D. Steve DENNIS¹ Robert J. LAVIGNE² Jeanne G. DENNIS³

¹1105 Myrtle Wood Drive, St. Augustine, Florida 32086, USA, e-mail: dstevedennis@msn.com

²Honorary Research Associate. Entomology, South Australia Museum, North Terrace, Adelaide, South Australia 5000; and Professor Emeritus, Entomology, Department of Renewable Resources, College of Agriculture, University of Wyoming, Laramie, WY 82070, USA, e-mail: robert.lavigne@samuseum.sa.gov.au; hexapoda55@gmail.com

³P.O. Box 861161, St. Augustine, Florida 32086, USA, e-mail: sj34den@msn.com

ABSTRACT

There are many references on the Internet and in the published literature to robber flies preying upon spiders. However, an evaluation of available data summarized in the Asilidae Predator-Prey Database reveals that spiders make up only a small percentage of the robber fly diet (less than 1% of approximately 58,000 prey listed in the Database). The types of spider chosen as prey are discussed and examined in relation to robber fly classification. Robber fly methods of capturing spiders are examined and comments about spiders preying upon robber flies are provided.

Key words: Araneae, spiders, prey, robber flies, Diptera, Asilidae.

INTRODUCTION

There are approximately 43,000 described species of spiders (Araneae) (Platnick 2011) that are found world-wide on every continent except Antarctica. Because robber flies (Insecta: Diptera: Asilidae) are opportunistic predators that also can be found in many similar habitats, one would expect spiders to serve as prey in proportional numbers to other arthropod prey. The purpose of this paper is to discuss the role that spiders play as prey of robber flies.

MATERIALS AND METHODS

Published literature and information on the Internet contain numerous references, often based on casual observations, to robber flies preying upon spiders. In order to provide more information on the role of spiders as prey of robber flies, the literature was reviewed and summarized in the Asilidae Predator-Prey Database (Lavigne, 2003). These data were evaluated in conjunction with detailed examination of relevant papers to ascertain which species of robber flies have fed on which species of Araneae, the numbers of spider prey and their identification. Also, select information on the Internet was examined for information on spiders as prey of robber flies.

Spiders are classified according to Platnick (2011). For Asilidae, Dikow, (2009a and b) has recognized 14 robber fly subfamilies. In this paper, however, we have retained the 11 subfamily classification of Geller-Grimm, (2003) so that the data can be more easily compared with other detailed robber fly prey evaluations published in Dennis and Lavigne (2007); Dennis *et al.* (2009, 2010); Londt (1993, 1999, 2006).

RESULTS

In the majority of the references cited in the Asilidae Predator-Prey Database (Lavigne, 2003), general comments have been made about robber flies preving upon spiders. Wood (1981) stated that, "Occasionally other invertebrates, especially spiders, are captured." Most of the records in the Database and information on the Internet are based on only one or a few prey for each robber fly and if one did not know this, it would appear that spiders make up a significant part of the prey of robber flies. Thus we find references, such as Chew et al. (2010) observing Leptogaster (Meigen, 1803) sp. capturing and feeding on a medium sized Silver Orbweaver [Tetragnathidae: Leucauge granulate (Walckenaer, 1842)] in its unfinished web; Overbeck, (2005) photographing Tipulogaster glabrata Wiedemann, 1828 feeding on an Orchard Orbweaver [Leucauge venusta (Walckenaer, 1842)] in its web; Sawaro (1952) reporting that Leptogaster trimucronotata Hermann, 1917 prevs on spiders and observing one flying while holding a spider in its tarsi; and Painter, (1926); reporting a male Psilocurus nudiusculus Loew, 1874 feeding on an immature lycosid. Bromley (1950) indicated that Stichopogon trifasciatus (Say, 1823) preyed upon spiders, including the black widow [Theridiidae: Latrodectus mactans (Fabricius, 1775)], while Lehr (1958a and c, respectively) commented that the robber flies, Aneomochtherus tricuspicatus (Engel, 1927) (as Neomochtherus Osten Sacken, 1878) and Promachus canus leontochlaenus Loew, 1871 (as P. leontochlaenus) preyed upon spiders.

Table 1. contains data from the more recent literature wherein large numbers of spiders as prey are reported. For the 27 robber fly genera and/or species taken with over 20 prey, 0.2 to 10% were spiders, with an average of 2.5%. In a regional context, Londt (2006), whose data has been incorporated in the Predator- Prey Database, evaluated 2,001 robber fly prey records in the South African Natal Museum and found that only 16 or 0.8% were spiders. This small percentage of spiders as prey of robber flies from a single region is in line with the results obtained in analyzing the Database where of the approximately 58,000 prey records, there are only 347 records for spiders or less than 1% of the prey (This assumes that there are only two prey where the Database indicates "common" or "spiders" for prey number).

Of note, spiders that have served as prey are not often identified beyond the order level. Early on, MacLeay (1838) commented that robber flies prey upon the genus *Clubiona* Latreille, 1804 (Clubionidae), but did not say how they were captured. As shown in Table 2, spiders represented in the Asilidae Predator-Prey Database are from only one (Araneomorphae) of the three suborders and 14 of the 110 families; however, 16 genera and seven species are listed. The Araneomorphae is the largest

Table 1.	Spiders	recorded i	n recent	literature a	s prey	of robber	flies.
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References	Species	Araneae (%)	Total Prey
	Comantella fallei (Back, 1909)	0.6	162
Dennis and Lavigne, 1975	Ospriocerus latipennis (Loew, 1866)	0.5	209
	Proctacanthella cacopiloga (Hine, 1909)	0.5	209
Dennis and Lavigne, 1976	Leptogaster parvoclava Martin, 1957	1.0	144
LaPierre, 2000	Holcocephala oculata (Fabricius, 1805)	1.6	379
Lavigne, 1979	avigne, 1979 Triorla argyrogaster (Macquart, 1846) (as Efferia Coquillet, 1893)		50
Lavigne and Dennis, 1985	Efferia subcuprea (Schaeffer, 1916)	5.3	19
Lavigne and Holland, 1969	Stichopogon trifasciatus (Say, 1823)	10.0	21
Lavigne <i>et al.,</i> 1983	Laphystia rufofasciata Curran, 1931	3.7	137
Lehr, 1958b	Stenopogon porcus Loew, 1871	2.5	488
	Holopogon claripennis (Loew in Rosenhauer, 1856)	4.0	96
	Machimus alatavicus Lehr, 1967	2.0	46
Lehr, 1964	Promachus canus leontochlaenus Loew, 1871	1.0	271
	Stenopogon avus Loew, 1874	0.2	403
	Stenopogon porcus Loew, 1871	3.0	96
L	Machimus alatavicus Lehr, 1967	1.6	61
	Machimus rusticus Meigen, 1820	0.4	236
	Damalis Fabricius, 1805	0.6	163
	Daspletis Loew, 1859	4.2	24
	Euscelidia Westwood, 1849	20.0	10
Landt 2006	Lasiocnemus lugens Loew, 1858	100.0	4
	Neolophonotus Engel, 1925	0.6	486
	Pegesimallus Loew, 1858	3.1	98
	Promachus Loew, 1848	0.6	169
	Rhabdogaster Loew, 1858	7.1	98
Newkirk, 1963	Psilonyx annulatus (Say, 1823) (as Leptogaster Meigen, 1803)	7.8	2,279
Scarbrough, 1978	Cerotainia albipilosa Curran, 1930	3.1	739
Scarbrough, 1981	<i>Eudioctria tibialis</i> Banks, 1917	0.2	462
Scarbrough 1982	Holcocephala abdominalis (Say, 1823)	2.4	340
- Scarbiougii, 1962	Holcocephala calva (Loew, 1872)	3.0	367
Scarbrough and Sraver, 1979	Atomosia puella (Wiedemann, 1828)	0.3	1,567

	Table 2. Spiders in the As	silidae predator-prey	database (Lavio	ine, 2003).
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Suborder	Superfamily	Family/Common Name	Genus/Species	Number
			<i>Alpaida grayi</i> (Blackwell, 1863) (as <i>Epeira</i> Walckenaer 1805)	2
		Araneidae/Orbweavers	Araneus Clerck, 1757 sp.	1
			Micrathena Sundevall, 1833 sp.	1
			Unidentified	4
		Linyphiidae/Sheetweb and Dwarf Weavers	Meioneta unimaculata (Banks, 1892)	1
	Araneoidea		Unidentified	2
		Nephilidae/Orbweavers	Nephila clavipes (Linnaeus,1767)	1
		Tetragnathide/Longjawed	Leucauge White, 1841 sp.	3
		Orbweavers	Tetragnatha Latreille, 1804 sp.	1
			Latrodectus mactans (Fabricius, 1775)	1
		Theridiidae/Cobweb Weavers	Oecobius Lucas, 1846 sp.	1
			Steatoda fulva (Keyserling, 1884)	1
Araneomorphae	Lycosoidea	Lycosidae/Wolf Spiders	Lycosa Latreille, 1804 sp.	1
			Pardosa C.L. Koch, 1847 sp.	1
			Unidentified	2
		Oxyopidae/Lynx Spiders	Unidentified	4
		Pisauridae/Nursery Web Spiders	Dolomedes Latreille, 1804 sp.	1
	Agelenoidea	Agelenidae/Funnel Weavers	Unidentified	8
	Sparassoidea	Sparassidae/Giant Crab Spiders	Unidentified	2
	Tengelloidea	Clubionidae/ Sac Spiders	Unidentified	5
	Gnaphosoidea	Gnaphosidae/Stealthy Ground Spiders	Unidentified	1
	Thomisoidea	Thomisidae/Crab Spiders	Synema Simon, 1864 (?) sp.	1
			Unidentified	4
	Salticoidea	Salticidae/Jumping Spiders	<i>Habronattus agilis</i> (Banks, 1893) (as <i>Pellenes</i> Simon, 1876)	1
			Unidentified	17
Unidentified				280
			Total	347

Subfamily	Genus	Number of Prey Records	Subfamily	Genus	Number of Prey Records
	Efferia Coquillet, 1893 Group	4			
Apocleinae	Neolophonotus Engel, 1925	4		Bathypogon Loew, 1851	3
	Proctacanthella Bromley,1934	1		Daspletis Loew, 1859	1
	Promachus Loew, 1848	8		Heteropogon Loew, 1847	1
		Total 17		Holopogon Loew, 1847	8
	Dysmachus Loew, 1860	1	Stenonogoninge	Jothopogon Becker, 1913	1
	Ktyr Lehr, 1967	2	Clonopogoninao	Ospriocerus Loew, 1866	1
	Machimus Loew, 1849	3		Plesiomma Macquart, 1838	3
Asilinae	Mauropteron Daniels, 1987	1		Rhabdogaster Loew, 1858	1
	Neoitamus Osten Sacken, 1878	7		Scylaticus Loew, 1858	1
	Zosteria Daniels, 1987	1		Stenopogon Loew, 1847	9
		Total 15			Total 29
	Brachyrhopala Macquart, 1847	1	Stichopogoninae	Stichopogon Loew, 1847	11
	Comantella Curran, 1923	1	Clichopogoninae		Total 11
	Dioamites Loew. 1866	2			
Dasypogoninae	Pegesimallus Loew. 1858	3	Trigonomiminae	Damalis Fabricius, 1805	1
	Thereutria Loew, 1851	1		Hoicocephala Jaennicke, 1867	18
		Total 8			Iotal 19
	Diactria Meigen, 1803	1			3
Dioctrinae	Eudioctria Wilcox & Martin 1941	1	Unidentified in Predator-Prey		Total 3
		Total 2	Database		Grand Total
	Atomosia Magguart 1929				347
	Corotainia Sabinar, 1969				
	Cuananadua Harmann, 1012	1			
	Eumococomo Sobinor 1966	1			
		Tatal 29			
	1 hu fi 4047	10(2)			
	Laphysia Loew, 1847	5			
Laphystiinae	Psilocurus Loew, 1874	2			
		lotal 7			
	Euscelidia Westwood, 1849	2			
Leptogastrinae	Lasiocnemus Loew, 1851	4			
	Leptogaster Meigen, 1803	16			
	Fisionyx Aldrich, 1923	183			
	Inpulogaster Cockerell, 1913	2			
		Tatal 000			
	1	IOTAI 208			

Table 3. Subfamilies and genera of robber flies in the Asilidae predator-prey database (Lavigne 2003) preying upon spiders (Araneae).

References	Method of	Species of Spider	Species of Robber Fly Taken
	Capture		Dysmachus cochleatus (Loew, 1854)
			Echthistus rufinervis (Meigen, 1820)
			Lasiopogon Loew, 1847 sp.
			Leptogaster cylindrical (De Geer, 1776)
Adamovic 1963		Araneidae:	Machimus annulines (Brullé 1832)
Adamovic, 1905	Web	Argiope bruennichi (Scopoli, 1772)	Machimus Loew 1849 sp
			Dasynogon (as Selidonogon)
			Diadema (Eabricius 1781)
			Stenopogon sabaudus (Fabricius, 1794)
		Araneidae:	
		Araneus bicentenarius (McCook, 1888) (as Epeira gigas Leach, 1815)	Promachus vertebratus (Say, 1823)
	Web	Araneus trifolium (Hentz, 1847) (as Epeira Walckenaer, 1805)	Promachus bastardii (Macquart, 1838)
Bilsing, 1920 (insects captured and eaten in the field)			Atomosia puella (Wiedemann, 1828)
		Araiope aurentia Lucas, 1833	Diogmites basalis (Walker, 1851) (as D. umbrinus Loew, 1866)
		(as A. riparia [Emerton, 1884)]	Leptogaster murina Loew, 1862 (as L. murinus)
			Promachus vertebrates (Say)
		Neoscona crucifera(Lucas, 1838) (as Epeira domiciliorum Emerton, 1884)	Promachus vertebratus (Say)
	Web	Araneidae: Metepeira foxi Gertsch and Ivie, 1936	Dicropaltum mesae (Tucker, 1907) (as Asilus Linnaeus, 1758)
Dennis & Lavigne, 1975	Stalk and Jump	Lycosidae: Schizocosa Chamberlin, 1904 sp.	Proctacanthus micans Schiner, 1867
	Stalk and Jump	Salticidae: Pellenes Simon, 1876 sp.	Dicropaltum mesae (Tucker) (as Asilus)
Lavigne, 1972	Stalk and Jump	Salticidae	Ablautus rufotibialis Back, 1909
Lavigne, 1992	Web	Araneidae: Eriophora transmarine (Keyserling, 1865) (as Araneus)	Colepia abludo (Daniels, 1983) (as Neoaratus Ricardo, 1913)
Lavigne et al., 1993	Not Specified	Salticidae: Habronattus hirsutus (Peckham and Peckham, 1888) (as Pellenes)	Holopogon seniculus Loew, 1866
Lavigne et al., 2009	Stalk	Sparassidae: Isopeda leishmanni Hogg, 1903	Mauropteron pelago (Walker, 1849)
Lehr, 1958d	1958d Web Not identified		Dasypogon octonotatus Loew, 1869 (as Selidopogon) Dioctria Meigen, 1803 sp.
Newkirk, 1963	Web	Araneidae: Gasteracantha Sundevall, 1833 sp.	Psilonyx annulatus (Say, 1823) (as Leptogaster Meigen, 1803)
Schmid ,1969	Stalk	Lycosidae	Choerades gilva (Linnaeus, 1758) (as Laphria Meigen, 1803)

Table 4. Spiders that prey upon robber flies.

spider suborder with over 40,000 species that are often readily visible. Members of the other two suborders (Mesothelae and Mygalomorphae) contain approximately 2,800 species, but their reclusive habits largely preclude them from being taken as prey. The Mesothelae are only found in Southeast Asia, China and Japan and belong to the family Liphistiidae (Coddington 2005). Most of these spiders live in silk-lined burrows or tubes with trapdoors. The suborder Mygalomorphae are generally large

spiders most of which also live in burrows. Members of this suborder include tarantulas, trapdoor spiders and the Australian funnel-web spider.

Table 3 presents data from the Predator-Prey Database showing that 10 of the 11 subfamilies of robber flies recognized by Geller-Grimm (2003) have been reported to prey upon spiders. The only subfamily not included is Ommatiinae, which are not well represented in collections although some species are quite large and can be presumed to feed on spiders as well. As can be seen from this table, the Leptogastrinae have the largest number of spider prey records (208), followed by the Stenopogoninae (29), Laphriinae (28), Trigonomiminae (19), Apocleinae (17), Asilinae (15), Stichopogoninae (11), Dasypogoninae (8), Laphystiinae (2), and Dioctriinae (2). The genera *Psilonyx* (Aldrich, 1923), *Cerotainia* (Schiner, 1866), *Holcocephala* (Jaennicke, 1867), *Leptogaster* and *Stichopogon* (Loew, 1847) have the largest number of prey records with 183, 22, 18, 16 and 11, respectively. These five genera account for approximately 72% of spider prey in the Database.

DISCUSSION

As indicated above, robber flies do not often take spiders as prey. It is assumed that this is, in part, because most robber fly prey are usually captured while they are in flight and predation does not ordinarily take place on the ground, except in the *Stenopogon* (Loew, 1847) group (Asilidae: Stenopogoninae).

While it might be expected that large robber flies would be most successful attacking spiders, the reverse seems to be the case. Many of the successful attacks noted in literature and on the Internet have been made by relatively small and weak robber flies, such as *Leptogaster* spp. (Leptogastrinae) (Sawaro 1952, Chew *et al.* 2010), *Atomosia* (Macquart, 1838; Laphriinae) (Scarbrough and Sraver, 1979) and *Stichopogon trifasciatus* (Stichopogoninae) (Bromley 1950, Lavigne and Holland 1969). Dikow (2003, 2008) observed that other species, representing different genera in the subfamily Leptogastrinae (*Euscelidia procula* (Walker, 1849) and *Ophionomima solocifemur* Enderlein, 1914, respectively) preys on spiders. He also commented (Dikow 2007) that robber flies in the genus *Lasiocnemus* (Loew, 1851) capture spiders in their grassland habitat.

It is believed that *Leptogaster* spp. are more often reported as preying upon spiders because of their method of foraging, generally close to the ground, weaving in-and-out of vegetation, and hovering in front of vegetation, and striking at resting prey (Dennis and Lavigne 1976; Dikow 2007, 2008; Melin 1923; Scarbrough and Sipes 1973). Bristowe (1968) commented similarly, "Asilids of the subfamily Leptogastrinae are more likely than other asilids to catch spiders because it is their custom to hunt amongst long grasses, etc., and attack victims at rest..." Newkirk (1963) reported *Psilonyx annulatus* (Say, 1823) (as *Leptogaster*) preying upon spiders on vegetation and noted that females capture more prey than males, presumably because they live longer. Lehr (1964) also observed *Leptogaster* sp. capturing prey including spiders, on the surface of grasses and bushes. Additionally Lehr (1964) observed a *Leptogaster*

cylindrica hispanica Meigen, 1838 that had captured a spider in its web, and reported that *Holopogon* (Loew, 1847) sp. also capture spiders moving on their cobwebs.

Dikow and Bayless (2009), and Londt (2006) commented on the long tarsal claws that *Schildia* species have and their resemblance to those of *Lipokophila eberhardi* Schuh, 1993 (Heteroptera: Plokiophilidae). This species of true bugs lives on the webs of *Tengella radiata* (Kulczynski, 1909) (Araneae: Tengellidae) and feeds on the spider's prey. Thus Dikow and Bayless (2009) indicated that the morphological similarity of the tarsal claws " might suggest that species of *Schildia* use spider webs as refuges, perching sites, feed on the spiders, or are perhaps even kleptoparasites "stealing" the spider's prey items directly from the web."

Among the larger robber fly species, Londt (2006) reported *Lasiocnemus lugens* Loew, 1858 captured spiders as the robber fly was searching and hovering near flowering heads of plants. Dennis and Lavigne (1975) observed that *Ospriocerus latipennis* (Loew, 1866), which also forage by weaving in-and-out of and hovering in front of plant stems and flower heads, captured one spider [Theridiidae: *Steatoda fulva* (Keyserling, 1884)].

Other robber flies have used a different strategy to capture spiders, for example, as they were "ballooning" or moving at the ends of suspended silken threads (*Cerotainia albipilosa* Curran, 1930 in Scarbrough 1978; *Heteropogon paurosomus* Pritchard, 1935 in Lavigne and Bullington 1999); as they moved from one spot to another by jumping; as they rested in their web or were actively engaged in constructing a web (*Plesiomma fuliginosum* Wiedemann, 1821 in Bristowe 1924; *Schildia jamaicensis* Farr, 1962 in Farr 1963; *Leptogaster* sp. in Chew *et al.* 2010; and *Ophionomima solocifemur* in Dikow 2008).

Although *Leptogaster* spp. are more frequently observed capturing spider prey, the published data suggests that robber flies that forage from vegetation or ground. although normally capturing flying prey, also may prey upon spiders. In Table 1 those species that forage mostly from vegetation include: Atomosia puella (Wiedeman, 1828) (Scarbrough and Sraver 1979), Cerotainia albipilosa(Scarbrough 1978), Efferia subcuprea (Schaffer, 1916) (Lavigne and Dennis 1985), Eudioctria tibialis Banks, 1917 (Scarbrough 1981), Heteropogon paurosomus (Lavigne and Bullington 1999), Holcocephala abdominalis (Say, 1823) and H. calva (Loew, 1872) (Scarbrough 1982), H. oculata (Fabricius, 1805) (LaPierre 2000), Machimus rusticus Meigen, 1820 (Lehr 1971), Psilonyx annulatus (Newkirk 1963), Stenopogon porcus Loew, 1871 (Lehr 1964) and Triorla argyrogaster (Macquart, 1846) (Lavigne 1979 as Efferia Coquillet, 1893). Species that forage primarily from the ground/rocks and capture spiders as prev include: Laphystia rufofasciata Curran, 1931 (Lavigne et al., 1983). Proctacanthella cacopiloga (Hine, 1909) (Dennis and Lavigne, 1975), and Stichopogon trifasciatus (Lavigne and Holland, 1969). Stenopogon porcus (Lehr 1958b, 1964) also was recorded capturing a spider crawling on a plant. Members of a related genus, Scleropogon Loew, 1866, have been observed to attack grasshoppers crawling across the soil surface (R. J. Lavigne unpublished data). Comantella fallei (Back, 1909) forages from both vegetation and soil and was reported to capture one spider (Lycosidae: *Pardosa* C. L. Koch, 1847 sp. in Dennis and Lavigne 1975). *Machimus alatavicus* Lehr, 1967 also forages from vegetation and the ground (Lehr, 1967) and preys upon spiders (Lehr, 1971).

Londt (2006) commented that, "Although spiders are incapable of flight, they can dangle from silken threads and jump into the air, and so such prey also may have been collected in "flight." Salticid spiders which also jump regularly, are commonly found in the same rangeland habitats as asilids and thus should be taken often, for example, a female *Efferia barbatus* (Scopoli, 1763) with a salticid [*Habronattus agilis* Banks, 1893 (as *Pellenes* Simon, 1876)] as prey (Painter 1926). The data in the Asilid Predator-Prey Database support this. The largest number of identified spiders preyed upon by robber flies are the Salticidae (18; jumping spiders), followed by the Araneidae (8; orb-weavers) and Agelenidae (8; funnel weavers). According to Platnick (2011), the Salticidae contains the largest number of species (5,368) and the Araneidae contains the third largest number of species (3,020) after the Linyphiidae (4,401 species) which supports the hypothesis that the more abundant species have a greater chance of being predated. . The Agelenidae have a smaller number of species with 1,148; but this is still a large number when one considers that the majority of spider families have less than 150 species.

Both the Salticidae and Araneidae live in a wide variety of habitats and their abundance could make them potentially more available as robber fly prey. The Agelenidae may be preyed upon by robber flies because many species build their webs in low vegetation and bushes.

Robber flies which paralyze prey almost instantly, are equally at risk according to Lehr (1958d) who found *Stenopogon macilentus* Loew, 1861 and its spider prey lying in a path and observed that they had apparently paralyzed each other simultaneously.

Robber Flies as Prey of Spiders

Spiders are not without defenses against robber fly predators. These include the use of webs, concealment, and the ability to move rapidly. Jumping spiders (Salticidae) often have a coloration which blends into the local environment such as that of the branches of shrubs on which the asilids routinely land, as in the case of *Holopogon seniculus* Loew, 1866 (Lavigne *et al.* 1993). Speed of some spiders and long forelimbs probably accounts for the observation of Hobby (1940) that the crab spider, *Xysticus loeffleri* Roewer, 1955 (Thomisidae) preys upon robber flies. It is not uncommon to observe asilids snared in webs constructed by large spiders, primarily members of the Araneidae, across open areas such as gullies (Lavigne 1992). Bromley (1914); Adamovic (1963) and Bilsing (1920) have recorded multiple instances of asilids serving as prey of spiders. Additional specific information has been provided on spiders in the families: Araneidae, Lycosidae and Salticidae (Table 4). Other authors, such as Castellarnau (1968), Cole (1958), Colyer and Hammond (1968), Lavigne *et al.* (1978) and Lehr (1958b and d, 1961) have mentioned spiders as enemies of asilids.

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