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Spiders as superhosts and secondary kleptoparasites

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Kleptoparasitism, broadly defined, is the *theft of extrinsic resources resulting in potential cost to the host*. The stealing of resources, often food gathered by another, is perhaps best known in birds and mammals, but is even more common and widespread in arthropods like ants, bees, flies and spiders. Spiders are involved in myriad kleptoparasitic interactions, best studied as obligatory kleptoparasites of other spiders. However, less attention has been paid to the critical role of spiders as “superhosts” to commensal and kleptoparasitic organisms, and their variety of facultative kleptoparasitic strategies. To understand obligatory kleptoparasitism in spiders, it is first necessary to examine their role and characteristics as hosts and as facultative kleptoparasites. Most spider kleptoparasites utilize other spiders as hosts, a link that is not coincidental, and facultative resource stealing, in its many forms, is generally assumed to provide an evolutionary bridge to obligate kleptoparasitism. Here, I provide a brief review of these two roles through a summary of literature on all kleptoparasitic spiders and over 200 hosts. The phylogenetic distribution of spider hosts is distinctly non-random, involving about 200 species, in 86 genera, and 23 families. These then pertain to a few select lineages, out of total spider diversity: 23/136 families, 86/4,427 genera, and 200/52,765 known species. The vast majority of argyrodine hosts belong to four Araneoidea families (Araneidae, Nephilidae, Theridiidae, Linyphiidae), while the majority of hosts of mysmenid kleptoparasites are mygalomorphs, mostly Dipluridae and Ischnothelidae. Key spider hosts like *Nephila*, *Trichonephila*, *Argiope*, *Cyrtophora*, and *Linothele*, build large, often structurally complex, and persistent webs. Three-dimensionality, often in the form of auxiliary webbing, provides safe refuges for kleptoparasites, and the abundant prey and extended prey handling time of large spiders provide resources and opportunities for theft. Many of the favored hosts either interlink webs or are social. Key host traits to counter kleptoparasitism include web takedown and relocation, food concealment, and direct aggression. Facultative resource stealing in spiders includes web takeover, male kleptoparasitism of females in webs, and opportunistic prey theft. Among these, kleptotany, the facultative abandonment of own web and the invasion of a larger host web, to steal it and/or to prey on the host (araneophagy) are the most likely to link to obligatory kleptoparasitism.

KEYWORDS

Kleptoparasitism, commensal, Theridiidae, spider webs, kleptotany

1 Introduction

1.1 Kleptoparasitism and kleptoparasite hosts

Kleptoparasitism is typically characterized by resource theft that comes at a cost to the host (Vollrath, 1987; Elgar, 1993; Iyengar, 2008). Scrounging may refer to individuals benefiting from food remnants left or ignored by the host, without direct conflict or the overt act of stealing valuable resources. Such behavior can occur in a social context and be tolerated or even cooperative. Yet, the apparent distinction between scrounging and kleptoparasitism is blurred, e.g. by the dynamic nature of many such foraging systems where the potential cost to the host ranges from negative to none (Trager et al., 2010, Figure 1) to potentially positive (Peng et al., 2013). When resources are limited the value of food items increases so that any theft may come at some cost. The same species may interact in environments, or during seasons, where resources are

abundant, and resource theft may occur less aggressively and have negligible impact on the host's energy budget. I emphasize kleptoparasitic systems where *theft of extrinsic resources results in potential cost to the host*. As pointed out by Coyle et al. (1991) while direct cost can be small and difficult to measure, even a single interruption where an invader distracts a host momentarily from feeding represents a potential cost to the host. As such, kleptoparasitism is usefully delimited from other forms of species-interactions that center on exploitation of innate properties of individuals (such as parasitism and predation) or involve intimate association of species that may be aggressive (competition over non-secured resources), or where species cohabit with neither player incurring even potential cost from overlapping resource use (commensalism, mutualism). The primary goal here is to set the stage for understanding the origin and evolution of obligatory kleptoparasitism and the ecological context that may render this strategy successful in the long term as an *evolutionarily stable strategy*. Pivotal to this endeavor is to examine facultative



FIGURE 1

The cost of resource theft to the 'host' varies dramatically across systems and can be challenging to estimate. Top: when hosts and kleptoparasites are comparable in size, the cost is high. Hyenas form packs that can sometimes steal prey captured by lions. The cost to the host is obvious and significant: a lion will risk fighting over the prey with potentially harmful consequences and may lose prey that is challenging to capture. Bottom: When kleptoparasites are tiny compared to the host their impact may be marginal. Left: a tiny argyrodine spider with the towering *Trichonephila* host in the background that as adults are over 100x its mass. Lower right: kleptoparasitic milichiid flies soak up some digestive fluids from the prey of a crab spider. The individual consumption of these small kleptoparasites has negligible impact on the host but collectively, over time, and in circumstances of low food availability, they still have the *potential* to reduce the host's fitness. Top, artwork modeled on a wirestock photo, lower left by I. Agnarsson, lower right by Jay Taylor.

kleptoparasitism as a strategy that is often presumed to precede—or be transitional to—the evolution of obligatory kleptoparasitism. It is also critical to understand the nature of hosts, whose relatively close relationships to kleptoparasites in numerous organisms (Wheeler, 1901; Iyengar, 2008) are not coincidental, but integral to the success of the strategy (a generalized form of Emery's rule, Emery 1909).

For kleptoparasites, resource theft may conserve energy that would otherwise be spent in foraging while simultaneously avoiding exposure to potentially hazardous prey or predators (Vollrath, 1987; Elgar, 1993; Iyengar, 2008). From the perspectives of the host, the cost of kleptoparasitism ranges from sublethal/lethal to minimal, even putatively positive, temporarily, and under certain circumstances. The potential cost and the long-term interaction of kleptoparasite and host, regardless, is expected to result in an arms race and the evolution of adaptive traits in the host to respond to kleptoparasite selection pressures.

1.2 The scope of this review

I initially envisioned this invited review as an opportunity for a comparative synthesis of kleptobiosis across the tree of life—through the eyes of spiders. During months of effort, I gradually started to appreciate the gargantuan size and challenge of such a task. On the one hand, inordinately vast literature must be surveyed that offers a great wealth of information on different taxa and strategies. On the other hand, despite its volume, the literature is incredibly sparse on the most pertinent data needed for such meta-analyses, namely phylogenetic context. As for most lineages, this information is also largely lacking for spiders (but see Su and Smith, 2014). I therefore shifted my focus to a synthesis of kleptoparasitism involving spiders, but this too turned out to be elusive. Spiders are involved in a great variety of kleptoparasitic interactions both as hosts to a great variety of kleptoparasitic lineages, as well as containing many species involved both in facultative as well as obligatory kleptoparasitism (Table 1; Supplementary Table S1). The scope of this paper is therefore focused on providing a platform for understanding obligatory kleptoparasitism through a review of spiders as hosts to kleptoparasitic groups, including facultatively kleptoparasitic spiders. I highlight some of the ways in which spiders are unique and important hosts for multiple lineages of kleptoparasites, defensive host strategies, and the variety of opportunistic kleptoparasitism seen across the order. Facultative kleptoparasitism is probably extremely widespread in spiders, with scattered records that I attempt to summarize. Araneophagy through web invasion is seen in several lineages, perhaps best known in salticids like *Portia*. Such behavior has been reviewed before (e.g. Jackson, 1986) and does not seem to be explicitly linked to kleptoparasitism in general, with the possible exception of the argyrodine theridiids where both traits occur. Therefore, I offer a brief overview to summarize the variety of web invasion behaviors in spiders, with emphasis on those that may be linked to the origin and evolution of kleptoparasitism.

Are there emerging shared patterns in the evolutionary 'pathways' to obligate kleptoparasitism across the countless independent evolutionary origins of kleptoparasitism? This

question is challenging to answer and to do so properly, requires phylogenetic comparative meta-analyses that will not be attempted here and may be as yet unachievable given scattered phylogenetic knowledge of the various lineages. An obvious and often cited hypothesis is that obligatory kleptoparasitism has transitioned from facultative kleptoparasitism (Iyengar, 2008; Breed et al., 2012). Such a route where opportunistic resource theft as a part of a broader foraging strategy can act as an evolutionary bridge to obligate kleptoparasitism is intuitively appealing. Candidate examples may come from *Koptothrips* thrips initially utilizing damaged galls then moving to actively usurping intact galls (Crespi and Abbot, 1999), *Lestrimellita* stingless bees gradually losing pollen-gathering structures to become reliant solely on stolen food (Breed et al., 2012), sphaerocerid flies that range from facultatively stealing food from scavengers like dung beetles to specialized reliance on host (Sirvinski et al., 1999), and *Ranzovius* bugs that belong to a lineage containing many facultative kleptoparasites but where some species have become entirely reliant on their social spider hosts to capture prey (Henry, 1984; Wheeler and McCaffrey, 1984). In other cases, like spiders, such a transition between facultative and obligate kleptoparasitism is not obvious given the evidence at hand. Another hypothesis that may be specific to spiders suggests an evolutionary link between stealing from or predating on a host, though the direction of such transition is debated, and in fact, this link has not been clearly established (but see Su and Smith, 2014, and below).

Kleptoparasitism exemplifies the complex interplay between ecological opportunity, behavioral flexibility, and evolutionary adaptation. This versatile strategy has evolved independently across diverse taxa implying important ecological function and fitness consequences favored by natural selection. Below I provide the groundwork necessary to further our understanding of obligatory kleptoparasitism in spiders.

2 Spider superhosts: webs provide refuge and resources

2.1 Spider webs as habitats

Spider webs vary greatly in their size and web tenacity (Eberhard, 2020). Larger and more permanent webs may form habitats for a variety of arthropods, including other spiders (Figure 2). Webs provide a stable environment rich in resources such as shelter, prey remnants, and protection from environmental extremes (Eberhard, 2020), attracting a range of organisms that engage in complex interactions with their spider hosts. Proctor (1992), for example, discussed the co-inhabitants in colonial *Cyrtophora moluccensis* webs in Moorea, French Polynesia. In five *Cyrtophora* colonies she found five additional spider species whose combined abundance far outnumbered the host spiders. These included web builders using *Cyrtophora* webs as support, as well as the kleptoparasitic *Argyrodes argentatus* and the likely araneophagic *Platnickina adamsoni*. Social spider webs form an even more diverse habitat, for example the webs of *Anelosimus*

TABLE 1 Known hosts among spiders (see [Supplementary Table S1](#) for detail).

Hosts	Kleptoparasites
MYGALOMORPHAE	
Dipluridae Simon, 1889	
<i>Diplura</i> C. L. Koch, 1850	<i>Curimagua bayano</i> , <i>Mysmenopsis cidrelicola</i> , <i>M. dipluramigo</i> , <i>M. gamboa</i>
<i>Linothele pukachumpi</i> Dupérré & Tapia, 2015	<i>Mysmenopsis otonga</i>
<i>Linothele quori</i> Dupérré & Tapia, 2015	<i>Mysmenopsis chiquita</i> , <i>M. fernandoi</i>
<i>Linothele tsachilas</i> Dupérré & Tapia, 2015	<i>Mysmenopsis awa</i> , <i>M. cube</i> , <i>M. lasrocas</i> , <i>M. fernandoi</i>
<i>Linothele yanachanka</i> Dupérré & Tapia, 2015	<i>Mysmenopsis fernandoi</i> , <i>M. onorei</i>
<i>Linothele zaia</i> Dupérré & Tapia, 2015	<i>Mysmenopsis fernandoi</i>
<i>Linothele</i> Karsch, 1879 indet.	<i>Faiditus atopus</i> , <i>Mysmenopsis alvaroi</i> , <i>M. angamarca</i> , <i>M. atahualpa</i> , <i>M. baerti</i> , <i>M. bartolozzii</i> , <i>M. choco</i> , <i>M. corazon</i> , <i>M. guaniza</i> , <i>M. hunachi</i> , <i>M. junin</i> , <i>M. lloa</i> , <i>M. otonga</i> , <i>M. otokiki</i> , <i>M. pululahua</i> , <i>M. salazarae</i> , <i>M. shushufindi</i> , <i>M. tepuy</i> , <i>M. tungurahua</i>
Dipluridae Simon, 1889 indet.	<i>Mysmenopsis huascar</i> , <i>M. pachacutec</i> , <i>Portia</i> sp.
Euagridae Raven, 1979	
<i>Allothele teretis</i> Tucker, 1920	<i>Isela okuncana</i>
Ischnothelidae F. O. P.-Cambridge, 1897	
<i>Ischnothele annulata</i> Tullgren, 1905	<i>Mysmenopsis ischnamigo</i>
<i>Ischnothele caudata</i> Ausserer, 1875	<i>Mysmenopsis dipluramigo</i> , <i>M. ischnamigo</i>
<i>Ischnothele digitata</i> (O. P.-Cambridge, 1892)	<i>Mysmenopsis palpalis</i>
<i>Ischnothele goloboffi</i> Coyle, 1995	<i>Mysmenopsis ischnamigo</i>
<i>Ischnothele guianensis</i> (Walckenaer, 1837)	<i>Mysmenopsis ischnamigo</i> , <i>M. gamboa</i>
<i>Ischnothele longicauda</i> Franganillo, 1930	<i>Mysmenopsis tibialis</i> , <i>Philoponella semiplumosa</i>
<i>Ischnothele reggae</i> Coyle & Meigs, 1990	<i>Mysmenopsis monticola</i>
<i>Ischnothele xera</i> Coyle & Meigs, 1990	<i>Mysmenopsis furtiva</i>
<i>Ischnothele</i> Ausserer, 1875 indet.	<i>Modisimus</i> sp., <i>Mysmenopsis furtiva</i> , <i>M. monticola</i>
<i>Thelacantha brevispina</i> (Doleschall, 1857)	<i>Argyroides argentatus</i>
<i>Thelechoris striatipes</i> (Simon, 1889)	<i>Isela inquilina</i>
SYNSPERMIATA	
Diguetidae F. O. P.-Cambridge, 1899	
<i>Diguetia</i> Simon, 1895	<i>Neospintharus baboquivari</i> (Exline & Levi, 1962), <i>Latrodectus</i> sp.
Pholcidae C. L. Koch, 1850	
<i>Holcnemus pluchei</i> (Scopoli, 1763)	<i>Argyroides argyroides</i> , <i>Holcnemus pluchei</i>
<i>Mesabolivar cyaneotaeniatus</i> (Keyserling, 1891)	<i>Mysmenopsis archeri</i>
<i>Mesabolivar togatus</i> (Keyserling, 1891)	<i>Mysmenopsis archeri</i>
<i>Mesabolivar</i> González-Sponga, 1998	<i>Mesabolivar</i> sp.
<i>Modisimus</i> Simon, 1893 indet.	<i>Modisimus</i> sp.
<i>Pholcus phalangioides</i> (Fuesslin, 1775)	<i>Argyroides antipodianus</i>
<i>Pholcus</i> Walckenaer, 1805 indet.	<i>Argyroides tripunctatus</i> , <i>Pholcus</i> sp.
Pholcidae C. L. Koch, 1850 indet.	<i>Argyrodella pusilla</i> , <i>Argyroides gracilis</i> , <i>Neospintharus syriacus</i> , <i>Rho. sagana</i>
Segestriidae Simon, 1893	

(Continued)

TABLE 1 Continued

Hosts	Kleptoparasites
Segestriidae Simon, 1893 indet.	<i>Portia</i> sp.
CY-SPIGOT CLADE	
Austrochilidae Zapfe, 1955	
Austrochilidae Zapfe, 1955 indet.	<i>Sofanapis antillanca</i>
<i>Thaida</i> Karsch, 1880 indet.	<i>Sofanapis antillanca</i>
ENTELEGYNAE	
ARANEOIDEA	
Araneidae Clerck, 1757	
<i>Aculepeira armida</i> (Audouin, 1826)	<i>Argyrodes argyrodes</i>
<i>Araneus bogotensis</i> (Keyserling, 1864)	<i>Argyrodes elevatus</i>
<i>Araneus cavaticus</i>	<i>Argyrodes elevatus</i>
<i>Araneus diadematus</i> Clerck, 1757	<i>Argyrodes antipodanus</i> , <i>A. nephilae</i>
<i>Araneus marmoreus</i> Clerck, 1757	<i>Argyrodes elevatus</i>
<i>Araneus pegnia</i> (Walckenaer, 1841)	<i>Argyrodes elevatus</i> , <i>A. nephilae</i>
<i>Araneus thaddeus</i> (Hentz, 1847)	<i>Argyrodes elevatus</i> , <i>A. nephilae</i>
<i>Araneus venatrix</i> (C.L. Koch, 1838)	<i>Argyrodes elevatus</i>
<i>Araneus ventricosus</i> (L. Koch, 1878)	<i>Argyrodes bonadea</i> , <i>A. cylindratus</i> , <i>A. flavescens</i>
<i>Araneus</i> Clerck, 1757 indet.	<i>Argyrodes bonadea</i> , <i>A. flavescens</i> , <i>Neospintharus trigonum</i> , <i>Rhomphaea fictitium</i> , <i>R. sp.</i>
<i>Araniella cucurbitina</i>	<i>Pholcus</i> sp.
<i>Araniella displicata</i> (Hentz, 1847)	<i>Araniella displicata</i>
<i>Argiope aemula</i>	<i>Argyrodes bonadea</i> , <i>A. flavescens</i>
<i>Argiope amoena</i> L. Koch, 1878	<i>Argyrodes bonadea</i>
<i>Argiope anasuja</i> Thorell, 1887	<i>Argyrodes argentatus</i> , <i>A. flavescens</i>
<i>Argiope appensa</i> (Walckenaer, 1841)	<i>Argyrodes argentatus</i> , <i>A. argyrodes</i>
<i>Argiope argentata</i> (Fabricius, 1775)	<i>Argyrodes elevatus</i> , <i>Faiditus caudatus</i> , <i>F. dracus</i> , <i>F. leonensis</i>
<i>Argiope aurantia</i> Lucas, 1833	<i>Argyrodes pluto</i> , <i>Faiditus cancellatus</i> , <i>F. globosus</i> , <i>Neospintharus trigonum</i> , <i>Salticidae</i> , <i>Argiope aurantia</i> , <i>A. trifasciata</i>
<i>Argiope bruennichi</i> (Scopoli, 1772)	<i>Argyrodes bonadea</i> , <i>A. miniaceus</i>
<i>Argiope florida</i> Chamberlin & Ivie, 1944	<i>Argyrodes</i> sp.
<i>Argiope lobata</i> (Pallas, 1772)	<i>Argyrodes argyrodes</i>
<i>Argiope minuta</i> Karsch, 1879	<i>Argyrodes bonadea</i> , <i>A. flavescens</i>
<i>Argiope pulchella</i> Thorell, 1881	<i>Argyrodes flavescens</i>
<i>Argiope sector</i> (Forsskal, 1776)	<i>Argyrodes argyrodes</i>
<i>Argiope trifasciata</i> (Forsskal, 1775)	<i>Argyrodes argyrodes</i> , <i>Rhomphaea</i> sp.
<i>Argiope</i> Audouin, 1826 indet.	<i>Argyrodes antipodanus</i> , <i>A. nephilae</i> , <i>A. scapulatus</i> , <i>Faiditus cochleaforma</i> , <i>Rhinoliparus rainbowi</i> , <i>Rhomphaea projiciens</i> , <i>Argiope</i>
<i>Caerostris darwini</i> Kuntner & Agnarsson, 2010	<i>Argyrodes</i> spp.
<i>Cyclosa confusa</i> Bösenberg & Strand, 1906	<i>Argyrodes bonadea</i> , <i>A. flavescens</i>
<i>Cyclosa huila</i> Levi, 1999 colonial	<i>Argyrodes elevatus</i>
<i>Cyclosa insulana</i> (Costa, 1834)	<i>Argyrodes argyrodes</i> , <i>Rhinoliparus kulczynskii</i>

(Continued)

TABLE 1 Continued

Hosts	Kleptoparasites
<i>Cyclosa mulmeinensis</i>	<i>Argyrodes bonadea</i>
<i>Cyclosa trilobata</i> (Urquhart, 1885)	<i>Argyrodes antipodianus</i>
<i>Cyclosa</i> Menge, 1866 indet.	<i>Argyrodes bonadea</i> , <i>A. gracilis</i> , <i>A. miniaceus</i>
<i>Cyrtophora citricola</i> (Forsskål, 1775)	<i>Argyrodella pusilla</i> , <i>Argyrodes argentatus</i> , <i>A. argyroides</i> , <i>A. insectus</i> , <i>A. nephilae</i> , <i>A. rostratus</i> , <i>Neospintharus syriacus</i> , <i>Cyrtophora citricola</i> , <i>Holocnemus pluchei</i> , <i>Pa. tepidariorum</i> , <i>Rhomphaea longicaudata</i>
<i>Cyrtophora cylindroides</i> (Walckenaer, 1841)	<i>Argyrodes fissifrons</i> , <i>Leucauge granulata</i>
<i>Cyrtophora exanthematica</i> (Doleschall, 1859)	<i>Argyrodes fissifrons</i>
<i>Cyrtophora hirta</i> L. Koch, 1872	<i>Argyrodes alannae</i> , <i>A. antipodianus</i> , <i>A. incisifrons</i> , <i>Rhinoliparus rainbowi</i>
<i>Cyrtophora ikomosanensis</i> (Bös. & Strand, 1906)	<i>Argyrodes fissifrons</i> , <i>A. kumadai</i> , <i>Leucauge granulata</i>
<i>Cyrtophora moluccensis</i> (Doleschall, 1857)	<i>Argyrodes alannae</i> , <i>A. antipodianus</i> , <i>A. argentatus</i> , <i>A. argyroides</i> , <i>A. bonadea</i> , <i>A. fissifrons</i> , <i>A. flavescens</i> , <i>A. gracilis</i> , <i>A. kumadai</i> , <i>A. nephilae</i> , <i>A. samoensis</i> , <i>A. unimaculatus</i> , <i>Pa. tepidariorum</i> , <i>Platnickina adamsoni</i> , <i>Rhinoliparus rainbowi</i> , <i>Cyrtophora moluccensis</i> , <i>Leucauge granulata</i> , <i>L. blanda</i> , <i>Lehtineniana tahitiensis</i> , <i>Uloborus</i> , <i>Pholcus ancoralis</i>
<i>Cyrtophora unicolor</i> (Doleschall, 1857)	<i>Argyrodes bonadea</i> , <i>A. fissifrons</i>
<i>Cyrtophora</i> Simon, 1864 indet.	<i>Argyrodes fasciatus</i> , <i>A. fissifrons</i> , <i>Mysmenopsis capac</i> , <i>M. cienaga</i> , <i>Neospintharus borbonicus</i> , <i>N. cognatus</i> , <i>Rhinocosmetus argentatus</i> , <i>R. kulczynskii</i> , <i>R. lanyuensis</i> , <i>R. nafithiamae</i> , <i>Philoponella vittata</i>
<i>Eriophora</i> Simon, 1864 indet.	<i>Argyrodes elevatus</i> , <i>Faiditus amplifrons</i>
<i>Eriovixia</i> Archer, 1951 indet.	<i>Rhomphaea</i> sp.
<i>Gasteracantha cancriformis</i> (Linnaeus, 1758)	<i>Argyrodes elevatus</i> , <i>A. flavescens</i> , <i>A. nephilae</i> , <i>Faiditus cochleaforma</i> , <i>F. cordillera</i> , <i>F. globosus</i> , <i>Rhinoliparus lanyuensis</i>
<i>Gasteracantha kuhli</i> C. L. Koch, 1837*	<i>Argyrodes bonadea</i> , <i>A. flavescens</i>
<i>Gasteracantha taeniata</i> (Walckenaer, 1841)	<i>Rhinoliparus kulczynskii</i>
<i>Gasteracantha theisi</i> Guérin, 1838	<i>Rhinoliparus kulczynskii</i>
<i>Gasteracantha Sundevall</i> , 1833 indet.	<i>Argyrodes antipodianus</i> , <i>A. argentatus</i> , <i>A. cylindricus</i> , <i>A. flavescens</i> , <i>Faiditus proboscifer</i> , <i>Rhinoliparus lanyuensis</i>
<i>Hortophora transmarina</i> (Keyserling, 1865)	<i>Argyrodes antipodianus</i> , <i>Rhinoliparus rainbowi</i>
<i>Lariniaria argiopiformis</i> (Bös. & Strand, 1906)	<i>Lariniaria argiopiformis</i>
<i>Larinioides cornutus</i> (Clerck, 1757)	<i>Faiditus cancellatus</i> , <i>Eustala</i> sp., <i>Larinioides cornutus</i> , <i>Tetragnatha laboriosa</i>
<i>Leviana dimidiata</i> (L. Koch, 1871)	<i>Rhinoliparus rainbowi</i>
<i>Lipocrea epeiroides</i> (O. P.-Cambridge, 1872)	<i>Rhomphaea nasica</i>
<i>Manogeta porracea</i> (C. L. Koch, 1838)	<i>Argyrodes elevatus</i> , <i>Faiditus caudatus</i> , <i>Gelanor zonatus</i> , <i>Mimetes</i> sp.
<i>Mecynogea lemniscata</i> (Walckenaer, 1841)	<i>Argyrodes elevatus</i> , <i>A. nephilae</i> , <i>Faiditus cancellatus</i> , <i>F. caudatus</i> , <i>F. leonensis</i> , <i>Neospintharus concisus</i> , <i>N. furcatus</i> , <i>N. trigonum</i>
<i>Metazygia gregalis</i> (O. P.-Cambridge, 1889)	<i>Eustala fuscovittata</i> , <i>Larinia directa</i> , <i>Metazygia gregalis</i> , <i>Tetragnatha</i> sp.
<i>Metazygia pallidula</i> (Keyserling, 1864)	<i>Eustala</i> sp.
<i>Metazygia zilloides</i> (Banks, 1898)	<i>Metazygia dubia</i>
<i>Metazygia</i> F. O. P.-Cambridge, 1904 indet.	<i>Rhomphaea projiciens</i>
<i>Metepeira incrassata</i> F. O. P.-Cambridge, 1903	<i>Argyrodes elevatus</i> , <i>Faiditus caudatus</i> , <i>F. leonensis</i> , <i>Neospintharus concisus</i> , <i>N. furcatus</i> , <i>Rhomphaea projiciens</i> , <i>Mecynogea lemniscata</i> , <i>Metazygia gregalis</i> , <i>Leucauge</i> sp., <i>Trichonephila clavipes</i>
<i>Metepeira labyrinthica</i> (Hentz, 1847)	<i>Argyrodes pluto</i> , <i>Faiditus cancellatus</i> , <i>Neospintharus trigonum</i> , <i>Metepeira labyrinthica</i>
<i>Micrathena clypeata</i> (Walckenaer, 1805)	<i>Faiditus amplifrons</i>
<i>Micrathena gracilis</i> (Walckenaer, 1805)*	<i>Argyrodes elevatus</i> , <i>Faiditus caudatus</i> , <i>F. leonensis</i> , <i>Neospintharus concisus</i> , <i>N. furcatus</i>
<i>Micrathena sagittata</i> (Walckenaer, 1841)	<i>Faiditus cancellatus</i>
<i>Micrathena schreibersi</i> (Perty, 1833)	<i>Faiditus amplifrons</i>

(Continued)

TABLE 1 Continued

Hosts	Kleptoparasites
<i>Neoscona adianta</i>	<i>Argyrodes argyroides</i>
<i>Neoscona arabesca</i> (Walckenaer, 1841)	<i>Larinioides cornutus</i>
<i>Neoscona crucifera</i> (Lucas, 1838)	<i>Argyrodes argyroides</i> , <i>A. elevatus</i>
<i>Neoscona domiciliorum</i> (Hentz, 1847)	<i>Argyrodes elevatus</i> , <i>A. nephilae</i> , <i>Faiditus cancellatus</i> , <i>F. globosus</i>
<i>Neoscona inusta</i> (L. Koch, 1871)	<i>Neoscona inusta</i>
<i>Neoscona nautica</i> (L. Koch, 1875)	<i>Argyrodes nephilae</i>
<i>Neoscona punctigera</i> (Doleschall, 1857)	<i>Neoscona punctigera</i>
<i>Neoscona sacra</i> (Walckenaer, 1841)	<i>Argyrodes nephilae</i>
<i>Neoscona scylla</i> (Karsch, 1879)	<i>Argyrodes bonadea</i> , <i>A. flavescens</i>
<i>Neoscona subpullata</i> (Bös. & Strand, 1906)	<i>Argyrodes bonadea</i> , <i>A. flavescens</i>
<i>Neoscona theisi</i> (Walckenaer, 1841)	<i>Argyrodes bonadea</i> , <i>A. flavescens</i>
<i>Neoscona</i> Simon, 1864 indet.	<i>Argyrodes argentatus</i> , <i>A. bonadea</i>
<i>Nuctenea umbratica</i> (Clerck, 1757)	<i>Pholcus</i> sp.
<i>Parawixia dehaani</i>	<i>Parawixia dehaani</i>
<i>Phonognatha graeffei</i> (Keyserling, 1865)	<i>Argyrodes alannae</i> , <i>A. antipodanus</i> , <i>A. samoensis</i> , <i>Rhinoliparus rainbowi</i>
<i>Phonognatha neocaledonica</i> Berland, 1924	<i>Rhinoliparus neocaledonicus</i>
<i>Plebs</i> Joseph & Framenau, 2012	<i>Spheropistha miyashitai</i>
<i>Socca pustulosa</i> (Walckenaer, 1841)	<i>Argyrodes antipodanus</i>
<i>Thelacantha brevispina</i> (Doleschall, 1857)	<i>Argyrodes argentatus</i> , <i>A. flavescens</i> , <i>A. nephilae</i>
<i>Verrucosa arenata</i> (Walckenaer, 1841)	<i>Faiditus cancellatus</i> , <i>F. globosus</i>
<i>Zealaranea crassa</i> (Walckenaer, 1841)	<i>Argyrodes antipodanus</i>
<i>Zygiella x-notata</i> (Clerck, 1757)	<i>Argyrodes argyroides</i> , <i>Pholcus</i> sp., <i>Zygiella x-notata</i>
Araneidae Clerck, 1757 indet.	<i>Argyrodes argentatus</i> , <i>Faiditus globosus</i> , <i>Neospintharus fur</i> , <i>Portia</i> sp., <i>Sofanapis antillanca</i> , <i>Rhomphaea nasica</i>
Nephilidae Simon, 1894	
<i>Clitaetra irenae</i> Kuntner, 2006	<i>Rugathodes</i> sp.
<i>Nephila pilipes</i> (Fabricius, 1793)	<i>Argyrodes antipodanus</i> , <i>A. argentatus</i> , <i>A. argyroides</i> , <i>A. bonadea</i> , <i>A. flavescens</i> , <i>A. miniaceus</i> , <i>Rhinocosmetus xiphias</i> , <i>Rhinoliparus kulczynskii</i> , <i>R. lanyuensis</i> , <i>Platnickina sterninotata</i> , <i>Rhomphaea</i> , <i>N. pilipes</i>
<i>Nephila</i> Leach, 1815 indet.	<i>Argyrodes bonadea</i> , <i>A. cylindratus</i> , <i>A. fasciatus</i> , <i>A. miniaceus</i> , <i>A. tripunctatus</i> , <i>Rhinocosmetus argentatus</i> , <i>Rhinoliparus nafithiamae</i> *
<i>Nephilengys malabarensis</i> (Walckenaer, 1841)	<i>Argyrodes flavescens</i> , <i>A. miniaceus</i> , <i>Portia fimbriata</i>
<i>Nephilengys</i> L. Koch, 1872 indet.	<i>Argyrodes antipodanus</i> , <i>A. tripunctatus</i>
<i>Nephilingis borbonica</i> (Vinson, 1863)	<i>Argyrodes</i> sp., <i>A. zonatus</i> , <i>Neospintharus borbonicus</i>
<i>Nephilingis cruentata</i> (Fabricius, 1775)	<i>Argyrodella pusilla</i> , <i>A. elevatus</i> , <i>A. fissifrontellus</i> , <i>A. rostratus</i> , <i>Neospintharus cognatus</i>
<i>Nephilingis dodo</i> (Kuntner & Agnarsson, 2011)	<i>Argyrodes argyroides</i> , <i>A. zonatus</i>
<i>Nephilingis livida</i> (Vinson, 1863)	<i>Argyrodes argyroides</i>
<i>Trichonephila clavata</i> (L. Koch, 1878)	<i>Argyrodes bonadea</i> , <i>A. flavescens</i> , <i>A. projeles</i> , <i>Spheropistha miyashitai</i> , <i>Platnickina sterninotata</i> , <i>Rhomphaea</i> sp.
<i>Trichonephila clavipes</i> (Linnaeus, 1767)	<i>Argyrodes elevatus</i> , <i>A. nephilae</i> , <i>A. minax</i> , <i>Faiditus acuminatus</i> , <i>F. altus</i> , <i>F. americanus</i> , <i>F. amplifrons</i> , <i>F. atopus</i> , <i>F. benedicti</i> , <i>F. cancellatus</i> , <i>F. caronae</i> , <i>F. caudatus</i> , <i>F. dracus</i> , <i>F. globosus</i> , <i>F. leonensis</i> , <i>F. mariae</i> , <i>F. morretensis</i> , <i>F. ululans</i> , <i>Neospintharus concisus</i> , <i>N. furcatus</i> , <i>N. trigonum</i> , <i>Philoponella tingens</i> , <i>Trichonephila clavipes</i>
<i>Trichonephila edulis</i> (Labillardière, 1799)	<i>Argyrodes antipodanus</i>

(Continued)

TABLE 1 Continued

Hosts	Kleptoparasites
<i>Trichonephila inaurata</i> (Walckenaer, 1841)	<i>Argyrodella pusilla</i> , <i>Argyroides argyroides</i> , <i>A. convivans</i> , <i>A. fissifrontellus</i> , <i>A. rostratus</i> , <i>A. sextuberculosus</i> , <i>A. stridulator</i> , <i>A. zonatus</i>
<i>Trichonephila plumipes</i> (Latreille, 1804)	<i>Argyroides alannae</i> , <i>A. antipodianus</i> , <i>A. miniaceus</i> , <i>Rhinoliparus kulczynskii</i> , <i>R. rainbowi</i> , <i>T. plumipes</i>
<i>Trichonephila senegalensis</i> (Walckenaer, 1841)	<i>Argyroides insectus</i>
<i>Trichonephila</i> Dahl, 1911 indet.	<i>Argyroides miniaceus</i> , <i>Rhinocosmetus argentatus</i> , <i>Rhinoliparus nafithiamae</i>
Tetragnathidae Menge, 1866	
<i>Leucauge argyra</i> (Walckenaer, 1841)	<i>Faiditus globosus</i>
<i>Leucauge argyrobapta</i> (White, 1841)	<i>Rhomphaea</i> sp.
<i>Leucauge blanda</i> (L. Koch, 1878)	<i>Argyroides bonadea</i> , <i>A. flavescens</i>
<i>Leucauge celebesiana</i> (Walckenaer, 1841)	<i>Rhomphaea</i> sp.
<i>Leucauge dromedaria</i> (Thorell, 1881)	<i>Argyroides antipodianus</i>
<i>Leucauge fastigata</i> (Simon, 1877)	<i>Rhomphaea</i> sp.
<i>Leucauge mariana</i> (Taczanowski, 1881)	<i>Faiditus globosus</i>
<i>Leucauge undulata</i> (Vinson, 1863)	<i>Argyroides bonadea</i> , <i>A. flavescens</i>
<i>Leucauge venusta</i> (Walckenaer, 1841)	<i>Argyroides elevatus</i> , <i>Faiditus caudatus</i> , <i>F. globosus</i> , <i>F. leonensis</i>
<i>Leucauge</i> White, 1841 indet.	<i>Argyroides argentatus</i> , <i>A. bonadea</i> , <i>A. gracilis</i> , <i>A. tripunctatus</i> , <i>Neospintharus concisus</i> , <i>N. furcatus</i> , <i>Rhinoliparus lanyuensis</i>
<i>Metabus gravidus</i> O. P.-Cambridge, 1899	<i>Metabus gravidus</i>
<i>Metellina segmentata</i> (Clerck, 1757)	<i>Enoplognatha ovata</i>
<i>Tetragnatha extensa</i> (Linnaeus, 1758)	<i>Pholcus</i> sp.
<i>Tetragnatha keyserlingi</i> Simon, 1890	<i>Tetragnatha keyserlingi</i>
<i>Tetragnatha</i> Latreille, 1804	<i>Argyroides rostratus</i> , <i>Enoplognatha ovata</i>
Tetragnathidae	<i>Neospintharus fur</i> , <i>Platnickina sterninotata</i> , <i>Portia</i> sp.
Indet. araneoid orb weavers	<i>Argyroides convivans</i> , <i>A. scintillulanus</i> , <i>A. stridulator</i> , <i>Faiditus proboscifer</i> , <i>F. solidao</i> , <i>Neospintharus nipponicus</i> , <i>Platnickina sterninotata</i> , <i>Leucauge marina</i> , <i>Meta segmentata</i> , <i>Nuctenea</i> spp., <i>Philoponella vicina</i>
Linyphiidae Blackwall, 1859	
<i>Erigone dentipalpis</i> (Wider, 1834)	<i>Dicymbium nigrum</i> , <i>Erigone atra</i> , <i>E. dentipalpis</i> , <i>Gnathonarium dentatum</i> , <i>Mermessus trilobatus</i> , <i>Micrargus herbigradus</i>
<i>Frontinella pyramitela</i>	<i>Neospintharus trigonum</i> , <i>Rhomphaea fictitium</i> , <i>Linyphia triangularis</i>
<i>Frontinella</i> sp.	<i>Rhomphaea sagana</i>
<i>Linyphia triangularis</i> (Clerck, 1757)	<i>Frontinella communis</i> , <i>Enoplognatha ovata</i>
<i>Linyphia</i> indet.	<i>Argyroides fissifrons</i> , <i>Rhomphaea sagana</i>
<i>Nerene litigiosa</i> (Keyserling, 1886)	<i>Nerene litigiosa</i>
<i>Orsonwelles falstaffius</i> Hormiga, 2002	<i>Argyroides laha</i>
<i>Orsonwelles graphicus</i> (Simon, 1900)	<i>Argyroides hawaiiensis</i>
<i>Orsonwelles macbeth</i> Hormiga, 2002	<i>Argyroides laha</i>
<i>Orsonwelles malus</i> Hormiga, 2002	<i>Argyroides ilipoepoe</i>
<i>Orsonwelles polites</i> Hormiga, 2002	<i>Argyroides laha</i>
<i>Orsonwelles</i> Hormiga, 2002 indet.	<i>Argyroides argentatus</i> , <i>A. ilipoepoe</i> , <i>A. laha</i> , 'Ariamnes' kahili, 'A.' laau, 'A.' makue, 'A.' melekalikimaka
<i>Tenuiphantes tenuis</i> (Blackwall, 1852)	<i>Lepthyphantes tenuis</i>

(Continued)

TABLE 1 Continued

Hosts	Kleptoparasites
Linyphiidae indet.	<i>Neospintharus fur</i> , <i>N. syriacus</i> , <i>Rhinocosmetus nasutus</i> , <i>Rho. sagana</i>
Pimoidae Wunderlich, 1986	
<i>Pimoida cona</i> Zhang & Li, 2020	<i>Gushangzao shiqian</i>
Theridiidae Sundevall, 1833	
<i>Achaearanea</i> Strand, 1929	<i>Argyrodes alannae</i> , <i>A. antipodanus</i> , <i>A. fissifrons</i> , <i>Rhinoliparus lanyuensis</i> , <i>Philoponella tingens</i>
<i>Anelosimus andasibe</i> Agnarsson & Kuntner, 2005	<i>Archaeidae</i> indet., <i>Miturgidae</i> indet.
<i>Anelosimus baeza</i> Agnarsson, 2006	<i>Argyrodes elevatus</i> , <i>Faiditus caudatus</i> , <i>F. spinosus</i>
<i>Anelosimus elegans</i> Agnarsson, 2006	<i>Faiditus caudatus</i>
<i>Anelosimus eximius</i> (Keyserling, 1884)	<i>Argyrodes flavescens</i> , <i>Faiditus alticeps</i> , <i>F. amplifrons</i> , <i>F. caudatus</i> , <i>F. coactatus</i> , <i>F. ululans</i> , <i>Rhomphaea projiciens</i>
<i>Anelosimus guacamayos</i> Agnarsson, 2006	<i>Argyrodinae</i> indet.
<i>Anelosimus domingo</i> Levi, 1963	<i>Argyrodes flavescens</i> , <i>Faiditus ululans</i>
<i>Anelosimus may</i> Agnarsson, 2005	<i>Argyrodes</i> sp., <i>Mimetes</i> sp., <i>Archaeidae</i> indet., <i>Miturgidae</i> indet.
<i>Anelosimus nazariani</i> Agnarsson & Kuntner, 2005	<i>Argyrodes</i> sp., <i>Neospintharus</i> sp., <i>Mysmenidae</i> indet., <i>Philoponella</i> spp.
<i>Anelosimus salut</i> Agnarsson & Kuntner, 2005	<i>Argyrodes</i> sp.
<i>Anelosimus studiosus</i> (Hentz, 1850)*	<i>Argyrodes elevatus</i> , <i>Neospintharus trigonum</i> , <i>Rhomphaea fictitium</i> , <i>Eris militaris</i> , <i>Tetragnatha</i> sp., <i>Mimetes</i> sp., <i>Ero</i> sp., <i>Synema parvulum</i> , <i>Araniella</i> , <i>Eriophora</i> , <i>Eustala</i> , <i>Metazygia</i> , <i>Nuctenea</i> , <i>Tetragnatha</i> , <i>Mimetes</i> , <i>Dipoena</i> , <i>Theridion</i> , <i>Florinda coccinea</i> , <i>Agelenopsis</i> , <i>Anyphaena</i> , <i>Castianeira</i> , <i>Clubiona</i> , <i>Dysdera</i> , <i>Hentzia palmarum</i> , <i>Hentzia</i> , <i>Hytia</i> , <i>Misumenops</i> , <i>Peckhamia</i> , <i>Peucetia viridans</i> , <i>Phidippus</i> , <i>Trachela</i>
<i>Anelosimus tosus</i> (Chamberlin, 1916)	<i>Argyrodes</i> sp.
<i>Anelosimus vondrona</i> Agnarsson & Kuntner, 2005	<i>Argyrodes</i> sp., <i>Archaeidae</i> indet., <i>Miturgidae</i> indet., <i>Scytodes</i> sp.
<i>Enoplognatha ovata</i> (Clerck, 1757)	<i>Pholcus</i> sp.
<i>Latrodectus antheratus</i> (Badcock, 1932)	<i>Argyrodes elevatus</i>
<i>Latrodectus bishopi</i> Kaston, 1938	<i>Argyrodes elevatus</i> , <i>Faiditus caudatus</i> , <i>Neospintharus furcatus</i>
<i>Latrodectus curacaviensis</i> (Müller, 1776)	<i>Argyrodes elevatus</i>
<i>Latrodectus geometricus</i> C.L. Koch, 1841	<i>Argyrodes antipodanus</i> , <i>A. elevatus</i>
<i>Latrodectus hesperus</i> Chamberlin & Ivie, 1935	<i>Argyrodes pluto</i> , <i>Neospintharus baboquivari</i> , <i>Enoplognatha ovata</i>
<i>Latrodectus revivensis</i> Shulov, 1948	<i>Latrodectus revivensis</i>
<i>Latrodectus variolus</i> Walckenaer, 1837	<i>Rhomphaea fictitium</i>
<i>Latrodectus</i> Walckenaer, 1805 indet.	<i>Neospintharus trigonum</i> , <i>Holocnemus pluchei</i>
<i>Nihonhimea japonica</i> (Bösenberg & Strand, 1906)	<i>Argyrodes fissifrons</i>
<i>Nihonhimea mundula</i>	<i>Spheropistha</i> sp., <i>Argyrodes incursus</i>
<i>Parasteatoda tepidariorum</i> (C.L. Koch, 1841)	<i>Argyrodes elevatus</i> , <i>Faiditus cancellatus</i> , <i>Neospintharus trigonum</i> , <i>Mimetes</i> sp.
<i>Parasteatoda wau</i> (Levi, Lubin & Robinson, 1982)	<i>Argyrodes</i> spp.
<i>Parasteatoda</i> Archer, 1946 indet.	<i>Argyrodes bonadea</i> , <i>Spheropistha melanosoma</i> , <i>Rhomphaea labiata</i>
<i>Phylloneta sisypheia</i> (Clerck, 1757)	<i>Enoplognatha ovata</i>
<i>Steatoda</i> Sundevall, 1833 indet.	<i>Spheropistha melanosoma</i>
<i>Theridion melanurum</i> Hahn, 1831	<i>Platnickina tinctoria</i>
<i>Theridion nigroannulatum</i> Keyserling, 1884	<i>Faiditus amplifrons</i> , <i>F. subdulus</i>

(Continued)

TABLE 1 Continued

Hosts	Kleptoparasites
<i>Theridion pictum</i>	<i>Neospintharus trigonum</i> , <i>Enoplognatha ovata</i>
<i>Theridion</i> Walckenaer, 1805 indet.	<i>Neospintharus baboquivari</i>
<i>Tidarren sisypoides</i> (Walckenaer, 1841)	<i>Argyroides elevatus</i> , <i>Neospintharus baboquivari</i> , <i>N. trigonum</i>
Theridiidae Sundevall, 1833	<i>Argyroides amboinensis</i> , <i>A. cylindricus</i> , <i>A. fasciatus</i> , <i>A. miniaceus</i> , <i>A. tripunctatus</i> , <i>Faiditus caudatus</i> , <i>F. leonensis</i> , <i>Gushangzao goemon</i> , <i>G. pelorosus</i> , <i>G. shiqian</i> , <i>Neospintharus concisus</i> , <i>N. furcatus</i> , <i>Rhinocometus nasutus</i> , <i>Rhomphaea labiata</i> , <i>R. sagana</i> , <i>Portia</i> sp.
ENTELEGYNAE other	
Uloboridae Thorell, 1869	
<i>Octonoba varians</i>	<i>Argyroides fissifrons</i>
<i>Philoponella congregabilis</i> (Rainbow, 1916)	<i>Portia fimbriata</i>
<i>Philoponella oweni</i> (Chamberlin, 1924)	<i>Faiditus subdulus</i> , <i>Neospintharus baboquivari</i> , <i>Rhomphaea fictitium</i>
<i>Philoponella republicana</i> (Simon, 1891)	<i>Philoponella republicana</i>
<i>Philoponella Mello-Leitão</i> , 1917	<i>Argyroides fissifrons</i>
<i>Uloborus</i> Latreille, 1806 indet.	<i>Faiditus dracus</i> , <i>Neospintharus baboquivari</i>
Uloboridae Thorell, 1869 indet.	<i>Portia</i> sp.
Eresidae C. L. Koch, 1845	
<i>Stegodyphus dumicola</i> Pocock, 1898	<i>Archaeodictyna ulova</i> , <i>Stegodyphus africanus</i> , <i>S. sabulosus</i>
<i>Stegodyphus lineatus</i> (Latreille, 1817)	<i>Stegodyphus lineatus</i>
<i>Stegodyphus mimosarum</i> Pavesi, 1883	<i>Archaeodictyna ulova</i> , <i>Portia schultzi</i>
<i>Stegodyphus sarasinorum</i> Karsch, 1892	<i>Argyroides argentatus</i> , <i>A. kumadai</i> , <i>A. projeles</i> , <i>Rhomphaea projiciens</i> , <i>R. sp.</i> , <i>Cheiracanthium sp.</i> , <i>Chrysilla sp.</i> , <i>Clubiona sp.</i> , <i>Drassodes sp.</i> , <i>Hyllus semicupreus</i> , <i>Icius alboterminus</i> , <i>Indoxysticus sp.</i> , <i>Madhyattus sp.</i> , <i>Menemerus sp.</i> , <i>Olios lamarcki</i> , <i>O. obesus</i> , <i>Oxyopes javanus</i> , <i>Philoponella feroxa</i> , <i>Phintella vittata</i> , <i>Plexippus sp.</i> , <i>Poecilochroa sp.</i> , <i>Rhene sp.</i> , <i>Stegodyphus tibialis</i> , <i>Tibellus sp.</i>
<i>Stegodyphus</i> Simon, 1873 indet.	<i>Stegodyphus africanus</i> , <i>S. sabulosus</i>
Eresidae C. L. Koch, 1845 indet.	<i>Portia</i> sp.
RTA clade	
Agelenidae C. L. Koch, 1837	
<i>Agelena labyrinthica</i> (Clerck, 1757)	<i>Phylloneta sisypbia</i>
<i>Agelena limbata</i> Thorell, 1897	<i>Argyroides fissifrons</i> , <i>Neospintharus fur</i>
<i>Agelena silvatica</i> Oliger, 1983	<i>Argyroides kumadai</i>
<i>Agelena</i> Walckenaer, 1805 indet.	<i>Argyroides bonadea</i> , <i>A. nephilae</i> , <i>Neospintharus furcatus</i> , <i>Rho.sagana</i>
<i>Agelenopsis aperta</i> (Gertsch, 1934)	<i>Agelenopsis aperta</i>
<i>Agelenopsis</i> Giebel, 1869 indet.	<i>Argyroides elevatus</i> , <i>A. pluto</i> , <i>Rhomphaea fictitium</i>
<i>Coelotes</i> Blackwall, 1841 indet.	<i>Oonops pulcher</i>
<i>Eratigena atrica</i> (C. L. Koch, 1843)	<i>Oonops pulcher</i> , <i>Pholcus</i> sp.
Agelenidae C. L. Koch, 1837 indet.	<i>Neospintharus nipponicus</i> , <i>Portia</i> sp.
Amaurobiidae Thorell, 1869	
<i>Amaurobius ferox</i> (Walckenaer, 1830)	<i>Oonops pulcher</i>
<i>Amaurobius similis</i> (Blackwall, 1861)	<i>Pholcus</i> sp.
Amaurobiidae Thorell, 1869 indet.	<i>Portia</i> sp.
Desidae Pocock, 1895	

(Continued)

TABLE 1 Continued

Hosts	Kleptoparasites
<i>Badumna insignis</i> (L. Koch, 1872)	<i>Portia fimbriata</i>
<i>Badumna longinqua</i> (L. Koch, 1867)	<i>Argyroides antipodianus</i>
<i>Cambridgea</i> L. Koch, 1872 indet.	<i>Argyroides antipodianus</i>
<i>Phryganoporus candidus</i> (social)	<i>Rhinoliparus rainbowi</i> , <i>Neosparassus diana</i> , <i>Simaetha paetula</i>
Hahniidae Bertkau, 1878	
Hahniidae Bertkau, 1878 indet.	<i>Sofanapis antillanca</i>
Lycosidae Sundevall, 1833	
<i>Aglaoctenus lagotis</i> (Holmberg, 1876)	<i>Lycosa erythronatha</i> , <i>L. poliostruma</i> , <i>Schizocosa malitiosa</i>
<i>Aglaoctenus</i> Tullgren, 1905 indet.	<i>Mysmenopsis amazonica</i> , <i>M. atahualpa</i> , <i>M. penai</i> , <i>M. shushufindi</i>
Lycosidae Sundevall, 1833 indet.	<i>Mysmenopsis bartolozzii</i> , <i>M. salazarae</i>
Pisauridae Simon, 1890	
<i>Dolomedes</i> Latreille, 1804 indet.	<i>Rhomphaea sagana</i>
Pisauridae Simon, 1890 indet.	<i>Rhinocosmetus carnicobarensis</i> , <i>Portia</i>
Psechridae Simon, 1890	
<i>Psechrus argentatus</i> (Doleschall, 1857)	<i>Argyroides fissifrons</i>
<i>Psechrus</i> Thorell, 1878 indet.	<i>Argyroides amboinensis</i> , <i>A. fasciatus</i> , <i>Gushangzao pelorosus</i> , <i>Rhinocosmetus nasutus</i>
Psechridae Simon, 1890 indet.	<i>[Deelemanella]* Theridion nodiferum</i>
Stiphidiidae Dalmat, 1917	
Stiphidiidae Dalmat, 1917	<i>Portia</i> sp.
<i>Stiphidion</i> Simon, 1902 indet.	<i>Argyroides antipodianus</i>
Zoropsidae Bertkau, 1882	
<i>Tengella radiata</i> (Kulczyński, 1909)	<i>Faiditus bryantae</i> , <i>Maymena rica</i> , <i>Mysmenopsis dipluramigo</i> , <i>M. tengellacompa</i>

This list is based on a survey of literature on kleptoparasitic spiders, and selected references on araneophagy. About 200 species have been identified, belonging to 86 genera and 23 families. In many cases hosts are identified only to genus or family. For references for each entry see [Supplementary Material](#), the table is based on references listed below the table, in addition to personal data and personal communications from Greg Anderson, Jillian Cowles, William Eberhard, Robert Jackson, Matjaz Kuntner, and Yuya Suzuki.

Table references (Abhijith et al., 2021; Agnarsson, 2003, 2006, 2011; Agnarsson et al., 2016, 2025; Alayón García, 1992; Andrade, 1996; Archer, 1946, 1948, 1966; Avilés et al., 2006; Baba and Miyashita, 2005; Baba et al., 2007, 2012, 2013; Baert, 1990; Baert and Murphy, 1987; Baptista, 1988; Berland, 1923, 1924; Berry 1987; Bhattacharya, 1936; Bilsing, 1920; Binford and Rypstra, 1992; Blanchong et al., 1995; Blanke, 1972; Blanke, 1974; Bosmans and Colombo, 2015; Bradoo, 1972, 1979, 1983, 1985, 1986; Bristow, 1930, 1941, 1958; Buskirk, 1975; Cangialosi, 1990a, b, 1991, 1997; Cerveira and Jackson, 2005; Chida and Tanikawa, 1999; Chinta et al., 2016; Christenson, 1984; Christenson and Goist, 1979; Chrysanthus, 1963; Chua and Lim, 2012; Clark and Jackson, 1994; Clyne, 1979; Cobbold, 2010; Coyle, 1995; Coyle and Meigs, 1989; Coyle et al., 1991; Crespo et al., 2009; Dippenaar-Schoeman et al., 2021a, 2021b; Downes, 1994; Drisya-Mohan et al., 2019; Dupérré and Tapia, 2015, 2020; Dönnitz, 1887; Eberhard, 1979, 1983, 2020; Eberhard and Briceño, 1983, 1985; Eberhard et al., 1978, 1993; Eichenberger et al., 2009; Elgar 1989, 1993, 1994; Elgar and Fahey, 1996; Elgar et al., 1983; Elias et al., 2024; Emerton, 1882, 1902, 1909; Enders, 1974; Exline, 1945a, 1945b; Exline and Levi, 1962; Fage, 1928; Farr, 1976; Forster and Platnick, 1977; Fowler and Venticinque, 1996; Gan et al., 2015; Gillespie and Rivera, 2007; González and Castro, 1996; González and Toscano-Gadea 2021; Gould, 2021; Gray, 1983; Gray and Anderson, 1989; Griswold, 1985; Griswold and Mekle-Griswold, 1987; Grostal, 1999; Grostal and Walter 1997, 1999; Guarisco, 1999, 2000; Hall, 2019; Hénaut, 2000; Hénaut et al., 2005; Hentz, 1850; Higgins and Buskirk, 1998; Hiramatsu, 2012, 2019; Hormiga, 2002; Houser et al., 2005, 2014; Jackson and Blest 1982; Jackson, 1985, 1986, 1987; Jackson and Whitehouse, 1986; Jäger and Praxaysombath, 2011; Javed et al., 2010; Justice et al., 2005; Kaston, 1948, 1965; Kerr, 2005; Kerr and Quenga, 2004; Keyserling, 1984, 1891, 1890; Kim, 2021; Kim and Kim, 2007; Kim et al., 2015; Koh and Li, 2003; Kraus, 1955; Kullmann, 1959a, b, 1960; Kumada, 1986, 1990; Kuntner, 2005, 2007; Lamore, 1957, 1958; Larcher and Wise, 1985; Lawrence, 1937; Le Peru, 2011; Leborgne et al., 1998; Legendre, 1960, 1961; Levi, 1967; Levy, 1985; Lin et al., 2024; Lopez, 1986, 1988, 1990; Lubin, 1974; Lubin and Robinson, 1982; Lubin et al. 1993; Luczak and Dabrowska-Prot 1970; Marples, 1955; Mascord, 1980; McCrate and Uetz, 2010; Meira et al., 2021; Michálek et al., 2017; Miyashita, 2001, 2002; Miyashita et al., 2004; Moran, 1993; Moura et al., 2017, 2020, 2021; Namkung, 2003; Nentwig and Christenson, 1986; Nyffeler and Benz, 1980; Opell, 1979; Pickard-Cambridge, 1872; Osses et al., 2007; Ovatt Mohanan Drisya-Mohan et al., 2019; Pasquet et al. 1997; Patel and Bradoo, 1981; Peng et al. 2013, 2024; Pekar and Lubin, 2011; Petrunkevitch, 1930; Platnick and Forster, 1989; Platnick and Shadab, 1978, 1979; Pocock, 1898; Prenter et al., 1994; Proctor 1992; Quero et al., 2023; Ramirez and Platnick, 1999; Reimoser, 1931; Responde et al., 2021; Riechert and Gillespie, 1986; Rivera and Gillespie, 2010; Roberts, 1952; Roberts, 1978; Robinson and Olazarri, 1971; Robinson and Robinson, 1973; Robinson and Robinson 1976; Rovner, 1968; Rypstra, 1979; Saaristo, 1978, 2000, 2010; Schmidt, 1980, 1999, 2005; Schmidt et al., 1994; Schneider and Lubin, 1996, 1997; Schneider, 1997; Scott and McCann, 2023; Sekhar and Sunil Jose, 2018; Shinkai, 1988; Shinkai, 1992; Shinkai, 2000; Sibi et al., 2022; Sierwald and Fenzl, 1999; Silveira and Japyassú, 2012; Simon, 1864, 1892, 1894; Smith-Trail 1980; Spear et al., 2018; Srinivasulu et al., 2013; Straus and Avilés, 2023; Striffler and Rembold, 2009; Struhsaker, 1969; Su 2012; Su and Smith, 2014; Su et al., 2018; Susuki et al. 2022, Taczanowski 1873; Tanaka, 1984, Tanikawa, 2017; Thorell, 1887; Tikader, 1970, 1977; Tso and Severinghaus, 1998, 2000; Vanuytven et al. 2024; Vinson, 1863; Vollrath, 1976, 1977, 1978, 1979a, b, 1980, 1982, 1984, 1987; Watson, 1990; Whitehouse, 1986, 1987b, 1988, 1991, 1997a, b, 2011, 2016; Whitehouse and Jackson, 1993, 1994, 1998; Whitehouse and Lubin, 2005; Wickler and Seibt, 1988; Wiehle, 1928; Wise, 1975, 1981, 1982, 2006; Wood et al., 2012; Yaginuma, 1956, 1986; Yoshida, 2001a; Yoshida et al., 1998; Zhang et al., 2020, 2022; Zhu and Song, 1991).

studiosus can contain numerous other spiders, and a range of other arthropods (Deyrup et al., 2004; Perkins et al., 2007; Mock, 2008), and Jani et al. (2023) reported 21 spider species and many other arthropods and even vertebrates making the webs of social

Stegodyphus sarasinorum their home. Further, in a survey of about 80 nests of subsocial *Anelosimus* in Madagascar Magnússon and Agnarsson (unpublished) found over 130 arthropod species associated with these nests.

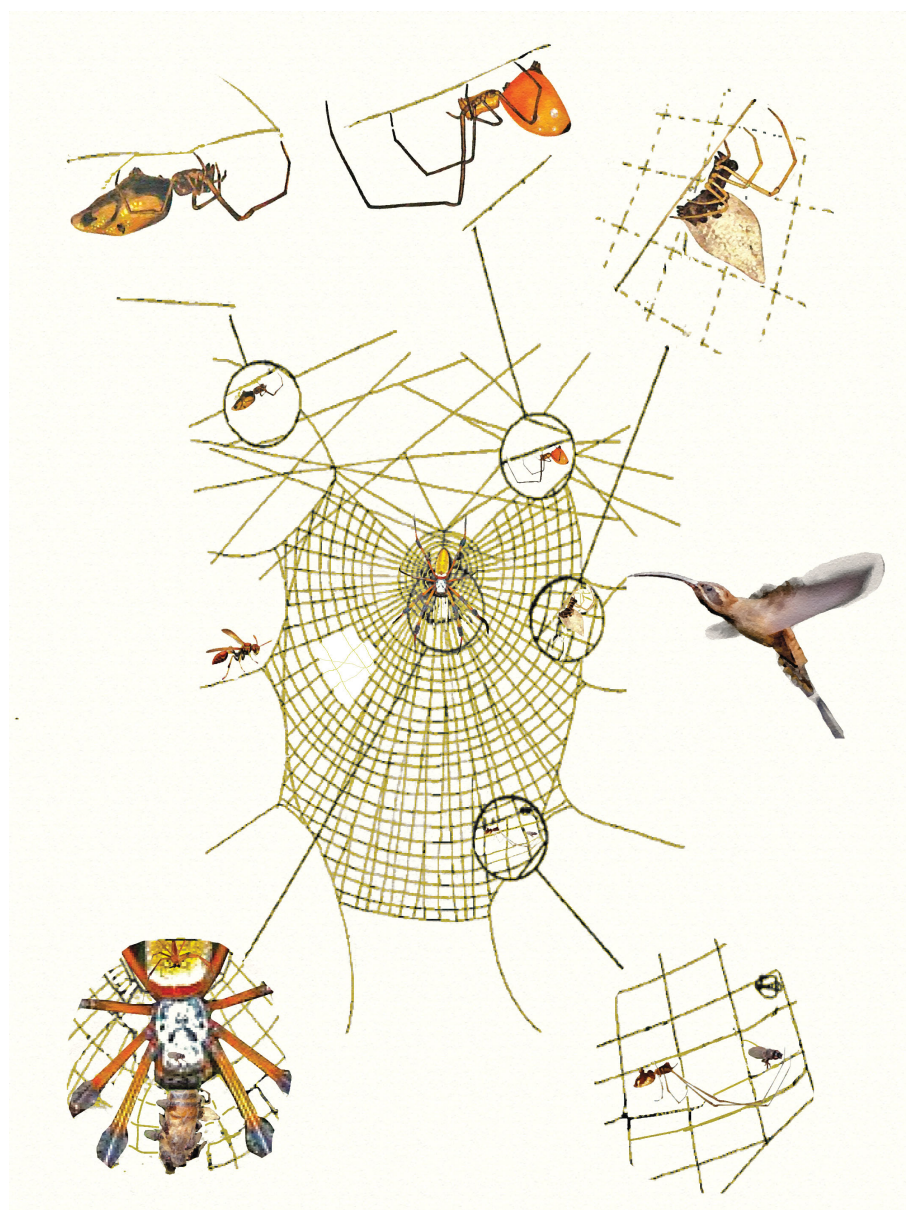


FIGURE 2

Spider webs are hosts for a variety of kleptoparasites. Here, a *Trichonephila* female sits at the hub of her web, feeding on prey. On her and the prey (inset lower left) kleptoparasitic flies share her prey. A wasp (left) and a hummingbird (right) may steal prey, and the latter also silk for its nest, from her web. Various obligatory kleptoparasite species (inset above and lower right) are constant guests in her web, gleaning insects, and prey packages, feeding with her, or on her juveniles. On the left side of the web, a hole has been cut out by a kleptoparasite, removing prey from the web. Artwork is a conceptual reproduction of figure 97 in Vollrath (1987).

The inhabitants of spider webs are varied. Some species, including certain beetles and lepidopteran larvae, act as scavengers, consuming waste materials and leftover prey within the web. In *Phryganoporus candidus* nests, scavengers like mealybugs thrive, benefitting from the sheltered environment and sometimes aiding in nest sanitation by breaking down waste (Downes, 1995). Some insects and spiders simply seek shelter in the nests of social spiders, while ants, wasps, assassin bugs, and other predatory insects have been documented as significant predators, sometimes killing spiders and stealing egg masses. Predatory wasps, for example—while not kleptoparasitic—invalidate

host webs and have a major impact on *Metepeira incrassata* colonies (Uetz et al., 2002). As discussed below, in addition to opportunistic predators, many types of kleptoparasites are also attracted to this community thriving in a prey capturing abode.

2.2 Ecology and biogeography of spider webs as islands

Spider webs function as fascinating examples of “habitat islands”, uniquely structured and highly distinct and quantifiable

ecosystems (Blackledge and Gillespie, 2002; Blackledge et al., 2011) that support various forms of life, notably among them, kleptoparasitic spiders (Elgar, 1989; Agnarsson, 2003). Spider webs resemble islands in the isolation of habitat, patchily dispersed within a matrix of strikingly contrasting habitats (Agnarsson, 2011). Therefore, general ecological models used for island biogeography and metapopulation biology (MacArthur and Wilson, 1967; Hanski, 1997) are applicable to spider webs as habitats. For kleptoparasites, host webs like those of golden orbweavers (*Nephila*, *Trichonephila*), are attractive due to their size, tenacity, and predictable provision of essential resources (Elgar, 1989; Grostal and Walter, 1999). Similarly, due to the size and ease of discovery and measurement, webs of golden orbweavers are a convenient system to study ecology, such as how kleptoparasites are distributed among ‘islands.’ Studies on nephilids (Robinson et al., 1973; Elgar, 1989; Grostal and Walter, 1997, 1999; Agnarsson, 2003, 2011), and other types of host webs (Cangialosi, 1990a, b; Rypstra and Binford, 1995) have clearly established that web size is the best predictor of kleptoparasite load (Su et al., 2021). Fernandez-Fournier and Avilés (2018) also showed that kleptoparasite diversity increases with web size across four different solitary and social host species, and McCrate and Uetz (2010) showed that the number of Argyrodinae kleptoparasite species increases with size of colonies made up by *Metepeira incrassata* and associated web builders. This is expected as large webs both contain more silk, and thus areas to occupy, and intercept more prey resulting in a relatively high-quality kleptoparasite habitat (Gregorič et al., 2021, 2024). What is intriguing is the scalability of the system—how abundance scales precisely with size (Agnarsson, 2011; Gregorič et al., 2024), down to some ‘minimum’ size where kleptoparasites are generally absent (Agnarsson, 2002; Miyashita, 2002; Whitehouse et al., 2002). Thus, total host web area in a given region or habitat can approximately predict the expected number of spider kleptoparasites. Another interesting result from these studies is that a) while web clustering and interconnectedness—a common feature of many nephilid species—facilitate immigration and stabilization of kleptoparasite populations (Agnarsson, 2003, 2011), b) even highly isolated webs have kleptoparasite abundances proportional to their size (Gregorič et al., 2024). This suggests that habitat quality trumps connectivity when individuals freely distribute according to resources and implies that isolation is not limiting in the distribution of kleptoparasites. Spider kleptoparasites therefore seem *both adept at locating host webs and highly mobile*. Accordingly, it has been shown that the distribution of kleptoparasites among host webs closely follows the Ideal Free Distribution model, where the free movement of individuals leads to an equilibrium in habitat occupancy in relation to suitability (Elgar, 1989; Agnarsson, 2003, 2011; Gregorič et al., 2024). The ability of kleptoparasitic spiders to detect and evaluate habitat islands suggests the use of airborne cues, likely pheromones produced by the host (Agnarsson et al., 2025), to locate suitable patches. In conclusion, spider webs provide a compelling model for studying habitat islands and the ecological relationships they support. Through examining the relationship between orb weavers and their kleptoparasitic guests, we can gain a

deeper understanding of how patch quality and connectivity shape community dynamics in isolated habitats (Agnarsson, 2011; Gregorič et al., 2024). The preference of kleptoparasitic spiders for larger webs, coupled with their impressive dispersal capabilities, demonstrates that for organisms in isolated ecosystems, the availability and quality of resources are paramount. Habitat islands, whether they are spider webs or isolated forest patches, illustrate the complex interactions between organisms and their environments, offering valuable insights into abundance distributions and resilience of ecological communities.

2.3 Web building spiders as ideal hosts for kleptoparasites

Spider webs provide a diverse habitat for a variety of organisms (Figures 2, 3 and text above) that alone makes them attractive to other foragers. The efficacy of these prey catching devices further renders them a predictable source of insect cadavers and the sedentary nature of web-building spiders creates a stationary and accessible resource for kleptoparasites (Vollrath, 1987; Eberhard, 2020). Vollrath (1984) suggests that web spiders are vulnerable to kleptoparasitism because they cannot run away or hide food. Web building spiders, furthermore, may capture both large prey that require extended handling times and more prey than they can consume at a given time, requiring storage within the web (Champion de Crespigny et al., 2001). Additionally, spiders lack mandibles and generally do not chew on prey but rather inject venom and digestive enzymes into the prey. The prey is thus partially digested externally and spiders feed exclusively by sucking up the digestive juices (Foelix, 1982). Combined, the prolonged prey handling, availability of predigested stored prey in the web, and slow absorption of food from the prey by the host, all represent excellent opportunities for kleptoparasitic organisms to join in feeding with the host or steal its wrapped prey items (Table 1; Supplementary Table S1). In addition, while spider webs are not well characterized as sieves (Eberhard, 2020) their design, even if well-tuned to capture ‘optimal’ prey, inevitably results in the by-catch of some very small insects that may not be important food source for the host. This presents an additional opportunity for kleptoparasites that are typically many times smaller than the host spider (regardless of developmental stage of either) or for whom such prey items represent valuable resources. It is no wonder then, that individual webs or colonies attract a great diversity of kleptoparasites, ranging from birds, large hymenopterans and scorpionflies, to tiny ants and ‘freeloader’ flies, in addition to the specialized spider kleptoparasites like *Argyrodes* (Thornhill, 1975; Nyffler and Benz, 1980; Vollrath, 1987; Henschel, 1998; Sivinski et al., 1999).

Spiders are potentially dangerous hosts, but large spiders may pay limited attention to smaller organisms in their webs, if they are not struggling or sending other similar vibratory signals to the web owner (Vollrath 1979b, 1987). While large spider webs thus attract a number of kleptoparasite species from diverse arthropod groups, the most numerous and speciose kleptoparasites in spider webs are

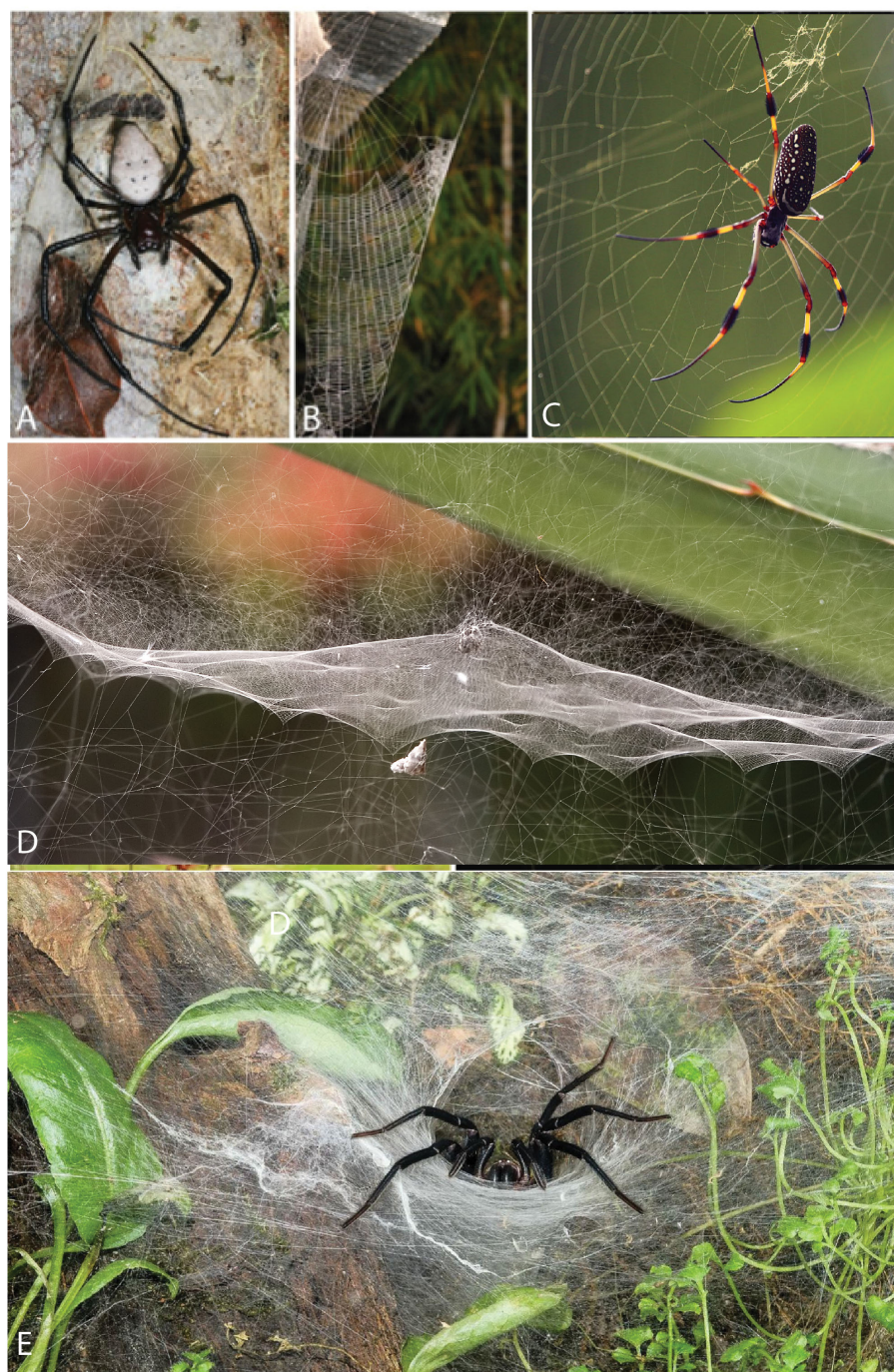


FIGURE 3

Key spider hosts. (A–D) the most important hosts of argyrodine kleptoparasites. (A–C) Nephilidae. (A) *Nephilingis livida* female and B, her large orb web (c.a. 1m in total length). (C) The mother of all hosts, *Trichonephila clavipes*, sitting on her golden orb. (D) *Cyrtophora citricola* web, representing the second most affected host lineage. Note the abundant auxiliary webbing above and below the horizontal orb. (E) *Linothele* sp. female sitting in her retreat, leading to her brushed sheet web—the favorite home of mysmenid kleptoparasites. (D) is reproduced from Cyrtophora.citricola.net.7626.jpg in Wikipedia commons under Creative Commons Attribution-Share Alike 2.5 Generic. (E) is by Bastian Drolshagen, reproduced with permission from the author.

other spiders. As pointed out by Vollrath (1987 p. 277) '[t]he spider web is a very special structure in terms of material, configuration and information transmission. It is not surprising that web spiders are the most successful inquilines in spider webs (Brignoli, 1966), since they are superbly preadapted.' In other words, spiders know

how to operate spider webs and spider kleptoparasites can move about in webs stealthily and without becoming stuck on the sticky capture spiral of many of the hosts. Non-spider kleptoparasites that inhabit spider webs are, in fact, most common in webs that do not contain sticky silk, particularly in the webs of subsocial and social

spiders that tend to show more tolerance toward other web inhabitants, many of which are, of course, their kin.

Kleptoparasites may impose significant costs on spider hosts. While some scavengers may only consume leftover prey, kleptoparasites often remove entire prey items, reducing the spider's available resources (Henschel and Lubin, 1992; Vollrath, 1987). In some cases, kleptoparasites like ants or certain *Argyrodes* species also attack spider broods or egg sacs, increasing their impact on spider populations (Schneider and Lubin, 1997; Agnarsson, 2002). The persistent threat of kleptoparasites and predators has led to the evolution of several adaptive responses in spiders. Spiders like *Stegodyphus lineatus* exhibit defensive behaviors to reduce the risk of ant raids, such as altering web structure or abandoning heavily invaded areas (Henschel, 1998; Rypstra, 1981). Hosts may also relocate webs when kleptoparasitic pressure becomes unsustainable (Rypstra, 1981; Whitehouse, 1997a) offering short term respite from kleptoparasite activities (Robinson et al., 1973).

In sum, while spiders are potentially dangerous hosts as major arthropod predators that have evolved various means of countering kleptoparasitism, spider webs offer many advantages making them an ideal host to other organisms, among which kleptoparasites are typically most abundant.

2.4 Characteristics and phylogenetic distribution of spider hosts

Even a cursorial look at the distribution of kleptoparasitic hosts across the spider phylogeny reveals a starkly non-random pattern (Figures 4–6). The inset figure on the left side shows in broad strokes that hosts are not spread proportionately across all spider diversity. A total of about 200 hosts have been recorded, including approximately 200 named species, 88 genera, and 23 families, a tiny fraction of spider diversity (Figures 5, 6). But even among these, the distribution of the most critical hosts—those home to the majority of kleptoparasites—is non-random. Rather, as depicted in Figure 4, preferred kleptoparasite hosts, labeled in bold and green font, are concentrated in relatively few genera within a small subset of web-building spiders. These key hosts exhibit unique characteristics—large, often structurally complex, and persistent webs—that make them particularly suitable for kleptoparasitic exploitation (Exline, 1945b; Vollrath, 1984, 1987, Elgar, 1993; Whitehouse et al., 2002; Whitehouse, 2011). Kleptoparasitic hosts are disproportionately found among large sheet or funnel web spiders like web building mygalomorphs (Dipluridae, Ischnothelidae) and RTA clade spiders (Agelenidae, Pisauridae, Psecridae, Tenggellidae), and among orbweavers (especially Nephilidae and *Cyrtophora*, but also in large Araneidae, Theridiidae, and Linyphiidae). Within these families, key genera like *Diplura*, *Linothele*, *Ischnothele*, *Agelena*, *Psecrus*, *Nephila*, *Trichonephila*, *Argiope*, *Cyrtophora*, *Latrodectus*, *Linyphia* and a few other araneoids emerge as primary hosts for kleptoparasites, through sharing some key traits. All build **large webs**, in absolute terms and certainly relative to confamilials, that are **long lasting**, either in being in constant construction and repair (mygalomorphs, RTAs, *Cyrtophora*, *Latrodectus*, *Linyphia*), undergoing only partial

reconstruction (*Nephilidae*), or webs that are reconstructed with high site fidelity (*Argiope*, *Gasteracantha*). Most of these webs are **3-dimensional** in primary architecture, or through **auxiliary webbing** in the form of voluminous non-capture areas, either elaborate retreats where the host gets protected rest, or 'barrier' webs that may serve to slow down prey or as protection against flying predators and parasitoids. The auxiliary webbing in these non-capture areas provides an excellent refuge for kleptoparasites where they can stay in contact with the prey capture web, but outside the prey monitoring zone of the host. In most cases, preferred hosts are also **large spiders** at least relative to the kleptoparasites. It is easier for a small kleptoparasite to go about unnoticed in a large host web, and some of the prey that gets stuck in large webs is so small as to be ignored by the host but represents an important meal for the kleptoparasite. Large prey items caught by large spiders may require **long prey handling times**, and excess capture results in **prey storing**, both of which provide additional opportunities for kleptoparasites (Champion de Crespigny et al., 2001). Finally, the most important host species tend to build **clustered webs** that may even be interconnected. For example, *Trichonephila* and *Cyrtophora* are the two genera that are hosts to the greatest diversity and highest abundances of kleptoparasitic spiders (Table 1; Supplementary Table S1). Both construct expansive orb webs that epitomize the key traits of 'good hosts', though nevertheless, they are architecturally strikingly different as orb webs. *Trichonephila* builds a huge 'modified' vertical orb (Kuntner et al. 2019) with extensive barrier webbing, especially as juveniles, while *Cyrtophora* constructs a horizontal modified 'sheet like' orb with extensive vertical network of dense threads that intercept the flight of insects (Figure 3). Both tend to build webs in close proximity to others, frequently forming interconnected web clusters that may span significant areas. Aggregated webs provide large "arenas" where kleptoparasites may freely wander among multiple provisioning hosts, supplying rich prey capture opportunities and ample shelters. The large-scale composition of colonies inherently diffuses the host's vigilance, creating a spatial limitation in policing and guarding resources effectively across the colony (Vollrath, 1984; Elgar, 1993). Clustered webs may also capture more prey, due for example to 'ricochet effects' (Uetz, 1989). The ultimate spider aggregations are found in **social spiders** constructing large communal webs housing hundreds or thousands of individuals (Avilés, 1997). It is no surprise then that social spiders complete the list of the most important host species for kleptoparasites (Vollrath, 1987; Cangialosi, 1990a, b, c; Straus and Avilés, 2018, 2023). *Stegodyphus* and *Anelosimus*, in particular, contain many social species all of which host kleptoparasites that in some cases are specialists, like *Argyrodes ululans* on *Anelosimus eximius* (Cangialosi, 1990a, b, –, 1991) and *Archaeodictyna ulova* in *Stegadyphus* webs (Griswold and Meikle, 1987). *Faiditus subdolos* also appears to prefer communal webs, hitherto found only in the nests of social *Theridion nigroannulatum* (Avilés et al., 2006) and the colonial *Philoponella oweni* (Smith Trail, 1980). Some particular traits of social spiders, in addition to web size, complexity, and permanence, are conducive to spider kleptoparasitism. Social spiders have generally reduced levels of aggression as—unlike typical solitary spiders—they must tolerate conspecifics sharing the web (Avilés, 1997; Agnarsson, 2002; 2004). Communal web-building and resource sharing also translates to

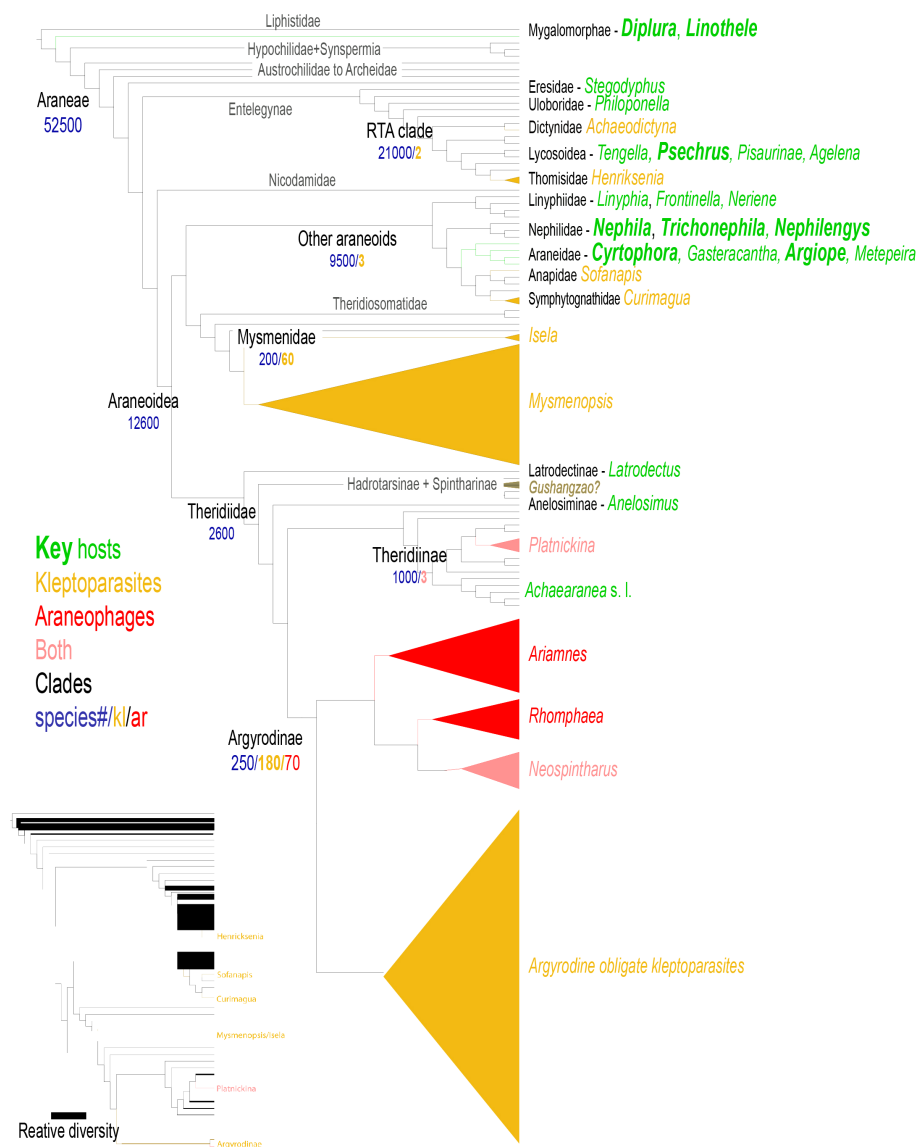


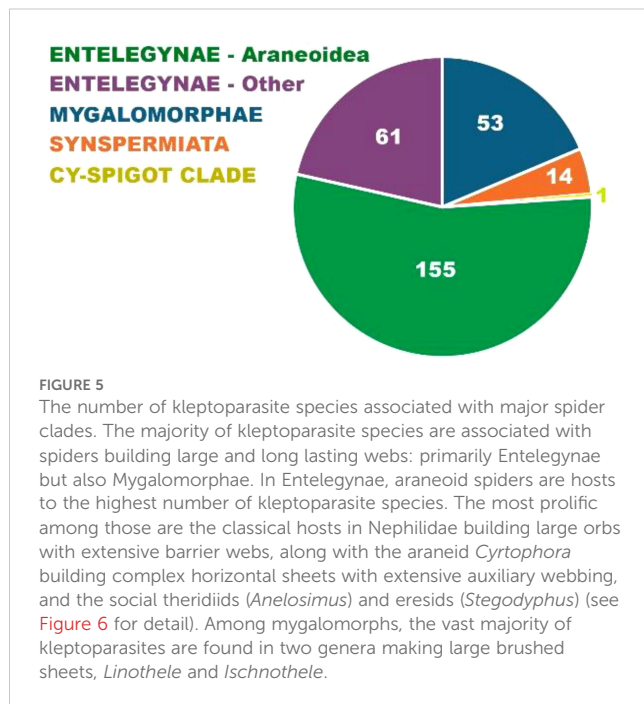
FIGURE 4

Phylogenetic distribution of major spider host species, obligate kleptoparasitic spiders, and theridiid araneophages. The inset figure highlights that both kleptoparasites and their hosts are clustered on certain branches unrelated to patterns of total species richness within the tree. This distribution indicates that while many spiders are web-builders, only a subset has evolved the necessary web traits to support kleptoparasitic lifestyles effectively (see also Figures 5, 6). This narrow host range likely reflects the stringent requirements that kleptoparasites have for host web characteristics—namely, webs that provide sustained resources, cover, and minimal interference from the host. It is notable, also, that kleptoparasitism is clustered within Theridiidae and symphytognathoids, even though multiple origins are implied. Hosts in bold appear to be the most important in terms of number and abundances of kleptoparasites in their webs. Species number (species#) indicates diversity of kleptoparasites (kl) and araneophages (ar). The phylogeny is an interpretive reconstruction of relationships within Theridiidae from Liu et al. (2016), while broader fundamental structure is from Wheeler et al. (2017) and Kulkarni et al. (2023). The putative placement of Nicodamidae and relationships within Araneoidae, especially the monophyly and interrelationships among ‘symphytognathoids’ reflect the stronger character set of Kulkarni et al. (2023). *Gushangzao* is tentatively placed among hadrotarsine theridiids, as proposed by Lin et al. (2024).

reduced individual control over web sections and increased ‘noise’ levels in the web, making it harder to detect invaders who are apt at navigating silk. Perhaps as a consequence of decreased host detection, kleptoparasites in social webs tend to be closer in size to the host spiders than kleptoparasites in solitary webs. As outlined above, social spiders are also favored hosts among non-spider kleptoparasites.

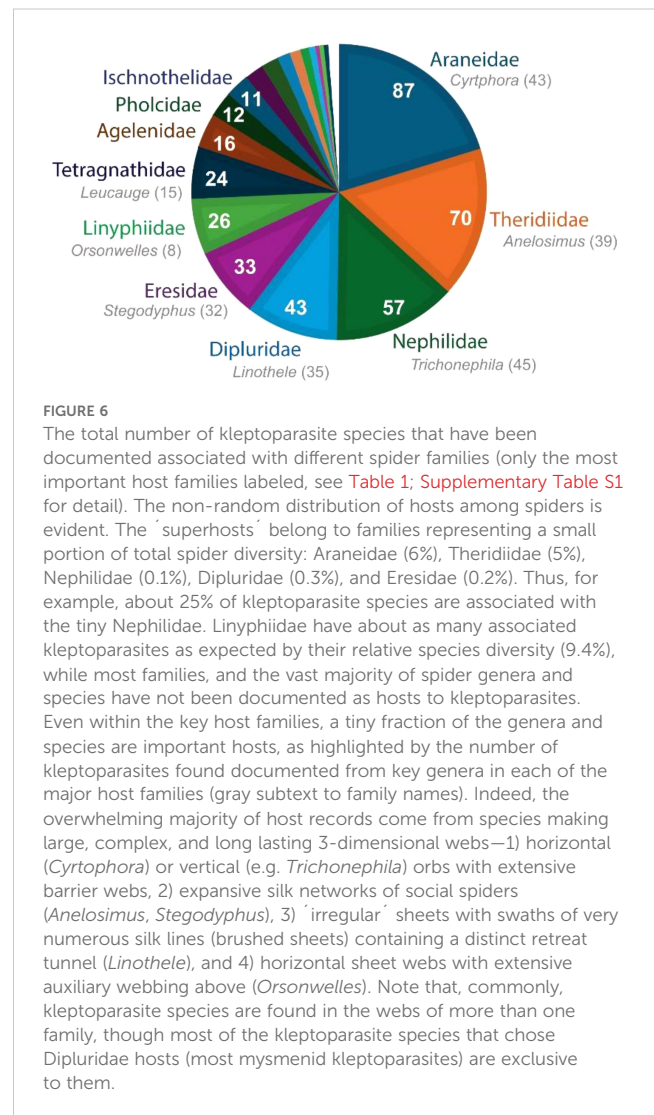
While preferred spider hosts share many traits, the stark divide in host use between argyrodoine and ‘symphytognathoid’ (*Mysmenopsis*,

Isela, *Curimagua*) kleptoparasites is intriguing and suggests we have a very partial understanding of host choice. The mygalomorphs *Diplura* and *Linothele* construct brushed sheet-like webs that span the ground or other surfaces and are key hosts for a clade of symphytognathoid kleptoparasites (excluding *Sofanapsis*) but are rarely used by argyrodoines. In turn, symphytognathoids are relatively rarely found in orb webs suspended above the ground that are favored by argyrodoines. Thus, it seems that the even ‘good hosts’, as characterized above, building large, complex, and permanent webs,



are not simply a free-for-all. Effective utilization of a given host type may require some adaptations. That two monophyletic lineages (argyrodes and mysmenids) have diverged to specialize on these different web types—sticky orbs vs mechanical (non-sticky) sheet and funnel webs, respectively—begs adaptive questions. It remains to be seen if we can identify traits that differ between argyrodine and symphytonathoid kleptoparasites and may help explain this division in host use. Certainly, certain kleptoparasite behaviors may be orb-web specific like silk consumption (spiders have not been documented consuming aciniform silks, used in the sheet of Diplurid webs) and stealing wrapped prey items. However, in both cases kleptoparasites feed with the host, possibly the primitive foraging mode of spider kleptoparasites. Curiously, the other symphytonathoid kleptoparasite, the anapid *Sofanapis*, is highly unusual in preferring host rarely used by the other two clades. It seems to prefer austrochilid hosts, while also found in the webs of Hahnidae, in addition to occurring in some classical orb webs. Regardless, *Sofanapis* displays the putatively primitive foraging mode of feeding with the host.

Of identified species, the host to the highest number of kleptoparasite species is probably also the best studied, the American *Trichonephila clavipes* where 21 species of mostly argyrodes have been documented (Table 1; Supplementary Table S1). While vastly less effort has been afforded to other nephilids as host, other species like *T. inaurata*, *T. clavata*, and *Nephila pilipes* are known to harbor multiple species of kleptoparasites (Table 1; Supplementary Table S1). Whitehouse et al. (2002) suggested a special importance of Nephilidae hosts globally, and field biologists certainly can confirm that large nephilid webs, as a rule, house multiple argyrodine individuals. In addition to *Nephila* and *Trichonephila*, larger *Nephilengys* and *Nephilingis* webs are rarely without kleptoparasites, that may also be found in *Herennia*. *Cyrtophora citricola*, and other *Cyrtophora* are similarly critical hosts harboring high abundances and



numerous species of kleptoparasites. These two groups seem to be the preferred hosts of the majority of argyrodine kleptoparasites, with some clear exceptions (Table 1; Supplementary Table S1), however, systematic research on kleptoparasite distributions and assembly into host webs is generally lacking. The tight link between *Linothele* mygalomorphs and *Mysmenopsis* kleptoparasites has become particularly clear recently with the effort of Dupérré and Tapia (2015, 2020), but again, almost no research on host choice and assembly into host webs exists on mysmenid kleptoparasites.

2.5 Deferred hosts

In contrast to the groups discussed above, the majority of web building spiders rarely host kleptoparasites and thus appear to be deferred hosts—that is their webs have much lower kleptoparasite loads than predicted based on web size. While many knowledge gaps exist and new research constantly adds to the list of kleptoparasitic species and their hosts, a ‘list’ of deferred hosts among web building spiders would be very long, approximately the

inverse of hosts listed in Table 1 (see also Supplementary Table S1). Even some found in Table 1, species that are utilized as hosts, are clearly deferred. For example spiders in the genus *Leucauge* are among the most common orbweavers in many habitats (own obs.). Yet they rarely contain kleptoparasitic spiders. In fact, many of the records of *Leucauge* as a host come from a study where McCrate and Uetz (2010) failed to find kleptoparasites in its webs, unless in multi-species colonies of web-builders associated with the colonial *Metepeira incrassata*. In some areas *Leucauge* webs are generally without kleptoparasites but may serve as interim hosts during seasons when preferred hosts are not available (Miyashita, 2002). Miyashita (2002) found *Argyrodes bonadea* and *A. flavescens* in *Leucauge blanda* webs in Japan but almost exclusively when preferred hosts (*Nephila pilipes* and *Trichonephila clavata*) were not in season. Regardless, Miyashita (2002 p. 34) found that *L. blanda* had "...significantly fewer [*Argyrodes*] ... on their webs than expected from their web area". *Tetragnatha* and other tetragnathids, most Araneidae genera, and nearly all small "orbicularians" (e.g. *Cyclosa*, *Eustala*, *Mangora* etc.), are further examples of extremely common, diverse, and abundant orbweavers that rarely host kleptoparasites. Similarly, amaurobiids, most pholcids, mysmenids, and most theridiids, are examples of diverse web builders underutilized by kleptoparasites (Supplementary Table S2). In fact, the vast majority of species of web-building spiders are deferred hosts, likely including many entire families of spiders like Theridiosomatidae, Symphytognathidae, and other groups of small spiders. The vast majority of species in the most diverse web-building groups Linyphiidae and Theridiidae are also deferred. In the latter two, nevertheless, certain species rank among clearly preferred hosts. It is logically obvious that what characterizes deferred hosts is lacking some or most of the traits of preferred hosts. There are vastly more species of small rather than large web builders, which may more readily detect similar-sized invaders and compete more directly with them for food. The majority of orbweavers make small webs with little auxiliary webbing, renew webs daily, and may frequently relocate. *Leucauge* are an exception in that their orbs are often associated with barrier webs, and indeed many kleptoparasites of many species have occasionally been found in their webs. However, these relatively small spiders are incredibly aggressive toward web intruders (Eberhard pers. comm.) which may explain why *Leucauge* webs seem mostly to be used as 'last resort' hosts when preferred hosts are absent. Smaller spiders and webs capture fewer insects, are likely to have faster prey handling time, and less reason to store prey. Most web builders, furthermore, do not form interconnected clusters. In some cases, a single trait may separate preferred from avoided hosts. Large orbweavers have many attributes that are attractive to kleptoparasites, yet only a portion of them commonly host them, likely due to lack of certain critical traits. A point in case can be made regarding *Gasteracantha* and *Micrathena*. The two genera are diverse and highly similar as large, spiny, brightly colored spiders that build big and highly regular symmetric orb webs, in relatively open areas. Numerous species of argyrodines have been documented in a number of *Gasteracantha* species that, at least in certain habitats, appear to

be among the most important hosts. In contrast, kleptoparasites are rarely encountered in *Micrathena* webs (except when associated with multi-species colonies McCrate and Uetz, 2010). While both genera remove webs at night and rebuild during the day, a key difference may be in what they do not remove. *Micrathena* removes the entire web leaving at most one or two lines while *Gasteracantha* leaves up a number of frame lines that that are reused as frames the following morning (Eberhard pers. comm.). Such minor differences may suffice to allow kleptoparasites to more easily find webs or web remains at night and stay associated with host webs that are taken down but rebuilt in the same spot.

2.6 Hosts from the perspective of kleptoparasites

It is clear that host choice is not random. First, only a small subset of web building spiders seem appropriate hosts. Second, even among spiders that build relatively large and permanent webs, kleptoparasite diversity and abundance is concentrated in the webs of a few host species. But how decisively do kleptoparasites chose among 'acceptable hosts'? There is a range of opinion but limited data on kleptoparasite host specialization. Vollrath (1984 p. 70), e.g. discussed argyrodines and claimed that '[o]f the 50-odd neotropical *Argyrodes* two are presently known to be specialists, about ten to be generalists...'. Specialists are, he claims, in large araneids (*Araneus*, *Cyrtophora*, *Argiope*, *Nephila*), while generalists are found in multiple additional hosts (Vollrath, 1977). Since Vollrath (1984, 1987) kleptoparasites are commonly referred to as either specialists or generalists in literature (e.g. Elgar, 1993; Whitehouse, 2011; Su and Smith, 2014). Yet the data at hand suggest a more subtle picture. In an extensive study of argyrodines (treated together under the genus *Conopistha* at the time) of Peru and Ecuador, Exline (1945b p. 506) stated 'There is no correlation between the various species of *Conopistha* and species of their hosts. They inhabit indifferently webs of *Gasteracantha*, *Argiope*, *Meta*, and *Aranea* [= *Araneus*], in localities where these orb weavers occur.' Similarly, as more data are gathered, species that once were thought to be specialists, like *Argyrodes elevatus*, have now been documented in a large sweep of hosts (Supplementary Table S2). On the other hand, Exline (1945b p. 506-507) discussed preferred and deferred hosts in general: 'Some field observations on the relationships of *Conopistha* to host species may be important if correctly interpreted. In most areas where the genus is common, species of orb-weavers, including *Meta*, *Gasteracantha*, *Aranea*, *Argiope*, *Tetragnatha*, *Cyclosa*, and *Leucauge*, are common. *Conopistha* nearly always is present in the webs of *Meta*, *Gasteracantha*, *Aranea*, and *Argiope*, but almost never in webs of *Tetragnatha*, *Cyclosa* or *Leucauge*. Spiders of the first groups, hosts of *Conopistha*, feed upon large insects—beetles, large flies, bees, and Orthoptera—and disregard the small prey in their webs. Orb-weavers which do not harbor *Conopistha* feed on such minute insects as small flies, mosquitoes, and midges.' Exline (1945a, b) believed host choice was essentially random and that kleptoparasites survived and thrived when they happened to be in

webs where they did not compete with the host for prey or fall prey to it. There is little evidence for host choice to be random, especially with respect to preferred and deferred webs in general. However, establishing true host specialization requires large amounts of data that simply do not exist for most species. Studies that have been made over a short period of time, in a particular region or season, or particular habitat, may find evidence suggesting specialization, while the strength of any proposed association with a particular host tends to break down as more data are added. Vollrath (1976, 1977, 1979b, 1984), for example, suggested that *Argyrodes elevatus* is a specialist on large hosts, principally found in webs of *Trichonephila clavipes* and *Argiope argentata*, which is an expert in stealing food bundles from the hosts' hub. Further studies on this species have found it utilizing a variety of host species, large and small. Thus, in stark contrast with Vollrath, Silveira and Japyassú (2012) instead consider *A. elevatus* to show extreme plasticity, employing diverse tactics to steal food from a great variety of hosts and web types. These include *Nephilengys*, various *Argiope* and *Araneus*, colonial *Metepeira incrassata* and *Cyclosa huila*, subsocial *Anelosimus baeza*, as well as in solitary webs of theridiid spiders such as *Latrodectus*, *Tidarren*, and *Parasteatoda*. What can we therefore claim about host specialization in argyrodine kleptoparasites? As proposed by Agnarsson et al. (2025) asking if one species is a specialist or a generalist is not a productive approach to understand the complex interplay between kleptoparasites and hosts. Rather “argyrodines may better be characterized as kleptoparasites generally capable of discriminating among host webs, but that choose hosts with varying degrees of astuteness or concern.” A more productive approach, therefore, will be to better assess kleptoparasite distribution and assembly into host webs at a community level, and the factors that impact host choice. In particular, what host traits do kleptoparasites cue in on and why do some species seem to choose hosts with greater astuteness than others?

3 Diversity of organisms as kleptoparasites of spiders

3.1 Non-spider kleptoparasites on spider hosts

A number of animals regularly exploit spider webs, ranging from commensals to kleptoparasites, to predators and parasitoids, depending on whether symbionts compete for the same resource and the manner of their foraging or reproductive strategy (Supplementary Table S3, Robinson and Robinson, 1977). Some arthropods may be purely commensal, such as mealybugs found in *Phryganoporus candidus* nests, or scavenging beetles that rummage leftover prey and waste (Downes, 1995), or lepidopteran larvae feeding mostly on plant material incorporated into the webs of social spiders. Kleptoparasites (Supplementary Table S3), in addition to other spiders, include species of hemipterans (Davis and Russell, 1969; Henry, 1984) panorpoid scorpionflies (Thornhill, 1975), lepidopteran larvae (Robinson, 1977), wasps (Jeanne, 1972), damselflies (Vollrath, 1977), numerous dipteran species of at least

10 families (Sivinski et al., 1999), rove beetles and other scavenging beetles, Cheyletidae mites, and other arthropods (Supplementary Table S1, Knab, 1915; Bristowe, 1931, 1941; Richards, 1953; Robinson and Robinson, 1977), and even birds, such as a hummingbird that steals both insect prey and silk (Young, 1971). Many of these are attracted to prey captured by the host spider or entangled in its web, others may be more generally predators in the host webs where they may prey on host or commensal spiders, their eggs or juveniles, or other arthropods in the web (Schneider and Lubin, 1997; Henschel, 1998). Ants, for example, enter webs and may steal prey from the web and/or prey on the host and its offspring (Schneider and Lubin, 1997; Henschel, 1998). Parasitoid wasps target host spiders, their eggs, or even other symbionts (Hieber and Uetz, 1990).

Kleptoparasites that compete with spiders for prey, remove prey items secured by the spider, or feed with the host, clearly can negatively impact the hosts (Henschel and Lubin, 1992). Probably the majority of non-spider kleptoparasites in spider webs are facultative. Scorpionflies (Panorpidae) opportunistically enter webs to feed on captured prey (Thornhill, 1975).

Other facultative kleptoparasites include damselflies (Zygoptera), apocritan wasps, and lepidopteran larvae that may occasionally steal prey from spider webs or use the web or webbing as nesting material (Jeanne, 1972; Robinson, 1977; Vollrath, 1977), and mites and beetles that scavenge on debris left by the host spider or consume parts of prey remains (Faust et al., 2012). Hummingbirds may occasionally use silk taken from spider webs as nesting material and grab prey items as they pass by (Young, 1971). The impact of facultative kleptoparasites can be difficult to evaluate. Secondary consumption on decomposing prey bodies or web-bound detritus, can be of no consequence to the host, or even beneficial if it results in effectively reducing waste within the web. Yet, all these taxa may remove resources with potential fitness consequences for the host spider. On the other end of the spectrum, there is clear evidence that facultative kleptoparasites can be very harmful to the host. Ants provide a stark example of harmful occasional kleptoparasites. When they wander into spider webs, they have the ability to recruit large raids of foragers that opportunistically steal resources and predate upon hosts (Schneider and Lubin, 1997; Henschel, 1998; Hölldobler and Wilson, 1998). As ants may continuously patrol a network of routes around their nests, they can pose a persistent and ominous challenge to web building spiders (Henschel, 1998; Hölldobler and Wilson, 1998). Furthermore, ants like *Veromessor pergandei*, *Oecophylla smaragdina*, and *Anoplolepis gracilipes* can not only steal prey and forage on egg sacs but may also dismantle spider webs e.g. to salvage trapped nestmates.

Many groups then rely mostly on kleptoparasitism, where spiders may be among their hosts, or their exclusive hosts. Dipterans are adept kleptoparasites often feeding on prey along with the predators, and numerous species in families including Milichiidae, Phoridae, Chloropidae, and others (Supplementary Table S3) approach or invade spider webs (Sivinski and Stowe, 1980; Sivinskii et al., 1999). Milichiid flies are chemically attracted to prey caught in spider webs and often hover near the web until an

opportunity arises to feed undetected. The majority of such flies apparently go unnoticed, perhaps adapted to hovering at a safe distance and landing on the spider carapace or on the prey only when the spider is occupied. Or the host opts to not detract them, however, some percentage of these flies may themselves end up as prey. *Ranzovius* bugs (Miridae) like *R. morens* and *R. contubernalis* are specialist kleptoparasites scavenging prey items in spider webs, many associated with the social *Anelosimus* spiders (Henry, 1984; Wheeler and McCaffrey, 1984; Guariso, 2000; Deyrup et al., 2004).

In conclusion, spider webs represent not only snares for prey capture but also complex habitats that sustain diverse communities where kleptoparasitic organisms are the most diverse. From the stealthy *Argyrodes* to opportunistic ants, each kleptoparasitic organism has developed strategies to exploit spider webs to its advantage. Clearly, spider webs play ecological roles beyond prey capture, providing important microhabitats within most terrestrial ecosystems.

4 Facultative kleptoparasitism in spiders and araneophages in kleptoparasitic lineages

4.1 Interactions among spider species in webs – webs as refuges and structural support, and web invasion

Spiders exhibit a fascinating array of web-invasive strategies exploiting the webs of other spiders in intra- and interspecific interactions including—in addition to kleptoparasitism—other resource usurpation, web takeover, predation, and mating.

Perhaps the least invasive usurpation of spider webs is using a stranger's web as a refuge from predators, as seen in some wandering spiders in social spider webs or using the structural lines of the web to support one's own web. Such connecting behavior characterizes colonial spiders that in addition to clustering around abundant resources may benefit from interconnectedness via 'ricochet effects' (Uetz, 1989), the ability to sense struggling prey in multiple webs, predator defense, and others (Rypstra, 1989). Colonial species such as *Metepeira incrassata* (McCrate and Uetz, 2010) and *Philoponella republicana* (Binford and Rypstra, 1992), and those that more facultatively interlink webs like *Cyrtophora* spp. (Rypstra, 1979; Leborgne et al., 1998) and *Trichonephila* spp (Rypstra, 1981; Agnarsson, 2011), may also connect their nests to heterospecific webs. Many other species facultatively connect their webs to others, particularly to webs of colonial or clustering species. *Leucauge*, *Uloborus*, *Micrathena*, *Holocnemus pulcei* and some other pholcids, various small orbweavers, linyphiids and theridiids are among those using 'host' webs as structural support (Bristowe 1941a, b, Eberhard et al., 1993; Leborgne et al., 1998; McCrate and Uetz, 2010, Magnússon and Agnarsson unpublished). As webs of inter- and intraspecific individuals are thus frequently contiguous (Krafft, 1970; Burgess and Uetz, 1982; Jackson and Hallas, 1986; Hénaut

et al., 2010), opportunities for web invasions abound. Indeed, spiders in interconnected complexes often enter neighboring webs to pursue insects (facultative kleptoparasitism, Supplementary Table S2), or opportunistically predate on the web owner (Kullmann, 1959a, b, 1960; Jackson and Hallas, 1986; Wise, 2006). Bristowe (1941a, b), for example, observed *Pholcus* sp. predate on the owners of various webs it connected to, including araneids, theridiids, amaurobiids, agelenids and other pholcids. Other spiders instead of linking their web will invade webs to aggressively steal prey from the host, kill the host, or attempt to take the web over. The best-known cases are wandering spiders like *Olios* (Sparassidae), *Simaetha* and *Portia* (Salticidae) that engage in aggressive facultative kleptoparasitism by removing the prey from their hosts (Jackson and Wilcox, 1990). *Portia* is unique in its versatility of foraging strategies, being among the very few jumping spiders that regularly build prey capture webs, in addition to hunting outside a web, and invading the webs of other species (Jackson and Hallas, 1986). It may or may not connect its own web to a host web and opportunistically forage kleptoparasitically or via araneophagy. Even though they will take insects, *Portia* species are specialized araneophages that will prey on eggs, juveniles, and capture host spiders using a variety of tactics including stealth and mimicry (Jackson, 1985, 1987, Jackson and Blest, 1982; Jackson and Hallas, 1986). Web building spiders may instead engage in web takeover. Kleptoteny refers to such theft were spiders abandon their own webs to invade and exploit the webs of others. While there are relatively few observations of web invasion by web building spiders (Enders, 1974; Buskirk, 1975; Eberhard et al., 1978; Wise, 1981, 2006, Wickler and Seibt, 1988; Eichenberger et al., 2009; Houser et al., 2014; Gan et al., 2015; Gould, 2021), web building spiders frequently abandon webs when insufficient prey is captured (Turnbull, 1964), providing an impetus to wander off web and possibly happen upon other webs inadvertently. It seems likely that web takeover is widespread as an opportunistic strategy (Bilsing, 1920, Bristowe 1941a, b). Web building spiders web takeover may take place intra- or interspecifically, can be passive or aggressive, and involve various life stages, including adult males. Enders (1974), in an experimental setup, observed passive (empty web) conspecific web takeover in *Larinioides cornutus* and *Argiope trifasciata*. Both species would also invade empty webs of some other orbweavers and *Eustala* sp. was observed taking over empty webs of *Larinioides cornutus* (Bilsing, 1920; Enders, 1974). Aggressive web takeover has been seen in a number of species. Colonial *Cyrtophora citricola* adults and juveniles will displace each other depending on the capture rate of individual webs (Blanke, 1972; Eberhard et al., 1978; Rypstra, 1979) and adult *Trichonephila clavipes* will displace smaller individuals from their webs (Farr, 1976; Christenson, 1984). *Cyrtophora citricola* often steal food from one another (Whitehouse and Lubin, 2005) and in some cases, rather than attempting to take over webs, some individuals may simply opt to be webless and operate as facultative kleptoparasites in conspecific webs. This has been observed, for example, in *C. citricola* and *Agelenopsis aperta* (Rypstra, 1979; Christenson, 1984). It is unclear if such 'intraspecific optional weblessness' differs from other facultative kleptoparasite strategies. Gan et al. (2015) observed

intra- and interspecific aggressive web takeover among various orbweaving species including *Lariniaria argiopiformis*, *Neoscona inusta*, *N. punctigera*, *Parawixia dehaani*, *Zygiella x-notata*, and *Tetragnatha laboriosa*. Webs built higher in the vegetation and those capturing more prey were more likely to be invaded, and typically, as in *C. citricola* and *T. clavipes*, the success rate of web takeover depends on the relative size of invader and host. Similarly, Eichenberger et al. (2009) observed interactions between the introduced linyphiid *Mermessus trilobatus* with native European sheetweb spiders (*Erigone dentipalpis*, *E. atra*, *Gnathonarium dentatum*, *Dicymbium nigrum* and *Micrargus herbigradus*). The impetus for the study was the indicated invasive takeover of webs by the introduced *M. trilobatus*, however, Eichenberger et al. (2009) found that all of these species may attempt web takeover. Like prior studies, they found that body size plays a critical role in the outcome of these interactions, whether intra- and interspecific web takeover. This kind of web takeover is a clear example of facultative kleptoparasitism (aggressive usurpation) where the stolen resource is not prey secured by the host, but its prey capturing device and, of course, the prey it subsequently entangles. Eberhard et al. (1978) observations of webs of *Metazygia* spp. in Colombia illustrate a form of web robbery in which male spiders seize webs from immature or conspecific individuals to capture prey. This is a particularly interesting case of size-based aggressive usurpation as the males themselves typically do not build webs. They observed a male *Tetragnatha* sp. invade the web of *M. gregalis* where it stole prey and eventually replaced the smaller owner in the hub of the web. Similarly, they saw males of *Eustala* sp. and *Larinia directa* take over webs of *Metazygia* and males of *Metazygia* taking over webs of conspecifics or other *Metazygia* species. The males would then capture prey in the stolen web. Male spiders may also feed on silk, male *Leucauge marina* may steal silk from the webs of larger orbweavers (Eberhard, 2020). Observations on male behavior after they molt to adulthood and abandon web building, but prior to courtship, is generally lacking. However, it is reasonable to assume that males wandering in search of females will opportunistically capture prey on and off webs and steal other resources. The males of many species that cohabit with females they (attempt to) mate with, will take prey from the webs (see below), and web building spiders are certainly capable of capturing prey outside their webs, Gould (2021), for example observed *Tetragnatha* sp. haul up a large dragonfly without the use of a web.

4.2 Mating and males as facultative kleptoparasites

Webs typically serve as mating sites, with males abandoning their own webs and seeking to invade the web of a female to court her. It is common that males cohabit with females in their webs for some time, guarding a subadult female until she molts to maturity, defending her against other males, or awaiting an opportunity to sneak in and mate (Foelix, 2010). In the case of large spiders with pronounced sexual size dimorphism (female biased extreme sexual size dimorphism, eSSD *sensu* Kuntner and Coddington, 2020)

males may even accumulate in significant numbers in female webs. In communal species, like *Philoponella* spp (Opell, 1979), it is also common to find males in the colonies and it seems likely they take prey opportunistically. Though observations are sparse for this aspect of male biology, the scattered records suggest that males may commonly act as facultative kleptoparasites in female webs. *Linyphia litigosa* males steal prey from females they cohabit with and will even fight her for prey (Rovner, 1968; Wise, 1975; Watson, 1990). Many male pholcids will, similarly, aggressively pursue food in female webs (Eberhard and Briceño, 1983, 1985, Blanchong et al., 1995). Males in some species are favored to win fights due to larger size (Eberhard and Briceño, 1983), or in species where the sexes are similarly sized, the larger individual tends to have the upper hand (Blanchong et al., 1995). *Latrodectus revivensis* males enter webs of females, even juveniles and subadults, and steal prey. The impact is particularly negative for younger females that may opt to relocate their webs to escape the male, at a high risk of mortality (Lubin et al., 1993). Male *Stegodyphus lineatus* cohabit with females and may steal and consume their eggs (if not their own) and steal prey from them, acting as costly kleptoparasites in female webs (Schneider and Lubin, 1996, 1997). Facultative male kleptoparasitism is typically less aggressive and costly to females. Male *Metellina segmentata* hang out at the edge of the female web and may enter the web when the female has captured prey and feed with her, both prior to and after mating (Blanke, 1974; Prenter et al., 1994; Elgar and Fahey, 1996). In the eSSD nephilids, where multiple males often cohabit with the giant female, their foraging behavior is quite similar to that of obligatory kleptoparasitic argyrodines. *Trichonephila clavipes* males, for example, await their opportunity in the barrier web and enter the web to glean insects ignored by the female, feed with the female, eat silk, or may even steal prey from argyrodines inside the female web (Christenson and Goist, 1979; Vollrath, 1977; 1980, 1987). In both *Nephila* and *Trichonephila* the largest male may reside near the hub and feed with the female while the smaller ‘satellite’ males glean insects and rival argyrodine kleptoparasites (Robinson et al., 1973, 1976, Kuntner pers. comm.). It is likely that males of other nephilids and of other eSSD orb weavers where males accumulate in female webs display similar kleptoparasitic behaviors (Robinson et al., 1973; Christenson and Goist, 1979; Vollrath, 1980, Kuntner pers. comm.).

Male cohabitation may in some cases be more mutualistic than parasitic in nature. Males of the pholcids *Blechnocelis* sp. and *Modisimus* spp. cohabit with female and capture prey in her web (Eberhard and Briceño, 1983, 1985). While the generally larger males will contest with the female over prey, the males appear to ‘concede’ the prey to females upon ‘begging’ gestures she makes, vibrating her abdomen. In some instances, males will capture and wrap prey, signal the female by plugging the web, and then leave the prey to her, or even carry the prey to her. Eberhard and Briceño (1983, 1985) suggest that this kind of ‘chivalry’ in *Blechnocelis* and *Modisimus* spp. may render the interaction between males and females mutualistic. On the other hand, where the sexes are similarly sized like in *Holocnemus pluchei*, the outcome of a struggle for prey depends on individual size, males not being favored in general. On such ‘equal terms’ males that happened to

secure a prey from a female, did not show any signs of 'chivalry' (Blanchong et al., 1995). Perhaps the lack of a general size advantage means that males cannot exert control over females by stealing prey at will and then secondarily offering it to them.

4.3 Facultative kleptoparasites and araneophages

In addition to web takeover scattered across multiple web building groups, and male facultative kleptoparasitism that is also widespread but rather poorly known, a few cases of facultative kleptoparasitism that involve neither web takeover nor male spiders are relatively well documented. Information on a few groups of such facultatively kleptoparasitic taxa are summarized below. In addition, some taxa specializing in araneophagy are treated below, although they may be similar to taxa discussed under section 5.1. These are examples taken to highlight groups like *Rhomphaea* and *Ariamnes* that due to details of strategies and/or phylogenetic position, may display transitional traits related to the evolution of kleptoparasitism. Information on further facultative spider kleptoparasite and araneophages can be found above and in [Supplementary Table S2](#), though it is far from exhaustive. It should be noted that not all spider kleptoparasites steal from other spiders. *Henriksenia* crab spiders take food from pitcher plants (Fage, 1928; Striffler and Rembold, 2009; Chua and Lim, 2012), and spiders may also take food from other predators and scavengers (Cushing, 2012). Jackson and Pollard (2008), for example, observed three Kenyan species of *Menemerus* jumping spiders snatch food from the mandibles of *Crematogaster* and *Camponotus* ants, a behavior first noted by Bhattacharya (1936) in the Indian *M. bivittatus* [as *M. melanognathus*]. Near the shores of a lake masses of Chaoboridae and Chironomidae midges that had emerged from a lake were found perishing on the walls of buildings scouted by ants. Jackson and Pollard (2008) describe how the spiders would track ants as they walked by and attack if they were carrying prey. The spiders would approach rapidly, grab the fly with their chelicerae and pull away as the ant let go of the prey. Only relatively small individuals would partake in prey theft, which complemented typical prey catching by these jumping spiders. Hence, the kleptoparasitic behavior is facultative and Jackson and Pollard (2008) suggest that it may secure fly prey more rapidly than stalking the fly directly. Further, as the flies are dead or dying, the spiders may use the ants as assessors picking out among the cadavers prey that is still palatable. This foraging tactic has been noted in multiple *Menemerus* species, but is not a common salticid behavior, suggesting this may be an adaptive, although facultative, strategy.

In most cases, spiders steal food from other spiders, and typically on the host's web. *Oonops* is a fairly large genus of Oonopidae spiders containing one species known to be kleptoparasitic. *Oonops pulcher* is a small spider that has been observed in a variety of habitats, hunting on the ground as typical for oonopids, sometimes found in birds' nests, but also in the webs of larger spiders (Bristowe, 1930, 1958). Bristowe (1930) observed

O. pulcher move among the retreat strands of its hosts, ignored by the host agelenid or amaurobiid spider, feeding on remnants of the hosts meals. *Oonops pulcher* is clearly a facultative kleptoparasite, most commonly found outside a host webs (Le Peru, 2011).

Platnickina is a theridiid genus containing 12 species some of which have been observed invading other spider webs. *Platnickina* is an anomaly in this summary of genera as it likely rarely steals prey. It is discussed here to highlight the need for further studies of the genus, and to consider the potential links between opportunistic web invasion and obligatory kleptoparasitism in spiders. *Platnickina* species build their own web, a simple network of threads, and commonly capture prey there (Suzuki et al., 2022). The majority of prey consists of insects like nematoceran flies and paraneopterans, but some 40% of the prey were spiders. *Platnickina* will wander outside its web and into webs of hosts including other theridiids, *Tetragnatha* and *Trichonephila* (Bristowe 1941a, b; Namkung, 2003; Suzuki et al., 2022). There, it will attempt to attack and kill the host but has a much lower success rate in killing hosts in the host's web than in capturing prey in its own web. The large size of potential spider host prey may make up for the challenge in capturing and killing it. *Platnickina* may be an opportunistic kleptoparasite as well, Suzuki (pers. comm.), for example, has observed *P. sterninotana* feeding on a large *Brachycera* fly in a theridiid web.

Rhomphaea contains 37 argyroline species that are primarily thought to be araneophages and are often discussed in the context of the origin of web invasion and kleptoparasitism. *Rhomphaea* species are typically elongated, with long 'tails' that they can move in a worm-like fashion (Archer, 1946)—their bodies appear well camouflaged, especially within host webs. While *Rhomphaea* species are often found in their own simple web consisting of several irregularly spaced threads, they are also frequent invaders in the webs of other spiders. 'Hosts' of *Rhomphaea* include a variety of smaller sheet (Linyphiidae) and cobweb (Theridiidae) spiders—including social theridiids—as well as orbweavers (Archer, 1946; Exline and Levi, 1962; Smith Trail, 1980; Whitehouse, 1987b; Guarisco, 2000; Kim and Kim, 2007; McCrate and Uetz, 2010; Srinivasulu et al., 2013). In most cases, *Rhomphaea* are reported as host predators, but they have also been observed stealing food from host webs (Eberhard, 1979; Yaginuma, 1986; Yoshida, 2001a, b). Suzuki et al. (2022) found that the diet of adult *Rhomphaea* consists mostly of spiders, with some 15% of predation attempts directed at insects, while juvenile *Rhomphaea* capture mostly insects. *Rhomphaea* had a high predation success on its own simple thread webs (95%), but in host webs it often fails to capture the host spider (25% success rate), especially when the host is large. It is likely that *Rhomphaea* ventures into host webs in an attempt to catch larger prey than it gets on its own web, even if less successful.

Ariamnes is an extraordinary genus of argyroline theridiids, containing 24 species with exceptionally elongated and worm-like abdomens (Vollrath, 1977). *Ariamnes* are relatively large spiders, and unlike most members of the subfamily, they appear to rarely wander into webs of other spiders (Clyne, 1979; Eberhard, 1979). Eberhard (1979) describes the web of *Ariamnes* as a sparse, irregular, three-dimensional network of long, non-sticky threads that can extend up to 1–2 meters. Rather than functioning as a snare,

this web serves as a resting site for the spider and as a base for ambush attacks. Juveniles of *A. attenuatus* primarily capture nematocorous flies that tend to hang on these threads, while adults capture juvenile spiders, typically non-web builders larger than themselves. They use a specialized predatory technique shared with *Rhomphaea*, throwing sticky silk with their hind legs to immobilize prey. Suzuki et al. (2022) found that spiders constitute about 75% of the prey of *Ariamnes*, with a preference for cursorial spiders over web builders, and including other araneophagic spiders like *Rhomphaea*, *Platnickina*, and even other *Ariamnes*. *Ariamnes* foraging behavior appears to be quite homogenous across species. The spider's resting posture, with legs outstretched, may be a camouflage resembling a pine needle caught in the web. Dönitz (1887) described the spider's unique egg sac, a bell-shaped structure suspended by threads and resembling an elongated cocoon with a wool-like interior, which the adult females guard (Eberhard, 1979).

Spiders employ diverse web invasion tactics, utilizing webs for predation, resource competition, shelter, and mating. Diverse groups of both web builders and web-less hunters enter webs in search of resources or mating opportunities. Facultative kleptoparasitism is found in most such species, opportunistically stealing prey, silk, or even the web itself, regardless of the ultimate objective ranging from courtship to cannibalism. Facultative kleptoparasitism is also found in some spiders stealing prey not from a web spider. For reasons outlined in the Introduction, I have not attempted to exhaustively review facultative kleptoparasitism in spiders. It is a compelling but underexamined facet of spider biology, marked by dynamic and often intricate interactions: overt contests for webs, covert theft of prey and silk by males wandering in search of females, sexual conflict on display in facultative male kleptoparasitism, opportunistic resource theft by versatile taxa, and specialized araneophagy. Opportunities for innovative future research abound—given the phylogenetic spread of observed species, and the somewhat haphazard nature of such observations. I predict that *facultative kleptoparasitism is far more widespread and common than currently appreciated*. Spiders that engage in opportunistic web invasions demonstrate an evolutionary flexibility, using webs of others to reduce the energetic costs of web building and prey capture. If as pervasive as hypothesized above, the occurrence of web invasions and facultative kleptoparasitism across diverse spider lineages may imply that the evolutionary bridge to obligatory kleptoparasitism in spiders is rather short.

4.4 Obligate spider kleptoparasites

In total there are probably between 200–300 species of obligate kleptoparasites among the ~53,000 spider species currently known (WSC, 2025). Some behavioral or habitat data (host webs) are available for a little over 100 species (see Table 1; Supplementary Table S1 and References, summarized in Agnarsson in prep.), while the majority of species expected to be kleptoparasitic lack such data. Many new species also doubtless await discovery and description (Agnarsson et al., 2013) as evidenced by a proliferation in descriptions of species and genera in recent years (Dupérré and Tapia, 2020; Lin et al., 2024;

Vanuytven et al., 2024). A synthesis on obligate kleptoparasitic spiders will be provided elsewhere (Agnarsson in prep.).

5 Host response to kleptoparasitism

The cost of kleptoparasitism is challenging to measure. In some cases, it is expected to be relatively small, when kleptoparasites only remove prey remains, prey ignored by the host, or silk. However, any removal of calories from the web has the potential to impact the host (Coyle et al., 1991; Whitehouse, 2011) and even calories contained in ignored prey and silk represent a cost as these could be ingested by the host when recycling the web. In many cases, kleptoparasitism inflicts a more readily measurable costs on host spiders, especially through prey depletion and its cascading effects on growth, reproductive output, and fitness (Vollrath, 1987; Elgar, 1993; Whitehouse, 2011). Studies on *Anelosimus eximius* demonstrate that *Faiditus ululans* may consume up to a quarter of the prey in a host's web (Cangialosi, 1990b), and research on *Trichonephila clavipes* shows that the daily caloric requirements of argyrorodine spiders can reach at least 20% of that of the host when kleptoparasite abundances are high—in this case when they reach about 40 per web (Vollrath, 1980; Elgar, 1993). While these may be extreme examples, even at a smaller cost, kleptoparasites divert significant energy reserves away from the host spider's reproductive efforts and thus fitness. It is obvious that such resource diversion can be particularly damaging in energy-constrained environments, where each prey item represents a critical contribution to the host's metabolic requirements. In social webs, the impact of kleptoparasites can amplify, as these webs represent a “public good” shared among colony members. The shared prey resources attract kleptoparasites who consume prey captured collectively, placing additional strain on the colony (Straus and Avilés, 2018, 2023). Thus, this resource-sharing model, though beneficial for maintaining the colony, becomes a point of vulnerability, making communal webs especially susceptible to kleptoparasitic exploitation and resource depletion (Leborgne et al., 2011). This highlights the ecological cost of maintaining large, accessible prey traps in communal settings (Vollrath, 1984), where kleptoparasitism can reach ‘sublethal’ levels (Straus and Avilés, 2023).

The behavior and phylogenetic distribution of kleptoparasitic hosts suggests an evolutionary trade-off, perhaps even an arms race between web-building spiders and kleptoparasites. Hosts in clades like Nephilidae, Araneidae, and Dipluridae have evolved ‘progressively’ (or repeatedly) larger and more intricate webs presumably under fecundity selection where larger females require ever more food to produce more offspring (see e.g. Kuntner et al., 2019; Kuntner and Coddington, 2020). However, large and elaborate webs with high prey capture success rate also attract kleptoparasites. This trade-off may have at least two consequences. First, one expects increased selective pressure on direct hosts countermeasures such as means of detecting and eliminating kleptoparasites while maintaining such webs. Second, the majority of orb weaving spiders take down their webs and rebuild daily. It is tempting to consider the possibility that daily web recycling, in addition to providing a fresh capture surface daily, is an example of a trade-off where the costs of kleptoparasitism outweigh the benefits of more

elaborate permanent webs. However, testing this hypothesis may be challenging, and if orb recycling evolved once, as the evidence may suggest (e.g. Eberhard, 2020 and references therein), putative causative factors will ever remain speculative. One observation casts doubt on such co-evolutionary scenario; spider kleptoparasitism likely evolved later (and mostly within Araneoidea), than daily web recycling in orb-weavers. Thus, the origin of web recycling does not relate to (at least extant) spider kleptoparasites. The hypothesis is still tenable given the negative impact of heavy kleptoparasite load (Vollrath, 1987; Elgar, 1993), and facultative web takedown and relocation by spiders suffering such heavy loads. It is plausible that kleptoparasitism maintains natural selection for web recycling, and that it plays a trade-off role in the evolution of large and permanent webs. *Nephila pilipes* (Robinson et al., 1973) for example will take down and relocate its web when kleptoparasite load is high. A new web location may offer a respite from kleptoparasites for up to 48 hours. Web relocation in social *Anelosimus* and extreme 'boom and bust' population growth in social *Theridion nigroannulatum* are both putatively linked to argyrodine kleptoparasites (Avilés et al., 2006; Straus and Avilés, 2018, 2023). Thus, kleptoparasite pressure can become a resource drain leading to colony fragmentation or collapse. These scenarios underscore the likely evolutionary arms race between resource conservation strategies and kleptoparasitic exploitation, with host spiders displaying adaptive flexibility in web structure, prey management, and interspecific interactions to mitigate the fitness impacts of kleptoparasitism (Whitehouse, 2011).

Certain solitary orb-weavers display a degree of tolerance toward minor kleptoparasitic activity, conserving energy by ignoring low-level incursions. Vollrath (1987) suggests that this tolerance may serve as an adaptive strategy, where active defense is reserved for more resource-intensive interactions. When implemented, hosts may engage in defensive behaviors aimed at excluding or confronting kleptoparasites. *Trichonephila clavipes*, for example, may respond to argyrodines with aggressive web shaking, or even pursuits. Many other host spiders have aggressive response to spider kleptoparasites that differs distinctly from their response to prey or predators (Vollrath, 1987). Further, the web itself may serve as a barrier modulating kleptoparasitic impact, e.g. through spatial separation of prey from potential kleptoparasites. For instance, layered retreats within *Anelosimus* colonies can limit direct access to prey-rich areas, creating a physical deterrent. It is likely that other traits, speed of prey capture and handling, retreats, and sensory biology are influenced by kleptoparasitism, but research is lacking on this front.

6 Conclusions

Certain spiders function as superhosts by providing structurally complex, resource-rich webs that support a wide range of kleptoparasites. Key superhost traits include large host and web size, high prey capture rates, web or website persistence, and three-dimensional auxiliary silk structures that offer refuges for kleptoparasites. These characteristics are most pronounced in genera such as the orbweaving *Nephila*, *Trichonephila* and

Cyrtophora, and sheet weaving mygalomorphs like *Diplura* and *Linothele*. The webs of these hosts attract diverse kleptoparasites from multiple arthropod lineages, including spiders, flies, ants and bugs. Social spiders are also favored hosts likewise building large and complex webs. The most diverse communities, indeed, form in social spider webs, which have hosts that are more tolerant of co-inhabitants than solitary spiders and generally lack sticky silk. In such webs kleptoparasites bound, but also many arthropods scavenge leftovers and detritus, like beetles and lepidopteran larvae.

The spectrum of kleptoparasitism in spider webs is broad, encompassing obligate kleptoparasites like argyrodine theridiids, facultative prey thieves, web invaders, and even commensals that exploit spider webs without stealing resources useful to the host. Some kleptoparasites feed opportunistically on prey remnants, while others engage in stealthy theft or aggressive food robbery.

Additionally, spiders themselves exhibit secondary kleptoparasitism, with some species abandoning their own webs to invade and exploit the webs of other spiders (kleptotany). This facultative kleptoparasitism is seen in multiple lineages and can involve resource theft, web takeover, or even direct predation on the host (*araneophagy*). These interactions suggest a complex evolutionary pathway, where facultative kleptotany may serve as a transition to obligate kleptoparasitism.

This review highlights the importance of spiders in kleptoparasitic networks and suggests that further phylogenetic and ecological analyses are necessary to fully understand the evolutionary history of kleptoparasitism, and the assembly of kleptoparasitic species into host webs.

7 Future directions

Despite substantial progress in understanding spiders as superhosts and secondary kleptoparasites, this review reveals several key areas that urgently require future research.

7.1 Phylogenetic context of kleptoparasitism

While facultative kleptoparasitism and kleptotany (here) have been hypothesized as precursors to obligate kleptoparasitism, robust phylogenetic analyses are necessary to establish evolutionary transitions. Future work should focus on constructing comprehensive phylogenetic trees incorporating all kleptoparasitic and host lineages to discern evolutionary patterns and seek signatures of possible coevolutionary arms race between kleptoparasites and host.

7.2 Mechanisms of host selection and assembly into host webs

Further investigation is needed into how kleptoparasites locate, evaluate, and establish themselves in host webs. Ecological studies

on species colonization, composition in host webs, and intra- and interspecific competition would clarify what rules may govern species assembly into these habitat islands. Studies employing behavioral assays and chemical ecology approaches should clarify the role of airborne cues, such as pheromones or web-borne signals, in host detection and selection.

7.3 Impact of kleptoparasitism on host fitness and web dynamics

Although some hosts appear resilient to kleptoparasitism, long-term studies tracking web persistence, prey capture rates, and reproductive success in the presence of kleptoparasites would provide a clearer picture of costs and benefits to hosts. Evaluating host responses to kleptoparasites in relation to species and kleptoparasite load could cast light on what strategies may be evolutionary responses to this type of resource theft. In particular, if both facultative and obligatory web takedown and relocation are influenced by kleptoparasitism, then web takedown may play a role in explaining the absence of kleptoparasites from the majority of spider webs.

7.4 Geographic and environmental influences

The distribution and abundance of kleptoparasites across different biogeographic regions remain underexplored. Comparative studies examining kleptoparasitism in varying climates, habitats, and ecological contexts, and the biogeography of kleptoparasites among geographical and habitat islands, would enhance understanding of environmental factors shaping these interactions.

7.5 Behavioral plasticity and evolutionary transitions

Some species exhibit facultative kleptoparasitism in specific contexts, suggesting behavioral plasticity that may facilitate evolutionary shifts. Experimental studies investigating the conditions under which facultative kleptoparasitism is expressed could illuminate pathways to obligate kleptoparasitism.

7.6 Community-level interactions in multi-species webs

Spider webs are often interlinked and can form multi-species assemblages. Given that existing studies suggest such web clusters are more than the combination of their parts, further research is needed to explore the dynamics of kleptoparasite assemblages in such transient communities. In particular, in what context do webs of species that are normally deferred become attractive to kleptoparasites? Understanding this context may offer key insight into the host traits that attract and detract kleptoparasites.

7.7 Application of (advanced) tracking technologies

An almost entirely unexplored field of study is that of tracking movement of kleptoparasites among host webs. Simple techniques like paint or dust tagging would allow the movement of individual kleptoparasites to be tracked and could provide novel insights into assembly into host webs, dispersal, and long-term site fidelity of kleptoparasitic spiders. The use of modern tracking tools, such as harmonic tags or miniature radio-frequency identification (micro RFID) tags would be ideal and is certainly feasible to track larger host species. The smallest harmonic tags may also be useful for tracking kleptoparasites and such data would lend themselves well to machine-learning-based behavioral analysis.

7.8 Molecular ‘tracking’ of kleptoparasites

A few studies have started to use modern sequencing methods to understand kinship and local adaptation in kleptoparasitic spiders. Population genomics offers tools that will advance our understanding on dispersal, kinship of individuals within host webs (potentially underlying some cooperative behavior), and host specialization. Such data may be pivotal in gaining complete understanding of species assembly into host webs.

Addressing these knowledge gaps will not only refine our understanding of kleptoparasitism in spiders but also contribute to broader ecological and evolutionary theories on community ecology, assembly rules, resource exploitation, parasitism, and host-parasite dynamics.

Data availability statement

The data analyzed in this study is subject to the following licenses/restrictions: Some unpublished sequence data from collaborative ongoing work was used to inform on the summary phylogeny. Requests to access these datasets should be directed to IA, iagnarsson@gmail.com.

Author contributions

IA: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

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Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

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