lavigne (1975) calculated that *P. micans* could feed on approximately 6 to 7 prey per day and Dennis (2012) estimated 7 to 8 prey per day for *P. brevipennis*. Other investigators have estimated that robber flies feed on from 1 to 35 prey per day (Baker and Fischer, 1975; Dennis, 2013; Dennis and Lavigne, 1975, 1976a and b; Joern and Rudd, 1982; Lavigne and Dennis, 1975; Lavigne *et al*., 2000; Lavigne and Pfadt, 1966; Lehr, 1958a, 1964, 1971).

Proctacanthus fulviventris's feeding on fewer prey per day than many other species of robber flies may be correlated with it feeding on larger prey as shown by the lower predator to prey ratio. Although *P. micans* also had a low predator to prey ratio (2.0:1.0), it had an average shorter feeding time (46 minutes) than *P. fulviventris*.

Prey

Proctacanthus fulviventris was very selective in its choice of prey, feeding on only Diptera (12.0%) and Hymenoptera (88.0%) (Table 2). Other species of *Proctacanthus* feed on a wide variety of prey from the orders Coleoptera, Diptera, Hemiptera, Hymenoptera, Isoptera, Lepidoptera, Neuroptera, Odonata, and Orthoptera (Baker and Fischer, 1975; Bouseman and Maier, 1977; Bromley, 1923, 1931a and b, 1934, 1946a and b, 1947, 1949, 1950; Dennis, 2012; Dennis and Lavigne, 1975, 2007; Dennis *et al*., 2009, 2010; Lavigne and Dennis, 1979; Lavigne *et al*., 1994; Rogers and Lavigne, 1972).

Table 2. Number and percent composition of orders of prey taken by *Proctacanthus fulviventris.*

	Male		Female		Total	
Order	Number	Percent	Number	Percent	Number	Percent
Diptera	2	12.5	7	11.9	9	12.0
Hymenoptera	14	87.5	52	88.1	66	88.0
Totals	16	100.0	59	100.0	75	100.0

Diptera and Hymenoptera made up approximately the same percentages of prey for both male and female *P. fulviventris*. However, in this study more females were captured with prey than males. Numerous other investigators have reported collecting more female than male robber flies with prey (Dennis, 1979; Dennis and Lavigne, 1975, 1976a and b, 1979; Dennis *et al*., 1986; Hobby, 1931a and b, 1935; Lavigne, 1970a, 1979, 1984, 1992; Lavigne and Dennis, 1985; Lavigne *et al*., 1976, 1983; Lavigne and Pogue, 2009; Lehr, 1958a and b; Londt, 1991; Poulton, 1906).

Dennis and Lavigne (1975) stated that it would seem advantageous for robber flies to be opportunistic predators since there would be more potential prey. Most of the prey of *P. fulviventris* were large bodied, suggesting selectivity rather than opportunism.

A number of different species of robber flies, including *Proctacanthus* spp. (Knisley and Hill, 2010; Lavigne, 1972, 1977; Wallis, 1913) prey on tiger beetles (Coleoptera: Cicindelidae). Tiger beetles, including *Cicindela hirtilabris* LeConte, 1875, walked or flew around *P. fulviventris*, but none were attacked.

The following is a list of prey taken by *P. fulviventris*. Number and sex of the predator is indicated following the prey record.

DIPTERA, Asilidae: *Efferia tabescens* (Banks, 1872), 9-VIII-13 (1♀); *Proctacanthus fulviventris,* 15-VIII-11 (1♀). Tabanidae: *Tabanus* sp., 4-VI-13 (1♂), 15-VIII-11 (1♀), 29-VIII-11 (1♂, 1♀), 2-IX-11 (3♂♂). HYMENOPTERA, Apidae: *Apis mellifera* L, 1758,

15-VIII-11 (1♀), 15-VIII-13 (1♀), 20-VIII-13 (2♀♀), 27-VIII-13 (3♀♀), 11-IX-13 (1♀), 24-IX-12 (1♀); *Bombus impatiens* Cresson, 1863, 7-VIII-12 (1♀), 9-VIII-13 (1♂), 16-VIII-13 (2♀♀), 21-VIII-13 (♀), 27-VIII-13 (4♀♀), 29-VIII-13 (2♀♀), 30-VIII-13 (1♀), 31-VIII-13 (1♀), 6-IX-13 (1♀), 13-IX-13 (1♀); *Bombus* sp., 11-VIII-11 (1♀). 4-IX-13 (1♀); *Bombus* sp. prob. *variabilis* (Cresson, 1872), 7-VIII-12 (1♀). Scoliidae: *Campsomeris plumipes fossulana* (Fabricius, 1804), 10-V-12 (♀); *Trielis octomaculata hermione* (Banks, 1912), 14-VIII-12 (1♀). Sphecidae: *Prionyx* sp., 12-VIII-11 (1♀), 17-VIII-11 (1♀). Tiphiidae: unidentified, 23-VI-12 (1♀), 29-VI-12 (1♂), 2-VII-12 (1♂), 6-VII-12 (1♀),15-VII-13 (1♂), 16-VII-13 (1♂), 30-VII-12 (1♀), 7-VIII-12 (1♀), 16-VIII-13 (1♀), 27-VIII-13 (♀), 31-VIII-12 (♂). Unidentified: 6-VII-12 (♀). Vespidae: *Polistes fuscatus* (Fabricius, 1793), 3-VIII-13 (1♀); *Vespula maculifrons* (Buysson, 1905), 31-V-12 (1♀); *Vespula* sp., 3-IX-13 (♀), *Vespula squamosa* (Drury, 1770), 5-VI-13 (1♀), 10-VI-13 (1♀), 29-VII-13 (2♀♀), 3-VIII-13 (1♂), 6-VIII-12 (1♀), 8-VIII-13 (1♂), 15-VIII-13 (♂), 21-VIII-13 (1♂, 1♀), 22-VIII-12 (1♂), 26-VIII-13 (1♀), 27-VIII-13 (1♂), 28-VIII-13 (1♀), 29-VIII-13 (2♀♀), 2-IX-13 (1♀), 11-IX-13 (1♂, 1♀), 13-IX-13 (1♂).

Mating Behavior

Male *P. fulviventris* performed searching flights for receptive females with which to mate. Flights consisted of a male flying 3-30 m, 30-40 cm above the ground in a straight or zig zag pattern up and down a road. Between flights a male would land for 2 to 7 minutes and then resume its periodic searching flights for up to a total of 49 minutes. Male searching flights in vertical undulations have been reported for *P. brevipennis* (Dennis, 2012) and *P. micans* (Dennis and Lavigne, 1975).

As part of the mate searching process, males frequently flew up to investigate other *P. fulviventris*. They would then briefly come into contact and hover in front of or the pair would circle each other before landing on the ground or vegetation.

Proctacanthus fulviventris usually initiated matings in-flight when the male would grasp the dorsum of the female's thorax and the struggling pair would fall to the ground in the male-over-female position. Two pairs fell to the ground before the males could clasp the female's genitalia and begin mating. The males subsequently attempted to clasp the female's genitalia for 7 and 19 minutes before they were successful.

After a mating was initiated, pairs would fly to nearby vegetation up to 2.5 m above the ground, typically in the shade of leaves or a plant stem. In the male-over-female position the male's abdomen curved to the right or left of the female's abdomen and clasped her genitalia from below (Fig. 3). The wings of both asilids were usually spread at a 30 to 45-degree angle to their bodies. The female's wings in this position passed between the male's mid and hind legs so that the male's mid tibiae were over the female's wing bases. Two females had their wings closed over their abdomens so that the male's mid and hind legs were around them. The male's fore tarsi rested on the female's eyes/head, anterior part of her thorax or vegetation. The male's mid tarsi rested on the anterior part of the female's thorax, sides of her eyes, vegetation or hung free below her thorax with the mid tibiae holding onto the female's thorax. The male's hind legs passed around the female's abdomen, the hind tarsi rested on the female's hind femora, vegetation or hung free below her abdomen with the hind tibiae holding onto the female's abdomen.

Fig. 3. Mating pair of *Proctacanthus fulviventris* in the male-over-female position.

During mating the asilids generally remained motionless, but were easily disturbed and would fly up to 10 m to other vegetation. If they were in the shade of vegetation and then exposed to the sun, the female would adjust their position so that they were in shade. One pair buzzed their wings twice when adjusting their position.

The author observed 11 complete matings that lasted 30 to 63.5 minutes, with an average of 40.6 minutes. Matings occurred when the air temperature at the height where the mated pair rested on vegetation ranged from 30.5-33.5ºC in the shade and 29.4-36.0ºC in the sun. *Proctacanthus brevipennis* mated for 78 to 111 minutes with an average of 90 minutes (Dennis, 2012); whereas, *P. micans* mated for 23 to 66 minutes with an average of 42 minutes (Dennis and Lavigne, 1975).

At the completion of mating, male *P. fulviventris* released the female and both flew off or the pair flew into the air in the tail-to-tail position and then separated. Towards the end of two matings, the females flexed their abdomens down and stroked or rubbed them with their hind tarsi.

Proctacanthus brevipennis mated in the tail-to-tail position (Dennis, 2012) and *P. micans* mated in the male-over-female position (Dennis and Lavigne, 1975). Rogers and Lavigne (1972) indicated that *P. micans* will mate in the tail-to-tail position, but Dennis and Lavigne (1975) did not believe this to be the normal mating position. They indicated that if *P. micans* assumed the tail-to-tail position, duration of matings was shortened. Lavigne and Dennis (1979) indicated that *Proctacanthus nearno* started mating in the male-over-female position and shortly after the initiation of mating assumed the tail-to-tail position, although these researchers were not certain if they had observed a complete mating or if it was shortened in the tail-to-tail position.

Oviposition Behavior

Like other species of *Proctacanthus* (Bromley, 1946b; Hine, 1911), *P. fulviventris* females have spines (acanthophorites) at the tips of their ovipositors and oviposit in the ground. Observed ovipositions typically occurred in the shade of vegetation or in depressions in the ground, such as horse hoof prints and antlion (Neuroptera, Myrmeleontidae: *Myrmeleon carolinus* Banks, 1943) larvae conical pit fall traps, unless the sky was cloudy, and then it was in more open areas. *Proctacanthus brevipennis* (Dennis, 2012) and *P. micans* (Dennis and Lavigne, 1975) also oviposit in the ground in the shade of vegetation.

Air temperatures 30 cm above the oviposition site ranged from 27.0-38.0°C with an average of 32.6°C. Ground surface temperatures at the oviposition site ranged from 27.2-48.3°C with an average of 34.3°C; whereas, temperatures beneath the surface of the ground where ovipositions occurred ranged from 26.0-43.9°C with an average of 32.9°C.

Proctacanthus fulviventris females either immediately inserted their ovipositors in the ground or walked along the ground and probed with their ovipositors in order to find a suitable place to deposit their eggs. They inserted their ovipositors in the ground with a lateral or tamping action for up to 155 seconds with an average of 55 seconds. The actual oviposition or deposition of eggs took 60 to 284 seconds with an average of 126 seconds, during which some females intermittently exhibited a tamping action. Following deposition of eggs, females withdrew their ovipositors from the ground with a sweeping action that usually continued on the ground surface around the oviposition hole, although some females did not sweep the surface of the ground. Ovipositor withdrawal and sweeping was done for a few seconds to 140 seconds with an average of 41 seconds. Average time for complete ovipositions was 222 seconds with a range from 75 to 457 seconds.

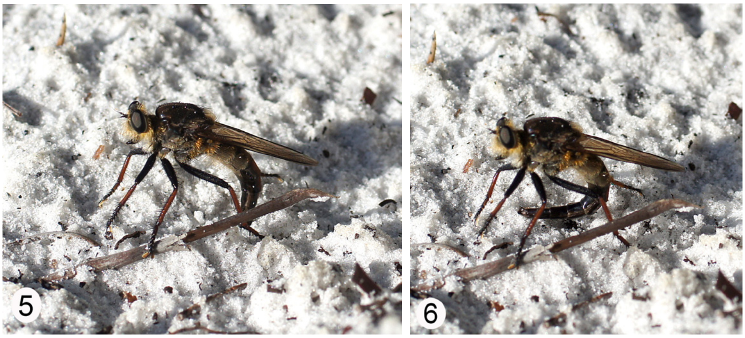
The depth that a female inserted her abdomen in the ground depended on the dryness of the ground. In dry ground, in particular in sugar sand that was loose and not compacted, a female would typically insert her ovipositor so that her abdomen was buried up to or almost up to the thorax (Fig. 4). In this position the female's abdomen was gently curved outward and her wings were usually spread at a 30 to 90-degree angle, although some females kept their wings folded over their abdomens with the wing tips buried in the ground.

In damp soil, following a rain when the soil was presumably more compacted, females would only insert the abdomen in the soil 1/4 to 1/2 of its length (Fig. 5). Most females then kept their wings folded over their abdomens, but a few spread their wings to a 30 to 45-degree angle.

Females took longer to insert their ovipositors and there was more tamping in damp soil. The length of time for depositing eggs, withdrawing ovipositors, and sweeping the ground around the oviposition hole was about the same in dry and damp soil.

Female robber flies that oviposit in the ground usually sweep the ground with the tips of their ovipositors following oviposition. *Proctacanthus fulviventris* females exhibited unusual behavior and swept the ground with both the tip of their ovipositors and with the dorsal surface of the last two to three abdominal segments by curving their abdomens under their bodies (Fig. 6).

Fig. 4. Female *Proctacanthus fulviventris* ovipositing in dry sugar sand.



Figs. 5-6. Female *Proctacanthus fulviventris* 5. ovipositing in damp sugar sand. 6. brushing with dorsal abdominal segments area around oviposition hole.

It was not unusual to see female *P. fulviventris* oviposit two to four times over a 15 to 20 minute period before being lost to sight. One female oviposited five times. Rogers and Lavigne (1972) observed a female *P. micans* oviposit six times over 31 minutes. According to Lavigne *et al*. (2000) robber fly females may oviposit several times.

One to six eggs were recovered from each of seven ovipositions, with an average of five eggs. For these ovipositons there was not any difference between the number of eggs deposited in dry or damp soil or the length of time for ovipositing.

Eggs were creamy-white and oblong like those of *P. brevipennis* (Dennis, 2012), *P. micans* (Dennis and Lavigne, 1975), and many other species of robber flies (Dennis *et al*., 2013). Some of the larger eggs were narrower at one end and a few were slightly shaped like a kidney bean. The 30 eggs collected ranged in length from 2.0-3.0 mm, with a mean of 2.5 mm; range in width was from 0.8-1.5 mm, with an average of 1.0 mm.

Grooming

Proctacanthus fulviventris groomed themselves in much the same way as reported for other species of robber flies (Dennis, 1979, 2012, 2013; Dennis and Lavigne, 1975, 1976a, 1979; Johnson, 1976; Lavigne and Pogue, 2009; Lehr, 1958c). They always used the fore legs to groom their faces, and the hind legs for grooming their wings, abdomen and genitalia. Before grooming of the face, they usually rubbed together the fore tarsi while extending and slightly elevating the fore legs. Asilids moved the fore tarsi back and forth along their long axes and then rubbed the dorsolateral part of the face and eyes with the inside of and distal part of either one or both front femora and proximal 1/2 of the tibiae. During this sequence some flies slightly rotated their heads and used their fore tarsi, tibiae, and femora to groom their faces and eyes.

Proctacanthus fulviventris rubbed their hind tarsi together prior to grooming the abdomen, genitalia, and wings. They then turned the hind tarsi inward to groom the abdomen, genitalia, and tops and bottoms of the wings of the posterior part of the wings. Generally they groomed the posterior 1/2 of the abdomen with it slightly curved down and often with their wings slightly spread. Grooming of the wings and abdomen was always from anterior to posterior as observed by Dennis (2012, 2013) and Lehr (1958c).

Grooming was common between foraging flights. Grooming of the face was particularly common after feeding, as was grooming of the abdomen and genitalia after mating and ovipositing.

Proctacanthus fulviventris never groomed its thorax.

Changes in Behavior from Mowing Vegetation

During the fall, 2012 the scrub habitat in which *P. fulviventris* had been studied was mowed. By 2013 the cut vegetation had grown to 30-60 cm in height before it was cut again in early September to a height of 15-20 cm. Cutting of the vegetation caused *P. fulviventris* to move from the cut areas to nearby roads with generally taller vegetation or forested areas on the sides of the roads. They then rarely foraged, mated, or oviposited in the cut areas and conducted most of these behaviors on and along the roads.

Daily Rhythm of Activity

Proctacanthus fulviventris exhibited a distinct diurnal or daily rhythm of activity between 8:00 AM and 4:00 PM for mating, oviposition, and feeding (Fig. 7). These behaviors had similar patterns and all peaked between 10:00 and 11:00 AM. *Proctacanthus fulviventris* also had the most activity for these behaviors during a similar time frame with 75.5%, 91.9%, and 66.7% of mating, ovipositing, and feeding, respectively, occurring between 9:00 AM and 12:00 noon.

The number of mating pairs increased earlier (between 8:00 to 9:00 AM) than oviposition and feeding behavior. Subsequently, a larger percentage of individuals continued to feed and oviposit between 11:00 AM and 3:00 PM. Thus, to a certain extent, as the frequency of occurrence of one behavior increased, others decreased as with some other species of robber flies (Adamovic, 1963; Dennis and Lavigne, 1975; Lavigne *et al*., 2000) and *P. brevipennis* (Dennis, 2012).

The peak periods of behavior between 10:00 and 11:00 AM were at the same time as when *P. fulviventris* moved from the ground to vegetation. During this time frame, air, ground and subsurface ground temperatures were often increasing 11-15°C.

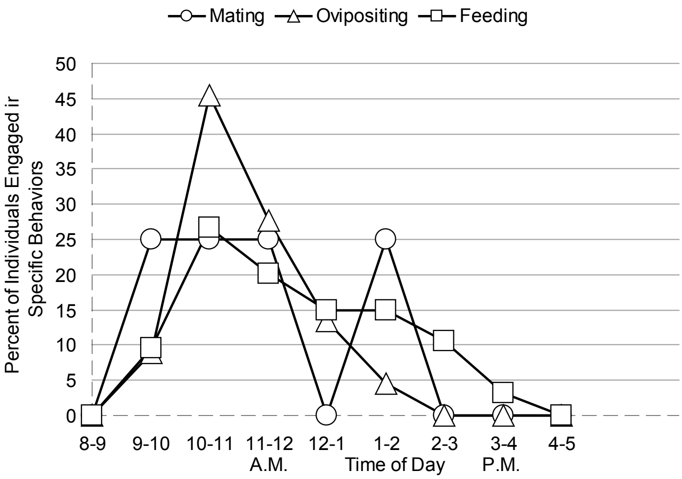


Fig. 7. Diurnal rhythm of activity for *Proctacanthus fulviventris* based on 53, 123, and 78 observations for mating, ovipositing, and feeding, respectively.

Dennis and Lavigne (1975) commented that most of the species of robber flies they studied engaged in feeding before they began mating and ovipositing suggesting the robber flies needed to be food satiated before engaging in other activities. This was not the case for *P. fulviventris*.

Pine and other trees surrounded the roads and the mowed scrub community in which *P. fulviventris* were studied. As a result these areas were mostly in shade until between 8:00 to 8:30 AM and after 4:00 PM. Thus, *P. fulviventris* did not move from its assumed nocturnal resting position on vegetation back to the roads and open areas of the mowed scrub community until they became exposed to the sun. Movement into an area during the day and out again at dusk or changing light conditions has been observed for *P. brevipennis* (Dennis, 2012) and a number of other robber fly species (Adamovic, 1963; Hespenheide and Rubke, 1977; Lavigne, 1970b; Lavigne and Holland, 1969; Musso, 1972; Scarbrough, 1981b; Scarbrough and Norden, 1977).

Robber flies are most active when the sun is shining. However, when the sky was overcast and the author could still see a very light shadow, *P. fulviventris* continued to forage, mate, and oviposit.

Predators and Parasites

Robber flies of the same species often prey on each other (Lavigne *et al*., 2000). This occurred once for *P. fulviventris* when a female attacked a male. A male captured another male, but after landing on the ground released the male when it played dead. Lehr (1961) indicated that cannibalism allowed *Stenopogon heteroneurus* (Macquart, 1838) to survive shortages of food, in particular after long periods of inclement weather.

Other species of robber flies also preyed on *P. fulviventris*. A male *P. brevipennis* and female *Promachus bastardii* (Macquart, 1838) fed on a male and female *P.*

fulviventris, respectively. Both male and female *Diogmites crudelis* Bromley, 1936 were recorded capturing *P. fulviventris.*

Mites were not observed attached to *P. fulviventris*, although they are often found on other robber flies (Lavigne *et al*., 2000).

There were a number of ants (Formicidae: *Formica* spp and *Solenopsis invicta* Buren, 1972) in the same habitats as *P. fulviventris*. When the ants crawled on the asilids' tarsi, the asilids would shake their tarsi and then often fly to a new location.

Lizards may consume robber flies (Lavigne *et al*., 2000). In the MCCA the six-lined racerunner [*Cnemidophorus sexlineatus* (Linnaeus, 1766)] is very common and often walked or ran by *P. fulviventris* on the ground. Although the racerunners are insectivorous, they were not observed to attack the robber flies.

CONCLUSIONS

There exists detailed information on the ethology of only 3 of 19 species of robber flies in the genus *Proctacanthus* (*P. brevipennis*, *P. micans*, and *P. nearno*) in the United States. This paper provides information on a fourth species, *P. fulviventris*. This species rested on the ground, on dead vegetation on the ground, and on the stems and leaves of live vegetation. *Proctacanthus fulviventris* maintained its body temperature by positioning itself on the ground or in the shady side of vegetation, depending on the air and ground temperature and location of the sun. Foraging was primarily from the ground in an attitude or posture that presumably allowed the asilids to better see prey. All prey were captured in flight and consisted of Hymenoptera (88%) and Diptera (12%, including cannibalism). During feeding, *Proctacanthus fulviventris* manipulated prey while hovering above its feeding site. There was no courtship prior to mating, which occurred in the male-over-female position. Females oviposited in the ground, and 1 to 6 eggs were recovered from each of seven ovipositions. Peak period for feeding, mating, and ovipositing was from 10:00 to 11:00 AM. Grooming was in much the same manner as other asilids. *Proctacanthus fulviventris* was preyed upon by three other species of robber flies (*P. brevipennis*, *Promachus bastardii*, and *Diogmites crudelis*).

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