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REVIEW

Parasites of spiders: Their impacts on host behavior and ecology

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Abstract. Parasites are some of the most abundant, diverse, and ecologically important organisms on the planet. Similarly, spiders are diverse, abundant, and play important roles in many terrestrial ecosystems. It is unfortunate that our understanding of the parasites that affect spiders is so underdeveloped relative to similar fields (e.g., parasites of insects). With this review, we describe characteristics of the major groups known to parasitize spiders and illustrate the ways in which spider biology presents unique challenges and opportunities for their parasites. Particularly promising avenues of future research include testing how parasites alter their spider hosts' behavior and ecology through density-dependent and trait-mediated effects. We close by providing future directions and testable hypotheses at the forefront of spider-parasite research.

Key words: Araneae, disease, infection, araneopathogen, host behavior

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The most frequent species interactions in which any animal engages are undoubtedly interactions with parasites. Parasitism is argued to be the most common lifestyle on earth (Windsor 1998; Sorci & Garnier 2018), and animals are constantly bombarded by microparasites (i.e., parasites that "multiply" in their hosts) and macroparasites (i.e., parasites that do not "multiply" in their hosts) (Lafferty et al. 2006). These interactions may be short-lived and relatively inconsequential, whereas others represent lifelong relationships with important effects on hosts' traits and ecology. Spiders remain disappointingly overlooked in parasite ecology research, despite their global abundance and boundless utility as models for studies in behavior and ecology (Wise 1993). Although there have been areas of detailed research (e.g., mermithid worms infecting spiders; Poinar 1987), there remains to be a comprehensive overview of the parasite groups most likely to affect spider populations and a framework for how parasites alter the role spiders play in ecological communities.

In this review, we present a history of research into spider-parasite interactions, attempt to synthesize this growing field, and present a framework for future experiments. We aim to (1) review the major groups known to parasitize spiders (see Fig. 1), (2) describe how spider biology presents unique challenges and opportunities for their parasites, (3) describe how parasites alter spider ecology through density- and trait-mediated effects, and (4) provide testable hypotheses that should be at the forefront of future studies using spiders and their parasites as test systems.

MAJOR GROUPS THAT PARASITIZE SPIDERS

We use the term parasite to include both macroparasites (e.g., nematodes and arthropods) and microparasites (e.g., bacteria, fungi, viruses, and protists). Here, we define parasites as organisms that extract nutrients from a living host and exert negative effects on host performance or fecundity. Although there are detailed criteria for how trophic relationships define parasitic lifestyles (Lafferty & Kuris 2002), we use a broader definition of parasitism since the study of spider parasites is still growing. We use the terms "araneopathogen" and "araneopathogenic" to refer to and describe parasites that cause pathology in spiders (i.e., Araneae). We do not include beneficial or neutral relationships between spiders and species from these taxonomic groups, though information regarding, for example, interactions between beneficial bacteria and spiders can be co-opted to better understand pathogenic bacteria. The following subsections cover the biology and pathology of the parasite, observed symptoms in the host, and some example relationships (Fig. 2). Some of these parasite groups are better characterized in other arthropod hosts, and we apply this information to fill in the knowledge gaps about spider parasites. We invite readers to see our list of reported spider-host and parasite (bacteria, virus, Acari and nematode) infections on our online Spider Parasite Digital Research (SPDR) Collection (https://www.keiserlab.com/spdr-literature-database).

Araneopathogenic fungi.—Parasitic fungi are perhaps the hallmark of arthropod parasites because infections by fungi are often readily identifiable post-mortem and widespread across the world (Fig. 1A,B). Parasitic fungi represent the best-studied group of spider-associated pathogens, often described as araneogenous or araneopathogenic (Evans & Samson 1987), arachnophilic (Rong & Grobbelaar 1998), and arachnogenous (Kubátová 2004). Here, we propose that the term araneopathogenic be used singularly in future studies. Although fungal parasites of spiders are relatively well documented, the field remains vastly understudied compared to entomopathogenic (i.e., insect) fungi. Most research focuses on morphological descriptions and phylogenetic relationships of araneopathogenic fungi. Evans & Samson (1987) were the first to identify the need for studying the interaction between

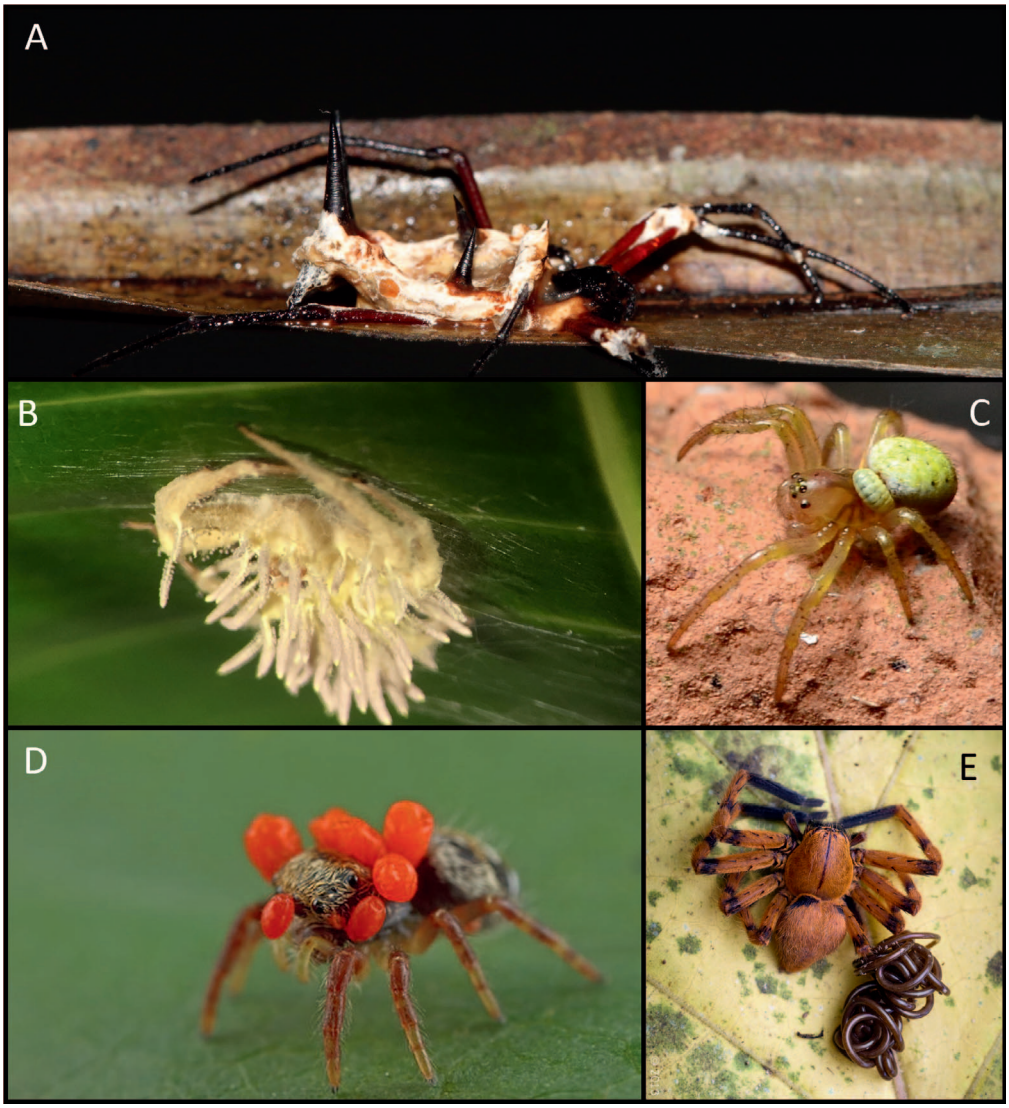

Figure 1.—Major groups that parasitize spiders. (A) Araneopathogenic fungus. In some cases, features of the host can be identified post-mortem, like the abdominal spines on this *Micrathena* in Brazil. Photo by João Araújo. (B) *Gibellula* sp. fungus emerging from a *Lyssomanes viridis* (Salticidae). Found on the underside of a leaf in Gainesville, FL. USA. Photo by Nick Keiser. (C) Ectoparasitoid insect larva attached to the abdomen of its host. Photo by Tone Killick. (D) Ectoparasitic Parasitigone mites on a juvenile salticid spider. Photo by Weng Keong Liew. (E) Mermithid worm recently emerged from an *Olios* (Sparassidae) in Belize. Photo by Thomas Shahan.

araneopathogenic fungi and their spider hosts, noting the global distribution of araneopathogenic fungi.

Two comprehensive reviews on fungal pathogens in spiders have recently been published: Evans (2013) and Shrestha et al. (2019). Evans (2013), notably, begins by announcing the dearth of information available to researchers and describes findings since the original fungal parasites of spiders review (Evans & Samson 1987). Shrestha et al. (2019) update findings since Evans (2013) and comprehensively lists all currently known species of araneopathogenic fungi, spider host species, and habitats in which they have been found.

Araneopathogenic fungi appear distinct from entomopathogenic fungi, with Evans (2013) suggesting a fungal clade specializing in spider hosts based on the phylogeny from Johnson et al. (2009). Shrestha et al. (2019) do not explicitly suggest a clade exclusive to araneopathogenic fungi, but implied some segregation between fungal araneopathogens and entomopathogens. There is certainly some overlap between these groups, where common entomopathogens have been found on spiders. For example, labouls (Laboulbeniales) are an order of fungi that contain many obligately parasitic species that infect mainly beetles but have been found on dwarf spiders (Linyphiidae; Noordam et al. 1998). These are non-lethal fungi but could potentially impose negative impacts to hosts by penetrating the integument and consuming hemolymph as they do in insects (Blackwell et al. 2020). There are at least 86 currently described species of araneopathogenic fungi from 16 genera belonging to the single order Hypocreales (Ascomycota). Four of these genera (*Akanthomyces, Gibellula, Hevansia, and Torrubiella*) are dominated by or exclusively obligate spider pathogens (Shrestha et al. 2019). Fungi from these four genera are known to parasitize spiders

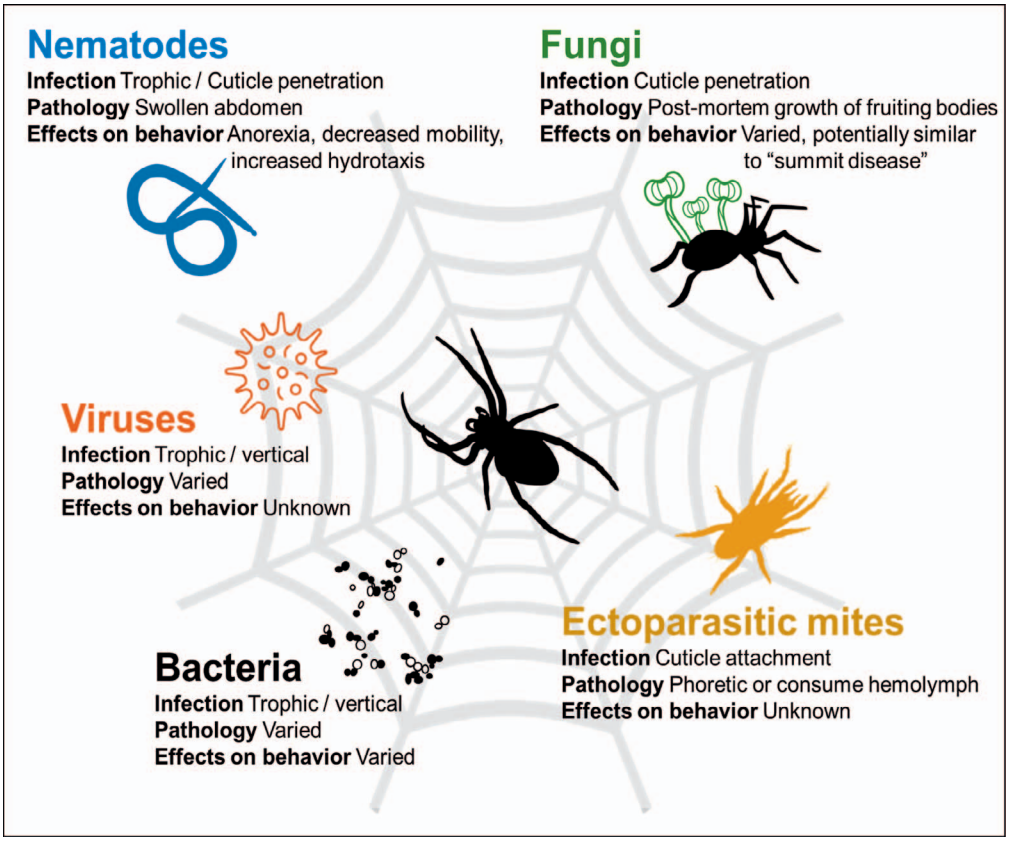

Figure 2.—Schematic description of the known routes of infection, pathology, and effects on behavior for the major groups of spider parasites. This information is not exhaustive, as there are likely many routes of infection, pathology, and effects on behavior that remain currently untested. All images sourced from The Noun Project (online at https://thenounproject.com/) and Phylopic (online at https://phylopic.org).

from 15 different families (Shrestha et al. 2019), although this is almost certainly an underestimation. Until recently, the vast majority of araneopathogenic fungi were found in the subtropics and tropics (Evans 2013; Shrestha et al. 2019) but this is likely due to lack of research in temperate zones. Infected spiders have indeed been found in the Pacific Northwest forests of the United States (Poinar 2019) and approaching the southern polar region on the summit of West French Peak, Falkland Islands (O'Donnell et al. 1977). This demonstrates the potential for araneopathogenic fungi to have greater representation outside the tropics than previously known. To avoid redundancy from recent reviews of this subject (i.e., Evans 2013; Shrestha et al. 2019), we focus on the four genera dominated by araneopathogens.

The four main genera of araneopathogenic fungi are part of Cordycipitaceae (Kepler et al. 2017) infecting a diversity of spider hosts across the globe, though concentrated in the tropics. *Akanthomyces* contains 10 species of araneopathogenic fungi whose infections are characterized as white to flesh-colored mycelium with stalks covered in laterally oriented spore-bearing structures (Evans 2013; Shrestha et al. 2019). Species in this genus are rarely found growing on non-spider hosts but have been found parasitizing moths (Sung et al. 2007; Aini et al. 2020). *Gibellula* is exclusively araneopathogenic and is likely the most commonly found fungal parasite of spiders. The genus has a global, mostly tropical, distribution (Samson & Evans 1992; Rong & Botha 1993). This highly conserved, exclusively araneopathogenic genus is characterized by large, often brightly colored stalks (Evans 2013). *Gibellula* has 17 described species, with several having been synonymized with or transferred from other species (Shrestha et al. 2019). *Granulomanus* is a synanamorph associated with *Gibellula* where it grows on or replaces *Gibellula* sporulating structures (Evans & Samson 1987; Evans 2013). *Hevansia* is an exclusively spider-pathogenic genus that contains eight species (Shrestha et al. 2019) named after Harry Evans, a plant pathologist who made seminal advancements to the field of araneopathogenic fungi (Evans 2013). This genus was recently split from *Gibellula* and is morphologically similar to both *Gibellua* in its sexual morph and *Akanthomyces* in its asexual morph (Kepler et al. 2017). *Torrubiella* is a large sexual polyphyletic genus across three families in Hypocreales (Shrestha et al. 2019). *Torrubiella*-like sexual morphs are associated with several other genera in Hypocreales (*Akanthomyces, Gibellula, Hevansia, Lecanicillium*, etc.) with 26 araneopathogenic species awaiting phylogenetic revision (Johnson et al. 2009; Kepler et al. 2017; Shrestha et al. 2019). Morphological similarities of the fruiting bodies between *Torrubiella* and *Akanthomyces* may suggest reclassification that encompasses *Torrubiella* into *Akanthomyces* (Kepler et al. 2017).

Fungi that parasitize arthropods have a similar general life cycle as the typical saprophytic fungus, with some key differences. Similarities include: (1) sexual and asexual

reproduction which releases spores that undergo germination (Watkinson et al. 2015); (2) mycelium growth, or root-like structures that make up the main body of the fungus; and (3) fruiting body development from mycelial growth that generates more spores (Watkinson et al. 2015). Unique characteristics of araneopathogenic fungi include: (1) spores adhere to the surface of their host's integument; (2) mycelia penetrate the integument by growing appressoria, which are single flattened hyphal cells using immense turgor pressure to enter their host (Howard et al. 1991; Shang et al. 2015); (3) once inside the host, parasitic fungi switch to a single-celled phenotype that allows for rapid propagation in the haemocoel (Shang et al. 2015). Although there are interesting exceptions in insects (Lovett et al. 2020a), an infecting fungus kills the host and then reproduces asexually by formation of conidia, or sexually by producing fruiting bodies (Shang et al. 2015). It has been suggested that spiders living near plants and decaying plant matter are at the greatest risk of infection by araneopathogenic fungi (Shrestha et al. 2019). Infected cadavers are also often discovered in caves (Keiser, Macias, Lovett, and Kasson unpublished data) and cellar spider cadavers infected with *Lecanicillium aranearum* (formerly *Engyodontium aranearum*; Zare & Gams 2001) are commonly found in basements. Therefore, like entomopathogenic fungi, araneopathogens may be most prevalent in damp habitats with the humidity necessary for sporulation.

As Evans (2013) points out, descriptions of araneopathogenic fungi are routinely published in mycology journals that usually do not reach arachnologist readers. As methods of host and fungal identification improve, it is imperative to identify and investigate host-parasite dynamics given the critical position spiders occupy in global ecosystems. Spider hosts are often difficult to identify due to identifying features covered in hyphae or conidia. However, Costa (2014) developed a method of cutting through the leaf substrate on which spiders are found to identify the host via epigynal structures. In order to properly understand the dynamics of araneopathogenic fungi and their spider hosts, more collaboration is required between arachnologists and mycologists to investigate this field with the same vigor as their entomological colleagues.

Araneopathogenic bacteria.—Unlike the araneopathogenic fungi described above, bacteria are unable to penetrate through the host integument and must enter via a pre-existing orifice (e.g., the oral cavity, genital openings, trachea, or punctures/abrasions in the cuticle; Ortiz-Urquiza & Keyhani 2013). Unfortunately, there are very few descriptions of bacterial infections in spiders. The symptoms of bacterial infections are not apparent and are, therefore, unlikely to be noticed or investigated. Those who most often interact with and observe spiders (e.g., researchers and hobbyists) may simply discard the cadavers upon discovery, the cause of death remaining unknown. Given the activity of the spider immune system, bacterial colonization is either cleared by haemocytes (see *Immune system* section below) or results in fatal sepsis. Here, we describe some notable studies on araneopathogenic bacteria and make some predictions given our understanding of entomopathogenic bacteria.

The genus *Pseudomonas* contains many cosmopolitan, generalist facultative pathogens that have been used in experimental studies with spider hosts. For example, *P. syringae*, a generalist pathogen of many plants and arthropods, reduces cold tolerance and subsequent survival in common house spiders, *Parasteatoda tepidariorum* (CL Koch, 1841), after consuming infected prey (Tanaka & Watanabe 2003). Wolf spiders (*Schizocosa ocreata* (Hentz, 1844)) have been experimentally infected with *P. aeruginosa* via ingestion of contaminated water, after which active bacteria were recovered in the hemolymph for up to five hours (Gilbert et al. 2016). Further studies are needed to investigate under what circumstances ingestion of bacteria via prey items is interrupted by antibacterial properties in venom (see the *Feeding physiology* section).

Some cuticular bacteria induce weight loss, mortality, and changes to host behavior when re-applied in large quantities, as has been shown in the grass spider *Agelenopsis pennsylvanica* (CL Koch, 1843) (Parks et al. 2018) and the social spider *Stegodyphus dumicola* Pocock, 1898 (Keiser et al. 2016b). It is unlikely that exposure to cuticular bacteria alone can induce these changes, but none of these studies identified the route by which bacteria enter the host body after a topical application. Spicer et al. (2019) applied a cocktail of cuticular bacteria onto *A. pennsylvanica* sex organs, and found that females who mated with males whose pedipalps were exposed to bacteria experienced reduced survivorship compared to females who had bacteria injected directly into the epigynum. Thus, the epigynum may not represent a potential route for the acquisition of environmental microbes but transfer from male intromittent organs (the embolus) warrants further study.

Rickettsia bacteria are obligate intracellular parasites and have been identified in multiple spider species (Haupt 2000; Vanthournout & Hendrickx 2015; Ceccarelli et al. 2016; White et al. 2020). Although the route of transmission was not identified, Haupt (2000) has described a rickettsial infection in the hepatopancreas of East Asian trapdoor spiders. The bacteria consume a large proportion of the spider's resources which inhibits molting. The spider's opisthosoma can appear swollen and white in color late in infection. Eventually, the spider dies, and when the opisthosoma decomposes, the bacteria are introduced back into the soil (Haupt 2000).

Just like many other arthropods, spiders possess a number of endosymbiotic bacteria belonging to multiple genera, including *Arsenophonus*, *Cardinium, Rhabdochlamydia, Rickettsia*, *Rickettsiela*, *Spiroplasma*, and *Wolbachia* (Wang et al. 2010; Goodacre 2011; Vanthournout & Hendrickx 2015; Ceccarelli et al. 2016; White et al. 2020). The functional relationships between endosymbiont and host can range from beneficial to detrimental and can change in different contexts (e.g., presence or absence of other endosymbionts). Co-infections within individual spiders are common; up to five different endosymbiotic bacteria have been found in an individual (Vanthournout & Hendrickx 2015; White et al. 2020). We will not thoroughly review endosymbiotic bacteria here because these endosymbionts have subtle but important differences compared to pathogenic bacteria. Endosymbiont infection does not induce temporary or fatal pathology but rather induces permanent changes to host life history traits, which typically promote the maintenance and spread of the bacteria. Endosymbiotic bacteria are often intracellular and vertically-transmitted (Engelstädter & Hurst 2009). However,

there is some evidence to suggest *Wolbachia* may be horizontally transmitted between closely-related funnel-web spider species (*Agelenopsis* spp. Giebel, 1869; Baldo et al. 2008). Generally, endosymbionts are poorly characterized in spiders, but there is recent work characterizing the endosymbionts of *Mermessus fradeorum* (Berland, 1932) (Linyphiidae). Their *Rickettsiella* endosymbiont causes cytoplasmic incompatibility, in which crosses between uninfected females and infected males causes offspring mortality (Engelstädter & Hurst 2009). *Wolbachia* is reported to skew the sex ratio of *Oedothorax gibbosus* (Blackwall, 1841) (Linyphiidae) clutches towards predominantly female (Vanthournout & Swaegers 2011). Future studies should follow discoveries made in insect study systems, such as their impacts on the ecology and evolution of host populations and how they might alter hosts' interactions with other parasites. For example, the facultatively endosymbiotic bacteria *Hamiltonella defensa* confers protection against some parasitoids (McLean & Godfray 2015).

Araneopathogenic viruses.—Despite the global ubiquity of viruses, very few studies describe the biology and pathology of araneopathogenic viruses. However, a combination of surveys and experiments have demonstrated that araneopathogenic viruses exhibit multiple modes of infection and diverse effects on hosts. Here, we describe surveys and more detailed studies on the interactions between viruses and their spider hosts, including studies which were unsuccessful at experimentally infecting spiders with viruses.

Invertebrates are host to a great diversity of RNA viruses, and the discovery of these viruses has shed massive light on their evolutionary history (Shi et al. 2016). Li et al. (2015) conducted a large survey of arthropods in search of negative-sense RNA viruses and identified seven negative-sense single-stranded RNA viruses in five spider host species. Debat (2017) detected RNA viruses in the whole body, the brain, venom glands and silk glands of the golden silk orb weaver, *Trichonephila clavipes* (Linnaeus, 1767).

In another survey, Rosario et al. (2018) found 14 species of spider belonging to 9 families (Agelenidea, Araneidae, Cybaeidae, Dysderidae, Linyphiidae, Pimoidae, Segestriidae, Tetragnathidae and Theridiidae) infected with a diversity of circular Rep-encoding single-stranded (CRESS) DNA viruses. Circular virus 1, 2, and 3 were the most commonly identified viruses in the surveyed spiders. Rosario et al. (2019) found SpOrbCV-1 in all life stages of spinybacked orb weavers, *Gasteracantha cancriformis* (Linnaeus, 1758). The high prevalence of this virus in all spider life stages suggests SpOrbCV-1 is vertically transmitted, which is the first evidence for a potential vertically-transmitted virus in spiders (Rosario et al. 2019). SpOrbCV-2 was also identified in spinybacked orb weavers but at a much lower prevalence and only in adults (Rosario et al. 2019). SpOrbCV-2 was present in multiple spider species in the survey of Rosario et al. (2019) and was previously identified in dragonflies (Rosario et al. 2012). For these reasons, Rosario et al. (2019) hypothesize that SpOrbCV-2 accumulates in spiders via ingestion of infected insect prey. These studies demonstrate that two closely related viruses can exhibit very different modes of infection.

Baculoviruses (family Baculoviridae) are a diverse group of DNA viruses that infect a wide range of invertebrates and are commonly used as insect-control agents. Morel (1978) described a fatal baculovirus infection of the hepatopancreas in a nursery web spider (*Pisaura mirabilis* (Clerck, 1757)) but provided no information on symptoms or pathology (Morel 1978; Lewbart 2011). Kring et al. (1988) fed velvetbean caterpillars, *Anticarsia gemmatalis*, infected with nuclear polyhedrosis virus, another baculovirus, to striped lynx spiders, *Oxyopes salticus* Hentz, 1845. Active virus was successfully collected from spider excreta, suggesting lynx spiders could spread the virus in the environment (Kring et al. 1988). Importantly, this study revealed that active polyhedrosis virus could traverse the digestive tract of spiders.

Chilo iridescent virus (family Iridoviridae) is a DNA virus that exhibits a host range of over 100 insects (Ohba & Aizawa 1979). Ohba & Aizawa (1979) attempted to infect a huntsman spider (*Heteropoda venatoria* (Linnaeus, 1767)) with this virus via injection, but the infection failed. It should be noted that this study attempted the infection of only a single juvenile spider (Ohba & Aizawa 1979); thus, whether spiders are hosts to this virus remains largely unknown. Strickman et al. (1997) sought to determine whether pholcid spiders (*Crossopriza lyoni* (Blackwall, 1867)) became infected with Dengue virus after consuming experimentally-infected mosquitoes. Spiders were later tested for Dengue virus using ELISA tests, but all were negative (Strickman et al. 1997). Overall, these studies have shed some light on the diversity of viruses infecting spiders. Further experimental studies are needed to identify how araneopathogenic viruses are transmitted, how they may affect the prey and predators of spiders and the degree to which spider viruses contribute to the origins and diversity of the arthropod virosphere (Li et al. 2015).

Araneoparasitic nematodes.—The vast majority of documented cases of naturally-occurring nematode infections refer to parasites in the family Mermithidae, which commonly infect arthropods (Fig. 1E). A baltic amber specimen containing a spider and its mermithid parasite indicates that the relationship between spiders and Mermithids dates back to at least 40 million years ago (Poinar 2000). Much of the work on nematode parasites in spiders was dominated by George Poinar and was summarized in 1987. A few studies have filled in detailed gaps since Poinar (1987), but many questions remain untested.

Mermithids are similar in ecology to gordiid horsehair worms (family Nematomorpha) which infect terrestrial insects (Hanelt et al. 2005). Mermithids have both direct and indirect life cycles. In direct life cycles, infective larvae hatch from eggs and directly penetrate the integument of spider hosts. Infective larval mermithids use their odontostylet to pierce and enter through mosquito larvae cuticle (Sanad et al. 2013); a similar mechanism is likely employed on spider hosts that are directly infected. Indirect life cycles are characterized by infective larvae first entering a paratenic host (a host in which little to no parasite development occurs; Penney & Bennett 2006). Spiders become infected when they consume an infected paratenic host. Infective-stage spider mermithids (*Aranimis giganteus*) have been identified in mayfly and caddisfly larvae in New Zealand (Poinar & Early 1990); it is likely common for aquatic prey to serve as paratenic hosts given that reproduction occurs primarily in freshwater. Mermithids grow and develop in the spider host (a "developmental host") and

emerge as third stage post-parasitic juveniles. Mermithids are notorious for manipulating their host's behavior to ensure their emergence into freshwater where they reproduce. Thus, infected spiders can also exhibit increased hydrotaxis (Poinar 1987; see *Parasite-mediated changes to spider behavior* section below). Once in the water, Mermithids emerge through the cuticle, which often results in host-death (Poinar 1987). Post-parasitic juveniles molt 3–4 weeks after host emergence and then mate. Adult worms deposit their eggs in an aquatic or semi-aquatic habitat (Poinar 1987). Late-stage symptoms in spiders can include a swollen abdomen, deformed legs, malformed epigyna, palpi, and secondary sexual characteristics (Leech 1966). Infected spiders can experience a reduction in organ size and even castration (Poinar & Benton 1986). Lastly, Penney & Bennett (2006) noted a reduction in guanine deposition in *Tenuiphantes tenebricola* (Wider, 1834) spiders supposedly infected with Mermithids.

Laboratory tests demonstrate that spiders are also susceptible to infection by nematodes in the order Rhabditida (Poinar & Thomas 1985). There are documented cases of tarantulas suffering from Panagrolaimidae (Nematoda, Rhabditida) nematode infections in nature. This infection is considered to be an emerging disease in captive tarantulas, and Pizzi (2009) provides a detailed description of this infection. In brief, the initial signs of infection include anorexia and reduced mobility. Infection is fatal and histopathological examinations of infected spiders indicate that this nematode infection remains in the mouthparts and is often associated with bacterial invasion of the surrounding tissues. The exact significance of this bacterial infection is unclear. Transmission of this nematode in tarantulas is also unclear. Nematodes belonging to Panagrolaimidae are typically bacteriophagic soil-dwellers, so soil may be a source of infection. However, hump-backed flies (Diptera: Phoridae) are hypothesized vectors (Pizzi 2009). What the author meant by "vector" is unclear. It is possible these flies serve as trophic vectors for these nematodes (i.e., the spider becomes infected upon consumption of the fly). However, it should be noted that Panagrolaimide nematodes are phoretic on insects (Poinar 1975). Perhaps the flies can act as vehicles by which these nematodes are transmitted to a spider's environment. Finally, there are recent reports of tarantulas infected with a newly described species of rhabditid nematode, *Tarantobelus arachnicida* (Abolafia & Peña-Santiago 2018). Captive tarantulas infected with this nematode exhibit anorexia, lethargy and white discharge (Wyrobisz-Papiewska et al. 2019). Small nematodes were found in the discharge and with post-mortem analysis, nematodes were found in the anterior portion of the intestines and in spider excrement (Wyrobisz-Papiewska et al. 2019).

Protists infecting spiders.—Parasitic protists represent a diverse paraphyletic group with vastly different infection mode and pathology in arthropod hosts. We were unable to find any documented cases of spiders infected with parasitic protists (i.e., single-celled eukaryotes). This is likely because it is an understudied area of research, rather than spiders being unaffected. For example, a review of the parasites of Opiliones (Arachnida: Opiliones) indicates that harvestmen are commonly infected with gregarines (Cokendolpher 1993), which have been verified with ribosomal RNA sequencing (Dabert & Dabert 2008). The similarities in physiology and ecology between harvestmen and some spiders suggest that they may be similarly affected.

Ectoparasitic Acari of spiders.—Mites (Acari) are the most abundant and diverse of the arachnid groups. Because of their small size and staggering diversity, identification of mites can be difficult and is likely one reason why there are few reports of mites on spiders (Welbourn & Young 1988). Amber specimens have preserved interactions between mites and spiders as far back as 50 million years ago (Wunderlich 2002). The relationships between ectosymbiotic mites and spiders are numerous and can range from commensal to parasitic, including kleptoparasitic mites of spiders found in Brazilian caves (Bernardi et al. 2017). Fain & Jocque (1996) published a list of parasitic and phoretic mites reported on spiders which included 34 mite species reported on spiders belonging to 16 different families. Although commensal mites do not cause direct harm to their hosts, it has been suggested that heavy commensal mite loads can be cause for health problems in spiders, such as occlusion of the moist surfaces in the book lung (Pizzi 2009). Here we focus on the parasitic mites (Fig. 1D).

Within Acariformes, many of the reported parasites of spiders are members of the taxonomic group Parasitengona which have a parasitic larval stage and active, free-living post-larval stages (Wohltmann 2000). Parasitengone mites are associated with many arthropods, and those reported to parasitize spiders belong to the families Erythraeidae, Trombidiidae, Eutrombidiidae and Microtrombidiidae. Mąkol & Felska (2011) describe many of the documented Parasitengone mite larvae parasitic on spiders. According to their latest evaluation, 26 named species of Parasitengone mites have been recorded on 34 spider species, representing 20 families (Mąkol et al. 2017). Previous observations indicate that the larvae of Trombidiidae are more commonly found on spider hosts than are erythraeid larvae (Welbourn & Young 1988; Mąkol & Felska 2011). Larvae seek out hosts, attach, and feed on host fluids. Once attached, a larva inserts its chelicerae into the host and drinks fluid from the wound (Zhang 1998). Eutrombidiid and microtrombidiid larvae have oral rings which encircle the wound and anchor them on the hosts. Feeding tubes (stylostomes) have been observed in trombidiid (Robaux 1974; Pflugfelder 1977) and trombiculid (Voigt 1970; Hase et al. 1978) larvae. After inserting their chelicerae into the host's cuticle, the larvae secrete a lytic substance from the salivary glands. This lytic substance is responsible for the histolysis of the host's tissues (Voigt 1970). Larvae then inject a second secretion which hardens on contact with the host's hemolymph to form the stylostome (Voigt 1970).

Welbourn & Young (1988) noted that the majority of *Eutrombidum lockleii* larvae attached to spider hosts were found along the lines of exuvial separation (pleura). They hypothesized that the pleura may allow for easy cheliceral penetration and increased survival of mites during host molting (Welbourn & Young 1988). Parasitengone larvae remain attached to their host for approximately 1–2 weeks and rarely change hosts during this time period (Zhang 1998; Wohltmann 2000). Once engorged, the larvae drop off the host and seek refuge to develop into subsequent life stages (Walter & Proctor 2013). As adults, Parasitengone mites are either

pollinivorous or predators of microinvertebrates (Wohltmann 2000).

Little is known about host defenses against Parasitengone larvae. Melanization at the wound frequently occurs but has little effect on the parasitic larvae (Åbro 1988; Forbes et al. 1999). The physiological effects of parasitengone mite larvae on spiders remain unknown. In insects, host survival and reproduction are affected, which is dependent on the relative size of the parasite and host as well as the number of mites per host (Zhang 1998). Whether parasitengone mite larvae transmit infectious agents to spiders is also unknown, but there are reports of larvae transmitting *Spiroplasma* bacteria in walking-stick hosts (DiBlasi et al. 2011).

Within Parasitiformes, members of Laelapidae are reported to parasitize spiders. Previous researchers claimed that *Ljunghia* spp. parasitized mygalomorph spiders (Domrow 1975; Welbourn & Young 1988; Moraza et al. 2009). However, in their review of *Ljunghia*, Halliday & Juvara-Bals (2016) point out that there is limited evidence to suggest these mites are true parasites of spiders. Studies that include descriptions of the mites' habits are enigmatic, such as a species described by Schwendinger & Ono (2011) which attaches to and leaves scars on the dorsal carapace of host spiders, but scurries to the ventral side when disturbed. However, Schwendinger & Ono (2011) later describe the host carapace as highly sclerotized; thus, it seems unlikely that mites are able to access host fluids from this location (Halliday & Juvara-Bals 2016). Halliday & Juvara-Bals (2016) caution researchers against making distinctions on the parasitic nature of mites based simply on their presence on host bodies. As one example, *Gromphadorholaelaps schaeferi,* a mite commonly found on the bodies of Madagascar hissing cockroaches (*Gromphadorina portentosa*) has later been described as a mutualist, as it does not feed on its host and cleans away old food debris which could cause infection (Halliday & Juvara-Bals 2016). Future studies should employ removal experiments to test whether mite presence has any detectable negative impacts on spider performance (e.g., growth, body condition, and behavior).

Parasitoids of spiders.—Parasitoids are functionally distinct from parasites in that they kill their host, typically upon completion of larval development. As such, parasitoids' impacts on host populations are more akin to predators than parasites (Lafferty & Kuris 2002). Regardless, we include parasitoids in this review because they employ parasite-like strategies for a large portion of their life cycle and exhibit long-term relationships with a single host while that host continues to interact with the environment. Over 1000 parasitoids of spiders have been reported from the insect orders Hymenoptera and Diptera (with some examples of egg parasitism/predation in Neuroptera and Lepidoptera; Austin 1985; Korenko 2017; Nyffeler & Birkhofer 2017), and their description goes back to 1771 (Viera & Gonzaga 2017). There is both fossil and molecular evidence to suggest that dipteran parasitoids of spiders from the family Acroceridae likely evolved during the Mesozoic period (reviewed in Gillung & Winterton 2018). Spider parasitoids may be specialists or generalists (Austin 1985; Fitton et al. 1987; Korenko 2017) and hosts range from highly mobile ground dwellers (e.g., Cobb & Cobb 2004; Machkour-M'Rabet et al. 2015) to more sedentary web building species (e.g., Matsumoto 2009; Fernandez-Fournier et al. 2019). Generally, parasitoids are divided into endoparasitoids which reside and develop inside the host, and ectoparasitoids which attach and develop on the host outer body surface (Fig. 1C). Parasitoids may be koinobionts, meaning they allow their host to continue to develop after infection, or idiobiont, meaning that once the host is parasitized, the host does not develop any further (Pennacchio et al. 2014).

Hymenoptera represent the best studied, most abundant, and most diverse parasitoids of spiders. Hymenopteran parasitoids seem to be primarily ectoparasitoids (except for egg endoparasitoids, e.g., Stevens & Austin 2007) and may be either koinobiontic or idiobiontic (Pollard 1982; Korenko 2017; Nyffeler & Birkhofer 2017). Female ectoparasitoid wasps lay an egg on the dorsal side of a host, commonly between the cephalothorax and abdomen where the host spider cannot reach (Quicke 2015), but other larval positionings have been observed (Matsumoto & Konishi 2007).The larva develops on the back of an active spider host, feeding on its body fluids. During the first few instars, larval development is slow and can last about a month or more depending on the species and environmental conditions (Matsumoto & Konishi 2007; Korenko et al. 2016). Development of the later instars is rapid, and immediately prior to pupation, the larva consumes the entire contents of the spider host and pupates (Fitton et al. 1987).

Within the order Diptera, only species from the families Acroceridae, Phoridae, Sarcophagidae, and Tachinidae are considered true parasitoids, some of which are endoparasitoids (e.g., Vincent 1985; Schlinger 1987; Machkour-M'Rabet et al. 2015) and others ectoparasitoids (Schlinger et al. 2013). The majority of spider endoparasitoids are members of Acroceridae (small-headed flies). Adult acrocerids typically scatter their eggs throughout the environment. The first instar larvae (called planidia) immediately seek out potential hosts upon hatching and use modified setae, spines, and/or suction cups to actively maneuver the environment (Schlinger 1987). For most species, there has not been direct observation of host infection by planidia. However, there are observations of *Acrocera orbicula* and the planidia of this species using their mouthparts to attach to a host and feed externally on the host for about a week (Nielsen et al. 1999; Toft et al. 2012). They then molt into second instar larvae, which are small and flexible, and enter the host spider through the wound created while feeding. Once in the host, the larvae attach their posterior spiracle to the book lung for respiration while they feed on the host and develop (Schlinger 1987). Schlinger (1987) proposed that the larvae enter a diapause stage, lasting months to years once inside the host. The host dies when it is completely consumed by the final instar just prior to its emergence (Schlinger 1987). Identifying parasitized spiders is difficult. Some researchers have reported an enlarged opisthosoma on infected spiders (Barraclough & Croucamp 1997) and altered host behaviors in the later stages of infection (see *Parasite-mediated changes to spider behavior* section). Gillung & Borkent (2017) provide a more detailed review of dipteran parasitoids.

Parasitoids may also target the egg sacs of their host (e.g., Foote 1984; Cobb & Cobb 2004). The nuanced details of their biology obscure the difference between egg predators and egg

parasites. Because egg sac parasitoids consume more than one egg, they may be defined as egg predators (Austin 1985; Gillung & Borkent 2017). Given that they consume the egg entirely, and an egg is not an individual with ecological consequences, we consider them egg predators and do not review them here. Similarly, larval mantispids actively search for spider egg prey. If the larvae cannot immediately locate host eggs, they engage in a behavior known as "spider boarding" where the larvae attach to a spider and potentially ectoparasitize the spider, feeding on hemolymph, as they wait for the spider to lay an egg case or for an opportunity to transfer to a different spider during mating or cannibalism (Redborg 1998).

SPIDER BIOLOGY RELEVANT TO PARASITES

Integument.—After avoidance behaviors, the integument is a spider's first line of defense against parasitic infection. Spider integument is composed of multiple cuticular layers (epi-, exo-, meso- and endocuticle). The epicuticle is the thin, outermost layer of the integument and is responsible for the permeability of the integument. Directly below the epicuticle lies the exocuticle, which is much thicker and is hypothesized to be the toughest of all of the cuticle layers (Foelix 2011). The meso- and endocuticle lie deep to the exocuticle and are similar in composition, except that the mesocuticle is more sclerotized. The exocuticle is found in "tougher" body regions of spiders like the prosoma and legs. Softer regions, such as the opisthosoma and joint membranes, completely lack a tough exocuticle (Barth 1973; Foelix 2011), making them more susceptible to invasion by certain parasites (e.g., the tendency of mites to attach to the soft pleural membrane; Welbourn & Young, 1988).

Spiders differ from insects in that they possess a mesocuticle layer their entire life (Foelix 2011), a trait only found in larval insects. The difference in cuticular anatomy between insects and spiders could be responsible, in part, for the differences between entomopathogenic and araneopathogenic fungi which must penetrate through the integument to infect hosts. For example, ten species of entomopathogenic fungi have been documented on the cuticles of the cave orb-weaver *Meta ovalis* (Gertsch, 1933) (Yoder et al. 2009). These fungi have been shown to be pathogenic to co-occurring cave crickets, but not the spiders (Yoder et al. 2009). There is evidence of coevolving interactions between the host cuticle and pathogenic fungi in insects (Ortiz-Urquiza & Keyhani 2013), suggesting that araneopathogenic fungi may have evolved mechanisms to penetrate the unique epicuticle–mesocuticle structure in spiders (Evans 2013).

Respiration.—Most extant araneomorph spiders respire using both a tracheal system and one to two pairs of book lungs (Weygoldt & Paulus 1979). However, some species completely lack book lungs, while the mygalomorphs do not possess tracheae and respire using two pairs of book lungs only (Schmitz 2016). The book lung is located anteriorly on the ventral side of the opisthosoma, where air travels through the narrow "lung-slit" and into the atrium, and extends into air pockets which are in contact with blood-filled lamellae (Foelix 2011). In most araneomorphs, the second pair of book lungs is reduced and replaced by tracheae. Tracheae are invaginations of the body wall or originate from lungs or other internal structures and connect to tissues, providing them with a direct supply of oxygen.

Just like in insects, both the tracheae and book lungs open to the external environment and provide an entry point for parasites. Gudowska et al. (2016) observed mite-infested carabid beetles to employ discontinuous gas exchange (DGE) more than uninfested beetles. During DGE, the spiracles (openings to the tracheal system) cycle through patterns of being open and closed. This respiration pattern has been hypothesized to have evolved as a defense mechanism against parasites (Chown et al. 2006). There is evidence for three species of mygalomorph spider engaging in DGE (Mason et al. 2013). However, it is unknown as to whether this method of respiration might be utilized in parasite defense.

Immune system.—Spiders, like most arthropods, have a relatively simple, broadly effective innate immune system. Unlike vertebrates and some invertebrates, there are no adaptive components such as immunoglobulin or antibodies. In general, the spider immune response does not depend on prior exposure to the invading pathogen. Interestingly, Gálvez et al. (2020) found evidence for immune priming (augmented response to a previously-encountered pathogen) against *Escherichia coli* in the scorpion *Centruroides granosus* (Thorell, 1876), but not in the spider *Lycosa cerrofloresiana* Petrunkevitch, 1925. Instead, it is thought that nearly every constitutive component of the spider's immune system is contained within small and abundant neutrophil-like cells called hemocytes. Plasmatocytes and granulocytes, the two most common cell types found in the hemolymph, have been shown to contain a variety of immune-related compounds such as antimicrobial peptides (AMPs; Fukuzawa et al. 2008) and glycine-rich peptides (Lorenzini et al. 2003; Fukuzawa et al. 2008; Baumann et al. 2010). Prohemocytes, mostly located in hematopoietic tissue, are known as 'precursor cells' which often mature into granulocytes or plasmatocytes (Fukuzawa et al. 2008; Foelix 2011). Cyanocytes, found only in spiders and horseshoe crabs, are mainly responsible for hemocyanin storage and production (Burmester 2013; Kuhn-Nentwig & Nentwig 2013). The final immune-related blood cell, the spherulocyte, has only been found in *Lasiodora* spp. CL Koch, 1850, and is thought to be involved in the coagulation response (Soares et al. 2013).

When a foreign object such as a parasite enters the hemolymph, hemocytes will detect biomarkers on the surface of the object. If the object is identified as a threat, the hemocytes will signal for the migration of more immune cells to the site of the infection (Fukuzawa et al. 2008). In the case of bacterial or fungal pathogens, hemocytes can release a variety of AMPs that will subsequently immobilize and destroy the pathogen. Additionally, hemocytes near the site of infection will release components of the coagulation cascade, a highly-conserved innate immune response involving Hemocyanin and von Willebrand factor-related proteins (Fukuzawa et al. 2008; Sanggaard et al. 2016). If the object is too large for AMPs to clear the infection (e.g., a nematode or parasitoid larva), then a large number of hemocytes will surround and encapsulate the object, simultaneously causing a melanization cascade to be initiated by pro-phenoloxidase and free hemocyanins in the hemolymph. The cellular capsule and

subsequent melanization will effectively suffocate the parasite and clear the infection. This type of immune response, called the encapsulation or phagocytic response, is mostly regarded as a secondary defense. The secretion of AMPs and the initiation of the coagulation cascade are the primary responses to the presence of infectious agents.

Similar to other animals, mounting an immune response requires energy, which can result in trade-offs between immune function and other life history traits in spiders. As one example, Calbacho-Rosa et al. (2012) compared the lytic (i.e., bacteria-killing) activity of pholcid spiders (*Physocyclus dugesi* Simon, 1893) that had previously engaged in reproductive activities (mating, oviposition and agonistic interactions) to those that had not. Those that engaged in reproductive activity exhibited a significant reduction in lytic activity. These results suggest a down-regulation of immunity associated with the expression of reproductive behaviors, which could leave spiders more susceptible to sexually-transmitted microbes (Spicer et al. 2019). Gilbert et al. (2016) found that the ingestion of bacteria as a juvenile leads to stronger immune responses in adult *S. ochreata* wolf spiders, but was also associated with decreased body condition and asymmetrical foreleg tufts, which is an important sexually-selected trait. Thus, the potential for immune priming in the absence of an adaptive immune system is a promising avenue of research. In fact, Gilbert & Uetz (2016, 2019) developed *S. ocreata* as a system for testing questions regarding male courtship, signaling, and infection status. They found that cuticular chemicals are reliable cues of bacterial infection to females observing male courtship (Gilbert & Uetz 2019), that females can become infected through mating, and that engaging in courtship behaviors can decrease immune function in males (Gilbert & Uetz 2016). A recent gene expression study of the jumping spider *Portia labiata* (Thorell, 1887) found that aggressive behavior towards conspecifics using a mirror test was negatively associated with the expression of a viral infection response gene (Chang et al. 2020). Further, aggressive spiders were found to contain more viral RNA for picorna-like virus and Duwamo virus, but docile spiders contained more Xinzhou Spider virus RNA (Chang et al. 2020). This was the first study linking spider behavioral traits with immune gene expression and viral RNA load. Finally, Albin et al. (2020) found that female burrowing wolf spiders (*Allocosa senex* (Mello-Leitão, 1945)) showed higher cellular immune responses compared to males, and that males who engaged in burrow-digging showed increased immune activity. We encourage researchers to utilize these systems to test more questions regarding behavior, sexual selection, and host-parasite interactions. For a more in-depth review of the spider immune system, see the book chapter by Kuhn-Nentwig & Nentwig (2013).

Feeding physiology.—A feature characteristic of all spiders is the consumption of an entirely liquid diet. Spiders have a narrow gut that can only process liquid food and engage in external digestion. External digestion occurs by exuding digestive enzymes, originating in the midgut, to liquefy solid prey tissues (Fuzita et al. 2016) or by macerating the prey using their cheliceral teeth and pedipalps while covering the prey with digestive enzymes (Foelix 2011). This presents an interesting challenge for trophically-transmitted parasites; few multicellular parasites could survive this aggressive entry into the host gut. Further, the vast majority of spiders use venom to immobilize their prey, which may kill any parasites present in those prey. Spider venoms have at least two functions: to impair the nervous system (neurotoxic) or to dissolve tissues in their prey (necrotic). Necrotic venoms are capable of breaking down azocoll, gelatin, and casein in their prey (Kaiser & Raab 1967), and perhaps any metazoan parasites therein. Further, spider venom has many anti-parasitic and antiseptic properties (described below). Despite these barriers against parasite infection, oral entry has been shown to be an effective mode of infection in several experimental systems.

In Gilbert et al. (2016), male wolf spiders (*S. ocreata*) that ingested 600 CFU/microliter were later found to have up to 100 CFU/microliter of active *P. aeruginosa* bacteria in their hemolymph. This suggests that, though there may be physical or immunological barriers limiting the amount of ingested microbes that cross into the hemolymph from the gut, trophic sources of infection are possible. In *Drosophila melanogaster*, there is evidence of a physical barrier in the gut called the peritrophic matrix, which protects from damage caused by pathogenic bacteria (Kuraishi et al. 2011). It remains unknown whether spiders possess a similar structure.

Antimicrobial properties have been described in several spider venoms. Venom extracted from the funnel weaver *Agelena labyrinthica* (Clerck, 1757), demonstrated antimicrobial activity against multiple strains of bacteria including but not limited to: *Bacillus subtilis*, *Escherichia coli,* and *Staphylococcus aureus* (Benli & Yigit 2008). Similarly, the VdTX-I toxin extracted from the tarantula *Vitalius dubius* (Mello-Leitão, 1923), has been shown to have antimicrobial activity against 12 species of *Candida, Trichosporiun, Staphylococcus* and *Micrococcus* (Sutti et al. 2015). A peptide fraction from a tarantula (*Acanthoscurria gomesiana* (Mello-Leitão, 1923)) venom also showed antimicrobial activity against *E. coli, Enterobacter cloacae and Candida albicans* strains (Abreu et al. 2017). Venom supernatant extracted from a wolf spider (*Lycosa terrestris* Butt, Anwar & Tahir, 2006) inhibited the growth of aerobic Gram-negative *Acinetobacter* sp. (Tahir et al. 2018). Lastly, venom from a recluse spider (*Loxosceles gaucho* Gertsch, 1967) has a complex effect on virulence of *Pseudomonas aeruginosa*; exhibiting antimicrobial properties but also the potential for increasing *P. aeruginosa* biofilm formation (de Oliveira Domingos et al. 2018; see *Medical arachnology* section in Future Directions). Overall, spider venoms provide ample opportunities for the discovery of novel antibacterial and therapeutic drugs (Alikhani et al. 2020). Escoubas et al. (2006) predict, globally, that spider venoms may contain more than 10 million bioactive peptides, of which only 0.01% has been characterized.

Given their diverse antimicrobial properties, it is particularly interesting that spider venom glands can also contain diverse living microbial communities (Esmaeilishirazifard et al. 2018). Dunaj et al. (2020) found that three species of the widow genus *Latrodectus* Walckenaer, 1805 and related theridiid species contain similar venom-associated microbiota (e.g., *Psychrobacter* and *Variovorax)*. The presence of virus RNA was found in the venom glands of golden orb weavers, *T. clavipes*, with NCPV1 being the most prevalent (Debat 2017). The working group *Initiative for Venom-Associated*

Microbes and Parasites (iVAMP) was recently established to study the microbes living in the venom glands of diverse organisms, and aims to integrate studies across fields and taxa (Ul-Hasan et al. 2019).

Silk use.—Another defining characteristic of all spiders is the production of silk (Brunetta & Craig 2010). Silk is used for an immensely diverse set of functions that have allowed spiders to adaptively radiate into nearly all ecosystems on earth. Some functions of silk include habitat building, prey capture, prey immobilization, dispersal, navigation, safety, mating, and egg protection (Miyashita et al. 2004; Bell et al. 2005; Sutherland et al. 2009; Brunetta & Craig 2010). Spiders can produce up to seven different types of silk produced by different glands: ampullate major (dragline), ampullate minor, flagelliform (capture-spiral), tubuliform (egg cocoon), aciniform (prey wrapping), aggregate (sticky globules), and piriform (Foelix 2011); individual insects generally produce only a single type (Sutherland et al. 2009). Each silk type has the potential for different antiseptic/antimicrobial properties. However, the nature, breadth, and magnitude of silk's antibacterial properties have not been definitively determined.

Heimer (1988) was the first to publish on antiseptic properties of silk and suggested that they are due to its acidity. Borders (2001) tested silk from 30 different spider species for their antiseptic properties. Although the results were inconclusive, Borders (2001) suggested silk partially inhibited growth of the Gram-negative bacteria *Pseudomonas fluorescens*, a relative of the known spider pathogen, *P. aeruginosa* (Gilbert & Uetz 2016). Silk from the Indian social spider *Stegodyphus sarasinorum* Karsch, 1892 was found to have antibacterial properties toward *Escherichia coli* and *Staphylococcus aureus* (Deshmukh & Pansare 2019). *Tegenaria domestica* (Clerck, 1757) spider silk inhibits the growth of Gram-positive *Bacillus subtilis* but not the Gram-negative *E. coli,* both of which are deleterious to the host spider (Wright & Goodacre 2012). Interestingly, this study also showed that the antimicrobial activity of the silk is diminished by soaking it in water or incubating it with Proteinase K, suggesting that some silk-based proteins may be playing an important role (Wright & Goodacre 2012). Silk from *Pholcus phalangioides* (Fuesslin, 1775) was found to inhibit the growth of two food-borne pathogens, *E. coli* and the Gram-positive *Listeria monocytogenes* (Roozbahani et al. 2014). The silk of *Argiope aurantia* Lucas, 1833 does not inhibit bacterial growth, but rather hindered bacterial adherence to the web (Sharma 2014). However, not all spider silks exhibit antimicrobial properties. Spider webs have been shown to be a source for detecting environmental DNA and an impressive diversity of fungi and bacteria have been found in spider webs, including many plant and arthropod pathogens (Gregorič et al. 2020). Silk from mygalomorph spiders had no effect against multiple bacterial species (*E. coli, P. aeruginosa, S. aureus,* and *Enterococcus faecalis*; Szymkowiak et al., 2020). Moreover, a recent study found that black widow gumfoot threads promote bacterial growth (Alicea-Serrano et al. 2020). This same study included a literature review that demonstrated the nuanced effects of silk on bacterial growth influenced by silk type, bacterial species, and experimental methods (Alicea-Serrano et al. 2020). However, a recent study (Fruergaard et al. in press 2021) examined silk from seven species of spiders and found no evidence for anti-microbial properties; they also concluded that published reports of anti-microbial activity suffered from risk of bacterial contamination and lack of control for effects of solvents, so that anti-microbial activities cannot be unequivocally attributed to spider silk. Given some of these mixed results, the protection silk provides from parasites is likely context- and species-specific and warrants additional investigation.

Mechanistically, spider silk may (1) actively kill bacteria (i.e., antimicrobial), or (2) inhibit or slow microbial growth (i.e., antiseptic; Zhang et al. 2019). Different levels of nitrogen availability on the silks of three different types of web builders (i.e., *Hippasa holmerae* Thorell, 1895, *Nephila pilipes* (Fabricius, 1793), *Cyrtophora moluccensis* Doleschall, 1857) determined the bacterial growth rate of four types of bacteria (i.e., *Bacillus altitudinis*, *B. subtilis*, *Enterobacter bugandensis*, *E. coli*; Zhang et al. 2019). When silk is the primary source of nitrogen, it appears to limit bacterial growth rate rather than killing bacteria outright. Keiser et al. (2015a) found that intact spider silk of *Stegodyphus dumicola* wrapped around a filter paper disk had a minor inhibitory effect on bacterial growth. However, ethyl acetate extractions, commonly used to isolate antibiotics from spider silk, showed no inhibitory effects. The exact mechanisms by which spider silk stifles bacterial proliferation remains to be determined, but it is clear that there may be multiple protein-based, structure-based, or resource-based components that differ across or even within species.

The study of the antimicrobial nature of spider silk remains primarily focused on creating tools to enhance human medicine. In the future, more research should focus on these properties in an ecological context. For example, are there differences in the antimicrobial effects of silks used for prey capture vs. egg case protection? Is the consumption of old silk a route for microbial colonization in spiders that build new orb-webs daily? Are these ephemeral webs less defended against microbial growth compared to the more permanent webs of other spiders like *Nephila* spp? Further, many spiders consume droplets of water directly from web surfaces, such as dew that has accumulated overnight, which represents an interesting potential route of microbial colonization.

SPIDER-PARASITE ECOLOGY

Parasite-mediated changes to spider behavior.—A hallmark of parasite infection is a change in host behaviors after infection. Parasite-induced behavioral changes can be divided into three categories (reviewed in Poulin 2010): (1) sickness behaviors which are beneficial responses by the host to reduce the negative effects of infection, (2) behavioral manipulation by the parasite to benefit parasite development or transmission, and (3) side-effects of infection which benefit neither the parasite nor the host. These are often difficult to differentiate without experimental investigation. For example, infection with endosymbiotic bacteria like *Wolbachia* and *Rickettsia* is often thought to manipulate host life history to benefit the bacterium. Rickettsial infection in a money spider, *Erigone atra* Blackwall, 1833, can reduce host dispersal behavior (Goodacre et al. 2009), but it is unknown whether this change in behavior benefits the parasite. Below we describe the best-known cases of parasite manipulation of host spiders, as we

are unaware of any definitive cases of adaptive sickness behaviors.

There are numerous reports of species from the *Polysphincta* clade of the subfamily Pimplinae (Hymenoptera: Ichneumonidae), all koinobiont ectoparasitoids of spiders, manipulating the web building behavior of their hosts (Gonzaga et al. 2017; Weinersmith 2019). When these parasitoids molt into their final larval instar, the host constructs a modified web which is often similar to the host's moulting, oviposition, and/or overwintering webs, on which the parasitoid larva kills and consumes its host and affixes a pupal cocoon (Korenko & Pekár 2011; Korenko et al. 2013; Gonzaga et al. 2017; Weinersmith 2019). Similar behavioral alterations have been observed in *Anelosimus* spp. Simon, 1891 parasitized by the wasp *Zatypota solanoi* (Ichneumonidae) (Eberhard 2010), where the modified web provides protection for the developing wasp larva with a protective sheet around a space where the larva suspends its cocoon (Eberhard 2010). Matsumoto (2009) found that removal of the protective modified web produced by *Agelena limbata* Thorell, 1897 when parasitized by *Brachyzapus nikkoensis* (Ichneumonidae) increases predation risk on the parasitoid before eclosion. The modified webs produced by parasitized spiders are often less effective at intercepting prey, but rather provide increased stability and safety for the parasitoids' cocoons (Gonzaga et al. 2017). Across diverse host-parasitoid systems, these analogous manipulations may result from similar underlying mechanisms, like the injection of psychotropic compounds related to or precursors of ecdysteroids (Takasuka et al. 2015; Kloss et al. 2017). In another system, parasitism by *Zatypota* wasps prompts the social spider *Anelosimus eximius* (Keyserling, 1884) to disperse from its natal colony to construct a solitary web, though it has been hypothesized that this manipulation may occur simply by starving their hosts or by exploiting an ancestral dispersal behavior in the host (Jones & Parker 2000; Fernandez-Fournier et al. 2019). Regardless of the mechanism, these cases of parasitoid-altered behavior hint at parasite manipulation, as they reduce host performance and benefit parasitoid development.

Infection by mermithid worms appears to increase the attraction of spider hosts to water (Poinar 1985) which may aid in the completion of the reproductive cycles of mermithids, given that they reproduce primarily in water. This phenomenon is similar to, but less studied, than the increase in water-seeking behavior in insect hosts infected by horsehair worms (phylum Nematomorpha; Hanelt et al. 2005). Herbison et al. (2019) used SWATH-mass spectrometry on the brains of insects infected by mermithids and nematomorphs and discovered protein dysregulation and downregulation of common mediators of synaptic plasticity and long-term potentiation (i.e., "memory") across a diversity of host-parasite pairs. This convergence in host manipulation mechanisms suggests similar alterations may occur in spider hosts, which warrants further study.

Manipulation of host behavior is a hallmark of many fungal pathogens of insects (Hughes et al. 2016). Although behavioral manipulation by araneopathogenic fungi has never been tested directly, most fungus-parasitized cadavers are found on the undersides of leaves, hinting at the potential for a "summit disease"-related phenomenon (Lovett et al. 2020b) where hosts die in a location where infectious fungal spores are more likely to contact susceptible hosts. Cursorial and fossorial spiders that become infected are also likely to position themselves such that spores will not become trapped in leaf litter or subterranean retreats.

Parasites and spider foraging ecology.—Spiders are some of the most common predators on earth, found in virtually every terrestrial habitat (Turnbull 1973). They are voracious predators that consume 1% of the global terrestrial net primary production (Nyffeler & Birkhofer 2017) with a diverse range in prey species from arthropods to plant material to vertebrates (McCormick & Polis 1982; Meehan et al. 2008; Foelix 2011). When spider biomass is high there is a direct reduction in herbivore populations from predation (Welti et al. 2020). Predation pressure from spiders can release plants from herbivore pressure (i.e., "trophic cascades"; Michalko et al. 2019) and thus they may be direct modulators of understory community dynamics. Therefore, any stressor, including parasites, that reduces predation pressure by spiders can alter these top-down dynamics.

Parasites have received much attention in the past few decades as influencing food webs in a way that mirrors predator's top-down regulation of communities (e.g., Lafferty et al. 2008). Considering spiders' potentially significant role as top predators for many ecosystems, parasites that affect spider abundance and distribution have the capability to induce trophic cascades, as has been found when spider populations are reduced via chemical pesticides (Satpathy et al. 2020). Perhaps the most enigmatic influence of spiders on community dynamics are the trait-mediated indirect effects they impose across the food web (reviewed in Ohgushi et al. 2012). Top predators, such as spiders, can modify prey traits via non-consumptive (e.g., fear-mediated) mechanisms like hunting in specific habitats which could change the foraging behavior of prey to avoid risky patches (i.e., landscape of fear; Brown et al. 1999). For example, in heterogeneous environments the spatial distributions of spiders and their springtail prey were found to be negatively correlated, suggesting an avoidance of habitats with greater risk of spider predation (Birkhofer et al. 2010). The magnitude of spider-induced trophic effects can depend on spider behavioral traits, like activity level (Keiser et al. 2015b). If sublethal infection alters spider activity level, then parasites could alter the magnitude of trophic cascades via non-consumptive effects. In a system where predatory wolf spiders and their prey (black-legged ticks) were housed with a shared araneopathogenic fungus, both spider and tick behavior changed under parasite presence, altering predator-prey dynamics (Fischhoff et al. 2018). Spiders may also avoid or alter their foraging behavior in high infection-risk habitats (i.e., landscape of disgust; Weinstein et al. 2018). For example, in an Arctic wolf spider (*Pardosa glacialis* (Thorell, 1872)) the average prevalence of nematode infection was estimated at 1%, though prevalence reaches 5% in riparian zones around streams (Leech 1966). Although no study has yet tested the community-wide effects of araneoparasite infection directly, complementary evidence from multiple systems suggests that parasites might alter spiders' top-down control of insect communities via changes in abundance or behavior, which may alter rates of herbivory on plant populations. This represents an exciting avenue of future research.

Disease outbreaks in social spiders.—Sociality is extraordinarily rare in spiders. Of the ~48,000 species of spiders described at the time this paper was written, only ~20 are permanently social (Avilés & Guevara 2017). Some have argued that sociality is an evolutionary dead-end for spiders, where the short-term benefits of sociality (cooperative nest building, prey capture, etc.) are outweighed by the long-term evolutionary costs associated with population subdivision and inbreeding (Agnarsson et al. 2006). Social spiders experience boom and bust population dynamics due, in part, to intense levels of colony extinction (Crouch & Lubin 2001). The drivers of colony extinction are often idiopathic, though a few studies have identified predators and parasites as potentially important selective pressures (e.g., Henschel, 1998; Crouch & Lubin 2001).

In a three year study in the Namib Desert, Henschel (1998) noted that 82% of colonies of the social spider *S. dumicola* (Araneae: Eresidae) succumbed to extinction, of which 5.7% occurred as a consequence of fungal pathogens after heavy rains. Interestingly, Henschel (1998) noted that only 1.3% of solitary *S. dumicola* succumbed to fungal infection. Dense aggregations and high levels of inbreeding within colonies may increase susceptibility to disease outbreaks. A recent survey found that populations in wetter climates are more likely to succumb to fungus-driven extinctions (McEwen et al. 2020), though the fungus has not yet been identified and it remains unknown whether it is pathogenic, opportunistic, or saprophytic (i.e., growing only after idiopathic colony death). The genus *Stegodyphus* Simon, 1873, in which sociality has evolved three times independently, has become a powerful test system for questions regarding the microbial communities of social spiders and the nests in which they reside. Keiser et al. (2019) showed that the silken retreats and capture webs of *S. dumicola* harbor highly consistent bacterial communities, even from colonies collected hundreds of kilometers apart. Busck et al. (2020) published a monumental paper characterizing distinct but overlapping microbial communities associated with all three social *Stegodyphus* spp. They identified a core microbiome (>50% prevalence) consisting of five to seven symbionts, three of which are putatively novel, and used fluorescence in situ hybridization to localize two genera (*Borrelia* and *Mycoplasma*) to the host midgut. Keiser et al. (2016a, 2018) also used electroporation to transform *Pantoea* sp. bacteria collected from *S. dumicola* cuticles to track microbial transmission among group mates. Horizontal transmission of cuticular microbes appears to be influenced by individual behavioral phenotypes and differs by group size.

FUTURE DIRECTIONS IN SPIDER-PARASITE RESEARCH

This review demonstrates that there are countless exciting questions yet to be answered regarding the parasites of spiders. Fortunately, arachnologists can utilize the vast literature on the parasites of insects as a baseline (Sanchez-Contreras & Vlisidou 2008; Six 2013; Engel & Moran 2013). The insect parasitology literature has spanned pathology (Tanada & Kaya 1993), ecoimmunology (Adamo 2012), and epizootiology (Fuxa & Tanada 1987). In addition to conceptual advances to ecology, evolution, and behavior, surveys of spider parasites across different regions of the world will provide insights into their underappreciated biodiversity. Recent regional surveys or literature reviews have been conducted in New Zealand (Thompson 2020) and Argentina (Manfrino et al. 2017). Below, we provide suggestions for future research and potential test systems.

Parasite manipulation and sickness behaviors.—Two hallmark systems in the study of parasite-induced changes to host behavior are the effects of *Ophiocorcyceps* fungal infection on ant "death grip" behavior and the effects of horsehair worm infection on insect water-seeking behavior. Two araneopathgenic corollaries of these systems are *Gibellula* fungal pathogens and Mermithid parasitic roundworms. *Gibellula*-infected spider cadavers are commonly found on the undersides of leaves. Of course, salticid spiders are commonly found on the undersides of leaves, but the parallels between this observation and how *Ophiocordiceps*-infected ants position themselves on the undersides of leaves to promote spore dispersal are noteworthy. The *Gibellula*-salticid system sorely lacks laboratory-based infections with detailed observations of host behavior. Although some *Gibellula* can be cultured in vitro, sporulation does not occur (Kuephadungphan et al. 2019). Mermithid infections require laborious collections due to the low infection prevalence. George Poinar (pers. comm) suggests that Mermithid larvae can be observed in the abdomens of wild-caught spiders by casting light through the specimen under magnification. Future research questions in these systems could include: (1) To what degree do seasonality and habitat type alter patterns in Mermithid host manipulation? (2) Do *Gibellula*-infected spiders climb vegetation before death or are they simply found near their retreats? (3) What is the timing of host manipulation in fungal araneopathogens, and does this differ between generalist and specialist parasites? To study host sickness behaviors, we recommend the use of lipopolysaccharides (LPS), bacterial surface proteins which are recognized by the host immune system and initiate immune responses and subsequent behavioral alterations. The use of LPS injection is common in insect pathology and allows researchers to assess the effects of sickness behaviors in the absence of other pathologies. We are not aware of any study which used LPS injections in a spider host. The best method is to infect hosts with pathogens or inject with LPS and observe behavioral changes compared to sham injections. If behavioral changes are observed, an additional experimental group where those changes in host behavior are impeded can suggest the mechanism of behavioral alterations. For example, if infection is associated with reduced activity level, then infected individuals can be forced to walk on a treadmill to impede the change in behavior. If infected individuals forced to walk on a treadmill exhibit reduced survival compared to other groups, then sickness behaviors are a likely scenario.

Ecological parasitology.—Spiders exert important top-down control in invertebrate food webs, either through direct predation and through fear-mediated herbivore abandonment of host plants (Riechert & Lockley 1984; Sunderland 1999). As described in the *Spider Foraging Ecology* section above, any parasite that alters spiders' direct or indirect effects on prey populations can have important effects on community dynamics. A particularly interesting avenue of research could utilize generalist entomopathogenic fungi, araneopathogenic

fungi, and generalist parasites that infect both spiders and their insect prey to ask: (1) do araneopathogens alter the top-down effects of predators directly via predator mortality or indirectly via changes to predator behavior? (2) Do spiders avoid parasitized prey? Jumping spiders have been shown to avoid unpalatable prey (Taylor et al. 2016), so perhaps similar patterns will be identified for infection avoidance. Interestingly, when predators avoid eating infected prey, the likelihood of prey extinction is increased because prey are being removed by predators and parasites independently (Roy & Chattopadhyay 2005).

Medical arachnology.—Much of the interest in spider-associated bacteria focuses on their potential role in spider bite pathology. Most arachnologists are well aware that, despite their undeserving reputation, spiders do not pose a great risk to human health. Unfortunately, medical professionals commonly misattribute dermonecrotic lesions (Benoit & Suchard 2006; Suchard 2011) and burns as spider bites (Vetter & Bush 2002). In fact, "necrotic arachnidism" is nearly always diagnosed without any actual evidence of a spider bite, and "loxoscelism" (symptoms associated with bites from recluse spiders of the genus *Loxosceles* Heiniken & Lowe, 1832) is diagnosed in American states where brown recluse do not occur (Vetter 2000). Detailed studies have found that the bacteria *Clostridium septicum* and *C. perfingens* isolated from the fangs of *Loxosceles* has been shown to play an important interactive role in the dermonecrotic process associated with loxoscelism diagnoses (Monteiro et al. 2002; Catalán et al. 2010). However, it was found that recluse spiders are highly unlikely to vector methicillin-resistant *S. aureus* (MRSA; Gaver-Wainwright et al. 2011). Further investigations have revealed little evidence for spiders' ability to carry or vector pathogenic bacteria to humans (Vetter et al. 2015). Some researchers are interested in spider venom as a potential source for novel antibacterial agents (Saez et al. 2010; Tan et al. 2013) and antiparasitic drugs. Nixon et al. (2020) found antiparasitic effects of crude venoms extracted from many venomous invertebrates, especially tarantulas. Spider-bacterial interactions will undoubtedly provide resources for future biomedical research, but an important responsibility of arachnologists continues to be dispelling myths regarding spider bites.

SPDR Collection.—As part of an initiative to strengthen spider-parasite research, the Spider Parasite Digital Research Collection (SPDR) has been established to maintain a collection of spider-parasite pairs, each identified, sequenced, georeferenced, and photographed and all information provided freely online in a searchable database. The SPDR collection is both a biodiversity collection and a catalog of ecological interactions and serves as an archive for photographs and literature associated with spider-parasite interactions. The SPDR collection focuses especially on fungal araneopathogens, parasitic nematodes, and spider parasitoids, and is currently housed in the Florida State Collection of Arthropods in Gainesville, FL and accessions are welcomed in the form of physical specimens or photographs (www.keiserlab.com/spdr).

LITERATURE CITED

Abolafia J, Peña-Santiago R. 2018. Morphological and molecular characterization of *Tarantobelus arachnicida* gen. n., sp. n. (Nematoda, Rhabditida, Brevibuccidae), a parasitic nematode of tarantulas. *Journal of Helminthology* 92:491–503.

Abreu TF, Sumitomo BN, Nishiyama MY, Oliveira UC, Souza GHMF, Kitano ES, et al. 2017. Peptidomics of *Acanthoscurria gomesiana* spider venom reveals new toxins with potential antimicrobial activity. *Journal of Proteomics* 151:232–242.

Åbro A. 1988. The mode of attachment of mite larvae (*Leptus* spp.) to harvestmen (Opiliones). *Journal of Natural History* 22:123–130.

Adamo SA. 2012. Comparative psychoneuroimmunology/ecoimmunology: Lessons from simpler model systems. Pp. 277–290. *In* The Oxford Handbook of Psychoneuroimmunology. (SC Segerstrom (ed.)), Oxford University Press.

Agnarsson I, Avilés L, Coddington JA, Maddison WP. 2006. Sociality in theridiid spiders: Repeated origins of an evolutionary dead end. *Evolution* 60:2342–2351.

Aini AN, Mongkolsamrit S, Wijanarka W, Thanakitpipattana D, Luangsa-ard JJ, Budiharjo A. 2020. Diversity of *Akanthomyces* on moths (Lepidoptera) in Thailand. *MycoKeys* 71:1–22.

Albín A, Simó M, Cargnelutti F, Aisenberg A, Calbacho-Rosa L. 2020. Sex and burrowing behavior and their implications with lytic activity in the sand-dwelling spider *Allocosa senex*. *Science of Nature* 107:1–8.

Alicea-Serrano AM, Htut KZ, Coonfield AJ, Karkosiak K, Dhinojwala A, Blackledge TA. 2020. Spider viscid silk sticks better to superhydrophobic surfaces. bioRxiv: 2020.05.15.098194.

Alikhani HK, Zargan J, Bidmeshkipour A, Mohammadi AHN, Hosseinpour M, Heydari A, et al. 2020. Antibacterial activity of the Iranian Scorpion's crude venom (*Odontobuthus bidentatus*) on gram-positive and gram-negative bacteria. *Iranian Journal of Toxicology* 14:105–109.

Austin AD. 1985. The function of spider egg sacs in relation to parasitoids and predators, with special reference to the Australian fauna. *Journal of Natural History* 19:359–376.

Avilés L, Guevara J. 2017. Sociality in spiders. Pp. 188–223. *In* Comparative Social Evolution. (D Rubenstein, P Abbot (eds.)), Cambridge University Press.

Baldo L, Ayoub NA, Hayashi CY, Russell JA, Stahlhut JK, Werren JH. 2008. Insight into the routes of *Wolbachia* invasion: High levels of horizontal transfer in the spider genus *Agelenopsis* revealed by *Wolbachia* strain and mitochondrial DNA diversity. *Molecular* 17:557–569.

Barraclough DA, Croucamp W. 1997. A new South African species of *Ogcodes* Latreille (Diptera: Acroceridae) reared from sac spider of the genus *Cheiracanthium* Koch (Miturgidae). *Annals of the Natal Museum* 38: 55–60.

Barth FG. 1973. Microfiber reinforcement of an arthropod cuticle - Laminated composite material in biology. *Zeitschrift für Zellforschung und Mikroskopische Anatomie* 144:409–433.

Baumann T, Kämpfer U, Schürch S, Schaller J, Largiadèr C, Nentwig W, et al. 2010. Ctenidins: antimicrobial glycine-rich peptides from the hemocytes of the spider *Cupiennius salei*. *Cellular and Molecular Life Sciences* 67:2787–2798.

Bell JR, Bohan DA, Shaw EM, Weyman GS. 2005. Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. *Bulletin of Entomological Research* 95:69–114.

Benli M, Yigit. N 2008. Antibacterial activity of venom from funnel web spider *Agelena labyrinthica* (Araneae: Agelenidae). *Journal of Venomous Animals and Toxins Including Tropical Diseases* 14:641–650.

Benoit R, Suchard JR. 2006. Necrotic skin lesions: spider bite- or something else? *The Consultant* 46:1386–1394.

Bernardi LFDO, Wohltmann A, Lorenzon IM, Ferreira RL. 2017. A novel symbiotic relationship between mites and recluse spiders (Sicariidae: *Loxosceles*), with a description of a new *Callidosoma* species (Trombidiformes: Erythraeidae). *Zootaxa* 4338:459–474.

Birkhofer K, Scheu S, Wiegand T. 2010. Assessing spatiotemporal

predator–prey patterns in heterogeneous habitats. *Basic and Applied Ecology* 11:486–494.
Blackwell M, Haelewaters D, Pfister DJ. 2020. Laboulbeniomycetes: evolution, natural history, and Thaxter's final word. *Mycologia* 112:1048–1059.
Borders WR. 2001. An investigation of spider webs' antibacterial properties. *Page Bulletin of the South Carolina Academy of Science* 24.
Brown JS, Laundre JW, Gurung M. 1999. The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* 80:385–399.
Brunetta L, Craig CL. 2010. Spider Silk: Evolution and 400 Million Years of Spinning, Waiting, Snagging, and Mating. Yale University Press.
Burmester T. 2013. Evolution and adaptation of hemocyanin within spiders. Pp. 3–14 *In* Spider Ecophysiology. (W Nentwig (ed.)), Springer, Berlin, Heidelberg.
Busck MM, Settepani V, Bechsgaard J, Lund MB, Bilde T, Schramm A. 2020. Microbiomes and specific symbionts of social spiders: Compositional patterns in host species, populations, and nests. *Frontiers in Microbiology* 11:1845.
Calbacho-Rosa L, Moreno-García MA, Lanz-Mendoza H, Peretti AV, Córdoba-Aguilar A. 2012. Reproductive activities impair immunocompetence in *Physocyclus dugesi* (Araneae: Pholcidae). *Journal of Arachnology* 40:18–22.
Catalán A, Espoz MC, Cortés W, Sagua H, González J, Araya JE. 2010. Tetracycline and penicillin resistant *Clostridium perfringens* isolated from the fangs and venom glands of *Loxosceles laeta*: Its implications in loxoscelism treatment. *Toxicon* 56:890–896.
Ceccarelli FS, Haddad CR, Ramírez MJ. 2016. Endosymbiotic Rickettsiales (Alphaproteobacteria) from the spider genus *Amaurobioides* (Araneae: Anyphaenidae). *Journal of Arachnology* 44:251–253.
Chang C-C, Connahs H, Tan ECY, Norma-Rashid Y, Mrinalini D, et al. 2020. Female spider aggression is associated with genetic underpinnings of the nervous system and immune response to pathogens. *Molecular Ecology* 29:2626–2638.
Chown SL, Gibbs AG, Hetz SK, Klok CJ, Lighton, JRB, Marais E. 2006. Discontinuous gas exchange in insects: A clarification of hypotheses and approaches. Pp. 333–343. *In* Physiological and Biochemical Zoology. The University of Chicago Press.
Cobb LM, Cobb VA. 2004. Occurrence of Parasitoid wasps, *Baeus* sp. and *Gelis* sp., in the egg sacs of the wolf spiders *Pardosa moesta* and *Pardosa sternalis* (Araneae, Lycosidae) in Southeastern Idaho. *Canadian Field-Naturalist* 118:122–123.
Cokendolpher JC. 1993. Pathogens and parasites of Opiliones (Arthropoda: Arachnida). *Journal of Arachnology* 21:120–146.
Costa PP. 2014. *Gibellula* spp. associadas a aranhas da Mata do Paraíso, Viçosa-MG. Universidade Federal de Viçosa.
Crouch T, Lubin Y. 2001. Population stability and extinction in a social spider *Stegodyphus mimosarum* (Araneae: Eresidae). *Biological Journal of the Linnean Society* 72:409–417.
Dabert M, Dabert J. 2008. Ribosomal DNA sequences reveal gregarine pathogens (Apicomplexa: Gregarinia) in mites and other arachnids (Arachnida). *Soil Organisms* 80:197–204.
de Oliveira Domingos M, Neves IV, Vigerelli H, Pimenta DC, de Carvalho Lins Fernandes Távora B, Lemos TJ, et al. 2018. The potential of *Loxosceles gaucho* spider venom to regulate *Pseudomonas aeruginosa* mechanisms of virulence. *Toxicon* 152:78–83.
Debat HJ. 2017. An RNA virome associated to the golden orb-weaver spider *Nephila clavipes*. *Frontiers in Microbiology* 8:2097.
Deshmukh US, Pansare AS. 2019. Antimicrobial activity of web of spider, *Stegodyphus sarasenorum* on *E. coli* and *S. aureus*. *Bioscience Biotechnology Research Communications* 12:787–789.
DiBlasi E, Morse S, Mayberry JR, Avila LJ, Morando M, Dittmar K. 2011. New *Spiroplasma* in parasitic *Leptus* mites and their *Agathemera* walking stick hosts from Argentina. *Journal of Invertebrate Pathology* 107:225–228.
Domrow R. 1975. *Ljunghia oudemans* (Acari: Dermanyssidae), a genus parasitic on mygalomorph spiders. *Records of the South Australian Museum* 17:31–39.
Dunaj SJ, Bettencourt BR, Garb JE, Brucker RM. 2020. Spider phylosymbiosis: Divergence of widow spider species and their tissues' microbiomes. *BMC Evolutionary Biology* 20:1–17.
Eberhard WG. 2010. New types of behavioral manipulation of host spiders by a parasitoid wasp. Psyche: A Journal of Entomology 2010: Article ID 950614.
Engel P, Moran NA. 2013. The gut microbiota of insects - diversity in structure and function. *FEMS Microbiology Reviews* 37:699–735.
Engelstädter J, Hurst GDD. 2009. The ecology and evolution of microbes that manipulate host reproduction. *Annual Review of Ecology, Evolution, and Systematics* 40:127–149.
Escoubas P. 2006. Molecular diversification in spider venoms: A web of combinatorial peptide libraries. *Molecular Diversity* 10:545–554.
Esmaeilishirazifard E, Usher L, Trim C, Denise H, Sangal V, Tyson GH, et al. 2018. Microbial adaptation to venom is common in snakes and spiders. bioRxiv: 348433.
Evans HC. 2013. Fungal pathogens of spiders. Pp. 107–121. *In* Spider Ecophysiology. (W. Nentwig (ed.)). Springer, Berlin, Heidelberg.
Evans HC, Samson RA. 1987. Fungal pathogens of spiders. *Mycologist* 1:152–159.
Fain A, Jocqué R. 1996. A new larva of the genus *Leptus* Latreille, 1796 (Acari: Erythraeidae) parasitic on a spider from Rwanda. *International Journal of Acarology* 22: 101–108.
Fernandez-Fournier P, Straus S, Sharpe R, Avilés L. 2019. Behavioural modification of a social spider by a parasitoid wasp. *Ecological Entomology* 44:157–162.
Fischhoff IR, Burtis JC, Keesing F, Ostfeld RS. 2018. Tritrophic interactions between a fungal pathogen, a spider predator, and the blacklegged tick. *Ecology and Evolution* 8:7824–7834.
Fitton MG, Shaw MR, Austin AD. 1987. The Hymenoptera associated with spiders in Europe. *Zoological Journal of the Linnean Society* 90:65–93.
Foelix RF. 2011. Biology of Spiders, 3rd ed. Oxford University Press, New York.
Foote BA. 1984. Biology of *Trimerina madizans*, a predator of spider eggs (Diptera: Ephydridae). *Proceedings of the Entomological Society of Washington* 86:486-492.
Forbes MR, Muma KE, Smith BP. 1999. Parasitism of *Sympetrum* dragonflies by *Arrenurus planus* mites: Maintenance of resistance particular to one species. *International Journal for Parasitology* 29:991–999.
Fruergaard S, Braad Lund M, Schramm A, Vosegaard T, Bilde T. 2021 in press. The myth of antibiotic spider silk, *iScience*, https://doi.org/10.1016/j.isci. 2021.103125
Fukuzawa AH, Vellutini BC, Lorenzini DM, Silva PI, Mortara RA, da Silva JMC, et al. 2008. The role of hemocytes in the immunity of the spider *Acanthoscurria gomesiana*. *Developmental & Comparative Immunology* 32:716–725.
Fuxa JR, Tanada Y. 1987. Epizootiology of Insect Diseases. Wiley-Interscience, New York, NY.
Fuzita FJ, Pinkse MWH, Patane JSL, Verhaert PDEM, Lopes AR. 2016. High throughput techniques to reveal the molecular physiology and evolution of digestion in spiders. *BMC Genomics* 17:716.
Gálvez D, Añino Y, Vega C, Bonilla E. 2020. Immune priming against bacteria in spiders and scorpions? *PeerJ* 8:e9285.
Gaver-Wainwright MM, Zack RS, Foradori MJ, Lavine LC. 2011. Misdiagnosis of spider bites: Bacterial associates, mechanical pathogen transfer, and hemolytic potential of venom from the hobo spider, *Tegenaria agrestis* (Araneae: Agelenidae). *Journal of Medical Entomology* 48:382–388.

Gilbert R, Uetz GW. 2016. Courtship and male ornaments as honest indicators of immune function. *Animal Behaviour* 117:97–103.

Gilbert R, Uetz GW. 2019. Male chemical cues as reliable indicators of infection in the wolf spider *Schizocosa ocreata*. *Ethology* 125:177–183.

Gilbert R, Karp RD, Uetz GW. 2016. Effects of juvenile infection on adult immunity and secondary sexual characters in a wolf spider. *Behavioral Ecology* 27:946–954.

Gillung JP, Borkent CJ. 2017. Death comes on two wings: a review of dipteran natural enemies of arachnids. *Journal of Arachnology* 45:1–19.

Gillung JP, Winterton SL. 2018. A review of fossil spider flies (Diptera: Acroceridae) with descriptions of new genera and species from Baltic Amber. *Journal of Systematic Palaeontology* 16:325–350.

Gonzaga MO, Kloss TJ, Sobczak JF. 2017. Host behavioural manipulation of spiders by ichneumonid wasps. Pp. 417–437. *In* Behaviour and Ecology of Spiders. (C Viera, MO Gonzaga (eds.)), Springer.

Goodacre SL. 2011. Endosymbiont infections in spiders. *Advances in Insect Physiology* 40:137–153.

Goodacre SL, Martin OY, Bonte D, Hutchings L, Woolley C, Ibrahim K, et al. 2009. Microbial modification of host long-distance dispersal capacity. *BMC Biology* 7:32.

Gregorič M, Kutnjak D, Bačnik K, Gostinčar C, Pecman A, Ravnikar M, et al. 2020. Spider webs as eDNA tool for biodiversity assessment of life's domains. bioRxiv: 2020.07.18.209999.

Gudowska A, Drobniak SM, Schramm BW, Labecka AM, Kozlowski J, Bauchinger U. 2016. Hold your breath beetle-mites! *Evolution* 70 249–255.

Halliday RB, Juvara-Bals I. 2016. Systematics and biology of the mite genus *Ljunghia* Oudemans in Southeast Asia (Acari: Laelapidae). *Systematic and Applied Acarology* 21:830–864.

Hanelt B, Thomas F, Schmidt-Rhaesa A. 2005. Biology of the phylum nematomorpha. *Advances in Parasitology* 59:243–305.

Hase T, Roberts LW, Hildebrandt PK, Cavanaugh DC. 1978. Stylostome formation by Leptotrombidium mites (Acari: Trombiculidae). *Journal of Parasitology* 64:712.

Haupt J. 2000. Fungal and rickettsial infections of some East Asian trapdoor spiders. *European Arachnology* 2000:45–49. Berlin.

Heimer S. 1988. Wunderbare Welt der Spinnen. Urania-Verlag.

Henschel JR. 1998. Predation on social and solitary individuals of the spider *Stegodyphus dumicola* (Araneae, Eresidae). *Journal of Arachnology* 26: 61–69.

Herbison R, Evans S, Doherty J-F, Algie M, Kleffmann T, Poulin R. 2019. A molecular war: convergent and ontogenetic evidence for adaptive host manipulation in related parasites infecting divergent hosts. *Proceedings of the Royal Society B: Biological Sciences* 286:20191827.

Howard RJ, Ferrari MA, Roach H, Money NP. 1991. Penetration of hard substrates by a fungus employing enormous turgor pressures. *Proceedings of the National Academy of Sciences of the United States of America* 88:11281–11284.

Hughes DP, Araújo JPM, Loreto RG, Quevillon L, de Bekker C, Evans HC. 2016. From so simple a beginning. The evolution of behavioral manipulation by fungi. Pp. 437–469. *In* Genetics and Molecular Biology of Entomopathogenic Fungi. (B Lovett, RJ St. Leger (eds.)), Elsevier.

Johnson D, Sung G-H, Hywel-Jones NL, Luangsa-Ard JJ, Bischoff JF, Kepler RM, et al. 2009. Systematics and evolution of the genus *Torrubiella* (Hypocreales, Ascomycota). *Mycological Research* 113:279–289.

Jones TC, Parker PG. 2000. Costs and benefits of foraging associated with delayed dispersal in the spider *Anelosimus studiosus* (Araneae, Theridiidae). *Journal of Arachnology* 28:61–70.

Kaiser E, Raab W. 1967. Collagenolytic activity of snake and spider venoms. *Toxicon* 4:251–255.

Keiser CN, DeMarco AE, Shearer TA, Robertson JA, Pruitt JN. 2015a. Putative microbial defenses in a social spider: immune variation and antibacterial properties of colony silk. *Journal of Arachnology* 43:394–399.

Keiser CN, Hammer TJ, Pruitt JN. 2019. Social spider webs harbour largely consistent bacterial communities across broad spatial scales. *Biology Letters* 15:20190436.

Keiser CN, Howell KA, Pinter-Wollman N, Pruitt JN. 2016a. Personality composition alters the transmission of cuticular bacteria in social groups. *Biology Letters* 12:20160297.

Keiser CN, Pinter-Wollman N, Ziemba MJ, Kothamasu KS, Pruitt JN. 2018. The primary case is not enough: Variation among individuals, groups and social networks modify bacterial transmission dynamics. *Journal of Animal Ecology* 87:369–378.

Keiser CN, Shearer TA, Demarco AE, Brittingham HA, Knutson KA, Kuo C, et al. 2016b. Cuticular bacteria appear detrimental to social spiders in mixed but not monoculture exposure. *Current Zoology* 62:377–384.

Keiser CN, Slyder JB, Carson WP, Pruitt JN. 2015b. Individual differences in predators but not producers mediate the magnitude of a trophic cascade. *Arthropod-Plant Interactions* 3:225–232.

Kepler RM, Luangsa-ard JJ, Hywel-Jones NL, Quandt CA, Sung G-H, Rehner SA, et al. 2017. A phylogenetically-based nomenclature for Cordycipitaceae (Hypocreales). *IMA Fungus* 8:335–353.

Kloss TG, Gonzaga MO, de Oliveira LL, Sperber CF. 2017. Proximate mechanism of behavioral manipulation of an orb-weaver spider host by a parasitoid wasp. *PLoS One* 12: e0171336.

Korenko S. 2017. Ecology of Spider Parasitoids: Koinobiont Ectoparasitoids from *Polysphincta* Genus Group (Ichneumonidae, Ephialtini). Palackỳ University Olomouc.

Korenko S, Pekár S. 2011. A parasitoid wasp induces overwintering behaviour in its spider host. *PLoS One* 6: e24628.

Korenko S, Potopová V, Satrapová J, Pekár S. 2016. Life history of the spider parasitoid *Zatypota percontatoria* (Hymenoptera: Ichneumonidae). *Entomological Science* 19:104–111.

Korenko S, Schmidt S, Schwarz M, Gibson GAP, Pekár S. 2013. Hymenopteran parasitoids of the ant-eating spider *Zodarion styliferum* (Simon) (Araneae, Zodariidae). *ZooKeys* 262:1–15.

Kring TJ, Young SY, Yearian WC. 1988. The striped lynx spider, *Oxyopes salticus* Hentz (Araneae: Oxyopidae), as a vector of a nuclear polyhedrosis virus in *Anticarsia gemmatalis* Hübner (Lepidoptera: Noctuidae). *Journal of Entomological Science* 23:394–398.

Kubátová A. 2004. The arachnogenous fungus *Gibellula leiopus* - second find from the Czech Republic. *Czech Mycol* 56:185–191.

Kuephadungphan W, Macabeo APG, Luangsa-ard JJ, Tasanathai K, Thanakitpipattana D, Phongpaichit S, et al. 2019. Studies on the biologically active secondary metabolites of the new spider parasitic fungus *Gibellula gamsii*. *Mycological Progress* 18:135–146.

Kuhn-Nentwig L, Nentwig W. 2013. The Immune System of Spiders. Pp. 81–91, *In* Spider Ecophysiology. (W Nentwig (ed.)), Springer, Berlin, Heidelberg.

Kuraishi T, Binggeli O, Opota O, Buchon N, Lemaitre B. 2011. Genetic evidence for a protective role of the peritrophic matrix against intestinal bacterial infection in *Drosophila melanogaster*. *Proceedings of the National Academy of Sciences of the United States of America* 108:15966–15971.

Lafferty KD, Kuris AM. 2002. Trophic strategies, animal diversity and body size. *Trends in Ecology and Evolution* 17:507-513.

Lafferty KD, Allesina S, Arim M, Briggs CJ, De Leo G, Dobson AP, et al. 2008. Parasites in food webs: the ultimate missing links. Ecology Letters 11: 533–546.

Lafferty KD, Dobson AP, Kuris AM. 2006. Parasites dominate food

web links. *Proceedings of the National Academy of Sciences of the United States of America* 103:11211–11216.
Leech RE. 1966. The spiders (Araneida) of Hazen Camp 81° 49′N, 71° 18′W. *Quaestiones Entomologicae* 2:153–212.
Lewbart GA. 2011. Invertebrate Medicine. Blackwell Publishing.
Li CX, Shi M, Tian JH, Lin XD, Kang YJ, Chen LG, et al. 2015. Unprecedented genomic diversity of RNA viruses in arthropods reveals the ancestry of negative-sense RNA viruses. *eLife* 2015.
Lorenzini DM, Fukuzawa AH, da Silva PI, Machado-Santelli G, Bijovsky AT, Daffre S. 2003. Molecular cloning, expression analysis and cellular localization of gomesin, an anti-microbial peptide from hemocytes of the spider *Acanthoscurria gomesiana*. *Insect Biochemistry and Molecular Biology* 33:1011–1016.
Lovett B, Macias A, Stajich JE, Cooley J, Eilenberg J, de F. Licht HH, et al. 2020a. Behavioral betrayal: How select fungal parasites enlist living insects to do their bidding. *PLoS Pathogens* 16:e1008598.
Lovett B, St. Leger RJ, de Fine Licht HH. 2020b. Going gentle into that pathogen-induced goodnight. *Journal of Invertebrate Pathology* 174:107398.
Machkour-M'Rabet S, Dor A, Hénaut Y. 2015. *Megaselia scalaris* (Diptera: Phoridae): an opportunistic endoparasitoid of the endangered Mexican redrump tarantula, *Brachypelma vagans* (Araneae: Theraphosidae). *Journal of Arachnology* 43:115–119.
Mąkol J, Felska M. 2011. New records of spiders (Araneae) as hosts of terrestrial Parasitengona mites (Acari: Actinotrichida: Prostigmata). *Journal of Arachnology* 39:352–354.
Mąkol J, Felska M, Król Z. 2017. New genus and species of microtrombidiid mite (Actinotrichida: Trombidioidea, microtrombidiidae) parasitizing spiders (Araneae: Araneidae) in Costa Rica. *Acarologia* 57:517–527.
Manfrino RG, González A, Barneche J, Tornesello Galván J, Hywell-Jones N, López Lastra CC. 2017. Contribution to the knowledge of pathogenic fungi of spiders in Argentina. Southernmost record in the world. *Revista Argentina de Microbiologia* 49:197–200.
Mason LD, Tomlinson S, Withers PC, Main BY. 2013. Thermal and hygric physiology of Australian burrowing mygalomorph spiders (*Aganippe* spp.). *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* 183:71–82.
Matsumoto R. 2009. "Veils" against predators: Modified web structure of a host spider induced by an ichneumonid parasitoid, *Brachyzapus nikkoensis* (Uchida) (Hymenoptera). *Journal of Insect Behavior* 22:39–48.
Matsumoto R, Konishi K. 2007. Life histories of two ichneumonid parasitoids of *Cyclosa octotuberculata* (Araneae): *Reclinervellus tuberculatus* (Uchida) and its new sympatric congener (Hymenoptera: Ichneumonidae: Pimplinae). *Entomological Science* 10:267–278.
McCormick S, Polis GA. 1982. Arthropods that prey on vertebrates. *Biological Reviews* 57:29–58.
McEwen BL, Lichtenstein JLL, Fisher DN, Wright CM, Chism GT, Pinter-Wollman N, et al. 2020. Predictors of colony extinction vary by habitat type in social spiders. *Behavioral Ecology and Sociobiology* 74:1–9.
McLean AHC, Godfray HCJ. 2015. Evidence for specificity in symbiont-conferred protection against parasitoids. *Proceedings of the Royal Society B: Biological Sciences* 282:1–8.
Meehan CJ, Olson EJ, Curry RL. 2008. PS 62-107: Exploitation of the *Pseudomyrmex-Acacia* mutualism by a predominantly vegetarian jumping spider (*Bagheera kiplingi*). 93rd ESA Annual Meeting.
Michalko R, Pekár S, Dul'a M, Entling MH. 2019. Global patterns in the biocontrol efficacy of spiders: A meta-analysis. *Global Ecology and Biogeography* 28:1366–1378.
Miyashita T, Maezono Y, Shimazaki A. 2004. Silk feeding as an alternative foraging tactic in a kleptoparasitic spider under seasonally changing environments. *Journal of Zoology* 262:225–229.
Monteiro CLB, Rubel R, Cogo LL, Mangili OC, Gremski W, Veiga SS. 2002. Isolation and identification of *Clostridium perfringens* in the venom and fangs of *Loxosceles intermedia* (brown spider): Enhancement of the dermonecrotic lesion in loxoscelism. *Toxicon* 40:409–418.
Moraza ML, Iraola V, Alemany C. 2009. A new species of *Ljunghia* Oudemans, 1932 (Arachnida, Acari, Laelapidae) from a mygalomorph spider. *Zoosystema* 31:117–126.
Morel G. 1978. Les maladies microbiennes des Arachnides (Acariens exceptés). Pp. 477–481. *In* Arachnology. 7th International Congress, Zoological Society of London Symposia 42. (P Merrett (ed.)), Academic Press, London.
Nielsen BO, Funch P, Toft S. 1999. Self-injection of a Dipteran parasitoid into a spider. *Naturwissenschaften* 86: 530–532.
Nixon S, Agwa, A, Robinson S, Walker A, Touchard A, Schroeder C, et al. 2020. Discovery and characterisation of novel peptides from Amazonian stinging ant venoms with antiparasitic activity. *Toxicon* 177:S60.
Noordam AP, Samson RA, Sudhaus W. 1998. Fungi and Nematoda on *Centromerus sylvaticus* (Araneae, Linyphiidae). Pp. 343–347. *In* Proceedings of the 17th European Colloquium of Arachnology, (PA Selden (ed.)), Edinburgh 1997.
Nyffeler M, Birkhofer K. 2017. An estimated 400-800 million tons of prey are annually killed by the global spider community. *Science of Nature* 104: 30.
O'Donnell KL, Common RS, Imshaug HA. 1977. A new species of *Torrubiella* on a spider from the Falkland Islands. *Mycologia* 69:618.
Ohba M, Aizawa K. 1979. Multiplication of Chilo iridescent virus in noninsect arthropods. *Journal of Invertebrate Pathology* 33:278–283.
Ohgushi T, Schmitz O, Holt RD. 2012. Trait-mediated Indirect Interactions: Ecological and Evolutionary Perspectives. Cambridge University Press.
Ortiz-Urquiza A, Keyhani NO. 2013. Action on the surface: entomopathogenic fungi versus the insect cuticle. *Insects* 4:357–374.
Parks OB, Kothamasu KS, Ziemba MJ, Benner M, Cristinziano M, Kantz S, et al. 2018. Exposure to cuticular bacteria can alter host behavior in a funnel-weaving spider. *Current Zoology* 64:721–726.
Pennacchio F, Caccia S, Digilio MC. 2014. Host regulation and nutritional exploitation by parasitic wasps. *Current Opinion in Insect Science* 6:74–79.
Penney D, Bennett S. 2006. First unequivocal Mermithid-Linyphiid (Araneae) parasite-host association. Journal of Arachnology 34:273–278.
Pflugfelder O. 1977. Wirttierreaktionen auf Zooparasiten. Gustav Fischer Verlag, New York.
Pizzi R. 2009. Parasites of tarantulas (Theraphosidae). *Journal of Exotic Pet Medicine* 18:283–288.
Poinar GO. 1975. Entomogenous Nematodes: a Manual and Lists of Insect-nematode Associations. E. J. Brill, Leiden, Netherlands.
Poinar GO. 1985. Mermithid (Nematoda) parasites of spiders and harvestmen. *Journal of Arachnology* 13:121–128.
Poinar GO. 1987. Nematode parasites of spiders. Pp. 299–308. *In* Ecophysiology of Spiders. (W. Nentwig (ed.)), Springer.
Poinar GO. 2000. *Heydenius araneus* n.sp. (Nematoda: Mermithidae), a parasite of a fossil spider, with an examination of helminths from extant spiders (Arachnida: Araneae). *Invertebrate Biology* 119:388–393.
Poinar GO. 2019. A Naturalist's Guide to Plant Communities of Pacific Northwest Dune Forests and Wetlands. Botanical Research Insitute of Texas.
Poinar GO, Benton CLB. 1986. *Aranimermis aptispicula* n. g., n. sp.

(Mermithidae: Nematoda), a parasite of spiders (Arachnida: Araneida). *Systematic Parasitology* 8:33–38.

Poinar GO, Early JW. 1990. A parasite of New Zealand mygalomorph spiders (Araneae: Arachnida). *Revue Nématologie* 13:403–410.

Poinar GO, Thomas GM. 1985. Laboratory infection of spiders and harvestmen (Arachnida: Araneae and Opiliones) with *Neoaplectana* and *Heterorhabditis* nematodes (Rhabditoidea). *Journal of Arachnology* 13:297–302.

Pollard SD. 1982. *Epipompilis insularis,* (Hymenoptera: Pompilidae), a parasitoid of hunting spiders. *New Zealand Journal of Zoology* 9:37–40.

Poulin R 2010. Parasite manipulation of host behavior: an update and frequently asked questions. *Advances in the Study of Behavior* 41:151–186.

Quicke DLJ. 2015. Idiobionts, koinobionts and other life history traits. Pp. 87–105. *In* The Braconid and Ichneumonid Parasitoid Wasps: Biology, Systematics, Evolution and Ecology. John Wiley & Sons, Ltd.

Redborg KE. 1998. Biology of the Mantispidae. *Annual Review of Entomology* 43:175–194.

Riechert SE, Lockley T. 1984. Spiders as biological control agents. *Annual Review of Entomology* 29:299–320.

Robaux P. 1974. Recherche sur le développement et la biologie des acariens "Thrombidiidae." *Mémoires du Muséum d'histoire Naturelle Paris* 85:1–186.

Rong E, Grobbelaar IH. 1998. South African records of associations between fungi and arthropods. *African Plant Protection* 4:43–63.

Rong IH, Botha A. 1993. New and interesting records of South African fungi XII. Synnematous Hyphomycetes. *South African Journal of Botany* 59: 514–518.

Roozbahani H, Asmar M, Ghaemi N, Issazadeh K. 2014. Evaluation of antimicrobial activity of spider silk *Pholcus phalangioides* against two bacterial pathogens in food borne. *International Journal of Advanced Biological and Biomedical Research* 2:2197–2199.

Rosario K, Dayaram A, Marinov M, Ware J, Kraberger S, Stainton D, et al. 2012. Diverse circular ssDNA viruses discovered in dragonflies (Odonata: Epiprocta). *Journal of General Virology* 93:2668–2681.

Rosario K, Mettel KA, Benner BE, Johnson R, Scott C, Yusseff-Vanegas SK, et al. 2018. Virus discovery in all three major lineages of terrestrial arthropods highlights the diversity of single-stranded DNA viruses associated with invertebrates. PeerJ 6:e5761.

Rosario K, Mettel KA, Greco AM, Breitbart M. 2019. Prevalence of a vertically transmitted single-stranded DNA virus in spinybacked orbweavers (*Gasteracantha cancriformis*) from Florida, USA. *Journal of General Virology* 100:1253–1265.

Roy S, Chattopadhyay J. 2005. Disease-selective predation may lead to prey extinction. *Mathematical Methods in the Applied Sciences* 28:1257–1267.

Saez NJ, Senff S, Jensen JE, Er SY, Herzig V, Rash LD, et al. 2010. Spider-venom peptides as therapeutics. *Toxins* 2:2851–2871.

Samson RA, Evans HC. 1992. New species of *Gibellula* on spiders (Araneida) from South America. *Mycologia* 84:300–314.

Sanad MM, Shamseldean MSM, Elgindi AEY, Gaugler R. 2013. Host penetration and emergence patterns of the mosquito-parasitic mermithids *Romanomermis iyengari* and *Strelkovimermis spiculatus* (Nematoda: Mermithidae). *Journal of Nematology* 45:30–38.

Sanchez-Contreras M, Vlisidou I. 2008. The diversity of insect-bacteria interactions and its applications for disease control. *Biotechnology and Genetic Engineering Reviews* 25:203–244.

Sanggaard KW, Dyrlund TF, Bechsgaard JS, Scavenius C, Wang T, Bilde T, et al. 2016. The spider hemolymph clot proteome reveals high concentrations of hemocyanin and von Willebrand factor-like proteins. *Biochimica et Biophysica Acta (BBA) - Proteins and Proteomics* 1864:233–241.

Satpathy S, Gotyal BS, Babu VR. 2020. Role of novel insecticides in crop protection and their selectivity to natural enemies: A review. *Journal of Environmental Biology* 41:149–160.

Schlinger EI. 1987. The biology of Acroceridae (Diptera): True endoparasitoids of spiders. Pp. 319–327. *In* Ecophysiology of Spiders. (W. Nentwig (ed.)), Springer.

Schlinger EI, Gillung JP, Borkent CP. 2013. New spider flies from the Neotropical Region (Diptera, Acroceridae) with a key to New World genera. *ZooKeys* 270:59–93

Schmitz A. 2016. Respiration in spiders (Araneae). *Journal of Comparative Physiology B* 186:403–415.

Schwendinger PJ, Ono H. 2011. On two *Heptathaela* species from southern Vietnam, with a discussion of copulatory organs and systematics of the Liphistiidae (Araneae: Mesothelae). *Revue Suisse de Zoologie* 118:599–637.

Shang Y, Feng P, Wang C. 2015. Fungi that infect insects: Altering host behavior and beyond. *PLoS Pathogens* 11:e1005037.

Sharma S. 2014. Investigation of Antimicrobial Properties of Spider Silk. University of Akron.

Shi M, Lin XD, Tian JH, Chen LJ, Chen X, Li CX, et al. 2016. Redefining the invertebrate RNA virosphere. *Nature* 540:539–543.

Shrestha B, Kubátová A, Tanaka E, Oh J, Yoon DH, Sung JM, et al. 2019. Spider-pathogenic fungi within Hypocreales (Ascomycota): their current nomenclature, diversity, and distribution. *Mycological Progress* 18:983–1003.

Six DL. 2013. The bark beetle holobiont: Why microbes matter. *Journal of Chemical Ecology* 39:989–1002.

Soares T, dos S. Cavalcanti MG, Ferreira FRB, do S. de M. Cavalcanti M, Alves LC, Brayner FA, et al. 2013. Ultrastructural characterization of the hemocytes of *Lasiodora* sp. (Koch, 1850) (Araneae: Theraphosidae). *Micron* 48:11–16.

Sorci G, Garnier S. 2018. Evolutionary ecology: Evolution of parasitism. *Encyclopedia of Ecology* 2:304–309.

Spicer ME, Pruitt JN, Keiser CN. 2019. Spiders, microbes and sex: Bacterial exposure on copulatory organs alters mating behaviour in funnel-web spiders. *Ethology* 125:677–685.

Stevens NB, Austin AD. 2007. Systematics, distribution and biology of the Australian "micro-flea" wasps,. *Zootaxa* 45:1–45.

Strickman D, Sithiprasasna R, Southard D. 1997. Bionomics of the spider, *Crossopriza lyoni* (Araneae, Pholcidae), a predator of Dengue vectors in Thailand. *Journal of Arachnology* 25:194–201.

Suchard JR. 2011. "Spider bite" lesions are usually diagnosed as skin and soft-tissue infections. *Journal of Emergency Medicine* 41:473–481.

Sunderland K. 1999. Mechanisms underlying the effects of spiders on pest populations. *Journal of Arachnology* 27:308–316.

Sung G-H, Hywel-Jones NL, Sung J-M, Luangsa-ard JJ, Shrestha B, Spatafora JW. 2007. Phylogenetic classification of *Cordyceps* and the clavicipitaceous fungi. *Studies in Mycology* 57: 5–59.

Sutherland TD, Young JH, Weisman S, Hayashi CY, Merritt DJ. 2009. Insect silk: One name, many materials. *Annual Review of Entomology* 55:171–188.

Sutti R, Rosa BB, Wunderlich B, da Silva Junior PI, da Rocha e Silva TAA. 2015. Antimicrobial activity of the toxin VdTX-I from the spider *Vitalius dubius* (Araneae, Theraphosidae). *Biochemistry and Biophysics Reports* 4: 324–328.

Szymkowiak P, Tsiareshyna M, Koczura R. 2020. Spider silk of *Linothele fallax* and *Linothele megatheloides* (Mygalomorphae, Dipluridae) does not affect the growth of bacteria. *Biologia* 75: 1679–1683.

Tahir HM, Zaheer A, Khan AA, Abbas M. 2018. Antibacterial potential of venom extracted from wolf spider, *Lycosa terrestris* (Araneae: Lycosiade). *Indian Journal of Animal Research* 52:286–290.

Takasuka K, Yasui T, Ishigami T, Nakata K, Matsumoto R, Ikeda K, et al. 2015. Host manipulation by an ichneumonid spider ectoparasitoid that takes advantage of preprogrammed web-building behaviour for its cocoon protection. *Journal of Experimental Biology* 218: 2326–2332.

Tan H, Ding X, Meng S, Liu C, Wang H, Xia L, et al. 2013. Antimicrobial potential of Lycosin-I, a cationic and amphiphilic peptide from the venom of the spider *Lycosa singorensis*. *Current Molecular Medicine* 13:900–910.

Tanada Y, Kaya HK (eds.). 1993. Insect Pathology, 1st ed. Academic Press.

Tanaka K, Watanabe M. 2003. Transmission of ice-nucleating active bacteria from a prey reduces cold hardiness of a predator (Araneae: Theridiidae). *Naturwissenschaften* 90:449–451.

Taylor LA, Amin Z, Maier EB, Byrne KJ, Morehouse NI. 2016. Flexible color learning in an invertebrate predator: *Habronattus* jumping spiders can learn to prefer or avoid red during foraging. *Behavioral Ecology* 27:520–529.

Thompson SA. 2020. Records of spider parasites in New Zealand. *Wētā* 54:65–72.

Toft S, Nielsen BO, Funch P. 2012. Parasitoid suppression and life-history modifications in a wolf spider following infection by larvae of an acrocerid fly. *Journal of Arachnology* 40:13–17.

Turnbull A. 1973. Ecology of true spiders (araneomorphae). *Annual Review of Entomology* 18:305–348.

Ul-Hasan S, Rodríguez-Román E, Reitzel AM, Adams RMM, Herzig V, Nobile CJ. 2019. The emerging field of venom-microbiomics for exploring venom as a microenvironment, and the corresponding Initiative for Venom Associated Microbes and Parasites (iVAMP). *Toxicon*: X 4: 100016.

Vanthournout B, Hendrickx F. 2015. Endosymbiont dominated bacterial communities in a dwarf spider. *PLoS One* 10: e0117297.

Vanthournout B, Swaegers J. 2011. Spiders do not escape reproductive manipulations by *Wolbachia*. *BMC Evolutionary Biology* 11:15.

Vetter RS. 2000. Myth: Idiopathic wounds are often due to brown recluse or other spider bites throughout the United States. *Western Journal of Medicine* 173:357–358.

Vetter RS, Bush SP. 2002. Reports of presumptive brown recluse spider bites reinforce improbable diagnosis in regions of North America where the spider is not endemic. *Clinical Infectious Diseases* 35:442–445.

Vetter RS, Swanson DL, Weinstein SA, White J. 2015. Do spiders vector bacteria during bites? the evidence indicates otherwise. *Toxicon* 93:171–174.

Viera C, Gonzaga MO (eds.). 2017. Behaviour and Ecology of Spiders: Contributions from the Neotropical Region. Springer International Publishing.

Vincent LS. 1985. The first record of a tachinid fly as an internal parasitoid of a spider (Diptera: Tachinidae; Araneae: Antrodiaetidae). *Pan Pacific Entomologist* 61:224–225.

Voigt B. 1970. Histologische untersuchungen am stylostome der Trombiculidae (Acari). *Zeitschrift fur Parasitenkunde* 34:180–190.

Walter DE, HC Proctor. 2013. Mites: Ecology, Evolution and Behaviour, 2nd ed. Springer, New York, NY.

Wang Z, Deng C, Yun Y, Jian C, Peng Y. 2010. Molecular detection and the phylogenetics of *Wolbachia* in Chinese spiders (Araneae). *Journal of Arachnology* 38:237–241.

Watkinson SC, Boddy L, Money N (eds.). 2015. The Fungi, 3rd edition. Academic Press.

Weinersmith KL. 2019. What's gotten into you?: a review of recent research on parasitoid manipulation of host behavior. *Current Opinion in Insect Science* 33:37–42.

Weinstein SB, Buck JC, Young HS. 2018. A landscape of disgust. *Science* 359:1213–1214.

Welbourn WC, Young OP. 1988. Mites parasitic on spiders, with a description of a new species of Eutrombidium (Acari, Eutrombidiidae). *Journal of Arachnology* 16:373–385.

Welti EAR, Prather RM, Sanders NJ, de Beurs KM, Kaspari M. 2020. Bottom-up when it is not top-down: Predators and plants control biomass of grassland arthropods. *Journal of Animal Ecology* 89:1286–1294.

Weygoldt P, Paulus HF. 1979. Untersuchungen zur morphologie, taxonomie, und phylogenie der Cherliceraten. II. Cladogramme und die entfaltung der Chelicerata. *Zeitschrift fur Zoologische Systematik und Evolutionsforschung* 17:177–200.

White JA, Styer A, Rosenwald LC, Curry MM, Welch KD, Athey KJ, et al. 2020. Endosymbiotic bacteria are prevalent and diverse in agricultural spiders. *Microbial Ecology* 79:472–481.

Windsor DA. 1998. Most of the species on earth are parasites. *International Journal for Parasitology* 28: 1939–1941.

Wise DH. 1993. Spiders in Ecological Webs. Cambridge University Press.

Wohltmann A. 2000. The evolution of life histories in Parasitengona (Acari: Prostigmata). *Acarologia* 41:145–204.

Wright S, Goodacre SL. 2012. Evidence for antimicrobial activity associated with common house spider silk. *BMC Research Notes* 5:326.

Wunderlich J. 2002. Ant mimicry by spiders and spider-mite interactions preserved in Baltic amber (Arachnida: Acari, Araneae). Pp. 355–358. *In* European Arachnology 2000: 19th European Colloquium of Arachnology.

Wyrobisz-Papiewska A, Kowal J, Łopieńska-Biernat E, Kornaś S, Basiaga M, Nosal P, et al. 2019. *Tarantobelus arachnicida* (Nematoda: Rhabditida) invasion of exotic spiders in Poland. Annals of parasitology 65: 83–86.

Yoder JA, Benoit JB, Christensen BS, Croxall TJ, Hobbs HH. 2009. Entomopathogenic fungi carried by the cave orb weaver spider, *Meta ovalis* (Araneae, Tetragnathidae), with implications for mycoflora transfer to cave crickets. *Journal of Cave and Karst Studies* 71:116–120.

Zare R, Gams W. 2001. A revision of Verticillium section Prostrata. VI. The genus *Haptocillium*. *Nova Hedwigia* 73: 271–292.

Zhang S, Piorkowski D, Lin WR, Lee YR, Liao CP, Wang PH, et al. 2019. Nitrogen inaccessibility protects spider silk from bacterial growth. *Journal of Experimental Biology* 222: jeb214981.

Zhang ZQ. 1998. Biology and ecology of Trombidiid mites (Acari: Trombidioidea). *Experimental and Applied Acarology* 22:139–155.

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