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Ethology of *Holopogon snowi* Back, 1909 (Diptera: Asilidae) in Northeastern Florida, U.S.A.

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ABSTRACT

Holopogon snowi Back, 1909 foraged from plant twig tips, capturing prey in flight, and immobilizing them in flight or at the feeding site. Identified prey came from eight orders: Araneae (0.5%), Blattodea (family Termitidae; 9.9%), Coleoptera (0.5%), Diptera (8.8%), Hemiptera (26.4%), Hymenoptera (11.0%), Psocoptera (11.0%), and Thysanoptera (27.5%). Male courtship preceded mating in the tail-to-tail position. Females dropped eggs on the twigs of scrub oak or directly onto the ground. This species demonstrated a distinct daily rhythm of activity for feeding, mating, and ovipositing. Grooming behavior did not occur often but resembled that of other species of Asilidae. Habitat, resting behavior, and predators also are discussed. This is the first record of *H. snowi* occurring in Florida.

Key words: Asilidae, behavior, robber flies, prey, new Florida record.

INTRODUCTION

Twenty-one species of robber flies in the genus *Holopogon* occur in the United States of America (U.S.A.) (Geller-Grimm, 2016). Despite their wide distribution, different aspects of the ethology of only seven species has been described: *H. albipilosus* Curran, 1923 (Dennis and Lavigne, 1975) and *H. seniculus* Loew, 1866 (Lavigne *et al*., 1993) in Wyoming; *H. caesariatus* Martin, 1959 in Idaho and Oregon (Martin, 1959); *H. currani* Martin, 1959 in Arizona (Martin, 1959); *H. phaeonotus* Loew, 1874 in Florida (Dennis, 2014); *H. stellatus* Martin, 1959 in California (Martin, 1959); and *H. wilcoxi* Martin, 1959 in Arizona (Hespenheide and Rubke, 1977).

This paper provides detailed information on the ethology of *H. snowi* Back, 1909 in the Moses Creek Conservation Area (MCCA), near the southern boundary of St. Augustine in northeastern Florida.

MATERIALS AND METHODS

The author studied a population of *H. snowi* from 24 March through 5 May 2016 on both sides of a sand road that follows an electrical transmission line corridor. During this period, two to 59 (mean of 16) asilids were observed during a day, each for up to 90 minutes. Total number of hours of observation was approximately 103. The

identification of *H. snowi* was confirmed using the key in Martin (1959) and description in Back (1909). Male and female specimens will be deposited in the Smithsonian Institution, National Museum of Natural History, Washington, D.C.

Observations began with the author standing, kneeling, or sitting on the ground and observing one or more flies until they were lost from sight in order to collect information on their various behaviors and diurnal activities. When sufficient data were gathered on an individual's behaviors, the author walked along the edges of the road to observe the activities of many flies. These actions also allowed for the collection of prey and the observation of mating pairs and ovipositing females. Some behaviors, such as prey manipulation and oviposition, 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. The author then identified the prey in the office using primarily prey that had been previously identified for *H. phaeonotus* (Dennis, 2014) by Research Entomologists at the U.S. Department of Agriculture, Agricultural Research Service, Systematic Entomology Laboratory, Beltsville, Maryland U.S.A. Some *H. phaeonotus* and *H. snowi* prey, was not identifiable to family, genus, or species because of the unavailability of specialists, inadequate keys, or poor condition of the specimens.

In the office, prey length was determined by measuring each prey to the nearest 0.5 mm with a clear, plastic ruler.

Temperature and wind are important environmental variables that determine the activities in which adult robber flies engage. A hand held Taylor thermometer and a Cooper-Atkins DPP400W Digital Thermometer were used to take air temperatures and a Dwyer Hand-Held Wind Meter was used to measure wind speed.

RESULTS AND DISCUSSION

Morphology and distribution

Like other *Holopogon*, *H. snowi* is a small (approximately 6-8.5 mm in length, excluding antennae) blackish species with white setae on the body. Back (1909) described the tibiae and tarsi as dark reddish. In the population studied in the MCCA, the fore- and mid-tibiae are light reddish brown to dark reddish, and at least the proximal 1/4-1/2 of the hind tibiae has similar coloration. The fore- and mid-tarsi are also light reddish brown as are at least the ventral part of the hind tibiae. The dorsal part of the hind tibiae may be black. Depending on the light conditions in the field and the angle of view, *H. snowi* tibiae and tarsi may look reddish black to black, and the setae may look yellowish to black.

Holopogon snowi has historically been reported to occur in Kansas, Oklahoma, and Texas (Back, 1909; Martin, 1959). More recently Williams (1999) observed it in Wisconsin. The observation of this species in Florida is a new record for the state and the first time that it has been reported in eastern U.S.A.

Habitat

The 8.6-14.2 m (mean 11.3 m) wide, 1,129 m long section of the electrical transmission line corridor and associated sparsely vegetated road, passes through a scrub vegetation community where *H. snowi* occurs (Fig. 1). This community grades into mesic flatwoods and upland mixed forest vegetation communities, and so there is some overlap in the vegetation. An area west of the road was sprayed with herbicide late Summer to Fall 2015 for up to 3.7 m (mean 1.5 m) and is dominated by dead scrub oak (*Quercus* spp.) with heights up to 2.7 m. The area east of the road was not sprayed and is dominated for a distance up to 3 m with live scrub oak that is up to 3.7 m tall. On either side of these areas taller vegetation grows, in particular sand pine [*Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarg.]. The vegetation in the *H. snowi* habitat is shown in Table 1.

Table 1. Vegetation in habitat in which *Holopogon snowi* was studied in the Moses Creek Conservation Area.

Family/Genus/Species/Common Name		**Family**/Genus/Species/Common Name
Annonaceae		**Fabaceae**
Asimina sp./Pawpaw		*Erythrina herbaceae* L./Coralbean
Aquifoliaceae		*Galactia* sp./Milkpea
Ilex opaca Alton/American holly		**Fagaceae**
Arecaceae		*Quercus geminata* Small/Sand live oak
Serenoa repens (W. Bartram) Small/Saw palmetto		*Quercus* spp. /Scrub oaks
Asteraceae		**Magnoliaceae**
Balduina angustifolia (Pursh) B. L. Rob./ Coastalplain honeycombhead		*Magnolia grandflora* L./Southern magnolia
Eupatorium sp. /Fennel		**Pinaceae**
Carphephorus corymbosus (Nutt.) Torr. and A. Gray/Coastalplain chaffhead (Florida paintbrush)		*Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarg./ Sand pine
Liatris tenuifolia Nutt. var. *quadriflora* Chapm./Shortleaf gayfeather		**Poaceae**
Pityopsis graminifolia (Michx.) Nutt./ Narrowleaf silkgrass		*Andropogon* sp./Bluestem
Solidago sp./Goldenrod		Other grasses
Cactaceae		**Smilaceae**
Opuntia humifusa (Raf.) Raf./Prickly pear cactus		*Smilax bona-nox* L./Saw greenbrier vine
Ericaceae		*Smilax glauca* Walter/Cat greenbrier vine
Lyonia ferruginea (Walter) Nutt./Rusty lyonia		**Vitaceae**
Lyonia lucida (Lam.) K. Koch/Fetterbush		*Vitis rotundifolia* Michx./Muscadine vine
Vaccinium myrsinitas Lam./Shiny blueberry		**Zamiaceae**
Euphorbiaceae		*Zamia integrifolia* L./Florida arrowroot (Coontie)
Cnidoscolus stimulosus (Michx.) Engelm. & A. Gray/Tread-softly		

Holopogon snowi occur primarily on the tips of 1-4 mm diameter scrub oak twigs (a small branch without leaves) and up to 7 mm diameter buds. In areas where there are a large number of scrub oak plants close together (within 15-30 cm of each other), flies rest on and forage from the outside of the plants facing open areas of habitat or on top of the plants.

Fig. 1. *Holopogon snowi* habitat along electrical transmission line corridor.

Some individuals also were observed on leaves of scrub oak, twigs of rusty lyonia (*Lyonia ferruginea* (Walter) Nutt.), 1/2 mm diameter tendrils of saw greenbrier vines (*Smilax bona-nox* L.), dead sand pine and sand live oak (*Quercus geminata* Small) branches, and the tips of dead bluestem (*Andropogon* sp.) grass stems, and shortleaf gayfeather (*Liatris tenuifolia* Nutt. var. *quadriflora* Chapm.) stems.

Williams (1999) found *H. snowi* on marbleseed (*Onosmodium molle* Michx.) plant and commented that some predator arthropod fauna hunted over an entire plant and others (presumably including *H. snowi*) "…hunted at the shoot tips and about the flowers, where insect activity was usually greatest." Other species of *Holopogon* in the U.S.A. also are known to forage from the tips of twigs and from low weeds or bushes: *H. albipilosus* (Dennis and Lavigne, 1975); *H. caesariatus* and *H. currani* (Martin, 1959); *H. guttulus* (Wiedeman, 1821) (Back, 1909; Bromley, 1931, 1946, 1950; Goslin, 1950; McAtee and Banks, 1920, all as *H. guttula*); *H. phaeonotus* (Dennis, 2014); *H. seniculus* (Lavigne *et al*., 1993); *H. stellatus* (Martin, 1959); and *H. wilcoxi* (Hespenheide and Rubke, 1977). Several species of *Holopogon* in the former Union of Soviet Socialist Republics (U.S.S.R.), occur on the tips of high grasses and twig tips of shrubs (Lehr, 1964, 1972). In France, Musso (1972) found *H. venustus* (Rossi, 1790) on the extreme tips of 2-3 mm diameter twigs.

Resting behavior

Holopogon snowi rests on and forages from twig tips (Fig. 2) 15 cm to 2.7 m above the ground, but are most frequently seen at an elevation of at least 30.5 cm. Other species of *Holopogon* are generally observed at heights from 10 cm to 3 m above the substrate (Dennis, 2014; Dennis and Lavigne, 1975; Hespenheide and Rubke, 1977; Lavigne *et al*., 1993; Lehr, 1972; Martin, 1959; Musso, 1972).

Individuals rest in a horizontal position on the twig tip or below (up to 1.9 cm) the tip with their bodies parallel to the bare branch. When on the branch they would often face away from the tip. Similar resting behavior was observed for *H. phaeonotus* (Dennis, 2014).

The twigs would often vibrate or wave in the wind when the wind gusted in excess of 14.5 km/hr. In these circumstances the flies move to lower elevations on the

vegetation (e.g., from 1.2 m to 0.3-0.6 m) where the wind blew less (6.4- 9.7 km/hr). Also, they would more often face away from the twig tips, hold themselves closer to the twigs, or move to the sides of the twigs with their heads turned down towards the twigs. When individuals remained on top of the twigs, one or both wings would often blow open when the wind gusted as low as 6.4-9.7 km/hr, in particular when the asilids faced away from the direction of the wind. *Holopogon phaeonotus* also made postural adjustments on twigs when the wind gusted 11-16 km/hr (Dennis, 2014).

Fig. 2. *Holopogon snowi* resting and grooming while on scrub oak twig tip.

While resting, *H. snowi* remains motionless for variable periods of time ranging from 1-5 seconds to 5 minutes. During this time they only move the head and body slightly as they watch other insects flying by or the author moving around. One individual rested for 45 minutes, with intermittent periods of motionless and slight movements, before resuming foraging and other activities. *Holopogon phaeonotus* would rest for up to 7 minutes before resuming other activities, in particular foraging (Dennis, 2014). Lehr (1972) commented on *H. claripennis avor* Lehr, 1972 turning its head and following a person and “not losing him from sight.”

Holopogon snowi, like H. phaeonotus (Dennis, 2014), usually did not turn so that one of its sides faced and was elevated to the sun or flatten themselves against the twig they were on, such as when the sun was obscured by clouds and air temperatures ranged from 24.0-35ºC. (n=21, mean 29.3ºC). Many other species of robber flies including *H. priscus* (Meigen, 1821) (Lehr, 1972), 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, 2016; Dennis and Lavigne, 1975; Lavigne and Holland, 1969).

According to Morgan *et al*. (1985), and Morgan and Shelly (1988), foraging neotropical and desert robber flies regulate their body temperatures by microhabitat selection and postural adjustments. Lehr (1972) commented that each species of *Holopogon* occupy a habitat with specific microclimate components. Thus, both *H. snowi* and *H. phaeonotus* (Dennis, 2014) may primarily use microhabitat selection to regulate their body temperature.

When resting and feeding, a few individuals expelled a drop of creamy-white to brownish liquid from their anus. Similar behavior was observed for *H. phaeonotus* (Dennis, 2014), and Lehr (1958c) commented that the expulsion of liquid from the anal opening is quite common in robber flies.

Foraging and feeding behavior

Holopogon snowi forages primarily from scrub oak twig tips. A few individuals infrequently foraged from scrub oak leaves, twigs of rusty lyonia, saw greenbrier vine tendrils, dead sand pine branches on the ground and on a fallen tree, dead sand live oak branches on the ground, tips of dead bluestem grass stems, and shortleaf gayfeather stems. Individuals are active in both sun and shade. Other species of *Holopogon* have been reported to forage primarily from twig tips (Dennis, 2014; Dennis and Lavigne, 1975; Lehr, 1972; Martin, 1959).

Foraging height depends on vegetation height and the location of sunlight on the twigs. *Holopogon snowi* generally forages higher in the vegetation in the morning. As these areas become shaded, the asilids move to lower areas in sunlight. This is similar behavior to that described for *H. phaeonotus* (Dennis, 2014). Hespenheide and Rubke (1977) speculated that *H. wilcoxi* spent the night in areas where they would be in sunlight earliest in the morning and then moved to areas better suited for foraging.

Holopogon snowi foraging individuals usually held their bodies at a 30 to 45 degree angle with their heads facing up or down. Foraging *H. priscus* hold their heads downward and their bodies at an angle to the side of the grass stem that they are on (Lehr, 1972).

A few *H. snowi* foraged from a horizontal position on the twig tip. In these postures and positions they would pivot and make quick movements (generally every 2-3 seconds) of their heads and bodies, often turning 180° to face another direction. *Holopogon albipilosus* also rapidly faces different directions while remaining on the same twig when foraging (Dennis and Lavigne, 1975), but *H. phaeonotus* does not (Dennis, 2014).

In the morning, once the sun was shining and until about 2:00-3:00 PM, *H. snowi* in the area on the western side of the road would face primarily south, southeast, and east. Then in the afternoon, because of increased shade on the western side, most flies moved across the road to the area on the eastern side where they would face west towards the sun. During cloudy weather, *H. snowi* more frequently face other directions in both areas on the western and eastern sides of the road.

The directions that *H. snowi* faces and their foraging postures or attitudes, presumably allows the flies to use backlighting to better see their prey because of their position relative to the prey and the sun. Also the body held at a 45-degree angle allows *H. snowi* to see potential prey more clearly because the incoming light is at right angles to the surface of the forward, flattened ommatidia. Similar observations have been made for *H. phaeonotus* and other species of robber flies (Dennis, 2014). According to Nation (2008), robber flies have higher visual acuity near the forward part of their eyes and this probably enhances their ability to see and capture prey.

A few foraging *H. snowi* made investigatory flights without making contact with potential prey. Flies made these flights when potential prey were 12.7-17.8 cm below or directly in front of its position, and they also often chased them for up to 30.5 cm. Investigatory flights are common for *H. phaeonotus* and many species of robber flies (Dennis, 2014).

A few *H. phaeonotus* captured insects and released them while still in flight (Dennis, 2014). Except in one case, *H. snowi* did not capture insects and release them in flight. Like *H. phaeonotus*, a number of *H. snowi* released captured insects after returning to their foraging twig tip and while manipulating the prey with their tarsi prior to insertion of their proboscis. One individual discarded the prey after insertion of its proboscis in flight, landing at its feeding site, and prior to manipulating the prey with its tarsi. This may indicate that *H. snowi* uses visual and other stimuli to select prey as mentioned by Dennis and Lavigne (1975). Lehr (1958) commented that robber flies often cannot determine whether a flying insect is acceptable prey.

Short flights about a foraging position without being directed towards any potential prey are called orientation flights (Dennis and Lavigne, 1975). *Holopogon snowi* made orientation flights within 5-91 cm of its foraging position, most often in a circle in front of its foraging twig tip.

Holopogon snowi would forage from the same twig tip for 30 seconds to 79 minutes with an mean of 28 minutes. During this period of time, an individual could feed on a number of prey and make numerous investigatory and orientation flights. When an individual moved to a new foraging position, it was within 15 cm to 1.2 m of its previous position.

Based on 44 prey capture records, *H. snowi* captured 31 of its prey in the air 2.5-75 cm (mean 21 cm) in front of its foraging position (Table 2). These prey were 2.5-30 cm above (n=16; mean 8.3 cm), at the same level (n=13; mean 24.8 cm), or 2.5-5 cm below (n=2; mean 3.8 cm) the level of the foraging position. Thus, *H. snowi* captured the largest number of prey in front of and above their foraging position, similar to *Holopogon albipilosus* that captured most prey 7.5-30 cm in front of and above their foraging position (Dennis and Lavigne, 1975). *Holopogon phaeonotus* captured its 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, 2014).

Holopogon snowi would forage until wind gusts reached 11.5 km/hr and as long as the twig they perched on was not waving excessively in the wind. Once the gusts reached 14.5-17.7 km/hr and the twig vibrated or waved in the wind, the robber flies stopped foraging, held their bodies closer and parallel to the twig, and often faced the interior of the plant. Also, similar to when they were resting, some flies moved lower down in the vegetation to forage where the wind gusts were not as high. For example, at 1:44 PM on 08.04.2016, at an elevation of 1.2 m above the ground the wind gusted to 16.1 km/hr and the flies moved to an elevation of 0.6 m (61 cm) where the wind was 6.4 km/hr. One asilid was blown off a waving twig during a sudden gust of 19.3-22.5 km/hr.

Table 2. Location, number, and distance of prey captured in relation to foraging level of *Holopogon snowi*.

Prey Location	Number of Prey	Horizontal Distance (cm) (Average cm)	Vertical Distance Above/Below (cm) (Average cm)
In Front of *H. snowi*			
At Same Foraging Level	13	2.5–75 (24.8)	N/A[1]
Above Foraging Level	16	2.5–45 (19.2)	2.5–30 (8.3)
Below Foraging Level	2	2.5–15 (8.8)	2.5–5 (3.8)
To Left of *H. snowi*			
At Same Foraging Level	4	5–25 (15.6)	N/A
Above Foraging Level	2	17.5–20 (18.8)	5 (5)
To Right of *H. snowi*			
At Same Foraging Level	2	30–45 (37.5)	N/A
Above Foraging Level	3	12.5–20 (15.8)	5 (5)
Behind *H. snowi*			
At Same Foraging Level	1	20 (N/A)	N/A
Straight Above *H. snowi*			
Above Foraging Level	1	N/A	10 (N/A)

[1] N/A = not applicable.

When it captured prey, *H. snowi* would most often return to its foraging twig tip and hold onto the twig tip with one of its mid-tarsi. However, one individual held onto the twig tip with its right fore tarsi during prey manipulation and a few individuals that had inserted their proboscis in flight, landed on the twig tip in normal resting posture without holding on with one of their mid-tarsi. If the robber fly had not inserted its proboscis in the prey before landing, it would insert it while holding the prey with the tarsi not used to hold onto the twig tip. Also, some individuals still held onto prey with the tarsi when the proboscis had been inserted in flight, possibly to prevent the prey's movement from dislodging from the fly's proboscis. *Holopogon phaeonotus* either inserted its proboscis in flight or at the feeding site while holding onto prey with tarsi not used to hold onto a twig (Dennis, 2014). Most prey of *H. albipilosus* were immobilized at the feeding site while the asilid held onto a twig with one of its mid-tarsi and held the prey with the rest of its tarsi; only a few flies immobilized prey in the air prior to landing to feed (Dennis and Lavigne, 1975).

Holopogon snowi would manipulate prey one to nine (n=42; mean four) times during feeding. When it manipulated prey, an asilid would hold onto the side of a twig tip with one of its mid-tarsi (Fig. 3) and manipulate the prey with the other tarsi. Then it would re-insert its proboscis and stand up on the twig tip to resume feeding. During prey manipulation, both *H. phaeonotus* (Dennis, 2014) and *H. albipilosus* (Dennis and Lavigne, 1975) held onto the twig tips with either their fore- or mid-tarsi.

In general, the number of times the flies manipulated prey depended upon the length (not including folded wings) and shape of the prey and the amount of time spent feeding. *H. snowi* fed on small prey (0.5 mm) such as thrips (Thysanoptera), for 1-5 minutes and did not manipulate them. They fed on larger prey (3-3.5 mm; Hemiptera: Cixiidae, *Cixius* sp.), for 9 1/2-13 1/2 minutes and either did not manipulate or manipulated them 1-2 times. *Holopogon snowi* fed on slightly larger prey with a narrower shape [3.5-4 mm; alate Blattodea (formerly Isoptera): Kalotermitidae, *Calcaritermes nearcticus* Snyder, 1933 and Rhinotermitidae, *Reticulitermes virginicus* (Banks, 1907)] for 8 1/2-20 minutes and manipulated them 2-9 times.

Fig. 3. *Holopogon snowi* manipulating prey holding onto scrub oak twig tip.

While *H. snowi* fed, prey hung free on their proboscises without support by the tarsi. Similar behavior was observed for *H. phaeonotus* (Dennis, 2014).

Female *H. snowi* fed on prey that averaged slightly longer than those fed upon by males. The mean prey length for females was 2.3 mm (n = 67) with a range from 0.5-5.0 mm; whereas, for males it was 1.9 mm (n = 32) with a range from 0.5 -4.0 mm. Overall mean prey length was 2.1 mm. Both female and male *Holopogon phaeonotus* fed on longer prey than *H. snowi* with a range from 1.0-7.0 mm (Dennis, 2014). Female and male *H. albipilosus* and *H. seniculus* fed on slightly smaller prey with prey length ranging from 1.6-1.9 mm (Dennis and Lavigne, 1975; Lavigne *et al*., 1993).

Mean predator to prey ratios 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 male and female *H. snowi* each, the mean predator to prey ratio is 3.3:1.0. This indicates that *H. snowi* is over three times the length of its prey. Mean predator to prey ratios for *H. albipilosus* (Dennis and Lavigne, 1975), *H. phaeonotus* (Dennis, 2014), and *H. seniculus* (Lavigne *et al*., 1993) are 3.5:1.0, 2.6:1.0, and 3.1:1.0, respectively. For *H. wilcoxi*, the overall range of prey sizes varied from 1/10 to 1/2 the length of the fly (Hespenheide and Rubke, 1977).

At the completion of feeding, *H. snowi* individuals discarded most prey (46 out of 79 observations) by pushing them off the proboscis with the fore tarsi while still at the feeding site. The second most common method of prey disposal was dropping prey in flight as the asilid left the feeding site (n=16), followed by allowing prey to drop off the

proboscis at the feeding site (n=9), and dropping during feeding while manipulating prey (n=8). The most common methods for *H. phaeonotus* (Dennis, 2014) and *H. seniculus* (Lavigne *et al*., 1993) to discard prey was to push it off their proboscis while still at the feeding site and to drop prey during feeding while manipulating them. *Holopogon albipilosus* pushed prey off its proboscis with the fore tarsi while still at the feeding site (Dennis and Lavigne, 1975).

The length of time *H. snowi* spent feeding on individual prey varied from 1-20 minutes (n=35), with an mean of 4.7 minutes. Time between feedings (interfeeding time) varied between 0-55 minutes (n=16), with an mean of 8.8 minutes. There were two - zero minute interfeeding times where individuals dropped prey at the feeding site or in flight after leaving the feeding site and immediately captured another prey.

The theoretical number of prey an individual *H. snowi* could feed on in one day can be calculated if it is assumed that, (1) it continually forages and feeds between 11:00 AM and 6:00 PM (the observed major period of foraging and feeding activity for 97.6% of the feedings), and (2) it captures and feeds on prey every 13.5 minutes (based on the mean feeding and interfeeding times). Thus, over a seven-hour period an individual could feed on approximately 31 prey. It was calculated that *H. phaeonotus* (Dennis, 2014) and *H. albipilosus* (Dennis and Lavigne, 1975) could feed on approximately 33 and 15 prey per day during 6 and 5.5-hour periods of foraging activity with mean 11 and 21 minute feeding and interfeeding times, respectively. This is in comparison to *H. claripennis avor* that Lehr (1964) calculated could feed on approximately 14 prey per day. Other investigators have estimated that asilids feed on 1 to 35 prey per day, as reported by Dennis (2014) and Lehr (1964).

Prey

Holopogon snowi individuals preyed primarily on Thysanoptera (27.5%) and Hemiptera (26.4%), followed by Hymenoptera (11.0%) and Psocoptera (11.0%), Blattodea (Isoptera alates, 9.9%), Diptera (8.8%), Araneae (0.5%), and Coleoptera (0.5%) (Table 3). In the U.S.A. other species of *Holopogon* have been reported to prey on insects representing similar orders including: Coleoptera, Diptera, Hemiptera (as Hemiptera and Homoptera), Hymenoptera, Lepidoptera, Plecoptera, Psocoptera, and Thysanoptera (Dennis, 2014; Dennis and Lavigne, 1975, 2007; Dennis *et al*., 2010; Hespenheide and Rubke, 1977; Lavigne *et al*., 1993). According to Musso (1970, 1972), *Holopogon venustus* fed on Hemiptera (Aphididae) in France. The Asilidae Predator-Prey Database has eight records of *Holopogon* feeding on spiders (Dennis et al., 2012). Lehr (1964, 1972) commented on *Holopogon* spp. in the U.S.S.R. feeding on Araneae, and the insect orders Coleoptera, Diptera, Hemiptera (as Hemiptera and Homoptera), and Hymenoptera.

Male and female *H. snowi* generally preyed on the same insect orders. Although males preyed more on Hemiptera and females preyed more on Thysanoptera. One female over a 23.5-minute period preyed on five Thysanoptera and one Hemiptera (Cixiidae, *Cixius* sp.). Approximately 2 1/2 times as many females as males were captured with prey. Other investigators have reported collecting more female than

male asilids with prey (Dennis, 2014; 2015a and 2015b).

Table 3. Number and percent composition of orders of prey taken by *Holopogon snowi.*

	Male		Female		Unknown sex		Total	
Order	Number	Percent	Number	Percent	Number	Percent	Number	Percent
Araneae	1	2.0	0	0	0	0	1	0.5
Blattodea (Isoptera)	4	7.8	14	10.9	0	0	18	9.9
Coleoptera	0	0	0	0	1	50.0	1	0.5
Diptera	4	7.8	12	9.3	0	0	16	8.8
Hemiptera	19	37.3	29	22.5	0	0	48	26.4
Hymenoptera	8	15.7	12	9.3	0	0	20	11.0
Psocoptera	4	7.8	16	12.4	0	0	20	11.0
Thysanoptera	10	19.6	40	31.0	0	0	50	27.5
Unidentified	1	2.0	6	4.6	1	50.0	8	4.4
Totals	51	100.0	129	100.0	2	100.0	182	100.0

The following is a list of prey taken by *H. snowi*. All prey was collected between 30 March and 5 May 2016. The number and sex (if known) of the predator follows the prey record.

ARANEAE, Unidentified, 11.04.2016 (1♂). BLATTODEA (ISOPTERA, alates), Kalotermitidae: *Calcaritermes nearcticus* (Snyder, 1933), 31.03.2016 (1♀), 19.04.2016 (1♀), 22.04.2016 (1♂), 25.04.2016 (1♂, 2♀♀), 27.04.2016 (1♀); Rhinotermitidae: *Reticulitermes virginicus* (Banks, 1907), 7.04.2016 (2♂♂, 2♀♀), 14.04.2016 (1♀), 23.04.2016 (4♀♀), 2.05.2016 (1♀), 5.05.2016 (1♀). COLEOPTERA, Curculionidae: *Dendroctonus* sp., 30.03.2016 (1 unknown sex). DIPTERA, Cecidomyiidae: unidentified, 18.04.2016 (1♂, 1♀), 19.04.2016 (1♂). Chironomidae: unidentified, 31.03.2016 (1♀), 3.04.2016 (2♀♀). Dolichopodidae: *Condylostylus* sp., 5.04.2016 (1♀). Sciaridae: unidentified, 19.04.2016 (1♀), 21.04.2016 (2♀♀). Unidentified, 4.04.2016 (1♀), 11.04.2016 (1♂), 19.04.2016 (1♂), 26.04.2016 (1♀), 27.04.2016 (1♀), 2.05.2016 (1♀). HEMIPTERA, Auchenorrhyncha, Cicadellidae: *Empoasca* sp., 31.03.2016 (1♂), 5.04.2016 (2♀♀), 7.04.2016 (1♂, 1♀), 8.04.2016 (1♂), 9.04.2016 (1♂, 1♀), 11.04.2016 (1♂), 18.04.2016 (1♀), 21.04.2016 (2♂), 22.04.2016 (1♀), 23.04.2016 (1♀), 26.04.2016 (1♀); unidentified, 30.03.2016 (2♂♂, 1♀), 3.04.2016 (3♀♀), 6.04.2016 (1♂), 18.04.2016 (1♂). Cixiidae: *Cixius* sp., 31.03.2016 (1♂), 1.04.2016 (♀), 6.04.2016 (2♀), 7.04.2016 (1♀), 8.04.2016 (1♂), 11.04.2016 (1♀), 12.04.2016 (1♀), 18.04.2016 (1♂), 19.04.2016 (1♂, 3♀♀), 21.04.2016 (3♀♀), 23.04.2016 (1♂), 26.04.2016 (2♀♀), 29.04.2016 (1♂); unidentified, 1.04.2016 (1♂), 21.04.2016 (2♀♀), 27.04.2016 (1♀). Sternorrhyncha, Aphididae: unidentified, 18.04.2016 (1♂). HYMENOPTERA, Chalcidoidea: 30.03.2016 (1♀), 05.04.2016 (2♂♂), 11.04.2016 (1♂), 13.04.2016 (1♂), 18.04.2016 (1♂). Cynipidae: *Andricus* sp., 6.04.2016 (1♀); *Callirhytis* sp., 4.04.2016 (1♀), 8.04.2016 (1♂); *Synergus* sp., 31.03.2016 (1♂), 3.04.2016 (1♀), 5.04.2016 (1♀), 7.04.2016 (1♀). Formicidae (alates): *Linepithema* sp., 31.03.2016 (1♀); unidentified, 31.03.2016 (1♀), 4.04.2016 (1♂), 15.04.2016 (1♀), 22.04.2016 (1♀); Sphecidae: unidentified, 8.04.2016 (1♀). Unidentified: 22.04.2016 (1♀). PSOCOPTERA, Unidentified, 31.03.2016 (5♀♀), 3.04.2016 (2♀♀), 4.04.2016 (2♀♀), 5.04.2016 (1♂, 1♀), 6.04.2016 (2♀), 7.04.2016 (1♂, 2♀), 9.04.2016 (1♂), 11.04.2016 (1♀), 25.04.2016 (1♀), 26.04.2016 (2♂♂). THYSANOPTERA, Unidentified, 3.04.2016 (1♀), 6.04.2016 (5♀♀), 7.04.16 (1♂), 8.04.2016 (1♂, 1♀), 9.04.2016 (1♂, 2♀♀), 11.04.2016 (2♀♀), 12.04.2016 (1♂, 1♀), 13.04.2016 (3♀♀), 14.04.2016 (1♂), 18.04.2016 (3♂♂, 3♀♀), 19.04.2016 (1♂, 7♀♀), 21.04.2016 (3♀♀), 25.04.2016 (2♀♀), 26.04.2016 (4♀♀), 27.04.2016 (3♀♀), 29.04.2016 (1♂, 1♀), 5.05.2016 (2♀♀). UNIDENTIFIED: 30.03.2016 (1♀, 1 unknown sex), 31.03.2016 (1♀), 11.04.2016 (2♀♀), 19.04.2016 (2♀♀), 26.04.2016 (1♂).

Courtship and mating behavior

Male courtship prior to mating has been described for five species of *Holopogon*: *H. albipilosus* (Dennis and Lavigne, 1975), *H. claripennis avor* and *H. priscus* (Lehr, 1972), *H. phaeonotus* (Dennis, 2014), and *H. seniculus* (Lavigne *et al*., 1993). Lavigne

(2003) suggested that male courtship is probably widespread in the genus.

Holopogon snowi males will court both females and other males with or without prey. *Holopogon phaeonotus* males also court both females and males (Dennis, 2014) and male courtship of prey-feeding females has been reported for *H. priscus* (Lehr, 1972) and *H. seniculus* (Lavigne *et al*., 1993).

The author observed 57 courtships, 12 mating pairs, and three complete matings. During courtship, most *H. snowi* males hovered 1.9-12.7 cm (mean 2.0 cm) in front of (n=17 out of 35) and slightly above (n=11) the level of the courted asilid. A few males also hovered to the side (n=3), behind (n=3), or directly above (n=1) the female. Only one of the three complete matings observed began with courtship; the other two were initially observed as the male landed on the female's dorsum to begin mating. The male of the complete mating that was observed from courtship, hovered in a stationary position 12.5 cm immediately in front of and 5.0-7.5 cm above the female for 5 seconds.

While hovering male abdomens were straight and the fore- and mid-legs were held against the thorax with the tibiae and tarsi pointed forwards. The hind legs were angled posteriorly at about a 30-45˚ angle to the thorax and the hind tibiae and tarsi hung straight down or bent slightly forward. Each courtship hover lasted 3-26 seconds with an mean of 10 seconds. During courtship the male remained stationary, had a slight forward or backwards motion, or moved sideways in an arc up to 7.5 cm.

When a male or non-receptive female was courted, they frequently flew off with the courting male in pursuit. A non-receptive female often assumed an agonistic posture by spreading her wings, usually at a 45° angle (range from 30-90˚) to her body and/or by crawling to the side of the twig. A female would often spread her wings up to three to four times.

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 away. One male intermittently courted a non-receptive female for 26 minutes with variable periods of rest, with the longest rest for 5 minutes.

The complete matings began when the male flew and landed on the female's dorsum, clasped her genitalia, and straightened out in the tail-to-tail position (Fig. 4). Most mating pairs (n=10) stayed in a straight tail-to-tail position or were at about 120° to each other, sometimes with their abdomens bent up to form an inverted "V". Two pairs mated in an inverted "V" position with their abdomens curved around the tip of a twig. Other species of *Holopogon* also mate in the tail-to-tail position (Dennis, 2014).

The complete matings lasted for 54-59 minutes (mean 57 minutes). Most matings ended when a male unclasped the female and immediately flew off. Two matings ended when the asilids flew up and separated in flight within 7.5-12.5 cm above the twig on which they mated. One mating ended when the male unclasped the female, then walked forward on the twig and flew away.

During mating, *H. snowi* remained relatively inactive and moved very little, with only slight adjustments on the twig they stood on. While a female is mating, other males may court the female, land on her dorsum and attempt to mate with her. One

male courted a mating female and landed on her dorsum four times before flying off.

Fig. 4. Mating pair of *Holopogon snowi* in the tail-to-tail position.

Matings took place in both the sun and shade, and when the sky was overcast. Air temperature at the height of the matings on the twigs ranged from 27.0-34.5ºC with a mean of 29.3°C. *Holopogon phaeonotus* also mated within a similar temperature range from 27.5-34.0ºC (Dennis, 2014).

Oviposition

Female robber flies with acanthophorite-bearing spines at the tips of their ovipositors generally oviposit in soil, as was observed for *H. phaeonotus* (Dennis, 2014). Although *H. snowi* females have acanthophorites with spines, they dropped eggs on the scrub oak twigs where they stood or onto the ground below the twigs. Five complete ovipositions were observed during which one to three eggs were quickly oviposited.

Females began to exhibit oviposition behavior when they curved their abdomen down and touched the twig with their ovipositor, turned perpendicular to the twig as they extended the abdomen, or they extended their abdomen over a twig tip (Fig. 5). During this process, some females also stroked their abdomens from anterior to posterior, with both hind tibiae and/or tarsi, presumably to help push the eggs out. One female also extended her abdomen prior to dropping a brown liquid and another female had an extended abdomen during mating.

Fig. 5. Female *Holopogon snowi* ovipositing with extended abdomen and wings blown open by wind.

No eggs were recovered from the ovipositions. They were lost in the wind as they were dropped on the ground or twigs, or the wind blew them off the twigs and they could not be found on the ground. The eggs were shiny or glistening white and oblong or elongate, similar to the eggs of *H. phaeonotus* (Dennis, 2014).

Temperatures at the height of the *H. snowi* ovipositions ranged from 28.5-35.0ºC with an mean of 31.7 ºC. Air temperature above two *H. phaeonotus* ovipositions in soil were 32ºC and 33ºC.

Grooming

Holopogon snowi, like *H. phaeonotus* (Dennis, 2014), did not frequently groom themselves. This may be because the asilids occupy various heights on vegetation and do not land on the ground. When *H. snowi* did groom it was in much the same way as reported for *H. phaeonotus* and other species of robber flies (Dennis, 2014).

Holopogon snowi always used the fore legs to groom their heads, and the hind legs to groom their wings (Fig. 2.) and abdomen. Generally grooming of the head followed feeding and grooming of the abdomen followed mating.

Grooming of the head was usually preceded and followed by the rubbing together of the fore tarsi. When grooming the head *H. snowi* used the distal part of the fore femora, the entire tibiae, and the proximal part of the tarsi, often as the asilid quickly turned its head.

Holopogon snowi sometimes rubbed its hind tarsi together, leaned forward and down, and then curved the abdomen down before grooming the abdomen and wings. Grooming of the wings and abdomen always proceeded from anterior to posterior with the hind tibiae and tarsi. When the wings were closed, only the top surface was groomed; when the wings were spread at a 45˚ angle to the body, both the tops and bottoms of the wings were groomed outward for about 3/4 of their length.

During separate matings, a male and female groomed the tops of their closed wings with their hind tarsi. Also, during feeding one female groomed the tops and bottoms of her spread wings and then the posterior 1/2 of the dorsal part of her abdomen with her hind tibiae.

Daily rhythm of activity

Each day, *H. snowi* began foraging high up (approximately 1.8-2.1 m) on the twigs of vegetation in the areas on the western side of the road where the sun was shining and the areas on the eastern side were still in shade. As the day progressed, the asilids on the western side moved down to lower twigs of vegetation as these areas became exposed to the sun. When the western areas of vegetation became shaded and sunlight was shining on some eastern areas of vegetation (1:00-2:00 PM), the flies began to move across the road to forage from these sunny areas. Between 4:30-6:30 PM, most of the western side of the road was in shade and the majority of asilids had moved to the sunlit areas on the eastern side of the road.

Holopogon snowi feeding began between 10:00-11:00 AM with the peak period (65.4% of feeding) from 12:00 noon to 3:00 PM, with a steady tapering off until between 6:00-7:00 PM (Fig. 6). The largest number of mating pairs (66.7%) occurred during

two peaks, the first peak between 2:00-3:00 PM and the second between 4:00-5:00 PM with seven of eight mating pairs on the eastern side of the road during these time periods. Peak period for ovipositing (three of five ovipositions) occurred between 1:00-2:00 PM with a smaller peak between 11:00 AM-12:00 noon; oviposition behavior (i.e., females extending their abdomens) was observed between 11:20 AM to 2:44 PM.

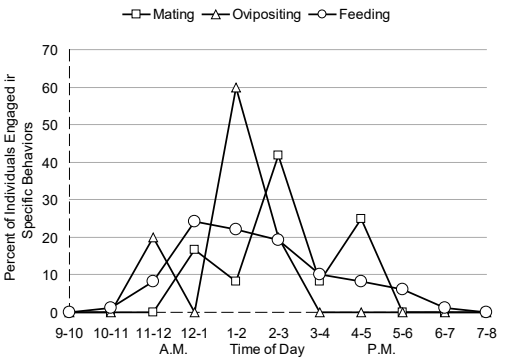

Fig. 6. Daily rhythm of activity of *Holopogon snowi* based on 12, 5, and 182 observations for mating, ovipositing, and feeding, respectively.

The peak period of feeding for *H. phaeonotus* occurred between 10:00 AM and 1:00 PM, and between 1:00-2:00 PM for mating and oviposition (Dennis, 2014). Based on the percent of flies with prey, *H. wilcoxi* had two peak periods of feeding from about 8:00-10:00 AM and 2:00-4:00 PM (Hespenheide and Rubke, 1977). *Holopogon albipilosus* also had two peak periods of feeding from 11:00 AM-12:00 noon and from 4:00-5:00 PM, with the peak period for mating from 2:00-3:00 PM (Dennis and Lavigne, 1975). *Holopogon claripennis avor* foraged primarily from 8:00-9:00 AM, 10:00-11:00 AM and 5:00-6:00 PM (Lehr, 1972).

In deserts, where there can be acute changes in weather over 24 hours, *Holopogon* forage early in the morning and evening and mate and oviposit during the daylight hours (Lehr, 1972).

Predators

The same species of robber flies often prey upon each other or exhibit cannibalism (Lavigne *et a*l., 2000). However, *H. snowi* did not prey upon each other. Cannibalism also has not been observed for other species of *Holopogon* (Dennis, 2014; Dennis and Lavigne, 1975; Hespenheide and Rubke, 1977; Lavigne *et al*., 1993; Lehr, 1964, 1972).

Proctacanthus brevipennis (Wiedemann, 1828) and *Laphria saffrana* Fabricius, 1805 occurred in the same habitat as *H. snowi*, but did not prey on them. In Texas, Bromley (1934) reported *Atomosia puella* (Wiedemann, 1828) preying on *H. snowi*.

One female *H. snowi* was caught in a basilica orbweaver [*Mecynogea lemniscata* (Walckenaer, 1841)] spider web between scrub oak twig tips approximately 60 cm above the ground. *Holopogon phaeonotus* (Dennis, 2014) and *H. seniculus* (Lavigne *et al*., 1993) also has been reported as prey of spiders.

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

CONCLUSIONS

Various details have been reported on the ethology of only four of twenty-one species of *Holopogon* (*H. albipilosus*, *H. phaeonotus*, *H. seniculus*, and *H. wilcoxi*) in the United States. This paper provides information on a fifth species, *H. snowi*. This species rested on and foraged from plant twig tips, primarily scrub oak. *Holopogon snowi* 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, each day individuals began foraging higher up in sun-exposed vegetation in areas on the western side of a road and as these areas became shaded, they moved to lower areas of vegetation and to sunlit vegetation on the eastern side of the road. All prey was captured in flight and consisted of Araneae, Blattodea (Isoptera, alates), Coleoptera, Diptera, Hemiptera, Hymenoptera, Psocoptera, and Thysanoptera. During feeding, *H. snowi* 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 extended their abdomens and oviposited on the twigs where they stood or dropped eggs directly onto the ground. Peak period for feeding occurred from 12:00 noon to 3:00 PM. Mating had two peaks from 2:00 to 3:00 PM and 4:00 to 5:00 PM, and the oviposition peak was from 1:00 to 2:00 PM. *Holopogon snowi* did not frequently groom themselves, possibly because they stayed on vegetation and were never observed on the ground. *Holopogon snowi* were not cannibalistic, but one female was caught in a spider's web.

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