

Ethology of *Promachus bastardii* (Macquart, 1838) (Diptera: Asilidae) in Northeastern Florida, U.S.A.

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ABSTRACT

Promachus bastardii (Macquart, 1838) foraged from both the ground and vegetation, capturing most prey in flight and then immobilizing them during a hover prior to landing to feed. Identified prey came from four insect orders (Coleoptera (15.6%), Diptera (8.3%), Hemiptera (4.2%), Hymenoptera (59.4%), and unidentified/uncollected (12.5%)). Mating occurred in the male over female position and ovipositing was in dried seed heads of plants and an oak bullet gall, typically in the shade of vegetation. This species exhibited a distinct daily rhythm for feeding, mating, and ovipositing, primarily between 09:00 AM and 12:00 noon. Other topics discussed include habitats, resting behavior, grooming behavior, and predators and parasites.

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

INTRODUCTION

The genus *Promachus* has 22 species in the Nearctic zoogeographic region of the world (Geller-Grimm, 2015). Some detail on different aspects of the ethology of only five species (*P. albifacies* Williston, 1885 (Hastings *et al.*, 1994; Lavigne, 2002); *P. bastardii* (Macquart, 1838) (Hull, 1942; Lavigne, 2002, as *P. bastardi*); *P. dimidiatus* Curran, 1927 (Lavigne, 2002; Lavigne and Holland, 1969); *P. giganteus* Hine, 1911 (Morgan and Shelly, 1988); and *P. rufipes* (Fabricius, 1775) (Lavigne, 2002)) has been described, with other publications limited to discussion of habitat and/or prey (*P. albifacies* (Dennis and Lavigne, 2007; James, 1938; Linsley, 1960); *P. bastardii* (Alex, 1948; Baker and Fischer, 1975; Bromley, 1914, 1930, 1931, 1934, 1942, 1946a and b (all as *P. bastardi*), 1948; Fattig, 1945; Riley, 1870a (as *P. bastardii* Loew); Thorp, 1973); *P. dimidiatus* (Cannings, 2014; Dennis *et al.*, 2010; Dennis and Lavigne, 2007); *P. giganteus* (Barnes, 2010; Beckemeyer and Charlton, 2000; Bromley, 1934; Dennis *et al.*, 2010; Hurd and Linsley, 1975); and *P. rufipes* (Bromley, 1930, 1946a, 1950a and b; Fattig, 1945).

Promachus bastardii is common in the eastern half of the United States of America (U.S.A.), occurring from Kansas north to Ontario, Canada and Maine, south to Texas and Florida (Fisher and Wilcox, 1997 (unpublished draft); Geller-Grimm, 2015). It is a robust, brownish-black species, varying in length from 20-35 mm, with the males generally smaller than the females. The mystax is creamy white/yellowish, the thorax is brown, the wings are uniformly brownish, and the abdomen is brown pollinose ventrally

and laterally, and black dorsally. On the posterior margin of the first four abdominal segments, there is a narrow dorsal and lateral white band. The male genitalia have dense, distinctive, bright white to silvery-white setae dorsally (Fig. 1) (Baker and Fischer, 1975; Bromley, 1934; Hine, 1911; McAtee and Banks, 1920).

This paper provides detailed information on the ethology of *P. bastardii* in the 2,173 acre Moses Creek Conservation Area (MCCA) in St. Augustine in northeastern Florida.



Fig. 1. Male *Promachus bastardii* on dead saw palmetto frond.

MATERIALS AND METHODS

Promachus bastardii is a widely distributed species in Florida and, generally occurs from April into August, depending on location. Observations were made over five field seasons: on 10.06.2011; 22.05.2012-10.07.2012; 15.06.2013-26.07.2013; 26.05.2014-08.08.2014 and 01.05.2015-14.07.2015. The author observed a number of *P. bastardii* in the MCCA in four vegetation communities: mowed edges of roads in mesic flatwoods and upland mixed forest (along Hidden Creek) communities, and in mowed scrub and scrubby flatwoods communities. When flies flew into the nearby woods, it was not possible to follow them because of dense vegetation.

Promachus bastardii was studied when it was most abundant in the previously mentioned vegetation communities and times in the MCCA. Observations involved an average of three individuals per day, each for up to 4.5 hours. Total number of hours of observation equaled approximately 126, not including the many hours looking for *P. bastardii* to observe.

The study involved 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, and slowly walking through a study area and observing the activities of many flies. This allowed for the collection of more prey and increased the probability of observing mating pairs and ovipositing females.

Collected prey were placed in glass vials with a label indicating the following: 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,

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Systematic Entomology Laboratory, Beltsville, Maryland, U.S.A. for identification. Prior to shipment, prey were measured with a clear, plastic ruler to the nearest 0.5 mm.

The author observed ovipositing females for as long as they exhibited oviposition behavior or until they were lost to sight as they flew about the habitat. When a female ceased oviposition behavior or the author lost visual contact, he collected the vegetation and associated eggs. The vegetation was then visually examined in the laboratory and the eggs were removed. Eggs were recovered from four ovipositions and placed in 95% ethyl alcohol for examination and measurement with 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.

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

RESULTS AND DISCUSSION

Habitat

The St. Johns River Water Management District (District) owns the MCCA. The District uses fire and mechanical (roller chopping and mowing) vegetation management in the scrub and scrubby flatwoods communities. To facilitate access to the MCCA, the roads and the sides or edges of roads are also mowed. The largest population of *P. bastardii* studied occurred along the mowed sides of a road in a mesic flatwoods community.

The mowed roads and sides of the roads are approximately 3-4 m and 4-7 m wide, respectively. The roads often have little vegetation or some sparsely distributed grasses and sedges. The mowed sides of the roads in the mesic flatwoods (Fig. 2) and upland mixed forest (along Hidden Creek) communities (habitats) and mowed scrubby flatwoods and scrub habitats, have the plants associated with the vegetation communities shown in Table 1. The dominant plants in the mesic flatwoods, scrubby flatwoods, and scrub habitats are 30 cm to 1 m tall cut earleaf and saw greenbrier vines, Elliott's (white) milk pea, highbush and shiny blueberry, saw palmetto, scrub oak, fetterbush, and rusty lyonia. The dominant plants in the area along Hidden Creek are common buttonbush, muscadine, and wild taro. Each habitat also has the following abundant plants at various locations: mesic flatwoods (coastalplain chaffhead, fennel, gallberry, live oak, myrtle oak, narrowleaf silkgrass, sand pine, tar flower, vanillaleaf, wiregrass); along Hidden Creek (cinnamon fern, grasses and sedges); scrubby flatwoods (coastalplain chaffhead, live oak, myrtle oak, narrowleaf silkgrass, wiregrass); and scrub (bushy and broomsedge bluestem, fennel, gallberry, live oak, sand pine, tailed bracken, wiregrass).



Fig. 2. *Promachus bastardii* habitat along road in mesic flatwoods community.

Promachus bastardii is found in a variety of habitats in the U.S.A. Bromley (1930) made the general comment that it "... is found more characteristically around the edges of fields, along road sides, overgrown walls, and fences, and in brushy pastures and similar locations..." In Texas, he (Bromley, 1934) reported it is a widespread species, in particular "... in the open upland post oak woods and adjacent cultivated fields." In Connecticut, Bromley (1946b) said that it is a characteristic species in woodlands occurring in oak and mixed mesophytic (moderate amount of moisture) regions, and brushy pastures also in these regions. In Arkansas, Scarbrough (1972) observed that *P. bastardii* is common in dry fields and also found it in a garden. Baker and Fischer (1975) indicated that in Michigan, this species was collected in a sandy and dry old burn area that had a large amount of dry dead leaves and twigs on the ground; whereas, McGravy and Baxa (2011) reported it in a recently (Spring 2005) burned prairie in west-central Illinois. In Virginia, Bedell (2010) found *P. bastardii* in an ungrazed and unmowed field.

Population levels of *P. bastardii* in the MCCA vary dramatically from year to year. From 2011 through 2014, only a few flies were found in any given area of a vegetation community, with the most occurring in the mowed scrub community. In May 2015, approximately 15-18 *P. bastardii* were found along the mowed (Fall 2014) sides of a road in a mesic flatwoods community (Fig. 2). The author had not previously seen *P. bastardii* along this road prior to it being mowed. In other communities it appeared that after *P. bastardii* emerged from their pupal cases, they rapidly dispersed throughout their habitat and did not stay long in one area. Haupt (2002) commented that adult *P. indigenus* (Becker, 1925) on the island of Iriomote (Yaeyama, Ryukyu, Japan) spread after their emergence and their perching sites could not be related to where the immatures were found.

Bromley (1948) found that from 1936 to 1948, *P. bastardii* had become rare in the Stamford Connecticut area. He attributed this to a decrease in white grub (*Phyllophaga fusca* (Frölich, 1792)) populations that appeared to be the principal food of the larvae.

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McCabe and Weber (1994) said that historically *P. bastardii* occurred in the Albany, New York scrub oak-pitch pine (*Quercus ilicifolia*-*Pinus rigida*) barrens, but apparently it had been extirpated.

Resting behavior

Early in the morning (08:00-09:30 AM) when air temperatures were 27-30°C, most *P. bastardii* rested on vegetation, but a few rested on the ground. Whether on vegetation or the ground they would often turn so that one of their sides faced and was elevated to the sun. As the day progressed and air temperatures increased, individuals rested primarily in the shade of leaves of live vegetation (e.g., fetterbush, rusty lyonia, and scrub oak) 7.5-60 cm above the ground. A few individuals rested on the tops of vegetation up to 1 m above the ground, and on the ground or dead vegetation on the ground. When *P. bastardii* rested in the shade of vegetation, they usually did not make changes in their position unless they became exposed to the sun, and then they crawled back into the shade or flew to a new location in the shade.

Some robber flies regulate their body temperature by moving to the shaded side of vegetation (Dennis and Lavigne, 1975). Both *P. dimidiatus* (Lavigne and Holland, 1969) and *P. giganteus* (Morgan and Shelly, 1988) made postural adjustments in relation to the sun's position, and as the sun rose and ground temperatures increased, assumed perch heights higher in vegetation. *Promachus giganteus* resumed perching on or near the ground at different times in the afternoon. Morgan *et al.* (1985) commented, "...the abdomen of a robber fly with physiological control over haemolymph (and thus heat flux) between the thorax and abdomen is a thermal window which enables the insect to manage its thermal balance by varying heat transfer between the thorax and abdomen; and by controlling heat loss from the abdomen by changes in orientation with respect to the sun."

If the sky became overcast while *P. bastardii* was resting or foraging, they would flatten themselves against the substrate they were on. Dennis and Lavigne (1975) found that robber flies on the ground apparently attempt to maintain their body temperature by changing their position and flattening themselves against the ground.

Promachus bastardii rested and foraged with its abdomen either parallel to the surface that it was on or at a 45-degree angle. When resting, individuals will usually ignore other insects flying by, although when a scoliid wasp hovered in front of one female she flew to a new location. Resting *P. bastardii* also sometimes groom their face, fore tarsi, abdomen, wings, hind tarsi and tibiae.

Promachus bastardii usually rested for 4 to 19 minutes before moving to a new location, although a few individuals remained in the same locations in the shade of vegetation for 34 to 39.5 minutes. When they flew to another location, their wings often made a high-pitched buzzing sound. Bromley (1934) described the buzz as resembling that of a megachilid bee (Hymenoptera: Megachilidae).

While resting, between foraging flights, and during and after feeding, it was common to see *P. bastardii* excrete wastes by expelling a drop of creamy-white to white liquid from the anus. This also has been observed for other robber flies (Dennis, 2015a; 2015b).

Table 1. Vegetation in communities in which *Promachus bastardii* was studied in the Moses Creek Conservation Area.

Vegetation Type Family/Genus/Species/Common Name	Mowed Sides of Road in Vegetation Community		Mowed Community	
	Mesic Flatwoods	Upland Mixed Forest (along Hidden Creek)	Scrubby Flatwoods	Scrub
Annonaceae				
<i>Asimina</i> sp./Pawpaw	X ¹	- ²	X	X
Aquifoliaceae				
<i>Ilex glabra</i> (L.) A. Gray/ Gallberry	X	-	X	X
Araceae				
<i>Colocasia esculenta</i> (L.) Schott/Wild taro (elephant-ear)	-	X	-	-
Araliaceae				
<i>Hydrocotyle</i> sp./Marshpennywort	-	X	-	-
Areaceae				
<i>Serenoa repens</i> (W. Bartram) Small/Saw palmetto	X	X	X	X
Asteraceae				
<i>Carphephorus corymbosus</i> (Nutt.) Torr. & A. Gray/ Coastalplain chaffhead (Florida paintbrush)	X	-	X	X
<i>Carphephorus odoratissimus</i> (J. F. Hamel) H. Hebert/Vanillaleaf (deer's tongue)	X	-	X	X
<i>Erigeron quercifolius</i> Poir./ Oakleaf fleabane	-	X	-	-
<i>Eupatorium</i> sp./Fennel	X	X	X	X
<i>Pityopsis graminifolia</i> (Michx.) Nutt./Narrowleaf silkgrass	X	-	X	-
<i>Senecio vulgaris</i> L./Common groundsel	X	X	X	X
<i>Solidago</i> sp./Goldenrod	X	-	X	X
<i>Liatris tenuifolia</i> Nutt./Shortleaf gayfeather	X	-	X	X
Cactaceae				
<i>Opuntia humifusa</i> (Raf.) Raf./ Eastern prickly pear cactus	-	-	X	X
Cyperaceae				
<i>Cyperus</i> sp./Flatsedge	X	-	-	X
<i>Cyperus surinamensis</i> Rottb./ Tropical flatsedge	-	X	-	-
<i>Rhynchospora colorata</i> (L.) H.Pfeiff./Starrush whitetop	-	X	-	-
<i>Rhynchospora</i> sp./Beaksedge	X	-	-	X

Footnotes: 1 = present; 2 = not present.

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Table 1. Continued.

Vegetation Type	Mowed Sides of Road in Vegetation Community		Mowed Community	
Family/Genus/Species/Common Name	Mesic Flatwoods	Upland Mixed Forest (along Hidden Creek)	Scrubby Flatwoods	Scrub
Dennstaedtiaceae				
<i>Pteridium aquilinum</i> L. (Kuhn) var. <i>pseudocaudatum</i> (Clute) Clute ex. A. Heller/Tailed bracken	X	-	X	X
Ericaceae				
<i>Bejaria racemosa</i> Vent./Tar flower (flyweed)	X	-	X	-
<i>Lyonia ferruginea</i> (Walter) Nutt./ Rusty lyonia	X	-	X	X
<i>Lyonia lucida</i> (Lam.) K. Koch/ Fetterbush	X	X	X	X
<i>Vaccinium arboreum</i> Marshall/Sparkleberry	X	-	-	-
<i>Vaccinium corymbosum</i> L./ Highbush blueberry	X	-	X	X
<i>Vaccinium myrsinitas</i> Lam./ Shiny blueberry	X	-	X	X
Fabaceae				
<i>Galactia elliotii</i> Nutt./Elliott's (white) milkpea	X	X	X	X
<i>Mimosa</i> sp./Sensitive plant	X	-	X	-
Fagaceae				
<i>Quercus incana</i> W. Bartram/ Bluejack oak	-	-	-	X
<i>Quercus myrtifolia</i> Willd./Myrtle oak	X	-	X	X
<i>Quercus virginiana</i> (P. Mill)/Live oak tree				
<i>Quercus</i> sp./Scrub oaks	X	X	X	X
Hypoxidaceae				
<i>Hypoxis juncea</i> Sm./Fringed yellow stargrass	X	-	-	-
Lamiaceae				
<i>Teucrium canadense</i> L./Wood sage	-	X	-	-
<i>Agalinis fasciculata</i> (Elliott) Raf./Beach false foxglove	X	-	-	-
Osmundaceae				
<i>Osmunda cinnamomea</i> L./ Cinnamon fern	-	X	-	-

Footnotes: 1 = present; 2 = not present

Table 1. Continued.

Vegetation Type	Mowed Sides of Road in Vegetation Community		Mowed Community	
Family/Genus/Species/Common Name	Mesic Flatwoods	Upland Mixed Forest (along Hidden Creek)	Scrubby Flatwoods	Scrub
Poaceae				
<i>Andropogon glomeratus</i> (Walter) Britton <i>et al.</i> / Bushy bluestem	X	-	X	X
<i>Andropogon virginicus</i> L./Broomsedge bluestem	X	-	X	X
<i>Aristida stricta</i> Michx. Var. <i>beyrichiana</i> (Trin. & Rupr.) D. B. Ward/Wiregrass	X	-	X	X
<i>Dactyloctenium aegyptium</i> (L.) Willd. Ex Asch. & Schweinf/Durban crowfootgrass	X	-	-	-
Other grasses	X	X	X	X
Polygalaceae				
<i>Polygala lutea</i> L./Orange Milkwort	-	-	-	X
Rubiaceae				
<i>Cephalanthus occidentalis</i> L./ Common buttonbush	-	X	-	-
Saururaceae				
<i>Saururus cernuus</i> L./Lizard's tail	X	-	X	X
Smilacaceae				
<i>Smilax auriculata</i> Walter/Earleaf greenbrier vine	X	-	X	X
<i>Smilax bona-nox</i> L./Saw greenbrier vine	X	X	X	X
Vitaceae				
<i>Vitis rotundifolia</i> Michx./ Muscadine	-	X	-	X
Zamiaceae				
<i>Zamia integrifolia</i> L./Florida arrowroot (Coontie)	-	-	-	X

Footnotes: 1 = present; 2 = not present

Foraging and feeding behavior

Promachus bastardii foraged primarily from the tops of vegetation up to 2.7 m above the ground. Only a few individuals foraged from the ground or debris on the ground. *Promachus dimidiatus* foraged from both the ground and vegetation, depending on ambient temperature (Lavigne and Holland, 1969). *Promachus noninterponens* Ricardo, 1920 (as *P. interponens*) foraged from vegetation 30 cm to 10 m above the ground (Daniels, 1976).

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Promachus bastardii that are actively foraging move to a new foraging site approximately every 10 seconds to 9 minutes. They change location by flying over the vegetation or by weaving in-and-out of vegetation for distances up to 7.6 m. Time spent at any one location varies with the individual and the weather (e.g., when clouds obscured the sun). Depending on the species, robber flies either forage from one location for variable periods of time or move frequently to new locations.

When foraging, *P. bastardii* frequently made investigatory flights without making contact with potential prey and followed prey with their abdomen gently curved up. Flights were for distances of 10 cm-3.7 m above, to the side of or in front of an individual's original foraging position and 30 cm-3.7 m above the ground. One female made a 1 m investigatory flight with a prey hanging from her proboscis. Following investigatory flights, *P. bastardii* typically landed at or within 46 cm of their original foraging locations. Investigatory flights are common for robber flies (Dennis, 2015a and b), possibly to help them identify suitable prey (Parmenter, 1952; Lavigne *et al.*, 2000).

Short flights around a foraging position without pursuing potential prey are called, "orientation flights" (Dennis and Lavigne, 1975). *Promachus bastardii* made orientation flights 2.5 cm-4.5 m (average 66 cm) away from its foraging position and 15-50 cm (average 26.5 cm) above the ground or moved to a new foraging site up to 3 m away. As summarized in Dennis (2015a and b), a number of investigators have commented on robber flies moving to new foraging locations to increase the probability of finding prey.

Many *P. bastardii* captured potential prey within approximately 2 m (average 55 cm) of their foraging position, 7.5 cm-2 m (average 33 cm) above the ground or up to 35.5 cm above or below its position on vegetation and released them while still in flight. Some species of robber flies may capture and release prey because they use both visual and other stimuli to select prey (Dennis and Lavigne, 1975).

Promachus bastardii captured all but three prey in the air when the prey were within 5 cm-1.5 m (average, 65 cm) in front of, to the side of, or behind their foraging positions and 5 cm-1.2 m (average, 45 cm) above the ground, at the same level as the robber fly or within 30 cm above the robber fly's position (three prey were captured within 20 cm below its position). Individuals captured prey on a grass blade and a rusty lyonia leaf; another prey might have been captured just as it landed on a scrub oak leaf. Both *P. dimidiatus* (Lavigne and Holland, 1969) and *P. noninterponens* (Daniels, 1976) captured prey in the air; *P. canus leontochlaenus* Loew, 1871 (as *P. leontochlaenus*) captured most of its prey in the air when they were within several cm to 3 m of their foraging position (Lehr, 1958).

Promachus bastardii would hold onto captured prey with all six tarsi during a hover, and manipulate the prey with its tarsi until it could insert its proboscis. The proboscis was generally inserted in the back of the prey's head, or in the dorsal or dorsolateral part of the prey's thorax. Both *P. dimidiatus* (Lavigne and Holland, 1969) and *P. noninterponens* (Daniels, 1976) inserted their proboscis in flight, generally in the cervical area of the prey.

Most *P. bastardii* moved at least once while feeding on a prey, to a new location up to 9 m from the previous location. It was not uncommon for some individuals to move two to eight times while feeding on a prey.

During feeding *P. bastardii* hovered above or near the feeding site, usually with the wings buzzing, and manipulated prey with all six tarsi for up to 32 seconds. Prey were manipulated one to seven times with an average of three times. Following prey manipulation, an asilid would land on the same feeding site or within 46 cm of the site. *Promachus dimidiatus* also hovered and manipulated prey near its feeding site (Lavigne and Holland, 1969).

The number of times that *P. bastardii* manipulates prey usually depended on both prey size and shape, and the amount of time spent feeding. A 9 mm long *Blauta falli* Brown, 1936 (Coleoptera: Elateridae) was fed on for 25.5 minutes and manipulated two times; a 11.5 mm unidentified pompilid wasp (Hymenoptera: Pompilidae) was fed on for 31.5 minutes and manipulated four times; and a 14 mm long *Bombus impatiens* Cresson, 1863 (Hymenoptera: Apidae) was fed on for 163.5 minutes and manipulated six times.

If *P. bastardii* initially inserted its proboscis in the prey's head or thorax, it would often manipulate the prey and insert the proboscis near the tip of the abdomen. Then after feeding for an irregular amount of time, the asilid would manipulate the prey again and insert the proboscis back in the thorax or another part of the abdomen. This sequence of manipulation and reinsertion of the proboscis could be repeated for up to three to four times.

When *P. bastardii* were feeding, prey hung free from the asilid's proboscis without being held by any tarsi.

Promachus bastardii often pumped the first one to three segments of the abdomen during feeding, and sometimes following foraging flights and during mating. Lavigne and Holland (1969) also observed abdominal pumping during feeding with *P. dimidiatus*. According to Musso (1968) and Lavigne and Holland (1969), abdominal pumping or contractions during feeding are associated with the injection of proteolytic enzymes into prey and ingesting liquefied food from prey. Abdominal pumping also might be for body temperature regulation. Morgan *et al.* (1985) found that periodic rapid contractions of the first three abdominal sternites of a tropical rainforest, light seeking *Promachus* species, indicated that heat transfer to the abdomen (i.e., transfer of warmed haemolymph from the thorax to the cooler abdomen) was reduced, and after the contractions stopped, heat transfer increased. Morgan and Shelly (1988) commented that physiological heat pumping might be important for thermoregulation in the desert robber fly *P. giganteus* during the hottest part of the day. This is accomplished by enhanced haemolymph flow from the thorax to the abdomen with contractions of the dorsal aorta and ventral diaphragm.

A male *P. bastardii* also exhibited abdominal pumping after it appeared to have been stung on his right fore leg by an unidentified wasp. The male captured and released the wasp in flight and when he landed on a barbed wire fence, he appeared

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disoriented, leaned forward at a 30° angle, had a difficult time walking, and limped when he tried to walk. These behaviors lasted approximately 4 minutes, then the male flew forward 15 cm to a scrub oak leaf, began shaking his right fore leg and pumping the first three segments of his abdomen. After about 1 minute, the male flew into nearby vegetation and was lost to sight.

As indicated in Dennis (2015a; 2015b), researchers have commented that the time robber flies spend feeding usually depends on prey length. *Promachus bastardii* fed on a 4.5 mm long scarab beetle (Coleoptera: Scarabaeidae) for 18.5 minutes. They fed longer on most larger prey, as for example 37 minutes on a 12.0 mm long pompilid wasp. Length of time that *P. bastardii* spent feeding on individual prey varied from 6.0 to 163.5 minutes, with an average of approximately 35 minutes for prey lengths of 3.5 to 15.0 mm, averaging 10.4 mm.

Male *P. bastardii* captured prey that were smaller than prey captured by females. Mean prey length for males was 9.0 mm (n = 11) with a range from 3.5-20.0 mm; for females mean prey length was 12.5 mm (n = 33) with a range from 4.0-31.0 mm. The overall mean prey length was 11.6 mm.

Mean predator to prey ratios show the relationship between predator to prey lengths, with a larger ratio indicating smaller prey. Based on the mean prey length and the mean length of 10 males and females each, the mean predator to prey ratio for *P. bastardii* was 2.4:1.0. This indicates that *P. bastardii* is almost 2 1/2 times as large as its prey. Mean predator to prey ratios for other species of robber flies range from 0.9:1.0 to 8.4:1.0 with a mean of 2.9:1.0 (Dennis, 2015a; 2015b).

At the completion of feeding, *P. bastardii* most frequently discarded prey by dropping them in flight, near or within 1.5 m of the feeding site, as it moved to a new location. At the feeding site it also, pushed prey off its proboscis with its fore tarsi; dropped prey during a hover while manipulating the prey with all of its tarsi; or allowed free-hanging prey to drop-off the proboscis. *Promachus dimidiatus* discarded prey by pushing it off its proboscis immediately after leaving the feeding site (Lavigne and Holland, 1969).

Interfeeding times for *P. bastardii* range from two to 42.5 minutes with an average of 18.4 minutes (n = 8).

One can calculate the theoretical number of prey an individual *P. bastardii* could feed on in one day if we assume that, it continually forages and feeds between 08:00 AM and 02:00 PM (the observed period of foraging and feeding activity for all individuals), and it captures and feeds on prey every 53.4 minutes (based on the average feeding and interfeeding times). Thus, over a 6-hour period an individual could feed on approximately 4 to possibly 5 prey. As summarized in Dennis (2015a; 2015b), other investigators have estimated that robber flies feed on from 1 to 35 prey per day.

Prey

Promachus bastardii fed primarily on Hymenoptera (59.4%), followed by Coleoptera (15.6%), Diptera (8.3%), and Hemiptera (4.2%) (Table 2). Other investigators have reported *P. bastardii* feeding on Coleoptera, Diptera, Hemiptera, Hymenoptera, and

Orthoptera (Bromley, 1914, 1931, 1934, 1946a, 1946b; Fattig, 1945; Hocking, 1952; Linsley, 1944, McAtee and Banks, 1920; Riley, 1870b, 1872 (both as *P. bastardi* Loew)). Lavigne and Holland (1969) reported that 87% of the 108 prey of *P. dimidiatus* were Hymenoptera, followed by Diptera (5.6%), Coleoptera (4.6%), Hemiptera (1.9%), and Lepidoptera (0.9%).

Table 2. Number and percent composition of orders of prey taken by *Promachus bastardi*.

	Male		Female		Total	
Order	Number	Percent	Number	Percent	Number	Percent
Coleoptera	6	19.4	9	13.8	15	15.6
Diptera	1	3.2	7	10.8	8	8.3
Hemiptera	2	6.5	2	3.1	4	4.2
Hymenoptera	17	54.8	40	61.5	57	59.4
Unidentified	5	16.1	7	10.8	12	12.5
Totals	31	100.0	65	100.0	96	100.0

Coleoptera and Hymenoptera made up the majority of prey for both male (74.2%) and female (75.3%) *P. bastardi*. However, about twice as many females as males were observed with prey. Numerous other investigators have reported collecting more female than male robber flies with prey, as discussed in Dennis (2015a; 2015b).

Promachus bastardi preyed on Hymenoptera primarily in the families Pompilidae, Scoliidae (*Campsomeris* spp.), Sphecidae, and Tiphiidae. However, *P. bastardi* frequently has been reported to feed on honeybees (*Apis mellifera* L.) (Apidae) (Alex, 1948; Bromley, 1930, 1931, 1934, 1942, 1946a, 1946b, 1947, 1948; Fattig, 1945; Linsley, 1960; Riley, 1870a, 1870b (both as *P. bastardi* Loew); Thorp, 1973). *Promachus fitchii* has been called the Nebraska bee-killer (Bromley, 1930, 1934, 1946b). *Promachus bastardi* has been called the false Nebraska bee-killer (Bromley, 1930, 1946b), because it was initially identified by Riley (1870b, 1872) as the same species as *P. fitchii*.

The following is a list of prey taken by *P. bastardi*. Number and sex of the predator (if known) is indicated following the prey record.

COLEOPTERA, Buprestidae: unidentified, 16.07.2013 (1♀). Elateridae: *Blauta cribraria* (Germar, 1844), 09.06.2015 (1♂, 1♀), 11.06.2015 (1♂), 15.06.2013 (1♀), 13.07.2013 (1♀); *Blauta falli* Brown, 1936, 10.06.2015 (2♂♂), 22.06.2015 (1♀), 01.07.2013 (1♀); *Blauta* sp., 10.06.2015 (1♂); Scarabaeidae: *Melanocanthus* sp. prob. *granulifer* (Schmidt, 1920), 06.07.2013 (1♀), 08.06.2015 (1♀); *Strigoderma pygmaea* (Fabricius, 1798), 06.07.2013 (1♂), 08.07.2013 (1♀). DIPTERA, Asilidae: *Proctacanthus fulviventris* Macquart, 1850, 29.06.2012 (1♀); *Proctacanthus longus* (Wiedemann, 1821), 05.06.2012 (1♀); *Proctacanthus* sp., 12.06.2012 (1♀), 26.07.2013 (1♀). Conopidae: unidentified, 13.05.2015 (1♂). Mydidae: *Mydas maculiventris* (Westwood, 1835), 17.06.2014 (1♀), 02-07.2012 (1♀); Unidentified:

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14.05.2015 (1♀). HEMIPTERA: Flatidae: *Ormenaria rufifascia* (Walker, 1851), 11.06.2015 (1♀); Membracidae: *Ophiderma* sp., 11.06.2015 (1♀); unidentified, 01.05.2015 (1♂), 10.06.2015 (1♂). HYMENOPTERA, Apidae: *Bombus impatiens* Cresson, 1863, 04.06.2015 (1♀); *Bombus* sp., 30.06.2014 (1♀), 08.08.2014 (1♀). Colletidae: *Colletes* sp., 22.05.2015 (1♂). Formicidae: unidentified (alate), 11.06.2015 (1♀). Ichneumonidae: unidentified, 04.06.2012 (1♂). Megachilidae: *Megachile* sp., 03.07.2015 (1♀). Mutillidae: *Dasymutilla* sp. (2 winged ♂♂), 08.07.2013 (♂), 12.07.2013 (1♀). Pompilidae: unidentified, 18.05.2015 (1♀), 26.05.2012 (1♀), 26.05.2014 (1♀), 10.06.2011 (1♀), 11.06.2012 (1♂), 01.07.2014 (1♀). Scoliidae: *Campsomeris plumipes fossulana* (Fabricius, 1804), 05.06.2012 (1♀), 10.06.2014 (1♂); *Campsomeris quadrimaculata* (Fabricius, 1775), 14.06.2012 (1♀), 18.06.2012 (1♀), 23.06.2012 (1♂); *Campsomeris* sp., 14.06.2012 (1♀). Sphecidae: unidentified, 26.05.2012 (1♀), 04.06.2012 (2♀♀), 13.06.2012 (1♀). Tiphidae: unidentified, 02.07.2012 (1♀), 10.07.2012 (1♀), 13.07.2013 (1♂, 1♀). Unidentified: 11.05.2015 (1♂), 13.05.2015 (1♂), 16.05.2015 (1♂), 18.05.2015 (♂), 03.06.2015 (2♂♂), 04.06.2015 (1♀), 05.06.2012 (1♀), 06.06.2015 (1♂), 08.06.2015 (1♀), 10.06.2015 (1♀), 12.06.2015 (1♀), 15.06.2012 (1♂), 18.06.2013 (1♂, 3♀♀), 02.07.2012 (1♀), 03.07.2014 (1♀), 04.07.2012 (1♀), 05.07.2013 (2♂♂). Vespidae: *Mischocyttarus mexicana cubacula* (Richards, 1978), 03.06.2015, (1♀), 06.06.2015 (1♂); *Monobia quadridens* (Linnaeus, 1763), 3.06.2015 (1♀); *Polistes* sp., 19.05.2015 (1♀); *Vespula* sp., 22.05.2015 (1♂); *Vespula squamosa* (Drury, 1770), 12.06.2015 (1♀), 18.07.2014 (1♀), 06.08.2014 (1♀). UNIDENTIFIED: 12.05.2015 (1♂), 19.05.2015 (1♂), 27.05.2015 (1♂), 04.06.2015 (1♀), 11.06.2012 (1♀), 15.06.2012 (1♂), 17.06.2013 (2♀♀), 18.06.2013 (1♂), 29.06.2012 (1♀), 01.07.2013 (1♀), 05.07.2013 (1♂, 1♀).

Courtship and mating behavior

Male *P. bastardii* perform searching flights for females with which to mate. Flights consist of a male flying 3-6 m, 15-61 cm above the ground or slightly above vegetation that varies from 15-76 cm in height, in a straight or zigzag flight weaving in and out of vegetation, often with slight vertical undulations. While in flight the male's wings may make a high pitched buzzing sound, the abdomen is straight to slightly curved up, the fore- and mid-legs are held against the thorax with the tibiae and tarsi extending forward, and the hind legs are also held against the thorax or hang down to the posterior at a 30-45° angle. *Promachus dimidiatus* males have been reported to have similar searching flights for receptive females with which to mate (Lavigne and Holland, 1969). Hastings *et al.* (1994) found that when male *P. albifacies* perch on shrubby plants used by females as oviposition sites, it enhances their finding and mating with females.

While *P. bastardii* males searched for receptive females with which to mate, they would often encounter and hover in front of or circle around other males with their wings buzzing loudly. A few males briefly came into contact or chased one another. Similar behavior has been observed for *P. albifacies* (Hastings *et al.*, 1994) and *P. dimidiatus* (Lavigne and Holland, 1969).

Upon locating a female on debris or branches on the ground or on vegetation up to 1.5 m above the ground, the male stops at the same level 15-25 cm directly in front of the female or to her side. He then hovers for 5-34 seconds (average approximately 18 seconds) with his wings making a loud, high pitched buzzing sound. The male's abdomen is straight to slightly curved up, while the fore- and mid-legs are held against the thorax with the tibiae and tarsi extending forward. The hind legs appear to hang down or to the posterior at a 30-45° angle with the hind tibiae and tarsi bent slightly forward or hanging straight down. In this position, the femora, in particular the hind femora, extend away from the thorax or almost straight out at a 90° angle and may hang down slightly (see Raney (2015) for a photograph of a courting male). During the hover most males remained stationary or had only a slight oscillation forward and backward, before flying forward to mate with the female. One male backed-up 45 cm from his courtship hover position, before flying forward to mate with the female. Hull (1942) reported similar courtship behavior for *P. bastardii* with the male backing up before flying forward to mate with a female. Variations of this type of aerial courtship with respect to length of time of male courtship, distance to female, and/or positions of the male's legs have been reported for an unidentified *Promachus* species (*Promachus* sp.) (Kershaw, 1912); *P. dimidiatus* (Lavigne and Holland, 1969); *P. noninterponens* (Daniels, 1976); and *P. latitarsatus* (Macquart, 1839) (Geller-Grimm and Geisthardt, 1996).

Many species of insects exhibit courtship behavior, including sound production, visual displays, ritualized movements (dancing), tactile stimulation, and nuptial gifting. The loud buzzing sound that the wings of the male *P. bastardii* and *P. dimidiatus* (Lavigne and Holland, 1969) make during the courtship hover may be a courtship cue for the female. According to Lavigne (2002), the white abdominal tips on male *P. bastardii*, *P. albifacies*, *P. dimidiatus*, and *P. latitarsatus*, and the hind leg color (shining silver-white hairs on the dorsal and anterior surfaces of the tibiae) of male *P. noninterponens* are visual cues for females during courtship.

Male *P. bastardii* sometimes courted and mated with females that had prey, although most females did not. Hull (1942) also observed a male *P. bastardii* successfully court and initiate mating with a female that was feeding on a honeybee. Lavigne and Holland (1969) found that male *P. dimidiatus* courted and mated with females that had prey.

Three male *P. bastardii* exhibited unusual courtship behavior. One courted another male *P. bastardii*, another courted a male *Proctacanthus longus* (Wiedemann, 1821), and yet another courted a grayish white sand pine cone (55 mm long, 25 mm at its base, tapering to 6 mm at its tip). With respect to the latter, the male briefly hovered about 10 cm from and at the same level as the pinecone, then flew forward and landed on the middle of the cone before flying away.

The majority of *P. bastardii* courtship hovers that resulted in mating were when the male courted the female from either her right or left side and not directly in front of her. If the female was receptive to mating, she did not move as the male flew forward, landed on her dorsum and initiated mating in the male-over-female position with his abdomen to the right or left of the female's abdomen and clasping her genitalia from below. Non-receptive females flew off during the male courtship hover or while the

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male was trying to clasp their genitalia. One female curved her ovipositor down so that the male was unable to clasp her genitalia and then flew off with the male chasing her.

Lavigne (2002) reported *P. bastardii* mating in both the male-over-female and tail-to-tail position, *P. dimidiatus* in the male-over-female position, and *P. fitchii* and *P. rufipes* in the tail-to-tail position. *Promachus canus leontochlaenus* mated all night in the tail-to-tail position (Lehr, 1958, 1961).

In the male-over-female position (Fig. 3), the wings of both male and female *P. bastardii* are usually spread at a 40 to 90-degree angle to their bodies, although some males have their wings spread only enough to go around their abdomens. The female's wings pass between the male's fore and mid legs or mid and hind legs so that the male's mid tibiae are over the female's wing bases. The male's fore tarsi either rest on the female's head, eyes or anterior part of her thorax, or grasp vegetation slightly to the side of the female's thorax. The male's mid tarsi may grasp either vegetation below the mating pair or the underside of the female's thorax; rest on her mid femora; or hang free with the male's mid femora and tibiae passing around or holding onto the female's thorax or near where the female's thorax and abdomen join. The male's hind legs pass around the female's abdomen. The hind tarsi and sometimes the tibia on the same side where the male's abdomen passes to the side of the female's abdomen, hang free or hold onto the underside of the female's abdomen. The male's opposite tarsi, tibia and possibly distal part of the femur, stroke the side and/or underside of the female's abdomen from anterior to posterior. Sometimes both the male's right and left tarsi and tibiae stroke the female's abdomen; although if on the same side as where the male's abdomen curves under the female's abdomen, the male's tarsi and tibia often are not in contact with the female's abdomen and still exhibit the stroking action. Because males are generally smaller than females, the posterior part of the female's abdomen was usually curved up or held straight up at a 90° angle.



Fig. 3. Mating pair of *Promachus bastardii* in the male-over-female position.

While a male *P. bastardii* strokes the female's abdomen, he also pulls or flexes her abdomen up and down. For some matings, stroking and flexing of the female's abdomen continued for the entire mating or stopped 1-3 minutes before the end of mating. Stroking and flexing usually took place for the first 8-23 minutes (average, 13 minutes) of mating, then alternately stopped for 5-78 seconds (average, 25 seconds) and resumed for 2-70 seconds (average, 17.4 seconds) until the end of mating.

Promachus bastardii matings were initiated in both the sun and shade. When in the sun, the mating pair would often move into a shaded area of vegetation where it is slightly cooler. Also, if a mating started in the shade and the pair was exposed to the sun, the female would often adjust their position so that they were again in the shade.

The mating pair generally remained motionless and males did not buzz their wings. However, in one partial mating, the male buzzed his wings three times for 24, 31 and 10 seconds, for 10, 8 and 5 minutes, respectively, before the end of mating; and in another complete mating the male briefly buzzed his wings twice, 3 minutes before the end of the mating. *Promachus dimidiatus* males buzzed their wings at least once during all matings, although there was not a discernable pattern (Lavigne and Holland, 1969).

The author observed 21 mating pairs, 9 of which were complete matings that lasted 12.5 to 25 minutes, with an average of 18.4 minutes. Matings occurred when the air temperature at the height where the mated pair rested on vegetation ranged from 29-33°C (average, 31.2°C) in the shade, to 30-34.5°C (average, 32.4°C) in the sun. *Promachus dimidiatus* mated for 2.5 to 5 minutes (Lavigne and Holland, 1969).

At the completion of mating, male *P. bastardii* usually released the female and both flew away. Two mating pairs flew into the air in the male-over-female position, then assumed the tail-to-tail position and separated. Multiple mating was not observed for either male or female *P. bastardii*. Lavigne and Holland (1969) noted that male *P. dimidiatus* mate with more than one female, but did not observe females mating with more than one male. Lehr (1958) marked both male and female *P. canus leontochlaenus* and determined that both sexes may mate several times. Based on the worn wings of two female *P. flavopilosus* Ricardo, 1920, Jackson (1954) made the observation that mating is not restricted to freshly emerged individuals.

Oviposition behavior

Promachus bastardii females searched for suitable oviposition sites by flying from one potential site to another and probing each site with their ovipositor. They probed a wide variety of both live and dead vegetation, including the stem of a vanillaleaf plant 45 cm above the ground; live oak tree branches and leaves 3.1 m above the ground; live saw greenbrier vine stem and dead live oak tree branch, both 1.2 m above the ground; between two live rusty lyonia leaves and on a branch 2.5 m above the ground; and a slash pine tree branch and small log, and under oak leaves on the ground. However, the successful ovipositions were in the dried seed heads of sparkleberry and rusty lyonia (Fig. 4), 1.8 m and 2.1 m above the ground, respectively; and in a cynipid wasp (Hymenoptera: Cynipidae) oak bullet gall.



Fig. 4. Female *Promachus bastardii* ovipositing in seed head of rusty lyonia.

Lavigne and Holland (1969) observed *P. dimidiatus* females searching for oviposition sites and probing with their ovipositors in both dead and live stalks of vegetation, but they only oviposited in dry, dead stalks or seed heads. Hastings *et al.* (1994) reported *P. albifacies* ovipositing on the dead flower stalks of soaptree (as narrow-leaf) yucca (*Yucca elata* (Engelm.) Engelm.) or a dead stem of tree or cane (as staghorn) cholla (*Cylindropuntia imbricata* (Haw.) F.M. Knuth; as *Opuntia arborescens*).

Kershaw (1912) observed *Promachus* sp. ovipositing on the upper end of grass stalks and the bare ends of twigs of woody herbs 61-91 cm above the ground. Yonezu (1998) reported *P. yesonicus* Bigot, 1887 ovipositing on a Eulalia or Chinese silver grass leaf (*Miscanthus sinensis* Andersson). *Promachus canus leontochlaenus* oviposited on "...thin branches of umbelliferous plants (most often ferula), panicle and the upper parts of grain stalks (meadow grass), wheat-ears, and dry branches of various other bushes" and tamarisk (Lehr, 1958). *Promachus canus* (Wiedemann, 1818) oviposited on the stalk of camelthorn (Fabaceae, *Alhagi maurorum* Medik.; Lehr, 1961).

Female *P. bastardii* probing potential oviposition sites have their heads and dorsal surfaces facing up or down, wings closed, and they curve or curl their abdomens under themselves so that the tip of the ovipositor touches the site. They then move their ovipositors rapidly around, feeling about with their tips. With their ovipositors in dried seed heads, the females would remain stationary for up to 91 seconds as they probed with their ovipositors. On branches and logs they would crawl about while probing. If a female did not find an acceptable location, she flew to another location to repeat the searching. Similar oviposition behavior has been observed for other species of *Promachus* (Hastings *et al.*, 1994; Kershaw, 1912; Lavigne and Holland, 1969; Lehr, 1958, 1961; Yonezu, 1998).

The sparkleberry and rusty lyonia dried seed head oviposition locations were 4-5 mm long and wide, with an approximate 4 mm wide opening where the female inserted her ovipositor into the bottom of the seed head. The female would then deposit eggs in two to three chambers of the seed head. One female oviposited twice in the chambers of a rusty lyonia seed head. The female that oviposited in the oak bullet gall inserted her ovipositor in a small opening in the gall where the gall attached to the oak tree branch. The gall was 9 mm wide and 6 mm high and was probably hollow, based on an examination of other nearby galls.

Like some other genera (i.e., *Mallophora*, *Megaphorus*, *Porasilus*) in the subfamily Asilinae (Dennis *et al.*, 2013), *P. bastardii* deposited their eggs in a frothy-white "case" that hardened to a porous material. Kershaw (1912) found that the eggs of *Promachus* sp. were deposited in an ootheca or egg case consisting of a whitish, waxy-looking colleterial material (i.e., sticky substance) that hardened after about an hour to a microscopically porous material. *Promachus canus leontochlaenus* and *P. canus* oviposited eggs in a foamy white secretion or covering, and *P. yesonicus* oviposited eggs in a white mousse type of exudate (Lehr, 1958, 1961; Yonezu, 1998).

While one female *P. bastardii* was probing a live oak branch with her ovipositor, a male courted her and mating ensued. Lavigne and Holland (1969) observed female *P. dimidiatus* moving from one oviposition site to another and being courted by males that resulted in mating.

Promachus bastardii oviposition took 165 to 496 seconds with an average of 312 seconds. Ovipositions were in both the sun and shade of surrounding vegetation. Air temperatures in the sun at the height of ovipositions ranged from 31.5-34°C with an average of 32.8°C; temperatures in the shade ranged from 30-33°C with an average of 32°C.

One female *P. bastardii* oviposited five times over an approximate 21 minute period before being lost to sight. Between the second and third ovipositions the female groomed her ovipositor with her hind tarsi. *Promachus dimidiatus* females also can have a sequence of ovipositions (Lavigne and Holland, 1969). According to Lavigne *et al.* (2000) females of many species of robber flies have been known to oviposit several times.

Thirty to 37 eggs (average 34 eggs) were recovered from each of four *P. bastardii* ovipositions. *Promachus dimidiatus* deposited two to 31 eggs per oviposition (Lavigne and Holland, 1969). It was estimated by Kershaw (1912) that *Promachus* sp. oviposited over 50 eggs in an ootheca 9.5 mm long and 4.8 mm wide and high. *Promachus canus leontochlaenus* deposited three to 18 eggs in a mass that varied from 3.2-10.0 mm long, 2.3-3.4 mm wide, and 2.0-3.7 mm high (Lehr, 1958).

Eggs of *P. bastardii* are shiny-white, oblong, and straight to slightly concave. They range in length from 1.2-1.5 mm, with a mean of 1.4 mm; range in width is from 0.3-0.5 mm, with an average of 0.5 mm. The eggs are like those of many other species of robber flies including *P. dimidiatus* (Dennis *et al.*, 2013; Lavigne and Holland, 1969) and *Promachus* sp. (Kershaw, 1912), although the eggs of *P. canus leontochlaenus* are a light yellow (Lehr, 1958).

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Promachus bastardii larvae from the eggs of one oviposition emerged 6-7 days after they were deposited. Lavigne and Holland (1969) and Kershaw (1912) observed a similar time frame for hatching of *P. dimidiatus* and *Promachus* sp. eggs. Lehr (1958) found that *P. canus leontochlaenus* eggs hatch after 5-8 days.

Grooming

Promachus bastardii groomed when resting on debris on the ground or on vegetation and during feeding (i.e., hind tarsi, tops and bottoms of wings, abdomen and genitalia). They groomed in much the same way as reported for other species of robber flies (Dennis, 2015a; b). They used the fore legs to groom their faces, and the hind legs to groom their wings, abdomen, and genitalia. Before grooming the face, they extended and elevated the fore legs slightly and usually rubbed together the fore tarsi. Also, prior to grooming the face, *P. bastardii* would often groom the fore tarsi and tibiae by moving the fore tarsi back and forth along their length or by wrapping the fore tarsi and distal part of the tibiae around each other and then alternately moving the legs back and forth. The face, including the eyes, would be groomed by rubbing with the inside of and distal part of both front femora, tibiae, and proximal part of the tarsi, or the front tibiae and proximal part of the tarsi. Often this would be accompanied by quick rotations of the head.

Promachus bastardii usually leaned forward and rubbed their hind tarsi together prior to grooming the abdomen, genitalia, and wings. The abdomen was then curved down to as much as a 90-degree angle, as they groomed the abdomen, genitalia, and tops and bottoms of the posterior part of the wings with the hind tibiae and/or hind tibiae and tarsi. Sometimes the abdomen appeared to be pulled down as they groomed its posterior third to half. They either closed their wings or spread them to a 30 to 45-degree angle while grooming up to the posterior half or tips, the latter from inside to outside. Grooming of the wings and abdomen was always from anterior to posterior as observed for other species of robber flies (Dennis, 2015a; b).

Promachus bastardii commonly groomed while resting and between foraging flights. The face was quite frequently groomed after feeding, as was grooming of the abdomen and genitalia after mating, and between and after ovipositing. Lavigne and Holland (1969) commented that *P. dimidiatus* spent considerable time grooming its proboscis, legs, and wings after feeding and before foraging again or another behavior. Lehr (1958) commented on female *P. canus leontochlaenus* resting and grooming after ovipositing.

Like most robber flies (Dennis, 2015a; b), *P. bastardii* never groomed its thorax.

Daily rhythm of activity

Promachus bastardii exhibited a distinct diurnal or daily rhythm of activity between 08:00 AM and 03:00 PM (all times are Eastern Daylight Saving Time) for mating, ovipositing, and feeding (Fig. 5). Individual flies fed primarily from 08:00 AM to 01:00 PM (86.5%), with the peak between 09:00 AM to 12:00 noon (62.5%). Most mating occurred from 09:00 AM to 12:00 noon (76.2%), with the peak from 10:00 to 11:00

AM (38.1%), which was in the middle of the peak feeding time. Oviposition peaked from 11:00 AM to 12:00 noon (85.7%), towards the end of both the feeding and mating peaks. The percentage of matings and ovipositions quickly dropped off after 12:00 noon to 01:00 PM; whereas, the percentage of feeding individuals was a more gradual decline during the afternoon. Twenty three percent of feedings were between 12:00 noon to 03:00 PM and 2.0% were between 04:00 and 06:00 PM. In general, as with some other species of robber flies, as the frequency of occurrence of one behavior increased, others decreased (Dennis, 2015a; 2015b).

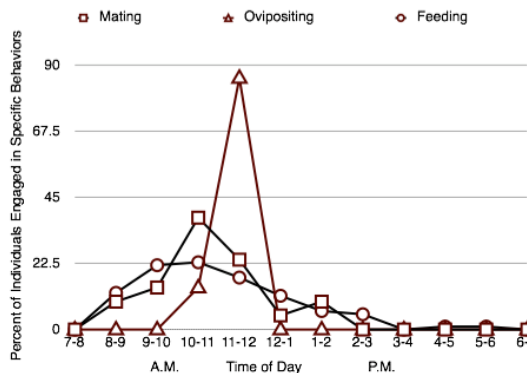


Fig. 5. Daily rhythm of activity of *Promachus bastardii* based on 21, 7, and 96 observations for mating, ovipositing, and feeding, respectively.

Hull (1942) observed a mating pair of *P. bastardii* as late as 04:00 PM. Lavigne and Holland (1969) found that *P. dimidiatus* mated during all times of the day, but most frequently in mid-morning and late afternoon. Most ovipositions for this species were in the late morning between 10:00 AM to 12:00 noon. Daniels (1976) reported that *P. noninterponens* engaged in courtship and associated mating, mainly between 10:00 AM and 03:00 PM.

Pine and other trees surrounded the mowed sides of the road in the mesic flatwoods community where the largest population of *P. bastardii* were studied. This area was mostly in shade until between 07:30 to 08:00 AM and after 04:30 to 05:00 PM. As a result, robber flies did not become active in this area until it was exposed to the sun. Late in the afternoon, when the area began to be in shade, *P. bastardii* would move to nearby, higher (2.5-3.5 m tall), uncut vegetation that was still in the sun. It is assumed that the asilids spent the night in this taller, more protected area of the habitat. *Promachus dimidiatus* spent the night on vegetation 15-30 cm above the ground (Lavigne and Holland, 1969).

Robber flies generally are most active when the sun is shining. However, even when the sky was overcast and the author could still see a dim shadow, *P. bastardii* continued to forage, mate, and oviposit. Dennis (2015a; 2015b) reported similar behavior in the MCCA for *Diogmites crudelis* Bromley, 1936 and *Proctacanthus fulviventris* Macquart, 1850.

Promachus bastardii also continued to forage, mate, and oviposit with a very light rain (scattered drops that did not completely wet an exposed surface regardless of

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duration), with a steady wind of 3.2-4.8 km/hr and wind gusts up to 8.9 km/hr. In general, robber flies decrease or stop activities in bad weather (overcast or cloudy sky, light to heavy rains, high winds).

Predators and parasites

The same species of robber flies often prey on one another (Lavigne *et al.*, 2000). This was not observed for *P. bastardii*, although one female captured and released another female. Lavigne and Holland (1969) also did not observe *P. dimidiatus* being cannibalistic. However, Riley (1870a) indicated that *P. bastardii* "... are cannibals, and quite ravenous...".

Barnes (2010) reported *P. bastardii* as prey of *Diogmites angustipennis* Loew, 1866.

Mites were observed on the thorax of *P. bastardii* and are often found on other robber flies (Lavigne *et al.*, 2000).

There are a number of ants (Formicidae, *Formica* spp. and *Solenopsis invicta* Buren, 1972) in the same habitats as *P. bastardii*. When the ants crawled on the asilids' tarsi, the asilids would shake them off and then usually fly to a new location. Also, if a number of ants crawled around the asilids or on the prey, *P. bastardii* would often relocate.

CONCLUSIONS

There exists information on some aspects of the ethology, not including prey and/or habitat, of only five of 22 Nearctic species of robber flies in the genus *Promachus* (*P. albafacies*, *P. bastardii*, *P. dimidiatus*, *P. giganteus*, and *P. rufipes*) in the United States. This paper provides more detailed information on *P. bastardii*. This species rests on the ground, on debris or dead vegetation on the ground, and on the stems and leaves of live vegetation. In this study, they rested mainly in the shade of vegetation, and as a result, in order to regulate their body temperature they usually did not make changes in their position in relation to the sun. Foraging took place primarily from vegetation, with only a few individuals foraging from the ground or debris on the ground. Most prey were captured in flight and consisted of Hymenoptera (59.4%), Coleoptera (15.6%), Diptera (8.3%), and Hemiptera (4.2%). During feeding, *P. bastardii* hovered above or near the feeding site and manipulated prey with all six tarsi. Males performed searching flights for females with which to mate. Mating occurred in the male-over-female position. Females oviposited in dried seed heads of sparkleberry and rusty lyonia, and an oak bullet gall; 30 to 37 eggs were recovered from each of four ovipositions. Peak period for feeding was from 09:00 AM to 12:00 noon; for mating 10:00 to 11:00 AM; and for ovipositing 11:00 AM to 12:00 noon. *Promachus bastardii* groomed both during resting and feeding.

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