The Evolution of Courtship Behaviour in Spiders

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The mating behaviour of spiders has been divided into three phases: sperm induction, courtship, and copulation. Although recent studies (Helsdingen, 1965; Rovner, 1966, 1967a) indicate that sperm induction need not always precede courtship and copulation, these categories are generally valid. Courtship in spiders consists of a ritualized series of actions preparatory to mating that serve as releasers of similar actions in the mate. This paper is an attempt to elucidate the functions, forms, and phylogeny of spider courtship, and its implications for systematics.

The functions of courtship

Courtship is conspicuous to us (and presumably to spider predators and parasites), and places the participants in considerable danger. It must, therefore have a great selective advantage over passive male approach. To discern this advantage it is necessary to examine the functions of courtship.

Bristow (1926) assigns courtship two functions: 1) gaining recognition for the male, thereby suppressing the female's predatory instincts, and 2) stimulating the female. Savory (1928) and Crane (1949) take exception to this analysis, on the basis that no real recognition occurs and that suppression of predatory instincts is a necessary correlative of stimulation. Both views rightly stress the selective value of inhibiting cannibalistic tendencies; unfortunately, they present courtship as a one-sided activity — a display by the male having certain effects on the female.

Tinbergen (1954) concluded that vertebrate courtship is a releaser system — that display serves to release a response in another individual, which in turn releases other actions in the initiator, and so on. As he puts it.

"... the releaser system involves a specific responsiveness to particular releasers in the reacting individual as well as a specific tendency to send out the signals in the initiator. The releaser system ties individuals into units of a super-individual order and renders these higher units subject to natural selection (. 234)."

For example, courtship of male *Lycosa rabida* consists of an alternate series of display sequences (involving foreleg, palpal, and abdominal movements) and quiescent periods. Female display, though more restricted in scope, is equal in importance: if receptive, her forelegs are waved during the male's quiescent period, and she moves toward him. Her display has measurable effects on the male: the length of the quiescent period diminishes and the display movements are heightened in intensity (Rovner, 1967b, 1968a).

Similar behaviour has been observed in other lycosids and salticids, and it seems likely that female response of some sort is typically present — indeed, in species in which non-receptivity is indicated by agression, the females remaining motionless during certain periods may be just as specific a response and just as effective a releaser as an active display.

Tinbergen's analysis of the functions of vertebrate courtship can be applied to the situation in spiders; courtship functions in: 1) synchronizing mating activities, 2) orienting the individuals, 3) suppression of non-sexual tendencies, and 4) insuring species-specific mating. The important point is that the combination of these functions is of sufficient magnitude to overweigh the selective pressures against conspicuous display, and hence that courtship has evolved as a releaser system based on male-female interactions.

The forms of courtship

The known patterns of spider courtship seem to fall into three phylogenetic levels based on the prime releaser of male display — the factor or factors that must be present for the male to initiate courtship. As such, this division does not take into account the few instances of vacuum activity (males courting in isolation) which have been reported. The prime releaser on the first level is direct contact with the female; on the second level, chemotactic perception of silk and distance chemoperception of pheromones;

on the third level, sight of the female.

Level I.

Males of some mygalomorphs and haplogynes, and most members of the clubionid-thomisid line, respond only to direct contact with the female. The theraphosid male taps the female with his forelegs; she assumes a defensive posture, raising her carapace off the ground and spreading her fangs, which are often caught and held by spurs on the male's forelegs; he then bends her cephalothorax back, taps her sternum, and inserts his palps (Petrunkevitch, 1911; Baerg, 1928). Ctenizid and diplurid males will enter female webs and burrows, emerge, and wait for the female to follow; the courtship then corresponds with the theraphosid pattern (McKeown, 1936; Levitt, 1961; Buchli, 1962), Chemotactic perception of silk may be the prime releaser in these two families, but data are lacking and they are best regarded as intermediate.

Typical first level haplogyne courtship involves interplay of the forelegs and palps on contact, the female raising her cephalothorax, and the male creeping under her and inserting his palps. This type of courtship has been reported for species in *Scytodes* by Berland (1914), Gerhardt (1926), and Bristowe (1930, 1931, 1958); in *Oonops* and *Dysderina* by Bristowe (1930, 1958); in *Loxosceles* by Hite, et. al. (1966) and Galiano (1967); and in *Dysdera* by Petrunkevitch (1910), Cloudsley-Thompson (1949), and Cook (1965). It is only in *Dysdera* that we have evidence as to the prime releaser of male display: Berland (1912) reports that male *D. erythrina* are never aware of females until they touch; Cooke (1965) reports that male *D. crocata* placed in containers where females were recently housed showed no reaction (evidence against the use of chemical stimuli) and that males blinded with black wax courted and mated successfully.

Species in the clubionid-thomisid line have the least developed courtship of any spiders. The typical pattern involves contact, the male climbing over the female, pulling one side of her abdomen toward him, and inserting a palp. Often the male will seize a leg or the pedicel of the female in his chelicerae as he mounts; Bristow (1958) argues that this is an adaptation to avoid loss of the female. Courtship of the typical pattern has been reported for species in

the Heteropodidae by Bristowe (1958) and Crome (1962); in the Thomisidae by Gerhardt (1924, 1926), Bristowe (1930, 1931, 1958), Kaston (1936), Gertsch (1939), Mathew (1954), Leech (1966), and others; in the Gnaphosidae by Montgomery (1910), Nielsen (1931), and Bristowe (1958); and in the Clubionidae by Savory (1928), Nielsen (1931), and Bristowe (1958). Some species have a small amount of close-range visual display, usually of vibrating palps (Dondale, 1964, 1967). Some male crab spiders spin a "bridal veil" by attaching numerous strands of silk from the female's carapace to the substrate; this has been observed in several species of *Xysticus* by numerous authors and in one species of *Tibellus* by Kaston (1936). Also, a few clubionids and gnaphosids may recognise the silken retreats of females; male gnaphosids have been reported to build a retreat adjoining that of an immature female, wait until she molts, and then mate before her new cuticle dries and she regains her strength (Montgomery, 1910; Nielsen, 1931; Bristowe, 1958). The ctenids and anyphaenids, associated with the clubionid line, have a more active courtship involving rapid leg and abdominal vibrations (Tretsel, 1957; Bristowe, 1958; Melchers, 1963; Gertsch, 1949; Braun, 1958).

The lycosids and pisaurids seem to be intermediate between levels I and II. In some species, chemoperception is a sufficient cause of courtship display, in others touch seems to be necessary. The literature has been reviewed by Kaston (1936) and supplemented by Nappi (1965), Vlijm and Dijkstra (1966), Rovner (1966, 1967b, 1968a), Bhatnagar and Sadana (1966), Hallander (1967), and Harrison (1969). Lycosid display can involve chemical, visual, and auditory signals; each species seems to have a unique pattern. Visual display is often enhanced by epigamic coloration and structures on legs and palps. Auditory display, used by only a few species, is probably a recent adaptation to enable mating activities to continue through the night when visual display is useless.

Pisaura mirabilis males kill a fly, wrap it in silk, and carry the prey in their chelicerae. When a female is found, and begins feeding on the proffered fly, the male proceeds to mate (Gerhardt, 1923, 1924; Bristowe and Locket, 1926). Leighton (1969) has shown that the male catches and wraps the prey between 18 and 23 days after the final molt, whether

a female is present or not. Male *Dolomedes* do not wrap a fly, but usually wait until a female is feeding before mating (Bonnet, 1924; Gerhardt, 1926).

Level II.

Spiders at this level are characterized by the use of chemotactic stimuli or pheromones or both as prime releasers of male courtship behaviour. It is difficult to distinguish between these two phenomena; many cases in which a male placed in the former haunts of a female immediately began courting have been ascribed to pheromones, but are probably due to chemotactic recognition of female draglines. For this reason, no attempt is made here to discriminate between the two senses. Spiders on level II include some mygalomorphs and haplogynes, all the web-building labidognaths, and possibly such families as Ctenizidae, Dipluridae, Lycosidae, and Pisauridae, discussed above.

Atypid females build a tube web extending above and below the ground for a few inches. When discovering a tube, the male taps on it with his legs and palps; the receptive female remains motionless and the male tears the tube and enters. If the female is immature or has already mated, she tugs at the tube and the male withdraws. Unlike the typical mygalomorph embrace described above, the male presses the female flat against one wall of the tube (Bristowe, 1958; Clark, 1969).

Among the haplogynes, the segestriids, pholcids, and sicariids are probably on level II. Segestriid males shake the threads outside the female's retreat; when she appears, he darts underneath, seizes her pedicel with his chelicerae, forces her cephalothorax upward and mates (Gerhardt, 1921; Bristowe, 1930, 1958). Pholcid courtship consists of the male advancing on the female's web with body vibrations and leg interplay on contact (Montgomery, 1903; Bristowe, 1958). The sicariids are predominantly desert spiders that bury themselves under the sand. The male is a wanderer and probably detects the female by some kind of chemical stimuli; at any rate, he will stop and dig, expose the female, tap her body, and mate (Levi, 1967).

Males courting on female webs have two serious problems to cope with besides the danger of being taken as prey: many females will desert the male during courtship or copulation if prey lands on the web, and mating may be disrupted if another male wanders onto the web (Proszynski, 1961; Rovner, 1968b). These problems are solved by a variety of mating area reducing adaptations that restrict the mobility of the female.

The agelenids and amaurobiids have met these problems directly. The male drums on the web as he approaches; if receptive, the female remains motionless; when they touch, the female is seized by the leg or pedicel, carried toward the retreat, and forcibly thrown on her side (Montgomery, 1903; Bristowe, 1930, 1931, 1958; Nielsen, 1931; Gertsch, 1949; Gering, 1953). Gregg (1961) reports that copulation is interrupted for sperm induction in *Ixeuticus,* and Locket (1926) reports that the male of *Amaurobius similis* attaches a thread to the female's web and pulsates his abdomen, producing vibration over a far larger part of the web than does palpal drumming.

An orb-weaver male remains on the outskirts of the female's web, tweaks threads with the forelegs, slowly approaches the female, builds a series of "mating threads" onto the web, and tweaks these threads until the female is coaxed onto them for mating. In these families (Araneidae, Tetragnathidae), courtship is generally lengthy and copulation short. Saito (1931) and Bristowe (1958) report that *Araneus ventricosus* and *Meta segmentata* males wait until the female is wrapping prey before approaching. The observations of Czajka (1963), while not directly bearing on courtship, are too interesting from an evolutionary point of view to be omitted. Female *Ero furcata* are apparently capable of imitating the mating signals of male *Meta segmentata;* in two cases *Ero* climbed onto the mating threads spun by the male during courtship. The males fled and the female *Ero* began plucking the mating threads, and over a period of three hours approached and captured the female *Meta.* A few species of these families build no webs. *Pachygnatha* males have little courtship but seize and hold the female's chelicerae in their own; this corresponds with the situation in *Tetragnatha,* which do build webs but also employ this cheliceral mechanism and dispense with special mating threads (Bristowe, 1941). Similar mating threads spun by the male have been reported in the unrelated family Oecobiidae (Glatz, 1967).

The linyphiids, theridiids, and dictynids differ from the orb-weavers by more typically biting away

threads from the female's web then spinning additional ones (Locket, 1927). Many theridiids and linyphiids (and scattered species in other families) possess stridulating organs that are probably used to impart species-specific vibrations to the female's web; athough this has never been demonstrated, many species have palpal and abdominal movements in their courtship that could easily bring these organs into play. The vibrations of the male are often returned by the female, allowing him to find her easily (Locket, 1926). The most spectacular cases of web-biting occur in the Linyphiidae – in *Lepthyphantes leprosus* and *Linyphia triangularis* the surface of the web is often reduced more than 90% (Helsdingen, 1965; Rovner, 1968b). Not all species conform with this pattern; some theridiids and a few linyphiids spin mating threads similar to those of araneids (Gerhardt, 1927; Braun, 1961); the dictynids apparently include species with both patterns (Montgomery, 1903; Locket, 1926; Bristowe, 1958).

Level III

Three families, of two lineages, rely primarily on vision as a releaser of male display: Oxyopidae, Salticidae, and Lyssomanidae. The oxyopids have evolved from the lycosid-pisaurid line; the lysso-manids and salticids, closely related to each other, probably evolved from the clubionid-thomisid line but have no living close relatives. From the evolutionary history of the former line and the different levels of complexity of courtship in the present-day forms of the latter line, it is clear that these families have in the past had courtship resembling that of present-day level I and II species.

Oxyopid spiders can recognize their partners at four to six inches; many males have epigamically darkened palps which undoubtedly play a large role in this recognition. Each species has a particular sequence of foreleg, palpal, and abdominal move-ments; there is considerable leg interplay on contact; mating usually takes place with both spiders hanging on a thread (Gerhardt, 1927, 1933; Bristowe, 1963; Whitcomb and Eason, 1965).

The lyssomanids are often considered a subfamily of Salticidae, but the courtship indicates otherwise. The mutual display of *Lyssomanes bradyspilus* has been described by Crane (1949). The male poses with the carapace high for prolonged periods of time while the female watches. The courtship consists of retinal motions of the anterior median eyes. The retina, being black, contrasts with the green carapace; muscular activity causes contraction and expansion of the black area; the female responds in kind, releasing an increase in the rate of color shifts in the male, and so on, until contact is finally made.

Crane (1949) has published a masterful synthesis of material on salticid display; later work has merely corroborated her results. She identified two stages in salticid courtship; in the first, all the species-specific differences are expressed; in the second, all species agree in that the male approaches the female with his forelegs extended forward. Active female response to male display was recorded in at least nine genera. Most important, Crane distinguished three evolu-tionary levels of salticids: 1) species with low visual acuity, high dependence on chemotactic stimuli, relatively simple courtship and no threat display, 2) species with good visual acuity, intermediate dependence on chemotactic stimuli, complex court-ship and a threat display not differentiated from courtship, and 3) species with extreme visual acuity, minimal dependence on chemotactic stimuli, complex courtship (sometimes secondarily simplified) and separate courtship and threat displays. That these groups do not coincide with the current systematic division of salticid species, casts more suspicion on the taxonomy than on Crane's analysis.

The phylogeny of courtship

Two problems will be considered here: first, from what aspect of the behaviour of the primitive spider was courtship developed; and second, how have the epigamic modifications of color and structure of many species arisen and been perpetuated.

Three theories have been put forth to explain the origin of spider courtship. Montgomery (1910) felt that courtship evolved from motions of self-defense and movements arising from physiological excite-ment. Berland (1922, 1927) considered courtship an external manifestation of the male's physiological excitement alone. Bristowe (1929 and elsewhere) argues that courtship behaviour has evolved from chemotactic searching movements.

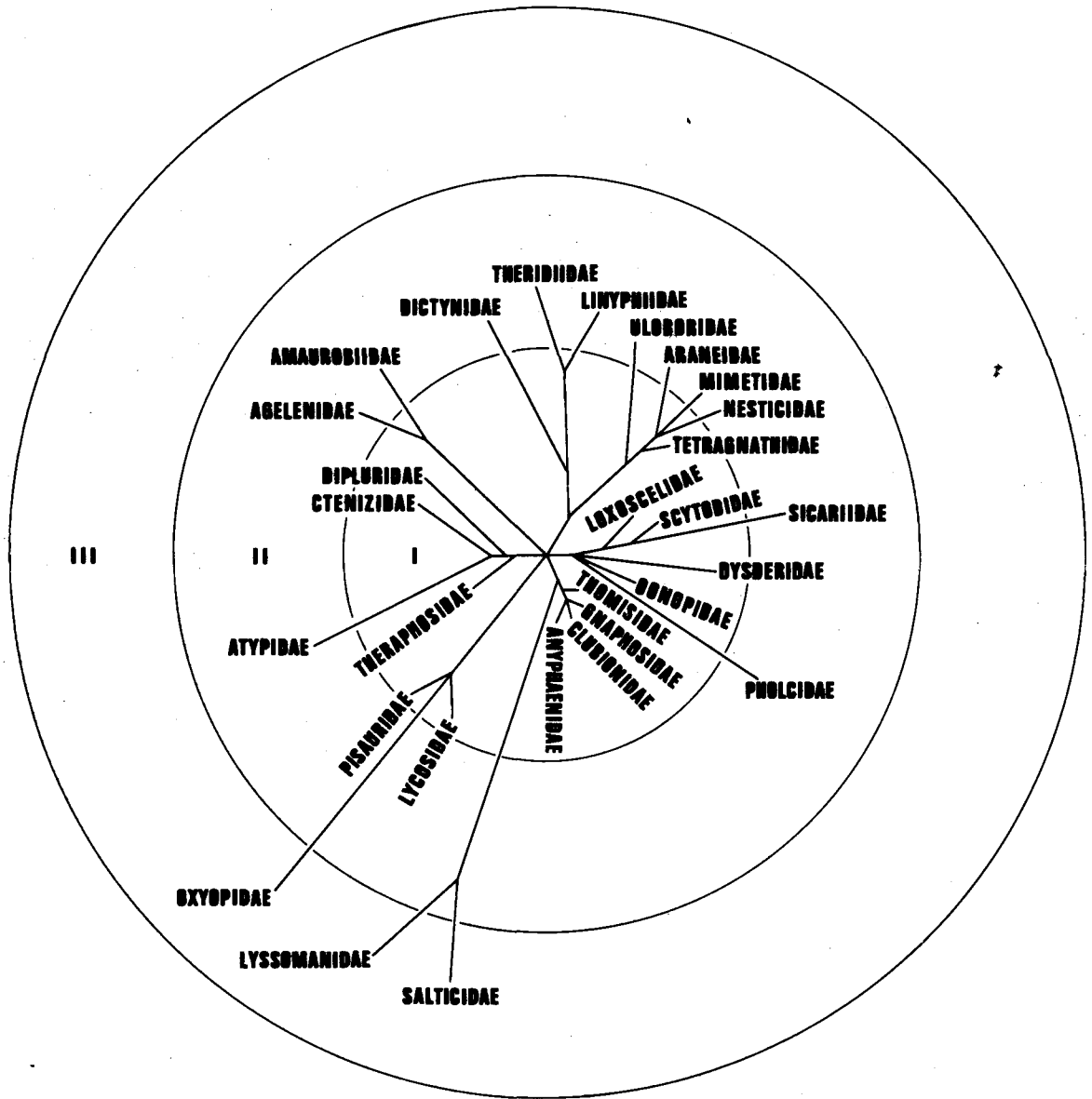The physiological excitement theory is unsup-ported by any evidence and appears nebulous.

FIGURE 1.

Possible phylogeny of the major Spider families
based on characteristics of courtship;
explanation in text.

Montgomery's self-defense theory is difficult to accept as these motions would hardly be made before contact of two primitive spiders (whose vision was almost certainly poor) and thus cannot be considered proto-courtship. All modern authors have agreed with Bristowe that courtship represents an exaggeration of ordinary chemotactic searching motions. This theory is supported by the fact that most of the living "primitive" spiders walk with their forelegs extended forward, occasionally tapping the ground with them. The possibility remains that courtship evolved from threat displays; both are really attempts to ward off intraspecific agression and it is likely that they developed together. That present-day mygalomorphs have radically different courtship and threat displays, and that some salticids lack threat displays, suggest a parallel rather than derivative origin, but these points are not conclusive.

On the origin of epigamic characters (modified structures or coloration used in mating), two major theories, those of Berland and the Peckhams, have been presented. Berland (1922, 1927), developing the theory cited above, felt that epigamic modifications are due simply to the extra vigor of the male. As Bristowe (1929) pointed out, this theory is deficient in that it cannot explain why these modifications are concentrated on specific parts of the body. If Berland's theory is correct, the modifications should be random instead of being concentrated on the forelegs and palps.

The Peckhams (1889, 1890) argued that these characters evolved by means of Darwinian sexual selection, i.e. that epigamic modifications are perpetuated because females are courted by a wide variety of males and themselves select the brightest, most outlandishly colored male and mate only with him, thereby keeping the selectively most disadvantageous genotypes in the gene pool. Although later authors hesitated to agree that the female consciously selects the most ornamented male, the theory did seem to contain some truth in that only sufficiently ornamented males seem capable of courting successfully. Further, while males will court virtually anything of the proper size (Drees, 1952), females will accept only males of their own species. Only after the work of Crane (1949) did it become clear that the level of activity of the male is far more important in determining reproductive success than

ornamentation; that the level of activity depends primarily on the length of time that has passed since the final molt and on daily fluctuations; and that almost all males are capable of success if they can court a receptive female at the height of their activity. When this is understood, one can accept the arguments of Bristowe (1929 and elsewhere) that natural selection is sufficient to account for epigamic modifications, in that the advantage they bring the male in speedy stimulation of the female and suppression of her predatory instincts far overweighs the disadvantage of conspicuousness.

Figure 1 shows a possible phylogeny of the major spider families in which the forms of courtship are known. The families within the inner circle are those placed on level I; those in the middle circle, on level II; and those in the outer circle, on level III. The branchings are not intended to represent evolutionary history in time, but merely the probable relationships of the groups involved. The cribellate families are tentatively placed in the lineages of ecribellate groups because it appears certain that at least in some cases ecribellate spiders have been derived from cribellate ancestors. Those families that cross the circles have a courtship intermediate in complexity or include species on both levels involved.

The implications of courtship for systematics

If our schemes of classification are to reflect the evolutionary history of organisms, it is clear that behaviour must be considered at least as important a character as morphology, if not more important, for, as Mayr points out, behaviour is the pacemaker of evolution:

> "A shift into a new niche or adaptive zone is, almost without exception, indicated by a change in behavior. The other adaptations to the new niche, particularly the structural ones, are acquired secondarily (1970, p. 363)."

If behaviour is an important systematic character, then courtship is one of the best, because it is in itself a method of reproductive isolation.

Courtship provides authoritative and useful characters on the specific, generic, and familial levels in spiders. The well-documented use of courtship to discover new species and authenticate older ones in such groups as *Philodromus* (Dondale, 1964, 1967),

Pardosa (Vlijm and Dijkstra, 1966), and *Theridion* (Braun, 1963, 1964) needs no comment here. Bristowe (1941, 1963) has ably demonstrated the usefulness of courtship as a generic character in lycosids, and it is made even more useful by the good predictive value of epigamic modification in tentatively assigning a probable type of courtship to preserved material. The work of Crane (1949) has shown us where to begin on the important task of reclassifying the salticids on the basis of their biology rather than the number of teeth on the cheliceral retromargin. Finally courtship can be used to validate some familial groupings, for example, in the Anyphaenidae and Lyssomanidae.

Acknowledgements

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