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ARGYRODES: PHYLOGENY, SOCIALITY AND INTERSPECIFIC INTERACTIONS—A REPORT ON THE *ARGYRODES* SYMPOSIUM, BADPLAAS 2001

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ABSTRACT. *Argyrodes* Simon 1864 is a large, cosmopolitan theridiid genus whose members exhibit a wide range of foraging techniques which usually involve exploiting other spiders, either by using their webs, stealing their food, or preying on them directly. We held a symposium on this genus at the 15th International Congress of Arachnology, Badplaas, South Africa in order to obtain a clearer perspective on the relationship between the phylogeny of the genus and the different foraging techniques. We concluded that *Argyrodes* forms a monophyletic group within the Theridiidae, and that there are clear monophyletic clades within the genus (already identified as species groups) that appear to share behavioral characteristics. We found no clear indication that foraging behaviors such as kleptoparasitism (stealing food) evolved from araneophagy (eating spiders) or vice versa. However, it appears that species that specialize in either kleptoparasitism or araneophagy use additional techniques in comparison to species that readily use both foraging modes. During our examination of *Argyrodes*/host interactions we noted the importance of *Nephila* species as hosts of *Argyrodes* species around the world and the impact of *Argyrodes* on *Nephila*. We also noted the fluid nature of the relationship between *Argyrodes* and the spiders with which they interact. For example, an *Argyrodes*/host relationship can change to an *Argyrodes*/prey relationship, and the type of kleptoparasitic behavior employed by an *Argyrodes* can change when it changes host species. The importance of eating silk was also noted and identified as an area for further research. We concluded that more work involving international collaboration is needed to fully understand the phylogeny of the genus and the relationships between the different types of foraging behaviors.

The large (over 200 species) cosmopolitan spider genus *Argyrodes* has attracted interest worldwide because of the gregarious nature of many of its species and their unusual foraging techniques (which include invading webs to steal food from and to attack other spiders). In response to increasing international attention in this group we decided to hold a symposium on *Argyrodes* to consolidate our knowledge and obtain an overall perspective on the genus. Our

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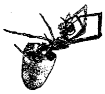
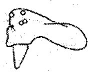
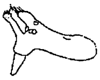
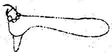
Species groups	**Male chephalo-thorax**	**Recognized feeding methods**					
		Glean insects 	Steal foodbundles 	Feed with host 	Attack moulting host 	Catch spiders by lunging 	Catch spiders with a net 
argyrodes		✓	✓	✓	✓	✓	x
cancellatus		✓	✓/x	✓/x	?	?	?
cordillera		?	?	?	?	?	?
trigonum		✓	✓	?	✓	✓	x
rhomphaea		?	x	x	?	x	✓
ariamnes		?	x	x	?	x	✓

Figure 1.—Chart of the six recognized species groups of *Argyrodes* (from the Americas) indicating the current known foraging behaviors and the standard form of the male cephalothorax for each group. A tick indicates that a species from that group performs the foraging technique, a cross indicates that a species is known not to perform this behavior, and a question mark indicates that nothing is known about the foraging method in relation to the species group. A tick and a cross for the same foraging method indicates that some species in this group use the foraging method while other species do not.

aim was to identify the direction that the research was leading, and develop future research programs that are more integrated.

The symposium was loosely focused on understanding how the phylogenetic relationships within the genus reflected the evolution of different types of relationships with other spider species. The ‘‘interaraneae’’ relationships of *Argyrodes* species are very diverse. Some species behave as kleptoparasites in that they invade the web of a (usually larger) host spider and eat the host’s web, glean insects off the host’s web, steal the host’s wrapped food bundles, and/or feed with the host. Some species attack the host when it is vulnerable such as during molting, or capture and eat small spiders by lunging at them and grabbing them with their front legs. Still others capture spiders by throwing a line of sticky silk over the victim. Phylogeny provided a framework in which we discussed 1) these diverse interspecific interactions, 2) sociality, and 3) specific foraging techniques. Below is a report on the conclusions we drew from the symposium and the areas that still require more research.

Evolution.—Evolutionary relationships within the genus *Argyrodes* are poorly understood. Currently there are six recognized species groups (Exline & Levi 1962) within the genus: Argyrodes, Rhomphaea, Ariamnes, Cordillera, Cancellatus, and Trigonum. Because these names refer to species groups and currently not to genera, they are not in italics. It is confusing that ‘‘Argyrodes’’ refers to the whole genus and to a particular species group. In this text, when we refer to the genus *Argyrodes* we will use italics, but when we refer to the species group Argyrodes, we will use normal script. The evidence to date suggests that animals in the species groups may use similar methods of web invasion (Fig. 1). For example, all species so far studied in the Rhomphaea and Ariamnes species groups seem to specialize on araneophagy (Eberhard

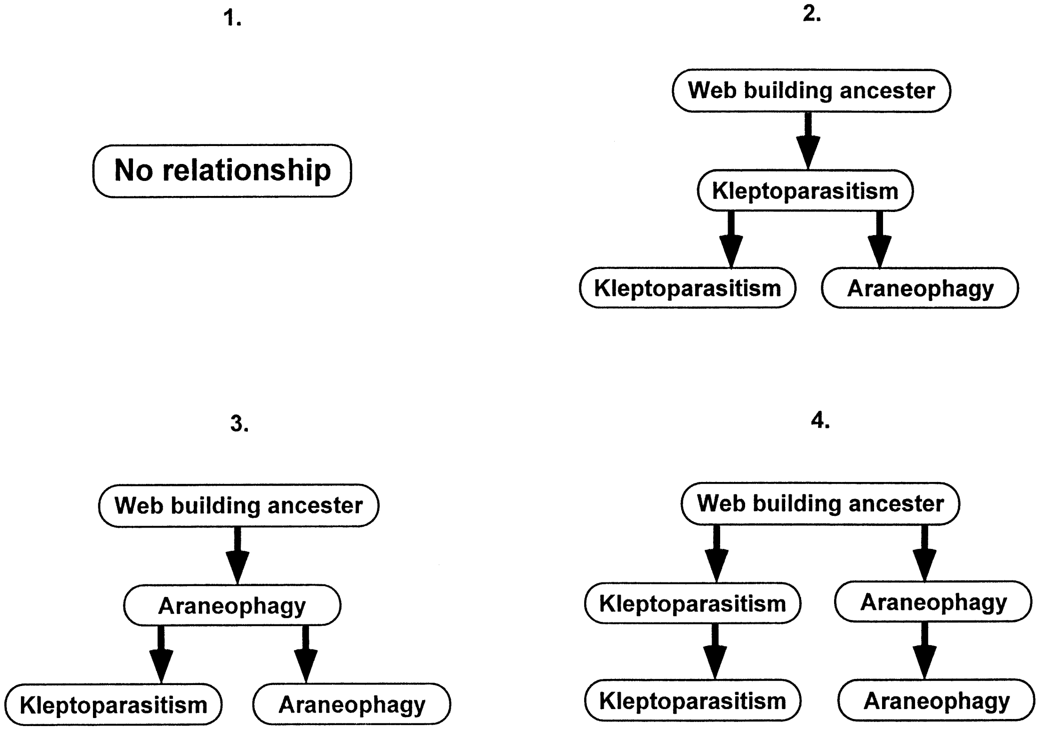


Figure 2.—Four ways in which the evolution of araneophagy and kleptoparasitism may be related. See text for details of each model.

1979; Horton 1982; Whitehouse 1987). They tend to be free-living and solitary, and capture spiders by throwing a sticky silk line over the victim. Species from the Argyrodes species group are gregarious and seem to specialize on kleptoparasitism. They will even feed with the host to obtain food: *A. antipodianus* O.P. Cambridge 1880 (Whitehouse 1986, 1997; Grostal & Walter 1997); *A. elevatus* Taczanowski 1872 (Vollrath 1979, 1984); *A. argentatus* O.P. Cambridge 1880 (Robinson & Robinson 1973); *A. argyrodes* 1842 (Kullmann 1959). Species that have been studied from the Trigonum species group forage using both kleptoparasitism and araneophagy: *A. trigonum* Hentz 1850 (Cangialosi 1997; Larcher & Wise 1985; Suter, et al 1989) and *A. baboquivari* Exline & Levi 1962 (Larcher & Wise 1985). However, the araneophagy that *A. trigonum* (at least) uses is distinct from that of Rhomphaea and Ariamnes species. Cangialosi reported in the symposium that it does not throw silk in order to capture the spider, but kills the spider by biting it. The species group Cancellatus contains some members that will only glean insects and eat the host's silk (*A. caudatus* Taczanowski 1874: Henaut & Ibarra-Nunez unpubl. data; Vollrath 1984) and other members that will also feed with the host (*A. globosus* Keyserling 1884: Henaut 2000) and others which will not feed with the host, but will steal food bundles (*A. ululans* O.P. Cambridge 1880: Cangialosi 1990a, b). Thus in the Cancellatus species group there is no consistency in the kleptoparasitic techniques used. No spiders from the Cordillera species group have been studied.

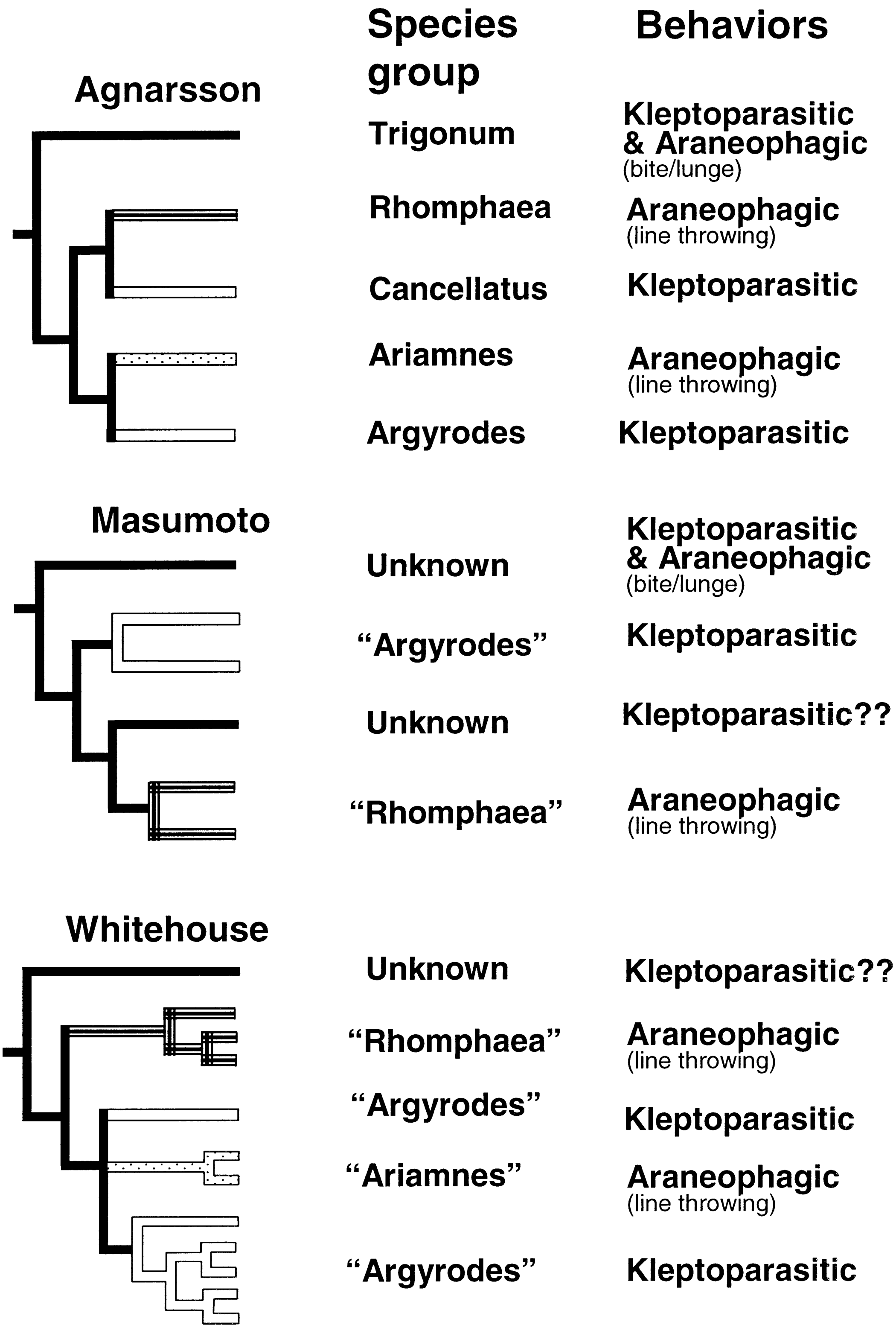
Four pathways have been proposed by which kleptoparasitism and free-living araneophagy may have evolved (Fig. 2). First, ecological pressures, rather than evolutionary history, may have dictated which behavior is expressed in each species so that there is no phylogenetic relationship between phylogeny and behavior (Model 1). Alternatively, araneophagy and kleptoparasitism may each have evolved once, in which case there are three possible models: Free-living araneophagy may have evolved from kleptoparasitism (Model 2). Smith Trail (1980) argued that the kleptoparasitic skills of interpreting the host's vibrations could preadapt *Argyrodes* for safely stalking and capturing the host itself. Alternatively, kleptoparasitism may have evolved from araneophagy (Model 3). Vollrath (1984) supported this model although he argued that *Argyrodes* would initially invade other spiders' webs and chase out the owner, and then later adopt araneophagic behaviors that would preadapt them to kleptoparasitism. Finally, both kleptoparasitism and araneophagy may have evolved separately (Model 4). Whitehouse (1987) proposed this argument based on differences in the araneophagic techniques of species from the predominantly araneophagic (Rhomphaea and Ariamnes) and kleptoparasitic (Argyrodes) species groups.

The three phylogenetic studies presented at this symposium examined the relationship between these different species groups and their foraging techniques, in particular the relationship between species that are predominantly kleptoparasitic, and those that are predominantly araneophagic (Fig. 3). Agnarsson presented a phylogenetic tree of *Argyrodes* (largely from the Americas) within the context of the family Theridiidae, and used sequences from the genes CO1, 16S, 18S and 28S and morphological characters to construct the tree. Masumoto, working on Japanese species, constructed his tree using sequences from the gene CO1, while Whitehouse presented trees of Australian *Argyrodes* based on sequences from the genes CO1 and 16S (for more information see Agnarsson et al this journal, Masumoto unpubl. data, Whitehouse et al. unpubl. data).

Superficially, all three trees appear to support different models: Agnarsson's tree seems to support model 1 (no evolutionary relationship between developing araneophagy and kleptoparasitism); Masumoto's tree seems to support model 2 (araneophagy developed from kleptoparasitism) and Whitehouse's tree seems to support model 3 (kleptoparasitism developed from araneophagy). However Bremer support for the lower nodes are not strong in any tree, and relationships between species could easily switch around. In addition the trees suggest that the basal species within the genus *Argyrodes* use both kleptoparasitic and araneophagic behaviors, even though they lack the more derived techniques of these foraging methods (such as the more derived kleptoparasitic behavior of ‘‘feeding with the host’’, or the araneophagic behavior of ‘‘throwing a sticky thread over the prey’’). The behavior of the basal species of both Agnarsson's and Masumoto's trees directly fit this model, while the behavior of the basal species in Whitehouse's tree is not known, except that it occurs on a larger spider's web. Consequently, the available evidence to date suggests that the araneophagic and kleptoparasitic foraging behaviors of *Argyrodes* species evolved concurrently, and latter species may have specialized, and/or refined these techniques.

In addition, all three trees support some general claims. For example, the trees of both Agnarsson and Whitehouse indicate that Argyrodes and Ariamnes are sister species groups, while all three trees suggest that the Rhomphaea species group is quite distinctive. This suggests that Rhomphaea and Ariamnes may have developed araneophagic foraging techniques independently of each other.

It is intriguing that Rhomphaea and Ariamnes may have developed araneophagy independently because the technique they both use to capture spiders (throwing silk) is distinctive from the technique used by the basal *Argyrodes* species (biting/lunging). At the symposium we debated whether the spider-catching behavior of Ariamnes and Rhomphaea was plesiomorphic or derived. Most symposium members (who have not seen Ariamnes or Rhomphaea catch spiders) regarded it as a plesiomorphic theridiid trait because most theridiids catch prey by wrapping them with sticky silk. Whitehouse argued that the behavior is derived because it is very distinctive from normal theridiid wrapping. Theridiids normally attack prey by throwing numerous threads of silk in quick succession with alternating legs IV over the victim until it is completely covered. When Rhomphaea and Ariamnes attack prey, the two legs IV move in unison towards the prey, and the spider will throw one to five sticky threads. Once the prey is immobilized Rhomphaea/Ariamnes will assume normal theridiid wrapping behavior. Whitehouse conceded that within these two species groups there might be a continuum in that some species may throw silk more like a standard theridiid while others may be more distinctive and more stylized. Agnarsson suggested that a solution would be to look for the spigots on the spinnerets that are responsible for producing sticky silk in theridiids. He noted that individuals in the Argy-


Species group
Behaviors
Agnarsson
Trigonum
Kleptoparasitic & Araneophagic (bite/lunge)
Rhomphaea
Araneophagic (line throwing)
Cancellatus
Kleptoparasitic
Ariamnes
Araneophagic (line throwing)
Argyrodes
Kleptoparasitic
Masumoto
Unknown
Kleptoparasitic & Araneophagic (bite/lunge)
"Argyrodes"
Kleptoparasitic
Unknown
Kleptoparasitic??
"Rhomphaea"
Araneophagic (line throwing)
Whitehouse
Unknown
Kleptoparasitic??
"Rhomphaea"
Araneophagic (line throwing)
"Argyrodes"
Kleptoparasitic
"Ariamnes"
Araneophagic (line throwing)
"Argyrodes"
Kleptoparasitic

rodes (‘‘kleptoparasitic’’) species group have lost one of the two aggregates on each PLS. Miyashita added that kleptoparasitic *Argyrodes* also lack an aggregate gland for producing sticky silk. If basal species do not have these spigots and an aggregate gland, then this would suggest that spider-catching method used by Rhomphaea and Ariamnes species is derived. If basal species do have these structures, then ‘‘throwing silk’’ is more likely to be a plesiomorphic trait.

Our discussions on the phylogeny of *Argyrodes* emphasized the need for more information. Firstly we need a more comprehensive phylogenetic tree to identify all species groups. We concluded that currently named species groups (Argyrodes, Rhomphaea, Ariamnes and Trigonum) appear to be monophyletic and therefore useful groupings of the species. However these species groups are only specific for American species, and that species in other continents, like Asia, Australia and Africa, may form different species groups. We concluded that we need an integrated, comprehensive phylogenetic tree that includes species found throughout the world, to establish if species groups within the *Argyrodes* complex are indeed monophyletic and should be recognized as separate genera.

Secondly, we acknowledged that there is a huge lack of behavioral data, and that it is unlikely that we can obtain behavioral data from each of the 200 species worldwide. We concluded that a better approach would be to identify the monophyletic species groups within the genus and then focus on particular species within these groups. Henaut expressed caution with this approach. His point was well taken as the large Cancellatus species group is known to contain a species (*A. globosus* Henaut 2000) that can do a range of kleptoparasitic techniques including feeding with the host, while it also contains a species (*A. caudatus*) which has been studied intensively (Vollrath 1984, Henaut & Ibarra-Nunez unpubl. data) but which only gleans insects from around the edge of webs. Because of the size of the group and the morphological diversity within the group it is possible that Cancellatus is not monophyletic. A comprehensive phylogeny would reveal this. Nevertheless we need to show caution when deciding which species will be representative of species groups.

Sociality.—An interesting aspect of the theridiid phylogeny that Agnarsson pointed out and which he discusses in this volume (Agnarsson et al 2001) was that *Argyrodes* form a monophyletic clade with the genera that contain social spiders. One of the striking characteristics of many species of *Argyrodes* is that they are gregarious, even forming mixed species groups around other spider’s webs. Their location within the theridiid phylogeny suggests that they may have a phylogenetic predisposition to form groups.

The significance of the group-forming behavior may be that it enhances the effectiveness of kleptoparasitism. For example, many *Argyrodes* on the same host’s web will be producing vibratory signals from numerous directions, confusing the host. Henaut pointed out that distraction had the effect of cooperation. He observed *A. globosus* distract the host while another *A. globosus* stole the food. He also saw *A. globosus* vary its degree of gregariousness—it was more gregarious on the webs of the more aggressive host (*Leucauge mariana* Taczanowski 1881, *L. venusta* Walckenaer 1842 and *L. argyra* Walckenaer 1842) than the less aggressive host (*Gasterancantha cancriformis* (Linnaeus 1758)).

Host-*Argyrodes* interactions.—Another important theme in the symposium was the relationship between hosts and *Argyrodes*. Firstly, Miyashita looked at the effect of different types of host species on the distribution of *Argyrodes* in Japan. He found that *Argyrodes* were limited by the distribution of their hosts and that *Nephila* spp. were particularly important. Li also pointed out the strong relationship between *Argyrodes* and *Nephila* in Singapore, and this relationship has also been noted in the Americas

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Figure 3.—Phylogenetic trees of species groups within *Argyrodes* reported by Agnarsson, Masumoto and Whitehouse at the symposium, indicating foraging behaviors associated with the species groups. Only spiders from the Americas (Agnarsson’s tree) have been formally assigned to the different species groups, so the speech-marks indicate the most probable species groups for the spiders from Japan (Masumoto) and Australia (Whitehouse).

(Vollrath 1979) and in Australia (Elgar 1989, 1993; Grostal & Walter 1997). As Smith noted, the importance of *Nephila* spp. as a host species for *Argyrodes* appears to be pandemic.

Secondly, the actual relationship between host and *Argyrodes* was explored. Li and Cangialosi emphasized that species of *Argyrodes* are often assumed to be kleptoparasitic (i.e. derogatory to the welfare of the host) when they could be commensal (have no effect on the host). Li provided evidence that *A. flavescens* O. P. Cambridge 1880 did have a direct affect on its host *Nephila pilipes* (Fabricius 1793). In the presence of the kleptoparasite, *N. pilipes* were smaller and produced fewer, but larger eggs. We concluded that the effect of *Argyrodes* on the fitness of the host was an area that could be expanded.

Thirdly, the relationship between the host and the *Argyrodes* can change depending on the type of host, and even the developmental stage of the *Argyrodes*. Cangialosi, working with a phylogenetically basal species *A. trigonum*, demonstrated that while this species exhibits both araneophagy and kleptoparasitism for all three hosts that she has studied; it is predominately a predator of *Neriene radiata* (Walckenaer 1842) (Linyphiidae) and predominately a kleptoparasite of *Pityohyphantes costatus* (Hentz 1850) (Linyphiidae) and *Achaearanea tepidariorum* (C. L. Koch 1841) (Theriididae).

Whether *A. trigonum* behaves as a kleptoparasite has to do not only with relative host size, but also with the developmental stage of *Argyrodes* independent of its relative size. For example, older *A. trigonum* are more likely to be aggressive compared to juveniles, regardless of host size.

Although *A. trigonum* switched between kleptoparasitism and araneophagy, the behavioral repertoire within each of these categories was limited. Kleptoparasitically, Cangialosi reported that *A. trigonum* gleaned insects and stole prey, but that it did not feed with its host (a kleptoparasitic behavior common in the Argyrodes species group) or eat silk. Araneophagically, Cangialosi reported that *A. trigonum* attacked spiders by biting them, but that it did not throw a silk line over a prey spider in order to catch it (the araneophagic method of species in the Rhomphaea and Ariamnes species groups).

Nevertheless the change in the relationship between *A. trigonum* and its host (from kleptoparasite/host to predator/prey) provides another dimension to the ‘‘interaraneae’’ interactions within the genus *Argyrodes*. The flexibility of the ability to change and the ecological ramifications of the change for both the host and the kleptoparasite were discussed and seen as important areas for future development.

Many questions remain concerning the factors contributing to changes in the relationship between *Argyrodes* species and their hosts. Basal species, such as those from the Trigonum species group which exhibit a wide repertoire of foraging behaviors, not only provide insight into the evolution of kleptoparasitism and araneophagy, but (as both Miyashita and Cangialosi pointed out) can also be good models for studying how shifting behavioral relationships between species can translate into complex patterns of population dynamics.

More subtle changes in the relationship between *Argyrodes* and their hosts were also presented at the symposium. Henaut showed that *A. globosus* would only use the behavior ‘‘feeding with the host’’ with the less aggressive hosts (*Gasterancantha cancriformis*, *Verrucosa arenata* (Walckenaer 1842), and *Nephila clavipes* (Linnaeus 1767)) and would form larger groups around the webs of the more aggressive host (*Leucauge mariana*, *L. venusta* and *L. argyra*) that had the effect of distracting the host.

An unusual relationship highlighted by Smith was that between an unnamed species of *Argyrodes* and plants protected by ants (Fowler & Venticinque 1996). In this case *Argyrodes* is not interacting with other spider species but with ants. How the *Argyrodes* interacts with the ants, and how this species of *Argyrodes* relates phylogenetically to other *Argyrodes* species, are two additional areas of research that need developing.

Silk eating.—Both Miyashita and Smith emphasized the importance of *Argyrodes* consuming the silk of its host. Miyashita pointed out that this behavior enables *Argyrodes* to survive periods of low prey abundance in the host’s web. It would be interesting to know how widespread this behavior is (Cangialosi reported that she has not seen *A. trigonum* feed on silk despite many hours of observations). Many species of spiders eat their own silk; do many species eat other spider’s silk as well? This area also needs further investigation.

Conclusions.—Research within the genus *Argyrodes* is at a very interesting stage. Our first priority is to improve our understanding of the phylogeny and its relationship to the multitude of foraging techniques common within the genus. With these points clarified we can more easily address ecological questions concerning interspecific interactions between *Argyrodes* and their ''hosts''. Our results suggest that different ecological questions may be particularly relevant for different species groups. For example, members of the Trigonum species group may be particularly useful for investigating a switch from kleptoparasitic behaviors to predatory behaviors. Species in the Argyrodes species group may be useful when asking questions either about host specificity or conditions under which an *Argyrodes* should change its kleptoparasitic techniques.

Obviously, these topics are only the tip of the iceberg. Our symposium only touched on the question of *Argyrodes* and sociality, the role of crypsis in determining the striking morphology of many *Argyrodes* species, and how *Argyrodes* locate their hosts. Mixed species groups of *Argyrodes* were not discussed, and we did not mention courtship behavior at all. All this indicates a very exciting and interesting future for behavioral-ecology research within the genus *Argyrodes*.

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