J. Entomol. Res. Soc., 14(3): 91-109, 2012 *ISSN:1302-0250*

Ethology of *Proctacanthus brevipennis* (Wiedemann, 1828) (Diptera: Asilidae) in Northeastern Florida, U.S.A.

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ABSTRACT

During 5 weeks of observation, *Proctacanthus brevipennis* (Wiedemann, 1828) foraged from both the ground and vegetation, capturing and immobilizing most prey in flight. Identified prey came from six insect orders (Coleoptera, Diptera, Hymenoptera, Isoptera, Lepidoptera, and Orthoptera), with Coleoptera making up 59.7%. Mating occurred in the tail-to-tail position and oviposition was in the ground, typically in the shade of vegetation. This species exhibited a distinct daily rhythm of activity for feeding, mating, and oviposition. Grooming behavior resembled that described for other species of Asilidae. Habitat, resting behavior, and predators and parasites also are discussed.

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

INTRODUCTION

Nineteen of the 30 described species of robber flies in the genus *Proctacanthus* occur in the United States (Geller-Grimm, 2012). Despite the widespread occurrence of species in the genus, only the ethology of *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, with other publications limiting themselves to observations on only habitat and/or prey (*P. micans* in Dennis *et al*., 2009, 2010; Lavigne, 2002; Lavigne *et al*., 1994; *P. nearno* in Bromley, 1930, as *P. arno*; Lavigne, 2002; Lavigne *et al*., 1994). Information primarily on habitat and/or prey for other *Proctacanthus* species has been reported for, *P. brevipennis* (Wiedemann, 1828) (Bromley, 1923, 1934, 1946a and b, 1950; Conradi and Eagerton, 1914; Vestal, 1913); *P. coquilletti* Hine, 1911 (Lavigne *et al*., 1994); *P. duryi* Hine, 1911 (Bromley, 1931a, 1947); *P. fulviventris* Macquart, 1850 (Bromley, 1950); *P. heros* (Wiedemann, 1828) (Bromley, 1930, 1946a, 1950); *P. hinei* Bromley, 1928 [Baker and Fischer, 1975; Bouseman and Maier, 1977; Bromley, 1923, as *P. rufus*, 1931a, 1934, 1947; Hine, 1911, as *P. rufus;* James, 1938; Knisley and Hill, 2010, as *P. heinei* Gromley (i.e., *P. hinei* Bromley)]; *P. longus* (Wiedemann, 1821) (Bromley, 1934, 1950; Clauson, 1940; Davis, 1919; Lavigne *et al*., 1994); *P. milbertii* Macquart, 1838 (Baker and Fischer, 1975; Blanton, 1939; Bromley, 1930, 1931a, 1934, 1947, 1949, 1950; Hine, 1911; Hull, 1962; James, 1938; Joern and Rudd, 1982; Lavigne *et al*., 1994; Lavigne and

Pfadt, 1966; Rau and Rau, 1916; Riley, 1870, as *Asilus missouriensis*; Wallis, 1913; Walton, 1914; Williston, 1885); *P. nigriventris* Macquart, 1838 (Bromley, 1930, as *P. arno*, 1931b, 1950); *P. occidentalis* Hine, 1911 (Bromley, 1930); *P. philadelphicus* Macquart, 1838 (Bromley 1914, 1930, 1931a and b, 1946b, 1948; Lavigne *et al*., 1994); *P. rodecki* James, 1933 (James 1938; Lavigne and Pfadt, 1966); *P*. spp. (Bromley, 1928, 1930; Dennis *et al*., 2009, 2010; Dennis and Lavigne, 2007; Hull, 1962; Wood, 1981); and *P. rufus* Williston, 1885 (Bromley, 1930, 1931b, 1934, 1946a and b, 1950; Wagner *et al*., 2003).

This paper provides detailed information on the ethology of *P. brevipennis* in an area near the southern boundary of St. Augustine in northeastern Florida, U.S.A.

MATERIALS AND METHODS

Proctacanthus brevipennis is widely distributed in Florida in open, forested areas, on sand roads and, depending on location, generally occurs from March through July. Most observations were made from 25 April to 30 May 2011 in an approximate ¼ hectare storm water drainage basin between State Road 206 and the Moses Creek Conservation Area (MCCA) (Fig. 1). The author observed a large number of *P. brevipennis* during his preliminary survey of the area and selected the drainage basin and the nearby MCCA for study and prey collection.

The period of study was based on the time when *P. brevipennis* was most abundant in the storm water drainage basin and the MCAA. Days when the asilids were most common were from 26 April through 05 May when seven to twenty asilids per day were followed, each for up to 2.5 hours. Total number of hours of observation was approximately 107.

The study began with the observation of single flies for as long as possible in order to collect information on their various behaviors and diurnal activities. When sufficient data was gathered on their behavior, the author slowly walked through the storm water drainage basin 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. Prey that the author could not identify were sent for identification to the U.S. Department of Agriculture, Agricultural Research Service, Systematic Entomology Laboratory, Beltsville, Maryland, U.S.A. Prior to shipment, the prey were measured with a clear, plastic ruler to the nearest 0.5 mm.

Ovipositing females were observed for as long as they continued to exhibit oviposition behavior or until they were lost as they flew about the habitat. When a female ceased to oviposit or was lost, the oviposition site was dug up with a small hand shovel. The eggs were then visually separated from the soil. Oftentimes eggs were not found, but those that were recovered (from two ovipositions) were placed in 95% ethyl alcohol for later examination and measurement with the plastic ruler.

Temperature and wind are important environmental variables that determine the activities in which adult asilids engage. A hand held Taylor thermometer was used to

take air, and surface and subsurface ground temperatures. Wind speed was measured with a Dwyer Hand-Held Wind Meter.

RESULTS AND DISCUSSION

Habitat

The storm water drainage basin study area (Fig. 1) had 8 to 13 cm high carpet grass (*Axonopus* sp.; Poaceae) and Elliott's (white) milkpea (*Galactia elliottii* Nutt.; Fabaceae). Quite a bit of dead grass lay on the ground. Dense growth of vegetation surrounded the basin, including sand pine trees [*Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarg.); Pinaceae], live oak trees [*Quercus virginiana* (P. Mill.); Fagaceae], oak shrubs (*Quercus* spp.; Fagaceae), rusty lyonia ([*Lyonia ferruginea* (Walter) Nutt.); Ericaceae], and some saw palmetto [*Serenoa repens* (W. Bartram) Small); Arecaceae]. The soil type is sand to sandy loam.

Fig. 1. *Proctacanthus brevipennis* storm water drainage basin habitat.

In the nearby MCCA, *P. brevipennis* occurred primarily on sand roads and on vegetation near the roads that included carpet grass, Elliott's (white) milkpea, various species of oak shrubs, gallberry [*Ilex glabra* (L.) A. Gray); Aquifoliaceae], tar flower (*Bejaria racemosa* Vent.; Ericaceae), rusty lyonia, and rusty staggerbush or coastal plain staggerbush [*Lyonia fruticosa* (Michx.) G.S. Torr.); Ericaceae].

Bromley (1934) said that *P. brevipennis* occurred in Texas in habitats similar to *P. longus*, specifically sandy fields and pastures near larger water courses; whereas, Bromley (1946b) listed this species as occurring in Connecticut in sand plains or "oak openings". Bromley (1928) also made the general statement that *Proctacanthus* " inhabit dry fields or pastures, several being restricted to dry sandy plains."

Resting Behavior

Proctacanthus brevipennis 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, asilids would often turn so that one of their sides faced and was elevated to the sun. They also flattened themselves against the substrate, in particular if clouds obscured the sun or the ground temperature was less than 33˚C. *Proctacanthus brevipennis* typically started to move onto live vegetation when the substrate temperature exceeded 34 to 35˚C. Movement to live vegetation was complete by the time the substrate temperature had reached 38˚C. When moving to live vegetation, a *P. brevipennis* would often land on the shaded side of a vertical grass blade with its body at a 45 degree angle to the blade.

Dennis and Lavigne (1975) observed that asilids on the ground apparently attempt to maintain their body temperature by changing their position and flattening themselves against the ground. *Proctacanthus brevipennis* also maintains its body temperature by its position on the ground 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. According to Lehr (1958c) the expulsion of liquid from the anal opening is quite common in robber flies.

Foraging and Feeding Behavior

Proctacanthus brevipennis foraged from both the ground and vegetation. They foraged from the ground early in the morning and late in the afternoon when ground temperatures were less than 34 to 35˚C and air temperatures 35 cm above the ground ranged from 30 to 33˚C. 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. brevipennis* would often have its body at a 45 degree angle to the substrate that it was on and face the sun. This foraging attitude, or posture, presumably allowed the asilids to better see their prey because of backlighting. Similar observations for several species of asilids have been made by other investigators including Dennis *et al*. (1986), Hespenheide (1978), Hespenheide and Rubke (1977), Lavigne (1970b, 1971), Lavigne and Dennis (1985), and Melin (1923). In addition, it is assumed that the body held at a 45 degree angle allowed the asilids to better see potential prey with the 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. brevipennis* frequently made investigatory flights without making contact with potential prey and/or other *P. brevipennis.* Flights were for distances of 15 cm to 1.5 m from the asilid's original foraging position and 15 cm to 1 m above the ground. Investigatory flights are common for asilids (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.* (1978) indicated that investigatory behavior is probably necessary because some asilids 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, the asilids typically landed in a different location than the original foraging location. Even if *P. brevipennis* did not make investigatory flights they changed their foraging location 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 the sun was obscured by clouds. 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, asilids 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 brevipennis* made orientation flights within 1 m and 45 cm above the ground or moved to a new foraging site up to 7 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 asilids 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).

A few asilids captured potential prey and released them while still in-flight (e.g., Coleoptera, Scarabaeidae, *Melanocanthon* sp. probably *granulifer* Schmidt, 1920). Dennis and Lavigne (1975) commented that some species may capture and release prey because the asilids use both visual and other stimuli to select prey.

Proctacanthus brevipennis captured most of its prey in the air when the prey were within 1.5 m in front of, to the side of or slightly behind, and within 15 cm above the asilid’s foraging position; although some prey were captured up to 60 cm above its foraging position. The preference for this species to capture prey in flight was shown when a female turned to watch a *Strigoderma pygmaea* (Fabricius, 1798) (Coleoptera, Scarabaeidae) crawling on the ground 10 cm away. When the beetle flew approximately 2.5 cm and 2.5 cm above the ground, the female immediately attacked and captured the beetle.

Height and distance that asilids fly in a habitat has been shown to decrease when the wind blows (Dennis and Lavigne, 1975; Lehr, 1961). In the storm water drainage

basin wind typically gusted up to 9 km/hr. This did not appear to decrease the distances or heights that the asilids flew in the basin.

Having captured prey an asilid would generally hold onto it with all six tarsi, often while hovering, and insert its proboscis in the dorsum or right side of the prey's thorax with the prey's head underneath the asilid's head. This indicated that the asilid attacked prey from behind and above, or from the side. A few prey were not immediately subdued and the asilid would fall to the ground and hold onto the prey until it stopped moving.

The asilid usually inserted its proboscis in the anterodorsal part of the abdomen of a captured Coleoptera, and this generally resulted in the elytra remaining open or spread. Both Lehr (1958c) and Wichmann (1956) also commented on similar behavior.

Proctacanthus brevipennis often did not manipulate prey during feeding. When it did manipulate prey, the method depended on the prey's size. It manipulated relatively small prey such as *S. pygmaea*, with all six tarsi while hovering above the feeding site. Larger prey such as *Vespula maculifrons* (Buysson, 1905) (Hymenoptera, Vespidae; Fig. 2) and *Polacantha gracilis* (Wiedemann, 1828) (Diptera, Asilidae), were held against vegetation or the ground with the tarsi and were crawled on while the asilid reinserted its proboscis.

Fig. 2. Female *Proctacanthus brevipennis* with *Vespula maculifrons* as prey.

Proctacanthus brevipennis manipulated individual prey up to five times. Both *P. micans* (Dennis and Lavigne, 1975; Rogers and Lavigne, 1972) and *P. nearno* (Lavigne and Dennis, 1979) demonstrate similar methods of prey manipulation.

When asilids were feeding, most prey hung free from the asilid's proboscis without support by the tarsi. An asilid used its body to hold large prey against the ground or vegetation while grasping the dead vegetation or a grass blade with all six tarsi.

As researchers have observed for other species of robber flies, time spent feeding usually depends on prey length (Dennis and Lavigne, 1975; Lavigne and Dennis, 1975). Feeding on prey with an average length of 5.5 mm (e.g., *S. pygmaea*) took

approximately 13 minutes. Larger prey such as *V. maculifrons*, with an average length of 13 mm, took about 46 minutes. Length of time that *P. brevipennis* spent feeding on individual prey varied from 5 to 89 minutes, with an average of 24.3 minutes.

Male *P. brevipennis* captured prey that averaged slightly longer than those captured by females. Mean prey length for males was 9.6 mm (n = 18) with a range from 5.5 to 21.0 mm; whereas, for females it was 8.1 mm (n = 15) with a range from 5.0 to 15.0 mm. The overall mean prey length was 8.9 mm with a predator to prey ratio of 3.0. Mean predator to prey ratios for other species of robber flies range from 0.9 to 8.4 with a mean of 2.9 (Dennis, 1979; 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, an asilid discarded prey in one of three ways, (1) it dropped prey in flight as it moved to a new location; (2) it pushed prey off of its proboscis with the fore tarsi while it was still at the feeding site; or (3) it allowed prey to drop-off at the feeding site. The latter was most common for large prey such as *V. maculifrons*, *P. gracilis* and *P. brevipennis*. *Proctacanthus 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); *P. micans* usually pushed prey off its proboscis with the fore tarsi as it moved to a new location (Dennis and Lavigne, 1975).

Time between feedings (interfeeding time) varied between 0 and 14.5 minutes, with an average of 7.8 minutes. The 0 minute interfeeding time was for a flying male that dropped the prey on which it was feeding to immediately capture another prey.

One can calculate the theoretical number of prey an individual *P. brevipennis* could feed on in one day if we assume that: (1) it continually forages and feeds between 9:00 AM and 1:00 PM (the observed major period of foraging and feeding activity), and (2) it captures and feeds on prey every 32 minutes 6 seconds (based on the average feeding and interfeeding times). Thus, over a 4-hour period an individual asilid could feed on approximately 7 to 8 prey. Dennis and Lavigne (1975) calculated that *P. micans* could feed on approximately 6 to 7 prey per day. Other investigators have estimated that asilids feed on from 1 to 35 prey per day (Baker and Fischer, 1975; 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).

Prey

Proctacanthus brevipennis was selective in its choice of prey with Coleoptera making up 59.7% of the 62 identified prey (Table 1). Hymenoptera, Diptera, Lepidoptera, Orthoptera, and Isoptera made up 17.7%, 9.7%, 8.1%, 3.2%, and 1.6% of the prey, respectively. Lavigne *et al*. (1994) reported *P. brevipennis* feeding on Coleoptera, Heteroptera, Lepidoptera, Odonata and Orthoptera. Other species of *Proctacanthus* feed on a wide variety of prey from the orders Coleoptera, Diptera,

Hemiptera, Hymenoptera, 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 and Lavigne, 1975; Lavigne and Dennis, 1979; Lavigne *et al*., 1994; Rogers and Lavigne, 1972).

Table 1. Number and percent composition of orders of prey taken by *Proctacanthus brevipennis*.

	Male		Female		Unknown Sex		Total	
Order	Number	Percent	Number	Percent	Number	Percent	Number	Percent
Coleoptera	27	67.5	9	45.0	1	50.0	37	59.7
Diptera	5	12.5	1	5.0	0	0.0	6	9.7
Hymenoptera	5	12.5	5	25.0	1	50.0	11	17.7
Isoptera	1	2.5	0	0.0	0	0.0	1	1.6
Lepidoptera	1	2.5	4	25.0	0	0.0	5	8.1
Orthoptera	1	2.5	1	5.0	0	0.0	2	3.2
Totals	40	100.0	20	100.0	2	100.0	62	100.0

Proctacanthus brevipennis preyed on only two species of Coleoptera, *Epitragodes tomentosus* (LeConte, 1866) and *S. pygmaea*. The latter made up 56.6% of the total prey. Bromley (1923, 1946b), and McAtee and Banks (1920) reported *P. brevipennis* preying upon *Anomala* spp. (Coleoptera, Scarabaeidae).

The large number of Coleoptera in the storm water drainage basin and captured by *P. brevipennis* indicates that prey availability was a major factor in prey selection. Similar observations have been made for other asilids (Adamovic, 1963; Dennis and Lavigne, 1975; Lavigne and Bullington, 1999; Lavigne *et al*., 2000; Lavigne and Holland, 1969; O'Neill, 1992; Scarbrough and Norden, 1977). Shelly (1984) compared the prey of *Atractia marginata* Osten Sacken, 1887 with sticky trap samples of available prey. He found that the prey selected or foraging rate was directly related to prey abundance.

A number of asilids, including *Proctacanthus* spp. (Knisley and Hill, 2010; Lavigne, 1972, 1977; Wallis, 1913) prey on tiger beetles (Coleoptera: Cicindelidae). Conradi and Eagerton (1914) observed *P. brevipennis* preying on *Cicindela rufiventris* Dejean, 1825. At one location in the MCCA a large number of *C. trifasciata ascendens* LeConte, 1851 were present. Although the tiger beetles crawled and flew around *P. brevipennis*, none were taken as prey.

Proctacanthus brevipennis preyed upon four species of asilids as listed below. A male *P. brevipennis* also captured and released a fifth species, *Stichopogon trifasciatus* (Say, 1823).

Male and female *P. brevipennis* preyed on the same insect orders. However, more males were captured with prey than females. It is assumed that this was because in the population studied in the storm water drainage basin there appeared to be more males than females, and males had shorter combined average feeding and interfeeding times than females (30.6 minutes for males and 41.9 minutes for females). This is

interesting because numerous other investigators have reported collecting more female than male asilids 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).

Scarbrough (1981b) noted that for the population of *Eudioctria tibialis* (Banks, 1917) that he studied, males begin to emerge slightly earlier than females and this temporarily produced a larger number of males; females became more abundant in the mid- to late-phases of the flight season. This also was observed for *P. brevipennis* when from 26 April through 05 May there were 2.1 males per female, but there was never a large number of females compared to males.

The following is a list of prey taken by *P. brevipennis*. All prey were collected between 21 April and 21 June 2011 primarily in the storm water drainage basin; a few prey were collected in the Moses Creek Conservation Area (MCCA) and are so indicated. Number and sex (if known) of the predator is indicated following the prey record.

COLEOPTERA, Scarabaeidae: *Strigoderma pygmaea*, 27-IV-11 (♀), 28-IV-11 (5♂♂, 2♀♀, sex unknown], 2-V-11 (6♂♂, ♀), 3-V-11 (2♂♂), 4-V-11 (6♂♂, 3♀♀), 5-V-11 (8♂♂); Tenebrionidae: *Epitragodes tomentosus*, 26-IV-11 (♀), 4-V-11 (♀). DIPTERA, Asilidae: *Efferia tabescens* (Banks in Hine, 1919) MCCA, 21-VI-11 (♂); *Ommatius floridensis* Bullington and Lavigne,1984, 19-V-11 (♀); *Polacantha gracilis*, 26-IV-11 (♂), 2-V-11 (2♂♂), 10-V-12 (♀); *Proctacanthus brevipennis* , 28-IV-11 (♂), 6-IV-12 (♂), 30-IV-12 (♀); Sarcophagidae: unidentified, 27-III-12 (♂); HYMENOPTERA, Sphecidae: unidentified, 7-V-11 (♂), 3-III-12 (♀); Vespidae: *Vespula maculifrons*, 26-IV-11 (2♀), 2-V-11 (♂), 16-V-11 (♀), 17-V-11 (♀, sex unknown), 8-IV-12 (♀); unidentified, 3-V-11 (♂), 23-III-12 (♂), MCCA, 13-V-11 (♂), 31-V-11 (♀). ISOPTERA, unidentified (alate), 3-V-11 (♂). LEPIDOPTERA, Crambidae (Odontiinae): *Microtheoris ophionalis ophionalis* (Walker, 1859), 27-IV-11 (♀), 28-IV-11 (♂, ♀), 7-V-11 (♀); Gelechiidae: unidentified, 7-V-11 (♀); unidentified, 4-IV-12 (♀); ORTHOPTERA, Acrididae, Oedipodinae, *Arphia* sp. nymphs, 28-IV-11 (♂), 19-V-11 (♀).

Mating Behavior

Male *P. brevipennis* performed searching flights for receptive females with which to mate. Flights consisted of a male flying 5 to 7 m, 15 to 30 cm above the ground weaving in and out of the vegetation or in a vertical undulation. Similar searching flights have been reported for *P. micans*, *Scleropogon neglectus* (Bromley, 1931) and *Stenopogon inquinatus* Loew, 1866 (Dennis and Lavigne, 1975); *Efferia* spp. and *Promachus dimidiatus* Curran, 1927 (Lavigne and Holland, 1969); *Stenopogon heteroneurus* (Macquart, 1838) (Lehr, 1961), *Efferia varipes* (Williston, 1885) (Dennis and Lavigne, 1976a), and *Efferia frewingi* Wilcox, 1966 (Lavigne and Dennis, 1975). They also were reported by Hayat and Çalışkan (2003) for *Dasypogon irinelae*, but they were not recognized as searching flights.

As part of searching for females to mate with, males frequently flew up to investigate other *P. brevipennis*. They would then briefly come into contact, hover in front of or circle each other before landing on the ground or grass. Lavigne *et al*. (2009) indicated that the purpose of male-to-male encounters for *Mauropteron pelago* (Walker, 1849) was not clear. “They could represent cases where males mistake each other for females or prey (via visual cues) and the encounter is essentially a “test” and “rejection” of the other male. Alternatively, they may represent protection of mating and foraging sites, as has been demonstrated for *Laphria fernaldi* (Back) (Lavigne and Bullington, 2001).”

Proctacanthus brevipennis 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 tail-to-tail or male-over-female position. They did not remain in the latter position for more than about 15 seconds before assuming the tail-to-tail position (Fig. 3). Once in the tail-to-tail position the mating pair moved onto grass blades where the male usually had his head to the sky and the female’s head was pointed to the ground. The mated pair also often moved so that they were at a 90º angle to each other, but still in the tail-to-tail position.

Fig. 3. Mating pair of *Proctacanthus brevipennis* in tail-to-tail position.

The asilids were very nervous and easily disturbed during mating, and often flew to a height of 3 m above the ground and for distances of 5 to 7 m, to a new location. Within about 4 minutes of the completion of mating, the mated pair became more nervous and frequently adjusted their positions on the vegetation or flew to a new location. During one of these flights, the mating was terminated when the male released the female and both asilids flew away.

The author observed three complete matings that lasted 78, 81, and 111 minutes, with an average of 90 minutes. Matings occurred when the air temperature at the height of the mated pair on vegetation ranged from 28.9º to 39º C. *Proctacanthus micans* mated for 23 to 66 minutes with an average of 42 minutes (Dennis and Lavigne, 1975).

Both *P. micans* (Dennis and Lavigne, 1975) and *P. nearno* (Lavigne and Dennis, 1979) mate in the male-over-female position. Rogers and Lavigne (1972) indicated

that *P. micans* 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.

Oviposition

Like other species of *Proctacanthus* (Bromley, 1946b; Hine, 1911), *P*. *brevipennis* females have spines on their ovipositors and oviposit in the ground. Ovipositions occurred in the shade of vegetation or tree bark on the ground, unless the sky was cloudy, and then it was in more open areas. Dennis and Lavigne (1975) also observed *P. micans* ovipositing in the ground in the shade of vegetation.

Proctacanthus brevipennis females walked along the ground and probed with their ovipositors in order to find a suitable place to deposit their eggs. They then inserted their ovipositor in the ground so that the abdomen was buried almost to the thorax. In this position the female's abdomen was gently curved outward and her wings were folded over her abdomen. At the completion of oviposition, females swept the soil around the oviposition hole for 10 to 15 seconds with lateral movements of their ovipositor. During oviposition the females did not rhythmically raise or lower (i.e., tamping action) their bodies as has been observed for *P. micans* (Dennis and Lavigne, 1975). Temperatures under the soil surface where ovipositions occurred ranged from 33.9° to 45° C.

Average time for a complete oviposition, not including sweeping of the surface soil, was 48.4 seconds with a range from 30 to 84 seconds. One and three eggs were recovered from a 30- second and the 84-second oviposition, respectively. Eggs were creamy-white and oblong like those of *P. micans* (Dennis and Lavigne, 1975) and many other species of robber flies. The eggs ranged in length from 1.25 to 1.50 mm, with a mean of 1.38 mm; range in width was from 0.50 to 0.70 mm, with an average of 0.57 mm.

Grooming

Proctacanthus brevipennis groomed themselves in much the same way as reported for other asilids (Dennis, 1979; 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. Grooming of the face was usually preceded and followed by the rubbing together of the fore tarsi while the fore legs were extended and slightly elevated. The fore tarsi were moved back and forth along their long axis and then the dorsolateral part of the asilid's face was rubbed with the inside of either one or both front femora. During this sequence some flies slightly rotated their head.

Grooming of the abdomen, genitalia and wings was preceded by *P. brevipennis* rubbing their hind tarsi together. Hind tarsi were then turned inward to groom the abdomen and genitalia, and tops and bottoms of the posterior part of the wings. Grooming of wings and abdomen was always from anterior to posterior as observed by 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 oviposition.

Proctacanthus brevipennis never groomed its thorax. This may be why mites occurred on a number of asilid's dorsolateral part of the thorax. A mite also was on one female's left hind femur.

Daily Rhythm of Activity

The population of *P. brevipennis* in the storm water drainage basin exhibited a distinct diurnal or daily rhythm of activity between 9:00 AM and 6:00 PM for feeding, mating and oviposition (Fig. 4). During this time frame as the frequency of one behavior increased, the probability of other simultaneous behaviors decreased. Adamovic (1963) commented that in a population of robber flies particular activities dominate at different times of day and that at least mating activity is related to light, temperature and humidity in the habitat.

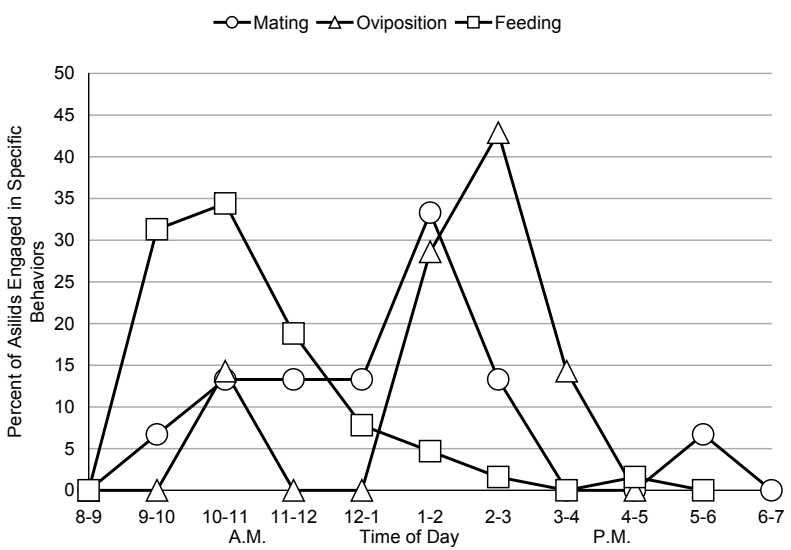

Fig. 4. Diurnal rhythm of activity for Proctacanthus brevipennis based on 15, 7 and 64 observations for mating, oviposition and feeding, respectively.

Peak period of feeding was from 9:00 to 11:00 AM, but some feeding occurred throughout the day until about 5:00 PM. Number of mating pairs observed was constant from 10:00 AM to 1:00 PM, and then peaked between 1:00 to 2:00 PM. Peak period for ovipostions occurred between 1:00 to 3:00 PM, with a smaller peak between 10:00 to 11:00 AM.

Each day from about 12:00 noon to 1:00 PM, the asilids were difficult to find and so their different behaviors showed a decrease. At this time the surface soil and air

temperatures generally exceeded 39.4ºC and 35.6ºC, respectively, and may reflect temperatures when *P. brevipennis* cannot "operate" as well as when they are lower. Morgan and Shelly (1988) showed that during midday, there was a difference in operative temperatures for *Promachus giganteus* Hine, 1911 and *Efferia texana* (Banks in Hine, 1911).

The storm water drainage basin was surrounded by pine and oak trees, and other vegetation, as described previously. Thus, the basin was mostly in shade until about 9:00 AM and after 7:00 PM. As the sun set in the evening, most asilids moved into vegetation surrounding the western side of the basin where the sunlight would reach earliest in the morning and be better suited for foraging. In the morning as more of the basin became exposed to the sun, the asilids moved further into the basin. Movement into an area during the day and out again at dusk or changing light conditions has been observed for a number of asilid species (Adamovic, 1963; Hespenheide and Rubke, 1977; Lavigne, 1970b; Lavigne and Holland, 1969; Musso, 1972; Scarbrough, 1981b; Scarbrough and Norden, 1977).

Because of the thickness of vegetation around the basin, the nocturnal resting position for *P. brevipennis* was not observed. Rau (1938) described the nocturnal resting position and showed a picture of *P. brevipennis* clinging to the side/underside of a plant with its wings bent down at right angles to its body. *Proctacanthus micans* and *Comantella fallei* (Back, 1909) rested on vegetation in a horizontal, upside-down position (Dennis and Lavigne, 1975). Rau and Rau (1916) indicated that *P. milbertii* has the same resting position on top of vegetation during the day and night, but grips its resting surface more firmly at night; whereas, Baker and Fischer (1975) said that *P. milbertii* in Michigan spent the night in or under dead leaves.

Predators and Parasites

Asilids of the same species are often observed to prey on each other (Lavigne *et al*., 2000). This occurred once for *P. brevipennis* when a male attacked another male who had just initiated mating with a female and the pair had not landed on the ground. Lehr (1961) indicated that cannibalism allowed *Stenopogon heteroneurus* to survive shortages of food, in particular after long periods of inclement weather.

Mites often are found on asilids (Lavigne *et al*., 2000), as was the case with *P. brevipennis*.

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

CONCLUSIONS

There exists detailed information on the ethology of only 2 of 19 species of robber flies in the genus *Proctacanthus* (*P. micans* and *P. nearno*) in the United States. This paper provides information on a third species, *P. brevipennis*. This species rested on the ground, on dead vegetation on the ground, and on the stems and leaves

of live vegetation. *Proctacanthus brevipennis* 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 from both the ground and vegetation in an attitude or posture that presumably allowed the asilids to better see prey. Most prey were captured in flight and consisted primarily of Coleoptera, followed by Hymenoptera, Diptera (including cannibalism), Lepidoptera, Orthoptera, and Isoptera. During feeding, *Proctacanthus brevipennis* manipulated prey while hovering above its feeding site or by crawling on larger prey. There was no courtship prior to mating, which occurred in the tail-to-tail position. Females oviposited in the ground, and 1 and 3 eggs were recovered from ovipositions that lasted 30 and 84 seconds, respectively. Peak period for feeding was from 9:00 to 11:00 AM, mating was from 1:00 to 2:00 PM, and oviposition from 1:00 to 3:00 PM. Grooming was in much the same way as other asilids.

ACKNOWLEDGEMENTS

The author would like to thank the staff of the St. Johns River Water Management District for the issuance of the Special Use Authorization that allows the study of robber flies in the Moses Creek Conservation Area (MCCA).

With gratitude, the author acknowledges the following Research Entomologists with the Systematic Entomology Laboratory (SEL), Agricultural Research Service, U. S. Department of Agriculture, Beltsville, Maryland, U.S.A. for their identification of prey: Matthew Buffington (Sphecidae, Vespidae); David A. Nickle (Acrididae); M. Alma Solis (Crambidae, Gelechiidae); and Natalia J. Vandenberg (Chrysomelidae, Scarabaeidae, Tenebrionidae; Isoptera). The SEL's Geoffrey B. White also is thanked for his handling of the prey and prompt Identification Reports.

I also thank the anonymous reviewers for their constructive comments on the manuscript.

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Received: May 31, 2012 Accepted: September 19, 2012