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Ethology of *Holopogon phaeonotus* Loew, 1874 (Diptera: Asilidae) in Northeastern Florida, U.S.A.

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ABSTRACT

Holopogon phaeonotus Loew, 1874 foraged from plant twig tips, capturing prey in flight, and immobilized them at the feeding site. Identified prey came from six insect orders: Coleoptera (4.0%), Diptera (33.0%), Hemiptera (17.0%), Hymenoptera (20.0%), Psocoptera (23.0%), and Thysanoptera (3.0%). Mating was preceded by male courtship and was in the tail-to-tail position. Eggs were laid in the soil, in the shade of overhanging vegetation and fallen dried oak leaves. There was a distinct daily rhythm of activity for feeding, mating, and oviposition. Grooming behavior was not common but when it did occur, resembled that described for other species of Asilidae. Information is also provided on habitat, resting behavior, and predators.

Key words: Asilidae, behavior, robber flies, prey.

INTRODUCTION

The robber fly genus *Holopogon* is widespread in the United States of America (U.S.A.) with twenty-one species (Geller-Grimm, 2013). Despite their broad distribution, the ethology of only three species has been described in some detail. Dennis and Lavigne (1975) and Lavigne *et al*. (1993) dealt with different aspects of the behavior of *H. albipilosus* Curran, 1923 and *H. seniculus* Loew, 1866, respectively, in Wyoming. Hespenheide and Rubke (1977) described the diurnal pattern of foraging and prey selection for *H. wilcoxi* Martin, 1959 in Arizona.

This paper provides detailed information on the ethology of *H. phaeonotus* Loew, 1874 near the southern boundary of St. Augustine in northeastern Florida, U.S.A.

MATERIALS AND METHODS

Holopogon phaeonotus is a small fly (approximately 6 mm in length, excluding antennae) that is widely distributed east of the Mississippi River, including Florida. It rests on the tips of twigs (a small branch without leaves) in open areas such as along forest roads or trails and, depending on location, generally occurs from March through April. Most observations were made from 27 March to 25 April 2012 in the Moses Creek Conservation Area (MCCA) and in an approximate 1/4 hectare storm water detention basin between State Road 206 and the MCCA.

The study period was based on the time when *H. phaeonotus* was most abundant in the MCCA. During this period, seven to 30 asilids were followed during a day, each for up to 83 minutes. Total number of hours of observation was approximately 67.

The study began with the author standing or sitting on the ground and observing single flies for as long as possible in order to collect information on their various behaviors and diurnal activities. When sufficient data were gathered on their behavior, the activities of many flies were observed by the author slowly walking along roads and trails in the MCCA and around the perimeter of the storm water detention basin. This also allowed for the collection of prey and the observation of mating pairs and ovipositing females. Some behaviors, such as prey manipulation, were confirmed by observing them with Pentax Papilio 8.5x21 binoculars.

Collected prey was placed in glass vials with the following information: sex of predator (if observed), date, time, and location. Prey that the author could not identify were sent for identification to the U.S. Department of Agriculture, Agricultural Research Service, Systematic Entomology Laboratory, Beltsville, Maryland, U.S.A. Prior to shipment, prey were measured to the nearest 0.5 mm with a clear, plastic ruler. Some prey was not identifiable to family, genus or species because specialists were not available, inadequate keys or poor condition of the specimens.

Ovipositing females were observed for as long as they continued to exhibit oviposition behavior or until they were lost as they flew about the habitat. When a female ceased to oviposit or was lost, the oviposition site was dug up with a small hand shovel. The soil was then examined with a compound microscope to find the eggs. Oftentimes eggs were not found, but those that were recovered (from two 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.

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

RESULTS AND DISCUSSION

Habitat

In the MCCA, *H. phaeonotus* occurs primarily on plant twigs along sand roads (Fig. 1) and trails, and in open areas of the forest. The twigs were from live oak trees [*Quercus virginiana* (P. Mill.); family Fagaceae], various species of oak shrubs (*Quercus* spp.; Fagaceae), sand pine [*Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarg.; Pinaceae], pond pine (*Pinus serotina* Michx.; Pinaceae), American holly (*Ilex opaca* Ait.; Aquifoliaceae), gallberry [*Ilex glabra* (L.) A. Gray; Aquifoliaceae], rusty lyonia [*Lyonia ferruginea* (Walter) Nutt.; Ericaceae], and rusty staggerbush or coastalplain staggerbush [*Lyonia fruticosa* (Michx.) G.S. Torr.; Ericaceae]. A few individuals also were occasionally on the dead tips of saw palmetto [*Serenoa repens* (W. Bartram)

Small; Arecaceae] and muscadine vine (*Vitis rotundifolia* Michx.; Vitaceae), live and dead grass leaves/stems (Poaceae) including lopsided indiangrass [*Sorghastrum secundum* (Elliott) Nash], and on the leaf tips of live oak trees and oak shrubs. The soil in these areas consists of sand mixed with organic matter.

Fig. 1. *Holopogon phaeonotus* habitat along edge of sand road.

Sand pine, muscadine vine, live oak trees, and oak shrubs are found around the edge of the storm water drainage basin. The habitat also included rusty lyonia and some saw palmetto, but *H. phaeonotus* was never observed on these plants. In the basin there was primarily 7-13 cm high carpet grass (*Axonopus* sp.; Poaceae) and Elliott's (white) milkpea (*Galactia elliottii* Nutt.; Fabaceae). The soil in and around the basin consisted of sand to sandy loam.

In Maryland, Scarbrough (1974) most frequently found *H. phaeonotus* at a wood-field interface and along sunlit paths. Occasionally he also found them in shaded woods with heavy undergrowth.

In the U.S.A. other species of *Holopogon* including *H. albipilosus* (Dennis and Lavigne, 1975), *H. guttulus* (Wiedeman, 1821) (Back, 1909; Bromley, 1931, 1946, 1950; Goslin, 1950; McAtee and Banks, 1920, all as *H. guttula*), *H. seniculus* (Lavigne *et al*., 1993), *H. snowi* Back, 1909 (Williams, 1999), and *H. wilcoxi* (Hespenheide and Rubke, 1977) also have been reported to occur on tips of twigs, and low weeds or bushes. In the former Union of Soviet Socialist Republics (U.S.S.R.) several species of *Holopogon* have been found on the tips of high grasses and twig tips of shrubs "… where constant winds cool the insects" (Lehr, 1964, 1972). In France, *H. venustus* (Rossi, 1790) (Musso, 1972) perch on the extreme tips of very thin twigs (2-3 mm in diameter).

In the United States, reference to *H. guttulus* may refer, in part, to *H. phaeonotus*. In 1959 Martin reorganized Lowe's *H. phaeonotus* as distinct from *H. guttulus*, and described *H. oriens* and *H. vockerothi* as new species, from material that previously would have been considered *H. guttulus*. Earlier references to *H. guttulus* or *H. guttula* therefore possibly include these species.

Resting Behavior

Holopogon phaeonotus rested and foraged from twig tips (Fig. 2) 10 cm to 3 m above the ground. Individuals were active in both sun and shade. Other species of *Holopogon* are generally found at heights from 30 cm to 3 m above the ground (Dennis and Lavigne, 1975; Hespenheide and Rubke, 1977; Lavigne *et al*., 1993; Lehr, 1972; Musso, 1972).

Fig. 2. Male *Holopogon phaeonotus* foraging from twig tip.

Individuals rested in a horizontal position on the twig tip or below (1-20 cm) the tip and parallel to the bare branch. When on the branch they would often face away from the tip. This behavior also was exhibited when the wind gusted 11-16 km/hr.

Holopogon phaeonotus would rest for up to 7 minutes before resuming other activities, in particular foraging. While resting the asilids were motionless or moved very little and did not react to other insects that flew around them.

Holopogon phaeonotus did not turn so that one of its sides faced and was elevated to the sun or flatten themselves against the twig that they were on, such as when the sun was obscured by clouds. This is unlike many other species of robber flies including *H. priscus* (Meigen, 1821) (Lehr, 1972), that attempt to maintain their body temperature by changing their position in relation to the sun, flattening themselves against the substrate that they are on, and/or resting on the shady side of vegetation (Dennis and Lavigne, 1975). Morgan *et al*. (1985), and Morgan and Shelly (1988) indicated that foraging neotropical and desert robber flies regulate their body temperatures by microhabitat selection and postural adjustments. Thus, *H. phaeonotus* may primarily use microhabitat selection to regulate their body temperature. According to Lehr (1972), each species of *Holopogon* occupy a habitat with specific microclimate components.

When resting and feeding, a number of individuals expelled a drop of creamy-white liquid from their anus. Lehr (1958c) commented that the expulsion of liquid from the anal opening is quite common in robber flies.

Foraging and Feeding Behavior

Holopogon phaeonotus foraged primarily from 0.75-3 mm diameter twig tips, but a few individuals infrequently foraged from dead grass stems, grass leaves, the dead tips of saw palmetto leaves, and on the edges of leaves of live oak trees and oak shrubs.

Foraging height depended on the location of sunlight on the twigs that the asilids were on. *Holopogon phaeonotus* generally foraged higher up in the vegetation in the morning and as these areas became shaded, the asilids moved to lower areas that were in sunlight. Hespenheide and Rubke (1977) speculated that *H. wilcoxi* spent the night in an area where they would be in sunlight earliest in the morning and then moved to areas better suited for foraging.

Foraging individuals held their bodies horizontal to the twig tip that they were on or at a 30 to 45 degree angle with their head down. In these postures they would make quick movements of their heads and slight movements of their bodies. They were most often in a horizontal position facing different directions from about 11:00 AM to 1:00 PM when the sun was directly overhead. From 9:00 to 11:00 AM and after 1:00 PM, they were more likely to be at an angle to the twig tip that they were on and facing the sun. *Holopogon phaeonotus* did not rapidly face different directions while on the same twig, as was observed for *H. albipilosus* by Dennis and Lavigne (1975). Lehr (1972) commented that foraging *H. priscus* had their heads directed downward and their bodies at an angle to the side of the grass stem that they were on.

The foraging postures or attitudes presumably allowed *H. phaeonotus* to use backlighting to better see their prey because of their position relative to it and the sun. Other investigators (Dennis, 2012; Dennis *et al*., 1986; Hespenheide, 1978; Hespenheide and Rubke, 1977; Lavigne, 1970b, 1971; Lavigne and Dennis, 1985; and Melin, 1923) have made similar observations for several species of robber flies. In addition, it is assumed that the body held at a 45-degree angle allowed *H. phaeonotus* to better see potential prey with their eyes (i.e., the incoming light would be at right angles to the surface of the forward, flattened ommatidia). According to Melin (1923), the central ommatidia "…have greater intensity of vision than the outer ones." Nation (2008) commented that robber flies have higher visual acuity near the forward part of their eyes and this probably allows them to better see and capture prey.

Foraging *H. phaeonotus* frequently made investigatory flights without making contact with potential prey. Flights were for distances of 5-45 cm from an individual's foraging location. Investigatory flights are common for asilids (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 asilids cannot identify suitable prey except at close range.

Lehr (1958c) noted that robber flies often cannot determine whether a flying insect is acceptable prey, and Dennis and Lavigne (1975) commented that some asilids use both visual and other stimuli to select prey. This may be true for *H*. *phaeonotus* since a few individuals captured potential prey and released them while still in flight; individuals released prey after returning to their foraging twig tip and while manipulating the prey with their tarsi prior to insertion of their proboscis; or individuals immediately discarded prey after insertion of their proboscis and standing up on the twig tip.

Dennis and Lavigne (1975) referred to short flights about a foraging position without being directed towards any potential prey as, orientation flights. *Holopogon phaeonotus* made orientation flights within 5-45 cm and typically in front of its foraging twig tip.

Holopogon phaeonotus would forage from the same twig tip for up to 83 minutes with an average of approximately 48 minutes. During this period of time, an individual could feed on a number of prey, and make numerous investigatory and orientation flights. Depending on the species, asilids forage from one location for variable periods of time or frequently move to a new location. Hayat and Çalışkan (2003) observed that male *Dasypogon irinelae* Weinberg, 1986 remain at one location for longer periods of time than females.

Holopogon phaeonotus captured all prey in the air within 7.5-45 cm in front of or 5-15 cm to the side or slightly behind their foraging position. Dennis and Lavigne (1975) reported that *H. albipilosus* captured most prey 7.5-30 cm above and in front of their foraging site.

Height and distance that asilids fly in a habitat has been shown to decrease when the wind is blowing (Dennis and Lavigne, 1975; Lehr, 1961). In the storm water drainage basin there typically was wind gusting up to 7 km/hr. This did not appear to decrease the distances or heights that the asilids flew until wind gusts exceeded 10 km/hr.

When prey were captured, *H. phaeonotus* would return to its foraging twig tip and generally hold onto the twig tip with one of its mid-tarsi, manipulate or hold onto the prey with its other tarsi, and insert its proboscis in the prey's thorax or abdomen. One individual captured its prey, returned to its foraging twig tip and held on with both fore tarsi, while manipulating the prey with the other tarsi before inserting its proboscis. Large prey, such as *Andricus* sp., were captured and often manipulated with all six tarsi in a hover while the asilid inserted its proboscis and then landed on its foraging twig tip. Only one individual captured a prey and inserted its proboscis without a hover before returning to its twig tip. Dennis and Lavigne (1975) indicated that most prey of *H. albipilosus* were immobilized at the feeding site while the asilid held onto a twig with one of its mid-tarsi; only a few prey were immobilized in the air prior to an asilid landing to feed.

Holopogon phaeonotus often would manipulate prey up to three to four times during feeding; one individual manipulated prey five times. When it did manipulate prey, an asilid usually would dangle from the side of the twig tip with one of its mid-tarsi and manipulate the prey with the other tarsi, re-insert its proboscis, and then stand erect on the twig tip to resume feeding. However, a number of individuals also held onto the twig tip with one of their fore tarsi, in particular with larger prey (e.g., *Andricus* sp.), and manipulated prey with the rest of their tarsi. During prey manipulation, *H. albipilosus* also used its mid- and fore-tarsi to hold onto a twig (Dennis and Lavigne, 1975).

When *H. phaeonotus* were feeding, prey hung free on their proboscises without support by the tarsi.

Female *H. phaeonotus* fed on prey that averaged slightly longer than those fed upon by males. The mean prey length for females was 2.6 mm (n = 42) with a range from 1.0-7.0 mm; whereas, for males it was 2.0 mm (n = 35) with a range from 1.0-4.0 mm. Overall mean prey length was 2.3 mm. Both male and female *H. albipilosus* and *H. seniculus* feed on slightly smaller prey with prey length ranging from 1.6-1.9 mm (Dennis and Lavigne, 1975; Lavigne *et al*., 1993). Hespenheide and Rubke (1977) indicated that for *H. wilcoxi*, the overall range of prey sizes varied from 1/10 to 1/2 the length of the fly. Lehr (1964) said that when asilids such as *Holopogon* spp., have a shortened abdomen, it indicates that they feed on small prey.

Mean predator to prey ratios are used to show the relationship between predator to prey lengths, with a smaller ratio indicating larger prey. Based on the mean prey length and the mean length of 10 males and females each, the mean predator to prey ratio for *H. phaeonotus* is 2.6. Mean predator to prey ratios for *H. albipilosus* (Dennis and Lavigne, 1975) and *H. seniculus* (Lavigne *et al*., 1993) are 3.5 and 3.1, respectively. Mean predator to prey ratios for other species of robber flies range from 0.9 to 8.4 with a mean of 2.9 (Dennis, 1979, 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, most prey was discarded by *H. phaeonotus* individuals pushing it off their proboscis with their fore tarsi while still at the feeding site. The second most common method was to drop prey during feeding while they were being manipulated. Some prey also were discarded by, (1) being dropped in flight as the asilid chased potential prey or captured prey, and (2) being dropped in flight without pursuing potential prey. *Holopogon seniculus* allowed prey to drop off its proboscis either at the feeding site or in flight after leaving the feeding site (Lavigne *et al*., 1993); whereas, *H. albipilosus* pushed prey off its proboscis with the fore tarsi while still at the feeding site (Dennis and Lavigne, 1975).

Length of time that *H. phaeonotus* spent feeding on individual prey varied from 1-7.5 minutes, with an average of 3.5 minutes. Time between feedings (interfeeding time) varied between 0 and 27 minutes, with an average of 7.5 minutes. The 0 minute interfeeding times were for individuals that dropped prey in flight and immediately captured another prey.

The theoretical number of prey an individual *H. phaeonotus* could feed on in one day can be calculated if it is assumed that, (1) it continually forages and feeds between 9:00 AM and 3:00 PM (the observed major period of foraging and feeding activity), and (2) it captures and feeds on prey every 11 minutes (based on the average feeding and interfeeding times). Thus, over a six-hour period an individual could feed on approximately 33 prey. Dennis and Lavigne (1975) calculated that *H. albipilosus* could feed on approximately 15 prey per day during a 5.5-hour period of foraging activity with an average 21 minute feeding and interfeeding time. Lehr (1964) calculated that *H. claripennis avor* Lehr, 1972 could feed on 14 1/2 prey per day. Other investigators have estimated that asilids 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).

After capturing and releasing potential prey in flight or releasing prey during manipulation prior to insertion of the proboscis, a few individuals landed or stood erect on their foraging twig tip and then spread their wings at a 45° angle. One time this was accompanied by an asilid fluttering its wings. These unusual behaviors may have indicated that the asilids were frustrated at not capturing suitable prey, or the prey was an unsuitable size or distasteful.

Prey

Holopogon phaeonotus individuals preyed primarily on Diptera (33.0%), followed by Psocoptera (23.0%), Hymenoptera (20.0%), Hemiptera (17.0%), Coleoptera (4.0%), and Thysanoptera (3.0%) (Table 1). In the U.S.A. other species of *Holopogon* have been reported to prey on Coleoptera, Diptera, Hemiptera (as Hemiptera and Homoptera), Hymenoptera, Lepidoptera, Plecoptera, Psocoptera, and Thysanoptera (Dennis and Lavigne, 1975, 2007; Dennis *et al*., 2010; Hespenheide and Rubke, 1977; Lavigne *et al*., 1993). *Holopogon venustus* in France has been reported to feed on Hemiptera (Aphididae; Musso, 1970, 1972). In the U.S.S.R., *Holopogon* spp. feed on Araneae, Coleoptera, Diptera, Hemiptera (as Hemiptera and Homoptera), and Hymenoptera (Lehr, 1964, 1972). The Asilidae Predator-Prey Database has eight records of *Holopogon* feeding on spiders (Dennis *et al*., 2012)

Male and female *H. phaeonotus* generally preyed on the same insect orders. A few more females were captured with prey than males. Numerous other investigators have reported collecting more female than male asilids with prey (Dennis, 1979, 2013; 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).

Table 1. Number and percent composition of orders of prey captured by *Holopogon phaeonotus*.

	Male		Female		Unknown sex		Total	
Order	Number	Percent	Number	Percent	Number	Percent	Number	Percent
Coleoptera	3	7.0	0	0	1	12.5	4	4.0
Diptera	17	39.6	15	30.6	1	0	33	33.0
Hemiptera	8	18.6	8	16.3	1	12.5	17	17.0
Hymenoptera	5	11.6	11	22.5	4	50.0	20	20.0
Psocoptera	9	20.9	13	26.5	1	12.5	23	23.0
Thysanoptera	1	2.3	2	4.1	0	0	3	3.0
Totals	43	100.0	49	100.0	8	100.0	100	100.0

The following is a list of prey taken by *H. phaeonotus*. All prey was collected between 28 March and 17 April 2012 primarily in the Moses Creek Conservation

Area; a few prey were collected in the storm water detention basin (SWDB) and are so indicated. The number and sex (if known) of the predator follows the prey record.

COLEOPTERA, Curculionidae: *Hypothenemus dissimilis* (Zimmermann, 1868), 29-III-12 (♂). Staphylinidae: 17-IV-12 (♂) (SWDB). Unidentified, 3-IV-12 (♂, unknown sex). DIPTERA, Cecidomyiidae: Cecidomyiinae, Lasiopteridi, 30-III-12 (♂); Cecidomyiini, 5-IV-12 (♀); *Contarinia* sp., 28-III-12 (♂), 29-III-12 (♂, unknown sex); *Dasineura* sp. 1, 30-III-12 (♂); *Dasineura* sp. 2, 3-IV-12 (♀), 4-IV-12 (♂, ♀), 12-IV-12 (♀); *Lestodiplosis* sp., 4-IV-12 (♂); *Micromya* sp., 4-IV-12 (♂); unidentified, 5-IV-12 (♂), 6-IV-12 (♂, ♀). Chironomidae: unidentified, 2-IV-12. Chloropidae: unidentified, 2-IV-12 (♂, 2♀♀). Dolichopodidae: *Chrysotus* sp., 5-IV-12 (♂); *Condylostylus* sp., 5-IV-12 (♀); *Condylostylus* sp. near *viridis* Parent, 1929, 30-III-12. Lauxaniidae: *Melanomyza* sp., 2-IV-12 (♂), 6-IV-12 (♀). Muscidae: unidentified, 2-IV-12 (♂). Phoridae: unidentified, 4-IV-12 (♀), 5-IV-12 (♀). Sciaridae: unidentified, 4-IV-12 (♂), 5-IV-12, 6-IV-12 (♂, ♀), 10-IV-12 (♀). Unidentified, 30-III-12 (♂), 2-IV-12 (2♂♂, ♀), 3-IV-12 (♂), 6-IV-12 (♀); 11-IV-12 (♀) (SWDB). HEMIPTERA, Auchenorrhyncha, Cicadellidae: *Empoasca* sp., 5-IV-12 (♀), 10-IV-12 (♂) (SWDB). Cixiidae: *Cixius* sp., 2-IV-12 (♀), 10-IV-12 (♂); unidentified, 10-IV-12 (♀) (SWDB). Unidentified, 2-IV-12 (♂, ♀), 12-IV-12 (♂, unknown sex) (SWDB). Heteroptera, Miridae: unidentified, 29-III-12 (♂), 30-III-12 (♂). Sternorrhyncha, Aphididae: *Aphis craccivora* Koch, 1854, 4-IV-12 (♀); *Aphis* sp., 4-IV-12 (♂); *Myzus persicae* (Sulzer, 1776), 10-IV-12 (♀) (SWDB); *Myzus* sp., 5-IV-12 (♀); *Tetraneura* sp., 4-IV-12 (♂); *Therioaphis trifolii* (Monell, 1882), 6-IV-12 (♀). HYMENOPTERA, Cynipidae: *Andricus* sp., 3-IV-12 (♀, unknown sex), 4-IV-12 (♀), 6-IV-12 (♀, unknown sex); *Callirhytis* sp., 2-IV-12 (♂), 11-IV-12 (♂), 12-IV-12 (♀), 17-IV-12 (♀); *Synergus* sp., 4-IV-12 (♂). Eucharitidae: *Orasema* sp., 2-IV-12 (♀), 10-IV-12 (♂) (SWDB), 12-IV-12 (♀). Eulophidae: *Omphale taborskyi* Boucek, 1984, 2-IV-12 (♀). Eupelmidae: *Brasema* sp., 12-IV-12 (♀). Eurytomidae: *Sycophila* sp., 4-IV-12 (♀). Formicidae: Formicinae, 10-IV-12 (♂); *Linepithema* sp., 29-III-12, 2-IV-12 (♀). Pteromalidae: unidentified, 30-III-12. PSOCOPTERA, Unidentified, 29-III-12 (♂), 2-IV-12 (♀), 3-IV-12 (2♀♀), 4-IV-12 (2♀♀) (SWDB), 5-IV-12 (2♂♂, ♀), 6-IV-12 (2♂♂, ♀), 10-IV-12 (♀), 11-IV-12 (♂, 3♀♀, unknown sex) (♂, SWDB), 12-IV-12 (2♂♂, 2♀♀). THYSANOPTERA, Phlaeothripidae: unidentified, 30-III-12 (♂), 4-IV-12 (♀), 5-IV-12 (♀).

Courtship and Mating Behavior

Lavigne (2002) indicates that male courtship prior to mating is probably widespread in the genus *Holopogon.* It has been described for *H. albipilosus* (Dennis and Lavigne, 1975), *H. claripennis avor* and *H. priscus* (Lehr, 1972), and *H. seniculus* (Lavigne *et al*., 1993). It has been observed but not described for *H. phaeonotus* (Lavigne, 2002).

Holopogon phaeonotus males will court both females and other males with or without prey. Male courtship of prey-feeding females has been reported for *H. priscus* (Lehr, 1972) and *H. seniculus* (Lavigne *et al*., 1993).

During courtship, *H. phaeonotus* males generally hovered 2.5-5 cm in front of, slightly above, to the side of, and behind the courted asilid. While hovering the males held their front and mid legs up against their thorax and their hind legs were angled posteriorly at about a 45˚ angle to their thorax. Courtship usually lasted 5-49 seconds with an average of 23 seconds, but some males courted for 106-160 seconds. When a male or non-receptive female was courted, they would frequently fly off with the courting male in pursuit. A non-receptive female also would assume an agonistic posture by spreading her wings at a 45˚angle to her body, tilt her body upward at a 45˚angle, and/or crawl to the side of the twig. A female would spread her wings up to three to four times and often vibrate or flutter them concurrently. Following courtship, a male would land on or next to a female and attempt to clasp her genitalia. When unsuccessful, the male would either fly off or repeat the courtship sequence before flying off.

There was only one courtship that resulted in mating. During this courtship the male hovered immediately in front of the female for 4-5 seconds, swaying from side-to-side in about a 3 mm arc. The male's eyes were very close to and possibly touching the female's eyes. The male then flew to the female's left side, landed dorsolaterally on the female for 5-7 seconds during which he clasped her genitalia and then straightened out in the tail-to-tail position (Fig. 3) so that he was slightly on the side of the twig (rusty staggerbush). After 38 minutes, the male released the twig and swung under the female so that he was at a 90˚ angle to the female and grasping the twig below the female. After 4 minutes in this position, the male let go of the twig and swung up onto the twig so that both the male and female were on top of and parallel to the twig. The mating pair remained on top of the twig for another 2 minutes and mating was terminated when the male unclasped the female and flew off. The mating lasted 44 minutes.

During mating, *H. phaeonotus* remained relatively inactive and moved very little. At various times during the complete mating the female reacted with slight movements of her head and body when other insects flew by. Also, during one of the incomplete matings two males simultaneously courted the same female, landed on her dorsum and attempted to mate with her. Two male *H. albipilosus* also have been recorded as simultaneously courting a female (Dennis and Lavigne, 1975).

There were five incomplete matings of *H. phaeonotus* when the air temperature at their height on the twigs varied between 27.5-34ºC. The one complete mating took place when the temperature was 34ºC at the mating pairs' height 1.2 m above the ground.

During courtship male *H. albipilosus* hover 7.5-30 cm in front of, above, and to the side of females. While courting, male *H. albipilosus* frequently touch a female's eyes with his fore tarsi (Dennis and Lavigne, 1975). This was not observed for *H. seniculus*, instead males appeared to touch females with their hind tarsi as they fly to their sides (Lavigne *et al*., 1993). Lehr (1972) said that *H. clarpennis avor* males make a circular flight around females in a radius of 10-15 cm. Non-receptive *H. albipilosus* and *H. seniculus* females exhibit agonistic behavior similar to that observed for *H. phaeonotus*.

Other species of *Holopogon* also mate in the tail-to-tail position and during mating *H. albipilosus* (Dennis and Lavigne, 1975), *H. claripennis avor* (Lehr, 1972), and *H. seniculus* (Lavigne *et al*., 1993) females and males may assume up to a 90º angle to each other. *Holopogon albipilosus* and *H. seniculus* complete matings last for 27 and 25 minutes, respectively. A partial mating of *H. albipilosus* lasted 31 minutes.

Fig. 3. Mating pair of *Holopogon phaeonotus* in tail-to-tail position with the female on the left and the male on the right.

Oviposition

Three complete and two partial ovipositions occurred on the western edge of a sand road in the shade of overhanging vegetation and fallen, dried oak leaves (Fig. 4). Females began to exhibit oviposition behavior when they flew 4-7 cm above the ground for a few seconds, then landed on oak leaves on the ground and as they walked around, probed with their ovipositors in order to find sand to deposit their eggs. Generally this was between and under oak leaves where the females barely inserted their ovipositor and posterior abdominal segments in the sand. In this position, a female's abdomen was slightly curved and her wings were spread at a 45° angle to her abdomen. At the completion of oviposition, females briefly (3-5 seconds) swept the soil around the oviposition hole with lateral movements of their ovipositors. Dennis and Lavigne (1975) speculated that *H. albipilosus* females also oviposit in the soil because of the spines on their genitalia. Lehr (1972) commented that *H. claripennis avor* females oviposit "…deep in the bushes."

Fig. 4. Female *Holopogon phaeonotus* ovipositing on edge of sand road underneath oak leaves.

Time for the three complete *H. phaeonotus* ovipositions, not including sweeping of the surface soil, was 234, 244, and 268 seconds. Six and nine eggs were recovered from the first two ovipositions, respectively; eggs were not recovered from the third oviposition. The two partial ovipositions were not completed because the author or ants disturbed the females. Temperatures on and under the soil surface where ovipositions occurred ranged from 33-35ºC.

Eggs are glistening white and oblong or elongate, like many other species of robber flies. The eggs range in length from 0.9-1.2 mm, with a mean of 1.1 mm; range in width is from 0.4-0.5 mm, with a mean of 0.4 mm.

Grooming

Holopogon phaeonotus did not frequently groom themselves. This may be due, in part, to the asilids occupying various heights on vegetation and only females visiting the ground to oviposit. However, when they did groom it was in much the same way as reported for other asilids (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 heads, and the hind legs for grooming their wings and abdomen. Grooming of the head was usually preceded and followed by the rubbing together of the fore tarsi while the fore legs were extended and slightly elevated. The fore tarsi were moved back and forth along their long axis and then the dorsolateral part of the asilid's head was rubbed with the inside of either of one or of both front femora (distal part) and tibiae (proximal part).

Grooming of the abdomen and wings was sometimes preceded by *H. phaeonotus* rubbing their hind tarsi together. Hind tarsi were then turned inward to groom the abdomen, and tops and bottoms of the wings. Grooming of the wings and abdomen was always from anterior to posterior as observed by Lehr (1958c). Also, the wings were often spread at a 45˚ angle to the body and they were groomed outward from about 3/4 their length.

Daily Rhythm of Activity

Holopogon phaeonotus did not appear on vegetation twig tips in the morning until about 9:00 AM, when the sun was shining on the twigs and the temperature exceeded 24.5˚C. Lehr (1972) commented that in the morning *H. claripennis avor* became active when air temperatures reached 17-18°C. In the afternoon *H. phaeonotus* were difficult to find after 3:30 to 4:00 PM because most of their habitat was in shade. Between these times they exhibited a distinct diurnal or daily rhythm of activity for feeding, mating and oviposition, and as the frequency of one behavior increased, the probability of other simultaneous behaviors decreased (Fig. 5). Adamovic (1963) commented that in a population of robber flies particular activities dominate at different times of day and that at least mating activity is related to light, temperature, and humidity in the habitat.

Peak period of feeding was from 10:00 AM to 1:00 PM, but some feeding occurred both before and after these times. One mating pair was observed between 10:00 and 11:00 AM, and six from 1:00 to 4:00 PM, with 5 of these between 1:00 and 3:00 PM. Peak period for ovipostions occurred between 1:00 to 3:00 PM.

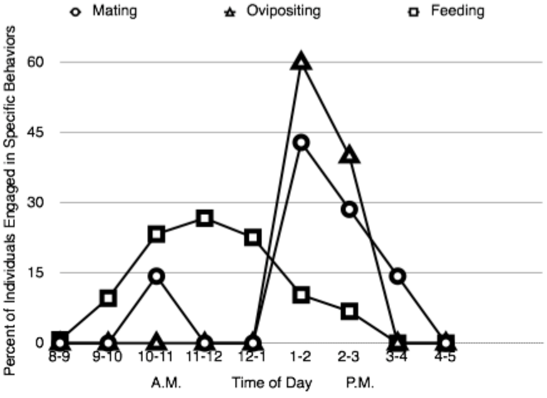

Fig. 5 Diurnal rhythm of activity of *Holopogon phaeonotus* based on 7, 5, and 146 observations for mating, oviposition, and feeding, respectively.

Holopogon wilcoxi had peak periods of feeding from about 8:00 to 10:00 AM and 2:00 to 4:00 PM, based on the percent of flies with prey (Hespenheide and Rubke, 1977). *Holopogon albipilosus* also had two peak periods of feeding between 11:00 AM and 12:00 noon and from 4:00 to 5:00 PM; and the peak period for mating was between 2:00 and 3:00 PM (Dennis and Lavigne, 1975). *Holopogon* in deserts, where there can be acute changes in weather over 24 hours, forage early in the morning and evening, and mate and oviposit during the daylight hours. *Holopogon claripennis avor* foraged primarily from 8:00 to 9:00 AM, 10:00 to 11:00 AM and 5:00 to 6:00 PM (Lehr, 1972).

Predators

Asilids of the same species are often reported to prey on each other (Lavigne *et al*., 2000). However, *H. phaeonotus* did not exhibit cannibalism. It also has not been observed for other species of *Holopogon* (Dennis and Lavigne, 1975; Hespenheide and Rubke, 1977; Lavigne *et al*., 1993; Lehr, 1964).

On two occasions spiders captured individual *H. phaeonotus*. One *H. phaeonotus* was captured on a twig tip by a green lynx spider [Oxyopidae: *Peucetia viridans* (Hentz, 1923)] and a jumping spider (Salticidae) was found approximately 7.5 cm from a twig tip with an asilid. Another *H. phaeonotus* was briefly caught in an unidentified spider's web but was able to free itself with its frantic movements. Lavigne *et al*. (1993) reported *H. seniculus* as prey of the jumping spider, *Habronattus hirsutus* (Peckham and Peckham, 1888; as *Pellenes*).

Evans (1973) reported that the sphecid wasp *Steniolia elegans* Parker, 1929, preyed on *H*. *atripennis* Back, 1909.

CONCLUSIONS

There is some detail on the ethology of only 3 of 21 species of *Holopogon* (*H. albipilosus*, *H*. *seniculus*, and *H. wilcoxi*) in the United States. This paper provides information on a fourth species, *H. phaeonotus*. This species rested on and foraged from plant twig tips. *Holopogon phaeonotus* did not attempt to maintain its body temperature by changing its position on the twig tips such as by turning one side towards the sun or by moving into shade of surrounding vegetation. However, individuals foraged higher up in the vegetation in the morning and as these areas became shaded, they moved to lower areas that were in sunlight. All prey were captured in flight and consisted of Coleoptera, Diptera, Hemiptera, Hymenoptera, Psocoptera, and Thysanoptera. During feeding, *H. phaeonotus* most frequently manipulated prey by holding onto the side of a twig tip with one of its mid-tarsi and manipulating prey with the other tarsi. Males courted females prior to mating, which occurred in the tail-to-tail position. Females oviposited in the ground, and 6 and 9 eggs were recovered from ovipositions that lasted 234 and 244 seconds, respectively. Peak period for feeding was from 10:00 AM to 1:00 PM, mating was from 1:00 to 4:00 PM, and oviposition from 1:00 to 3:00 PM. *Holopogon phaeonotus* did not frequently groom themselves, possibly because they stayed on vegetation above the ground, except when females oviposited. Spiders preyed upon this species by jumping on them.

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REFERENCES

Adamovic, Z. R., 1963, Ecology of some asilid-species (Asilidae, Diptera) and their relation to honey bee (*Apis mellifica* L.). *Museum d'Histoire Naturelle de Beograd*, Hors serie 30: 1-102. (In Serbian, English summary)

Back, E. A., 1909, The robber-flies of America, north of Mexico, belonging to the subfamilies Leptogastrinae and Dasypogoninae. *Transactions of the American Entomological Society*, 35: 137-400, 12 plates.

Baker, N. T., Fischer, R. L., 1975, A taxonomic and ecologic study of the Asilidae of Michigan. *Great Lakes Entomologist*, 8: 31-91.

Bromley, S. W., 1931, A preliminary annotated list of the robber flies of Ohio. *Ohio State Museum Science Bulletin*, 1: 1-18.

Bromley, S. W., 1946, Guide to the insects of Connecticut. Part VI. The Diptera or true flies of Connecticut. Third Fascicle. Asilidae. *Connecticut State Geological and Natural History Survey Bulletin* No. 69, 1-48.

Bromley, S. W., 1950, Florida Asilidae (Diptera) with description of one new species. *Annals of the Entomological Society of America*, 43: 227-239.

Dennis, D. S., 1979, Ethology of *Holcocephala fusca* in Virginia (Diptera: Asilidae). *Proceedings of the Entomological Society of Washington*, 81: 366-378.

Dennis, D. S., 2012, Ethology of *Proctacanthus brevipennis* (Wiedemann, 1828) (Diptera: Asilidae) in Northeastern Florida, U.S.A. *Journal of the Entomological Research Society,* 14: 91-109.

Dennis, D. S., 2013, Ethology of *Stichopogon trifasciatus* (Say, 1823) in Northeastern Florida, U.S.A. *Journal of the Entomological Research Society*, 15: 37-50.

Dennis, D. S., Lavigne, R. J., 1975, Comparative behavior of Wyoming robber fliesII (Diptera: Asilidae). *Agricultural Experiment Station University of Wyoming-Laramie Science Monograph* No. 30, 68 pp.

Dennis, D. S., Lavigne, R. J., 1976a, Ethology of *Efferia varipes* with comments on species coexistence (Diptera: Asilidae). *Journal of the Kansas Entomological Society*, 49: 48-62.

Dennis, D. S., Lavigne, R. J., 1976b, Ethology of *Leptogaster parvoclava* in Wyoming (Diptera: Asilidae*). Proceedings of the Entomological Society of Washington,* 78: 208-222.

Dennis, D. S., Lavigne, R. J., 1979, Ethology of *Machimus callidus* with incidental observations on *M. occidentalis* in Wyoming (Diptera: Asilidae). *The Pan-Pacific Entomologist*, 55: 208-221.

Dennis, D. S., Lavigne, R. J., 2007, Hymenoptera as prey of robber flies (Diptera: Asilidae) with new prey records. *Journal of the Entomological Research Society*, 9: 23-42.

Dennis, D. S., Lavigne, R .J., Bullington, S. W., 1986, Ethology of *Efferia cressoni* with a review of the comparative ethology of the genus (Diptera: Asilidae). *Proceedings of the Entomological Society of Washington*, 88: 42-55.

Dennis, D. S., Lavigne, R. J., Dennis, J. G., 2010, Hemiptera (Heteroptera/Homoptera) as prey of robber flies (Diptera: Asilidae) with unpublished records. *Journal of the Entomological Research Society*, 12: 27-47.

Dennis, D. S., Lavigne, R. J., Dennis, J. G., 2012, Spiders (Araneae) as prey of robber flies (Diptera: Asilidae). *Journal of the Entomological Research Society*, 14: 65-76.

Dennis, D. S., Roehrkasse, G. P., Lavigne, R. J., 1975, Prey recognition by *Efferia frewingi* (Dipera: Asilidae). *Annals of the Entomological Society of America*, 68: 404-408.

Evans, H. E., 1973, Notes on the nesting behavior of *Steniolia elegans* (Hymenoptera: Sphecidae). *Great Basin Naturalist*, 33: 29-30.

Geller-Grimm, F., 2013, Robber flies (Asilidae), database, catalog of species. Available from http://www.geller-grimm.de/catalog/species.htm (accessed 28 May 2013).

Goslin, R. M., 1950, Some robber flies from Campbell County Tennessee. *Journal of the Tennessee Academy of Science*, 25: 303-306.

Hayat, R., Çalışkan, H., 2003, Ethology of the robber fly *Dasypogon irinelae* Weinberg, 1986 (Diptera, Asilidae). *Zoology in the Middle East*, 30: 91-94.

Hespenheide, H. A., 1978, Prey, predatory and courtship behavior of *Nannocyrtopogon neoculatus* Wilcox and Martin (Diptera: Asilidae). *Journal of the Kansas Entomological Society*, 51: 449-456.

Hespenheide, H. A., Rubke, M. A., 1977, Prey, predatory behavior, and the daily cycle of *Holopogon wilcoxi* Martin (Diptera: Asilidae). *The Pan-Pacific Entomologist*, 53: 277-285.

Hobby, B. M., 1931a, The British species of Asilidae (Diptera) and their prey. *Transactions of the Entomological Society of South England*, 6: 1-42.

Hobby, B. M., 1931b, The relationship between courtship and predaceous habits in *Dioctria rufipes* De. G. and *D. atricapilla* Meig. (Dipt., Asilidae). *Proceedings of the Entomological Society of London* (Ser. A), 6: 74-75.

Hobby, B. M., 1935, Rhodesian Asilidae (Diptera) and their prey collected by Mr. C.F.M. Swinnerton. *Journal of Animal Ecology*, 4: 90-112.

Joern, A., Rudd, N. T., 1982, Impact of predation by the robber fly *Proctacanthus milbertii* (Diptera: Asilidae) on grasshopper (Orthoptera: Acrididae) populations. *Oecologia*, 52: 42-46.

Johnson, P. E., 1976, A preliminary investigation of the behavior of adult *Holcocephala abdominalis* (Say) (Diptera: Asilidae) in Putnam County, Indiana; with a description of the larvae and eggs. Unpublished M.S. Thesis, DePauw University, Greencastle, Indiana.

Lavigne, R. J., 1964, Notes on the distribution and the ethology of *Efferia bicaudata* (Diptera: Asilidae), with a description of the eggs. *Annals of the Entomological Society of America*, 57: 341-344.

Lavigne, R. J., 1970a, Courtship and predatory behavior of *Cyrtopogon auratus* and *C. glarealis* (Diptera: Asilidae). *Journal of the Kansas Entomological Society*, 43: 163-171.

Lavigne, R. J., 1970b, Courtship and predation behavior of *Heteropogon maculinervis* (Diptera: Asilidae). *Journal of the Kansas Entomological Society*, 43: 270-273.

Lavigne, R. J., 1971, *Backomyia seminoensis* sp. n. from Wyoming with ethological notes on *B. limpidipennis*. *Journal of the Kansas Entomological Society*, 44: 337-342.

Lavigne, R. J., 1979, Notes on the ethology of *Efferia argyrogaster* (Diptera: Asilidae) in Mexico. *Proceedings of the Entomological Society of Washington*, 81: 544-551.

Lavigne, R. J., 1984, Ethology of *Neocerdistus acutangulatus* (Diptera: Asilidae) in South Australia. *Proceedings of the Entomological Society of Washington*, 86: 422-431.

Lavigne, R. J., 1992, Ethology of *Neoaratus abludo* Daniels (Diptera: Asilidae) in South Australia, with notes on *N. pelago* (Walker) and *N. rufiventris* (Macquart). *Proceedings of the Entomological Society of Washington*, 94: 253-262.

Lavigne, R. J., 2002, Evolution of courtship behavior among the Asilidae (Diptera), with a review of courtship and mating. *Studia dipterologica*, 9: 703-742.

Lavigne, R. J., Bullington, S. W., 1984, Ethology of *Laphria fernaldi* (Back) (Diptera: Asilidae) in southeast Wyoming. *Proceedings of Entomological Society of Washington*, 86: 326-336.

Lavigne, R. J., Bullington, S. W., 1999, Ethology of *Heteropogon paurosomus* Pritchard (Diptera: Asilidae) in Mexico. *Journal of the Entomological Research Society*, 1: 9-19.

Lavigne, R. J., Bullington, S. W., Stephens, G., 1993, Ethology of *Holopogon seniculus* (Diptera: Asilidae). *Annals of the Entomological Society of America*, 86: 91-95.

Lavigne, R. J., Dennis, D. S., 1975, Ethology of *Efferia frewingi* (Diptera: Asilidae). *Annals of the Entomological Society of America*, 68: 992-996.

Lavigne, R. J., Dennis, D. S., 1985, Ethology of three coexisting species of *Efferia* (Diptera: Asilidae) in Mexico. *Proceedings of the Entomological Society of Washington*, 87: 146-160.

Lavigne, R. J., Dennis, D. S., Gowen, J. A., 2000, Asilid literature update 1956-1976 including a brief review of robber fly biology (Diptera: Asilidae). *Agricultural Experiment Station University of Wyoming Science Monograph* 36, 134 pp.

Lavigne, R. J., Holland, F. R., 1969, Comparative behavior of eleven species of Wyoming robber flies (Diptera: Asilidae). *Agricultural Experiment Station University of Wyoming Laramie Science Monograph* No. 18, 61 pp.

Lavigne, R. J., Pfadt, R. E., 1966, Parasites and predators of Wyoming rangeland grasshoppers. *University of Wyoming Agricultural Experiment Station Science Monograph* 3, 31 pp.

Lavigne, R. J., Pogue, M. G., 2009, Ethology of *Omninablautus nigronotum* (Wilcox) (Diptera: Asilidae) in Wyoming. *Proceedings of the Entomological Society of Washington*, 111: 1-6.

Lavigne, R. J., Pogue, M., Johnson, P., 1983, Ethology of *Laphystia rufofasciata* Curran (Diptera: Asilidae) in Wyoming. *Proceedings of the Entomological Society of Washington*, 85: 121-127.

Lavigne, R. J., Rogers, L., Lavigne, F., 1976, Ethology of *Efferia benedicti* (Diptera: Asilidae) in Wyoming. *Proceedings of the Entomological Society of Washington*, 78: 145-153.

Lehr, P. A., 1958a, The biology of a robber fly feeding on locusts. *Doklady Kazakhstan Akademii selskokhoz*. Nauk, Alma-Ata, 3: 16 -23. (In Russian)

Lehr, P. A., 1958b, Information on the biology of *Promachus leontochlaenus* Loew (Diptera- Asilidae). *Trudy nauchno-issledovaniya Instituta Zaschti Rasteniy, KazASKhN* (*Proceedings of the Scientific Research Institutee of Protection of Plants, Kazakhstan*), Alma-Ata, 4: 210-224. (In Russian)

Lehr, P. A., 1958c, On the biology and behavior of robber flies (Asilidae-Diptera). *Trudy Instituta Zoologii, Akademiya Nauk Kazakhstan*, SSR, 8: 173-196. (In Russian)

Lehr, P. A., 1961, The robber fly *Stenopogon heteroneurus* Macquart (Diptera: Asilidae), its behavior and feeding. *Trudy nauchno-issledovaniya Instituta Zaschti Rasteniy, KazASKhN* (*Proceedings of the Scientific Research Institute for Protection of Plants, Kazakhstan*), Alma-Ata, 6: 96-130. (In Russian)

Lehr, P. A., 1964, On the nutrition and significance of Asilidae. *Trudy nauchno-issledovaniya Instituta Zaschti Rasteniy, KazASKhN* (*Proceedings of the Scientific Research Institute for Protection of Plants, Kazakhstan*), Alma-Ata, 8: 213-244. (In Russian)

Lehr, P. A., 1971, Review of life style and significance of *Machimus rusticus* Meig. (Diptera: Asilidae) and closely related species of robber flies. *Biological Sciences, Kazakhstan State University*, Alma-Ata, 3: 203-213. (In Russian)

Lehr, P. A., 1972, The robber flies of the genera *Holopogon* Loew and *Jothopogon* Becker (Diptera, Asilidae) in the fauna of the USSR. *Entomological Review*, 51, 99-109.

Londt, J. G. H., 1991, Afrotropical Asilidae (Diptera) 21. Observations on the biology and immature stages of *Damalis femoralis* Ricardo, 1925 (Trigonomiminae). *Annals of the Natal Museum*, 32: 149-162.

Martin, C. H., 1959, The *Holopogon* complex of North America, excluding Mexico, with the descriptions of a new genus and a new subgenus (Diptera, Asilidae). *American Museum Novitates*, Number 180, 40 pp.

McAtee, W. L., Banks, N., 1920, District of Columbia Diptera: Asilidae. *Proceedings of the Entomological Society of Washington*, 22: 13-33.

Melin, D., 1923, Contributions to the knowledge of the biology, metamorphosis, and distribution of the Swedish asilids in relation to the whole family of asilids. *Zoologiska Bidrag Fran Uppsala*, 8: 1-317.

Morgan, K. R., Shelly, T. E., 1988, Body temperature regulation in desert robber flies (Diptera: Asilidae). *Ecological Entomology*, 13: 419-428.

Morgan, K. R., Shelly, T. E., Kimsey, S., 1985, Body temperature regulation, energy metabolism, and foraging in light-seeking and shade-seeking robber lies. *Journal of Comparative Physiology*, 155: 561-570.

Musso, J. J., 1970, Contribution à l'étude des Asilides de la Basse Provence (Dip. Asilidae) listes de proies. *Annales de la Faculté des Sciences de Marseille*, 44: 143-153.

Musso, J. J., 1972, Observations sur les moeurs prédatrices de quelques Asilides [Dipt. Brachycera] de la Basse Provence. *Annales de la Societe Entomologique de France (N.S.)*, 8: 409-421.

Nation, J. L., 2008, *Eyes and vision*. *In* J. L. Capinera, ed. Encyclopedia of Entomology (2nd edition). Springer, New York, New York. 4346 pp.

Parmenter, L., 1952, Notes on the Asilidae (robber flies). *Entomologist's Record*, 64: 229-234, 263-266, 295-299.

Poulton, E. B., 1906, Predaceous insects and their prey. *Transactions of the Royal Entomological Society of London* 1906: 323-409.

Scarbrough, A. G., 1974, A faunistic study of Asilidae (Diptera) at three locations in northern Baltimore County, Maryland: incidence, relative abundance and seasonal distribution. *Proceedings of the Entomological Society of Washington*, 76: 385-396.

Scarbrough, A. G., 1978, Ethology of *Cerotainia albipilosa* Curran (Diptera: Asilidae) in Maryland: predatory behavior. *Proceedings of the Entomological Society of Washington*, 80: 113-127.

Scarbrough, A. G., 1979, Predatory behavior and prey of *Diogmites missouriensis* Bromley in Arkansas (Diptera: Asilidae). *Proceedings of the Entomological Society of Washington*, 81: 391-400.

Scarbrough, A. G., 1981, Ethology of *Eudioctria tibialis* Banks (Diptera: Asilidae) in Maryland: prey, predator behavior, and enemies. *Proceedings of the Entomological Society of Washington*, 83: 258-268.

Scarbrough, A. G., 1982, Coexistence in two species of *Holcocephala* (Diptera: Asilidae) in Maryland habitat: predatory behavior. *Proceedings of the Entomological Society of Washington*, 84: 349-365.

Scarbrough , A. G., Sraver, B. E., 1979, Predatory behavior and prey of *Atomosia puella* (Diptera: Asilidae). *Proceedings of the Entomological Society of Washington*, 81: 630-639.

Shelly, T. E., Pearson, D. L., 1980, Predatory behavior of *Proctacanthella leucopogon* (Diptera: Asilidae): prey recognition and prey records. *Environmental Entomology*, 9: 7-9.

Williams, A. H., 1999, Arthropod fauna using marbleseed in Wisconsin. *Proceedings of the Sixteenth North American Prairie Conference*, 16: 165-171.

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