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Ethology of *Proctacanthus longus* (Wiedemann, 1821) (Diptera: Asilidae) in Northeastern Florida, U.S.A.

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ABSTRACT

Proctacanthus longus (Wiedemann, 1821) forage from the soil, dead vegetation on the soil (detritus), and vegetation, capturing and immobilizing prey in flight. Identified prey came from seven insect orders (Coleoptera, Diptera, Hemiptera, Hymenoptera, Neuroptera, Lepidoptera, and Orthoptera), with Diptera and Orthoptera making up 43.3 and 24.3%, respectively. Mating initially occurs in the male-over-female position and then the pair straightens out into the tail-to-tail position. Females oviposit in the soil, typically in the shade of vegetation. This species exhibits a daily rhythm of activity for feeding, mating, and ovipositing. Grooming behavior resembles 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

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INTRODUCTION

There are 19 described species of robber flies in the genus *Proctacanthus* in the United States of America (U.S.A.; Geller-Grimm, 2017). Of these species only the ethology of *P. brevipennis* (Wiedemann, 1828) (Dennis, 2012), *P. fulviventris* Macquart, 1850 (Dennis, 2015), *P. micans* Schiner, 1867 (Dennis & Lavigne, 1975; Rogers & Lavigne, 1972), and *P. nearno* Martin, 1962 (Lavigne & Dennis, 1979) have been described in detail. Dennis (2012) listed other publications that reported observations on habitat and/or prey for the other species.

This paper provides detailed information on the ethology of *P. longus* (Wiedemann, 1821) in the Moses Creek Conservation Area (MCCA) in St. Augustine in northeastern Florida, U.S.A. *P. longus* is 32-39 mm in length and its body is grayish to brownish pollinose. The proboscis is slender and the mystax is yellowish-white. The wings are uniform brown, wide and long, extending to at least the middle of the posterior margin of abdominal segment 7 (Figs. 1 and 2).

Fig. 1. Male *P. longus* on detritus on soil (Photograph: D.S. Dennis, 11.06.2012, 9:11 AM).

MATERIALS AND METHODS

P. longus is widely distributed in Florida and, depending on location, generally occurs from May through August. Observations were made over a period of 7 years, from: 21.06.2011-16.08.2011; 04.05.2012-05.07.2012; 01.07.2013-16.08.2013; 26.05.2014-29.07.2014; 27.05.2015-22.07.2015; 13.05.2016-27.07.2016, and 12.06.2017-17.08.2017. The author observed *P. longus* in the MCCA in the mowed edges of roads in upland mixed forest and mesic flatwoods vegetation communities, and in mowed scrub, scrubby flatwoods, and in sandhill vegetation communities, including their roads.

The times when *P. longus* was most abundant in the previously mentioned vegetation communities determined the periods of study. Up to 16 robber flies were observed per day with an average of three, with observations of individuals lasting

as long as 163 minutes. Total number of hours of observation equaled approximately 138, not including the time spent looking for *P*. *longus* to study.

Fig. 2. Female *P. longus* on saw palmetto leaflet (Photograph: D.S. Dennis, 22.05.2012, 8:44 AM).

During the study the author sat on the soil (mostly sand) or stood and observed single flies, mating pairs, and ovipositing females for as long as possible in order to collect information on their various behaviors and diurnal activities. In addition, after gathering sufficient data on their behavior, the author slowly walked through a study area and recorded the activities of as many flies as possible. During these walks data also was collected on prey selected and numbers of times specific behaviors occurred.

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

Ovipositing females were observed for as long as they exhibited oviposition behavior or until they moved out of sight. 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 eggs, if found, were removed. Those eggs that were recovered (from four ovipositions) were placed in 95% ethyl alcohol for subsequent examination and measurement to the nearest 0.1 mm. Equipment used was a Wild Heerbrugg M8 stereomicroscope with a transmitted light base, a 1.6x objective, and a 20x-focusing eyepiece for magnifications up to 160x. The eyepiece was equipped with a 5-mm/100-division reticle for measuring the eggs. The reticle was calibrated using a dual axis 1 mm/100 division/0.01 mm and linear 50-mm/500 division/0.1 mm multi-function scale/stage micrometer.

While in the field a hand held Taylor thermometer and a Cooper-Atkins DPP400W Digital Thermometer were used to take air, and surface and subsurface soil temperatures. A Dwyer Hand-Held Wind Meter measured wind speed.

RESULTS AND DISCUSSION

Habitat

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 scrub, scrubby flatwoods, and sandhill communities. The District also mows along roads and the sides or edges of roads in these communities, and the upland mixed forest and mesic flatwoods vegetation communities to facilitate access to the MCAA. Most *P. longus* were found and studied in the mowed scrub community (Fig. 3).

Fig. 3. *P. longus* habitat in mowed scrub vegetation community (Photograph: D.S. Dennis, 31.05.2014, 8:34 AM).

The *P. longus* study areas have the plants associated with the vegetation communities shown in Table 1. The dominant plants in all areas are 30 cm to 1 m tall saw palmetto, scrub oak, staggerbush (*Lyonia* spp), grasses (*Andropogon* spp.), and sedges (*Cyperus* spp.). Over time, the same plant species have invaded the mowed areas in the various habitats.

Bromley (1950) recorded that *P. longus* occurred in Florida in sandy fields and pastures, and on Panama City beach and dunes. Previously, Bromley (1934) had indicated that in Texas this species "Occurs in sandy fields and pastures near the larger water courses." Bromley (1928) made the general statement that *Proctacanthus* "…inhabit dry fields or pastures, several being restricted to dry sandy plains." Hull (1962) observed that *Proctacanthus* are found in "…rank grassland and shrubs on the edges of woodlands in swampy country and some prefer sandy river banks." Dennis (2012) found *P. brevipennis* primarily on sand roads in the MCCA, and *P. fulviventris* (Dennis, 2015) in a mowed scrub community and the mowed edges or roads in scrub, scrubby flatwoods, and upland mixed forest vegetation communities.

Table 1. Vegetation communities in which *P. longus* was studied in the Moses Creek Conservation Area.

Vegetation Type	Mowed Edges of Roads in Vegetation Communities		Mowed Vegetation Communities and Edges of Roads		
Family/Genus or Species/Common Name	Upland Mixed Forest	Mesic Flatwoods	Scrub	Scrubby Flatwoods	Sandhill
Agavaceae					
Yucca filamentosa L./ Adam's needle	—[1]	X	—	—	X
Amaranthaceae					
Froelichia floridana (Nutt.) Moq./cottonweed (plains snakeweed)	X	—	—	X	X
Annonaceae					
Asimina sp./pawpaw	X	X	X	X	X
Aquifoliaceae					
Ilex glabra (L.) A. Gray/ gallberry	—	X	X	—	—
Arecaceae					
Serenoa repens (W. Bartram) Small/saw palmetto	X	X	X	X	X
Asteraceae					
Carphephorus corymbosus (Nutt.) Torr. & A. Gray/ coastalplain chaffhead (Florida paintbrush)	—	X	X	X	—
Carphephorus odoratissimus (J. F. Hamel) H. Hebert/ vanillaleaf (Deer's tongue)	—	X	X	X	—
Erechtites hieraciifolius (L.) Raf. ex DC./ American burnweed (fireweed)	—	—	X	—	—
Eupatorium sp./fennel	X	X	X	X	X
Liatris gracilis Pursh/ slender gayfeather	X	—	—	—	—
Liatris tenuifolia Nutt./ shortleaf gayfeather	X	X	X	X	—
Pityopsis graminifolia (Michx.) Nutt./ narrowleaf silkgrass	X	X	—	X	X
Solidago spp./goldenrod	X	X	X	X	X
Cactaceae					
Opuntia humifusa (Raf.) Raf./ Eastern prickly pear cactus	X	X	X	X	X
Convolvulaceae					
Ipomoea sp./morning glory	—	—	—	—	X

Table 1. Continued.

Vegetation Type	Mowed Edges of Roads in Vegetation Communities		Mowed Vegetation Communities and Edges of Roads		
Family/Genus or Species/Common Name	Upland Mixed Forest	Mesic Flatwoods	Scrub	Scrubby Flatwoods	Sandhill
Cyperaceae					
Cyperus spp./flatsedge	X	X	X	X	—
Dennstaedtiaceae					
Pteridium aquilinum L. (Kuhn) var. *pseudocaudatum* (Clute) Clute ex A. Heller/ tailed bracken	X	X	X	X	X
Ericaceae					
Bejaria racemosa Vent./ tar flower (flyweed)	—	X	X	X	—
Ceratiola ericoides Michx./ Florida rosemary (sand heath)	—	—	X	—	—
Lyonia ferruginea (Walter)Nutt./rusty lyonia	X	X	X	X	X
Lyonia fruticosa (Michx.) G. S. Torr./ coastalplain staggerbush	—	—	X	—	—
Lyonia lucida (Lam.) K. Koch/fetterbush	X	X	X	X	—
Vaccinium corymbosum L./ highbush blueberry	—	X	X	X	—
Vaccinium myrsinitas Lam./ shiny blueberry	—	X	X	X	—
Eriocaulaceae					
Lachnocaulon spp./ bogbutton	—	—	X	X	—
Euphorbiaceae					
Cnidoscolus stimulosus Michx. Engelm & A. Gray/tread-softly	—	X	X	X	X
Fabaceae					
Centrosema virginianum (L.) Benth./spurred butterfly pea	—	X	—	—	X
Galactia elliottii Nutt./Elliott's (white) milkpea	X	X	X	X	X
Galactia spp./milkpea	X	—	X	—	—
Mimosa sp./sensitive plant	—	X	—	—	X

Table 1. Continued.

Vegetation Type	Mowed Edges of Roads in Vegetation Communities		Mowed Vegetation Communities and Edges of Roads		
Family/Genus or Species/Common Name	Upland Mixed Forest	Mesic Flatwoods	Scrub	Scrubby Flatwoods	Sandhill
Fagaceae					
Quercus incana W. Bartram/ bluejack oak	X	—	X	—	—
Quercus laevis Walter/turkey oak	—	—	—	—	X
Quercus virginiana (P. Mill.)/live oak tree	X	X	X	X	X
Quercus sp. /scrub oaks	X	X	X	X	X
Magnoliaceae					
Magnolia grandiflora L./southern magnolia	—	X	—	—	—
Pinaceae					
Pinus clausa(Chapm. ex Engelm.) Vasey ex Sarg./sand pine	X	X	X	X	X
Pinus elliottii Engelm./slash pine	X	X	X	—	—
Pinus palustris Mill./ longleaf pine	—	X	—	X	X
Poaceae					
Andropogon glomeratus (Walter) Britton et al./ bushy bluestem	X	X	X	X	X
Andropogon virginicus L./broomsedge bluestem	X	X	X	X	X
Aristida stricta Michx. Var. beyrichiana (Trin. & Rupr.) D. B. Ward/ wiregrass	X	X	X	X	X
Cenchrus sp./sandbur	—	X	X	—	—
Setaria spp./foxtail	X	X	X	—	—
Sorghastrum secundum (Elliott) Nash/lopsided indiangrass	—	X	—	—	—
Other grasses	X	X	X	X	X
Saururaceae					
Saururus cernuus L./ Lizard's tail	X	X	X	X	X

Table 1. Continued.

Vegetation Type	Mowed Edges of Roads in Vegetation Communities		Mowed Vegetation Communities and Edges of Roads		
Family/Genus or Species/Common Name	Upland Mixed Forest	Mesic Flatwoods	Scrub	Scrubby Flatwoods	Sandhill
Smilaceae					
Smilax auriculata Walter/earleaf greenbrier	—	X	X	—	X
Smilax bona-nox L./saw greenbrier vine	X	X	X	X	X
Smilax glauca Walter/ cat greenbrier	X	X	X	X	X
Vitaceae					
Vita rotundifolia Michx./muscadine	X	X	X	X	X
Zamiaceae					
Zamia integrifolia L./ Florida arrowroot (Coontie)	X	—	X	—	—

Footnote: — = not present; X = present.

Resting behavior

P. longus rests on the soil, on dead vegetation on the soil (detritus), and on the stems and leaves of live vegetation. In early morning, when on the soil or dead vegetation on the soil, individuals would flatten themselves against the substrate with their dorsal surface to the sun; turn so that one of their sides faced and was slightly elevated to the sun; or face the sun and elevate themselves on their fore tarsi so that their bodies are at a 45-degree angle. Flattening against the soil is particularly common when the surface soil temperatures are 28-30˚C or less and/or the wind is gusting 4.8-9.6 km/hr.

When resting on the soil or vegetation, individuals tend to groom themselves. At the same time, they generally ignore other insects flying by, even insects as close to the asilid as 15-30 cm.

P. longus generally started to move from the soil onto vegetation between 9:30 to 11:30 AM when the soil temperature reach 35-37˚C and the air temperature is 31-36˚C. When moving to vegetation to continue grooming or foraging, a *P. longus* would usually land on vegetation in the sun; whereas, if it moved to continue resting, it would land in the shade of vegetation with its body at a 45-degree angle, parallel to the vegetation, or vertical to the soil. After moving to vegetation, one male rested in the shade with its body at a 45-degree angle to a grass blade for 43 minutes. Both *P. brevipennis* (Dennis, 2012) and *P. fulviventris* (Dennis, 2015) show similar movement from the soil to vegetation as the day progresses and soil temperatures increase.

P. longus apparently maintain their body temperature by changing their position and flattening themselves against the substrate that they are on (in particular while on the soil), and moving to vegetation that is in shade. *Proctacanthus brevipennis*

(Dennis, 2012), *P. fulviventris* (Dennis, 2015), *P. nearno* (Lavigne & Dennis, 1979), and *P. micans* (Dennis & Lavigne, 1975) also maintain their body temperature by postural adjustments and microhabitat selection. Similar behavior is shown by many other species of robber flies (Dennis & Lavigne, 1975; Morgan, Shelly, & Kimsey, 1985; Morgan & Shelly, 1988).

While resting, abdominal pumping of the first one to two segments was observed in both male and female *P*. longus. This was observed for one male during feeding. In the laboratory *Promachus giganteus* Hine, 1911 pumped haemolymph into the abdomen to regulate thoracic temperatures (Morgan & Shelly, 1988). *P. longus* may exhibit similar behavior in the field to regulate its body temperature. Abdominal pumping or contractions during feeding generally have been attributed to the injection of proteolytic enzymes into prey and food pumping (Musso, 1968; Lavigne & Holland, 1969).

Foraging and feeding behavior

P. longus foraged from the soil, detritus on the soil, and from vegetation, often with their bodies at a 45-degree angle and facing the sun. Both *P*. *brevipennis* (Dennis, 2012) and *P*. *fulviventris* (Dennis, 2015) exhibited similar foraging behavior, and *P*. *micans* (Dennis & Lavigne, 1975) and *P*. *nearno* (Lavigne & Dennis, 1979) foraged from vegetation with their bodies at a 45-degree angle. These foraging postures presumably allow the robber flies to better see potential prey, and when they face the sun this may highlight potential prey by backlighting. Other authors have made similar observations for a number of species of robber flies (Dennis, 2012, 2015).

P. longus make flights around a forging position that are not directed at potential prey (i.e., orientation flights) and flights directed at potential prey without coming into contact with them (i.e., investigatory flights). Over periods of 9-18 minutes (average 13.5 minutes), individuals made orientation or investigatory flights 3-8 times (average 5 times). As part of an investigatory flight, often times the robber fly would follow or hover near the potential prey. *P. longus* also make foraging flights when they hit or capture and release potential prey.

Orientation flights took place within 2.5 cm-13.7 m (average 1.6 m) of an individuals foraging location. Investigatory flights were for distances of 5.0 cm-2.1 m (average of 74.0 cm) behind, above, to the side of or in front of a foraging position, and 5.0 cm-1.2 m (average 45.5 cm) above the soil.

The majority of *P. longus* foraging flights are made in front of an individual's foraging location, but they also take place to the side or behind a foraging location. Foraging flights occur from 5.0 cm-3.0 m (average 73.7 cm) around an individual's location and are conducted 5.0-75.0 cm (average 40.6 cm) above the soil.

After orientation, investigatory, and foraging flights, individuals often re-land at or near (within 15.0 cm) their starting location. If they move to a new foraging location, it is 22.9 cm -6.1 m (average 3.5 m) from its original location. Robber flies may move to new foraging locations to increase the probability of finding prey (Dennis, 2016).

P. longus captured all of its prey in the air when the prey were within 12.7-91.4 cm (average 54.4 cm) in front of, to the side of or behind its foraging location, and

within 15.0-61.0 cm (average 31.8 cm) above the soil. *Proctacanthus fulviventris* also captured all of its prey in flight; whereas, *P. brevipennis* (Dennis, 2012), *P. micans* (Dennis & Lavigne, 1975), and *P. nearno* (Lavigne & Dennis, 1979) captured most of their prey in flight.

When capturing prey, *P. longus* would either immediately insert its proboscis in the dorsal or dorsolateral part of the prey's thorax or hover and manipulate the prey with all six tarsi before inserting its proboscis. After initially landing on soil or vegetation in the sun, the asilids would generally then fly to the shade of nearby vegetation to feed.

Most *P. longus* move to a new location one to four times while feeding on prey. When they move it is to a location up to 1.8 m from the previous location, and it is often from an area in the sun to the shade of vegetation.

During feeding, *P. longus*, (1) did not manipulate prey, (2) manipulated prey in a hover above the feeding site, or (3) held prey against vegetation and crawled on them before reinserting their proboscises. In general, smaller prey [e.g., 11.5 mm long *Blauta falli* Brown, 1936 (Coleoptera: Elateridae)] were not manipulated or were manipulated in a hover; whereas, larger prey [20 mm long *Mydas maculiventris* Westwood, 1835 (Diptera: Mydidae)] were crawled on. *Proctacanthus fulviventris* manipulated prey in a hover above the feeding site (Dennis, 2015). *Proctacanthus brevipennis* (Dennis, 2012), *P. micans* (Dennis & Lavigne, 1975; Rogers & Lavigne, 1972), and *P. nearno* (Lavigne & Dennis, 1979) manipulate prey during a hover and held larger prey against the soil or vegetation and crawl on them before reinserting their proboscises.

When *P. longus* were feeding, prey less than 13 mm long generally hung free from the asilid's proboscis without support by the tarsi or being held against vegetation. For longer prey greater than approximately 18 mm, an asilid used its body to hold prey against vegetation while grasping the vegetation with all six tarsi.

Only four *P. longus* complete feedings were observed and these ranged from 17-119 minutes with an average of approximately 60 minutes. Based on this limited data, the time spent feeding depended on prey length. *Blauta falli* with a length of 11.5 mm was fed on for 52 minutes and *Mydas maculiventris* with a length of 20 mm was fed on for 119 minutes. Other researchers also have observed that for a number of robber fly species the time spent feeding usually depends on prey length (Dennis, 2016).

Male *P. longus* captured prey that were slightly longer than those captured by females. Mean prey length for males was 19.8 mm (n=12) with a range from 6.6-32.0 mm; whereas, for females it was 18.5 mm (n=14) with a range from 5.5-31.0 mm. The overall mean prey length was 19.1 mm with a predator to prey ratio of 1.7:1.0 which indicates that *P. longus* was between 1.5 to 2 times as large as its prey. Mean predator to prey ratios for *P. brevipennis* (Dennis, 2012), *P. fulviventris* (Dennis, 2015), and *P. micans* (Dennis & Lavigne, 1975), were 3.0:1.0, 1.9:1.0, and 2.0:1.0, respectively. Mean predator to prey ratios for other species of robber flies range from 0.9:1.0 to 8.4:1.0 (Dennis, 2016) with a mean of 2.9:1.0.

At completion of feeding, each individual *P. longus* 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 one or both fore tarsi while it was still at the feeding site; (3) it allowed prey to drop-off its proboscis at the feeding site; or (4) it dropped prey during a hover at the feeding site Other species of *Proctacanthus* use similar methods to discard prey (Dennis, 2015). In addition, *P. micans* pushed prey off its proboscis with the fore tarsi during a flight to a new location (Dennis & Lavigne, 1975).

Interfeeding times (time between feedings) for *P. longus* were extremely difficult to obtain because of the speed and distance flown by individuals after feeding. Additionally, the asilids tended to be lost to sight as they weaved in and out of vegetation. Consequently only one partial interfeeding time of 44 minutes was recorded.

One can calculate the theoretical number of prey an individual *P. longus* could feed on in one day if we assume that: (1) it continually forages and feeds between 9:00 AM and 3:00 PM (the period when individuals were found with prey), and (2) it captures and feeds on prey every 104 minutes (based on the average feeding time and the one partial interfeeding time). Thus, over a 6-hour period an individual could feed on approximately 3 to 4 prey. Dennis (2012, 2015) estimated 7 to 8 and 3 to 4 prey per day for *P. brevipennis* and *P*. *fulviventris*, respectively. Dennis & Lavigne (1975) calculated that *P. micans* could feed on approximately 6 to 7 prey per day. Other investigators have estimated that robber flies feed on from 1 to 35 prey per day (Dennis, 2016).

P. longus feeding on fewer prey per day than many other species of robber flies may be because they have longer feeding and interfeeding times and they feed on larger prey as shown by the lower predator to prey ratio. *Proctacanthus micans* (Dennis & Lavigne, 1975) also had a low predator to prey ratio (2.0:1.0), but it had average shorter feeding (46 minutes) and interfeeding times (21 minutes) than *P*. *longus*.

Prey

P. longus fed on Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Neuroptera, and Orthoptera. However, the majority of prey was Diptera (43.3%) and Orthoptera (24.3%) (Table 2). Other researchers record *P. longus* feeding on Diptera, Hemiptera (Homoptera), Hymenoptera, Lepidoptera, Odonata, and Orthoptera (Clauson, 1940; Bromley, 1934, 1950; Lavigne, Nelson, & Schreiber, 1994).

Both *P. brevipennis* and *P. fulviventris* occur in some of the same habitats with *P. longus*. Dennis (2012) reported *P. brevipennis* feeding on six insect orders (Coleoptera, Diptera, Hymenoptera, Isoptera, Lepidoptera, and Orthoptera); whereas, he (2015) indicated that *P. fulviventris* fed on only Diptera and Hymenoptera.

Male and female *P. longus* generally fed on the same insect orders and approximately the same number of prey was collected for both sexes. However, many investigators have reported collecting more females than males with prey (Dennis, 2016). For *P. brevipennis* and *P. rufus* Williston, 1885, Bromley (1923) attributed this to the females being "…larger and more powerful than the males…"

Table 2. Number and percent composition of orders of prey captured by *P. longus*.

	Male		Female		Total	
Order	Number	Percent	Number	Percent	Number	Percent
Coleoptera	2	11.8	2	10.0	4	10.8
Diptera	9	52.8	7	35.0	16	43.3
Hemiptera	1	5.9	0	0	1	2.7
Hymenoptera	2	11.8	3	15.0	5	13.5
Lepidoptera	0	0	1	5.0	1	2.7
Neuroptera	1	5.9	0	0	1	2.7
Orthoptera	2	11.8	7	35.0	9	24.3
Totals	17	100.0	20	100.0	37	100.0

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

COLEOPTERA, Elateridae: *Blauta falli* Brown, 1936, 13.06.2012 (1 ♂), 10.06.2014 (1 ♂, 1 ♀), 30.06.2014 (1 ♂). Scarabaeidae: *Melanocanthon* sp. prob. *granulifer* (Schmidt, 1920), 29.06.2012 (1 ♀). DIPTERA, Asilidae: *Efferia tabescens* (Banks, 1872), 17.06.2014 (1 ♀), 17.08.2017 (1 ♀); *Polacantha gracilis* (Wiedemann, 1828), 06.06.2014 (1 ♀); *P. longus,* 07.05.2012 (1 ♀), 11.07.2017 (1 ♂); *Proctacanthus rufus* Williston, 1885, 09.07.2015 (1 ♀); *Promachus bastardii* (Macquart, 1838), 20.07.2017 (1 ♂); unidentified, 30.06.2014, (1 ♂). Mydidae: *Mydas maculiventris* Westwood, 1835, 11.06.2012 (1 ♀), 04.06.2014 (1 ♂), 10.06.2014 (1 ♂, 1 ♀), 12.06.2014 (1 ♂), 13.06.2014 (2 ♂♂), 16.06.2014 (1 ♂). HEMIPTERA, Heteroptera: unidentified, 14.06.2012 (1 ♂). HYMENOPTERA, Apidae: *Bombus* sp., 03.07.2014 (1 ♀), 18.07.2014 (1♀). Formicidae: *Tetramorium* sp., 12.06.2012 (1♂). Scoliidae: unidentified, 20.06.2012 (1 ♂). Unidentified: 07.05.2012 (1 ♀). LEPIDOPTERA: Blastobasidae, *Holcocera immaculella* (McDunnough, 1930), 02.07.2015 (1 ♀). NEUROPTERA, Myrmeleontidae: *Myrmeleon* sp., 29.06.2012 (1 ♂). ORTHOPTERA: Acrididae, *Chortaphaga australior* Rehn and Hebard, 1911, 27.05.2015 (1 ♀); *Orphulella pelidna* (Burmeister, 1838), 3-VI-14 (1 ♂); *Psinidia fenestralis* (Serville, 1839), 25.07.2017 (1 ♀); *Spharagemon crepitans* (Saussure, 1884), 11.06.2014 (1 ♀); unidentified, 04.06.2014 (1 ♀), 07.07.2014 (1 ♀), 15.07.2014 (1 ♀), 11.07.2017 (1 ♂), 01.08.2017 (1 ♀).

Mating behavior

Male *P. longus* performed searching flights for receptive females with which to mate. Flights consisted of males making one to five vertical undulations as they flew a straight or zigzag pattern above vegetation or they weaved in and out of vegetation. They flew for distances of 1-12 m and 7.5 cm-2.4 m above the soil. Male searching flights in vertical undulations have been reported for *P. brevipennis* (Dennis, 2012), *P. fulviventris* (Dennis, 2015), and *P. micans* (Dennis & Lavigne, 1976). One male *P. longus* buzzed his wings during his searching flights and a few males had their abdomens slightly curved up without buzzing their wings.

As part of searching for females with which to mate, males frequently flew up to investigate other male *P. longus* without coming into contact. A few males also would either briefly hover in front of or circle each other and sometimes come into contact before landing on the soil or vegetation.

P. longus usually initiated matings in-flight when the male would land on the dorsum of the female's thorax and then clasp the female's genitalia. One male grasped and released a female in flight when she played dead (i.e., thanatosis) and then fell to the soil where she remained for 30 seconds before flying off. Another male landed on the dorsal surface of a female resting on a dead saw palmetto leaflet, approximately10 cm above the soil. The female immediately fell to the soil on her back with her legs extended and bent inward at the joints between the femora and tibiae. She remained in this position for 149 seconds, then stood up and flew off. A female also played dead when captured in a small jar. Dennis & Lavigne (1976) commented that when female *Efferia varipes* [(Williston, 1885); as *Erax*)] played dead, "…the males did not receive the necessary stimuli to continue mating attempts."

After mating started, the pair would fly in the male-over-female position to nearby vegetation and land up to 2.5 m above the soil (e.g., on the trunk of a live oak tree), in the shade of surrounding vegetation 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. The wings of at least the female were usually spread at a 30 to 45-degree angle to her body. The female's wings in this position usually passed between the male's mid and hind legs so that the male's mid tibiae were over the female's wing bases. One female's wings passed over the male's mid and hind legs. The male's wings were either closed or intermittently, briefly opened to a 30 to 45 degree angle to his body. The males fore tarsi rested on the female's eyes/head, on the anterior part of her thorax or on vegetation. The male's mid tarsi held on to the female's thorax or on to the anterior part of her abdomen. The male's hind tarsi held on to the females abdomen or his hind legs passed around the female's abdomen with the hind tarsi holding onto vegetation.

Fifteen partial matings and two complete matings were observed. The mating pairs generally remained in the male-over-female position for 10-52 minutes and then assumed the tail-to-tail position while in flight to another location on vegetation (Fig. 4). The female of one mating pair appeared agitated and after being in the male-over-female position for 5 minutes, she initiated flight and the pair straightened out in to the tail-to-tail position. When in the tail-to-tail position, both the male and female periodically had their wings spread at 30 to 45-degree angles, although the previously mentioned agitated female held her wings straight down at a 90-degree angle to her body.

Fig. 4. Mating pair of *P. longus* in the tail-to-tail position (Photograph: D.S. Dennis, 16.06.2014, 2:27 PM).

The two complete matings lasted 116 minutes and 106 minutes. Matings occurred when the air temperature at the height where the mating pair rested on vegetation ranged from 28.5-32.5ºC (average 30.1ºC) in the shade and 29.5-33.5ºC (average 31.4ºC) in the sun. *Proctacanthus brevipennis* mated for 78 to 111 minutes with an average of 90 minutes (Dennis, 2012); *P. fulviventris* mated for 30 to 63.5 minutes with an average of 40.6 minutes (Dennis, 2015); and *P. micans* mated for 23 to 66 minutes with an average of 42 minutes (Dennis & Lavigne, 1975).

Proctacanthus fulviventris (Dennis, 2015) and *P. micans* (Dennis & Lavigne, 1975) mated in the male-over-female position. *Proctacanthus nearno* started mating in the male-over-female position and shortly after the initiation of mating assumed the tail-to-tail position (Lavigne & Dennis, 1979). *Proctacanthus brevipennis* mated in the tail-to-tail position (Dennis, 2012).

At the completion of mating, like *P. fulviventris* (Dennis, 2015), male *P. longus* 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 mating, females did not flex or stroke their abdomen such as was observed for two matings of *P. fulviventris* (Dennis, 2015).

Oviposition behavior

The females of all described species of *Proctacanthus* (Bromley, 1946; Hine, 1911) have spines (acanthophorites) on their ovipositors and oviposit in the soil. Female *P. longus* ovipositions occurred in the soil, often in sugar sand (fine silt made up of ultrafine mineral sand mixed with a large percentage of organic granules), in the shade of vegetation (Fig. 5). *Proctacanthus brevipennis* (Dennis, 2012), *P. fulviventris* (Dennis, 2015), and *P. micans* (Dennis & Lavigne, 1975), also oviposit in the soil in the shade of vegetation.

Fig. 5. Female *P. longus* withdrawing her abdomen from oviposition hole in sugarsand (Photograph: D.S. Dennis, 22.07.2013, 10:01 AM).

Seventeen ovipositions were observed. Air temperatures 30 cm above the oviposition sites in the shade ranged from 29.0-37.0°C with an average of 33.6°C. In comparison, air temperatures in the sun ranged from 32.0-33.0°C with an average of 32.7°C. Soil surface temperatures at the oviposition sites ranged from 29.0-36.0°C with an average of 33.8°C; temperatures beneath the surface of the soil where ovipositions occurred also ranged from 29.0-36.0°C with an average of 33.7°C.

P. longus females either landed on the soil and immediately inserted their ovipositors into the soil or walked along the soil and probed with their ovipositors in order to find a suitable place to deposit their eggs. They inserted their ovipositors into the soil with a lateral action for up to 38 seconds with an average of 20 seconds. One female exhibited a tamping action while inserting her ovipositor. The actual deposition of eggs took 69 to 135 seconds with an average of 107 seconds. Following deposition of eggs, females withdrew their ovipositors from the soil with a sweeping action that continued on the soil surface around the oviposition hole for 25 to 183 seconds, with an average of 114 seconds. Average time for complete ovipositions was 240 seconds with a range from 211 to 276 seconds.

Like *P. fulviventris* females (Dennis, 2015), the depth that a *P. longus* female inserts her abdomen in the soil depends on the dryness of the soil and/or the amount of organic matter/roots in the soil. In dry soil a female would typically insert her abdomen in to the soil to about 1/2 its length.. In this position the female's abdomen was gently curved outward and her wings were folded over her abdomen, often with the wing tips buried in or touching the soil.

In damp soil, following a rain when the soil was presumably more compacted, or soil-containing lots of organic matter/roots, a female would barely insert her abdomen into the soil. The female then kept her wings folded over her abdomen and the tips were not buried in the soil.

The length of time for depositing eggs, withdrawing ovipositors and sweeping the soil around the oviposition hole was about the same in dry and damp soil. Dennis (2015) also observed this for *P. fulviventris*.

One female *P. longus* oviposited four times over a 26-minute period before being lost to sight. Female *P. fulviventris* oviposited up to five times over a 15 to 20 minute period (Dennis, 2015). Rogers & Lavigne (1972) observed a female *P. micans* oviposit six times over 31 minutes.

Two to six eggs in a "packet" were recovered from each of four *P. longus* ovipositions. For these ovipositons more eggs (four and six eggs) were deposited in damp than dry soil (two eggs).

Eggs are shiny, glistening white to creamy-white, and are similar to those of many other species of robber flies (Dennis, Barnes, & Knutson, 2013) including, *P. brevipennis* (Dennis, 2012), *P. micans* (Dennis & Lavigne, 1975), and *P. fulviventris* (Dennis, 2015). The eggs of *P. longus* range in length from 2.0-2.6 mm, with an average of 2.3 mm; range in width is from 0.7-1.2 mm, with an average of 0.9 mm. These are the same dimensions as the eggs of *P. fulviventris* (Dennis, 2015).

Grooming

P. longus groomed themselves in much the same way as reported for other species of *Proctacanthus* and robber flies in general (Dennis, 2012, 2013, 2015; Dennis & Lavigne, 1975). They used the fore legs to groom their faces, and the hind legs for grooming their wings, abdomen and genitalia. Sometimes *P. longus* would groom their forelegs prior to rubbing 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.

P. longus often rub their hind tarsi together prior to grooming the abdomen, genitalia, and wings. They then curve their abdomen down up to a 90-degree angle, and groom the abdomen, genitalia, and tops and bottoms of the wings with their hind tibiae and proximal part of the tarsi. Generally they groom the posterior 1/2 of the abdomen and often their wings when they are slightly spread. Grooming of the wings and abdomen was always from anterior to posterior as observed for *P. brevipennis* and *P. fulviventris* by Dennis (2012, 2015).

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

P. longus never groomed its thorax as was observed for *P. fulviventris* (Dennis, 2015).

Daily rhythm of activity

P. longus exhibited a diurnal or daily rhythm of activity between 9:00 AM and 3:00 PM for mating, ovipositing, and feeding (Fig. 6). Most of these behaviors occurred between 9:00 AM to 2:00 PM with 93.3%, 94.2%, and 97.3% for mating, ovipositing, and feeding, respectively.

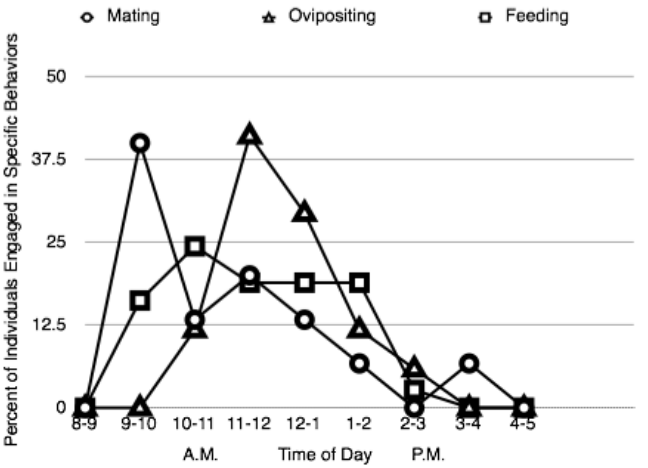

Fig. 6. Daily rhythm of activity of *P. longus* based on 15, 17, and 37 observations for mating, ovipositing, and feeding, respectively.

The number of mating pairs peaked early in the day between 9:00 to 10:00 AM, with a smaller peak from 11:00 AM to 12:00 noon. Also, ovipositing peaked during the latter time period. Both mating and ovipositing declined from 10:00 to 11:00 AM when feeding peaked. Then, from 12:00 noon to 2:00 PM more *P. longus* engaged in feeding than mating and ovipositing. After 3:00 PM all three behaviors generally steadily declined.

Dennis & Lavigne (1975) observed that most of the species of robber flies they studied engaged in feeding before their peak periods of mating and ovipositing. This also was the case for *P. brevipennis* (Dennis, 2012), but not for *P. fulviventris* (Dennis, 2015) or *P. longus*.

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, both *P. longus* and *P. fulviventris* (Dennis, 2015) continued to forage, mate, and oviposit. This may be because as long as air and soil temperatures are high enough, these species continue with their normal behaviors.

Predators and parasites

Both male and female *P. longus* preyed on males. One male grabbed another male in flight and the pair fell to the soil where they separated facing each other. They then quickly grabbed each other and one of the males inserted his proboscis in the left side of the other male's thorax.

Two female *P. bastardii* preyed on male *P. longus*. Also, a female *Diogmites crudelis* Bromley, 1936 preyed upon a female *P. longus.*

After a mating pair of *P. longus* straightened out in the tail-to-tail position on the trunk of a live oak tree, a regal jumping spider (Salticidae: *Phidippus regius* C.L. Koch, 1846) captured the female. When the author captured the spider, the male *P. longus*

took flight with the dead female hanging behind him. The male did not release the female until the author captured the pair and took the dead female.

Mites are often found on robber flies (Lavigne, Dennis, & Gowen, 2000), in particular on their thorax, but no mites were found on *P. longus.*

There are a number of ants (Formicidae, *Formica* spp. and *Solenopsis invicta* Buren, 1972) in the same habitats as *P. longus*. When the ants crawl on the asilids' tarsi, the asilids would shake their tarsi and then usually either walk or fly to a new location. One male stood up on its tarsi so that the ants could walk underneath and another male buzzed his wings when disturbed by ants.

Lizards may attack robber flies (Lavigne et al, 2000). In the MCCA the six-lined racerunner [*Cnemidophorus sexlineatus* (Linnaeus, 1766)] is very common and one caused a female *P. longus* to move to a new location. Racerunners are known to be insectivorous but they did not attack *P. longus*.

CONCLUSIONS

There exists detailed information on the ethology of only four of 19 species of robber flies in the genus *Proctacanthus* (*P. brevipennis*, *P. fulviventris*, *P. micans*, and *P. nearno*) in the United States. This paper provides information on a fifth species, *P. longus*. This species rested on the soil, on dead vegetation on the soil, and on the stems and leaves of live vegetation. *P. longus* maintains its body temperature by positioning itself on the soil or in the shady side of vegetation, depending on the air and soil temperature, and location of the sun. Foraging is from the soil, detritus on the soil, and from vegetation in an attitude or posture that presumably allows the asilids to better see prey. All prey are captured in flight and consist of Coleoptera (10.8%), Diptera (43.3%, including cannibalism), Hemiptera (2.7%), Hymenoptera (13.5%), Lepidoptera (2.7%), Neuroptera (2.7%), and (Orthoptera 24.3%). During feeding, *P. longus* sometimes did not manipulate prey, manipulated prey while hovering above its feeding site or held prey against vegetation and crawled on them before reinserting their proboscises. There was no courtship prior to mating, which occurrs in the male-over-female position and then the tail-to-tail position. Female's oviposite in the soil, and 2 to 6 eggs were recovered from each of four ovipositions. Peak period for mating is from 9:00 to 10:00 AM, feeding is from 10:00 to 11:00 AM, and ovipositing was from 11:00 AM to 12:00 noon. Grooming was in much the same manner as other asilids. Two other species of robber flies (*Promachus bastardii* and *Diogmites crudelis*), and a regal jumping spider (Salticidae: *Phidippus regius*) preyed on *P. longus*.

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