

Ethology of *Prolepsis tristis* (Walker, 1851) (Diptera: Asilidae) in Northeastern Florida, U.S.A.

D. Steve DENNIS

1105 Myrtle Wood Drive, St. Augustine, Florida 32086-4838, U.S.A.
e-mail: dstevedennis@msn.com; ORCID ID: 0000-0002-4832-4026

ABSTRACT

Prolepsis tristis (Walker, 1851) foraged from vegetation, capturing prey in flight and immobilizing them in flight or at the feeding site. Seven of the 10 prey were instances of cannibalism with females preying on other females and one male. Mating occurs in the tail to tail position. Female oviposition is in the soil. Feeding and mating peaks are from 10:00-11:00 AM, with two smaller peaks in the afternoon from 1:00-3:00 PM and 3:00-4:00 PM, respectively. Grooming behavior did not occur often and was brief, but resembles that of other species of Asilidae. Morphology, habitat, flight patterns, resting behavior, and predators and parasites also are discussed.

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

INTRODUCTION

Prolepsis is predominantly a genus of Neotropical robber flies with 17 species (Geller-Grimm, 2019). *Prolepsis tristis* (Walker, 1851) is the only Nearctic species and is found in about the southern half of the United States from California to Missouri and North Carolina south to Texas and Florida, as well as in Mexico (Fisher & Wilcox, 1997; Geller-Grimm, 2019). Despite the relatively widespread distribution of *P. tristis*, limited information has been published on this species.

This paper provides information on the ethology of *P. tristis* in the Moses Creek Conservation Area (MCCA) in St. Augustine in northeastern Florida. The main behaviors described are flight patterns, resting, foraging and feeding, courtship and mating, oviposition, grooming, and daily rhythm of activity. Male and female morphology, prey, and predators and parasites are also discussed.

MATERIALS AND METHODS

Prolepsis tristis is a widely distributed species in Florida, generally occurring from May into October. In the MCCA observations were made over nine field seasons: 01-14.09.2011; 16-31.08.2012; 12.09.2013; 28.07.2014-09.10.2014; 19.08.2015-04.09.2015; 13-17.05.2016; 15-30.08.2017; 05-07.09.2018; and 21.05.2019-04.10.2019. Some years had shorter periods of study because of inclement weather and low populations of flies.

Prolepsis tristis was studied when it was most abundant in the Moses Creek floodplain marsh and mesic flatwoods vegetation communities. Observations involved an average of 3 individuals per day, each for up to 89 minutes. Total number of hours of observations equaled approximately 97, not including the many hours searching for individuals or populations of *P. tristis* to observe.

Prolepsis tristis was studied by the author sitting or standing and observing single flies for as long as possible in order to collect information on their various behaviors and diurnal activities. The author also slowly walked through a study area and observed the activities of a number of flies, primarily to collect prey and to locate mating pairs and ovipositing females.

Collected prey was placed in glass vials with a label indicating the sex of the predator, 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 (SEL), Beltsville, Maryland, U.S.A. for identification. Prior to shipment, prey was measured with a clear, plastic ruler to the nearest 0.5 mm.

While in the field, a hand-held Taylor thermometer and/or a Cooper-Atkins DPP400W Digital Thermometer were used to take air, surface and subsurface ground temperatures. A Dwyer Hand-Held Wind Meter measured wind speed and a UYIGAO Digital Light Meter (UA-962) measured light levels.

RESULTS AND DISCUSSION

Morphology

Proleptis tristis is 14-28 mm long and is dimorphic with the male and female differently colored (Fig. 1). In the MCCA the overall color of males is black to dark reddish brown with four variations in color observed on the abdominal segments as follows, (1) all black abdomen; (2) segments 2 and 3 with circular faint white to triangular bright white spots laterally; (3) in the bright white forms, the dorsal apex of the base of the triangle runs toward the mid-dorsal line, often coalescing there; (4) segments 4 or 5-7 mostly dorsally and laterally orangish to reddish brown with similar dorsal lighter spots on segments 2 or 3; (5) mesonotum of thorax reddish brown and an abdomen that is entirely black except the sides of segment 2 and the lateral posterior margins of segment 3, which are dark reddish brown.



Fig. 1. Mating pair of *Proleptis tristis* in the tail-to-tail position with the female left and male right (Photograph: D.S. Dennis, 25 August 2015, 11:48 AM).

Females are yellowish brown to reddish brown with color variation on the abdominal segments mostly consisting of dorsal and lateral bands that become lighter ventrally or are missing as follows, (1) segments 2-5 with combination of reddish brown, yellow, orangish, and black bands, (2) segments 2 and 3 with combination of orangish to reddish brown, yellow, and black bands and segments 4-7 black; and (3) segments 2 and 3 with yellow and reddish brown bands with mid-dorsal black spot, segment 4 black with dorsal posterior reddish brown stripe, and segments 5-7 dorsally and laterally reddish brown.

Bromley (1934, 1950) indicated that *P. tristis* is a wasp mimic with the males mimicking Pompilidae or Sphecidae and the females resembling *Polistes* (Vespidae). In the Moses Creek floodplain marsh habitat discussed below, black pompilid wasps (e.g., *Anoplius* sp.) and *Polistes metricus* Say, 1831 are often seen.

Habitat

Proleptis tristis was found in the Moses Creek floodplain marsh (Fig. 2), and mowed and roller-chopped mesic flatwoods vegetation communities shown in Table 1. At the times this species was studied the dominant plants in the floodplain marsh were pickerelweed (Pontederiaceae, *Pontederia cordata* L.), saltmarsh fingergrass (Poaceae, *Eustachys glauca* Chapm.), danglepod (Fabaceae, *Sesbania herbacea* (Mill.) McVaugh), and pond cypress (Cupressaceae, *Taxodium ascendens* Brongn.). In the mesic flat woods the dominant plants were staggerbush (Ericaceae, *Lyonia* spp.)

and saw palmetto (*Arecaceae*, *Serenoa repens* (W. Bartram) Small). The dominant plants in the roads passing through the study areas were grasses (*Poaceae*) and sedges (*Cyperaceae*), and soft rush (*Juncaceae*, *Juncus effuses* L. subsp. *solutus* (Fernald & Wiegand) Hämet-Ahti) in the floodplain marsh.

Table 1. Vegetation communities in which *Prolepsis tristis* was studied in the Moses Creek Conservation Area.

Vegetation Type Family/Genus/Species/Common Name	Vegetation Community	
	Moses Creek Floodplain Marsh	Mowed and Roller Chopped Mesic Flatwoods
Altingiaceae		
<i>Liquidambar styraciflua</i> L./Sweetgum	X ¹	- ²
Annonaceae		
<i>Asimina</i> sp./Pawpaw	-	X
Apiaceae		
<i>Cicuta maculata</i> L./Spotted water hemlock	X	-
Apocynaceae		
<i>Asclepias perennis</i> Walter/ Swamp milkweed	X	-
Aquifoliaceae		
<i>Ilex glabra</i> (L.) A. Gray/ Gallberry	-	X
Arecaceae		
<i>Sabal palmetto</i> (Walter) Lodd. ex Shult. & Shult. f./Cabbage palm	X	-
<i>Serenoa repens</i> (W. Bartram) Small/Saw palmetto	X	X
Asteraceae		
<i>Carphephorus corymbosus</i> (Nutt.) Torr. & A. Gray/Coastalplain chaffhead (Florida paintbrush)	-	X
<i>Carphephorus odoratissimus</i> (J. F. Hamel) H. Hebert/Vanillaleaf (deer's tongue)	-	X
<i>Coreopsis leavenworthii</i> Torr. & A. Gray/ Leavenworth's tickseed	X	-
<i>Elephantopus elatus</i> Bertol./Tall elephantsfoot	X	-
<i>Erechtites hieracifolius</i> (L.) Raf. Ex DC./American burnweed	X	X
<i>Eupatorium</i> sp./Fennel	X	X
<i>Pityopsis graminifolia</i> (Michx.) Nutt./Narrowleaf silkgrass	-	X
<i>Pluchea</i> sp./Camphorweed	X	-
<i>Senecio vulgaris</i> L./Common groundsel	-	X
<i>Solidago</i> sp./Goldenrod	-	X
<i>Liatris tenuifolia</i> Nutt./Shortleaf gayfeather	-	X

Ethology of *Prolepsis tristis* (Walker, 1851) (Diptera: Asilidae)

Table 1. Continued.

Vegetation Type Family/Genus/Species/Common Name	Vegetation Community	
	Moses Creek Floodplain Marsh	Mowed and Roller Chopped Mesic Flatwoods
Convolvulaceae		
<i>Ipomoea</i> sp./Morning-glory	X	-
Cupressaceae		
<i>Taxodium ascendens</i> Brongn./Pond-cypress	X	-
Cyperaceae		
<i>Cyperus</i> spp./Flatsedges	X	X
<i>Cyperus surinamensis</i> Rottb./ Tropical flatsedge	-	X
<i>Juncus megacephalus</i> M.A. Curtis/Bighead rush	X	-
<i>Rhynchospora</i> spp./Beaksedges	X	X
<i>Scirpus</i> sp./Bulrush	X	-
Dennstaedtiaceae		
<i>Pteridium aquilinum</i> L. (Kuhn) var. <i>pseudocaudatum</i> (Clute) Clute ex. A. Heller/ Tailed bracken	X	X
Ericaceae		
<i>Bejaria racemosa</i> Vent./Tar flower (flyweed)	-	X
<i>Lyonia ferruginea</i> (Walter) Nutt./ Rusty lyonia	-	X
<i>Lyonia lucida</i> (Lam.) K. Koch/ Fetterbush	-	X
<i>Vaccinium arboreum</i> Marshall/Sparkleberry	-	X
<i>Vaccinium corymbosum</i> L./ Highbush blueberry	-	X
<i>Vaccinium myrsinitas</i> Lam./ Shinyblueberry	-	X
Fabaceae		
<i>Chamaecrista</i> sp./Sensitive pea or Partridge pea	X	-
<i>Galactia elliotii</i> Nutt./Elliott's (white) milkpea	-	X
<i>Lupinus diffuses</i> Nutt./Sky-blue lupine	X	-
<i>Mimosa</i> sp./Sensitive plant	-	X
<i>Sesbania herbacea</i> (Mill.) McVaugh/Danglepod	X	-
<i>Sesbania sericea</i> (Wild.) Link/Silky sesban	X	-
Fagaceae		
<i>Quercus laurifolia</i> Michx./Laurel oak	X	-
<i>Quercus myrtifolia</i> Willd./Myrtle oak	-	X
<i>Quercus virginiana</i> (P. Mill)/Live oak tree	X	X
<i>Quercus</i> sp./Scrub oaks	X	X

Table 1. Continued.

Vegetation Type Family/Genus/Species/Common Name	Vegetation Community	
	Moses Creek Floodplain Marsh	Mowed and Roller Chopped Mesic Flatwoods
Hypoxidaceae		
<i>Hypoxis juncea</i> Sm./Fringed yellow stargrass	-	X
Juncaceae		
<i>Juncus effusus</i> L. subsp. <i>solutus</i> (Fernald & Wiegand) Hämet-Ahti/Soft rush	X	-
Lamiaceae		
<i>Agalinis fasciculata</i> (Elliott) Raf./Beach false foxglove	-	X
Onagraceae		
<i>Ludwigia</i> sp./Primrosewillow	X	-
Osmundaceae		
<i>Osmunda cinnamomea</i> L./Cinnamon fern	?	X?
Pinaceae		
<i>Pinus clausa</i> (Chapm. Ex Engelm.) Vasey ex Sarg./Sand pine	-	X
<i>Pinus elliotii</i> Engelm./Slash pine	-	X
Poaceae		
<i>Andropogon glomeratus</i> (Walter) Britton et al./Bushy bluestem	-	X
<i>Andropogon virginicus</i> L./Broomsedge bluestem	-	X
<i>Andropogon virginicus</i> L. var. <i>glauca</i> Hack./Chalky bluestem	X (northern edge)	-
<i>Aristida stricta</i> Michx. Var. <i>beyrichiana</i> (Trin. & Rupr.) D. B. Ward/Wiregrass	-	X
<i>Dactyloctenium aegyptium</i> (L.) Willd. Ex Asch. & Schweinf/Durban crowfootgrass	-	X
<i>Digitaria</i> sp./Crabgrass	X	-
<i>Eustachys distichophylla</i> (Lag.) Nees/Weeping fingergrass	X	-
<i>Eustachys glauca</i> Chapm./Saltmarsh fingergrass	X	-
<i>Panicum virgatum</i> L./Switchgrass	X	-
<i>Setaria</i> sp./Foxtail	X	X
Other grasses	X	X
Polygalaceae		
<i>Polygala lutea</i> L./Orange Milkwort	-	X

Ethology of Prolepsis tristis (Walker, 1851) (Diptera: Asilidae)

Table 1. Continued.

Vegetation Type Family/Genus/Species/Common Name	Vegetation Community	
	Moses Creek Floodplain Marsh	Mowed and Roller Chopped Mesic Flatwoods
Polygonaceae		
<i>Persicaria glabra</i> (Wild.) M. Gómez/Denseflower knotweed	X	-
Pontederiaceae		
<i>Pontederia cordata</i> L./Pickerelweed	X	-
Rubiaceae		
<i>Oldenlandia corymbosa</i> L./Flattop clustered mille	X	-
Sapindaceae		
<i>Acer rubrum</i> L./Red maple	X	-
Saururaceae		
<i>Saururus cernuus</i> L./Lizard's tail	X	X
Smilacaceae		
<i>Smilax auriculata</i> Walter/Earleaf greenbrier vine	-	X
<i>Smilax bona-nox</i> L./Saw greenbrier vine	-	X
Vitaceae		
<i>Vitis rotundifolia</i> Michx./Muscadine	X	X
Xyridaceae		
<i>Xyris</i> sp./Yelloweyed grass	-	X

1 = present; 2 = not present. There are no 1 or 2 is it correct.



Fig. 2. *Prolepsis tristis* habitat along road in Moses Creek floodplain marsh (Photograph: D.S. Dennis, 24 August 2012, 9:27 AM).

The vegetation in the floodplain marsh community is thick, approximate 83 m long and 35.7 m wide, and is mostly along a “U” shaped road in an electrical transmission

line corridor. As part of vegetation height management, some plants in the corridor are periodically sprayed with herbicide. Thus, when *P. tristis* was initially studied in 2011, there was more danglepod, pickerelweed, and pond cypress than in subsequent years.

Bromley (1934) said that *P. tristis* is "Found along water courses or cultivated fields where vegetation is rank." Lavers (2011) and Raney (2019) both found this species near or along sandy beaches near rivers.

Flight patterns

Dennis & Lavigne (1975) classified robber fly flight patterns as, orientation flights; investigatory flights; foraging flights; and searching flights. Orientation flights are short flights around a robber fly's location to change its field of vision and are not directed towards potential prey. Investigatory flights are directed toward potential prey without the asilid making contact. Foraging flights are when an asilid makes contact with potential prey. Searching flights are, "Vertical undulating flight patterns or weaving in and out of the vegetation by male asilids in their search for receptive females with which to mate."

After making an orientation flight, many asilids return to or within a few cm of their original foraging location. *Prolepsis tristis* sometimes return to within 15 cm to 1 m of their original foraging position, but usually move to a new location 1.8-18.9 m away, flying up to 4.6 m above the ground or up to 3.4 m above the vegetation. The flights are relatively straight and take from 3-65 seconds. It is believed that these flights allow the asilids to survey the habitat and to select new resting and foraging locations. Some flights spanned Moses Creek (up to 8.1 m wide) to other parts of the habitat

During the longer flights the asilids slowly fly with the femora of the fore- and mid-legs held up against the thorax, and the tibiae and tarsi hanging down at about a 30-45° angle or the tibiae and tarsi are held closer to the thorax and extend forward. The hind legs also hang below the asilid at about a 45° angle. Sometimes the abdomen is gently curved up. Wasps flying slowly in the habitat held their legs in similar positions.

Diogmites crudelis Bromley, 1936 also made long orientation flights within 3-8 m of its foraging position (Dennis, 2015). Lavigne (1992) assumed that the long orientation flights (in excess of 10 m) that *Colepia abludo* (Daniels, 1983) made were in response to the lack of potential prey in the vicinity of its foraging location or were males relocating when no females had been seen. This also may be true for *P. tristis*.

Prolepsis tristis investigatory and foraging flights are discussed below under Foraging and Feeding Behavior. Searching flights are discussed under Courtship and Mating Behavior.

Resting behavior

Prolepsis tristis rests on and forages from vegetation, primarily on grass stems and blades. When they initially land on a grass blade, the blade generally bends over so that it is parallel to the ground. As the grass blade bends over the asilids balance themselves by spreading their wings for up to 44 seconds and curving their abdomen

Ethology of Prolepsis tristis (Walker, 1851) (Diptera: Asilidae)

over the edge of the blade. When having trouble balancing on a grass blade, some asilids buzz their wings. If an asilid lands on the edge of a grass blade, they usually keep their body at a 30-45° angle. One female rested on the side of a foxtail (*Poaceae*, *Setaria* sp.) spike vertical to the ground.

While resting, *P. tristis* are mostly still, but may make brief, quick movements of their head and abdomen, in particular when other insects fly over 45 cm to 1.2 m above their location. One female also reacted to a bird flying over 3 m above her. Individuals rest for up to 24 minutes before resuming other activities.

Most *P. tristis* rest 20 cm to 1.5 m above the ground with their sides to the sun. One asilid rested 6.1 m above the ground on scrub oak on the western side of the Moses Creek floodplain marsh habitat. However, when air temperature in the sun reached 36.5°C, some individuals move down to the shade of vegetation, 5-30 cm above the ground, where it is slightly cooler, 34.5-35°C. Many species of robber flies maintain their body temperature by changing their position in relation to the sun and/or rest on the shady side of vegetation (Dennis, 2018; Dennis & Lavigne, 1975; Lavigne & Holland, 1969).

While resting, one male *P. tristis* excreted a white drop from its anus. When resting and feeding, other species of robber flies in the MCCA have expelled a drop of creamy-white to brownish liquid from their anuses including: *Proctacanthus brevipennis* (Wiedemann, 1828) (Dennis, 2012), *P. longus* (Wiedemann, 1821) (Dennis, 2019), *Stichopogon trifasciatus* (Say, 1823) (Dennis, 2013), *Holopogon phaeonotus* Loew, 1874 (Dennis, 2014), *H. snowi* Back, 1909 (Dennis, 2018), *Diogmites crudelis* Bromley, 1936 (Dennis, 2015), and *Promachus bastardii* (Macquart, 1838) (Dennis, 2016). Lehr (1958) observed that the expulsion of liquid from the anal opening is quite common in robber flies.

Prolepsis tristis spent the night on vegetation, generally 30-60 cm above the ground, in either a horizontal or vertical position with their head up. One female was observed in a horizontal position with early morning dew on her thorax (Fig. 3).



Fig. 3. Female *Prolepsis tristis* with early morning dew on thorax (Photograph: D.S. Dennis, 24 August 2012, 8:13 AM).

Foraging and feeding behavior

Proleptis tristis forage from vegetation 15 cm-1.5 m above the ground. Investigatory flights are made within 15 cm-1.5 m and generally above an asilid's foraging position. Flights are for distances up to 1.5 m. One investigatory flight involved a female chasing a male, and three other flights were both female and male *P. tristis* chasing *Polistes metricus* wasps. Following investigatory flights, the asilids land at least 1 m from their original foraging location.

Foraging flights, when *P. tristis* capture and release potential prey, are made within 30 cm-1 m of an asilid's foraging position. Prey is generally released in flight, but one male captured a potential prey, fell to the ground, and then released it. Two males captured and released *P. metricus* while in flight. Like the investigatory flights, *P. tristis* did not return to its original foraging position after foraging flights.

Male and female *P. tristis* have modified foraging flights when they weave in and out of vegetation and then hover in front of and briefly hit grass stems and foxtail spikes. Males did not exhibit this behavior as much as females.

Only three prey captures were observed and all involved cannibalism when females captured other females. All prey were captured approximately 1 m from a female's foraging position and then the predator and prey fell into the vegetation where feeding ensued. Also, one male captured a female in flight and when the pair fell to the ground, the female inserted her proboscis in the venter of the male's head.

During feeding small prey hang free from the asilid's proboscis without being held by the tarsi and are not manipulated. Larger prey (i.e., other *P. tristis*) are held against the vegetation and the asilid crawls on the prey and manipulates the prey with a number of tarsi or holds onto vegetation with one or both fore tarsi and mid-tarsi and manipulates the prey with the other tarsi prior to reinserting its proboscis. As feeding progresses, prey is manipulated up to six times.

Only one complete feeding was observed and involved a female *P. tristis* feeding on another female. When the female captured the other female (prey), she inserted her proboscis in the venter of the prey's head, which indicates that the prey was attacked from below. The feeding took 129.5 minutes during which the prey was manipulated six times. Following the first manipulation the female reinserted her proboscis in the anteroventral part of the other female's abdomen. This was followed by manipulation and reinsertion of the proboscis in the female's ventral tip of the abdomen, right anterolateral part of the thorax, dorsal tip of the abdomen (two times in a row), and then the dorsal surface of the thorax. Following feeding the female dropped her prey at the feeding site and the author lost her as she flew to another location in the habitat.

During feeding some robber flies pump the first one to three segments of their abdomen. This abdominal pumping (or contractions) has been associated with the injection of proteolytic enzymes into prey and the ingestion of liquefied food from prey (Musso, 1968; Lavigne & Holland, 1969), as well as thermoregulation (Morgan, Shelly, & Kimsey, 1985; Morgan & Shelly, 1988). *Proleptis tristis* did not exhibit abdominal pumping.

Prey

Very few *P. tristis* were found with prey. The following is a list of prey taken by *P. tristis* with the number and sex of the predator following the date.

COLEOPTERA, Chrysomelidae: *Lema daturaphila* Kogan & Goeden, 1970, 25.09.19 (1 ♀). Meloidae: *Epicauta* sp. prob. *torsa* LeConte, 1853, 08.09.2014 (1 female). DIPTERA, Asilidae: female *P. tristis*, 17.08.2012 (1 ♀), 20.08.2012 (3 ♀♀) 21.08.2015 (1 ♀), male *P. tristis*, 17.08.2012 (1 ♀), 26.08.2015 (1 ♀). LEPIDOPTERA, Crambidae: *Herpetogramma bipunctalis* (Fabricius, 1794), 24.08.2015 (1 ♀).

As shown in the list of prey, the largest number of prey is from females preying upon both male and female *P. tristis*. Raney (2019) photographed a male *P. tristis* feeding on another male.

The records of cannibalism reported here occurred during periods of good weather without rain or high winds. Lehr (1961) observed that female *Stenopogon heteroneurus* (Macquart, 1838) preyed on males and cannibalism enabled the asilids to survive a shortage of food after a long period of inclement weather.

Bromley (1934) observed a female *P. tristis* (as *Dizonias tristis*) with *Epicauta* sp. (Coleoptera, Meloidae) as prey. Bromley (1950) also said that they (as *D. tristis*) feed on slow flying beetles and observed a female feeding on *Epicaerus formidosus* Boheman, 1842 (Coleoptera, Curculionidae). Fattig (1945) reported *P. tristis* (as *D. tristis*) preying on *Eristalis dimidiata* (Wiedemann, 1830) (as *Tubifera dimidiatus*; Diptera, Syrphidae), *Apis mellifera* L., 1758 (Hymenoptera, Apidae), and *Epicauta trichrus* (Pallas, 1798).

Courtship and mating behavior

Some of the previously mentioned orientation flights, in particular when the male weaves during flight (30-120 cm above the vegetation), may have been searching flights for receptive females with which to mate. However, most male searching flights involve the male slowly weaving in-and-out of vegetation, generally 30-90 cm above the ground, often hovering in front of vegetation.

Male and female *P. tristis* would fly up to investigate and briefly hover or oscillate back and forth within 7.5-10 cm in front of each other and up to 3 m above the ground. Some also hovered in a half circle in front of each other. A few came into contact with each other and one male grasped a female and the pair fell to the ground where they separated. One male also captured another male and the pair separated when they fell into vegetation.

Males initiate mating by flying from vegetation, 1.0-1.2 m above the ground, grasp the female and straighten out in the tail-to-tail position (Fig. 1) while still in flight, or alternately the pair falls into vegetation and then they straighten out in the tail-to-tail position. One pair when they fell into vegetation were facing and pushing each other with their tarsi before straightening out in the tail-to-tail position.

While mating, the asilids were easily disturbed, even by wind blowing vegetation, and they would often fly to other nearby vegetation. Mating pairs generally moved two

to four times, depending on the length of the mating. One pair after the initiation of mating, was unable to find vegetation that could support their weight. So they moved eight times before finding vegetation that was sturdy enough to support them.

If after moving the male or female could not immediately grasp vegetation, they would hang free until they were able to reach and hold onto vegetation. Females usually took the lead when flying and were most frequently head up when on vegetation and the male was head down.

Between flights to other vegetation, the mating pair would generally remain motionless except for grooming of the fore tarsi. However, during the longest mating (91 minutes), after 41 minutes of its initiation, the male arched or flexed up his abdomen twice, and then opened and closed his wings seven times over a 12 minute period. The male left his wings open at approximately a 45° angle, for five to 47 seconds with an average of 30 seconds.

The author observed seven complete and 11 partial matings. The complete matings lasted 30-91 minutes with an average of 48 minutes 42 seconds. At the completion of mating, males usually released the female and both flew off. Only one mating pair separated in flight.

Prolepsis tristis matings occurred when the air temperature ranged from 26-36.5°C at the height where the mating pair rested on vegetation, with an average of 31.5°C.

Oviposition Behavior

One oviposition was observed in the soil. The female flew 12-15 cm above the ground, 6 m from her previous location in thick vegetation, and landed on the soil in a small opening in the vegetation. The female's body was at a 45° angle to the soil, with her wings closed, and her ovipositor was barely inserted in the soil, which was moist from recent rains. She remained in this position for 33 seconds, then briefly swept the soil with the tip of her ovipositor, and flew off. Soil was recovered and examined for eggs, but none were found.

The air temperature above the oviposition site was 31°C; both at the surface and just below the surface, soil temperature was 33°C.

Grooming

Robber fly grooming behavior is often associated with other behaviors such as following the completion of feeding, mating, and oviposition. However, this was not observed for *P. tristis*. This species, like *Holopogon phaeonotus* (Dennis, 2014) and *H. snowi* (Dennis, 2018), did not frequently groom themselves. Dennis (2018) commented that for *H. phaeonotus* and *H. snowi*, "This may be because the asilids occupy various heights on vegetation and do not land on the ground." The same may be true for *P. tristis*.

When *P. tristis* did groom it was in much the same way as reported for other species of robber flies (Dennis, 2014). They always use the fore legs to groom their heads, and the hind legs to groom their wings, abdomen, and genitalia while resting and during feeding and mating.

Ethology of Prolepsis tristis (Walker, 1851) (Diptera: Asilidae)

Some robber flies groom for extended periods of time (e.g., *Diogmites crudelis* Bromley, 1936) (Dennis, 2015). However, *P. tristis* grooming is brief, lasting for seven seconds or less.

Prolepsis tristis often groom only the fore tarsi by placing the tarsi together and then moving them back and forth along their length. They also groom the fore tarsi and then groom their eyes and the sides of their face with their fore tibiae. They did not groom their proboscis, even after feeding.

When they groom their wings and abdomen, they would often briefly groom the hind tarsi and tibiae, and then groom the posterior half of the abdomen and wings from anterior to posterior with the hind tibiae and tarsi. The abdomen is often slightly curved down during grooming. When the wings are closed, only the top surface is groomed; when the wings are spread at a 30-45° angle to the body, both the tops and bottoms of the wings are groomed outward for about 3/4 of their length.

Daily rhythm of activity

Prolepsis tristis had one peak period for both feeding (40.0%) and mating (33.3%) between 10:00-11:00 AM (Fig. 4). Feeding had a second peak (22.2%) between 1:00-3:00 PM. A smaller mating peak (5.9%) occurred in the afternoon between 3:00-4:00 PM. Only one oviposition was observed, at 12:10 PM.

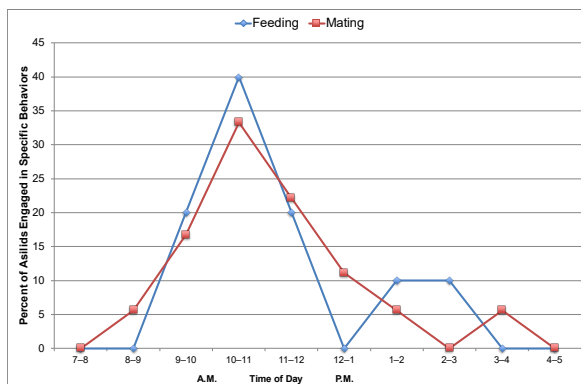


Fig. 4. Daily rhythm of activity of *Prolepsis tristis* based on 9 and 18 observations for feeding and mating, respectively.

The observations of daily rhythm of activity were made in the Moses Creek floodplain marsh habitat. This habitat has live oak, red maple, sweet gum and cabbage palm trees on both the eastern and western sides so that the habitat is in shade until about 8:17 AM when sun shines on some of the western side. By 10:40 AM about half the habitat is in sunshine and it is in full sun by about 12:00 noon. As the day progresses the western area starts to be in shade about 3:47 PM and the habitat is completely in shade by 5:00 PM.

The peak period of feeding and mating for *Prolepsis tristis* appears to be coordinated with when a large part of the habitat is in the sun, when light levels are

86,510-87,730 lux. However, even when the sky is overcast and the author can see a dim shadow with light levels ranging from 10,090-10,710 lux, *P. tristis* continues to forage and mate. Resting and some flying takes place in the shade with light levels of 1,619-1,754 lux.

Predators and parasites

As indicated above, female *P. tristis* prey upon both males and other females. According to Lavigne, Dennis, & Gowen (2000) cannibalism is common among robber flies.

Both male and female *P. tristis* were caught in the webs of the black-and-yellow orb weaver (*Argiope aurantia* Lucas, 1833; Araneae, Araneidae) orb weaver webs. Once caught in the webs, the robber flies were wrapped by the spiders in a cocoon of silk for later consumption. One male *P. tristis*, when resting on a grass stalk, was captured by a regal jumping spider (*Phidippus regius* C.L. Koch, 1846; Araneae, Salticidae) (Fig. 5).

Mites are often found on robber flies, in particular on the thorax. However, none were found on *P. tristis*.



Fig. 5. Regal jumping spider (*Phidippus regius*) with male *Proleptis tristis* as prey (Photograph: D.S. Dennis, 20 August 2012, 11:25 AM).

CONCLUSIONS

Proleptis tristis rests on and forages from vegetation. All prey were captured in flight and consisted of seven Diptera (70.0%), two Coleoptera (20.0%), and one Lepidoptera (10.0%). All of the Diptera were instances of cannibalism when females preyed on other females and males. During feeding small prey were not manipulated and larger prey (i.e., other *P. tristis*) were crawled on and manipulated with a number of tarsi. Mating occurred in the tail-to-tail position and oviposition was in the ground. This species exhibited a daily rhythm of activity with peak feeding and mating from 10:00-11:00 AM, with smaller peaks from 1:00-3:00 PM and 3:00-4:00 PM, respectively. The one oviposition observed was at 12:10 PM. Grooming behavior did not occur often and was brief, but resembles that of other species of Asilidae. Male and female *P.*

Ethology of Prolepsis tristis (Walker, 1851) (Diptera: Asilidae)

tristis were caught in the webs of the black and yellow orb weaver, *Argiope aurantia*. A regal jumping spider, *Phidippus regius*, captured one male.

ACKNOWLEDGMENTS

The author thanks 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) and for their interest in the research.

With gratitude, the author acknowledges Alma Solis (SEL) for her identification of the Lepidoptera (Crambidae) prey and Alexey Tishechkin (Department of Entomology, Louisiana State Arthropod Museum, Baton Rouge) for his identification of the Coleoptera (Meloidae) prey. The author also would like to thank the SEL's Michele Touchet for handling of the prey and the prompt Identification Reports.

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

REFERENCES

- Bromley, S.W. (1934). The robber flies of Texas (Diptera, Asilidae). *Annals of the Entomological Society of America*, 27(1), 74-113.
- Bromley, S.W. (1950). Florida Asilidae (Diptera) with description of one new species. *Annals of the Entomological Society of America*, 43(2), 227-239.
- Dennis, D.S. (2012). Ethology of *Proctacanthus brevipennis* (Wiedemann, 1828) (Diptera: Asilidae) in Northeastern Florida, U.S.A. *Journal of the Entomological Research Society*, 14(3), 91-109.
- Dennis, D.S. (2013). Ethology of *Stichopogon trifasciatus* (Say, 1823) (Diptera: Asilidae) in Northeastern Florida, USA. *Journal of the Entomological Research Society*, 15(2), 37-50.
- Dennis, D.S. (2014). Ethology of *Holopogon phaeonotus* Loew, 1874 (Diptera: Asilidae) in Northeastern Florida, U.S.A. *Journal of the Entomological Research Society*, 16(2), 141-158.
- Dennis, D.S. (2015). Ethology of *Diogmites crudelis* Bromley, 1936 (Diptera: Asilidae) in Northeastern Florida, U.S.A. *Journal of the Entomological Research Society*, 17(1), 23-44.
- Dennis, D.S. (2016). Ethology of *Promachus bastardii* (Macquart, 1838) (Diptera: Asilidae) in Northeastern Florida, U.S.A. *Journal of the Entomological Research Society*, 18(3), 69-92.
- Dennis, D.S. (2018). Ethology of *Holopogon snowi* Back, 1909 (Diptera: Asilidae) in Northeastern Florida, U.S.A. *Journal of the Entomological Research Society*, 20(1), 95-112.
- Dennis, D.S. (2019). Ethology of *Proctacanthus longus* (Wiedemann, 1821) (Diptera: Asilidae) in Northeastern Florida, U.S.A. *Journal of the Entomological Research Society*, 21(1), 37-56.
- Dennis, D.S. & Lavigne, R.J. (1975). Comparative behavior of Wyoming robber flies II (Diptera: Asilidae). *Agricultural Experiment Station University of Wyoming-Laramie Science Monograph No. 30*, 68 pp.
- Fattig, P.W. (1945). The Asilidae or robber flies of Georgia. *Emory University Museum Bulletin 3*, 33 pp.
- Fisher, E.M. & Wilcox, J. (1997, unpublished). Catalog of the robber flies (Diptera: Asilidae) of the Nearctic Region. California Department of Food & Agriculture; Sacramento.
- Geller-Grimm, F. (2019, July 10). Robber flies (Asilidae), database, catalog of species. Retrieved from <http://www.geller-grimm.de/catalog.species.htm>
- Lavers, N. (2011, September 4). The Robber Flies of Crowley's Ridge, Arkansas: An Illustrated Field Guide. Retrieved from <http://www.normanlavers.net/>

- Lavigne, R.J. (1992). Ethology of *Neoratus abludo* Daniels (Diptera: Asilidae) in South Australia, with notes on *N. pelago* (Walker) and *N. rufiventris* (Macquart). *Proceedings of the Entomological Society of Washington*, 94(2), 253-262.
- Lavigne, R.J., Dennis, D.S., & Gowen, J.A. (2000). Asilid literature update 1956-1976 including a brief review of robber fly biology (Diptera: Asilidae). *Agricultural Experiment Station University of Wyoming Science Monograph* 36, 93 pp.
- Lavigne, R.J. & Holland, F.R. (1969). Comparative behavior of eleven species of Wyoming robber flies (Diptera: Asilidae). *Agricultural Experiment Station University of Wyoming Laramie Science Monograph* No. 18, 61 pp.
- Lehr, P.A. (1958). On the biology and behavior of robber flies (Asilidae-Diptera). *Trudy Instituta Zoologii, Akademiya Nauk Kazakhstan. SSR*, 8, 173-196. (In Russian)
- Lehr, P.A. (1961). The robber fly *Stenopogon heteroneurus* Macquart (Diptera, Asilidae), its behavior and feeding. *Trudy nauchno-issledovaniya Instituta Zashchi Rasteniy, Kazaskhn (Proceedings of the Scientific Research Institute of Protection of Plants, Kazakhstan)*, Alma-Ata, 6, 131-146. (In Russian)
- Morgan, K.R. & Shelly, T.E. (1988). Body temperature regulation in desert robber flies (Diptera: Asilidae). *Ecological Entomology*, 13, 419-428.
- Morgan, K.R., Shelly, T.E., & Kimsey, L.S. (1985). Body temperature regulation, energy metabolism, and wing loading in light-seeking and shade-seeking robber flies. *Journal of Comparative Physiology*, 155, 561-570.
- Musso, J.J. (1968). Digestion extra-intestinale chez *Stenopogon sabaudus* F. et *Machimus pilipes* Meig. (Dipt. Asilidae). *Bulletin de la Société Zoologique de France*, 93(3), 487-497.
- Raney, H. (2019, July 10). Robber Flies. Retrieved from <http://www.hr-ma.com/RNA/Robber%20main%20page.htm>

Received: August 12, 2019

Accepted: June 26, 2020