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REVIEW

Death comes on two wings: a review of dipteran natural enemies of arachnids

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Abstract. Though the best known natural enemies of arachnids are Hymenoptera, Diptera also form an important group of arachnid enemies, attacking 31 spider families in all three suborders of Araneae, as well as members of the Acari, Amblypygi and Scorpiones. Some species of Bombyliidae, Chloropidae, Drosophilidae, Ephydridae, Phoridae and Sarcophagidae are known to attack eggs of several families of arachnids, acting as predators, parasitoids and/or parasites of egg sacs. Alternatively, members of Acroceridae and Tachinidae are internal parasitoids, attacking juvenile and/or adult spiders. One species of Sarcophagidae is reported as a predator of individual Liphistiidae (Mesothelae) spiders. We summarize the available information on all lineages of Diptera known to attack arachnids, including predators, parasites, kleptoparasites and parasitoids. A table including host records pertaining to the aforementioned dipteran families is presented. Particular emphasis is given to Acroceridae, the only lineage of Diptera known to develop exclusively on arachnids, and one of the most significant groups of natural enemies of spiders.

Keywords: Araneae, parasitoid, spider egg sacs, scorpions, amblypygids

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1. INTRODUCTION

Some of the best known natural enemies of arachnids belong to the order Hymenoptera, with species either feeding on the individual arachnid, or on its eggs. Several groups of Hymenoptera develop on arachnid hosts, including wasps in the families Diapriidae, Eulophidae, Eupelmidae, Eurytomidae, Ichneumonidae, Platygastridae sensu lato, Pompilidae, Pteromalidae and Sphecidae (Fitton et al. 1987; Noyes 2016). Hymenopteran parasitoids and predators exhibit a breadth of life strategies, including species that feed in cocooned spider egg masses, endoparasitoids that develop individually within eggs, external koinobiont parasitoids of mobile spiders, and idiobionts that paralyze one or more spiders as prey (Austin 1985; Gauld & Dubois 2006).

Species in the order Diptera are also significant natural enemies of arachnids. As opposed to the large taxonomic diversity of hymenopteran arachnid enemies, dipteran parasites, parasitoids and predators of arachnids are restricted to fewer families and vary considerably in their mode of action. All species of Acroceridae and a single species of Tachinidae are internal parasitoids of juvenile or adult spiders, while a few members of the Chloropidae, Drosophilidae, Ephydridae, Phoridae and Sarcophagidae are known to attack egg sacs of several arachnids, acting as parasitoids and/or predators of arachnid eggs (Clausen 1940; Vincent 1985; Schlinger 1987; Marshall 2012). One species of Sarcophagidae is a predator of Mesothelae spiders, attacking both adult and immature prey (Schwendinger & Pape 2000).

Although a clear cut distinction between predator and parasite is not always possible in nature, the three extremes of the spectrum (i.e., true parasite vs. true predator vs. true parasitoid) can be easily distinguished. Predators are organ-

isms that consume one or multiple prey during their lifetime, thus establishing a relationship that positively affects the predator and negatively affects the prey. Parasites, in general, live on/in the body of the organism they feed upon, and in contrast to predators, only take resources from one host, which they tend not to kill. Parasitoids, like parasites, only attack one host, but they enter or attach to their host, feed upon it, and ultimately kill it. Thus, the essential difference between parasites and parasitoids is that parasitoids always kill their hosts, while parasites tend to not kill their hosts. Additionally, the main difference between predators and parasitoids relates to the number of individuals attacked; predators usually kill multiple prey during their lifetime, while parasitoids only kill one host (Price 1980).

Parasitoids are found in five orders of holometabolous insects: Hymenoptera, Diptera, Coleoptera, Lepidoptera, and Neuroptera. Hymenopteran parasitoids account for nearly 78% of the estimated number of species, and consequently have served as models for nearly all recent research on insect parasitoids (Feener & Brown 1997). However, parasitoids in the Hymenoptera represent a single evolutionary lineage in contrast to the hundreds of parasitoid lineages in Diptera, Coleoptera, and other orders (Eggleton & Belshaw 1992). There are over 16,000 species of described dipteran parasitoids, which are distributed in 21 families and represent about 20% of the known parasitoid diversity (Eggleton & Belshaw 1992). Dipteran parasitoids are hypothesized to be derived from over 100 independent lineages, thus offering an unparalleled system for understanding the origin, evolution and diversification of parasitoid life history.

In this review, we summarize the available information on all lineages of Diptera that are known to attack arachnids, including predators, parasites, kleptoparasites and parasitoids. A table summarizing the egg parasitoids and/or predators, as well as internal parasitoids of adults and immature arachnid hosts is presented. Predators and kleptoparasites of individual arachnids were not included in the table because they represent opportunistic rather than adaptive interactions. All species and genus names given in the literature were checked and updated using current dipteran and arachnid taxonomy (Pape & Thompson (2013) and World Spider Catalog (2016) respectively).

2. DIPTERAN NATURAL ENEMIES OF ARACHNIDS

2.1 Predators.—Species of Asilidae are among the best known dipteran predators, but it has been indicated that arachnids do not comprise a significant portion of robber fly diet, making up less than 2% of all their consumed prey (Dennis et al. 2012). Robber flies are found worldwide and may occasionally take spiders as prey, especially species in the asilid genera *Daspletis* Loew, 1858, *Efferia* Coquillett, 1893, *Euscelidia* Westwood, 1850, *Holopogon* Loew, 1847, *Laphystia* Loew, 1847, *Psilonyx* Aldrich, 1923 and *Stichopogon* Loew, 1847 (Dennis et al. 2012). Robber flies are recorded to prey on spiders belonging to the suborder Araneomorphae, mainly in the families Agelenidae, Araneidae, Clubionidae, Lycosidae, Salticidae and Theridiidae, among others (Dennis et al. 2012). This suborder comprises species that are generally readily visible, including orbweavers, crab spiders and jumping spiders. In contrast, spiders in the other two suborders of Araneae (Mygalomorphae and Mesothelae) generally have reclusive habits (such as trapdoor and funnel-web spiders) or are highly mobile. There are also smaller dipterans that play a role as predators of small arachnids. For instance, larvae of species in the gall midge genus *Feltiella* Rubsaamen, 1910 (Cecidomyiidae) are specialized predators of all spider mite life stages (Acarina: Tetranychidae), as are many members of the gall midge tribe Lestodiplosini (Gagné 1995). One species of Ceratopogonidae, *Forcipomyia araneivora* Clastrier & Legrand, 1991, also plays a role as an enemy of spiders by feeding directly on their haemolymph (Clastrier & Legrand 1991). Other common dipteran predators (e.g., Muscidae and several families in Empidoidea) may take arachnids as prey, but no records of these were found.

2.2 Kleptoparasites.—Kleptoparasitism is a form of competition that involves the stealing of a portion of already acquired food items, and is one of the most common types of exploitation between animals. Kleptoparasites steal food that is either already in a predator's possession, or which the predator has already spent energy pursuing and capture by the predator is imminent. In this interaction, the kleptoparasite is benefited and the host may potentially be negatively affected by the loss of food resources (Brockmann & Barnard 1979; Barnard 1984). Some fly species in the families Cecidomyiidae, Ceratopogonidae, Chloropidae, Dolichopodidae, Lonchaeidae, Milichiidae and Phoridae are known kleptoparasites of spiders. These organisms typically exploit cadavers captured by spiders, feeding on the semi-digested prey. In general, spiders most commonly attacked by kleptoparasites are orbweavers (Araneidae and Nephilidae), crab spiders (Thomisidae) and jumping spiders (Salticidae). The most common spider kleptoparasites are species in the genera *Didactylomyia* Felt, 1911 (Cecidomyiidae), *Microphor* Macquart, 1827 (Dolichopodidae), *Desmometopa* Loew, 1866, *Neophyllomyza* Melander, 1913, *Paramyia* Williston, 1897, and *Phyllomyza* Fallen, 1810 (Milichiidae) and *Megaselia* Rondani, 1856 (Phoridae) (Robinson & Robinson 1977; Sivinski & Stowe 1980; Weinmann & Disney 1997; Sivinski et al. 1999; Brake 2000; Brake & von Tschirnhaus 2010; van Helsdingen 2011; Marshall et al. 2015).

Due to their generalistic feeding nature (taking a range of taxa as prey/host), predators and kleptoparasites of individual arachnids were not included in the summary table.

2.3 Egg parasitoids and predators.—A large variety of Diptera attack the eggs of arachnids, either as parasitoids or predators; it is often difficult to distinguish between these alternatives due to the limited number of natural history and rearing observations. Therefore, we have decided not to distinguish between these modes, in order to avoid making incorrect assumptions about poorly known dipteran-spider interactions. Each dipteran family is discussed in more detail below.

2.3.1 Family Bombyliidae: Bombyliidae is a large group of Diptera commonly known as bee flies. Despite the great number of species (over 5,000 valid species), the habits of most immature stages (>80%) are still poorly understood (Yeates & Greathead 1997). Known species are mostly ecto- or endoparasitoids on the larvae and/or pupae of other insects, mainly in the Lepidoptera, Hymenoptera, Coleoptera, Diptera and Neuroptera. The only known exception is *Petrorossia feti* Zaitsev & Charykuliev, 1981, which develops as a parasitoid or predator on egg sacs of oecobiid spiders (Zaitsev & Charykuliev 1981; Yeates & Greathead 1997). It is unknown

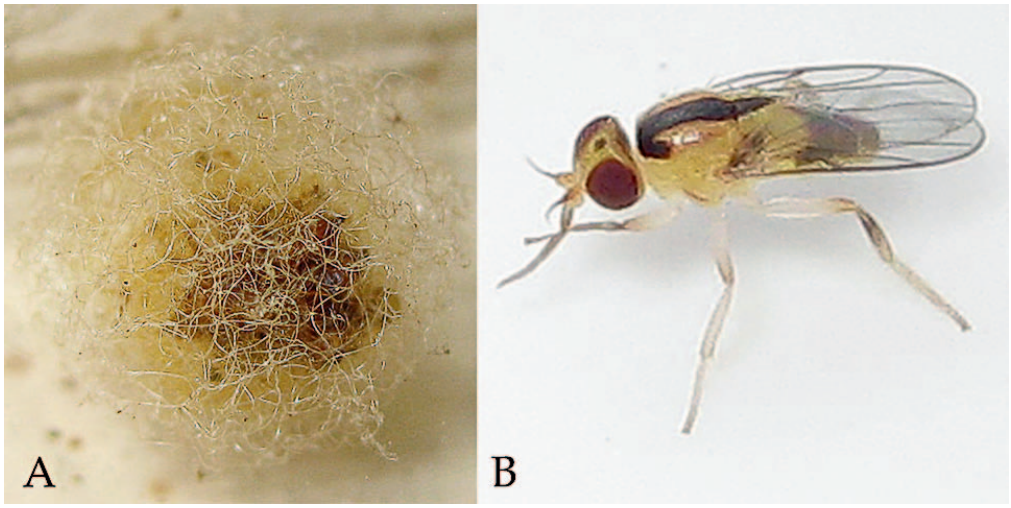

Figure 1.—Chloropidae development on spider egg sac. A. Egg mass of *Mimetus puritanus* Chamberlin, 1923 containing larvae of *Pseudogaurax anchora* (Loew, 1866). B. Adult *P. anchora*. Photos: John R. Maxwell.

whether or not this species has a specific host association with these spiders (Zaitzev & Charykuliev 1981).

2.3.2 Family Chloropidae: Several species of Chloropidae are known to be either parasitoids or predators of arachnid eggs. Genera of chloropids that have been reported as arachnid egg predators include *Conioscinella* Duda, 1929, *Gaurax* Loew, 1863, *Oscinella* Becker, 1909, *Oscinisoma* Lioy, 1864, *Pseudogaurax* Malloch, 1915, *Siphonella* Macquart, 1835, and *Tricimba* Lioy, 1864 (Barnes et al. 1992). Eason et al. (1967), Rollard (1984) and Barnes et al. (1992) provide a review of host records for several groups of Diptera and Hymenoptera, including chloropids. Several species of *Gaurax* and *Pseudogaurax* are suggested to be parasitoids of arachnid eggs (including amblypygids (Viquez & de Armas 2009; Chapin & Hebet 2016)) and have been raised from a variety of host eggs (see details in Table I) (Figs. 1 & 2). However, very little is known about the life histories of most of these species, and there is an indication that the larvae do not complete their development on a single egg, consuming a few or several eggs and, as such, must be considered as predators (Barnes et al. 1992). Some species are apparently opportunists, utilizing a variety of host species or even hosts of different orders, including lepidopteran cocoons and mantid oothecae. *Pseudogaurax signatus* (Loew, 1876) has been suggested as a biocontrol agent of black widow spiders, *Latrodectus* Walckenaer, 1805, since many specimens have been reared from egg sacs of this spider (Barnes et al. 1992; Vetter et al. 2012), with infestation rates reported to range from 6% (Vetter et al. 2012) to 40%, and estimated spider mortality >90% (Barnes et al. 1992). Female *P. signatus* flies lay the eggs on the surface of the host egg sac. Once hatched, larvae enter the egg sacs and consume multiple eggs, developing inside the sac.

2.3.3 Family Drosophilidae: Most species of Drosophilidae feed on decaying fruit and fungal material, as well as on fresh sap and nectar from flowers. Species in the subgenus *Titanochaeta* Knab, 1914 (genus *Scaptomyza* Hardy, 1850), however, differ from all other drosophilids in being parasitoids (or predators) of spider eggs. Unlike the remaining species of *Scaptomyza*, species in the subgenus *Titanochaeta* exhibit a slender, sharply pointed, stylet-like ovipositor, which is likely an adaptation to a lifestyle as a spider egg sac parasitoid or predator (O'Grady et al. 2003). The group is endemic to Hawaii and comprises 11 species known to develop on spider egg sacs (Wirth 1952; Eason et al. 1967; O'Grady et al. 2003). Little biological information is available on the host usage of species of *Titanochaeta*, but available rearing data indicate a preference for spiders in the family Thomisidae (Hardy 1965; Lapoint et al. 2013). Further study is needed in order to investigate the number of eggs consumed by each individual, thus confirming whether species of *Titanochaeta* are predators or parasitoids of spider eggs.

2.3.4 Family Ephydridae: The vast majority of species of Ephydridae feed primarily on autotrophic microorganisms such as algae (Foote 1984). One exception is *Trimerina madizans* (Fallen, 1813), which has been indicated as an egg parasitoid of marsh-inhabiting spiders (Wirth et al. 1987). The fly has been reported to attack egg sacs of the linyphiid *Hypselistes florens* (O. Pickard-Cambridge, 1875) (Wirth et al. 1987). However, it has been shown that each fly larva consumes on average six eggs of *H. florens* during its development (Foote 1984); in this case, the species is better regarded as a predator rather than a parasitoid.

2.3.5 Family Phoridae: Although most species of Phoridae associated with arachnids are merely saprophagous, some are known to be associated with living rather than dead arachnids. Most of these are predators of arachnid eggs. However, specimens of *Apocephalus borealis* Brues, 1924 have been reared from black widow egg sacs, *Latrodectus mactans* (Fabricius, 1775), (Araneae: Theridiidae), and this has been suggested to be a case of true parasitism, although further research is needed for proper confirmation (Disney 1994). Several species in *Megaselia* Rondani, 1856 and *Phalacrotophora* Enderlein, 1912 (Fig. 3) are known to prey on eggs of spiders in the families Araneidae (*Argiope* Audouin, 1826, *Gasteracantha* Sundevall, 1833, and *Larinioides* Caporiacco, 1934), Linyphiidae (*Pityohyphantes* Simon, 1929), Salticidae (*Phidippus* C. L. Koch, 1846), Tetragnathidae (*Meta* C. L. Koch, 1836) and Theridiidae (*Enoplognatha* Pavesi, 1880,

Figure 2.—Amblypigid female carrying pupae of *Pseudogaurax* (Diptera: Chloropidae) that were egg parasitoids of her egg case as larvae. Photographed at the Soltis Center, San Juan de Peñas Blancas, San Ramón, Costa Rica, by Kristie Reddick and Jessica Honaker.

Latrodectus and *Robertus* O. Pickard-Cambridge, 1879) (Disney & Evans 1980; Disney 1982, 1994, 1999).

2.3.6 Family Sarcophagidae: Sarcophagidae is a large family of Diptera with species exhibiting a breadth of habits and life histories. Most species are generalist scavengers and insect predators, while some species are kleptoparasites of solitary bees and wasps (Pape et al. 2012). Several species in the genus *Sarcophaga* Meigen, 1826 are spider egg parasitoids or predators (e.g., Eason et al. 1967; Auten 1925; Prakash & Pandian 1977; Austin 1985; Souza Lopes 1985; Cantrell 1986; Hieber & Uetz 1990). However, as in the dipteran families mentioned above, more research is needed in order to confirm whether these species are parasitoids or predators. Schwendinger & Pape (2000) reported an unusual case of a predatory species of *Metopia* Meigen, 1803, a genus that mostly comprises kleptoparasites in nests of solitary aculeate Hymenoptera (Pape 1986). Larvae of *Metopia sinensis* Pape, 1986 apparently kill the spider host and complete most of their larval life on the carcass, behaving more like predators rather than parasites (following Price 1980).

2.3.7 Family Tachinidae: As discussed below, tachinids are well known as parasitoids of a range of insects. However, there is only a single record of a tachinid attacking spider eggs, a specimen of *Tachina* Meigen, 1803 which had been reared from egg sacs of the araneid *Larinioides cornutus* (Clerck, 1757) (Bertkau 1880).

2.4 Endoparasitoids.—The majority of dipteran endoparasitoids of arachnids are species of the family Acroceridae, which have exclusively been reared from a variety of spider families. There are also a few examples from other Diptera families (Phoridae, Sarcophagidae and Tachinidae). The specific details of the behaviors in each case are given below.

2.4.1 Family Acroceridae: Species of Acroceridae are commonly called spider flies due to their tight relationship with spiders as internal parasitoids. They are sometimes also referred to as small-headed flies in reference to the disproportionately small heads of some species. Spider flies represent a morphologically heterogeneous assemblage of lineages, currently classified into three subfamilies (Acrocerinae, Panopinae and Philopotinae), 55 genera and approximately 530

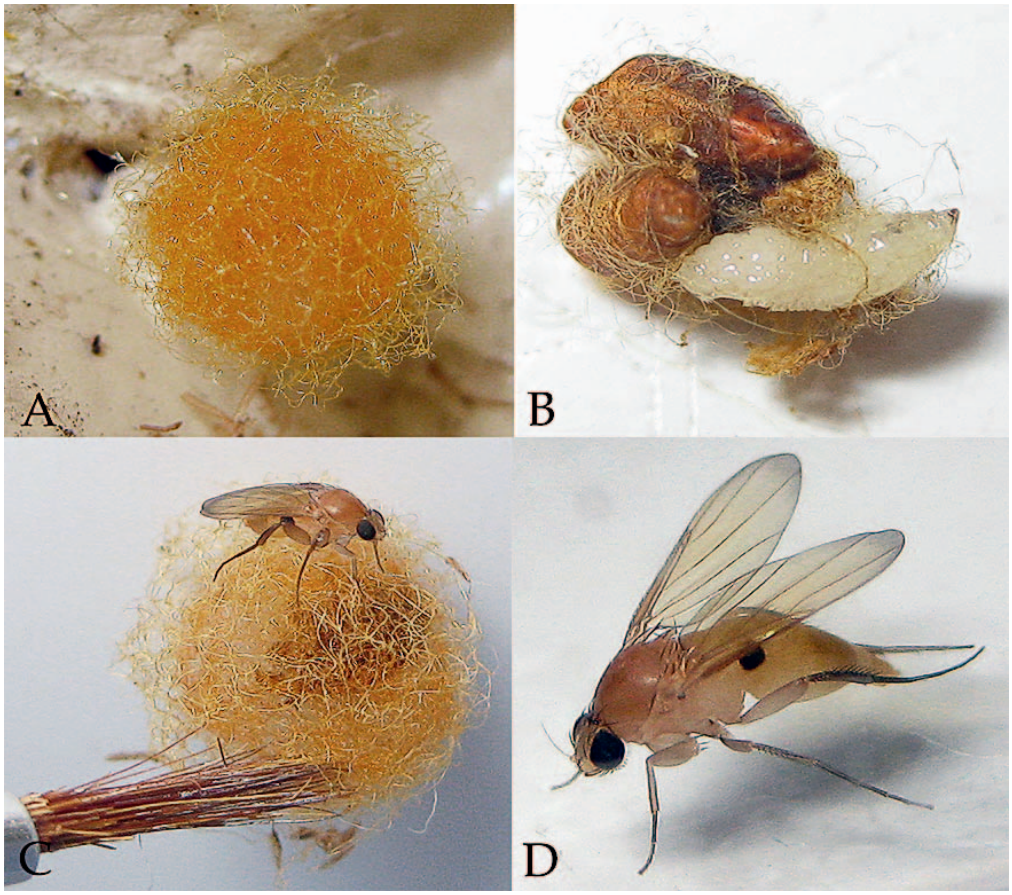

Figure 3.—Phoridae development on spider egg sac. A. Egg mass of *Mimetus puritanus* Chamberlin, 1923. B. Pupae and larva of *Phalacrotophora epeirae* (Brues, 1902). C. Spider egg mass, pupae and adult of *P. epeirae*. D. Adult *P. epeirae*, oblique view. Photos: John R. Maxwell.

species (Schlinger et al. 2013). Adults are morphologically very distinctive, usually with inflated or hunchbacked bodies, and occasionally with metallic coloration. Several species have long, modified mouthparts for nectar feeding and are considered important pollinators (e.g., Goldblatt et al. 1997; Potgieter et al. 1999; Pujol-Luz 2004; Carvalho & Machado 2006; Borkent & Schlinger 2008).

Spider fly larvae attack spiders in the Mygalomorphae (Fig. 4) and Araneomorphae. The only exception to the exclusive endoparasitic mode in Acroceridae is found in the Chilean genus *Carvalhoa* Koçak & Kemal, 2013 (= *Sphaerops* Philippi, 1865), which is reported to remain ectoparasitic on its host spider for at least three weeks (Schlinger 1987). It is still unknown whether the entire lifecycle is spent as an ectoparasite, but Schlinger (1987) reports this ectoparasitic behavior in multiple rearings of later instars of the species.

Records of acrocerids parasitizing Acari are extremely rare (Sferra 1986; Kerr & Winterton 2008), and no spider fly planidium has been reared from living mites to confirm, or identify, the acrocerid species in question. It is likely that the presence of acrocerid first instar larvae in mites is merely accidental parasitism, and the larvae probably do not develop further due to the small size of the mites relative to known acrocerid adults. Acrocerids are known to attack juvenile spiders, but even the smallest known spider hosts are several times larger than mites found in association with acrocerid planidia (Sferra 1986; Kerr & Winterton 2008). In the cases of mite parasitism, it is likely that the planidium is simply indiscriminately adhering to arachnids in an attempt to find a suitable host. In this case, the association between Acroceridae and Acari would not represent a true host-parasitoid relationship.

Generally, adult spider fly females scatter eggs during flight or oviposit large numbers of microtype eggs on twigs, branches or foliage (Schlinger 1987). In most species, oviposition seems to be entirely independent of the presence of a host, though naturally the flies occur in a habitat favorable to spider populations. Females of *Eulonchus* Gerstaecker, 1856 are reported to be attracted to burrows of trapdoor spiders in the genus *Antrodiaetus* Ausserer, 1871. Coyle (1971) reports a case in which, as trapdoor spider burrows were being excavated, a large number of spider flies quickly approached, hovering close to the ground and landing near closed burrow entrances, apparently attracted by some chemical released during the excavation process.

The first-instar acrocerid is a free-living planidium, which actively seeks out a spider host by crawling, looping or jumping, with the aid of well-developed setae, spines and a caudal suction disk (Schlinger 1981). Planidia in the genus *Acrocera* Meigen, 1803, however, differ from all other spider

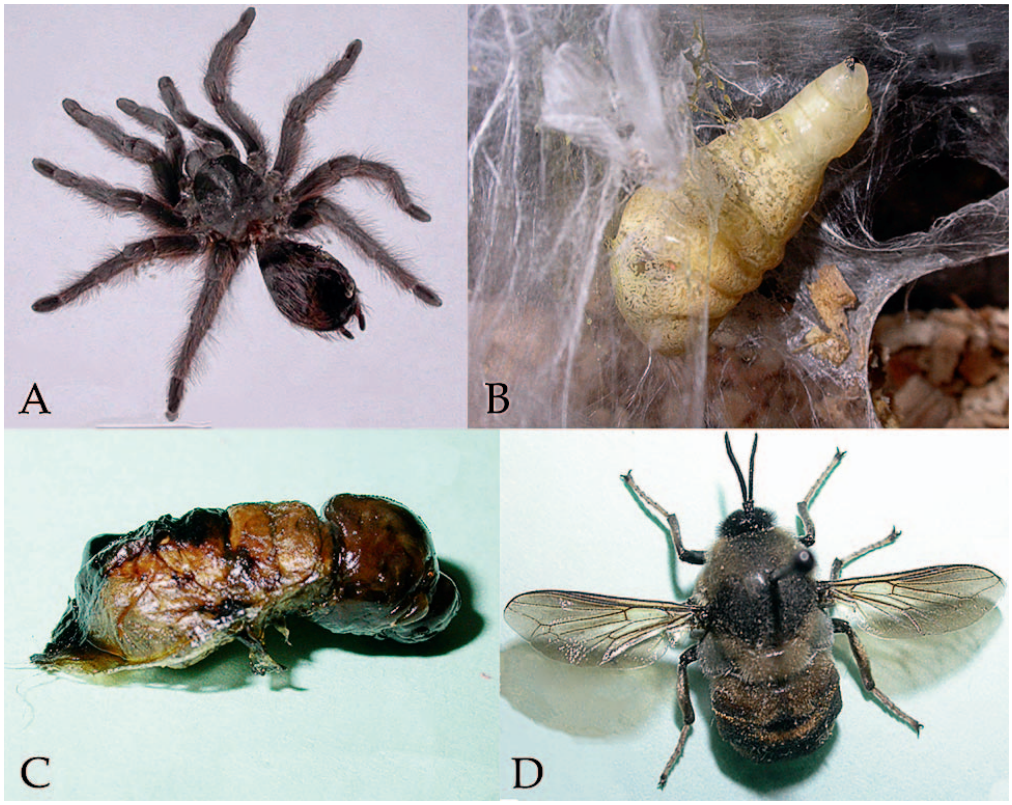

Figure 4.—Acroceridae development in the spider host. A. Spider host, *Aphonopelma duplex* (Chamberlin, 1925). B. Fourth instar larva of *Ocnaea* sp. C. Pupa of *Ocnaea* sp. D. Adult *Ocnaea* sp. Photos: Dr. A. Alagon.

flies in having a poorly sclerotized body and an abdomen with numerous annulations obscuring the regular body segmentation, as well as the absence of setal pile characteristic of acrocerid planidia (Schlinger 1981). *Acrocera* also exhibits a unique mode of entering its host, in which the first-instar larva injects itself into the spider. Planidia of *Acrocera orbicula* (Fabricius, 1787) have been observed entering a wolf spider through this sophisticated mode, in which first-instars firmly attach themselves to the host's cuticle by the mouthparts, presumably feeding externally for about a week (Overgaard Nielsen et al. 1999; Toft et al. 2012). Rather than entering the spider, the first-instar subsequently molts and the small, flexible, and glabrous second-instar is injected directly into the spider via the wound, leaving the exuvia of the ectoparasitic first-instar covering the site of infection. This mode of host invasion may reduce physical damage to the host in the initial phase of endoparasitism, thus enhancing parasitoid survival (Overgaard Nielsen et al. 1999). More research is needed in order to investigate whether this mechanism for infection is also present in other Acroceridae lineages.

Most host records for Acroceridae involve rearing of mature larvae from parasitized spiders, and observations of infestation of the host by the planidium stage are rare. The planidium presumably enters the host directly through the cuticle of the cephalothorax, opisthosoma or leg joints (Schlinger 1981, 1987; Nartshuk 1997), but these apparently have not been verified by direct observations. Acrocerid larvae eventually locate themselves in the opisthosoma and attach their posterior spiracle to the spider's book lung for respiration (Schlinger 1981, 1987). Schlinger (1987) proposed that upon entering the host, the larva may enter a state of diapause that can last for several months (Acrocerinae) up to 10 years (Panopinae), and, upon cessation of diapause, the actively feeding larva completes its life cycle relatively quickly (days to weeks), undergoing up to four instars. McQueen (1983) observed wolf spiders in the genus *Geolycosa* Montgomery, 1904 parasitized by *Pterodontia* Gray, 1832 spider flies and stated that infected spiders carry the larvae for approximately a year until they are entirely consumed by the parasitoid. However, further evidence is needed to support the hypothesis of diapause within the host and to verify the actual number of larval instars in Acroceridae, because the typical number of instars in lower brachyceran flies is three.

Many parasites and parasitoids have evolved remarkable strategies to manipulate the behavior of their hosts in order to promote their own survival and reproduction. These behavioral manipulations may include alterations in phototaxis, locomotion, foraging and defensive behaviors (Moore 2002). Most spider hosts of acrocerids, however, do not exhibit any obvious external indication of parasitism, although there are reports of enlargement of the spider's opisthosoma due to the presence of spider fly larvae (e.g., Lamore 1960; Barraclough & Croucamp 1997). It has been repeatedly reported that the host displays some abnormal, agitated behavior during the final stages of parasitism, in which the spiders walk aimlessly and incessantly scratch the lateral portions of the opisthosoma with the legs, presumably where the parasitoid is located (Cady et al. 1993; Barneche et al. 2013). In some species,

especially in the Mygalomorphae, the emergence of the parasite seems to correspond with the premolting behavior of the spider (e.g., Montgomery 1903; Cady et al. 1993; Barneche et al. 2013). However, a causative relationship between the production of the premolting web and parasitoid emergence can only be speculative at this time, but the presence of hook-like processes on the head and/or abdomen of the spider fly larva, which are supposedly used as attachment to the web, suggests that this is not coincidental. Lamore (1960) reported an example in which a larva of *Ogcodes dispar* (Macquart, 1855) parasitizing a basilica spider, *Mecynogea lemniscata* (Walckenaer, 1841), hung itself on the spider web while also hanging on to the spider on one end for a while, then released its hold on the exoskeleton in order to pupate. The last instar acrocerid larva typically only kills the host shortly prior to emergence, when it consumes the entire contents of the host body, leaving an empty, unbroken exoskeleton (Schlinger 1987; Nartshuk 1997).

While super-parasitism is common in early instars, usually only a single acrocerid adult ultimately emerges from its host (Cady et al. 1993; Overgaard Nielsen et al. 1999). Multiple emergences of larvae from a single host are more likely found in Panopinae, which attack large Mygalomorphae spiders capable of sustaining multiple parasitoids (Schlinger 1987; Cady et al. 1993).

Host records for acrocerids parasitizing spiders are known for at least 60 species, recorded from about 25 spider families (Schlinger 1987). Schlinger (1987, table 24) presented an extensive list of spider taxa parasitized by acrocerids, while Winterton et al. (2007) mapped host use onto a DNA-based phylogeny of the family. These studies clearly demonstrate that Panopinae are host-specific to Mygalomorphae spiders (Fig. 4), while Acrocerinae and Philopotinae are host-specific to the Araneomorphae. Only the genera *Acrocera* and *Carvalhoa* have been reared from Haplogynae spiders, while Philopotinae and all remaining Acrocerinae have only been recorded to attack Entelegynae. The cosmopolitan genera *Acrocera*, *Ogcodes* Latreille, 1797 and *Pterodontia* have been reared from numerous hosts in multiple spider families, but most geographically restricted and species-poor genera tend to be more host-specific, generally attacking only a single spider family (Schlinger 1987). Strict host specificity between particular acrocerid and spider species seems to be rare, but some trends are evident where host preference generally follows spider guilds instead of lineages (Schlinger 1987; Cady et al. 1993). Spiders most susceptible to parasitism by Acroceridae belong to guilds of cursorial or fossorial species (e.g., Mygalomorphae: Antrodiaetidae, Ctenizidae, Migidae, Theraphosidae; Araneomorphae: Anyphaenidae, Clubionidae, Lycosidae, Salticidae, Thomisidae), or those that occupy sac, tangle or funnel-like web retreats that are close to the ground, have webs with many connections to vegetation, or visit surrounding vegetation or substrate frequently (e.g., Agelenidae, Amaurobiidae, some Araneidae, Dipluridae, Segestriidae) (Schlinger 1987; Cady et al. 1993; Overgaard Nielsen et al. 1999). There are very few records of acrocerids parasitizing true web-dwelling spiders and exceptions typically involve comb-footed spiders (e.g., Theridiidae), where the spider may still be proximal to the substrate (e.g., Lamore 1960).

2.4.2 Family Sarcophagidae: As discussed above, the majority of members of Sarcophagidae are generalist scavengers and insect predators (Pape et al. 2012). However, there is one example of a sarcophagid acting as an endoparasitoid of a scorpion. *Sarcophaga dux* (Thomson, 1869), a species generally considered to be of forensic importance, was found to attack the Chinese scorpion *Mesobuthus martensii* (Karsch, 1879) (Scorpiones: Buthidae). Multiple larvae (3–6) attacked more than 50 individuals of this scorpion species, with more than 100 flies emerging as adults by the end of the study (Shi et al. 2015).

2.4.3 Family Tachinidae: Species of Tachinidae are internal parasitoids on a wide range of arthropod hosts. The most commonly used hosts are phytophagous insects, primarily Lepidoptera, Coleoptera, Hymenoptera, Heteroptera, and Orthoptera. Several genera of tachinids attack non-insect arthropods, including centipedes and scorpions (Stireman et al. 2006). There is a single record of a spider serving as a tachinid host (Vincent 1985). Two tachinid larvae in the genus *Lypha* Robineau-Desvoidy, 1830 emerged from the abdomen of immature individuals of *Antrodiaetus riversi* (O. Pickard-Cambridge, 1883) in the laboratory. The two larvae pupated outside of the host but neither adult emerged. Other known hosts of *Lypha* species are Lepidoptera in the families Gelechiidae and Tortricidae, and it is likely that the two spiders may have been accidental hosts that did not manage to survive and become adults. Vincent (1985) reported rearing over 340 spiders, which were examined and inspected for signs of parasitism, and only two contained larval tachinids.

The tachinid *Spilochaetosoma californicum* Smith, 1917 has been found to be an endoparasitoid of two Nearctic scorpions, *Anuroctonus phaiodactylus* (Wood, 1863) and *Paravaejovis spinigerus* (Wood, 1863) (Scorpiones: Vaejovidae). Multiple larvae of *S. californicum* emerged from wild caught individuals of both species and it is likely that this tachinid is a general parasitoid of burrowing scorpions (Williams et al. 1994).

3. CONCLUSION

In this review we summarized the available information on all lineages of Diptera known to attack arachnids, including predators, parasites, kleptoparasites and parasitoids. A summary table (Table 1) containing over 200 host records for eight families of Diptera attacking 36 arachnid families is included. Even though hymenopterans are among the best known natural enemies of arachnids, species of Diptera clearly also comprise a large component of arachnid enemies, attacking families in four orders of arachnids and all three suborders of Araneae.

A single species of Sarcophagidae, one species of Tachinidae and all species of Acroceridae are internal parasitoids, attacking juvenile and/or adult arachnids. Spider flies (family Acroceridae) comprise the only lineage of Diptera known to develop exclusively on arachnid hosts, representing some of the most significant natural enemies of spiders. Multiple species of Chloropidae, Drosophilidae, Ephydridae, Phoridae and Sarcophagidae are known to attack eggs of 11 families of arachnids, acting as predators and/or parasitoids of arachnid egg sacs (see Table I). Some of these species are known to be true predators, while some are known to be true parasitoids. However, in most cases, the life history strategy is not clear,

Table 1.—Host records for the known natural enemies of arachnids in the order Diptera, organized by arachnid order and family. Due to their generalist feeding habits, predators and kleptoparasites of individual arachnids were not included. Host stage exploited by the dipteran is noted as egg, adult, immature or stage unknown (Adult/Immature). EIS = E.I. Schlinger Collection database record.

Host order	Host family	Arachnid host	Host stage	Fly family	Fly parasitoid/ parasite/predator	Reference
Amblypygi	Phrynidae	*Paraphrynus laevifrons* (Pocock, 1894)	Adult	Chloropidae	*Pseudogaurax* sp.	Viquez & De Armas 2009
		Phrynus pseudoparvulus Armas & Viquez, 2001	Adult	Chloropidae	*Pseudogaurax* sp.	Viquez & De Armas 2009
Araneae	Agelenidae	*Agelenopsis naevia* (Walckenaer, 1841)	Adult/ Immature	Acroceridae	*Turbopsebius sulphuripes* (Loew)	Melander 1902
		Agelenopsis oregonensis Chamberlin & Ivie, 1935	Adult/ Immature	Acroceridae	*Acrocera bakeri* Coquillett	Schlinger 1987
		Agelenopsis sp.	Adult/ Immature	Acroceridae	*Acrocera melanderi* Cole	EIS database
		Agelenopsis sp.	Adult/ Immature	Acroceridae	*Ogcodes dispar* (Macquart)	Schlinger 1987
		Agelenopsis sp.	Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Guarisco 1990
		Barronopsis sp.	Adult/ Immature	Acroceridae	*Acrocera bimaculata* (Loew)	Schlinger 1987
		Coras montanus (Emerton, 1890)	Adult/ Immature	Acroceridae	*Acrocera bimaculata* (Loew)	Cady et al. 1993
		Coras montanus	Adult/ Immature	Acroceridae	*Pterodontia flavipes* Gray	Sabrosky 1948
		Coras montanus	Adult/ Immature	Acroceridae	*Turbopsebius sulphuripes* (Loew)	Cady et al. 1993
		Eratigena sicana (Brignoli,1976)	Adult/ Immature	Acroceridae	*Ogcodes* sp.	Brignoli 1976
		Hololena curta (McCook, 1894)	Adult/ Immature	Acroceridae	*Acrocera subfasciata* Westwood	EIS database
		Hololena curta	Immature	Acroceridae	*Ogcodes adaptatus* Schlinger	Schlinger 1960
		Hololena curta	Adult and immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Schlinger 1960
		Hololena curta	Immature	Acroceridae	*Turbopsebius diligens* (Osten Sacken)	Schlinger 1952
		Hololena sp.	Adult/ Immature	Acroceridae	*Acrocera melanderi* Cole	Cole 1969
		Hololena sp.	Adult/ Immature	Acroceridae	*Acrocera subfasciata* Westwood	Schlinger 1987
		Rualena sp.	Adult/ Immature	Acroceridae	*Turbopsebius diligens* (Osten Sacken)	Schlinger 1987
		Textrix denticulata (Olivier, 1769)	Adult/ Immature	Acroceridae	*Acrocera sanguinea* Meigen	Koch 1872
Araneae	Amaurobiidae	*Amaurobius erberi* (Keyserling, 1893)	Immature	Acroceridae	*Acrocera orbicula* (Fabricius)	Kehlmaier & Almeida 2014
		Amaurobius sp.	Immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Schlinger 1960
		Callobius bennetti (Blackwall, 1846)	Adult/ Immature	Acroceridae	*Acrocera fasciata* Wiedemann	Emerton 1890
		Undetermined genus	Adult/ Immature	Acroceridae	*Megalybus pictus* Philippi	Schlinger 1987
		Undetermined genus	Adult/ Immature	Acroceridae	*Thyllis* sp.	Schlinger 2003
Araneae	Amphinectidae	*Metaltella* sp.	Adult/ Immature	Acroceridae	*Holops cyaneus* Philippi	Schlinger 1987
Araneae	Antrodiaetidae	*Aliatypus californicus* (Banks, 1896)	Adult/ Immature	Acroceridae	*Eulonchus tristis Loew*	Coyle & Icenogle 1994
		Aliatypus erebus Coyle, 1974	Adult	Acroceridae	*Eulonchus tristis* Loew	Coyle & Icenogle 1994

Table 1.—Continued.

Host order	Host family	Arachnid host	Host stage	Fly family	Fly parasitoid/ parasite/predator	Reference
Araneae	Antrodiaetidae	*Aliatypus* sp.	Adult/ Immature	Acroceridae	*Eulonchus tristis* Loew	Schlinger 1987
		Antrodiaetus riversi (O. Pickard-Cambridge, 1883)	Adult/ Immature	Acroceridae	*Eulonchus sapphirinus* Osten Sacken	EIS database
		Antrodiaetus riversi	Adult/ Immature	Acroceridae	*Eulonchus* sp.	Vincent 1986
		Antrodiaetus riversi	Adult	Tachinidae	*Lypha* sp.	Vincent 1985
		Antrodiaetus unicolor (Hentz, 1842)	Adult/ Immature	Acroceridae	*Eulonchus marialiciae* Brimley	Coyle 1971; Adler et al 1997
		Antrodiaetus sp.	Adult/ Immature	Acroceridae	*Eulonchus* sp.	Schlinger 1987
Araneae	Anyphaenidae	*Anyphaena californica* (Banks, 1904)	Adult/ Immature	Acroceridae	*Ogcodes* sp.	Cady et al. 1993
		Wulfila saltabundus (Hentz, 1847)	Adult/ Immature	Acroceridae	*Ogcodes borealis* Cole	Sabrosky 1948
		Wulfila saltabundus	Adult/ Immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Sabrosky 1948
Araneae	Araneidae	*Alpaida veniliae* (Keyserling,1865)	Egg	Chloropidae	*Pseudogaurax cingulatus* Sabrosky	Sabrosky 1966
		Araneus angulatus Clerck, 1757	Egg	Chloropidae	*Pseudogaurax signatus* (Loew)	Davidson 1896
		Araneus ejusmodi (Boesenberg & Strand, 1906)	Egg	Chloropidae	*Gaurax chiyokae* (Kanmiya)	Kanmiya 1972, 1983
		Araneus gemma (McCook, 1888)	Egg	Chloropidae	*Pseudogaurax signatus* (Loew)	Pierce 1942
		Argiope aemula (Walckenaer, 1841)	Egg	Phoridae	*Megaselia araneivora* Goto	Goto 1985
		Argiope argentata (Fabricius,1775)	Egg	Sarcophagidae	*Sarcophaga davidsonii* Coquillett	Davidson 1894
		Argiope aurantia Lucas, 1833	Egg	Phoridae	*Megaselia* sp.	Kaston & Jenks 1937
		Argiope aurantia	Egg	Chloropidae	*Pseudogaurax anchora* (Loew)	Kaston & Jenks 1937
		Argiope aurantia	Egg	Chloropidae	*Pseudogaurax signatus* (Loew)	Coquillet 1898
		Argiope aurantia	Egg	Chloropidae	*Pseudogaurax signatus* (Loew)	Lockley & Young 1993
		Argiope aurantia	Egg	Sarcophagidae	*Sarcophaga litsingeri* (Shinonaga & Barrion)	Davidson 1896
		Argiope catenulata (Doleschall, 1859)	Egg	Sarcophagidae	*Sarcophaga litsingeri* (Shinonaga & Barrion)	Shinonaga & Barrion 1980
		Argiope pulchella Thorell, 1881	Egg	Sarcophagidae	*Sarcophaga banksi* Senior-White	Prakash & Pandian 1977
		Argiope trifasciata (Forsskål, 1775)	Egg	Sarcophagidae	*Tricharaea* (*Sarcophagula*) Thomson	de Armas & Garcia 1986
		Argiope sp.	Egg	Phoridae	*Megaselia argiopephaga* Disney	Disney 1982
		Cyrtophora moluccensis (Doleschall, 1857)	Egg	Sarcophagidae	*Sarcophaga arachnivora* (Lopes)	Cantrell 1986
		Cyrtophora moluccensis	Egg	Sarcophagidae	*Sarcophaga cyrtophorae* (Cantrell)	Cantrell 1986
		Cyrtophora moluccensis	Egg	Sarcophagidae	*Sarcophaga reposita* (Lopes)	Cantrell 1986

Table 1.—Continued.

Host order	Host family	Arachnid host	Host stage	Fly family	Fly parasitoid/ parasite/predator	Reference
Araneae	Araneidae	*Gasteracantha cancriformis* (Linnaeus, 1785)	Egg	Phoridae	*Phalacrotophora epeirae* (Brues)	Muma & Stone 1971
		Gasteracantha cancriformis	Egg	Chloropidae	*Pseudogaurax lancifer* (Coquillett)	Hall 1937
		Larinioides cornutus (Clerck, 1757)	Egg	Chloropidae	*Conioscinella frontella* (Fallen)	Krijger 1910
		Larinioides cornutus	Egg	Chloropidae	*Oscinella halterata* (Lamb)	Auten 1925
		Larinioides cornutus	Egg	Sarcophagidae	*Sarcophaga sexpunctata* (Fabricius)	Auten 1925
		Larinioides cornutus	Egg	Tachinidae	*Tachina* sp.	Bertkau 1880
		Larinioides sclopetarius (Clerck, 1757)	Egg	Chloropidae	*Oscinella halterata* (Lamb)	Auten 1925
		Larinioides sclopetarius	Egg	Phoridae	*Phalacrotophora epeirae* (Brues)	Brues 1902, 1903; Auten 1925
		Larinioides sclopetarius	Adult/ Immature	Acroceridae	*Pterodontia flavipes* Gray	King 1916
		Larinioides sclopetarius	Egg	Sarcophagidae	*Sarcophaga sexpunctata* (Fabricius)	Auten 1925
		Mecynogea lemniscata (Walckenaer, 1841)	Adult	Acroceridae	*Ogcodes dispar* Macquart	Lamore 1960
		Metepeira atascadero Piel, 2001	Egg	Sarcophagidae	*Sarcophaga lindae* (Lopes)	Hieber & Uetz 1990
		Metepeira incrassata O. Pickard-Cambridge, 1903	Egg	Sarcophagidae	*Sarcophaga lindae* (Lopes)	Hieber & Uetz 1990
		Neoscona nautica (L. Koch, 1875)	Egg	Chloropidae	*Gaurax chiyokae* (Kanmiya)	Kanmiya 1972, 1983
		Ordgarius magnificus (Rainbow, 1897)	Egg	Sarcophagidae	*Sarcophaga arachnivora* (Lopes)	Souza Lopes 1985
		Singa nitidula C. L. Koch, 1844	Egg	Chloropidae	*Conioscinella frontella* (Fallen)	Vachon 1952
		Zygiella x-notata (Clerck, 1757)	Adult/ Immature	Acroceridae	*Ogcodes fumatus* (Erichson)	Holl et al. 1983
		Undetermined genus	Egg	Phoridae	*Megaselia longifurca* (Lundbeck)	Disney 1999
Araneae	Clubionidae	*Clubiona leucaspis* (Simon, 1932)	Immature	Acroceridae	*Ogcodes reginae* Trojan	Kehlmaier & Almeida 2014
		Clubiona putris nom. dub. C. L. Koch, 1839	Adult/ Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Emerton 1890
		Clubiona putris nom. dub.	Adult/ Immature	Acroceridae	*Ogcodes pallipes* Latreille	Menge 1866
		Clubiona sp.	Immature	Acroceridae	*Acrocera orbicula* (Fabricius)	Millot 1938
Araneae	Ctenizidae	*Bothriocyrtum californicum* (O. Pickard-Cambridge, 1874)	Adult/ Immature	Acroceridae	*Ocnaea smithi* Sabrosky	Jenks 1938, 1940
		Cyrtocarenum cunicularium (Olivier, 1811)	Adult/ Immature	Acroceridae	*Astomella hispaniae* Lamarck	Brauer 1869
Araneae	Desidae	*Matachia ramulicola* Dalmas, 1917	Adult/ Immature	Acroceridae	*Ogcodes brunneus* (Hutton)	Dumbleton 1940
Araneae	Dipluridae	*Linothele cousini* (Simon, 1889)	Adult/ Immature	Acroceridae	*Lasia ecuadorensis* Bequaert	Schlinger 1987
Araneae	Euctenizidae	*Aptostichus stanfordianus* Smith, 1908	Adult/ Immature	Acroceridae	*Eulonchus smaragdinus* Gerstaecker	Schlinger 1987

Table 1.—Continued.

Host order	Host family	Arachnid host	Host stage	Fly family	Fly parasitoid/ parasite/predator	Reference
Araneae	Eutichuridae	*Cheiracanthium punctorium* (Villers, 1789)	Egg	Sarcophagidae	*Sarcophaga sexpunctata* (Fabricius)	Krehenwinkel et al. 2016
		Cheiracanthium sp.	Adult/ Immature	Acroceridae	*Ogcodes croucampi* Barraclough	Barraclough & Croucamp 1997
		Cheiracanthium sp.	Immature	Acroceridae	*Ogcodes* sp.	Schlinger 2003
Araneae	Gnaphosidae	*Herpyllus* sp.	Immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Schlinger 1960
		Zelotes sp.	Adult/ Immature	Acroceridae	*Acrocera melanderi* Cole	Schlinger 1987
		Zelotes sp.	Adult/ Immature	Acroceridae	*Ogcodes gibbosus* (Linnaeus)	Nielsen 1932
Araneae	Linyphiidae	*Hypselistes florens* (O. Pickard-Cambridge, 1875)	Egg	Ephydridae	*Trimerina madizans* (Fallen)	Wirth et al. 1987
		Pityohyphantes costatus (Hentz, 1850)	Egg	Phoridae	*Phalacrotophora epeirae* (Brues)	Manuel 1984
Araneae	Liphistiidae	*Liphistius lahu* Schwendinger, 1998	Adult/ Immature	Sarcophagidae	*Metopia sinensis* Pape	Schwendinger & Pape 2000
		Liphistius sp.	Adult	Sarcophagidae	*Metopia sinensis* Pape	Schwendinger & Pape 2000
Araneae	Lycosidae	*Alopecosa accentuata* (Latreille, 1817)	Adult/ Immature	Acroceridae	*Ogcodes pallipes* Latreille	Eason et al. 1967
		Alopecosa barbipes (Sundevall, 1833)	Adult	Acroceridae	*Ogcodes gibbosus* (Linnaeus)	Locket 1930
		Alopecosa barbipes	Adult/ Immature	Acroceridae	*Ogcodes pallipes* Latreille	Locket 1930
		Alopecosa kochi (Keyserling, 1877)	Immature	Acroceridae	*Ogcodes melampus* (Loew)	Schlinger 1960
		Geolycosa domifex (Hancock, 1899)	Adult/ Immature	Acroceridae	*Pterodontia flavipes* Gray	McQueen 1978, 1983
		Lycosa godeffroyi L. Koch, 1865	Immature	Acroceridae	*Ogcodes basalis* (Walker)	Humphreys 1976
		Lycosa godeffroyi	Immature	Acroceridae	*Pterodontia melli* Erichson	Humphreys 1976
		Pardosa alacris (C. L. Koch, 1833)	Adult	Acroceridae	*Ogcodes gibbosus* (Linnaeus)	Langer 2005
		Pardosa distincta (Blackwall, 1846)	Adult/ Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Sabrosky 1948
		Pardosa lapidicina Emerton, 1885	Adult/ Immature	Acroceridae	*Acrocera fasciata* Wiedemann	Eason 1966
		Pardosa lapidicina	Adult/ Immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Eason 1966
		Pardosa littoralis Banks, 1846	Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Kaston 1937
		Pardosa littoralis	Immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Kaston 1937
		Pardosa lugubris (Walckenaer, 1802)	Adult/ Immature	Acroceridae	*Ogcodes fumatus* (Erichson)	de Jong et al. 2000
		Pardosa milvina (Hentz, 1844)	Adult/ Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Eason et al. 1967
		Pardosa milvina	Immature	Acroceridae	Undetermined genus	Allard & Robertson 2003
		Pardosa prativaga (L. Koch, 1870)	Immature	Acroceridae	*Acrocera orbicula* (Fabricius)	Toft et al. 2012
		Pardosa pullata (Clerck, 1757)	Adult/ Immature	Acroceridae	*Ogcodes gibbosus* (Linnaeus)	Duffey 2000
		Pardosa pullata	Adult/ Immature	Acroceridae	*Ogcodes pallipes* Latreille	Schlinger 1987
		Pardosa pullata	Adult/ Immature	Acroceridae	*Ogcodes rufoabdominalis* Cole	Eason et al. 1967
		Pardosa saxatilis (Hentz, 1844)	Immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Kaston 1937

Table 1.—Continued.

Host order	Host family	Arachnid host	Host stage	Fly family	Fly parasitoid/ parasite/predator	Reference
Araneae	Lycosidae	*Pardosa sternalis* (Thorell, 1877)	Adult/ Immature	Acroceridae	*Acrocera convexa* Cole	Schlinger 1987
		Pardosa sternalis	Immature	Acroceridae	*Ogcodes adaptatus* Schlinger	Schlinger 1960
		Pardosa sternalis	Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Schlinger 1960
		Pardosa sternalis	Adult/ Immature	Acroceridae	*Pterodontia misella* Osten Sacken	Schlinger 1987
		Pardosa tuoba Chamberlin, 1919	Adult/ Immature	Acroceridae	*Ogcodes adaptatus* Schlinger	Schlinger 1987
		Pardosa utahensis Chamberlin, 1919	Adult/ Immature	Acroceridae	*Ogcodes rufoabdominalis* Cole	Capelle 1966
		Pardosa vancouveri Emerton, 1917	Adult/ Immature	Acroceridae	*Acrocera convexa* Cole	Schlinger 1987
		Pirata sedentarius Montgomery, 1904	Adult/ Immature	Acroceridae	*Ogcodes dispar* (Macquart)	Eason et al. 1967
		Schizocosa crassipes (Walckenaer, 1837)	Adult/ Immature	Acroceridae	*Acrocera fasciata* Wiedemann	Montgomery 1903, Johnson 1915
		Schizocosa ocreata (Hentz, 1844)	Adult/ Immature	Acroceridae	*Acrocera fasciata* Wiedemann	Montgomery 1903, Johnson 1915
		Schizocosa rovneri Uetz & Dondale, 1979	Adult/ Immature	Acroceridae	*Ogcodes borealis* Cole	Cady et al. 1993
		Schizocosa rovneri	Adult/ Immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Cady et al. 1993
		Tigrosa helluo (Walckenaer, 1837)	Adult/ Immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Eason et al. 1967
		Trochosa hispanica Simon, 1870	Adult/ Immature	Acroceridae	*Ogcodes lautereri* Chvala	Canzoneri & Hansen 1996
		Trochosa terricola Thorell, 1856	Adult/ Immature	Acroceridae	*Pterodontia flavipes* Gray	King 1916
Araneae	Migidae	*Moggridgea crudeni* Hewitt, 1913	Adult/ Immature	Acroceridae	*Astomella capensis* Schlinger	Barraclough 1984
Araneae	Mimetidae	*Mimetus notius* Chamberlin, 1923	Egg	Phoridae	*Phalacrotophora epeirae* (Brues)	Guarisco 2001
Araneae	Miturgidae	*Griswoldia* sp.	Immature	Acroceridae	*Thyllis crassa* (Fabricius)	Schlinger 1987
		Griswoldia sp.	Adult/ Immature	Acroceridae	*Thyllis* sp.	Schlinger 2003
Araneae	Nephilidae	*Nephila clavipes* (Linnaeus, 1767)	Egg	Chloropidae	*Pseudogaurax higginsi* Sabrosky	Barnes et al. 1992
		Nephila clavipes	Egg	Chloropidae	*Pseudogaurax mexoculatus* Sabrosky	Barnes et al. 1992
		Nephila inaurata (Vinson, 1863)	Egg	Chloropidae	*Pseudogaurax coyleae* Cogan	Cogan 1977
		Nephila pilipes (Fabricius, 1793)	Egg	Chloropidae	*Pseudogaurax seguyi* (Sabrosky)	Sabrosky 1990
Araneae	Oecobiidae	*Uroctea limbata* (C. L. Koch, 1843)	Egg	Bombyliidae	*Petrorossia feti* Zaitsev & Charykuliev	Zaitzev & Charykuliev 1981
Araneae	Oxyopidae	*Oxyopes lineatus* Latreille, 1806	Adult/ Immature	Acroceridae	*Ogcodes fumatus* (Erichson)	Schlinger 1987
		Oxyopes salticus Hentz, 1845	Adult/ Immature	Acroceridae	*Ogcodes dispar* (Macquart)	Eason et al. 1967
		Oxyopes salticus	Adult/ Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Eason et al. 1967
Araneae	Philodromidae	*Philodromus aureolus* (Clerck, 1757)	Egg	Sarcophagidae	*Sarcophaga sexpunctata* (Fabricius)	Auten 1925

Table 1.—Continued.

Host order	Host family	Arachnid host	Host stage	Fly family	Fly parasitoid/ parasite/predator	Reference
Araneae	Philodromidae	*Philodromus cespitum* (Walckenaer, 1802)	Immature	Acroceridae	*Ogcodes fumatus* (Erichson)	Kehlmaier et al. 2012
		Philodromus cespitum	Egg	Chloropidae	*Oscinella halterata* (Lamb)	Auten 1925
		Philodromus cespitum	Egg	Sarcophagidae	*Sarcophaga sexpunctata* (Fabricius)	Auten 1925
		Philodromus sp.	Immature	Acroceridae	*Ogcodes adaptatus* Schlinger	Schlinger 1960
Araneae	Phyxelididae	*Ambohima sublima* Griswold, 1990	Immature	Acroceridae	*Thyllis* sp.	Schlinger 2003
Araneae	Plectreuridae	*Kibramoa* sp.	Adult/ Immature	Acroceridae	*Acrocera arizonensis* Cole	Schlinger 1987
Araneae	Salticidae	*Aelurillus v-insignitus* (Clerck, 1757)	Adult	Acroceridae	*Ogcodes pallipes* Latreille	Millot 1938
		Aelurillus v-insignitus (Clerck)	Adult/ Immature	Acroceridae	*Ogcodes varius* Latreille	Séguy 1926
		Cobanus sp.	Adult/ Immature	Acroceridae	*Terphis* sp.	Schlinger 1987
		Cosmophasis bitaeniata (Keyserling, 1882)	Adult/ Immature	Acroceridae	*Ogcodes basalis* (Walker)	Schlinger 1987
		Cosmophasis bitaeniata	Adult/ Immature	Acroceridae	*Ogcodes doddi* Wandolleck	Wandolleck 1906, Dodd 1906
		Eris militaris (Hentz, 1845)	Immature	Acroceridae	*Acrocera* sp.	Larrivée & Borkent 2009
		Evarcha jucunda (Lucas, 1846)	Immature	Acroceridae	*Ogcodes reginae* Trojan	Kehlmaier & Almeida 2014
		Habronattus hallani (Richman, 1973)	Adult/ Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Schlinger 1987
		Heliophanus sp.	Immature	Acroceridae	*Ogcodes pallipes* Latreille	Millot 1938
		Heliophanus sp.	Immature	Acroceridae	*Ogcodes zonatus* Erichson	Millot 1938
		Lyssomaninae gen. sp.	Adult/ Immature	Acroceridae	*Ogcodes guttatus* (Costa)	Schlinger 1987
		Metaphidippus manni (Peckham & Peckham, 1901	Adult/ Immature	Acroceridae	*Pterodontia vix* Townsend	Schlinger 1987
		Metaphidippus sp.	Adult/ Immature	Acroceridae	*Acrocera bulla* Westwood	Schlinger 1987
		Metaphidippus sp.	Adult/ Immature	Acroceridae	*Ogcodes boharti* Schlinger	Schlinger 1987
		Pelegrina aeneola (Curtis, 1892)	Adult/ Immature	Acroceridae	*Acrocera bulla* Westwood	Beckwith et al. 1987
		Pelegrina aeneola	Adult/ Immature	Acroceridae	*Ogcodes boharti* Schlinger	Beckwith et al. 1987
		Pelegrina aeneola	Adult/ Immature	Acroceridae	*Ogcodes borealis* Cole	Schlinger 1987
		Pelegrina proterva (Walckenaer, 1837)	Immature	Acroceridae	*Ogcodes eugonatus* Loew	Larrivée & Borkent 2009
		Pelegrina proterva	Immature	Acroceridae	*Ogcodes melampus* Loew	Larrivée & Borkent 2009
		Phidippus ardens Peckham & Peckham, 1901	Adult/ Immature	Acroceridae	*Ogcodes boharti* Schlinger	Schlinger 1987
		Phidippus audax (Hentz, 1845)	Egg	Phoridae	*Phalacrotophora epeirae* (Brues)	Jones 1940
		Phidippus comatus Peckham & Peckham, 1901	Adult/ Immature	Acroceridae	*Ogcodes boharti* Schlinger	Schlinger 1987

Table 1.—Continued.

Host order	Host family	Arachnid host	Host stage	Fly family	Fly parasitoid/ parasite/predator	Reference
Araneae	Salticidae	*Phidippus johnsoni* (Peckham & Peckham, 1883)	Adult/ Immature	Acroceridae	*Ogcodes adaptatus* Schlinger	Schlinger 1987
		Phidippus johnsoni	Adult/ Immature	Acroceridae	*Ogcodes boharti* Schlinger	Schlinger 1987
		Phidippus johnsoni	Adult/ Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Schlinger 1987
		Phidippus octopunctatus (Peckham & Peckham, 1883)	Egg	Sarcophagidae	*Sarcophaga davidsonii* Coquillett	Coquillet 1892; Davidson 1896
		Phidippus princeps (Peckham & Peckham, 1883)	Adult/ Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Schlinger 1987
		Phidippus regius C. L. Koch, 1846	Egg	Phoridae	*Phalacrotophora epeirae* (Brues)	Manuel 1984
		Phidippus rimator nom. dub. (Walckenaer, 1837)	Adult/ Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Schlinger 1987
		Phidippus sp.	Adult/ Immature	Acroceridae	*Acrocera* sp.	Schlinger 1987
		Phlegra fasciata (Hahn, 1826)	Immature	Acroceridae	*Ogcodes pallipes* Latreille	Millot 1938
		Sassacus sp.	Adult/ Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Schlinger 1987
		Sidusa sp.	Adult/ Immature	Acroceridae	*Terphis* sp.	Schlinger 2003
Araneae	Segestriidae	*Ariadna maxima* (Nicolet, 1849)	Adult/ Immature	Acroceridae	*Carvalhoa appendiculata* Philippi	Schlinger 1987
Araneae	Tetragnathidae	*Meta menardi* (Latreille, 1804)	Egg	Phoridae	*Megaselia melanocephala* (Roser)	Decou-Burghele 1961
		Tetragnatha sp.	Egg	Chloropidae	*Pseudogaurax silbergliedi* Sabrosky	Sabrosky 1990
		Tetragnatha sp.	Egg	Chloropidae	*Siphonella* sp.	Kintner 1935
Araneae	Theraphosidae	*Acanthoscurria sternalis* Pocock, 1903	Immature	Acroceridae	*Exetasis jujuyensis* Gillung	Barneche et al. 2013
		Aphonopelma duplex (Chamberlin, 1925)	Adult/ Immature	Acroceridae	*Ocnaea* sp.	Alagon & Odell 2004
		Aphonopelma hentzi (Girard, 1852)	Adult/ Immature	Acroceridae	*Lasia purpurata* Bequaert	Baerg 1958; Eason et al. 1967
		Aphonopelma sp.	Adult/ Immature	Acroceridae	*Ocnaea* sp.	Schlinger 1987
		Chaetopelma sp.	Adult/ Immature	Acroceridae	*Astomella gravis* Erichson	Schlinger 1987
		Grammostola actaeon (Pocock, 1903)	Adult	Acroceridae	*Exetasis* sp.	Vellard 1934
		Lasiodora klugi (C. L. Koch, 1841)	Immature	Acroceridae	*Exetasis eickstedtae* Schlinger	Eickstedt 1971; Schlinger 1972
		Phrixotrichus scrofa (Molina, 1788)	Immature	Acroceridae	*Arrhynchus maculatus* Schlinger	Schlinger 1968
Araneae	Theridiidae	*Enoplognatha ovata* (Clerck, 1757)	Adult/ Immature	Acroceridae	*Ogcodes gibbosus* (Linnaeus)	Pichka 1977
		Enoplognatha sp.	Egg	Phoridae	*Megaselia tenebricola* Schmitz	Evans 1969
		Enoplognatha sp. or *Robertus* sp.	Egg	Phoridae	*Megaselia angusta* Wood	Disney & Evans 1980; Disney 1999
		Enoplognatha sp. or *Robertus* sp.	Egg	Phoridae	*Megaselia longifurca* (Lundbeck)	Disney & Evans 1980; Disney 1999

Table 1.—Continued.

Host order	Host family	Arachnid host	Host stage	Fly family	Fly parasitoid/ parasite/predator	Reference
Araneae	Theridiidae	*Latrodectus geometricus* C.L. Koch, 1841	Egg	Chloropidae	*Pseudogaurax signatus* (Loew)	Vetter et al. 2012
		Latrodectus hesperus Chamberlin & Ivie, 1935	Egg	Chloropidae	*Pseudogaurax signatus* (Loew)	Vetter et al. 2012
		Latrodectus mactans (Fabricius, 1775)	Egg	Phoridae	*Apocephalus borealis* Brues	Disney 1994
		Latrodectus mactans	Egg	Chloropidae	*Pseudogaurax signatus* (Loew)	Davidson 1896
		Latrodectus mactans	Egg	Chloropidae	*Pseudogaurax* sp.	Baerg 1959
		Parasteatoda tepidariorum (L. Koch, 1841)	Egg	Chloropidae	*Pseudogaurax signatus* (Loew)	Kaston & Jenks 1937
		Robertus sp.	Egg	Phoridae	*Megaselia tenebricola* Schmitz	Disney & Evans 1980
		Steatoda palomara Chamberlin & Ivie, 1935	Immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Schlinger 1960
Araneae	Thomisidae	*Diaea* sp.	Adult/ Immature	Acroceridae	*Ogcodes nitens* (Hutton)	Schlinger 1987
		Mecaphesa sp.	Immature	Acroceridae	*Ogcodes eugonatus* Loew	Cokendolpher et al. 1979
		Misumena vatia (Clerck, 1757)	Adult/ Immature	Acroceridae	*Ogcodes fumatus* (Erichson)	de Jong et al. 2000
		Thomisus onustus (Walckenaer, 1806)	Adult/ Immature	Acroceridae	*Ogcodes fumatus* (Erichson)	de Jong et al. 2000
		Xysticus cunctator Thorell, 1877	Immature	Acroceridae	*Ogcodes adaptatus* Schlinger	Schlinger 1960
		Xysticus cunctator	Immature	Acroceridae	*Ogcodes melampus* (Loew)	Schlinger 1960
		Xysticus luctuosus (Blackwall, 1836)	Adult/ Immature	Acroceridae	*Ogcodes pallipes* Latreille	Trojan 1956
		Xysticus montanensis Keyserling1887	Immature	Acroceridae	*Ogcodes borealis* Cole	Schlinger 1960
		Xysticus montanensis	Immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Schlinger 1960
		Xysticus sp.	Adult/ Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Schlinger 1987
		Undetermined genus	Egg	Drosophilidae	*Scaptomyza (Titanochaeta)* 11 spp.	Wirth 1952; Hardy 1965; Lapoint et al. 2013
Araneae	Trachelidae	*Trachelas mexicanus* Banks, 1898	Adult/ Immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Schlinger 1987
Araneae	Unknown	Undetermined genus	Egg	Phoridae	*Megaselia oviaraneae* Disney	Disney 1999
Scorpiones	Buthidae	*Centruroides margaritatus* (Gervais, 1841)	Adult/ Immature	Sarcophagidae	*Sarcodexia sternodontis* Townsend	Townsend 1893
		Mesobuthus martensii (Karsch, 1879)	Adult/ Immature	Sarcophagidae	*Sarcophaga dux* Thomson	Shi et al. 2015
Scorpiones	Vaejovidae	*Anuroctonus phaiodactylus* (Wood, 1863)	Adult	Tachinidae	*Spilochaetosoma californicum* Smith	Williams et al. 1994
		Vaejovis spinigerus (Wood, 1863)	Adult/ Immature	Tachinidae	*Spilochaetosoma californicum* Smith	Williams et al. 1994
Trombidiformes	Anystidae	Undetermined genus	Adult/ Immature	Acroceridae	Undetermined genus	Kerr & Winterton 2008
Trombidiformes	Erythraeidae	*Abrolophus* sp.	Adult/ Immature	Acroceridae	*Pterodontia flavipes* Gray	Sferra 1986
Trombidiformes	Trombidiidae	*Podothrombium* sp.	Adult/ Immature	Acroceridae	*Pterodontia flavipes* Gray	Sferra 1986

and deeper investigation is needed in order to verify whether the species in question are predators, parasitoids, or both.

In general, there is still much to be learned about the interactions between Diptera and the arachnids they attack. Many more large rearing studies of spiders and other arachnids would be the best approach to fill this gap in knowledge, as the majority of reports of natural enemies are the result of individual incidental rearings. Unfortunately, there are still large numbers of arachnid species that we know almost nothing about in terms of their habits, habitats, mating behavior and natural enemies. This lack of basic natural history information seriously limits the ability of arachnologists and dipterists to address these issues, though this problem is not limited to these groups or questions (Tewksbury et al. 2014; Barrows et al 2016). It is imperative that we as biologists spend time observing our chosen study organisms in their natural environment, if we are to have any hope of both discovering and understanding the ecological web of organisms that covers our planet.

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