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Ethology of *Diogmites crudelis* Bromley, 1936 (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

ABSTRACT

Diogmites crudelis Bromley, 1936 (during 106 hours of observation) foraged from the ground and vegetation, capturing and immobilizing prey in flight. Identified prey came from three insect orders (Diptera, Hemiptera, and Hymenoptera), with Hymenoptera making up 81.7%. Mating occurred in the tail-to-tail position and oviposition was in the ground, typically in the shade of vegetation when the sun was shining. This species exhibited a distinct daily rhythm of activity for feeding from 10:00 AM to 3:00 PM and oviposition from 10:00 AM to 1:00 PM. Habitats, resting behavior, grooming behavior, and predators and parasites also are discussed.

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

INTRODUCTION

The genus *Diogmites* has 175 species and is found only in the Nearctic and Neotropical zoogeographic regions of the world (Barnes, 2010; Geller-Grimm, 2013). There are 22 species in the United States of America (U.S.A.) part of the Nearctic region and the ethology of two species [*D. angustipennis* Loew, 1866 (Lavigne and Holland, 1969) and *D. missouriensis* Bromley, 1951 (Scarbrough, 1979)] has been described in detail, with other publications limiting themselves to habitat and prey (*D. angustipennis* in Barnes, 2010; Bromley, 1930 as *Deromyia angustipennis* and *Deromyia symmacha*, 1934 as *D. angustipennis* and *D. symmachus*, 1936 as *D. angustipennis*, *D. grossus*, and *D. symmachus*; Cole, 1969 as *D. angustipennis* and *D. grossus*; Dennis *et al*., 2010; James, 1938 as *D. angustipennis* and *D. symmachus*; Lavigne and Pfadt, 1966; Linsley, 1958 as *D. symmachus*, 1960 as *D. angustipennis*, *D. symmachus*, and *D. grossus*; Scarbrough, 1972 as *D. symmachus*; and *D. missouriensis* in Artigas, 1966; Bromley, 1950b; Dennis *et al*., 2010; Scarbrough, 1972).

Information primarily on habitat and/or prey and some behavioral observations for other species of *Diogmites* has been reported for: *D. basalis* (Walker, 1851) (Artigas, 1966; Baker and Fischer, 1975; Bromley, 1914, 1930, 1931a and b, all as *Deromyia umbrina* Loew, 1866); Bromley, 1936, 1942, 1946b, 1947, 1950b, all as *D. umbrinus*; Goslin, 1950 as *D. umbrinus*; Linsley, 1958 as *D. umbrina*, 1960 as *D. umbrinus*; McAtee and Banks, 1920 as *Deromyia umbrina*); *D. bilobatus* Barnes, 2010 (Barnes, 2010); *D. contortus* Bromley, 1936 (Bromley, 1936; Cole, 1969); *D. crudelis* Bromley, 1936 (Artigas, 1966; Bromley, 1936, 1946a, 1950a; Fattig, 1945); *D. discolor* Loew, 1866 (Artigas, 1966; Baker and Fischer, 1975; Bromley, 1930, 1931a both as *Deromyia*, 1936, 1942, 1946a and b, 1947, 1948, 1950b; Fattig, 1945; McAtee and Banks, 1920 as *Deromyia*; Reinhard, 1924 as *Deromyia*; Scarbrough, 1974); *D. esuriens* Bromley, 1936 (Artigas, 1966; Bromley, 1936, 1946a, 1950a as *D. esuriens* and *D. bilineata*; Fattig, 1945); *D. misellus* Loew, 1866 (Artigas, 1966; Baker and Fischer, 1975; Bromley, 1914 as *Deromyia winthemi* Wiedemann, 1821, 1931a and b as *Deromyia misella*, 1936, 1946a and b, 1950a; Fattig, 1945; Goslin, 1950; McAtee and Banks, 1920 as *Deromyia winthemi*; Scarbrough, 1972); *D. neoternatus* (Bromley, 1931) (Artigas, 1966; Baker and Fischer, 1975; Bromley, 1931a and c as *Deromyia neoternata*, 1934, 1936, 1946a, 1950a and b as *D. neoternatus*; Cole, 1969; Dennis and Gowen, 1978; Fattig, 1945; Goslin, 1950; James, 1938; Scarbrough, 1974 as *D. neoternatus*); *D. perplexus* (Back, 1909) (Walton, 1914 as *Deromyia perplexa*); *D. platypterus* Loew, 1866 (Artigas, 1966; Baker and Fischer, 1975; Bromley, 1950a; Lavigne, 2002; Scarbrough, 1972); *D. properans* Bromley, 1936 (Bromley, 1936); *D. salutans* Bromley, 1936 (Artigas, 1966; Bromley, 1936, 1946a, 1950a); *Diogmites* spp. (Artigas, 1966; Dennis and Lavigne, 2007; Dennis *et al*., 2009, 2010, 2012; Bromley, 1936, 1946b; Linsley, 1958, 1960); *D. ternatus* Loew, 1866 (Rau, 1938 as *Deromyia*); and *D. texanus* Bromley, 1934 (Bromley, 1934; Linsley, 1958, 1960).

This paper provides detailed information on the ethology of *D. crudelis* in areas of the Moses Creek Conservation Area (MCCA) in St. Augustine in northeastern Florida, U.S.A. *Diogmites crudelis* is a light reddish to reddish brown, large species varying in length from 24-48 mm. There are two short, darker lines on the mesonotum and sometimes two small dark spots. The abdomen has dark dorsal bands fading into reddish brown medially in some specimens and more or less interrupted in others (Artigas, 1966; Bromley, 1936).

MATERIALS AND METHODS

Diogmites crudelis is widely distributed in Florida and, depending on location, generally occurs from May through September. Observations were made over three field seasons, from: 5 July through 19 October 2011; 5 July through 25 September 2012; and 6 July through 16 September 2013. The author observed a number of *D. crudelis* in the MCCA along the mowed roads in three vegetation communities (scrub, scrubby flatwoods, and mesic flatwoods) and in a mowed scrub community. Some individuals flew into the nearby woods, but because of the thick or dense vegetation it was not possible to follow them.

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

The times when *D. crudelis* were most abundant in the previously mentioned areas in the MCCA determined the periods of study. Observations during these times involved an average of three individuals per day, each for up to 189 minutes. Total number of hours of observation equaled approximately 106.

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

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

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

Some ovipositions were in sugar sand. This is a fine silt made up of ultrafine mineral sand mixed with a large percentage of organic granules. It resembles fine sugar.

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

RESULTS AND DISCUSSION

Habitat

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

Bromley (1950) stated that *D. crudelis* occurred in Florida "in tall grass." Artigas (1966) noted that *D. crudelis* occurs in tall grass in open areas and that *Diogmites* "…commonly occur along woodland edges, the shores of streams, and in open fields with low vegetation." Hull (1962) commented that *Diogmites* "…prefer rather dense, rank, low growing vegetation in damp or swampy areas" and are sometimes abundant in old fields.

Fig. 1. *Diogmites crudelis* habitat in scrub community.

Resting Behavior

Diogmites crudelis rested primarily in the shade of leaves on live and dead vegetation (e.g., Elliott's white milk pea, scrub oak, and tailed bracken) 7.5-30 cm above the ground. A few individuals rested on the tops of vegetation up to 50 cm above the ground, and on the ground or dead vegetation on the ground. Because *D. crudelis* rested mainly in the shade of vegetation, they usually did not make changes in their position in relation to the sun in order to regulate their body temperature as some other species of robber flies do. One individual resting on vegetation in the sun, appeared to change position so that its right side was to the sun. Dennis and Lavigne (1975) observed that some robber flies regulate their body temperature by moving to the shaded side of vegetation.

Diogmites crudelis rests and forages with its abdomen either parallel to the surface that it is on or at a 45-degree angle. When resting, individuals will move their heads vertically and laterally in response to other insects flying by. They also may groom their face, fore tarsi, abdomen, wings, and hind tarsi and tibiae. *Diogmites angustipennis* (Lavigne and Holland, 1969) and *D. missouriensis* (Scarbrough, 1979) exhibited similar head and body movements when on their foraging perches.

Diogmites crudelis usually rested for 4 to 12 minutes before moving to a new location, although a few individuals remained in the same locations in the shade of vegetation for 19 to 36 minutes.

Table 1. Vegetation in areas in which *Diogmites crudelis* was studied in the Moses Creek Conservation Area.

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

[1] Footnote: X = present; - = not present.

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

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

[1] Footnote: X = present; - = not present.

While resting and feeding, a number of *D. crudelis* expelled a drop of creamy-white to white liquid from the anus. According to Lehr (1958c) the expulsion of liquid from the anal opening is common in robber flies.

Foraging and Feeding Behavior

Diogmites crudelis foraged primarily from the tops of vegetation 20-75 cm above the ground. Only a few individuals foraged from the ground. *Diogmites angustipennis* foraged from both the ground and vegetation, depending on ambient temperature (Lavigne and Holland, 1969). *Diogmites missouriensis* usually foraged from the tops of low growing vegetation less than 60 cm above the ground (Scarbrough, 1979).

Diogmites crudelis that are actively foraging move to a new foraging site approximately every 1 to 7 minutes. They change location by flying over the vegetation or by weaving in-and-out of vegetation.

When foraging, *D. crudelis* frequently made investigatory flights without making contact with potential prey. Flights were for distances of 45 cm to 2 m slightly behind, above, to the side of or in front of an individual's original foraging position and 10 cm to 1 m above the ground. Investigatory flights are common for robber flies (Dennis, 2012, 2013; Dennis and Lavigne, 1975; Dennis *et al*., 1975; Lavigne, 1964; Lavigne and Dennis, 1975; Lavigne and Holland, 1969; Melin, 1923). Parmenter (1952) and Lavigne *et al*. (2000) indicated that investigatory behavior is probably necessary because some robber flies cannot identify suitable prey except at a short distance. Lehr (1958c) noted that robber flies often cannot determine whether a flying insect is an acceptable prey.

Following investigatory flights, *D. crudelis* typically landed near their original foraging locations, although one individual moved approximately 3 m from its first location. Even if *D. crudelis* did not make investigatory flights they changed their foraging locations after periods ranging from a few seconds to 24 minutes. Time spent at any one location varied with the individual and the weather (e.g., when clouds obscured the sun). Hayat and Çalışkan (2003) observed that male *Dasypogon irinelae* Weinberg, 1986 remain at one location for longer periods of time than females.

Dennis and Lavigne (1975) called short flights around a foraging position without pursuing potential prey, “orientation flights.” *Diogmites crudelis* made orientation flights within 3-8 m of its foraging position and 5-45 cm above the ground or moved to a new foraging site up to 30 m away. Lavigne (1992) observed *Colepia abludo* (Daniels, 1983) (as *Neoaratus*) making orientation flights in excess of 10 m after the asilids stayed in one location for an extended period. He presumed the long flight was in response to the lack of potential prey in the immediate vicinity or was a strategy used by males to relocate when no females had been seen. Other researchers also have commented on robber flies moving to new foraging locations to increase the probability of finding prey (Lavigne and Holland, 1969; Hespenheide and Rubke, 1977; Scarbrough, 1979, 1981a; Scarbrough and Sraver, 1979).

Some *D. crudelis* captured potential prey within 7 m of their foraging position, 15 cm to 1.5 m above the ground and released them while still in-flight or landed on vegetation and released them following manipulation with a combination of tarsi not used to hold onto the vegetation. It appeared that the robber flies released prey because they were unable to insert their proboscis. Dennis and Lavigne (1975) commented that some species may capture and release prey because robber flies use both visual and other stimuli to select prey.

Diogmites crudelis captured all of its prey in the air when the prey were within 15 cm to 3 m in front of or to the side of their foraging positions and 20-75 cm above the ground. One individual captured a prey a little over 2 m directly above its foraging position. Both *D. angustipennis* (Lavigne and Holland, 1969) and *D. missouriensis* (Scarbrough, 1979) captured prey in the air and on vegetation; *D. angustipennis* also captured some prey on the ground. Bromley (1946b) observed *D. misellus* capturing worker ants on grass stems.

Height and distance that robber flies fly in a habitat has been shown to decrease when the wind is blowing (Dennis and Lavigne, 1975; Lehr, 1961). *Diogmites crudelis* was relatively inactive, unless disturbed, when wind blew in excess of 16 km/hr.

Diogmites crudelis would hold onto captured prey with all six tarsi, fly to the shade of nearby vegetation and hold onto the vegetation with one or both fore tarsi, and manipulate the prey with the rest of its tarsi until it could insert its proboscis. *Diogmites basalis* (Bromley, 1946b as *Deromyia umbrinus*), *D. angustipennis* (Lavigne and Holland, 1969) and *D. missouriensis* (Scarbrough, 1979) held onto vegetation with one of the fore tarsi and manipulated prey with the rest of their tarsi.

Diogmites crudelis generally inserted their proboscis shortly after landing on vegetation. However, if the prey continued to move and/or Hymenoptera prey tried to sting the robber fly, the asilid would hold it away from its body with its tarsi, and manipulate the prey for up to 4 1/2 minutes before successfully inserting its proboscis. One female fell to the ground after capturing a prey that continued to actively move, manipulated the prey with all of her tarsi, inserted her proboscis, and then flew to the shade of nearby vegetation. *Diogmites crudelis* manipulated prey in a way that held the prey's wings tightly against their bodies. Lavigne and Holland (1969) commented that *D. angustipennis* avoided being stung by Hymenoptera prey by holding them from above and behind so that they faced the same direction as the robber fly.

Diogmites missouriensis captured prey on vegetation with one fore tarsus, while supporting itself with the other tarsi. It then grasped the prey with all tarsi before flying to a new location (Scarbrough, 1979).

Diogmites crudelis often inserted the proboscis in the dorsum or dorsal lateral part of the thorax, unless the robber fly was having difficulty inserting its proboscis and then it typically inserted the proboscis near the tip of the abdomen. Both *D. angustipennis* (Lavigne and Holland, 1969) and *D. missouriensis* (Scarbrough, 1979) initially immobilized prey by inserting the proboscis in the neck region or thorax, and the latter also inserted its proboscis in a prey's head.

Diogmites crudelis usually moved at least once during feeding to a new location up to 9 m from its previous location. It was not uncommon for some individuals to move four to seven times. A robber fly would remove its proboscis from the prey and carry the prey with all six tarsi when flying to a new location and upon landing, manipulate the prey with whatever tarsi were not being used to hold onto vegetation, and then reinsert its proboscis. *Diogmites missouriensis* sometimes flew to new locations during feeding (Scarbrough, 1979) and *D. angustipennis* moved when disturbed (Lavigne and Holland, 1969).

During feeding, *D. crudelis* manipulated prey three to 21 times (average of nine times) with the tarsi that were not being used to hold onto vegetation. The number of times that prey was manipulated depended on prey length, with the 32.5-35 mm long robber fly *Proctacanthus longus* (Wiedemann, 1821) manipulated the most times. One prey, a mud dauber [*Isodontia auripes* (Fernald, 1906); 21-23.5 mm long], was not manipulated at all, possibly because the elongate petiole between the thorax and abdomen made it difficult to manipulate the wasp. Lavigne and Holland (1969) observed *D. angustipennis* manipulating prey multiple times with a small Lepidoptera manipulated 23 times. Scarbrough (1979) commented on *D. missouriensis* manipulating prey three to nine times depending on prey size.

When *D. crudelis* were feeding, prey were usually held with those tarsi not being used to hold onto vegetation. A few individuals fed with the prey hanging free from the asilid's proboscis without support by the tarsi.

Diogmites crudelis did not pump the first two to three segments of the abdomen during feeding, and Lavigne and Holland (1969) did not observe it with *D. angustipennis*. According to Musso (1968) and Lavigne and Holland (1969), abdominal pumping or contractions during feeding are associated with the injection of proteolytic enzymes into prey and extraction of dissolved substances.

As researchers have observed for other species, the time robber flies spend feeding usually depends on prey length (Dennis, 2012, 2013; Dennis and Lavigne, 1975; Lavigne and Dennis, 1975). *Diogmites crudelis* fed on prey with an average length of 15.4 mm (e.g., male *Campsomeris* spp.) for approximately 43 minutes. Most larger prey such as female *Campsomeris* spp, with an average length of 23.9 mm, took about 93 minutes. Length of time that *D. crudelis* spent feeding on individual prey varied from 22.5 to 159 minutes, with an average of 65.5 minutes.

Male and female *D. crudelis* captured prey that averaged about the same length, although males captured some slightly larger prey. Mean prey length for males was 20.3 mm (n = 18) with a range from 13.0-32.5 mm; whereas, for females it was 20.4 mm (n = 33) with a range from 12.5-30.0 mm. The overall mean prey length was 20.4 mm with a predator to prey ratio of 1.4:1.0 which indicates that *D. crudelis* was almost 1 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, 1979, 2012, 2013; Dennis and Lavigne, 1975, 1976a and b, 1979; Hespenheide, 1978; Lavigne, 1979, 1984, 1992; Lavigne and Bullington, 1984, 1999; Lavigne and Dennis, 1975, 1985; Lavigne *et al*., 1983, 1993; Lavigne and Holland, 1969; Lehr, 1958c, 1971; Scarbrough, 1978, 1979, 1981a, 1982; Scarbrough and Sraver, 1979; Shelly and Pearson, 1980).

At the completion of feeding, each individual *D. crudelis* discarded prey in one of four ways: (1) it dropped prey in flight as it moved to a new location; (2) it pushed or pulled prey off its proboscis with a combination of the tarsi not being used to hold onto vegetation; (3) it dropped prey during manipulation with a combination of the tarsi not being used to hold onto vegetation; or (4) it allowed prey hanging free to drop-off the proboscis. *Diogmites missouriensis* discarded most prey during manipulation and dropped a few prey in flight when the robber flies moved to a new location, or while still at the feeding site it pushed prey off its proboscis with the fore tarsi (Scarbrough, 1979).

Interfeeding times (between feedings) for *D. crudelis* were extremely difficult to obtain because the speed of flight, distance flown by individuals, and the height of flight in relation to that of vegetation, made the flies hard to follow. This resulted in the recording of only two interfeeding times of 15 1/2 minutes and 189 minutes for an average of approximately 102 minutes. There also was a partial interfeeding time of 79 minutes.

One can calculate the theoretical number of prey an individual *D. crudelis* could feed on in one day if we assume that: (1) it continually forages and feeds between 9:00 AM and 3:00 PM (the observed major period of foraging and feeding activity for 96.8% of individuals), and (2) it captures and feeds on prey every 167.5 minutes (based on the average feeding time and average of two interfeeding times). Thus, over a 6-hour period an individual could feed on approximately 1 to possibly 2 prey. Other investigators have estimated that robber flies feed on from 1 to 35 prey per day (Baker and Fischer, 1975; Dennis, 2012, 2013; Dennis and Lavigne, 1975, 1976a and b; Joern and Rudd, 1982; Lavigne and Dennis, 1975; Lavigne *et al*., 2000; Lavigne and Pfadt, 1966; Lehr, 1958a, 1964, 1971). *Diogmites crudelis'*s feeding on fewer prey per day, than many other species of robber flies, may be correlated with it feeding on longer or larger prey as shown by the lower predator to prey ratio.

Prey

Diogmites crudelis was very selective in its choice of prey, feeding on only Diptera (14.0%), Hemiptera (4.3%), and Hymenoptera (81.7%) (Table 2). Other species of Diogmites feed primarily on Hymenoptera followed by Diptera, Coleoptera, and Hemiptera; a few species are reported to feed on Araneae, Ephemeroptera, Lepidoptera, Neuroptera, Odonata, and Orthoptera (Artigas, 1966; Baker and Fischer, 1975; Barnes, 2010; Bromley, 1914, 1930, 1931a and b, 1934, 1936, 1942, 1946a and b, 1947, 1948, 1950a and b; Cole, 1969; Dennis, 2012; Dennis and Gowen, 1978; Dennis and Lavigne, 2007; Dennis et al., 2009, 2010, 2012; Fattig, 1945; Lavigne and Holland, 1969; Lavigne and Pfadt, 1966; Linsley, 1958, 1960; McAtee and Banks, 1920; Reinhard, 1924; Scarbrough, 1979; Walton, 1914).

Table 2. Number and percent composition of orders of prey captured by *Diogmites crudelis.*

	Male		Female		Unknown sex		Total	
Order	Number	Percent	Number	Percent	Number	Percent	Number	Percent
Diptera	7	29.2	5	10.9	1	4.3	13	14.0
Hemiptera	1	4.2	2	4.3	1	4.3	4	4.3
Hymenoptera	16	66.6	39	84.8	21	91.4	76	81.7
Totals	24	100.0	46	100.0	23	100.0	93	100.0

Diptera and Hymenoptera made up the majority (about 96%) of prey for both male and female *D. crudelis*. However, more females were captured with prey than males. Numerous other investigators have reported collecting more female than male robber flies with prey (Dennis, 1979; Dennis and Lavigne, 1975, 1976a and b, 1979; Dennis *et al*., 1986; Hobby, 1931a and b, 1935; Lavigne, 1970a, 1979, 1984, 1992; Lavigne and Dennis, 1985; Lavigne *et al*., 1976, 1983; Lavigne and Pogue, 2009; Lehr, 1958a and b; Londt, 1991; Poulton, 1906).

Diogmites crudelis preyed on Hymenoptera primarily in the families Scoliidae (*Campsomeris* spp.), Vespidae (*Polistes* spp.), and Sphecidae [*Sceliphron caementarium* (Drury, 1773) and *Isodontia auripes*]. This species has been reported to prey on Pompilidae [*Tachypompilus ferrugineus* (Say, 1824) as *Arachnophroctonus*] (Bromley, 1936), honey bees (*Apis mellifera* Linnaeus, 1758) (Bromley, 1936), and bees and wasps (Artigas, 1966; Bromley, 1950a). A number of species of *Diogmites* are known to prey on honeybees and cause economic damage (Bromley, 1930).

The following is a list of prey taken by *D. crudelis*. Date of capture, and the number and sex of the predator (if known) is indicated following the prey record.

DIPTERA, Asilidae: *Diogmites crudelis*, 7-VIII-12 (1♀); *Diogmites esuriens* Bromley, 1936, 3-VIII-12 (1♀); *Proctacanthus fulviventris* Macquart, 1850*,* 12-VIII-11 (1♂); 28-VIII-13 (2♂♂), 29-VIII-13 (♂), 3-IX-13 (♀), 11-IX-13 (1♂); *Proctacanthus longus*, 16-VIII-13 (1♀), 19-VIII-13 (♂). Calliphoridae: unidentified, 3-IX-13 (1♂); Mydidae: *Mydas clavatus* Drury, 1773, 31-VII-12 (♀); *Mydas* sp. poss. *maculiventris* (Westwood, 1835), 4-VII-11 (sex unknown). HEMIPTERA: Cicadidae: *Diceroprocta olympusa* (Walker, 1855), 2-VIII-12 (1♀), 30-VIII-13 (1♀); unidentified, 13-IX-13 (sex unknown). Membracidae: unidentified, 20-VIII-13 (1♂). HYMENOPTERA, Apidae: *Bombus pennsylvanicus* (DeGeer, 1773), 3-IX-13 (1♀). Mutillidae: *Dasymutilla* sp., 15-VIII-12 (sex unknown), 30-VIII-13 (1♂); unidentified, 26-VIII-13 (1♀), 5-IX-13 (sex unknown). Pompilidae: unidentified, 8-VIII-12 (1♀), 11-IX-12 (1♂), 6-IX-13 (1♂). Scoliidae: *Campsomeris plumipes fossulana* (Fabricius, 1804), 2-VIII-11 (1♀), 2-VIII-12 (♀), 3-VIII-12 (2♀♀), 3-VIII-13 (1♀); 7-VIII-12 (2♀♀), 10-VIII-12 (sex unknown), 14-VIII-12 (1♀), 17-VIII-12 (1♂), 3-IX-12 (1♀), 5-IX-12 (1♀), 6-IX-12 (sex unknown), 11-IX-12 (1♀), 25-IX-12 (1♀); *Campsomeris quadrimaculata* (Fabricius, 1775), 5-VII-11 (1♀, 2 sex unknown), 11-VII-12 (1♂), 13-VII-13 (1♂), 29-VII-13 (1♀), 2-IX-13 (1♀), 13-IX-13 (1♀), 14-IX-11 (1♂); *Campsomeris* spp., 30-VII-12 (sex unknown), 7-VIII-12 (sex unknown), 7-VIII-13 (sex unknown); 10-VIII-13 (sex unknown), 26-VIII-13 (sex unknown). Sphecidae: *Isodontia auripes*, 29-VIII-13 (1♀), 2-IX-13 (3♀♀), 5-IX-13 (1♀); *Sceliphron caementarium*, 3-IX-13 (1♀), 4-IX-13 (♂), 6-IX-13 (♀); *Sphex pennsylvanicus* Linnaeus, 1763, 27-VIII-13 (1♀), 28-VIII-13 (1♀), 4-IX-13 (sex unknown). Tiphiidae: unidentified, 28-VIII-13 (♀), 3-IX-12 (sex unknown), 13-IX-13 (1♀). Unidentified: 6-VII-12 (1♀), 27-VIII-13 (sex unknown), 28-VIII-13 (1♂, 2 sex unknown), 30-VIII-13 (1♂, sex unknown), 4-IX-13 (sex unknown), 5-IX-13 (1♀, sex unknown), 6-IX-13 (sex unknown). Vespidae: *Monobia quadridens* (Linnaeus, 1763), 19-VIII-13 (1♀); *Polistes fuscatus* (Fabricius, 1793), 17-VIII-11 (♂), 16-VIII-13 (1♂); *Polistes metricus* Say, 1831, 2-IX-13 (1♂, 2♀♀), 4-IX-13 (♂); 6-IX-13 (1♀), 9-IX-13 (1♂), 11-IX-13 (sex unknown); *Polistes* sp., 26-VIII-13 (1♀); *Vespula* sp., 28-VIII-13 (1♂); *Vespula squamosa* (Drury, 1770), 15-VIII-13 (1♀), 3-IX-13 (1♀), 4-IX-13 (sex unknown).

Mating Behavior

Male and female *D. crudelis* flew back and forth along the roads and around their habitat with their fore legs held straight up above their heads, their mid legs below their thorax at a 45-degree angle, and their hind femora parallel to their abdomen with the hind tibiae and tarsi extended up at a 45 to 90-degree angle. It is believed that the males were searching for receptive females with which to mate and the females were making it easier for the males to see them. These flights were 60 cm to 1.33 m above the ground and for distances up to 480 m. *Diogmites angustipennis* (Lavigne and Holland, 1969) and *D. missouriensis* (Scarbrough, 1979) males have been reported to perform similar behavior or searching flights for receptive females with which to mate.

Male and female *D. crudelis* would frequently fly up to investigate each other with their legs in the previously mentioned positions. They would then briefly come into contact, or hover in front of or circle each other before landing on the ground or vegetation. Males also would hover in front of females that were on vegetation or the ground, and both males and females would hover in front of other insects (e.g., *Apis mellifera* Linnaeus, 1758) that were on vegetation.

It is uncertain whether *D. crudelis* exhibited courtship behavior similar to that reported for *D. angustipennis* (Lavigne and Holland, 1969; Lavigne, 2002 as *D. grossus*; Linsley, 1960 as *D. grossus*) because male *D. crudelis* hovered in front of females and other insects. However, two complete matings and an attempted mating of *D. crudelis* were initiated without courtship, in-flight when the male flew up from vegetation and grasped the dorsum of the female's thorax, then the pair straightened out in the tail-to-tail position or fell to the top of vegetation where they straightened out in the tail-to-tail position (Fig. 2). Other species of *Diogmites* mate in the tail-to-tail position (Lavigne, 2002; Lavigne and Holland, 1969).

Fig. 2. Mating pair of *Diogmites crudelis* in tail-to-tail position.

After a mating was initiated, the pair usually would fly to the shade of nearby vegetation up to 30 cm above the ground. In the tail-to-tail position the male's genitalia clasped the female's genitalia from below. During mating, the wings of both asilids were either spread at a 30 to 45-degree angle to their bodies or were folded over their abdomens.

While mating, the asilids generally remained motionless, but were easily disturbed and would often fly to other nearby vegetation. If the male or female could not immediately grasp vegetation, they would hang free until they were able to reach vegetation and hold onto it. After about 1 hour, the female would briefly buzz her wings once or twice. One female repeated this behavior again, 83 minutes after mating was initiated.

The author observed 2 complete and 2 partial or incomplete matings. The complete matings lasted 135 and 144 minutes, with an average of approximately 140 minutes. The partial matings lasted 25 and 110 minutes. At the completion of mating, male *D. crudelis* released the female and both flew off. A partial mating of *Diogmites angustipennis* was observed for 205 minutes (Lavigne and Holland, 1969).

Diogmites crudelis matings occurred when the air temperature at the height where the mated pair rested on vegetation ranged from 31.5-33.5ºC in the shade and 32.0-35.0ºC in the sun.

Oviposition Behavior

Like other species of *Diogmites, D. crudelis* females have spines (acanthophorites) at the tips of their ovipositors and oviposit in the ground (Dennis *et al*., 2013; Hull, 1962; Lavigne and Holland, 1969). Observed ovipositions typically occurred in the shade of vegetation, unless the sky was cloudy, and then it was in more open areas (Fig. 3).

Air temperatures 30 cm above the oviposition site ranged from 29.0-36.0°C with an average of 31.7°C. Ground surface temperatures at the oviposition site ranged from 28.0-38.0°C with an average of 31.5°C; whereas, temperatures beneath the surface of the ground where ovipositions occurred ranged from 28.0-36.5°C with an average of 32.3°C.

Diogmites crudelis females either immediately inserted their ovipositors in the ground or walked along the ground and probed with their ovipositors in order to find a suitable place to deposit their eggs. They inserted their ovipositors in the ground with a lateral or tamping action for up to 30 seconds with an average of 7 seconds. The actual oviposition or deposition of eggs took 27 to 210 seconds with an average of 75 seconds, during which some females intermittently exhibited a tamping action. Following deposition of eggs, females withdrew their ovipositors from the ground with a sweeping action that usually continued on the ground surface around the oviposition hole, although some females did not sweep the surface of the ground. Ovipositor withdrawal and sweeping was done for up to 93 seconds with an average of 41 seconds. Average time for complete ovipositions was 47 seconds with a range from 27 to 333 seconds.

The depth that a female inserted her abdomen in the ground depended on the dryness of the soil and its composition. In dry soil, in particular in sugar sand that was loose and not compacted, a female would often insert her ovipositor in the ground so that her abdomen was buried about half way to the thorax. In damp soil and/or soil with a lot of organic matter, a female would barely insert her abdomen in the soil or up to only 1/4 its length. While ovipositing, the female's abdomen was bent down at an 80 to 90-degree angle to her thorax and her wings were usually folded over her abdomen, although some females kept their wings at a 45-degree angle to their abdomen. *Diogmites angustipennis* females usually oviposted with the abdomen buried up to the first abdominal segment. In this position the wings were apart (Lavigne and Holland, 1969).

It was not unusual to see female *D. crudelis* oviposit two to five times over a 12 to 16 minute period before being lost to sight. One female oviposited eight times over 40 minutes. *Diogmites angustipennis* females also may have a sequence of ovipositions (Lavigne and Holland, 1969). According to Lavigne *et al*. (2000) individual robber fly females may oviposit several times.

One to four eggs were recovered from each of five ovipositions, with an average of three eggs. For these ovipositons there was not any difference between the number of eggs deposited in dry or damp soil or the length of time for ovipositing. *Diogmites angustipennis* deposited five to 14 eggs per oviposition (Lavigne and Holland, 1969).

Eggs were creamy-white and oblong like those of many other species of robber flies including *Diogmites angustipennis* (Dennis *et al*., 2013; Lavigne and Holland, 1969). The eggs ranged in length from 2.1-2.4 mm, with a mean of 2.2 mm; range in width was from 0.9-1.0 mm, with an average of 1.0 mm.

Grooming

Diogmites crudelis groomed themselves when resting on the ground or vegetation and during feeding. They groomed in much the same way as reported for other species of robber flies when resting on the ground or vegetation (Dennis, 1979, 2012, 2013; Dennis and Lavigne, 1975, 1976a, 1979; Johnson, 1976; Lavigne and Pogue, 2009; Lehr, 1958c). They always used the fore legs to groom their faces, and the hind legs for grooming their wings, abdomen, and genitalia. Before grooming the face, they usually rubbed together their fore tarsi while extending and slightly elevating the fore legs. Asilids moved the fore tarsi back and forth along their long axes and then rubbed the dorsolateral part of the face and eyes with the inside of and distal part of either one or both front femora and proximal 1/2 of the tibiae (Fig. 4).

Figs. 3-4. Female *Diogmites crudelis* 3. ovipositing in ground. 4. grooming her head.

Diogmites crudelis rubbed their hind tarsi together prior to grooming the abdomen, genitalia, and wings. They then groomed the abdomen, genitalia, and tops and bottoms of the posterior part of the wings with the hind tibiae and tarsi. The abdomen and wings were curved down slightly or up to 80 and 45-degree angles, respectively, and the wings were slightly spread. Grooming of the wings and abdomen was always from anterior to posterior as observed by Dennis (2012, 2013) and Lehr (1958c).

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

During feeding, *Diogmites crudelis* also groomed the tibiae and tarsi that were not being used to hold onto vegetation or prey. They would curl the tarsi of one or more legs around the tibia of another and groom from the proximal to the distal part of the legs. Grooming of the tibiae and tarsi was repeated a number of times during feeding, often for extended periods.

Like most robber flies, *Diogmites crudelis* never groomed its thorax.

Changes in Behavior from Mowing Vegetation

During the fall, 2012, the scrub habitat in which *D. crudelis* had been studied was mowed. By 2013 the cut vegetation had grown to 30-60 cm in height before it was cut again in early September to a height of 15-20 cm. Cutting of the vegetation caused *D. crudelis*, (1) to forage more from the ground or cut vegetation on the ground; (2) once prey were captured in flight, to fly further to find vegetation to hold onto with the fore tarsi while feeding; (3) to fall to the ground when prey were initially captured and hold onto them with all tarsi while the proboscis was inserted into the prey; and (4) to fly lower to the ground (45 cm above the ground) with their fore legs extended over their heads.

Daily Rhythm of Activity

Diogmites crudelis exhibited a distinct diurnal or daily rhythm of activity between 9:00 AM and 4:00 PM (all times are Daylight Savings Time) for ovipositing and feeding (Fig. 5). These behaviors had similar patterns and peaked between 10:00 and 11:00 AM. *Diogmites crudelis* females oviposited primarily between 10:00 AM and 1:00 PM (86.6%); whereas, the major period of feeding was from 10:00 AM to 3:00 PM (87.2%). Thus, in the afternoon as the number of ovipositing females rapidly decreased, the number of foraging robber flies increased up to about 3:00 PM and then tapered off. To a certain extent, as the frequency of occurrence of one behavior increased, others decreased as with some other species of robber flies (Adamovic, 1963; Dennis, 2012; Dennis and Lavigne, 1975; Lavigne *et al*., 2000) and *P. brevipennis* (Dennis, 2012).

The mating diurnal rhythm of activity is based on only four observations and indicates that mating activity was steady from 9:00 AM to 2:00 PM, with a dip between 12:00 noon to 1:00 PM. Additional observations may show a more definitive pattern for mating. Most *D. angustipennis* mating activity occurred in the middle of the day (Lavigne and Holland, 1969).

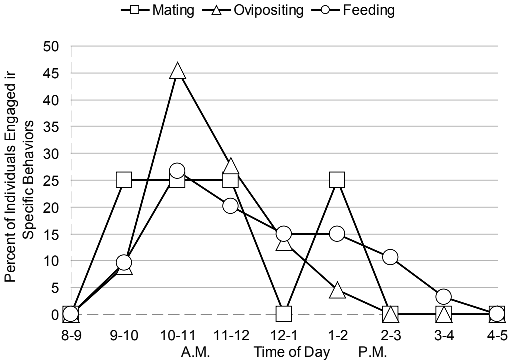

Fig. 5. Diurnal rhythm of activity for *Diogmites crudelis* based on 4, 106, and 94 observations for mating, ovipositing, and feeding, respectively.

Pine and other trees surrounded the roads and the mowed scrub community in which *D. crudelis* were studied and these areas were mostly in shade until between 8:00 to 8:30 AM and after 3:00 PM. As a result, *D. crudelis* did not move from its assumed nocturnal resting position on vegetation back to the roads and open areas of the mowed scrub community until they became exposed to the sun. Movement into an area during the day and out again at dusk or changing light conditions has been observed for a number of robber fly species (Adamovic, 1963; Dennis, 2012; Hespenheide and Rubke, 1977; Lavigne, 1970b; Lavigne and Holland, 1969; Musso, 1972; Scarbrough, 1981b; Scarbrough and Norden, 1977).

Diogmites angustipennis spent the night on vegetation (Lavigne and Holland, 1969). *Diogmites missouriensis* spent the night clinging to the underside of a leaf or in a plant's interior (Scarbrough, 1979).

Robber flies are most active when the sun is shining. However, when the sky was overcast and the author could still see a dim shadow, *D. crudelis* continued to forage and oviposit.

Predators and Parasites

Robber flies of the same species often prey on each other (Lavigne *et al*., 2000). This occurred once for *D. crudelis* when a female attacked a male (Fig. 6). *Diogmites angustipennis* (Lavigne and Holland, 1969) and *D. missouriensis* (Scarbrough, 1979) also are cannibalistic. Lehr (1961) indicated that cannibalism allowed *Stenopogon heteroneurus* (Macquart, 1838) to survive shortages of food, in particular after long periods of inclement weather.

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

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

Fig. 6. Female *Diogmites crudelis* feeding on a male.

CONCLUSIONS

There exists detailed information on the ethology of only two of 22 species of robber flies in the genus *Diogmites* (*D. angustipennis* and *D. missouriensis*) in the United States. This paper provides information on a third species, *D. crudelis*. This species rested on the ground, on dead vegetation on the ground, and on the stems and leaves of live vegetation. *Diogmites crudelis* rested mainly in the shade of vegetation, and as a result, they usually did not make changes in their position in relation to the sun in order to regulate their body temperature. Foraging was from the ground and vegetation. All prey were captured in flight and consisted of Hymenoptera (81.7%), Diptera (14.0%), and Hemiptera (4.3%). During feeding, *D. crudelis* manipulated prey with a combination of the tarsi that were not used to hold onto vegetation. Mating occurred in the tail-to-tail position. Females oviposited in the ground, and 1 to 4 eggs were recovered from each of five ovipositions. Peak period for feeding and ovipositing was from 10:00 to 11:00 AM. Grooming behavior depended on whether *D. crudelis* was resting or feeding. There was one instance of cannibalism when a female preyed upon a male.

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