SHARING A WEB—ON THE RELATION OF SOCIALITY AND KLEPTOPARASITISM IN THERIDIID SPIDERS (THERIDIIDAE, ARANEAE)

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ABSTRACT.   Sociality and kleptoparasitism occur commonly in theridiid spiders. In both behaviors a number of conspecifics occupy a single web; gregariousness entails tolerance. Sociality has evolved several times in theridiids, but kleptoparasitism seems to have arisen only once. All four or more instances of sociality in theridiids are concentrated within a clade of relatively distal theridiids. This distribution of sociality suggests common cause, i.e. the presence of some characteristics that may facilitate the evolution of social behavior. The monophyletic genus *Argyrodes*, many of which are kleptoparasitic, is sister to the clade containing all social theridiids. Sociality and kleptoparasitism may thus be phylogenetically related in theridiid spiders; behaviors that facilitated the evolution of sociality could also have facilitated kleptoparasitism. Both may have their roots in maternal care.

Keywords: *Argyrodes*, kleptoparasitism, maternal care, social behavior

Permanent sociality, or quasi-sociality, is known in only about 20 of the more than 37,000 described species of spiders, but based on the current classification, this represents at least 12–16 independent origins of sociality (Avilés 1997). Living in a group is atypical spider behavior; spiders are famously solitary. In most species even conspecifics are only tolerated while mating (although aggression even here is common) and as very young juveniles. Living in a group therefore requires overcoming this kind of innate aggression. Many authors have pointed out that sociality in spiders is not randomly distributed but rather concentrated in a few lineages (Shear 1970; Burgess 1978; Krafft 1979; Buskirk 1981; D'Andrea 1987; Kraus & Kraus 1988, 1990; Avilés 1997). Presumably such lineages may exhibit traits that facilitate sociality, or, in other words, predispose the spiders to group living.

Spider kleptoparasitism, the occupation of a heterospecific web to steal prey or silk, occurs in several families (Anapidae, Dictynidae, Eresidae, Sparassidae, Mysmenidae, Oonopidae, Salticidae, Symphytognathidae, Theridiidae and Uloboridae) (Struhsaker 1969; Wickler & Seibt 1988; Elgar 1993; Ramirez & Platnick 1999). Most of these instances represent opportunistic kleptoparasitism by solitary spiders: the eresids *Stegodyphus africanus* (Blackwall 1866) and *S. sabulosus* Tullgren 1910 (Wickler & Seibt 1988), the salticids *Simaetha paetula* (Keyserling 1882) (Jackson 1985) and several species of *Portia* Karsch 1878 (Jackson & Blest 1982), the sparassid genus *Olios* Walckenaer 1837 (Jackson 1987) [note: Elgar (1993) presumably misread Jackson's paper and indicates that these occur in groups], the symphytognathid *Curimagua bayano* Forster & Platnick 1977 (Vollrath 1978), the uloborid *Philoponella republicana* (Simon 1891) (Struhsaker 1969), and probably the oonopid *Oonops pulcher* Templeton 1835 (Bristowe 1958). In some cases, however, many conspecific kleptoparasites (or even a number of species of spiders and non-spider arthropods (Eberhard et al. 1993)) occupy the same host web; examples are *Sofanapis antillanca* Platnick & Forster 1989 (Anapidae) (Ramirez & Platnick 1999), *Archaeodictyna ulova* Griswold & Meikle-Griswold 1987 (Dictynidae) (Griswold & Meikle-Griswold 1987), *Isela okuncana* Griswold 1985 (Mysmenidae) and many other mysmenids (Griswold 1985; Coyle & Meigs 1989) in addition to *Argyrodes* Simon 1864 (Theridiidae) (e.g. Vollrath 1987)). These animals interact frequently and
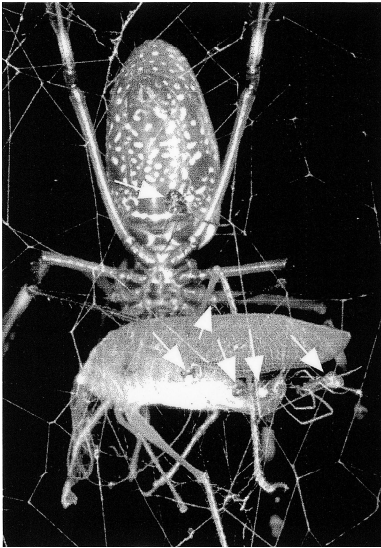
Figure 1.—Communal feeding of several individuals (arrows) of two *Argyrodes* species with their host, *Nephila clavipes*.

may even feed together (Fig. 1, see also Robinson & Robinson 1973). As in sociality, such gregariousness and communal feeding must require diminished agonism.

Theridiids are behaviorally diverse, ranging from solitary web-less hunters (e.g. species of the genus *Dipoena* Thorell 1869 (Levi 1953)), to species in which thousands of individuals cooperate to build webs several cubic meters in size e.g., *Anelosimus eximius* (Keyserling 1884). Most social spider species are theridiids (Avilés 1997) as are the equally famous kleptoparasites, *Argyrodes*. These are the most conspicuous spider kleptoparasites, found worldwide in the webs of *Nephila* Leach 1815, and numerous other spiders. Although both sociality and most instances of kleptoparasitism typically involve web sharing (i.e., the presence of more than one individual of the same species in a single web—excluding, of course, mating pairs) the two behaviors have hitherto been considered entirely unrelated (but see Whitehouse & Jackson 1993). Recent phylogenetic research suggests otherwise. In this paper three main points are made: first, I point out that the two types of behaviors appear phylogenetically juxtaposed in theridiid spiders; second I suggest that this may be due to a fundamental similarity between the two, namely web sharing, stemming

from maternal care; third, I discuss how the notion of web sharing implies a clear distinction between territorial and non-territorial sociality.

Although no detailed phylogeny of the family Theridiidae has ever been published, Agnarsson et al. (2001), and Arnedo et al. (2001) presented a preliminary theridiid phylogeny of 74 taxa at the XI Congress of Arachnology in Badplaas, South Africa, based on morphological and molecular data. This phylogenetic analysis will be published elsewhere, but Fig. 2 summarizes the clades relevant to this argument, based on a combined analysis of the morphological and molecular data. This arrangement has been consistently found in previous analyses. This phylogeny is included here to illustrate the argument; this admittedly speculative hypothesis does not require this particular cladistic structure to be valid.

All social theridiids occur in a relatively distal part of the cladogram, *Anelosimus* plus the "lost colulus clade" (Fig. 2). Both the current classification and the provisional phylogeny suggest at least four origins of sociality in this clade, within the genera *Theridion* Walckenaer 1805, *Achaearanea* Strand 1929 and *Anelosimus*. The predominance of solitary *Theridion* and *Achaearanea* species makes independent origin in these lineages very probable. Cladistic analysis further suggests a dual origin of sociality in *Anelosimus* (Fig. 2). Although not all *Argyrodes* are kleptoparasites, the behavior seems to have arisen once in the common ancestor of the whole lineage (see Whitehouse et al. this volume). *Argyrodes* is sister to the *Anelosimus* plus lost colulus clade. Thus all five instances of group living, or sharing a web, seem to be juxtaposed in theridiid phylogeny. Does this distribution require explanation, or is it simply coincidental? The definitive answer to this question must await the finished phylogenetic product. Maddison (1990) proposed a "concentrated changes test" to calculate the probability of obtaining, by chance alone, X independent events in a subclade of size Y in a phylogeny of Z terminals. Given the preliminary nature of both the phylogenetic and natural history data currently available, a calculation based on such data certainly cannot be definitive. However, even a marginally significant result at this point would support the notion that something unusual has occurred in this branch of theri-
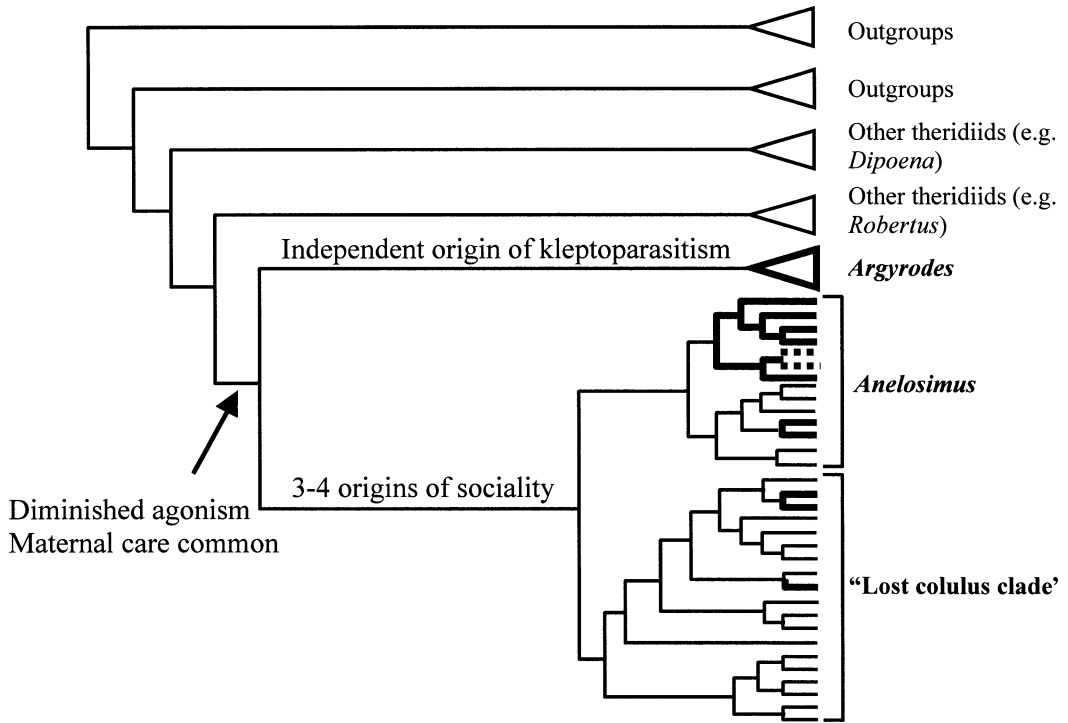
Figure 2.—Major theridiid clades ex Agnarsson et al. (2001) and Arnedo et al. (2001). Triangles represent subsidiary lineages, bold branches are group-living taxa, dotted branches unknown behavior. Web sharing (sociality plus kleptoparasitism) is notably clumped in the distal part of the cladogram suggesting a common cause.

diids, and therefore justifies some conjecture as to its genesis. In fact, the test says that sociality (four occurrences in the *Anelosimus* plus lost colulus clade) is significantly concentrated, a fact that in and by itself calls for explanation. In addition, the juxtaposition of sociality plus kleptoparasitism (five occurrences in the *Argyrodes* plus *Anelosimus* plus lost colulus clade) is significant. Of course, if the number of independent instances were to decrease in the final analysis the distribution might be attributed to chance. Likewise, augmenting the overall size of the cladogram would increase significance. As an increase in the size of the theridiid cladogram is much more certain than the discovery of novel instances of sociality or kleptoparasitism, it seems safe to conclude that their cladistic juxtaposition demands explanation if, as is argued below, sociality and kleptoparasitism are fundamentally similar. I argue that kleptoparasitism and sociality are both more likely to evolve in the presence of a trait that reduces agonism.

Many authors have argued that features required for maternal care can result in post-juvenile tolerance and sociality if siblings continue to cohabit after leaving the egg sac (Shear 1970; Kullmann 1972; Burgess 1978; Krafft 1979; Cangialosi & Uetz 1987, Avilés 1997). It should be pointed out here that maternal care is itself a vaguely defined phenomenon that may require more than one behavioral mechanism (Krafft 1982). The most obvious form of tolerance, and the one that authors presumably have in mind when they speak of the precursor to social behavior, is tolerance between peers. "Peer tolerance" among juvenile spiders is very widespread phylogenetically; most newly emerged spiderlings "tolerate" each other at least briefly (Krafft 1982). "Offspring tolerance" requires the inhibition of predation on smaller individuals, or at least on the egg sac. Finally, small spiders quite generally flee their webs if threatened by a large animal. Maternal care may additionally require inhibition of the

flight response, or "maternal tolerance" on the part of the juveniles.

Kraus & Kraus (1990) suggested that neotenic retention of juvenile tolerance "obviously" explained sociality in the eresid genus *Stegodyphus*. For example, they explained the smaller size of social *Stegodyphus* species in comparison to their solitary congenerics as neoteny. In a similar manner Whitehouse (1986) suggested that kleptoparasitism might have arisen through neoteny as an extension of a fundamental "feeding with host" response of juveniles. Elgar (1993) showed that obligatory kleptoparasitic (and thus group living) *Argyrodes* are smaller than their free living/opportunistic kleptoparasitic congenerics, but did not claim neoteny. Both Kraus & Kraus (1990) and Elgar (1993) treated taxa as statistically independent units, which of course inflates sample size and the potential for Type I errors, due to the failure to account for shared history (Ridley 1983; Felsenstein 1985). Thus the trends on which they based their conclusions should be re-analyzed.

In this view, sociality is homologous to the juvenile tolerance exhibited in cases of maternal care. Offspring tolerance (minimally as egg sac guarding), maternal tolerance and peer tolerance seem all necessary prerequisites for maternal care but the prolongation of juvenile peer tolerance may alone explain sociality, as tolerant juveniles become tolerant adults.

Could kleptoparasitism also be modified maternal care? The latter, from the juvenile's point of view, also means living and feeding in the web of a much bigger spider (the mother) who at some point becomes a potential predator (Whitehouse 1986). If sociality is the prolongation of the tolerance required for maternal care, kleptoparasitism can be viewed as co-opting or the exaptive application of juvenile tolerance in a novel context in which the much larger host is no longer a conspecific relative but an entirely different species. As in maternal care, the kleptoparasites (both adults and juveniles) occur in groups that feed together with the host. Interestingly, *Argyrodes* kleptoparasites exhibit a wide range of "tolerance" behaviors, from obligatory kleptoparasitism in which adults tolerate the juveniles and vice versa to facultative kleptoparasites that abandon their eggsacs and presumably are opportunistically cannibalistic (Larcher & Wise 1985). In addition, kleptoparasitism in

Argyrodes has other characteristics of cooperative living. Many *Argyrodes* moving on the host web will produce vibratory signals from numerous directions, which may confuse the host and can be considered a form of cooperation. Such effects have been identified as benefits of sociality (Allee 1931).

As Avilés (1997) pointed out, the hypothesis that sociality evolved from maternal care predicts that sociality should be concentrated in lineages already exhibiting maternal care and that maternal care should precede sociality phylogenetically. Although more phylogenetic and natural history information is required for a strong test, current evidence does suggest that sociality in theridiid spiders is indeed concentrated in a lineage where maternal care is common. Maternal care may be necessary, but it certainly is not sufficient because it occurs in many solitary spider lineages (e.g. Araneidae (Patel & Nigram 1991), Lycosidae (Eason 1964; Fujii 1979), Oxyopidae (Randall 1977; Willey & Adler 1989), Thomisidae (Castanho & Oliveira 1997; Evans 1998), and Uloboridae (Patel & Bradoo 1981) to name but a few. Avilés (1997) pointed out that all but one of the social spiders belong to the infraorder Araneomorphae, but this is not surprising as Araneomorphae comprises the vast majority of all spiders. However, she and others have also pointed out that most social spiders build webs (Shear 1970; Krafft 1979 & 1982; Buskirk 1981; D'Andrea 1987), while about half of all spider families (and the majority of spider species) do not build prey capture webs. The importance of webs may lie with the silk itself, e.g. Krafft (1982) likened spider silk to the social pheromones of insects because the vibratory information allows communication from a distance. Krafft (1979) further suggested that sociality is relatively more common in species that build three-dimensional webs than in orb weavers. Krafft, Buskirk, and D'Andrea attributed the relative absence of sociality in orb weavers to the difficulty of cooperatively building and using an orb-web (see also Cangialosi & Uetz 1987). (Note: from the perspectives of *Argyrodes* kleptoparasites, *Nephila* host orbs with their extensive barrier webs are effectively three dimensional). Theridiid web architecture varies greatly; some theridiids do not even make webs. Theridiid sociality, however, occurs

only among lineages where three dimensional webs are prevalent.

But is the concurrence of maternal care and three dimensional webs sufficient to explain why members of this particular subset of theridiids are so prone to web sharing? Other spiders beside this clade of theridiids have three dimensional webs and maternal care but lack further web sharing. Either web sharing simply has not evolved in these groups despite propitious conditions, or other unknown factors are involved, for example peer tolerance. Peer tolerance typically entails suppression of both hetero- and conspecific aggression. In a shared web, vibrations caused by conspecifics and even quite unrelated spider species walking around are generally ignored (Krafft 1982), although struggling prey, of course, trigger aggressive responses. Direct touch, however, typically triggers aggression towards heterospecific spiders only. In *Agelena consociata* Denis 1965 a pheromone on the integument seems responsible for the inhibition of mutual biting (Krafft 1975). Very little is known about spider pheromones and their possible role in social communication (see Tietjen & Rovner 1982, for review). Mutual feeding leads to exchange of digestive fluids that may contain pheromones (Krafft 1969). Kullmann (1972) suggested that contact chemoreceptors in *Stegodyphus sarasinorum* might function to receive colony pheromones. Such pheromones may be laid down on webs; recently sex pheromones have been isolated from spider webs (Schulz & Toft 1993). The study of such tolerance and communication mechanisms may cast additional light on patterns of social and kleptoparasitic web-sharing, and the relationship between the two.

The ideas presented in this paper can be tested in several ways. First, the current phylogeny juxtaposes kleptoparasitism and sociality; if the phylogeny changes in such a way that the two are no longer adjacent, behavioral homology is falsified, although maternal care might still coincide with each independently. Second, if maternal care does not evolve at the node subtending kleptoparasitism and sociality in theridiids, the hypothesis of common cause is suspect. Third, the hypothesis would be strongly corroborated if an increase in the length of time juveniles spend in their natal web evolves at the kleptoparasitism-sociality node. Fourth, this hypothesis predicts that maternal care will be common and widespread within this particular clade of theridiid spiders; at present such data are lacking for most theridiid species. Finally the ideas presented here may also apply to cases of social web sharing in unrelated spider lineages and can be tested there.

The argument followed in this paper suggests that spider "sociality" that consists of sharing a web may be fundamentally different from spider "sociality" that consists of tightly aggregated individual webs. "Web sharing" means two or more conspecifics in a single web. Whether permanent or periodic, sociality and communal kleptoparasitism are web sharing, and all might have arisen from maternal care (often labeled the "maternal care route" to sociality). In contrast, territorial "sociality," the tight concentrations of interconnected webs, differs distinctly. Known mainly from orb weavers such as *Cyclosa* Menge 1866, *Cyrtophora* Simon 1864, *Nephila*, and *Metepeira* F.O.P.-Cambridge 1903 (Burgess 1978; Krafft 1982; Aviles 1997; Burgess & Witt 1976; Burgess & Uetz 1982; Cangialosi & Uetz 1987), in these cases each individual maintains its territory (i.e., its own web) and communal feeding does not occur. Although such aggregations have been described as possibly "a colonial social organization intermediate between the solitary behavior typical of most spiders and the communal behavior of the "social" spiders" (Cangialosi & Uetz 1987 p. 237), it is not likely to be intermediate between solitarity and web-sharing sociality because it never involves web sharing. Territorial sociality in the same genus may also be periodic or permanent. *Metepeira labrynthea* (Hentz 1847) aggregates facultatively around resources, (called "fortuitous aggregations" by Buskirk & Uetz 1982), but *M. spinipes* F.O.P.-Cambridge 1903 forms permanent territorial colonies. Thus territorial "sociality" rather, as suggested by Burgess (1978), represents communal living that may arise through a different evolutionary pathway, that could be termed the "web aggregations route."

To conclude, I suggest that sociality and kleptoparasitism in theridiids can both be viewed as forms of web-sharing social behavior. The origin of both may have its roots in maternal care, via the retention of juvenile peer tolerance, sharing a three dimensional

web. Web-sharing sociality and territorial sociality seem unrelated.

ACKNOWLEDGMENTS

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