

Spiders in a hostile world (Arachnoidea, Araneae)

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Abstract: Spiders are powerful predators, but the threats confronting them are numerous. A survey is presented of the many different arthropods which waylay spiders in various ways. Some food-specialists among spiders feed exclusively on spiders. Kleptoparasites are found among spiders as well as among Mecoptera, Diptera, Lepidoptera, and Heteroptera. Predators are found within spiders' own population (cannibalism), among other spider species (araneophagy), and among different species of Heteroptera, Odonata, and Hymenoptera. Parasitoids are found in the orders Hymenoptera and Diptera. The largest insect order, Coleoptera, comprises a few species among the Carabidae which feed on spiders, but beetles are not represented among the kleptoparasites or parasitoids.

Key words: aggressive mimicry, araneophagy, cannibalism, kleptoparasitism, parasitoid

Spiders are successful predators with important tools for prey capture, viz, venom, diverse types of silk for snaring and wrapping, and speed. But spiders are prey for other organisms as well. This paper presents a survey of all the threats spiders have to face from other arthropods (excluding mites), based on data from the literature and my own observations. Spiders are often defenceless against the attacks of others, just as most spider victims are defenceless against the spiders and their methods of capturing prey. In this article I look at the spider in its environmental context from four angles: when it is preyed on by other spiders; when it is the victim of kleptoparasites (spiders and insects) which steal food from its web; when it is preyed on by other invertebrates (other than spiders); and when the individual spider falls victim to parasitoids. The subjects are dealt with in this order (Fig. 1). The present study is restricted to arthropods.

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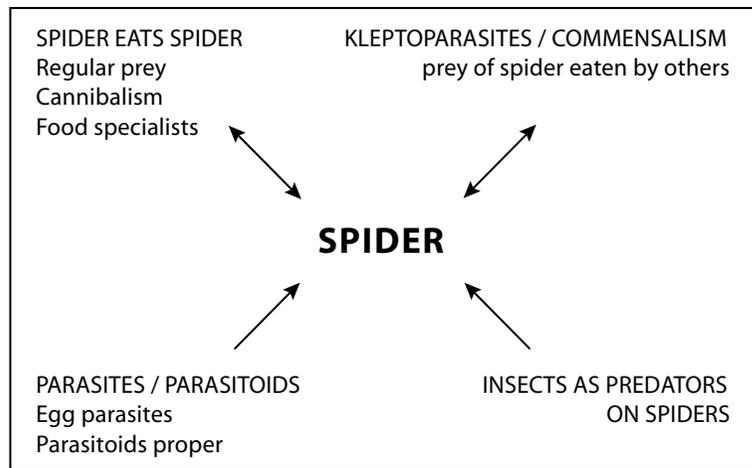


Figure 1: The spider in its environmental web.

Spiders and their prey

The regular prey of spiders consists of insects and other invertebrates, including other spiders. The methods employed are hunting, by sight or other senses, or catching with a web which has sticky threads or is made to entangle the prey. Prey can be wrapped up in silk or held with the legs and chelicerae but as a rule are killed with venom and digested externally by regurgitating digestive fluid over the prey after which the resulting fluid is sucked up. Walking, stalking, waiting, and wrapping are terms which fit. Although the bulk of spider prey consists of insects, preying on spiders is not an exception.

A general phenomenon in spiders is cannibalism which can already take place inside the egg batch or within the population. SAMU et al. (1999) demonstrated, for *Pardosa agrestis* (Westring), that when food is scarce preying on individuals in the

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same population becomes common. Usually not all specimens in a population are of the same age and size as they come from different egg batches and larger individuals then tend to eat the smaller members of the population. Some spiders have distinct food preferences. It is common knowledge that *Dysdera* species specialize on woodlice (Isopoda), bolas spiders (Araneidae: *Mastophora*, *Ordgarius*) attract male moths with chemical compounds which resemble the moth's pheromones, while *Zodarion* species feed on ants. Mimetidae and some Salticidae feed exclusively on other spiders, while some Pholcidae hunt other spiders as well (see section "Insects and spiders as predators on spiders").

Kleptoparasites

Kleptoparasitism is found in spiders as well as in many insect orders. Prey in spider webs are apparently an easily obtainable source of food once one has developed a method of getting at it without alarming the owner of the web and becoming its prey. Examples are summed up by order.

Araneae

Kleptoparasites "steal" the prey of the spider from the spider's web. It is debatable if this might be called commensalism, which is defined as using the food of the host species without causing any harm or negative influence. In many instances, e.g. with web-building species, a spider obtains food by locating the prey in the web, biting it and injecting venom, regurgitating digestive fluid over the prey, and wrapping the victim. All these actions are energy investments made by the host spider and thus are of negative influence on its energy balance, however slight. A kleptoparasite profits from the host spider's energy investment without giving anything in return. True kleptoparasites are able to walk along sticky silk without being trapped. This is not so surprising for kleptoparasitic spiders in which the ability to walk on webs is common in many groups. For other invertebrates this quality must have evolved.

Kleptoparasitism occurs in a large number of spider families (Anapidae, Dictynidae, Eresidae, Mysmenidae, Oonopidae, Salticidae, Sparassidae, Symphytognathidae, Theridiidae, and Uloboridae) (for a summary and literature references, see AGNARSSON 2002). *Argyrodes* species (Theridiidae) are the best-known examples of kleptoparasitism and are found with orb web building Araneidae and Tetragnathidae, and social and subsocial spiders with large communal webs, such as *Anelosimus* (AGNARSSON 2003). *Argyrodes*

steals the prey and may carry it off to the margin of the web (AGNARSSON 2003). Larger webs, such as those of *Nephila*, often catch more small prey than the owner needs. Small prey specimens just stick to the spiral threads and are not even bitten or wrapped and *Argyrodes* often eats from such neglected prey. The habit runs through the whole genus. *Argyrodes bryantae* Exline & Levi was found as kleptoparasite in the webs of *Tengella radiata* (Kulczynski) (EBERHARD et al. 1993). *Argyrodes antipodanus* O.P.-Cambridge shows a transition to araneophagy (WHITEHOUSE 1986). Social Uloboridae have been observed as solitary kleptoparasites in the webs of other spiders. *Philoponella republicana* (Simon) is known to occur in webs of *Cyrtophora nympa* Simon (ROBINSON 1977) and also in *Anelosimus* webs in French Guiana (LOPEZ 1987). *P. tingena* (Chamberlin & Ivie) has been recorded from webs of *Nephila clavipes* L. and "*Achaearana* spec." (OPELL 1979). Two species of *Mysmenopsis* (Mysmenidae) lead a kleptoparasitic life in webs of *Tengella radiata* (Kulczynski) (Tengellidae) (EBERHARD et al. 1993). Both have a broad host spectrum. *M. tegellacompta* Platnick is found in webs of *Tengella radiata* as well as in a diplurid web and an agelenid web (species not established), while *M. dipluramigo* Platnick & Shadab has been found in webs of *T. radiata*, a ctenid web and a pisaurid web (EBERHARD et al. 1993).

Mecoptera

Scorpionflies (Mecoptera) of the family Panorpidae have been observed to land directly onto a spider web or walk into it from the surrounding vegetation and eat from the prey they find there. When the owner of the web approaches the scorpion fly it may ward the spider off by hitting it with the thick end of its abdomen. Scorpionflies have been found in webs of Agelenidae, Tetragnathidae, Theridiidae, and Araneidae (THORNHILL 1975).

Diptera

Diptera also have their kleptoparasitic species. The gall midge *Didactylomyia longimana* (Nematocera, Cecidomyiidae) was detected as a very common kleptoparasite in orb webs of *Nephila clavipes* (Tetragnathidae), *Argiope aurantia* Lucas, *Mastophora bisaccata* (Emerton), *Eriophora ravilla* (C.L. Koch), and *Scoloderus cordatus* (Taczanowski) (all Araneidae) (SIVINSKI & STOWE 1980). The females were found on the prey of the spider, while the males were hanging inactively in the web. Among the biting midges

(Ceratopogonidae) a number of species associated with spider webs have also been found (SIVINSKI & STOWE 1980).

Among the suborder Brachycera there are several families which comprise species with kleptoparasitic behaviour. Examples of species of Chloropidae and Milichiidae (both of acalyptrate fly families) are listed by NENTWIG (1985). *Desmommetopa* species (Milichiidae) were observed to feed on the prey (honey bee, *Apis mellifera*) of a lynx spider (Oxyopidae, probably *Oxyopes heterophthalmus* (Latreille)) and also of other spiders (RICHARDS 1953; ROBINSON & ROBINSON 1977): *Phyllomyza* spec. (Milichiidae) on prey of *Nephila clavipes* (L.), *Conioscinella* spec. in the web of *Argiope argentata* (Fabricius). Best known, relatively, are the members of the genus *Microphor* (Microphoridae) with eight species and eight further species of related genera in Europe (PAPE 2010). Most of the *Microphor* species, if not all, are seen in association with spiders and their prey. They usually sit on the prey item while the spider is sucking on it. CHVALA (1986) stressed that MACQUART (1827) previously noted an association with spiders. *Megaselia scalaris* Loew (Phoridae) was found on the webs of *Tengella radiata* (Kulczynski) (EBERHARD et al. 1993).

Lepidoptera

Caterpillars of some lepidopteran families are known to feed on spider prey. POCOCK (1903) states that the larvae of *Batrachedra stegodyphobius* Walsingham (Batrachedridae) live in the communal web of a *Stegodyphus* species (Eresidae) in South Africa. According to Pocock pupation of the noctuid moth occurs in the spider web and the adult moths are seen fluttering about the web. ROBINSON (1977) reported the larvae of *Neopalthis madates* Druce (Noctuidae) living in the communal web of *Anelosimus eximius* Simon in Panama. The caterpillars of *Tallula watsoni* Barnes & McDunnough (Lepidoptera, Pyralidae) seem to live exclusively in the webs of *Anelosimus studiosus* (Hentz), where they eat dead and living leaves from the supporting tree or shrubs and attack or eat the spiders (DEYRUP et al. 2004). All these species are not only kleptoparasites but also inquilines which live in the web permanently.

Heteroptera

Among the bugs (Hemiptera-Heteroptera) there exist kleptoparasitic specialists in several families. *Arachnocoris* (Nabidae) is a genus which occurs with nine species (2–5 mm) in the Neotropical Region

(Lopez-Moncet 1997). An upside-down position in the spider web is typical for this taxon. The different species were found in webs of Araneidae (*Micrathena*) (with sticky silk), Theridiidae (*Tidarren fordum* (Keyserling) (= *Tidarren sisypoides* (Walckenaer)), *Anelosimus eximius* (Keyserling)) (sticky) as well as those of Pholcidae (*Physocyclus* sp.) (non-sticky silk). Strangely, specimens of *Arachnocoris trinitatis* Bergroth, one of the best studied species of the genus, are usually found in empty webs of the pholcid *Mesobolivar aurantiacus* (Mello-Leitao). It is hypothesized that the bug uses the web for catching prey and finding a mate (SEW-LAL & STARR 2008). It is not clear whether the bug emptied the web by capturing and devouring the spider or by chasing it away.

The genus *Ranzovius* (Miridae) comprises at least four species which are associated with spiders (WHEELER & MCCAFFREY 1984). All specimens in this genus are very small (2–2.5 mm) and are found in orb webs as well as in sheet webs. *R. fennabi* Carvalho lives in large webs of the social *Anelosimus eximius* (Keyserling) while *R. contubernalis* Henry occurs in the communal webs of the social *Anelosimus studiosus* (Hentz). In the large spatial webs of the latter a lot of prey remnants are scattered throughout the web which attract pyralid larvae, cockroaches and ants which behave as scavengers. *R. californicus* (Van Duzee) consumes prey in the webs of *Hololena curta* (McCook) (Agelenidae). *R. agelenopsis* Henry can be found in high numbers in the webs of the common *Agelenopsis pennsylvanica* (C.L. Koch) where *R. contubernalis* can be found as well. *Agelenopsis* species are often common in shrubs and hedges. The webs of other common spider species in the same habitat, such as the linyphiid *Frontinella pyramitela* (Walckenaer) and various araneids (probably *Zygiella* species) were checked for the presence of *Ranzovius* but none were found (WHEELER & MCCAFFREY 1984). Apparently *Ranzovius* prefers *Anelosimus* and *Agelenopsis* for its kleptoparasitic practises.

In the Reduviidae the relatively common species *Reduvius personatus* L. has been found in webs of “house spiders”, a name used in the U.S.A. for *Parasteatoda tepidariorum* (C.L. Koch) (AMYOT & SERVILLE 1843). There are a number of striking examples of kleptoparasites within the subfamily Emesinae (Reduviidae), viz. the genera *Eugubinus*, *Ploiaria*, *Emesa*, *Empicoris*, and *Stenolemus*. They all feed on the prey of the spiders the webs of which they invade. In the case of *Eugubinus araneus* Distant this was a theridiid (in Bombay) (DISTANT 1904), while

E. intrudans Distant and *E. reticolus* Distant were seen in webs of *Cyrtophora cicatrosa* (Stoliczka) (India) (DISTANT 1915). *Stenolemus* represents a transition to araneophagy.

More web-invading heteropteran species can be found in the Anthocoridae, viz., *Cardiastethus inquilinus* China & Myers in South Australia, in the web of a gregarious oxyopid (CHINA & MYERS 1929).

Species of the Plokiophilidae, with the genera *Plokiophila*, *Plokiophiloides*, *Lipokophila*, and *Embiophila* are found in the webs of Dipluridae and Tengelidae in the southern hemisphere (MCGAVIN 1993). The very small *Plokiophila cubana* (China & Myers) occurs on the webs of *Diplura macrura* (C.L. Koch) (Dipluridae) in Cuba. *Lipokophila eberhardi* Schuh and *L. tengella* Schuh were found on the webs of *Tengella radiata* (Kulczynski) (Tengellidae) (EBERHARD et al. 1993). According to CARAYON (1974) Plokiophilidae spend their whole life in the webs of spiders. They live there from egg stage to death. The egg is deposited on a thread in the spider's web and the young bug hatches immediately. *Plokiophiloides asolen* Carayon lives in webs of the social *Agelena consociata* Denis, while *P. balachowskyi* Carayon lives in webs of the social *Agelena republicana* Darchen. *P. biforis* Carayon was collected from webs of *Lathrothele catamita* (Simon) (Dipluridae). The reduviids *Themonocoris bambesanus* Carayon and two Anthocoridae (*Cardiastethus affinis* Poppius and *C. lateralis* Poppius) live there too.

When reduviid bugs live in a spider web these are free of kleptoparasitic spiders (LOPEZ-MONCET 1997). Possibly bugs live in spider webs because they are safe there from ants which are everywhere but hardly ever enter spider webs (LOPEZ-MONCET 1997).

Insects and spiders as predators on spiders

Araneae

For spiders any other spider is potential prey when it falls within the limits of its range of possibilities (size, danger, risk, defence of prey, etc.). Some spiders have made a habit of eating spiders of other species, a habit called "araneophagy". For cannibalism (occasional eating of specimens of the own species), see above.

Mimetidae are specialized predators on other spiders which they attack in the web of the prey by producing signals resembling those of an entangled insect or a potential mate wanting to pair, so-called "aggressive mimicry" (JACKSON & WHITEHOUSE 1986). From observations made by Bristowe (1958) it is clear that Mimetidae have very strong, paraly-

zing venom. Salticidae of the subfamily Spartaeninae are specialized in capturing spiders in their webs by stealthy approach combined with aggressive mimicry. The genus *Portia* is the best known genus (five species) which exploits this type of prey capture, but there are three other genera which show this type of behaviour as well, viz. *Brettus* (two species), *Gelotia* (one species), and *Cyrba* (two species) (WANLESS 1984). All these salticids share the characters of good vision with the ability to walk over sticky and non-sticky webs (JACKSON 1986). The pholcid *Pholcus phalangoides* ventures into the webs of other spiders and overwhelms the owner (JACKSON & BRASSINGTON 1987). Some Palpimanidae invade the web and lure the host out (HENSCHEL et al. 1992).

There are many examples of insects which are predators of spiders. The following examples are listed by order.

Heteroptera

Stenolemus species (Reduviidae, Emesinae) can be found in the surroundings of the spider webs which they penetrate to prey on the spider. *Stenolemus* are large, up to 1 cm overall body length, with long, thin legs. The 1990 catalogue of the Reduviidae of the world (MALDONADO CAPRILES 1990) listed 78 species, four of which are known to be predators on spiders. *S. arachniphagus* Maldonado-Capriles & Van Doesburg from Dutch Guiana (Surinam) was found in the communal web of *Anelosimus rupununi* Levi. They have peculiarly modified antennae which may be an adaptation to their habit of walking through webs (MALDONADO-CAPRILES & VAN DOESBURG 1966). *S. lanipes* Wygodzinski has been observed to eat juveniles of *Achaearanea tepidariorum* (C.L. Koch) (= *Parasteatoda t.*) (HODGE 1984). *S. giraffa* Wygodzinski (Australia) has a striking, elongate prothorax, hence its name. *S. edwardsi* Bergroth has been recorded as preying on young specimens of *Badumna* (Desidae) in Australia (Wignall & Taylor 2008). *Stenolemus bituberus* Stal was found in the webs of – and seen actually feeding on – spiders of the families Desidae, Pholcidae, Theridiidae, and Uloboridae. Most likely araneophagy will be found subsequently among the many other *Stenolemus* species known.

Neuroptera

The subfamily Mantispinae of the Mantispidae are predators of spider eggs. The front legs resemble those of the praying mantis, hence the name mantispid flies. They are fairly long, up to 5 cm. The stalked eggs are

deposited on the substratum. Different strategies are employed to reach the spider's eggs (REDBORG 1998). The larvae of one group of mantispids, the "boarders", attach themselves to a passing bee, beetle, or spider. The larva then rides along on the spider, usually curled around the pedicel, feeding itself with haemolymph fluid from the spider, acting as a leech. Their final destination is the egg cocoon or egg batch. When a mantispid larva has settled on a young spider it has to get on the newly emerging next instar of the spider when it moults. It may seek refuge temporarily in a book lung during the moulting process. They wait for the construction of the egg cocoon, slip into it, feed on the eggs and pupate in the cocoon or egg batch. In the other strategy, that of the "borers", the larva is attracted by spider silk and thus finds an egg sac and bores into it to feed on the eggs. Spiders which suffer from mantispid egg predation by spider boarders belong to a wide range of families of web builders as well as active hunters (REDBORG 1998), while the independent egg sac penetrators all feed exclusively on the eggs of hunting spiders.

Odonata

All Pseudostigmatidae ("Helicopter damsel flies") in which the adult feeding habits are known prey exclusively on web-building spiders. Gifted with very good vision they aim directly at the spider. Species showing this behaviour are *Mecistogaster linearis* (Fabricius), *M. modesta* Selys, *M. ornata* Rambur, *Megaloprepus coerulatus* (Drury), and *Pseudostigma accedens* Selys (CORBET 1999). *M. coerulatus* was seen preying on small *Argyrodes* spec. (Theridiidae) at a *Nephila* web (YOUNG 1980). *M. modesta* was seen at work near orb webs, as well as at the lampshade-shaped webs of pholcids.

Hymenoptera

Species from the Vespoidae, such as the hornet (*Vespa crabro* L.), and *Vespula* species capture spiders as food for their brood. Because the colonies of these social living insects are often very large the impact on the

local spider fauna must be considerable. *Vespa crabro* acts as a regular kleptoparasite as well as predator on *Argiope bruennichi* (Scopoli) (Figs. 2-3).

Ants are about the largest and ever present group of predator insects, often occur in very high numbers in certain habitats and are known to bring all types of prey to their nests, among which spiders do not fail. I have not found any literature on the relative importance of spiders in the ants' diet.

Coleoptera

Carabid beetles are known to feed on spiders on agricultural fields, but no quantitative data are available.



Figures 2, 3: *Vespa crabro* in web of *Argiope bruennichi* stealing the spiders prey (2) (Photo Jeanette Hoek), and with remnant of *Argiope bruennichi* (3) (Photo Marcel Wasscher).



Figure 4: *Tromatobia ornata* on egg cocoon of *Argiope bruennichi*. Photo Gerben Winkel.

Parasites and Parasitoids

Egg parasitoids

Some Pimplinae (Hymenoptera, Ichneumonidae) are predators of spider eggs (*Gelis*, *Hemiteles*, *Tromatobia*, *Zaglyptus*, some Scelionidae) (RICHARDS 1977). The pimpline larva eats from the eggs in the spider's egg sac. Species of *Tromatobia* parasitize the egg sacs and adults of spiders. *Tromatobia* is a species-rich genus (FITTON et al. 1988). A striking example is *Argiope bruennichi* (Scopoli), a species which has spread relatively quickly under its own power and of which the egg cocoons are parasitized by *Tromatobia ornata* Gravenhorst (Fig. 4). The parasite may have travelled along with the spider when it spread over the Netherlands over the last 25 years.

True parasitoids

Among Hymenoptera, the Ichneumonidae are also parasitoids of adult insects and spiders. They paralyze their prey, place an egg and after hatching the larva feeds on it while it remains in a stable, paralysed condition (endoparasitoids); or they place an egg on the victim which then continues its normal life until it succumbs because it is slowly weakened by its uninvited ecto-parasitic guest.

Spider-wasps (Hymenoptera, Pompilidae) are specialized parasites of spiders. Their search for and capture of spider specimens is followed by a paralyzing sting. The spider is then brought to a suitable

place where it is burrowed, an egg is put on the spider, and the burrow is closed. The pompilid larva when full-grown pupates in the burrow. Most pompilid wasps are polyphagous and hunt for spiders in general or specialize on webspiders. Some are monophagous, at least regionally, such as *Homonotus sanguinolentus* Fabricius which exclusively hunts for *Cheiracanthium erraticum* (Walckenaer) (Miturgidae) which is then left in its own silken nest (NIELSEN 1936). There are exceptions in this sequence. *Eoferreola rhombica* (Christ) parasitizes on *Eresus sandaliatus* (Martini & Goeze) (Eresidae). This

spider lives in a burrow with a cribellate web above the entrance. Having located the spider in its burrow the wasp enters, paralyzes the spider, places its egg on the animal and leaves the burrow without closing it. It does not make a burrow of its own (HAUPT 1927). Neither does *Aporus unicolor* Spinola, which locates *Atypus* (Atypidae) in its burrow and leaves it there after having paralyzed it and provided an egg. *Ceropales* species (Pompilidae) are known as kleptoparasites of other Pompilidae in that they follow other pompilid wasps with prey and put an egg on the prey just before the prey is buried by the true hunter (OEHLKE & WOLF 1987).

Within the Ichneumonidae the Pimplinae comprise the spider-ectoparasitoids of the *Polysphincta* group of genera of which we often see the larva externally on the abdomen (RICHARDS 1977). Species of the *Polysphincta* genus-group of the Pimplinae attack spiders. They first immobilize the spider, then put an egg on the spider, usually on the abdomen. The spider regains consciousness and leads a normal life until the larva is full-grown and pupates in the body of the dead spider. Many genera are distinguished, such as *Dreisbachia*, *Schyzopyga*, *Polysphincta*, *Acrodactyla*, *Synarachna*, and *Zatypota* (FITTON et al. 1988; GAULD et al. 2006).

A curious phenomenon in this respect is a procedure which is called "manipulation of the host behaviour". When the larva of *Hymenoepimecis argyraphaga*

Gauld (Ichneumonidae) is ready to pupate it stimulates the host spider *Plesiometa argyra* (Walckenaer) (= *Leucauge argyra* (Walckenaer)) (Tetragnathidae) just before it will die to produce a hub for a new web and repeat this over and over again, thus fabricating a “cocoon web” for its own parasitoid wasp (EBERHARD 2000, 2001), this process probably stimulated by chemicals brought into the host’s body. I am not aware of any other cases of manipulation of behaviour by parasitoids of spiders.

Within the Apoidea, the Crabronidae or digger wasps, comprise species which specialize on spiders and show a behaviour equivalent to that of the Pompilidae. Species of the genus *Miscophus* hunt for small spiders, and *Trypoxylon* species capture larger spiders, which they put in a cell and close off with mud.

Diptera

When the larvae of Acroceridae (Cyrtidae, Oncodidae) hatch they try to find a spider and climb on it, enter the book lungs and develop inside the abdomen. The spider dies when the parasitoid is full-grown and pupates. More than 500 species are known worldwide, mostly in the tropics. Recent additional data of acrocerid infestations in the Nearctic Region are given by LARRIVÉE & BORKENT (2009).

Discussion

Spiders are strongly armed, well-equipped predators: they have fangs to inject their venom, different types of silk for their webs – sticky or cribellate – and methods to wrap up their victims very quickly, and they have very short reaction time. For spiders the transition from hunting to invading a strange web, to kleptoparasitism, to becoming predator of a non-specific spider species, or to cannibalism, is nearly a continuum. The driving force in all instances is the search for food to meet the requirements of the individual’s energy balance. Food shortage will force spiders to eat individuals of their own kind. Other spiders, being live objects, are always on the menu. Once it is possible for an individual spider to enter a strange web unobserved or with misleading behaviour the intruder can benefit from available food (kleptoparasitism), protection from other organisms which cannot enter the web (such as ants), or capture the owner by surprise (araneophagy). There are many examples of insects that follow the same strategies. There are also many invertebrates that have found ways and means to master spiders: they have won the arms race.

It is clear that spider kleptoparasites benefit from using the prey collected by others. They do not have to invest in silk for webs, venom, or energy needed for hunting, jumping and overwhelming, while silk production for wrapping can be omitted. One may expect that exclusively kleptoparasitic spider species even have lost their capacity to produce venom, while the glands for silk production may have undergone reduction. The kleptoparasitic spider also gains protection from other predators, such as the ever present ants, which, however, have been observed only in a few spider species to enter the web. For the host spider the stealing of food means loss of invested energy but for a larger host (*Nephila*, communal *Anelosimus*) this may be negligible, also because the kleptoparasites often eats from smaller prey for which the web owner has no interest.

Aggression towards kleptoparasites by the web owner is nearly always negligible too, partly because of size differences (small kleptoparasites in the webs of larger species), partly because of subdued aggression (spiders in communal webs). Kleptoparasitism appears to be not so rare a phenomenon, although the number of spider species which employ this feeding behaviour is relatively restricted as far as we know now. The number of insects that play a kleptoparasitic role in relation with spiders probably is larger than we know now. It may be expected that observations of spiders in their natural environment may reveal more kleptoparasitic relationships, especially in the acalyprate Diptera and reduviid Heteroptera.

Spiders are not defenceless against predators. They can defend themselves with their chelicerae and fight back, but against most stinging Hymenoptera they seem to hardly have a chance, although we do not know how many attempts by Ichneumonidae, Crabronidae, and Pompilidae meet with failure. Spiders can drop from the web, change colour when hitting the ground, run away, hide in self spun cells, or flee to the other side of the web, putting the web between himself and predator (JACKSON et al. 1993). However, their chances of defence against predators which successfully deploy “aggressive mimicry” seem to be very slight. In the described cases the victim spiders were lured within striking distance of the predators “on perfidious pretexts” and the victim had very slight chances to escape. Apparently the “behavioral” arms race has been won by the predators, although we do not register where such methods are developing right now and have a lower percentage of successful attempts. It is difficult to detect evolution at work and

understand the direction the selective forces might move into.

If we look at the orders of invertebrates (other than spiders) which have developed scavengers, kleptoparasites, or predators, and parasitoids of spiders we must conclude that the largest order, the Coleoptera with 359,891 described species, has hardly developed any (carabid beetles can feed on spiders on arable land if no other food is available), that the Diptera (152,244) have some kleptoparasites among them but are under-represented as to predators (none) and parasitoids (only one family). Lepidoptera (156,793 species) are represented with noctuid kleptoparasites, but this feature seems to be rather exceptional in the order. The Odonata are a small order (5,680 species) of which only few genera have developed into spider predators. By far the most kleptoparasites are found among the Hemiptera (100,428 species), while some have become predators. The largest number of general predators, parasites and parasitoids are found in the Hymenoptera (144,695 species), which all possess poison glands and thus are able to overwhelm and/or parasitize spiders. They have developed a weapon of their own and are clearly ahead in the arms race. (All data on species numbers after ADLER & FOOTTIT 2008.)

Reflections

Interactions as brought together and discussed in this paper are of importance for understanding the biology of the species, of spiders as well as of the many insects involved. Discovering new relationships and interactions will help us to understand the many interesting behavioural patterns and food chains which exist in the invertebrate world. They illuminate an important aspect of the “web of life” and demonstrate the intricacies of food chains. It is clear that this asks for collecting observations in the field more than collecting specimens. Pitfalls and canopy fogging yield specimens and give insight in the composition of the fauna but they do not help us to find patterns of behaviour, parasitic relationships or food chains. This paper is meant to stimulate the observing type of invertebratologists who sits down amidst the invertebrates at work and tries to discover the patterns of interactions between organisms, the way organisms react to each other.

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