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Stratton, Gail E.; Hebets, Eileen; Miller, Patricia R.; and Miller, Gary L., "PATTERN AND DURATION OF COPULATION IN WOLF SPIDERS (ARANEAE, LYCOSIDAE)" (1996). *Eileen Hebets Publications*. 5.
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PATTERN AND DURATION OF COPULATION IN WOLF SPIDERS (ARANEAE, LYCOSIDAE)

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ABSTRACT. The temporal patterns of insertion of male palps, expansion of the hematodocha and duration of copulation are reported for 10 species of *Schizocosa* Chamberlin 1904, three species of *Rabidosia* Roewer 1955, one species of *Gladicosa* Brady 1986, one species of *Hogna* Simon 1885, two species of *Isohogna* Roewer 1960, one species of *Trochosa* C.L. Koch 1848, one species of *Geolycosa* Montgomery 1904, two species of *Arctosa* C.L. Koch 1848, three species of *Alopecosa* Simon 1885 and six species of *Pardosa* C.L. Koch 1847. In all species of *Schizocosa* examined so far, males showed a pattern composed of a series of insertions with one palp followed by a switch to the opposite side and a separate series of insertions with the other palp. During each insertion there was a single expansion of the hematodocha. These copulations generally lasted from 1–4 hours. Males of *Gladicosa bellamyi* (Gertsch & Wallace 1937) and *Hogna georgicola* (Walckenaer 1837) likewise showed a series of insertions on one side followed by insertions on the other side, with a single expansion of the hematodocha with each insertion. Males of *Arctosa littoralis* (Hentz 1844), *A. sanctaerosae* Gertsch & Wallace 1935 and *Geolycosa rogersi* Wallace 1942 each copulated by alternating palps with a single insertion and single expansion of the hematodocha. The alternating pattern of insertions was also seen in *Rabidosia rabida* (Walckenaer 1837), *R. hentzi* (Banks 1904) and *R. punctulata* (Hentz 1844). *Isohogna lenta* (Hentz 1844) (a single individual) alternated between multiple expansions of the hematodocha during one insertion and alternating sides with a single insertion and expansion per side. A second member of *Isohogna* showed a single insertion on one side with multiple expansions of the hematodocha. Comparisons with published descriptions of copulatory pattern suggest that *Schizocosa* and *Trochosa* Koch 1848 may form a monophyletic clade in the “*Trochosa* group” of the Lycosinae. The copulations that involved multiple insertions of the male’s palp on one side with a single expansion per insertion were long copulations (1–4 hours). This may provide for multiple opportunities of *in copula* courtship. *Arctosa* copulations were very short (18–46 sec), while the *Geolycosa* copulations were relatively short (5–7 min). Thus, the copulations of the burrowing spiders were much shorter than the nonburrowing spiders.

Copulatory behavior in spiders has long fascinated arachnologists (Clerck 1757 in Kaston 1936; Montgomery 1903, 1909; Britton 1926; Gerhardt & Kaestner 1937; Savory 1928; other references in Bonnet 1945; Robinson 1982) partly because there is an impressive array of copulatory positions and patterns. Also, in spiders, the potential for sexual cannibalism exists (Arnqvist 1992; reviewed in Elgar 1992), strongly reinforcing the need for clear communication both before and dur-

ing copulation. Although there have been numerous studies on copulatory behavior in a variety of spiders, relatively few have focused on the patterns of insertion of the male palp during copulation in the Lycosidae (Engelhart 1964; Rovner 1973, 1974; Costa & Sotelo 1994). We here present the patterns of palpal insertion, hematodochal expansion and duration of copulation seen in numerous lycosid species. We also present the first attempt to look at these behaviors in spiders in a phylogenetic context.

In wolf spiders (Lycosidae), the male mounts the female so that they face opposite directions, and the ventral surface of the anterior portion of the male’s prosoma is against

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the dorsal surface of the female's abdomen. The relative positions of males and females in *copula* were described by Gerhardt & Kaestner (1937) who categorized five different copulatory positions for spiders. The position described for wolf spiders (above) is also seen in pisaurid genera *Thalassius* Simon 1885 (Sierwald 1988), *Dolomedes* Latreille 1804 (Arnqvist 1992), and *Pisaurina* Simon 1898 (Bruce & Carico 1988) and Agelenidae (Fraser 1986; Gering 1953; Foelix 1982), as well as most "advanced" wandering spiders, including Philodromidae, Clubionidae and Salticidae (Foelix 1982). The *Pisaurina* shows the same position, but with both spiders hanging from a silken thread during copulation.

Once mounted, the lycosid male touches the anterior end of the female's abdomen, causing her to rotate the abdomen. He then scrapes the side of the female's abdomen with his palp, and most times the palp engages with the epigynum apparently by the median apophysis of the palp catching on the epigynal hood (unpubl. data, based on examination of high magnification videorecording from the ventral aspect of *Schizocosa* sp. nr. *crassipes* [Walckenaer 1837]). The right palp engages with the right side of the epigynum; the left palp engages the left side. Once engaged, the male expands the hematodocha which causes the embolus to coil into the female's copulatory duct and at some point, sperm is transferred. The timing of sperm transfer in groups with multiple insertions or with multiple hematodochal inflations has never been determined for any species. We call the physical act of the coupling of the male palp with the female epigynum an "insertion". The hematodocha may expand one or more times during a single insertion. If the male spider inserts the same palp multiple times before switching sides, a "series" of insertions or "multiple insertions" occurs (Rovner 1974).

Behavior has provided useful characters in the phylogenetic studies of the Lycosoidea clade. Carico (1986, 1993) looked at method of egg sac transport, structure of egg sac seam, method of maternal care, silking of female during copulation, the structure of the web retreat, reattachment of the egg sac, as well as the structure of the nursery web. Merrett (1988) used several behavioral traits in placing *Ancyclometes bogotensis* (Keyserling 1876) in the Pisauridae. Griswold (1993) used two behavioral characters (nursery web and

method of egg sac transport) in his phylogenetic analysis of Lycosoidea. Copulatory pattern has not yet been used in phylogenetic constructions as it has been reported only for a few species outside of the Lycosidae.

In 1973, Rovner suggested that Gertsch & Wallace's (1937) placement of *Schizocosa avida* (Walckenaer 1837) into the genus *Schizocosa* was supported by the copulatory pattern demonstrated by that species (Rovner 1973). Rovner noted that the pattern of palpal insertions in *Rabidosa rabida* was qualitatively distinct from the patterns demonstrated by *Schizocosa*, particularly *S. saltatrix* (Hentz 1844) observed by Rovner (1972) and *S. bilineata* (Emerton 1885) and *S. ocreata* (Hentz 1844) observed by Montgomery (1903). This was the first time copulatory behavior was used to investigate taxonomic placement in *Schizocosa*. Costa & Sotelo (1994) provided a brief review of copulatory patterns in wolf spiders and suggested that generally there are few differences in copulatory patterns among closely related species, but the differences become more notable at higher taxonomic levels.

We here report on the patterns of palpal insertion, hematodochal expansion, and copulation duration that we have observed in 10 species of *Schizocosa*. For many of these, we have observed copulatory behavior in several populations from a wide geographic range. We also report on the copulatory pattern seen in eight other North American lycosid species representing five genera. Additional data are provided for *Pardosa*, *Hogna*, *Geolycosa* (Dondale & Redner unpubl. data), for *Sosipus* Simon 1888 (Rovner unpubl. data) and for *Alopecosa* and *Hygrolycosa* Dahl 1908 (Kronstedt 1979, unpubl. data) and are discussed in the context of our observations. While this is still a relatively small proportion of the 2200 species of wolf spiders that exist worldwide (Coddington & Levi 1991), the patterns observed so far warrant some discussion. We also hope this report may stimulate other researchers to examine more species of lycosids for patterns in copulatory behavior.

METHODS

Wolf spiders were collected throughout the southeastern USA during the spring, summer and fall of 1993, 1994, 1995 and in the spring of 1996. Immature and mature individuals

were returned to the laboratory at the University of Mississippi where they were individually maintained in vials (8.5 cm × 5 cm) with wicks that extended into a water tray providing a constant source of moisture. Appropriately sized crickets were offered twice weekly as food for the spiders. Temperature in the laboratory ranged from 22–25 °C. Temperature during copulation was 22–25 °C. Spiders were kept on an L:D schedule of 14:10. Animals were only used once in a courtship/copulation observation and were generally used a few days to a few weeks after collection.

Courtship and copulation were observed for most species by setting the female in a culture dish with a piece of filter paper 6–12 hours before observations. Males and females were then placed with the filter paper in an observation chamber where their interactions were videotaped using a Panasonic HD-5000 video-camera with a 105mm Macrolens. *Arctosa* species and *Geolycosa rogersi* were observed by placing the female in a clear plastic cup with sand and allowing her to burrow. A day after she burrowed, a male was introduced and the interactions on the surface of the sand were videorecorded through the clear plastic cup. In some instances only the first half-hour of copulation was video-recorded. In these instances the copulating pair was watched to note the duration of copulation. The end of copulation was taken at the moment when the spiders physically separated.

Vouchers of all species studied are deposited at the Mississippi Entomological Museum at Mississippi State University, Mississippi State, Mississippi. Table 1 summarizes the species and collecting localities for all individuals used in this study. Observations by Dondale and Redner were field observations made shortly after the spiders were collected. Localities for these species are provided in Table 2. Additional observations were provided by T. Kronstedt and J. Rovner. The cladograms were produced using the computer program MacClade (Maddison & Maddison 1992).

RESULTS

Copulatory pattern, intraspecific variation.—The overall pattern of palpal insertion and hematodochal expansion showed little intra-specific variation in the species where we

were able to observe multiple individuals (*S. crassipes*, *S. duplex*, *S. ocreata*, *S. nr ocreata*, *S. retrorsa* and *G. rogersi*; Tables 1, 2), suggesting that there is not much variability in the overall pattern within a species when the first hour of copulation is observed. However, we also observed a few instances in which a male mounted a female facing the wrong direction or was unable to engage the palp in the epigynum apparently because his position was wrong. *Hogna helluo* (Walckenaer 1837) showed some variability in insertion pattern (Nappi 1975; Dondale & Redner unpubl.; Table 2), and one observation of the insertion pattern of *Rabidosia rabida* was inconsistent with other studies (Kaston 1936; compare with Montgomery 1903; Table 2). These observations suggest that conclusions of patterns based on single observations warrant some caution.

Copulatory pattern, interspecific variation.—Copulatory patterns varied both in the number of insertions on a side as well as the number of expansions of the hematodocha per insertion when different species were compared (Table 2; Figs. 1, 2). In four of the six *Pardosa* species observed by Dondale & Redner, members of the subfamily Pardosinae showed a single insertion on a side but with multiple expansions of the hematodocha with each insertion (Dondale & Redner unpubl. data; Table 2). In the subfamilies Sosippinae, Venoniinae and Allocosinae, all examples so far (four species total) demonstrate single insertions of the palps and multiple expansions of the hematodocha.

In the “*Lycosa* group” of the subfamily Lycosinae (as defined by Dondale 1986), *Arctosa littoralis* and *A. sanctaerosae* both showed a single insertion with a single expansion of the hematodocha. Both of these species are burrowing spiders, although only the latter is an obligate burrower. *Alopecosa* spp. and *Hygrolycosa* sp. both demonstrated single insertions of the palps with many expansions of the hematodocha (Kronstedt 1979 and pers. comm.).

In the “*Trochosa* group” of the Lycosinae there is remarkable consistency in *Schizocosa* species: 12 species examined to date demonstrated the pattern of multiple insertions on a side with a single expansion per insertion (Table 2; Figs. 1, 2). The 12 species of *Schizocosa* are from four different species groups within the genus (Stratton unpubl. data). This pattern held

Table 1.—Summary of taxa observed in this study. Collection locality (state and county) and dates are provided as are number of trials, courtships and copulations observed. (MS = Mississippi, AL = Alabama, FL = Florida, LA = Louisiana, OH = Ohio, TX = Texas, KY = Kentucky).

Species name	Locality	Date collected	Date of observations	# of trials/ # copulations
<i>Arctosa littoralis</i> (Hentz 1844)	MS. Grenada Co.	21 May 1994	9 June 1994	2/1
<i>Arctosa sanctaerosae</i> Gertsch & Wallace 1935	AL. Baldwin Co.	13 May 1994	19 May 1994	1/1
<i>Geolycosa rogersi</i> Wallace 1942	MS. Lafayette Co.	17, 23 March 1996	19 April 1996	3/3
<i>Gladicosa bellamyi</i> (Gertsch & Wallace 1937)	MS. Washington Co.	9 April 1993	29 April 1993	2/1
<i>Hogna georgicola</i> (Walckenaer 1837)	FL. Alachua Co.	4 May 1993	28 June 1993	1/1
<i>Isohogna</i> sp. A	AL. Baldwin Co.	13 May 1994	19 May 1994	4/1
<i>Isohogna lenta</i> (Hentz 1844)	MS. Marshall Co.	2 June 1994	14 June 1994	2/1
<i>Rabidoso hentzi</i> (Banks 1904)	AL. Baldwin Co.	14 May 1994	19 May 1994	8/2
<i>Rabidoso punctulata</i> (Hentz 1944)	MS. Tate Co.	25 Oct. 1995	20 Nov. 1995	2/1
<i>Rabidoso rabida</i> (Walckenaer 1837)	LA. Cameron Parish	22 May 1993	2 July 1993	2/1
<i>Schizocosa avida</i> (Walckenaer 1837)	MS. Marshall Co.	1 June 1993	26, 28 June 1993	5/2
<i>S. crassipes</i> (Walckenaer 1837)	FL. Alachua Co.	4 May 1993	4 June 1993	12/1
<i>Schizocosa</i> sp. nr. <i>crassipes</i>	MS. Grenada Co.	13 April 1995	18–31 May 1995	10/5
	TX. Nacogdoches Co.	12 April 1995	5 June 1995	2/2
<i>S. duplex</i> Chamberlin 1925	FL. Santa Rosa Co.	21 March 1995	April 1995	10/4
<i>S. floridana</i> Bryant 1934	FL. Alachua Co.	3 May 1993	9 May 1993	1/1
<i>S. ocreata</i> (Hentz 1844)	FL. Alachua Co.	3 May 1993	9 May 1993	
	OH. Clermont Co.	Fall 1994	Dec. 1994	53/26
<i>Schizocosa</i> sp. nr. <i>ocreata</i>	MS. Washington Co.			
	Stoneville Woods	14 April 1995	19–31 May 1995	10/8
	Leroy Percy St. Pk.	13 April 1995	19–31 May 1995	10/8
<i>S. retrorsa</i> (Banks 1911)	MS. Marshall Co.	29 June 1993	8 July 1993	5/1
	MS. Lafayette Co.	28 April 1993	30 June 1993	5/1
<i>S. stridulans</i> Stratton 1991	KY. Powell Co.	16–23 June 1993	29 June 1993	2/1
<i>S. saltatrix</i> (Hentz 1844)	MS. Lafayette Co.	10 March 1993	20–21 April 1993	22/1
<i>Schizocosa</i> sp. nr. <i>saltatrix</i>	MS. Adams Co.	9 April 1993	16–23 April 1994	4/2
<i>Schizocosa</i> n. sp.	MS. Lafayette Co.	15 June 1993	13 July 1993	5/2
	LA. Natchitoches Par.	23 May 1993	10 July 1993	5/3
<i>Trochosa avara</i> Keyserling 1877	MS. Tate Co.	25 Oct. 1995	Nov. 1, 1995	3/1

true for all instances where numerous populations were observed (Table 2). This pattern is consistent with four species of *Trochosa* studied by Engelhart (1964) in Europe. However, in *Trochosa avara* Keyserling 1877 (single observation from southeastern USA), we observed multiple insertions of each palp and multiple ex-

pansions of the hematodocha without disengaging. The failure to disengage the palp before each expansion made this individual different from the *Schizocosa* species and other *Trochosa* species. More observations on *Trochosa avara* and on the other North American *Trochosa* species are needed.

There was more variability in *Hogna* species than the *Schizocosa* species (Dondale & Redner unpubl. data; Table 2; Figs. 1, 2). *Hogna helluo*, *H. aspersa* (Hentz 1844), and *H. frondicola* (Emerton 1885) each showed a single insertion on a side (expansions of hematocha not recorded); *H. radiata* showed multiple insertions with one expansion per insertion, as did *H. georgicola* and one example of *H. helluo*.

There was also variability in the *Geolycosa* species although the number of observations are still relatively few for this genus. *Geolycosa rogersi* showed a single insertion on a side with a single expansion of the hematocha (Table 2). *Geolycosa domifex* (Hancock 1899) performed multiple insertions on each side. The number of hematochal expansions was not observed (Dondale & Redner unpubl. data).

The *Rabidosia* spp. and *Gladicosa gulosa* (Walckenaer 1837) showed a single insertion on a side and a single expansion of the hematocha. *Gladicosa bellamyi* showed multiple insertions on a side with a single expansion per insertion. *Isohogna lenta* (a single individual) switched between a single insertion with one expansion, and multiple insertions with multiple expansions, making it the most variable individual observed in this study. A second species of *Isohogna* (species A) showed multiple insertions with multiple expansions.

Duration of copulations.—Within the “*Trochosa* group” copulations ranged in duration from 5 min for *Geolycosa domifex* and *G. rogersi* to over 8 h for *S. saltatrix*. The *Schizocosa* spp. ranged from 1–8 h with most values from 1–4 h (Table 2); *Trochosa* spp. ranged from 20 min–6 h 48 min. The copulations for *Hogna* species were all longer than 1 h except for a single observation reported by Kaston (1936).

Within the “*Lycosa* group” the *Arctosa* spp. both showed very short copulations (18–33 sec). There was variability in the durations of copulation reported on and observed in *Gladicosa* spp. (short times reported by Kaston for *G. gulosa*; a longer time was observed for *G. bellamyi*). Copulation duration for *Rabidosia* spp. ranged from 25 min–1 h 30 min.

DISCUSSION

Comparisons between subfamilies of Lycosidae.—Costa & Sotelo (1994) reported

that there appears to be some consistency in the copulatory pattern within the lycosid subfamilies identified by Dondale (1986). For example, in the Sosippinae, Venoniinae, and Allocosinae, the three most basal subfamilies, all known examples showed a single insertion on a side with multiple expansions of the hematocha (see Figs. 1, 2). These examples included *Porrmosa lagotis* (Holmberg 1876), subfamily Sosippinae (Costa 1982 in Costa & Sotelo 1994); *Pirata Sundevall* 1833 sp., subfamily Venoniinae (Gerhardt 1924 in Costa & Sotelo 1994); and *Allocosa* Banks 1900 sp. subfamily Allocosinae (Costa unpubl. data).

Costa & Sotelo (1994; see also Kaston 1936) summarized five examples of copulatory pattern in the Pardosinae. These examples all showed a single insertion on a side but the authors did not report the number of expansions. Dondale & Redner (unpubl. data) added six more species in *Pardosa*; with two exceptions these showed single insertions with multiple expansions (Figs. 1, 2). This suggests that no one pattern characterizes this genus and subfamily and that there is more variability than noted by Costa & Sotelo (1994).

The Lycosinae, the most derived subfamily according to Dondale’s 1986 study, stands out in having all combinations of insertions and expansions (Figs. 1, 2). The vast majority of the studies of insertion pattern have been in Lycosinae. It appears that when numerous studies are available at the subfamily level, there is variability in copulatory pattern. Clearly, more studies are needed in the other subfamilies of lycosids to more fully understand the evolution of patterns of copulation.

Comparisons within the Lycosinae.—Dondale (1986) suggested that the Lycosinae can be subdivided into two groups based on palpal characteristics: the “*Lycosa* group” (including *Lycosa* Latreille 1804 [Europe only], *Arctosa*, *Alopecosa*, *Varacosa* Chamberlin & Ivie 1942 and *Hygrolycosa*); and the “*Trochosa* group” (including *Trochosa*, *Hogna*, *Geolycosa*, *Schizocosa*, *Gladicosa*, and *Rabidosia*). Within species of the “*Lycosa* group” (six species examined in this study) all individuals demonstrated single insertions on a side, but there was variability in the number of expansions (Table 2). Within species of the “*Trochosa* group” (33 species examined in this study), there was the consistent pattern noted for species of *Schizocosa* and most of

Table 2.—Pattern of palpal insertion and duration of copulation for many Lycosoidea, including Ctenidae, Pisauridae and Lycosidae plus examples from the Amaurobiidae and the Agelenidae. This table includes examples from the literature, unpublished observations by C. Dondale, J. Redner, J. Rovner and T. Kronstedt, in addition to the species observed by us. Initials for state localities as in Table 1. Sample sizes for durations are $n = 1$ unless otherwise noted by multiple entries or by means. Notes in table are as follows. ¹The pattern of expansions of hematodocha not stated for *Ancyclometes* and *Thalassius*. ²*Pardosa dromaea* showed multiple “pulses while the hematodocha remained expanded” (Dondale & Redner unpubl. data). ³For *Alopecosa* and *Hygrolycosa*, for each palpal application, numerous hematochochal swellings occurred. There was no disengagement of the palp between the numerous swellings, (Kronstedt, pers. comm.). ⁴Expansions not observed for some observations of *Hogna helluo*, nor for observations of *Hogna aspersa*, *Hogna frondicola*, *Hogna radiata*, *Schizocosa avida* (Ontario), *Schizocosa communis* and *Geoloycosa domifex*, (Dondale & Redner, unpublished data). ⁵In *Rabidososa rabida*, “contrary to Montgomery’s observation, there was not always strict alternation in the use of the palps” (Kaston 1936). ⁶For *Hololena adnexa* “each palpus was used in a single long series of insertions” (Fraser 1986), number of expansions per insertion not specified.

Species, location of study, source	Number of insertions on a side before switching sides		Number of expansions of hematodocha per insertion		Duration
	one	more than one	one	more than one	
Family Ctenidae					
<i>Cupiennius salei</i> Melchers 1963	XX		XX		25 min
Family Pisauridae					
<i>Pisaurina mira</i> Bruce & Carico 1988	XX		XX		
<i>Ancyclometes bogotensis</i> ¹ Merrett 1988	XX				10–15 min
<i>Thalassius spinosissimus</i> ¹ Sierwald 1988	XX				
<i>Dolomedes tenebrosus</i> Sierwald and Coddington 1988	XX				4–5 min
<i>Dolomedes scriptus</i> ($n = 4$) CT. New Haven Co. Kaston 1936	XX				5, 15, 20, 30 sec
<i>Dolomedes fimbriatis</i> ($n = 3$) Gerhardt 1926	XX		XX		
<i>Pisaura mirabilis</i> ($n = 3$) Gerhardt 1923	XX		XX		
Family Lycosidae, Subfamily Sosippinae					
<i>Sosippus janus</i> Rovner unpubl. data	XX		XX		
<i>Porrmosa lagotis</i> Costa 1982 in Costa & Sotelo 1994	XX		XX		
Family Lycosidae, Subfamily Venoniinae					
<i>Pirata</i> spp. Gerhardt 1924 in Costa & Sotelo 1994	XX		XX		
Family Lycosidae, Subfamily Allocosinae					
<i>Allocoa</i> sp. Costa unpubl.	XX		XX		

Table 2.—Continued.

Species, location of study, source	Number of insertions on a side before switching sides		Number of expansions of hematodocha per insertion		Duration
	one	more than one	one	more than one	
Family Lycosidae, Subfamily Pardosinae					
<i>Pardosa concinna</i> Colorado Dondale & Redner unpubl. 1983	XX		XX		15 min
<i>Pardosa fuscula</i> Ontario Dondale & Redner unpubl. 1983	XX		XX		15 min
<i>Pardosa mackenziana</i> Ontario Dondale & Redner unpubl.	XX		XX		60 min
<i>Pardosa groenlandica</i> Quebec Dondale & Redner unpubl. 1972	XX		XX		42 min
Colorado ($n = 3$) Montana Dondale & Redner unpubl. 1985	XX	XX	XX	XX	20, 68 & 15 min 45 min
<i>Pardosa dromaea</i> ² Alberta Dondale & Redner unpubl. 1985	XX		XX		25–30 min
<i>Pardosa amentata</i> ($n = 3$) Gerhardt 1923	XX		XX		
Family Lycosidae, Subfamily Lycosinae, "Lycosa group"					
<i>Alopecosa pulverulenta</i> ³ Sweden Kronestedt 1979	XX			XX	
<i>Alopecosa aculeata</i> Sweden Kronestedt 1979	XX			XX	
<i>Alopecosa taeniata</i> Sweden Kronestedt 1979	XX			XX	
<i>Arctosa littoralis</i> MS. Grenada Co. this study	XX		XX		18 sec
<i>Arctosa sanctaerosae</i> AL. Baldwin Co. this study	XX		XX		46, 33 sec
<i>Hygrolycosa rubrofasciata</i> ³ Sweden Kronestedt 1979	XX			XX	
Subfamily Lycosinae, "Trochosa group"					
<i>Geolycosa domifex</i> ⁴ Canda, Ontario Dondale & Redner 1990		XX			5 min
<i>Geolycosa rogersi</i> ($n = 3$) this study	XX		XX		$\bar{x} = 7$ min 9 sec

Table 2.—Continued.

Species, location of study, source	Number of insertions on a side before switching sides		Number of expansions of hematodocha per insertion		Duration
	one	more than one	one	more than one	
<i>Gladicosa bellamyi</i> MS. Washington Co. this study		XX	XX		1 hr 15 min
<i>Gladicosa gulosa</i> CT. New Haven Co. Kaston 1936	XX		XX		10 min, 30 min
<i>Hogna georgicola</i> FL. Alachua Co. this study		XX	XX		58 min
<i>Hogna helluo</i> CT. New Haven Co. Kaston 1936	XX		XX		8 min
CT. Central Ct. State Coll. Nappi 1965			XX		
Dondale & Redner unpubl. ⁴	XX	XX			1 h + 1 h 45 min
<i>Hogna aspersa</i> Dondale & Redner unpubl. ⁴	XX				
<i>Hogna frondicola</i> Dondale & Redner unpubl. ⁴	XX				2 h 45 min
<i>Hogna radiata</i> (Europe) Dondale & Redner unpubl. ⁴		XX	XX		1 h 3 min
<i>Isohogna</i> sp. A AL. Baldwin Co. this study		XX		XX	30 min
<i>Isohogna lenta</i> MS. Marshall Co. this study	XX		XX		
<i>Rabidosia hentzi</i> AL. Baldwin Co. this study	XX		XX		25 min, 40 min
<i>Rabidosia punctulata</i> OH. Athens Co. Rovner unpubl. data	XX		XX		
MS. Tate Co. this study	XX		XX		
<i>Rabidosia rabida</i> MS. Lafayette Co. this study	XX		XX		1 h 30 min
OH, Athens Co. Rovner 1972	XX		XX		1 h
CT, New Haven Co. ⁵ Kaston 1936; Montgomery 1903	XX	XX	XX		71 min
<i>Schizocosa avida</i> MS. Marshall Co. this study		XX	XX		2 h 15 min
OH. Athens Co. Rovner 1973		XX	XX		
Ontario Dondale & Redner unpubl.		XX			2 h 55 min

Table 2.—Continued.

Species, location of study, source	Number of insertions on a side before switching sides		Number of expansions of hematodocha per insertion		Duration
	one	more than one	one	more than one	
<i>Schizocosa bilineata</i> Montgomery 1903		XX	XX		
<i>Schizocosa communis</i> Ontario Dondale & Redner unpubl. 1966 ⁵		XX			1 h 3 min
<i>Schizocosa crassipes</i> FL. Alachua Co. this study		XX	XX		
<i>Schizocosa</i> sp. nr. <i>crassipes</i> MS. Grenada Co. this study ($n = 5$)		XX	XX		$\bar{x} = 2\text{h } 24\text{ min}$
MS. Claiborne Co. this study		XX	XX		4 h 35 min
TX. Nacogdoches Co. this study ($n = 2$)		XX	XX		
<i>Schizocosa duplex</i> FL. Santa Rosa Co. this study ($n = 4$)		XX	XX		$\bar{x} = 1\text{ h } 31\text{ min}$
<i>Schizocosa floridana</i> FL. Alachua Co. this study ($n = 2$)		XX	XX		3 h 31 min
<i>Schizocosa ocreata</i> FL. Alachua Co. this study		XX	XX		3 h 30 min, 2 h 28 min
OH. Hocking Co. Stratton & Uetz 1983		XX	XX		1–4 h
OH. Brown Co. Stratton & Uetz 1983		XX	XX		1–4 h
OH. Clermont Co. this study ($n = 26$)		XX	XX		$\bar{x} = 3\text{ h } 28\text{ min}$
<i>Schizocosa</i> sp. nr. <i>ocreata</i> MS. Washington Co. this study (Stoneville, Leroy Percy) ($n = 15$)		XX	XX		$\bar{x} = 2\text{ h } 17\text{ min}$
MS. Adams Co. this study		XX	XX		1 h 40 min
<i>Schizocosa retrorsa</i> MS. Marshall Co. this study		XX	XX		2 h 30 min
MS. Lafayette Co. this study		XX	XX		2 h 40 min
<i>Schizocosa rovneri</i> KY. Boone Co. Stratton & Uetz 1983		XX	XX		1–4 h
<i>Schizocosa saltatrix</i> MS. Lafayette Co. this study		XX	XX		>8 h
OH. Athens Co. Rovner 1973, 1974		XX	XX		$\bar{x} = 2\text{ h } 48\text{ min}$

Table 2.—Continued.

Species, location of study, source	Number of insertions on a side before switching sides		Number of expansions of hematodocha per insertion		Duration
	one	more than one	one	more than one	
<i>Schizocosa</i> sp. nr. <i>saltatrix</i> MS. Adams Co. this study (<i>n</i> = 2)		XX	XX		
<i>Schizocosa stridulans</i> MS. Lafayette Co. this study		XX	XX		
IL. Mason Co. Stratton unpubl.		XX	XX		
<i>Schizocosa</i> n. sp. MS. Lafayette Co. this study (<i>n</i> = 2)		XX	XX		1 h 55 min, 1 h 55 min
LA. Natchitoches Parish this study (<i>n</i> = 2)		XX	XX		1 h 30 min, 2 hr 10 min
<i>Trochosa avara</i> MS. Tate Co. this study		XX		XX	
<i>Trochosa terricola</i> Engelhardt 1964		XX	XX		\bar{x} = 2 h 9 min
<i>Trochosa ruricola</i> Engelhardt 1964		XX	XX		\bar{x} = 20 min
<i>Trochosa spinipalpis</i> Engelhardt 1964		XX	XX		\bar{x} = 1 h 32 min
<i>Trochosa robusta</i> Engelhardt 1964		XX	XX		\bar{x} = 2 h 24 min (max 6 h 48 min)
Family Amaurobiidae					
<i>Ixeuticus martius</i> Costa 1993		XX	XX		2 h 24 min
<i>Amaurobius ferox</i> (<i>n</i> = 2) Gerhardt 1923	XX		XX		
<i>Amaurobius fenestralis</i> Gerhardt 1924a	XX		XX		
<i>Titanoeca quadriguttata</i> (<i>n</i> = 2) Gerhardt 1928	XX		XX		
Family Agelenidae					
<i>Hololena adnexa</i> ⁶ Fraser 1986		XX	XX		
<i>Histopona torpida</i> Gerhardt 1927	XX			XX	
<i>Coelotes atropos</i> (<i>n</i> = 2) Gerhardt 1928	XX		XX		

the *Trochosa* but variability in the copulation pattern in *Hogna*, *Isohogna*, and *Geolycosa* (Table 2; Figs. 1, 2). With the exception of a single individual observed by Kaston (1936),

the *Rabidosa* were consistent with alternating insertions and a single expansion.

Comparisons with other Lycosoidea.—The sister group to the Lycosidae is currently

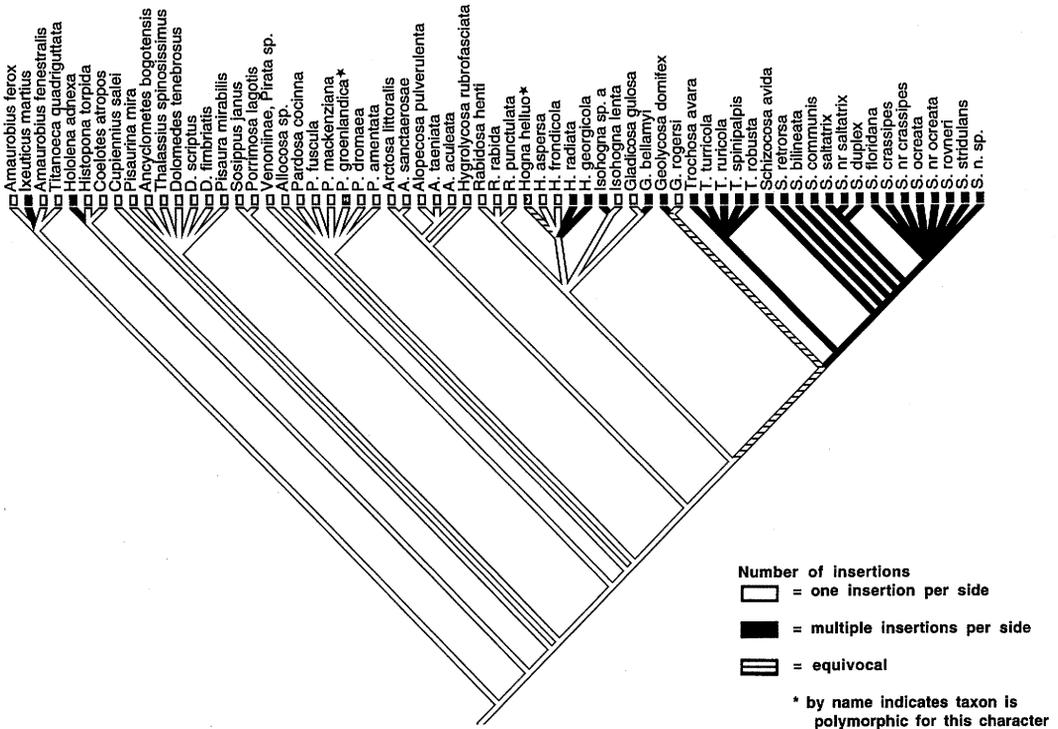


Figure 1.—Phylogeny of Lycosoidea (based on Griswold 1993; Carico 1993; Sierwald 1990), subfamilies of Lycosidae (based on Dondale 1986) plus Agelenidae and Amaurobiidae (from Coddington & Levi 1991) with overlay of pattern of insertion. The arrangement of *Schizocosa* species is based on an unpublished study; the *Rabidosa*, *Hogna* and *Isohogna* are each shown as polytomies that are clustered by genus name. Open bar is one insertion per side; filled bar is multiple insertions per side. Multiple insertions evolved either on the branch that includes *Geolycosa*, *Trochosa* and *Schizocosa* or on the branch that includes *Trochosa* and *Schizocosa*. The large lycosids of the “*Trochosa* group” (*Rabidosa*, *Hogna*, *Isohogna*, *Gladicosa* and *Geolycosa*) are variable for this character. The “*Lycosa* group” of the Lycosinae (*Arctosa*, *Alopecosa*, and *Hygrolycosa*) all show one insertion per side. Two species are polymorphic for this character; these are indicated with an asterisk.

recognized as the Trechaleidae (Carico 1986, 1993; Sierwald 1990; Griswold 1993); the Pisauridae and Ctenidae are also closely related (Figs. 1, 2) (Coddington & Levi 1991).

The insertion pattern for the Trechaleidae is not known (Carico pers. comm.). Members of four genera of the Pisauridae showed the pattern of alternating insertions (Table 2; Fig. 1). In *Pisaurina mira* (Walckenaer 1837) there was “a total of 3–5 insertions with a shift in the body between each insertion” (Bruce & Carico 1988); the palpal bulb expanded for 20–30 sec. Likewise, in *Ancylometes bogotensis* “each palp was inserted several times, alternately; the mating lasting about 10–15 min” (Merrett 1988). In her study of the African species of *Thalassius spinosissimus* Karsch 1876, Sierwald (1988) noted that both

palpi were used alternately, with 3–5 insertions occurring during copulation. Insertions lasted 5–20 sec for each palp. In these studies, the number of expansions was not noted.

The insertion pattern for *Cupiennius salei* Keyserling 1877, the one available example of Ctenidae, was of multiple expansions of the hematodocha during a single insertion followed by a switch to the opposite side. The ctenid showed 96 expansions in 12 min and typically only two insertions (one on each side) (Melchers 1963).

For the examples available in the Ctenidae and the Pisauridae, there was a single insertion on a side. The basal subfamilies of the Lycosidae also showed a single insertion on a side. This suggests that for insertion pattern, a single insertion on a side before switching

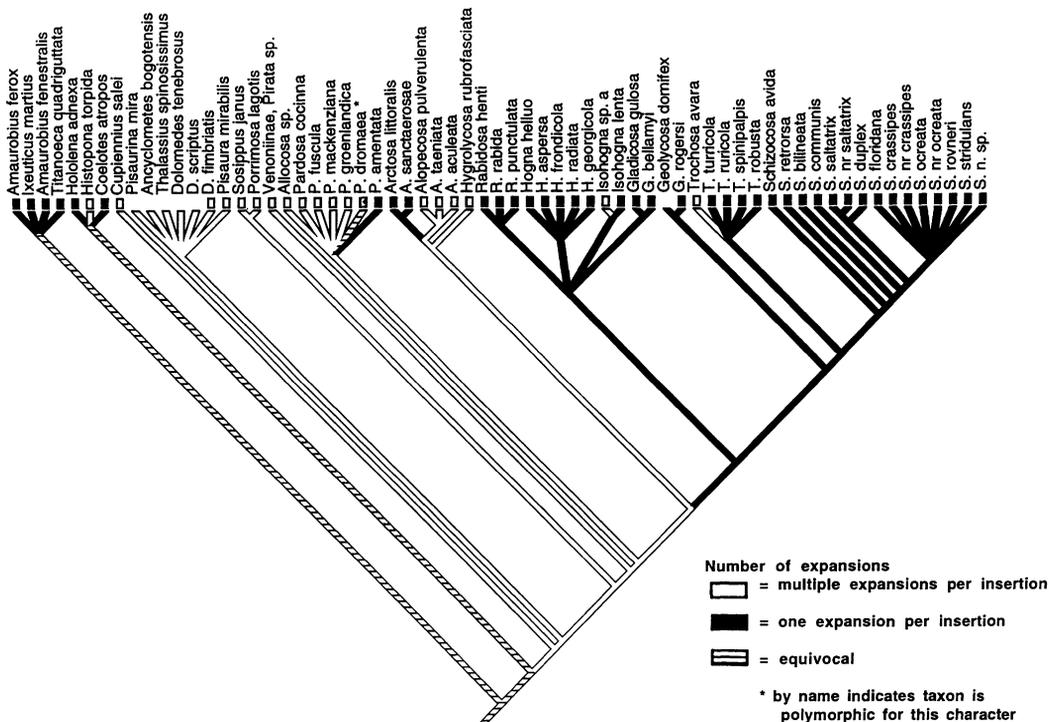


Figure 2.—Phylogeny of Lycosoidea plus Agelenidae and Amaurobiidae with overlay of pattern of embolus expansion. Arrangement of taxa is as in Figure 1. Open bar is multiple expansions per insertion; filled bar is one expansion per insertion. A single expansion per insertion is seen in most of the “*Trochosa* group” of the Lycosinae. The “*Lycosa* group” (*Arctosa*, *Alopecosa* and *Hygrolycosa*) are mixed for this character. One species is polymorphic for this character and is indicated with an asterisk.

may be the primitive pattern and multiple insertions on a side is the derived pattern (Fig. 1).

There are too few examples from the Ctenidae and Pisauridae to draw strong conclusions about the origin of the pattern of expansions (for several of the examples, the pattern of expansion was not given) (Fig. 2). However, the presence of multiple expansions of the hematodocha in *Cupiennius salei*, and in the three basal subfamilies of the Lycosidae suggests that multiple expansions may be primitive. An increase in the number of observations in the other subfamilies of lycosids will help clarify this picture.

The large number of different patterns seen in the Lycosinae may partly be a function of the number of studies done on this group; and since the sample sizes for the other subfamilies of lycosids and families of Lycosoidea are small, these data should be considered preliminary. Also, the diversity of patterns seen in the Lycosinae, and especially the “*Trochosa*

group”, suggests that the copulatory pattern may be fairly maleable in evolution, at least within that clade.

Evolution of copulatory pattern in Lycosidae.—It appears that in some taxa (such as *Schizocosa* spp.) the pattern of copulatory behavior shows some consistency while in other taxa (such as *Hogna* spp.) the overall pattern may vary between closely related species. It is interesting to speculate on the possible function of the differences in insertion and expansion patterns. The pattern seen consistently in *Schizocosa*, that of multiple insertions on one side, with one expansion of the hematodocha per insertion and palpal grooming between insertions, might allow for multiple opportunities for copulatory courtship (Eberhard 1994). Prior to each insertion in *Schizocosa* spp., the male scrapes the sides of the female’s abdomen, and while there may not be many sensory sensilla directly on the female’s epigynum (Huber 1993), there are many sensilla on the female’s abdomen in the

region surrounding the epigynum. Additionally, in the *S. ocreata* species group, males have a finger-like process on the palea of the palpal bulb and each expansion of the hematocha results in the paleal process scraping or pinching the sides of the epigynum (unpubl. data based on high magnification video from the ventral aspect of *Schizocosa* sp. nr. *ocreata*). This is consistent with Eberhard's sexual selection prediction (Eberhard 1985, 1986) that species-specific traits found on male genitalia are likely to be in direct contact with the female. Each separate insertion could therefore provide for stimulation of the female both as the palp of the male scrapes the side of her abdomen and then additionally (for the *S. ocreata* group) from the paleal process as it pinches the sides of the epigynum as the hematocha expands.

The species that showed multiple insertions on a side with a single expansion during each insertion had far longer copulations than the species that had multiple expansions (Table 2). Why should copulations be so long in these spiders? A long copulation may be a means for a male to restrict access to that female by other males (seen in *S. avida* [Walckenaer 1837], J. Latimore pers. comm.). A second possibility is that within the *Schizocosa* and *Trochosa* there is "in-copula" courtship (Eberhard 1994) as discussed above. A long copulation with many courtship movements on the part of the male could allow for many opportunities for the female to assess the male and for the male to induce favorable female responses. A third possibility is that the morphology of the male and female genitalia does not constitute as good a "fit" as a lock and key description may imply. Multiple insertions may be a mechanism that would assure at least one or a few successful insertions of the embolus by the male into the female. On several occasions we have observed males that mounted the female backwards and attempted to copulate from the wrong position. In other cases, the male oriented correctly but was not quite in the right position for the palp to engage with the epigynum. Multiple insertions would increase the probability of getting some insertions right.

The obligate burrowing spiders, *Arctosa sanctaerosae* and *Geolycosa* species all showed short copulations with the copulations happening at the top of the burrow. We ob-

served three instances in which males of *G. rogersi* attempted to copulate while a female was not in a burrow; in each of these, the male mounted backwards and did not copulate successfully. In the burrowing species, the burrow may be critical for correct orientation of the copulating pair.

Further work on copulation duration and pattern and in particular, studies on the timing of sperm transfer are necessary to further clarify the evolution of this behavior in lycosids.

ACKNOWLEDGMENTS

Financial support from the National Geographic Society (grants # 4916-92 and 5312-94) to G. Stratton and G. Miller and Hewlett Mellon Faculty Research funds from Albion College to G. Stratton are appreciated. We also thank W. Miller, E. Leighton, J. Hardy, J. Latimore, G. B. Edwards and P. Klawinski for help with field collections. Some specimens were obtained with support from the William H. Cross Expedition Fund of the Mississippi Entomological Museum and from NSF Grant BSR-90244810 (R.L. Brown, P.I.). J. Hardy videotaped the *Arctosa* behavior. J. Rovner, P. Sierwald and T. Kronstedt brought literature to our attention; D. Tingley provided translations of some of the German articles. This manuscript was greatly improved by the comments from several individuals. We thank P. Sierwald, C. Dondale, J. Rovner, W. Eberhard, T. Kronstedt and J. Carico for reading it closely and for providing additional examples and interpretations. C. Dondale & J. Redner shared data on *Pardosa*, *Hogna* and *Geolycosa*; J. Rovner provided data on *Sosippus* and T. Kronstedt provided data on *Alopecosa* and on *Hygrolycosa*. We are very grateful for these data and for fruitful discussions of copulatory patterns.

LITERATURE CITED

- Arnqvist, G. 1992. Courtship behavior and sexual cannibalism in the semi-aquatic fishing spider, *Dolomedes fimbriatus* (Clerck) (Araneae: Pisauridae). *J. Arachnol.*, 20:222-226.
- Bonnet, P. 1945. *Bibliographia Araneorum*. Tome I. Toulouse.
- Bristowe, W.S. 1926. The mating habits of British thomisid and sparassid spiders. *Ann. Mag. Nat. Hist.*, 18:114-131.
- Bruce, J.B. & J.E. Carico. 1988. Silk use during mating in *Pisaurina mira* (Walckenaer) (Araneae, Pisauridae). *J. Arachnol.*, 16:1-4.

- Capocasale, R.M. 1982. Las especies del género *Porrmosa* Roewer, 1959 (Araneae, Hippansinae). *J. Arachnol.*, 10:145–156.
- Carico, J.E. 1986. Trechaleidae: A “new” American spider family. P. 305, *In Proc. 9th Intern. Cong. Arachnol.*, Panama 1983 (W.G. Eberhard, Y.D. Lubin, & B.C. Robinson, eds.). Smithsonian Institution Press.
- Carico, J.E. 1993. Revision of the genus *Trechalea* Thorell (Araneae, Trechaleidae) with a review of the taxonomy of the Trechaleidae and Pisauridae of the Western Hemisphere., *J. Arachnol.*, 21: 226–257.
- Clerck, C. 1757. *Aranei suecci* (Svenska Spindlar) pp. 91–92. Stockholm.
- Coddington, J.A. & H.W. Levi. 1991. Systematics and evolution of spiders (Araneae). *Annu. Rev. Ecol. Syst.*, 22:565–92.
- Costa, F.G. 1993. Cohabitation and copulation in *Ixeuticus martius* (Araneae, Amaurobiidae). *J. Arachnol.*, 21:258–260.
- Costa, F.G. & J.R. Sotelo. 1994. Stereotypy and versatility of the copulatory pattern of *Lycosa malitiosa* (Araneae, Lycosidae) at cool versus warm temperatures. *J. Arachnol.*, 22:200–204.
- Dondale, C.D. 1986. The subfamilies of wolf spiders (Araneae: Lycosidae). *Actas X Congr. Int. Aracnol. Jaca/Espana*, 1:327–332.
- Dondale, C.D. & J.H. Redner. 1978. Revision of the Nearctic wolf spider genus *Schizocosa* (Araneida: Lycosidae). *Canadian Entomol.*, 110: 143–181.
- Dondale, C.D. & J.H. Redner. 1990. The Insects and Arachnids of Canada. Part 17. The wolf spiders, nurseryweb spiders, and lynx spiders of Canada and Alaska. *Agricul. Canada, Publ. 1856*. 383 pp.
- Eberhard, W.G. 1985. Sexual selection and animal genitalia. Harvard Univ. Press, Cambridge, Massachusetts. 244 pp.
- Eberhard, W.G. 1986. Why are genitalia good species characters? Pp. 53–59, *In Proc. 9th Intern. Congr. Arachnol.*, Panama. 1983 (W.G. Eberhard, Y.D. Lubin, & B.C. Robinson, eds.). Smithsonian Institution Press.
- Eberhard, W.G. 1994. Evidence for widespread courtship during copulation in 131 species of insects and spiders, and implications for cryptic female choice. *Evolution*, 48:711–733.
- Elgar, M.A. 1992. Sexual cannibalism in spiders and other invertebrates. Pp. 128–155, *In Cannibalism: ecology and evolution among diverse taxa.* (M.A. Elgar & B.J. Crespi, eds.) Oxford Univ. Press.
- Engelhart, W. 1964. Die mitteleuropäischen Arten der Gattung *Trochosa* C.L. Koch, 1848 (Araneae, Lycosidae). *Morphologie, Chemotaxonomie, Biologie, Autökologie. Z. Morph. Ökol. Tiere*, 54:219–392.
- Foelix, R. 1982. *Biology of Spiders*. Harvard Univ. Press., Cambridge, Massachusetts.
- Fraser, J.B. 1986. Courtship and copulatory behavior of the funnel-web spider *Hololena adnexa* (Araneae, Agelenidae). *J. Arachnol.*, 15:257–262.
- Gering, R.L. 1953. Structure and function of the genitalia in some American agelenid spiders. *Smithsonian Misc. Coll.*, 121:1–83.
- Gerhardt, U. 1923. Weitere sexualbiologische Untersuchung an Spinnen. *Arch. f. Naturg., Abt. A.*, 87:78–247.
- Gerhardt, U. 1924. Weitere Studien über die Biologie der Spinnen. *Arch. Naturgesch.*, 90:85–192.
- Gerhardt, U. & A. Kaestner. 1937. Araneae. Pp. 3: 395–656, *In Handbuch der Zoologie, Kükenthal*. W. de Gruyter, Berlin.
- Gertsch, W.J. & H.K. Wallace. 1937. New American Lycosidae with notes on other species. *American Mus. Novit.*, No. 919:1–22.
- Griswold, C.E. 1993. Investigations into the phylogeny of the lycosoid spiders and their kin (Arachnida: Araneae: Lycosoidea), *Smithsonian Contrib. Zool.*, 539:1–39.
- Huber, B.A. 1993. Genital mechanics and sexual selection in the spider *Nesticus cellulanus* (Araneae: Nesticidae). *Canadian J. Zool.*, 71:2437–2447.
- Kaston, B.J. 1936. The senses involved in the courtship of some vagabond spiders. *Entomol. Americana*, 16:97–167.
- Maddison, W.P. & D.R. Maddison. 1992. *MacClade: analysis of phylogeny and character evolution. Version 3.0.* Sinauer and Associates, Sunderland, Massachusetts.
- Melchers, M. 1963. Zur Biologie und zum Verhalten von *Cupiennius salei* (Keyserling), einer amerikanischen Ctenidae. *Zool. Jb. Syst. Bd.*, 91: 1–90.
- Merrett, P. 1988. Notes of the biology of the neotropical pisaurid, *Ancylometes bogotensis* (Keyserling) (Araneae: Pisauridae). *Bull. British Arachnol. Soc.*, 7:197–201.
- Montgomery, T.H. Jr. 1903. Studies on the habits of spiders, particularly those of the mating period. *Proc. Acad. Nat. Sci. Philadelphia*, 55:59–149.
- Montgomery, T.H. Jr. 1909. Further studies on the activities of Araneads, II. *Proc. Acad. Nat. Sci. Philadelphia*, 61:548–569.
- Nappi, A.J. 1965. Notes on the courtship and mating habits of the wolf spider *Lycosa helluo* Walckenaer. *American Midl. Nat.*, 74:368–373.
- Robinson, M.H. 1982. Courtship and mating behavior in spiders. *Ann. Rev. Entomol.*, 27:1–20.
- Rovner, J.S. 1972. Copulation in the lycosid spider *Lycosa rabida* Walckenaer: a quantitative study. *Anim. Behav.*, 20:133–138.
- Rovner, J.S. 1973. Copulatory pattern supports ge-

- neric placement of *Schizocosa avida* (Walckenaer) (Araneae: Lycosidae). *Psyche*, 80:245–248.
- Rovner, J.S. 1974. Copulation in the lycosid spider *Schizocosa saltatrix* (Hentz): an analysis of palpal insertion patterns. *Anim. Behav.*, 22:94–99.
- Savory, T. 1928. *The Biology of Spiders*. Sidgwick & Jackson, London.
- Sierwald, P. 1988. Notes on the behavior of *Thalassius spinosissimus* (Arachnida: Araneae: Pisauridae). *Psyche*, 95:243–252.
- Sierwald, P. 1990. Morphology and homologous features in the male palpal organ in Pisauridae and other spider families, with notes on the taxonomy of Pisauridae (Arachnida: Araneae). *Nemouria, Occ. Pap. Delaware Mus. Natur. Hist.*, 35:1–59.
- Sierwald, P. & J.A. Coddington. 1988. Functional aspects of the male palpal organ in *Dolomedes tenebrosus*, with notes on the mating behavior (Araneae, Pisauridae). *J. Arachnol.*, 16:262–265.
- Stratton, G.E., & G.W. Uetz. 1983. Communication via substratum-coupled stridulation and reproductive isolation in wolf spiders. *Anim. Behav.*, 31:164–172.
- Manuscript received 20 August 1995, revised 10 June 1996.*