

Australasian social spiders: what is meant by 'social'?

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Abstract – The number of social spider species in Australasia may be as few as three, or as many as there are species of spiders, given the present lack of consensus on the definition of a social animal. This is part of the reason why a unified theory of sociobiology has been elusive, and is especially regrettable for arachnologists because spiders are unusually promising subjects for testing theoretical ideas about social behaviour. A review of these problems, with special reference to Australasian social spiders, argues that cooperation among mutually tolerant individuals, in behaviour other than courtship, mating and parental care, is the sole defining criterion of sociality.

INTRODUCTION

There are three species of social spiders in Australasia. Or seven, or ten, or as many as there are species of spiders, depending on how 'social' is defined. Shear (1970) saw the need to distinguish sociality from contiguity when he wrote that "a meaningful definition of sociality must avoid being too broad". Other authors, e.g. Wilson (1975) and Jackson (1978, 1979), have urged caution in defining sociality in a way that narrows our intuitive understanding of the concept. My own belief is that the benefits of definitions in science outweigh their faults, so here (cautiously) I review the problem. Because most arachnologists have understandably been reluctant to probe this question, the literature on the social biology of spiders refers to these animals as being in a state of temporary aggregation, permanent integration and anything and everything in between. In doing so, it reflects certain problems of sociobiology in general, such as whether social behaviour is a consequence of the properties of social groups (Slobodchikoff and Shields 1988) or vice versa. Chronic terminological *laissez-faire*, allowing even interspecific interactions as social (Chapman and Reiss 1992), may be one reason why West Eberhard's (1975) hope of a "comprehensive theory of social behaviour" and Wilson's (1975) vision of "a more inclusive theory" of sociobiology are as yet unrealised, and may never be realised while the key term is seen as a lay word impossible or unwise to define.

The present paper brings together what is relevant about those Australasian spiders that, for one reason or another, have been explicitly referred to as social (excluding, for example, Main's (1964) reference to aggregations of *Gasteracantha minax*). Using these and other examples, it reviews the

criteria of sociality and categorizes Australasian social spiders in terms consistent with a derived definition and reconcilable with animal sociality in general. It is offered here as a token of appreciation to one of the major players in this drama, Barbara Main.

THE SPECIES

Achaearanea wau Levi, Theridiidae

The webs of this theridiid occur in groups along montane forest edges or in treefall clearings in Papua New Guinea. The spiders occupy curled-leaf retreats hung in the barrier web of the snare. Juveniles grow and mature together, and inbreed. Some females (mostly adult and gravid) then swarm *en masse* to establish a new site, while others remain in the parent web which may persist for several generations (Levi *et al.* 1982; Lubin and Robinson 1982; Lubin and Crozier 1985). Evidence strongly suggests that there is a primary sex ratio bias towards females in *A. wau* (Lubin 1991). The spiders jointly undertake web maintenance and together capture and share their prey (Lubin 1986). The young feed on prey captured by adult females; these are not necessarily their own parents (Lubin 1982).

Achaearanea vervoorti Chrysanthus, Theridiidae

The attribution of sociality to *A. vervoorti* is apparently based on there being four specimens in Father Chrysanthus's original collection, and on the discovery of two females and a male living together in a web (Levi *et al.* 1982). It is probably wise to withhold comment on this western New Guinean species until more information is available.

***Achaeearanea mundula* (L. Koch) and *Achaeearanea kaindi* Levi, Theridiidae**

The young feed on prey captured by their mothers, in these species (Lubin 1982), both of which are sympatric with *A. wau* (Levi *et al.* 1982; Lubin 1982). Juveniles of *A. mundula*, referred to by Lubin and Robinson (1982) as a solitary species, often remain together in the maternal web until their last instar.

***Achaeearanea tepidariorum* (C.L. Koch), Theridiidae**

Cosmopolitan in distribution, spiderlings of *A. tepidariorum* feed on prey captured by their mother (Lemasle 1977, in D'Andrea 1987). They are mutually tolerant before they disperse (Bonnet 1935).

***Argyrodes antipodiana* (O. Pickard-Cambridge), Theridiidae**

The webs of this kleptoparasitic theridiid may occur in temporary clusters on the webs of its primary host, the orb-weaver *Araneus pustulosus*, in New Zealand (Whitehouse 1986; Whitehouse and Jackson 1993). Interactive behaviour, other than that between the sexes, is not tolerant or cooperative (Whitehouse and Jackson 1994).

***Diaea socialis* Main, Thomisidae**

This species occurs in the karri and jarrah forests of southwest Western Australia, and is remarkable for being the only previously described thomisid documented as social (Main 1988); but other social crab spiders of the genus *Diaea* are now recognized (see Evans, this volume). A single gravid founder female establishes a nest, and she and her offspring subsequently enlarge this carton-like structure. No snare web is built (Main 1988; Evans and Main 1993). The spiders ambush prey individually but assist any successful hunter to subdue a captured victim, and many siblings afterwards feed on it. They mature and inbreed after at least two years in the home nest, a life history pattern that generates a female-biased sex ratio in this species (Rowell and Main 1992). There is evidence that in *D. socialis*, as in *Anelosimus eximius* (Vollrath 1986) and possibly in *Phryganoporus candidus* (Downes 1993), some females never mature, but represent a division of reproductive labour, i.e. act as 'workers' (Main 1988).

***Philodromus* sp., Thomisidae**

The nests of this unidentified thomisid are found in the canopies of ironbark and other eucalypts in southeastern Queensland (Brimblecombe 1962). They are reminiscent of those of *D. socialis*, and thus suggest that these spiders may also have a social life.

***Phryganoporus candidus* (L. Koch), Amaurobioidea**

This species is widespread in Australia (Gray 1983; Colgan and Gray 1992). Its nests, each founded by a solitary female in summer, may develop initially as aggregations of individual snares set by the early juveniles, but the mature nests are structurally and functionally amodular (Main 1971; Downes 1993, 1994a). Several to many individuals may together subdue prey and feed on it, and their predatory behaviour is at least in part cooperative (Downes 1994b). The current generic placement is that advocated by Dr M. Gray (personal communication).

***Badumna socialis* (Rainbow), Amaurobioidea**

Each of the shawl-like webs of *B. socialis* is the work of numerous individuals. The surface is peppered with retreat-tube entrance holes, and the spiders' egg sacs are scattered over the outside (Rainbow 1905). *B. socialis* is found in the Jenolan and Abercrombie caves of New South Wales (Rainbow 1905; Colgan and Gray 1992).

***Philoponella congregabilis* (Rainbow), Uloboridae**

The webs of this Australian species are aggregated and interconnected (Rainbow 1916; Main 1976; Clayton-Jones 1983), and the egg sacs are suspended outside of the orb frame (Rainbow 1916). Regurgitation feeding of young occurs, and juveniles attack prey in groups in captivity (Clayton-Jones 1983).

***Cyrtophora citricola* Forskal, Araneidae**

The webs of this orb-weaver are usually interconnected in clusters, but isolated webs may occur. Wheeler (1926) gave an inexplicit account of feeding "in common" in *C. citricola*. Tolerance exists among early young and adult females (Blanke 1972). Australasia is part of the worldwide range of *C. citricola*.

***Cyrtophora moluccensis* (Doleschall), Araneidae**

Present in New Guinea and Guam, *C. moluccensis* is also common in northeast Queensland (Main 1976). Its territorial web-complexes are like those of *C. citricola* (Lubin 1974; Main 1976). Most aggressive interactions are triggered by the capture of large prey. Individuals may travel far from their own orb to repair and maintain structural supporting threads on the periphery of web complexes (Lubin 1974).

***Arachnura higginsii* (C.L. Koch), Araneidae**

Widespread in mainland temperate Australia and Tasmania (J.F. Jones, in Mckeown 1963; Main 1976), females of this species are territorial, but their orb webs may occur in groups of up to 70,

among which males are vagrant beyond the confines of the orbs. The supporting frame threads "appear to be the general concern, and are evidently strengthened and extended by the work of many spiders" (J.F. Jones, in Mckeown 1963).

Scytodes fusca Walckenaer, Scytodidae

Web complexes of this pantropical spider occur on tree trunks in North Queensland and may consist of up to 50 units, each typically occupied by an adult female (with or without offspring). Males are usually located on the interstitial silk that links the territorial units. Modifications of this pattern do occur, however. Tolerance among conspecifics varies; adult females are least tolerant of intruders. Parent females provide prey for their early-instar young to feed upon (Bowden and Jackson 1988; Bowden 1991).

Delena cancerides Walckenaer, Heteropodidae

Endemic and widespread in Australia, extending to Tasmania and other southern islands (Main 1976), this species may occur in groups of one to three adult males, up to six adult females and up to 300 young of the next generation (Rowell 1985, 1988). According to Hickman (1967), the young remain with their mother until they are half grown, but Rowell (1985) observed that they stay together with their mother until they mature, and often share prey. Moreover, they hunt together under laboratory conditions. While group members are mutually tolerant, individuals from other groups are killed (Rowell 1985).

DEFINING 'SOCIAL'

Emerson (1958), insisting on systematic division of labour as a necessary criterion, claimed that "social behaviour in the strict sense is found only among social insects and humans". It is often defined loosely, however, for example as "behaviour that either is stimulated by or has a stimulating effect on one or more members of the same species" (Scott 1983), and sometimes (e.g. Fuller and Thompson 1978) explicitly includes sexual and/or parental behaviour. Wilson (1971) advocated a definition of sociality that excludes sexual interactions but includes parent-offspring interactions provided they involve "reciprocal communication of a cooperative nature", which he regarded as "the essential intuitive criterion of a society". A society he defined as "a group of individuals that belong to the same species and are organized in a cooperative manner". D'Andrea (1987), citing Tinbergen's (1953) acceptance of a parent and egg as a society, expressed misgivings about definitions that are too inclusive.

In contrast to definitions of sociality in general,

the terms developed by Wheeler (1923, 1928), Evans (1958), Michener (1969) and Wilson (1971) to classify sociality in the termites and the social hymenopterans are relatively rigorous and narrow. Although not originally designed to be relevant to other taxa, the process of legitimizing these terms in reference to spiders and other animals involved Wilson (1971) himself and is at present all but a *fait accompli* of sociobiology (e.g. Jarvis *et al.* 1994). Some arachnologists (e.g. Brach 1977; Vollrath 1986; Darchen and Delage-Darchen 1986) have explicitly evaluated the social status of spiders in terms of this entomological classification. Others have used the entomological terms along with, or instead of, colloquial ones or ones introduced specifically to define spider societies. As a result the arachnological literature refers to 'social' spiders as aggregated, affiliated, associated, collective, colonial, communal, coordinated, cooperative, eusocial, fraternal, friendly, gregarious, group-living, interattracted, maternal-social, matrifilial, noncooperative, nonsolitary, presocial, quasisocial, social, subsocial or tolerant, terms sometimes qualified as advanced, completely, facultative, highly, incipient, limited, loosely, non-territorial, obligate, periodic, permanent, semi, territorial or truly.

Some of the above terms have figured in more or less influential schemes of classification of spider sociality, e.g. those of Kullmann (1968, 1972), Burgess (1978), Jackson (1978) and Krafft (1982). Kullmann's diagnosis of spider sociality, which used interattraction, tolerance and cooperation as jointly defining criteria, proved particularly seminal. Interattraction, or "the tendency to form a group" (D'Andrea 1987) is a complex, heterogenic concept that reflects pheromonal, tactile and other influences in the lives of spiders. It is described by Kullmann (1972) as "an urge for associating", and characterized by Lindauer (1974) as an intraspecific, sex-independent, attracting stimulus. Thompson (1958) had earlier envisaged the equivalent concept of 'cohesiveness' as "the psychological counterpart of density". Despite the difficulty of defining it, interattraction has been interpreted and measured as a propensity to aggregate (Downes 1994b), and in the case of eusocial insects and 'permanent-social' spiders (Kullmann 1968, 1972), such aggregations may be essential to the survival of individuals (Darchen and Delage-Darchen 1986). But whatever might be the meaning, role or significance of interattraction, it does not demand inclusion in a definition of sociality involving cooperation, because it is neither sufficient nor necessary. Its insufficiency has been argued by Krafft (1970), using cockroaches as examples of asocial animals that display interattraction (but see Scott 1929; Gautier *et al.* 1988). It is unnecessary because, apart from

some human behaviour made possible by modern technology, the possibility of cooperation is predicated upon some form of interattraction, environment-mediated or otherwise: interattraction is possible without cooperation, but not vice versa.

Tolerance, on the other hand, is possible without cooperation, and vice versa: *Cyrtophora citricola* and *C. moluccensis* are examples of territorial species whose members are mutually intolerant and aggressive but cooperate (as defined below) in web-complex construction and maintenance. Here a choice presents itself: equate sociality with cooperation, or accept tolerance as a necessary criterion. I follow Kullmann (1968, 1972) and Main (1988) in choosing the latter, because while intraspecific intolerance can be, and often is, part of the behavioural repertoire of social species, it is their other, tolerant, behaviour that has traditionally and conceptually prevailed as characterizing a social species. Tolerance is not, however, itself sufficient as a criterion of sociality, because it is, for example, "exercised by early instars of all spiders" (Main 1988). These considerations underlie the following definitions:

1. A social species is one in which some or all of its members must, or normally do, perform one or more social acts in order to complete their life histories.

2. A social act is a naturally-occurring, cooperative act other than courtship, mating or parental care, performed by two or more free-living members of the same species that are mutually tolerant, at least for the duration of the act concerned.

While very few commentators would question the exclusion of sexual behaviour, the exclusion of parental care requires justification. Some level of parental care has been used as a sufficient criterion of sociality or incipient sociality by Kullmann (1972), D'Andrea (1987) and others. The level concerned is normally left unspecified (see, e.g. Polis and Lourenco 1986); this is possible because of the flexibility of the term 'subsocial', usually considered (e.g. by Wilson 1971, 1975) as a degree of sociality, but sometimes taken to represent both this and the conceptual space between the solitary and societal states (e.g. D'Andrea 1987). 'Subsocial' was defined by Michener (1969) for species of bees in which the female parent survives to feed and protect the young, but dies before the young mature. Wilson (1971) omitted Michener's reference to feeding, and licensed the use of the term 'subsocial' for any animal taxon. Krafft (1982) redefined subsocial species (of spiders) as those "whose young cooperate, without intervention by the mother...but disperse before adulthood". Krafft's modification, unfortunately, did not prevail. Thus, for this and other reasons, the definition of a subsocial species simply as one in

which adults care for their own offspring for some period of time has been effectively legitimized for all taxa, and is applied routinely to spiders (e.g. Ruttan 1990).

There are problems with this, primarily that by this criterion, vast numbers of vertebrates and invertebrates normally considered asocial (including numerous agelenids, eresids, lycosids, pisaurids, clubionids, salticids and theridiids) must be included among the social animals (see, e.g. Gillespie 1990). Yet there is a fundamental reason for denying parental care as a sufficient criterion of sociality, namely that models of natural selection based on individual fitness are sufficient to explain "the coming together of the sexes and parental care", but not "behaviour more positively social" than that (Hamilton 1964). Tolerance and cooperation between conspecific individuals other than parents and their offspring, i.e. behaviour interpreted in terms of inclusive fitness, is best considered the domain of sociality.

DEFINING 'COOPERATION'

Almost all of the seminal statements about the nature of sociality, whether or not intended as formal definitions, involve the concept of cooperation (e.g. Wheeler 1928; Michener 1969; Kullmann 1968, 1972; Wilson 1971; Krafft 1982). Arachnologists have explicitly cited cooperation as the key factor in any diagnosis of sociality in spiders (e.g. Jackson 1979; Buskirk 1981; D'Andrea 1987), but its meaning has remained largely intuitive. Packer and Ruttan (1988) do not define it, other than implicitly to acknowledge simultaneity as a necessary condition for behaviour to be called cooperative. Simultaneity is not, however, a sufficient condition (Curio 1976; Jackson 1979).

Cooperation among mutually tolerant individuals is a wider concept than sociality, because cooperation can be interspecific, e.g. between cleaner fish and their 'clients' (Trivers 1985). The definition I propose, and defend below, is as follows:

The act of working together simultaneously for mutual benefit, where 'working' involves more than movements that produce a change in dispersion.

An important aspect of this definition is its exclusion of the coming together of individuals in clusters that limit the worst effects of heat loss or desiccation. Penguins, for example, may huddle in a blizzard but the change in spatial aggregation involved should not in itself be admitted as social behaviour. Among spiders, such (usually overwintering) aggregations normally represent dormant phases of the life cycle (Main 1988). Another important feature of the definition is that

it does not disallow territoriality. Furthermore, not only is it possible for spiders to be both territorial and cooperative, it is possible for such species to be social, if they cooperate tolerantly, as in the case of *Eriophora bistrata* (Fowler and Diehl 1978).

The definition differs from Trivers' (1985) definition of a cooperative act by being unambiguous about simultaneity and by disallowing the possibility that a cooperative act can be performed by one animal, or that one participant can be passive. An insistence upon simultaneity endorses the view of Packer and Ruttan (1988), and distinguishes between cooperation and reciprocal altruism (Trivers 1971), which may or may not be cooperative. The timescale implied by 'simultaneously' in the definition is a function of the behavioural act concerned. The construction of a nest by two birds, for example, is a cooperative act even if one always rests or feeds while the other works, because the timescale is not the seconds or minutes of twiglet manipulation but the hours or days of nest construction. This example has direct parallels in the behaviour of social spiders that build or maintain nests or web-complexes. Furthermore, the acknowledgement of the timescale factor resolves an apparent problem of reconciling simultaneity with division of labour: termite soldiers may cooperate with each other during a minute-long battle; they may also cooperate with workers over a whole season, in rearing a viable brood of siblings to maturity.

As yet nothing has been said about communication, although it has been called "the crucial issue" of sociality (Darchen and Delage-Darchen 1986), and its mediation by web silk and associated pheromones is a preadaptation to sociality in spiders and a means of maintaining the integrity of spider societies (Shear 1970; Evans and Main 1993). A rigorous exploration of the definition of 'communication' cannot be attempted here; but it is clearly not the case that communication is a sufficient criterion of cooperation, or of sociality. Communication is normally, if not invariably, an integral part of all territorial and agonistic behaviour, most or all of which is not cooperative by almost any definition. It is also an important part of the behaviour of animals such as frogs, moths and butterflies, most species of which are normally regarded as asocial. If communication were a sufficient criterion of sociality, all web-building spiders would be social, a conclusion implicit in Witt's (1975) account of the web.

It is probably indisputable, however, that communication is necessary for cooperation (Krafft 1979), and I have argued above that cooperation is necessary for sociality; hence, communication is necessary for sociality. Nonetheless, it need not be

part of the latter's definition so long as cooperation is such a part.

COMING TO TERMS WITH SOCIAL SPIDERS

I have argued that species that must, or at least normally do, tolerantly cooperate in activities other than courtship, mating and parental care should be recognized as social, and those that do not as asocial. This has two major effects on the attribution of sociality to spiders. One is that many theridiids, eresids and other spiders in which the young are actively or passively fed by the mother are not thereby social. Another is that those species (especially araneids and uloborids) whose webs commonly or typically aggregate in clusters are also not thereby social, even if an interconnecting and supporting web-frame is constructed and maintained cooperatively. Available evidence supports the view that the clustering of orb webs of *Nephila clavipes* is a stochastic phenomenon driven by habitat availability and population density (Farr 1977). I recommend the term 'communal' for those species whose webs may occur in more or less dense aggregations but are otherwise territorial and mutually intolerant. The term 'colonial' is well-established and may prove hard, and perhaps unnecessary, to dislodge. Kullmann (1968, 1972) suggested that it is appropriate for insect societies in which brood production is the main aim; but 'colonial' is best reserved for those invertebrates in which asexually produced units remain united physically and physiologically. The term 'aggregated' remains clearly appropriate for overwintering clusters of salticids, etc.

Of the Australasian spiders that are the subjects of this review, only *Achaearanea wau*, *Diaea socialis* and *Phryganoporus candidus* are social by the given definition. *Badumna socialis* and *Philodromus* sp. are likely to be included when the necessary evidence is obtained; so too will be *Delena cancerides* when and if its cooperative hunting is observed in nature. Of the orb weavers, *Cyrtophora citricola*, *C. moluccensis* and *Arachnura higginsi* must be considered asocial unless and until tolerantly cooperative behaviour in their web-complex building is shown to be necessary or at least normal. This is also the case for *Scytodes fusca*. The findings of Clayton-Jones (1983) on the cooperative hunting of captive juvenile *Philoponella congregabilis* need to be confirmed and also shown to reflect natural behaviour, before that species could be admitted as social. Table 1 summarizes these designations and shows how they differ from those of the most recent review of sociality in spiders, that of D'Andrea (1987), which recalled and compared the merits of the prevailing terminology but did not undertake a critical review of it.

Table 1 Cooperative behaviour present (+), absent (-) or undecided (?) in Australasian spiders that have been referred to by various authors as social. The social status under present definitions, and according to D'Andrea (1987), is given as asocial, periodically social (period-soc), permanently social (perm-soc), social with duration undecided (social) or social status undecided (?). Asterisked entries are likely suppositions. xx = not listed in D'Andrea (1987).

Species	Cooperative behaviour			Social status	
	Nesting	Brooding	Hunting	Present	D'Andrea
<i>Achaearana wau</i>	+	+	+	perm-soc	perm-soc
<i>Achaearana verwoorti</i>	?	?	?	?	xx
<i>Achaearana mundula</i>	-	-	-	asocial	xx
<i>Achaearana kaindi</i>	-	-	-	asocial	period-soc
<i>Achaearana tepidariorum</i>	-	-	-	asocial	period-soc
<i>Argyrodes antipodiana</i>	-	-	-	asocial	xx
<i>Diaea socialis</i>	+	-	+	period-soc	xx
<i>Philodromus</i> sp.	+*	-*	+*	period-soc*	xx
<i>Phryganoporus candidus</i>	+	-	+	period-soc	social
<i>Badumna socialis</i>	+*	-*	+*	social	social
<i>Philoponella congregabilis</i>	-*	-	?	?	asocial
<i>Cyrtophora citricola</i>	-*	-	-	asocial*	perm-soc
<i>Cyrtophora moluccensis</i>	-*	-	-	asocial*	perm-soc
<i>Arachnura higginsii</i>	-*	-	-	asocial*	perm-soc
<i>Scytodes fusca</i>	-*	-	-	asocial*	xx
<i>Delena cancerides</i>	-*	-*	+*	social*	xx

TOWARDS A UNIFIED THEORY OF ANIMAL SOCIALITY

If studies of social spiders are to contribute as effectively as possible to "one of the great manageable problems of biology", namely "the formulation of a theory of sociobiology" (Wilson 1971), they should specify their relationships with the relevant theoretical ideas that operate proximally and are in turn explicable in genetical and evolutionary terms by inclusive fitness models such as Hamilton's (1964). Such bodies of theory include cooperative hunting theory (Packer and Ruttan 1988), optimal foraging theory (Mangel and Clark 1986), clutch theory (Godfray *et al.* 1991) and life history theory (Stearns 1992). Progress will continue to be hampered or thwarted, however, while the term 'social' remains fugitive (Shear 1970), or while prevailing and influential definitions of sociality conclude that social behaviour can be displayed by asocial animals (Slobodchikoff and Shields 1988).

Spiders that hunt cooperatively are "social in the same sense as wild dogs or wolves" (Buskirk 1981) and may therefore be valid models, in many respects, for studies of cooperative hunting, but their use of webs can make comparisons difficult: in Packer and Ruttan's (1988) analysis of hunting success, *Stegodyphus mimosarum* proved to be anomalous because it hunted cooperatively despite a high level of solo hunting success (Ward and Enders 1985). The 'hunting success' of the web alone, however, must be considered when calculating solo or group hunting success: the web may be more efficient than the spiders in prey

capture (Jackson 1979). Social spiders such as *Agelena consociata*, whose webs are not sticky traps, would be superior subjects for comparison with other cooperative hunters (see Jackson 1979). In addition, the relative ease and ethical legitimacy with which spiders can be manipulated experimentally makes them potentially as important to sociobiology as *Drosophila* has been to genetics.

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