Spider reproductive behaviour: a review of Gerhardt's work from 1911–1933, with implications for sexual selection

Bernhard A. Huber
Escuela de Biología,
Universidad de Costa Rica,
Ciudad Universitaria, Costa Rica*

Summary

Between 1911 and 1933, the German Ulrich Gerhardt compiled an unequalled amount of data on the reproductive behaviour of 151 spider species from 102 genera and 38 families. The present paper attempts to condense his more than 1,000 pages into three tables which contain the modern names of all the species he studied, as well as information on precopulatory and copulatory behaviour, and male sperm induction. Gerhardt's data are used to discuss several topics of current interest in sexual selection: (1) evidence is presented against the "conflict of interest hypothesis" for the evolution of genitalia; (2) the limited value of some reproductive behaviour patterns for systematic research at higher taxonomic levels is explained by the fact that these behavioural characters may evolve by sexual selection and therefore evolve rapidly and several times convergently; (3) "flubs" (unsuccessful intromission attempts) are shown to be both common and widespread in spiders, suggesting the possibility that they play an important role in the evolution of genitalia; (4) copulatory courtship is shown to be common in spiders, which probably means that cryptic female choice has been an important factor in the evolution of spiders.

Introduction

There has almost certainly never been anyone who observed and described the reproductive behaviour of as many spider species and families as Ulrich Gerhardt between 1911 and 1933. However, Gerhardt's findings are often ignored or cited superficially in modern arachnological work on spider sexual behaviour. There are several reasons for this neglect: (1) almost 50% of the spider names used by Gerhardt are different from those used now, making comparisons difficult; (2) the work comprises a total of 1,064 pages, divided into 12 papers, making it a formidable task to search for certain pieces of information; (3) Gerhardt published in German, in a style that now appears long-winded, and often used words in slightly different meanings from those in modern German; (4) some of Gerhardt's theoretical considerations are now regarded as wrong (e.g. the assumption that simple genitalia in spiders are primitive), which may give the impression that his work is only a historically important pioneer work.

The present paper aims to assist in overcoming some of these difficulties. It presents a list of the modern names of all the spider species which Gerhardt observed, with precise citations of the papers in which they were mentioned (Table 1). Two summary tables (Tables 2,3) provide information on 18 characters of copulation and sperm induction behaviour in all the species he observed. In addition, Gerhardt's data are used to discuss several topics of current interest in sexual selection.

This paper is in no way meant to substitute for the original works. It is intended to facilitate access to the existing information, of which only a small part can be presented here.

*Present address: Dept. of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA.

About Gerhardt (after Bonnet, 1945; Savory, 1961; Herre, 1952; Gerhardt, 1911, 1921)

Ulrich Gerhardt was born in Würzburg, Germany, in 1875. At secondary school and then during his studies of medicine he made his first observations of spider copulations. He received his doctorate of medicine in Berlin in 1899, and in 1905 became a lecturer in zoology at Breslau (now Wrocław in Poland). While his primary study subjects at that time were mammals, in particular rabbits, he also started to study the reproductive behaviour of orb weavers more systematically, which resulted in his 1911 paper. In 1911 he received the title of professor, and incidentally but persistently continued his studies of spiders. These were summarised in his large 1921 paper which he thought would close his contribution to this subject. Instead it became the starting point for a series of 10 more works, which he produced until 1933. His call to Halle as director of the veterinary institute in 1924 apparently did not reduce his dedication to spiders, which were only one of several groups of invertebrates he studied (including cockroaches, millipedes, and slugs). Why Gerhardt did not continue with spiders after 1933 is open to speculation. One reason may be the difficulty he experienced in obtaining representatives of unstudied families or genera, and his apparently growing conviction that he would not be able to answer some of his central theoretical questions even with increasing numbers of species studied (e.g. the question about the reasons for behavioural and morphological variety, or the question about the relationship between behaviour patterns and phylogeny). Other reasons might have been the approaching Second World War, and after the war, his commitment to German reconstruction. Gerhardt died in Halle, in 1950.

Strong points in Gerhardt's work

Intriguingly, some of the major virtues of Gerhardt's work were cited above as problems for modern arachnology. The formidable total of more than 1,000 pages reflects an unequalled comprehensiveness, and a lack of limitation in space. While modern papers on the subject are usually restricted to a few pages, Gerhardt's longest paper was 225 pages long. Another, even more important aspect, is the lack of theoretical or thematical limitations. While modern work often concentrates on answering one or a few specific questions, eliminating data that are not related to that topic, Gerhardt apparently made a note of everything he observed. He often noted down observations that appeared completely uninteresting at the time but which have subsequently proved of interest. He also recorded observations that he

Table 1: List of spider species studied by Gerhardt, with location of information (years in italic). Bold page numbers refer to main text, others to minor notes. Taxonomic advice was kindly provided by K. Thaler (pers. comm.).

Family	Current name	Remarks and references
Atypidae	*Atypus muralis* Bertkau	*1929*: **729**
	Atypus piceus (Sulzer)	*1929*: 729; *1933*: **11**
Theraphosidae	*Avicularia avicularia* (L.)	*1929*: **709**; identity uncertain
	Avicularia halensis (Gerhardt)	sub *Eurypelma halensis* n.sp.: *1933*: **4**; species inquirenda
	Grammostola mollicoma (Ausserer)	sub *G. longimana* Mello-Leitão: *1933*: **8**
	Phormictopus cancerides (Latreille)	*1929*: **704**; identity uncertain
Filistatidae	*Filistata insidiatrix* (Forskål)	*1923*: 49; *1928*: **578**; *1930*: **187**
	Zaitunia schmitzi (Kulcz.)	sub *Filistata s.*: *1933*: **12**
Sicariidae	*Loxosceles rufescens* (Dufour)	*1927*: 157; *1928*: **585**
Scytodidae	*Scytodes thoracica* (Latreille)	*1926*: **62**; *1927*: **152**; *1930*: **201**, **208**; *1933*: **20**
	Scytodes velutina Heineken & Lowe	*1930*: **205**
Pholcidae	*Holocnemus caudatus* (Dufour)	*1933*: **21**
	Holocnemus pluchei (Scopoli)	sub *H. rivulatus* (Forskål): *1927*: **148**
	Hoplopholcus forskali (Thorell)	*1924a*: **144**
	Pholcus opilionoides (Schrank)	*1921*: **154**; *1923*: 23, **99**; *1924a*: **140**
	Pholcus phalangioides (Fuesslin)	*1927*: **142**; *1929*: 752
Segestriidae	*Segestria bavarica* C. L. Koch	*1929*: **737**
	Segestria florentina (Rossi)	*1933*: **14**
	Segestria senoculata (L.)	*1921*: 121, 122, 128, **189**; *1923*: 23, **104**; *1924a*: **149**; *1925*: **568**, 576
Dysderidae	*Dysdera erythrina* (Walck.)	*1923*: **106**; *1924a*: **152**; *1925*: **575**; *1933*: **14**
	Dysdera westringi O.P.-Cambr.	*1933*: **13**
	Harpactea hombergi (Scopoli)	sub *Harpactes h.*: *1921*: 194; *1923*: **110**; *1924a*: **153**; *1924b*: 527; *1927*: 159
	Harpactea rubicunda (C.L. Koch)	sub *Harpactocrates rubicundus*: *1927*: **158**
Oonopidae	*Oonops placidus* Dalmas	*1930*: **195:** *1933*: **16**
	Xestaspis nitida Simon	*1933*: **17**
Palpimanidae	*Palpimanus orientalis* Kulcz.	sub *P. gibbulus* Dufour: *1927*: **100** (see Gerhardt, 1933: 23)
	Palpimanus schmitzi Kulcz.	*1933*: **23**
Mimetidae	*Ero aphana* (Walck.)	*1926*: **21**
	Ero furcata (Villers)	*1924a*: **137**; *1926*: **27**; *1933*: **43**
Eresidae	*Eresus cinnaberinus* (Olivier)	sub *E. niger* (Petagna): *1928*: **601**; identity uncertain — for the taxonomy of Central European *Eresus* see Ratschker (1993), Ratschker & Bellmann (1995)
	Eresus walckenaeri Brullé	*1928*: **595**, 660
	Stegodyphus lineatus (Latreille)	*1928*: **592**; *1933*: **22**
Oecobiidae	*Oecobius cellariorum* (Dugès)	*1928*: **589**
	Uroctea durandi (Walck.)	*1933*: **23**
Hersiliidae	*Hersiliola simoni* (O.P.-Cambr.)	sub *H. simonis*: *1933*: **26**
Uloboridae	*Hyptiotes paradoxus* (C.L. Koch)	*1923*: **50**, **115**; *1924a*: **115**, 172
	Polenecia producta (Simon)	sub *Sybota producta*: *1933*: **46**
	Uloborus walckenaerius Latreille	*1924a*: **108**; *1933*: **46**
	Zosis geniculatus (Olivier)	sub *Uloborus g.*: *1927*: **124**
Nesticidae	*Nesticus cellulanus* (Clerck)	*1927*: **114**
Theridiidae	*Achaearanea lunata* (Clerck)	sub *Theridium formosum* (Clerck): *1923*: **63**
	Achaearanea tepidariorum (C.L. Koch)	sub *Theridium tepidariorum*: *1923*: **17**, **61**
	Argyrodes argyrodes (Walck.)	sub *A. gibbosus* (Lucas): *1928*: **619**
	Crustulina conspicua (O.P.-Cambr.)	*1933*: **41**
	Enoplognatha ovata (Clerck)	sub *Theridium lineatum* (Clerck): *1921*: 116, 124, **160**; sub *Phyllonethis lineata*: *1923*: **16**, **60**
	Latrodectus schuchi (C.L. Koch)	sub *L. tredecimguttatus* var. *lugubris* (Dufour): *1928*: **621**; identity uncertain — name proposed for geographical reasons. Hadjissarantos (1940) mentions this species from the same region, Attica.
	Neottiura bimaculata (L.)	sub *Theridium bimaculatum*: *1924b*: **513**
	Steatoda bipunctata (L.)	*1923*: **66**; *1924a*: **136**; *1925*: 586
	Steatoda castanea (Clerck)	*1926*: **13**
	Steatoda grossa (C.L. Koch)	sub *Teutana grossa*: *1925*: **585**; *1926*: **11**
	Steatoda paykulliana (Walck.)	sub *Lithyphantes paykullianus*: *1933*: **39**
	Steatoda triangulosa (Walck.)	sub *Teutana triangulosa*: *1933*: **40**
	Theridion melanurum Hahn	sub *Theridium denticulatum* (Walck.): *1926*: **10**; *1927*: **113** (see Wiehle, 1952)
	Theridion varians Hahn	sub *Theridium v.*: *1923*: **60**; *1924a*: **133**; *1927*: 113
Theridiosomatidae	*Theridiosoma gemmosum* (L. Koch)	*1933*: **62**
Linyphiidae — Linyphiinae	*Labulla thoracica* (Wider)	*1921*: **167**; *1923*: **12**, **85**; *1925*: 581; *1928*: **631**
	Lepthyphantes leprosus (Ohlert)	sub *Leptyphantes l.*: *1925*: 581; *1933*: **43**
	Linyphia triangularis (Clerck)	*1921*: 102, **164**; *1923*: 12, **78**; *1925*: 581; *1928*: 627

Table 1: *Continued*

Family	Current name	Remarks and references
Linyphiidae — Linyphiinae	*Megalepthyphantes nebulosus* (Sund.)	sub *Leptyphantes n.*: *1923*: **14**, **72**; *1928*: 628
	Microlinyphia pusilla (Sund.)	sub *Linyphia* (*Microl.*) *pusilla*: *1928*: **629**
	Neriena clathrata (Sund.)	sub *Linyphia c.*: *1928*: **628**
	Neriene emphana (Walck.)	sub *Linyphia e.*: *1928*: **629**
	Neriene montana (Clerck)	sub *Linyphia m.*: *1921*: 130; *1923*: **78**; *1925*: **580**
Linyphiidae — Erigoninae	*Dismodicus elevatus* (C.L. Koch)	*1924b*: **516**; identity uncertain
	Erigone dentipalpis (Wider)	*1927*: **122**
	Erigone longipalpis (Sund.)	*1923*: **15**, **70**, **115** (on p. 71 Gerhardt erroneously writes "*E. atra*"); *1924a*: **129**; identity uncertain (maybe *E. atra* Blackwall?)
	Gonatium rubellum (Blackwall)	sub *Gonatium isabellinum* (C.L. Koch): *1924a*: **131**
	Gongylidium rufipes (L.)	*1924a*: **129**
	Hylyphantes graminicola (Sund.)	sub *Tmeticus graminicolus*: *1928*: **626**
Tetragnathidae	*Meta menardi* (Latreille)	*1928*: **642**
	Metellina merianae (Scopoli)	sub *Meta m.*: *1927*: **136**
	Metellina segmentata (Clerck)	sub *Meta s.*: *1911*: **656**; *1921*: 130, **147**; *1926*: **48**
	Nephila inaurata madagascariensis (Vinson)	sub *N. madagascariensis*: *1933*: **48**
	Pachygnatha clercki Sund.	*1923*: **95**
	Pachygnatha degeeri Sund.	*1924a*: **128**
	Pachygnatha listeri Sund.	*1921*: **152**; *1924a*: **126**
	Tetragnatha extensa (L.)	*1923*: **18**, **94**
	Tetragnatha montana Simon	sub *T. extensa*: *1921*: **149** (see Gerhardt, 1923: 94, footnote, and 1924a: 125); *T. solandrii* Thorell: *1924a*: **124**
	Tetragnatha nigrita Lendl	*1928*: **649**
Araneidae	*Aculepeira ceropegia* (Walck.)	sub *Aranea ceropegia*: *1927*: **131**
	Agalenatea redii (Scopoli)	sub *Aranea r.*: *1927*: **130**
	Araneus alsine (Walck.)	sub *Aranea a.*: *1927*: **133**
	Araneus circe (Audouin)	sub *Aranea c.*: *1928*: **637**
	Araneus diadematus Clerck	sub *Epeira* (*Aranea*) *diadema*(*ta*): *1911*: **646–664**; *1921*: 123, 129, 141; *1924a*: **121**, 172; *1924b*: 531; *1925*: 594, 603
	Araneus marmoreus Clerck	sub *Epeira marmorea*: *1911*: **646–664**; *1921*: 141
	Araneus quadratus Clerck	sub *Epeira quadrata*: *1911*: **646–664**; *1921*: 141
	Araneus sturmi (Hahn)	sub *Aranea s.*: *1933*: **67**
	Araniella cucurbitina (Clerck)	sub *Miranda* (*Epeira*, *Aranea*) *c.*: *1923*: **92**; *1924b*: **519**
	Argiope bruennichi (Scopoli)	*1924b*: **522**, 532; *1928*: 662
	Argiope lobata (Pallas)	*1928*: **634**, 662; *1933*: **60**; identity of specimens studied in 1933 uncertain
	Cyclosa conica (Pallas)	*1921*: 121; *1923*: **90**; *1926*: **34**
	Cyrtophora citricola (Forskål)	*1928*: **644**, 663
	Gibbaranea bituberculata (Walck.)	sub *Aranea dromedaria* Walck.: *1928*: **639**
	Larinioides cornutus (Clerck)	sub *Aranea cornuta*: *1926*: **35**
	Larinioides sclopetarius (Clerck)	sub *Epeira* (*Aranea*) *sclopetaria*: *1921*: **144**; *1925*: **596**
	Mangora acalypha (Walck.)	sub *Aranea acalypha*: *1928*: **639**
	Nuctenea umbratica (Clerck)	sub *Aranea* (*Epeira*) *umbratica*: *1921*: 122; *1925*: **593**
	Singa nitidula C.L. Koch	sub *Singa heerii* (Hahn): *1928*: **641** (see Wiehle, 1931: 45)
	Zilla diodia (Walck.)	sub *Aranea d.*: *1928*: **638**
	Zygiella atrica (C.L. Koch)	sub *Zilla a.*: *1924b*: **516**; *1926*: 41
	Zygiella x-notata (Clerck)	sub *Zilla atrica*: *1921*: 115, **148** (see Gerhardt, 1926: 41); sub *Zilla x-n.*: *1926*: **40**
Lycosidae	*Alopecosa albofasciata* (Brullé)	sub *Lycosa* (*Tarentula*) *a.*: *1933*: **30**
	Pardosa amentata (Clerck)	sub *Lycosa a.*: *1923*: **26**, **115**
	Pirata piraticus (Clerck)	*1921*: 122, 125, **136**; identiy uncertain (maybe *P. tenuitarsis* Simon?)
Pisauridae	*Dolomedes fimbriatus* (Clerck)	*1926*: **2**
	Pisaura mirabilis (Clerck)	*1923*: **28**; *1924a*: **89**
Oxyopidae	*Oxyopes heterophthalmus* Latreille	*1933*: **28**
	Oxyopes ramosus (Panzer)	*1927*: **105**
Agelenidae	*Agelena gracilens* C.L. Koch	sub *A. similis* Keyserling: *1921*: **174**; *1924a*: 167
	Agelena labyrinthica (Clerck)	*1921*: 108, 116, 123, **174**; *1923*: 20, 24; *1924a*: 167
	Coelotes atropos (Walck.)	*1928*: **617**; identity uncertain (maybe *C. terrestris* (Wider)?)
	Histopona torpida (C.L.Koch)	*1927*: **108**
	Tegenaria sp.	*1933*: **33**
	Tegenaria atrica C.L. Koch	*1921*: 103, 113, 120–123, **178**; *1924a*: 172
	Tegenaria domestica (Clerck)	sub *T. derhami* (Scopoli): *1921*: 112, 115, 122, 123, 127, **176**
	Tegenaria ferruginea (Panzer)	sub *T. domestica*: *1921*: 112, 121, 122, 130, **179**
	Tegenaria parietina (Fourcroy)	*1933*: **32**
Cybaeidae	*Cedicus israeliensis* Levy	sub *C. flavipes* Simon: *1933*: **34** (classification according to Levy, 1996)
	Cybaeus angustiarum L. Koch	*1921*: **182**

Table 1: *Continued*

Family	Current name	Remarks and references
Argyronetidae	*Argyroneta aquatica* (Clerck)	*1921*: 112, 123, **183**; *1924a*: 180; *1924b*: 527
Dictynidae	*Dictyna arundinacea* (L.)	*1921*: 115, 122, 130, **170**; *1923*: **8**
	Dictyna uncinata Thorell	*1924a*: **104**
	Nigma walckenaeri (Roewer)	sub *Dictyna viridissima* (Walck.): *1921*: 112, 122, 126, **172**; *1923*: **10**, 20
Amaurobiidae	*Amaurobius fenestralis* (Stroem)	*1923*: **46**; *1924a*: **106**, 168
	Amaurobius ferox (Walck.)	*1923*: **45**; *1924a*: 168
Titanoecidae	*Titanoeca quadriguttata* (Hahn)	*1928*: **606**
Liocranidae	*Mesiotelus mauritanicus* Simon	*1930*: **215**
Clubionidae	*Cheiracanthium* sp.	sub *Chiracanthium* sp.: *1928*: **609**
	Cheiracanthium pennatum Simon	sub *Chiracanthium permatum*: *1933*: **38** (orthography corrected, see Bonnet, 1956: 1065)
	Clubiona germanica Thorell	*1923*: **42**, **115**
	Clubiona pallidula (Clerck)	*1924b*: **511**
	Clubiona terrestris Westring	*1924a*: **94**
Zodariidae	*Zodarion elegans* (Simon)	sub *Zodarium e.*: *1928*: **607**
Gnaphosidae	*Drassodes lapidosus* (Walck.)	sub *Drassus lapidicola* (Latreille): *1924a*: **92**
	Gnaphosa lucifuga (Walck.)	*1928*: **616**
	Gnaphosa montana (L. Koch)	*1928*: **615**; identity uncertain
	Zelotes sp.	sub *Prosthesima erebea* (Thorell): *1924a*: **94** (for taxonomic confusion concerning this species see Job, 1969)
Heteropodidae	*Eusparassus walckenaeri* (Audouin)	*1933*: **37**; sub *Sparassus* sp.: *1928*: **612** (classification according to Levy, 1989)
	Micrommata virescens (Clerck)	*1921*: 121; *1925*: **604**
Philodromidae	*Philodromus aureolus* (Clerck)	*1923*: **34**; identity uncertain
	Philodromus dispar Walck.	*1924a*: **96**
	Philodromus fuscomarginatus (De Geer)	sub *Artanes f.*: *1923*: **36**: *1924a*: **96**
	Tibellus oblongus (Walck.)	*1923*: **38**; classification not sure (maybe *T. maritimus* (Menge)?)
	Thanatus sp.	sub *Thanatus fagei* n.sp.: *1933*: **35**; nomen dubium (Levy, 1977)
Thomisidae	*Misumena vatia* (Clerck)	sub *M. calycina* (L.): *1924a*: **100**; *1924b*: 530
	Xysticus cristatus (Clerck)	sub *X. viaticus* (L.): *1924a*: **97**; 172; identity uncertain (maybe *X. audax* (Schrank)?)
	Xysticus lanio C.L. Koch	*1924a*: **99**
	Xysticus tristrami (O.P.-Cambr.)	*1933*: **36**; identity uncertain (maybe *X. rectilineus* (O.P.-Cambr.) or *X. ferus* O.P.-Cambr.?)
Salticidae	*Evarcha falcata* (Clerck)	sub *Ergane f.*: *1924b*: **509**
	Heliophanus cupreus (Walck.)	*1924b*: **509**, **510**
	Marpissa muscosa (Clerck)	*1923*: **24**, **115**
	Salticus scenicus (Clerck)	sub *Epiblema scenicum*: *1921*: 102, 120, **131**
	Sitticus pubescens (Fabr.)	sub *Attus p.*: *1921*: 83, 113, 126, **133**

could not explain, and observations that contradicted his own views. Despite looking for a generalised pattern of behaviour for each species, he noted ‘‘abnormal’’ behaviour, aberrations and exceptions. Thus his descriptions appear relatively unfiltered by preconceptions.

Weak points in Gerhardt’s work

Some obvious flaws should be kept in mind when using Gerhardt’s results. First, sample size is often very small. Copulation behaviour is described in 151 species — in 40 of these (26%), the results are based on the observation of a single pair. This is even more pronounced in sperm induction behaviour: in 35 of 82 species (43%), descriptions are based on the observation of a single male. Obviously, Gerhardt was more interested in accumulating data on as many species as possible than in studying intraspecific variation. Secondly, it is often not clear whether the female was virgin or not. It has been shown several times that the female’s reproductive history may produce significant differences, both in qualitative and quantitative aspects (e.g. Blanke, 1986; Uhl, 1993; Eberhard & Huber, in press on *Leucauge mariana*). Finally, Gerhardt was not as interested in courtship as he was in copulation, which may explain his often vague descriptions of the former. Precopulatory courtship is therefore omitted in Table 2.

Discussion

In the following paragraphs Gerhardt’s data are related to some topics of sexual selection that have attracted interest recently. The point I try to make is that if certain restrictions are kept in mind (see above), Gerhardt’s data can usefully be incorporated into comparative studies of spider reproductive behaviour, and into more general discussions about reproductive behaviour and sexual selection.

Genitalic evolution by male-female conflict?

A widely accepted hypothesis to explain the common pattern of genitalia to be species-specific is the ‘‘female choice hypothesis'' (Eberhard, 1985). This assumes that females discriminate between males on the basis of their genitalia, and that females selectively co-operate with males (Eberhard, 1996). Recently, a competing hypothesis has been proposed by Alexander *et al*. (1997): the ''conflict of interest hypothesis''. This hypothesis ties the evolution of complex and species-specific genitalia to coercive mating acts, i.e. to males that evolve to coerce females, and females that evolve to evade this coercion (Alexander *et al*., 1997: 22). On the other hand, luring or persuasive mating acts, in which the female is in ''control over continuation of the mating sequence from the start of rapprochment until the point of genitalic contact'' are thought to be correlated with rather simple, uniform genitalia. Alexander *et al*. (1997) cite grasshoppers and field crickets as examples for ''seekers and seizers'' versus ''signallers'' (pp. 17–18), but they generalise their hypothesis to at least pterygote insects (p. 18). Furthermore, by proposing it as an exclusive alternative to the female choice hypothesis which is meant to be valid for all animals with internal fertilisation, the conflict of interest hypothesis purports to provide a general explanation for the evolution of genitalia (p. 25).

Gerhardt's data provide ample evidence against the validity of the ''conflict of interest hypothesis'' in spiders. Table 2 lists 10 types of active female co-operation preceding successful insertion. Female co-operation, which is a sign for luring mating acts, occurs in all major taxa studied (mygalomorphs, haplogynes, rta-clade, orbicularians), and is recorded in 75 of the 151 species. This obviously places male spiders into the category of signallers that lure the female into co-operation, rather than into the category of coercive seizers. At the same time it is evident from taxonomic literature that spider genitalia are almost universally the best characters for species discrimination. Thus, Gerhardt's observations do not support a general correlation between coercive mating acts and rapid evolution of genitalia.

Behavioural characters under sexual selection

One of Gerhardt's primary aims was to detect phylogenetic relationships by observing reproductive behaviour (e.g. Gerhardt, 1926: 1; 1927: 170). It is ironic that some of the characters he studied most intensively appear largely unusable for systematic research at higher taxonomic levels since they show extreme interspecific variation and have obviously evolved several times convergently. In this section I will argue that these characters have evolved so fast and convergently because they are at the same time relatively simple and under sexual selection.

The first concerns rhythmic movements of the male genitalia during insertion. Table 2 lists 80 species with rhythmic movements, and 48 without (in the other species the presence or absence of rhythmic genitalic movements is not explicitly mentioned). Nine families include representatives both with and without rhythmic movements (Oecobiidae, Agelenidae, Cybaeidae, Philodromidae, Oxyopidae, Uloboridae, Theridiidae, Linyphiidae, Tetragnathidae). The possible function of these movements has been discussed in detail by Huber & Eberhard (1997). Stimulation rather that sperm expulsion or removal was found to be the most probable explanation. Female choice may thus be responsible for the rapid divergence of this character. I predict that more detailed studies into the exact nature of the movements will reveal a vast range of species-specific modifications.

Another such character that shows high variation within families is insertion duration. This is correlated with the presence or absence of rhythmic genitalic movements: most species with insertion duration of more than 1 min show rhythmic movements (64 of 72 species), whereas most species with short insertions (less than 1 min) do not have rhythmic movements during insertion (38 of 44 species). This may indicate that there are two principal ways in which a male spider can prolong copulation: either by making rhythmic movements or by repeatedly withdrawing and inserting the genitalia, as in some linyphiids which make hundreds of short insertions. Such withdrawals and renewed insertions may exert similar stimuli to the female as rhythmic movements during insertion. Thus, the reason why the pattern of insertion (whether each palp is applied only once or several times; see Table 2) and the insertion-duration are so variable within families may be that these characters are also under sexual selection by female choice.

There is no correlation between pattern of insertion and insertion-duration (Table 2). Thus, a male spider seems to have three principal possibilities as to the pattern of copulation: (1) make only one short insertion with each palp, without rhythmic movements; (2) make only one long insertion with each palp, which usually requires rhythmic movements; (3) make several insertions, either long with rhythmic movements, or short without rhythmic movements. All of these possibilities have evolved convergently in several families and should be used very carefully for the reconstruction of phylogenetic relationships.

Flubs and copulatory courtship

The term ''flub'' was coined by Watson (1991) who used it for ''unsuccessful intromissions (i.e. obvious misses or incomplete penetrations, where the male's pedipalp does not completely expand)'', in the linyphiid spider *Neriene litigiosa* (Keyserling). The ratio of ''flubs to hits'' (hit = successful intromission) was used as a measure of the male's competency in copulation. Flubs may have a variety of causes, including both morphological and behavioural problems of the male or the female, and they probably reflect the difficulties males encounter and try to solve. Most published accounts on spider copulation have focused on successful intromissions, but recent studies show that flubs sometimes are the rule rather than the exception: in a study on the tetragnathid *Leucauge mariana* (Taczanowski), Eberhard & Huber (in press) found that the frequency of failed insertion attempts averaged more than 50%. Gerhardt's data support the

Table 2: List of 11 characters of precopulatory and copulatory behaviour in the spiders studied by Gerhardt. The order of species is as in Table 1. N=number of pairs observed.

1. Female co-operation: Only active co-operation is included, although there are probably many forms of passive, "cryptic" co-operation, such as not moving, allowing male to spin female's legs together, etc. Code: (1) female turns to male; (2) female approaches male; (3) female assumes copulatory position, either by lifting prosoma from ground or by lowering it from a thread; (4) female positions abdomen, either by bending it ventrally, or lifting or rotating it; (5) female becomes cataleptic; (6) female opens vulva, or erects scape; (7) female opens chelicerae to engage a male structure, or presents her chelicerae to male to grasp them; (8) female helps male palp with legs, chelicerae or palps to find genital opening; (9) female positions male correctly; (10) unspecified "helpfulness" or "co-operation".
2. Female rejection: Only active rejection is included, although there are probably many forms of passive rejection, such as not approaching male, etc. Code: (1) female attacks male; (2) female prevents insertion by holding legs III over genital opening; (3) female terminates copulation by moving, or by rotating opisthosoma; (4) female pushes or brushes away inserted bulb.
3. Insertion behaviour: (1) male extends bulb to female genital opening; (2) male moves pedipalp over female genital area, "searching", "groping" or "hammering"; from female perspective either from anterior to posterior (2a) or from posterior to anterior (2p); (3) male "flings" or "pushes" pedipalp against female genital area; (4) male "jumps" or rapidly "glides" to female from a distance.
4. "Flubs" are defined as unsuccessful attempts to couple, either genitalic (g) or cheliceral (c). A plus (+) indicates "often", "regularly" or "usual".
5. Cheliceral contact: (1) female chelicerae engage apophyses on male tibia I; (2) male chelicerae contact or clasp female ventrally; (3) male and female chelicerae locked together.
6. Palpal or bulbal movements during insertion: (1) rhythmic expansions of haematodocha; (2) rhythmic twisting movements of pedipalp or bulb; (3) vibrating or "quivering" of palp; (4) rhythmic expansions of paracymbium ("procursus" of pholcids); (−) explicit absence of rhythmic movements.
7. Non-genitalic movements during copulation: (1) male rhythmically "taps", "quivers", or "jerks" with one or more legs; (2) male rhythmically "quivers", "swings", "bobs", or "vibrates" his opisthosoma or entire body; (3) male rhythmically opens and closes chelicerae.
8. Pedipalps inserted simultaneously (s) or alternately (a). (a1): each palp only applied once; (a2) each palp applied more than once in more or less strict alternation; (a3) one palp applied several times, then the other one until termination of copulation.
9. Number of insertions during one copulation; (s) "some", which may be around 5–10; (m) "many", which may be more than 10.
10. Duration of insertion; (sds) "some seconds", i.e. about 5–10 s; (hrs) more than about 2 h.
11. Duration of copulation, i.e. from first intromission until last extraction, including pauses: (sds) and (hrs) as in 10.

Species	**N**	**female co-op.[1]**	**female reject.[2]**	**insert. behav.[3]**	**"flubs"[4]**	**chel. cont.[5]**	**palpal mov.[6]**	**other mov.[7]**	**sim./ alt.[8]**	**N ins.[9]**	**dur. ins.[10]**	**cop. dur.[11]**
Atypus m.	1	6		1		2	1		a2	13	sds − 20′	~1h
Atypus p.	4			1		2			a2	m	~3′(−15′)	hrs
Avicularia a.	13	3;6;7		1;2		1			a1	2	7–10″	~20″
Avicularia h.	13			1		1			a2	1–7	~10″	
Grammostola m.	34					1			a2	s		
Phormictopus c.	16	3;6;7		1;2	g+	1	−		a1	1–2	5–7″	5–10″
Filistata i.	13	4;6;8		1;2	g+		2		a1,2	1–4	sds	sds − 70′
Loxosceles r.	3	1;3		1;3					s	2–7	~2″	7–10′
Scytodes t.	33	1;3		2	g+	2	2	1	s	1	3–52′	3–52′
Scytodes v.	3	3			g	2		1;2	s	1	2–3′	2–3′
Holocnemus c.	2								s			>1h
Holocnemus p.	3					2	2	2	s	1	~1h	~1h
Hoplopholcus f.	1	1			c?		2	2	s	1	59′	59′
Pholcus o.	>3						2;4	1;2	s	1	42′ − hrs	− hrs
Pholcus p.	4	1;2;3;6			c+	2	2;4	2	s	1	58–85′	58–85′
Segestria b.	19					2	2;3		s	1	10–65′	10–65′
Segestria f.	3					2	2		s	1	6–13′	6–13′
Segestria s.	~70				c	2	2		s	1	2–3′	2–3′
Dysdera e.	9	4				2	2	3	s	1	19–84′	19–84′
Dysdera w.	?	4				2	2		s	1	~1h	~1h
Harpactea h.	30	2;4				2	2		s	1	~5′	~5′
Harpactea r.	7						2		a2	s	~1′	5–13′
Oonops p.	4	3					3		a1?	2?	~30″	~1′
Xestaspis n.	2								s	1	3′,14′	3′,14′
Palpimanus o.	4						−		a1	2(−3)	45–60′	90–163′
Palpimanus s.	2								a			
Ero a.	?	1;2;3		3	g		−		a1	2	~1″	
Ero f.	1						−		a	1	~1″	~1″
Eresus c. x *E. w.*	2						1		a	s		
Eresus w.	19	9			g+		1		a3	s	30″–4′	− hrs
Stegodyphus l.	15	2			g+		1	2	a2	s	~2(−10)′	~15–30′
Oecobius c.	3?	1			g+		−		a1	2	sds	~5′
Uroctea d.	1						1		a2	4	~2′	~30′
Hersiliola s.	1	3;6					−		a1	2	~1″	sds
Hyptiotes p.	5	3	3	4	g		−		a2	2–12	20–40″	~5′
Polenecia p.	1			1;2			1		a2	4	− 5′	~20′
Uloborus w.	7	2;4		4	g+		−		a1	2	4–5′	20–27′
Zosis g.	1	2;3		4	g		−		a1	2	sds	
Nesticus c.	9	1;8		1					a3	~2–12		~10′?

Table 2: *Continued*

Species	N	female co-op.[1]	female reject.[2]	insert. behav.[3]	"flubs"[4]	chel. cont.[5]	palpal mov.[6]	other mov.[7]	sim./ alt.[8]	N ins.[9]	dur. ins.[10]	cop. dur.[11]
Achaearanea l.	1						–			1	sds	sds
Achaearanea t.	20			4	g+		–	2	a1,2	1 – some	~5″	
Argyrodes a.	2	1;6					–		a1	2	~2″	sds
Enoplognatha o.	>4	1			g+		–	2	a2	m	~10″	13–45′
Latrodectus s.	1						1	2	a1	1	~4′	~4′
Neottiura b.	12	3			g		1	2	a1	2	~5′	~10′
Steatoda b.	3	4;10	3;4	1;3	g+		1	2	a1	1	~1–2h	~1–2h
Steatoda c.	6	3;8		1;3	g+		1	2	a2	s	2–5′	
Steatoda g.	5	1;3;4		1;3	g+		1	2	a1	1–2	5–17′	
Steatoda p.	6			3	g		1		a2	m	−6′	15–25′
Steatoda t.	2			3	g			2	a2		1.5–3′	~40′
Theridion m.	6	10			g				a2	m	~1′	~6h
Theridion v.	5	3			g+		–	2	a2	m	~40″	~2h
Theriodiosoma g.	2	6		4	g		1	1	a2	~15	30″–6′	~90′
Labulla t.	8				g		–		a2	m	28″–4′	hrs
Lepthyphantes l.	2								a2	m		hrs
Linyphia t.	2	2;3;6					–		a2	m	30″–2′	hrs
Megalepthyphantes n.	3	6					2	2	a2	m	~10–160″	hrs
Microlinyphia p.	3?						1	2	a2	m		hrs
Neriene c.	?						–	2	a2	m		hrs
Neriene e.	?								a2	m		
Neriene m.	?				g		–	1;2	a2	m	sds – 2′	hrs
Dismodicus e.	1						1					~30′
Erigone d.	?									m	sds – 35″	87′
Erigone l.	5?						–	2	a2	m	sds – 50″	hrs
Gonatium r.	5						1		a1	2	~50′	>1.5h
Gongylidium r.	1						1	2	a2	m	~3.5′?	~1h?
Hylyphantes g.	2								a2			
Meta m.	1	2;6		1;3			–				~2″	
Metellina m.	?	2		1;3	g		–	2	a1	1?	~3′	~3′
Metellina s.	>17	3				2	–	2	a1	1	2–3′	2–3″
Nephila i.m.	23		4	2			1		a2	s	~1–5′	
Pachygnatha c.	8	4		2		3	1	2	a1	2	~1h	~2h
Pachygnatha d.	1					3	1		a1	2		23′
Pachygnatha l.	3	4	4	2	c?	3	1		a1	2	2–64′	
Tetragnatha e.	many	7				3	1					
Tetragnatha m.	2	4;7		2	c?	3	1		a2	s	5–7′	30–40′
Tetragnatha n.	5	4				3	1		a2	s		10–12′
Aculepeira c.	2	2;3		4	g				a1	2	4–30″	~7′
Agalenatea r.	1	2;3		4			–		a2	8	~5″	~15′
Araneus a.	2	6		4	g+				a1	2	~2″	~3′
Araneus c.	1	6		4	g				a1	2	30–35″	~20′
Araneus d.	25	3;10	1	4	g		–	2	a1	2(–3)	3–20″	−15′
Araneus m.	1	3	2	4	g		–		a1	2(–3)	3–20″	
Araneus q.	11	3;10	2	4	g		–		a1	2(–3)	3–20″	~1′
Araneus s.	2?	6		4	g				a2	3	~4″	~32′
Araniella c.	2	2;3;6		4	g		–	2	a1	(1–)2	15″–30′	~2–8′
Argiope b.	6	3		2a	g		–		a1	1	~8″	~8″
Argiope l.	4	4;6		2a	g		–		a1	1–2	~7″	
Cyclosa c.	2	3		4	g		–		a1	1–2	2–3′	
Cyrtophora c.	2	2;3;6		1;4	g+		–		a1	2	~7″	~25′
Gibbaranea b.	1			4					a1		~7′	
Larinioides c.	1	2;3		4			–		a1,3	3	~10″	~16′
Larinioides s.	9	3		4	g		–		a1,3	2–3	~1′	~5′
Mangora a.	2			4	g		–		a2	4–13	~7″	
Nuctenea u.	6	3;6		4	g+		–		a1,2	2–3	~10–60″	
Singa n.	1	2;3;4;6		4	g		–		a1	1	~5″	~5″
Zilla d.	3								a1	2	~2″	
Zygiella a.	2	2;3		4	g+		–		a2	2	sds	~1′ – ?
Zygiella x-n.	8	3		2;4	g		–	2	a2	3–21	20–30″	16–81′
Alopecosa a.	1						1		a1	2		74′
Pardosa a.	3	4		2p			1		a2	m	~25′	
Pirata p.	3	1		2p			1		a1	1	2′	2′
Dolomedes f.	8			2p			1		a1	1–2	2–4′	~2–5′
Pisaura m.	6			2p			1		a1	1–2	30–40′	
Oxyopes h.	1			2	g		1		a		~2′	
Oxyopes r.	2						–		a1	1	~20″	~20″

Table 2: *Continued*

Species	N	female co-op.[1]	female reject.[2]	insert. behav.[3]	"flubs"[4]	chel. cont.[5]	palpal mov.[6]	other mov.[7]	sim./ alt.[8]	N ins.[9]	dur. ins.[10]	cop. dur.[11]
Agelena g.	?						–		a3	m		~2h
Agelena l.	3?	5		2p			–		a3	m	~80″	~90′
Coelotes a.	2	5			g		1	1;2	a2	2	40–100′	hrs
Histopona t.	1	5	3				1		a2	4	3–4′	19′
Tegenaria sp.	1			3	g		1		a1			
Tegenaria a.	6			2	g		1	1	a2		2–3′	hrs
Tegenaria d.	2						1		a2	1,3	~30–60″	15″–2.5′
Tegenaria f.	2			2p	g+		1	2			~2.5′	
Tegenaria p.	1	2;3		2	g		–		a1	2	~1′	
Cedicus i.	1	5					–	2	a2	m	5–10″	~1h
Cybaeus a.	1	5					1		a	3	3–32′	93′
Argyroneta a.	17	5	1				1		a1	1(−2)	20–60″	
Dictyna a.	?						1	2	a1?	1	46–60′	45–60′
Dictyna u.	2						1		a1	2	4–62′	
Nigma w.	4	4		2p	g	3	1		a1	2	15–20′	~30–40′
Amaurobius fen.	1	2		2			–		a1	1	sds	sds
Amaurobius fer.	2	2		2			–	2	a1	1	~2″	~2″
Titanoeca q.	2	2;3		1;3	g+		–	2	a	1–3	~10′	
Mesiotelus m.	1						1;2	2	a1	2	7′,15′	~30′
Cheiracanthium sp.	1						1		a2	3	35–145′	4h
Cheiracanthium p.	2				g		1		a2	s	~10–60′	hrs
Clubiona g.	3			2	g	2	1?		a2	−m	3–22′	28–99′
Clubiona p.	1								a2			>30′
Clubiona t.	1					2	1		a		−22′	~3h
Zodarion e.	34						–		a1,2	1–3	sds	sds
Drassodes l.	1						1		a2	3	−11′	21′
Gnaphosa l.	1						1		a1	2	~1h	~2h
Gnaphosa m.	1						1	2	a1	2	57′,67′	~2h
Zelotes sp.	1						1	2				
Eusparassus w.	4			2	g		1		a2	m	sds	~1.5h
Micrommata v.	2				g		1		a1	1	hrs	hrs
Philodromus a.	11				g		1		a1	1(−2)	−25″	−25″
Philodromus d.	1						1	2	a3	3		2′
Philodromus f.	1	4					–		a1	1	~20″	~20″
Tibellus o.	2						1		a2,3	3;10	1–4′	39′;98′
Thanatus sp.	1						1		a	2	~1′;15′	
Misumena v.	3						1		a1,2	1–3	~2′	
Xysticus c.	2				g		1	1;2	a1	1–2	30–60′	~90′
Xysticus l.	some				g		1	2	a2	s	−9′	hrs?
Xysticus t.	1						1?	1;2	a2	m		31′
Evarcha f.	3						1	1;2	a1	2	−hrs	−hrs
Heliophanus c.	1						1	1	a1	1	35′	35′
Marpissa m.	2		1	2	g		1		a1	1(−2)	15–25′	15–25′
Salticus s.	9	4?		2p			1	2	a1	1–2	8–14′	
Sitticus p.	4		3		g		1	1,2		1–2	3–15′	3–15′

idea that flubs are common and widespread among spiders. If the definition is extended to include unsuccessful attempts to couple the chelicerae in species where this precedes genitalic insertion, flubs were recorded in a total of 65 of 151 species (43%) from 49 genera (48%) and 23 families (61%). This is probably an underestimate, since flubs were recorded in only 20% of the species of which only one pair was observed, but in 56% of species of which five or more pairs were observed. In 20 species, flubs were noted to be "usual", or to occur "often". More detailed analyses of such flubs and of the associated male and female morphology and behaviour may help us to understand previously unexplained structures and behaviour.

Copulatory courtship (i.e. courtship following intromission) has been used as a conservative assay to infer cryptic female choice (Eberhard, 1991, 1994; see also Peretti, 1997). It was argued that "if . . . cryptic female choice does occur, then males will be selected to induce females to perform crucial post-intromission processes, and courtship behavior after intromission has begun may often evolve" (Eberhard, 1991: 2). In a literature survey, Eberhard (1991) found that 36% of 302 insect species performed apparent copulatory courtship. If the same criteria for copulatory courtship used by Eberhard (1991) are applied to Gerhardt's data (including the exclusion of genitalic movements), the result is very similar: 32% of 151 species performed apparent copulatory courtship (Table 2, column "other movements"). If the data are analysed by genera and by families (to reduce phylogenetic bias), the same trend is evident: 37% of 102 genera and 50% of 38 families had at

Table 3: List of 7 characters of sperm induction behaviour in the spiders studied by Gerhardt. The order of species is as in Table 1. N = number of males observed.
1. Time when sperm deposition takes place, usually after copulation; (bc) before copulation; (dc) during copulation, i.e. copulation is interrupted for sperm induction; (hrs) some hours; (mins) some minutes.
2. Position of male when sperm is ejaculated and deposited on sperm web; (a) standing above web; (b) hanging below web.
3. Position of male when sperm induction takes place; (a) standing above web; (b) hanging below web.
4. Sperm induction may occur either: (i) indirectly through sperm web; or (d) directly without web between sperm and bulb. (c): sperm drop transferred to chelicerae and taken up into palps from there.
5. Bulbs applied either: (s) simultaneously to drop of sperm; or (a) alternately; (a1) each bulb applied only once; (a2) each bulb applied more than once, usually in strict alternation.
6. Bulbs either: (s) brought into contact with drop and stay there for several s up to mins; or (d) briefly dipped into drop, up to about 3″, but usually less than 1″.
7. Duration of sperm uptake.

Species	N	when occurs[1]	deposit position[2]	uptake position[3]	dir./indir.[4]	alt./sim.[5]	drop contact[6]	duration[7]
Avicularia a.	6	~48h	b	a	d	a2	d	40–128′
Avicularia h.	2		b	a	d	s	s	~2h
Grammostola m.	2		b	a	d	s?	s?	2.5h
Filistata i.	1		a	b	d	s	s	~20′
Scytodes t.	2	−48h?				s	s	11′;20′
Holocnemus c.	2	~3h			d(c)	a2	d	~4′
Holocnemus p.	1	~3h			d(c)	a2	s(~30″)	3′
Hoplopholcus f.	5	bc	b	b	d(c)	a2	d	2′
Pholcus o.	2	3–4h	b	b	d(c)	a2	d	2′
Pholcus p.	3	1.5h–4.5h			d(c)	a2	s(~30″)	3′
Segestria b.	8	50′–10h	a	a		s	s	15–38′
Segestria f.	1	~9h	a	a	d?	s	s	30′
Segestria s.	12	10′–>2h	a	a	i?	s	s	6–22′
Dysdera e.	2		a	a	i	s	s	4′,10′
Dysdera w.	2	~8h	a	a		s	s	12′,17′
Harpactea r.	3	~2–4h		a	i	a		~7–8′
Oonops p.	4	~5–11′				s	s	30–45″
Palpimanus o.	1	4h	b	b	d	s	s	8′
Ero a.	5	1–2h	a	b	d	a2	d	9–11′
Ero f.	1			b	d	a2	d	>7′
Stegodyphus l.	9	mins?	b	b	i	a2	d	4–5′
Oecobius c.	3	~12′			d(c)	a2	d	~3′
Uroctea d.	1	~1h			d(c)	a2	d	47′
Hyptiotes p.	2	~45′	b	b	d	a2	s(~30″)	26′,36′
Uloborus w.	5	60–90′	a	b	d	a2	s(~90″)	14–20′
Zosis g.	1	~1h	a	b		a		3′
Nesticus c.	1	~4.5h	b	b	d	a2	d(~3″)	~7′
Achaearanea l.	1	39′	b	b	d	a2	d	8′
Enoplognatha o.	some	20′–4h	b	b		a1?	d	3–4′
Neottiura b.	8	mins?	b	b	d	a2	d	~2′
Steatoda b.	?	~2h	b	b		a2		24′
Steatoda c.	1	~1h	b	b	d?	a2	d	7′
Steatoda p.	1	50′				a	s(20–30″)	15′
Steatoda t.	2	~20′				a2	d	5′,6′
Theridion m.	?	dc						
Theridion v.	7	dc	b	b	d	a2	d	1.75–2′
Theriodiosoma g.	2	dc				a	d	2′;3′
Labulla t.	3	dc	a	b	d	a2	d	15″–4′
Lepthyphantes l.	1	dc	a	b				~15–30″
Linyphia t.	3	dc	a	b				~15″
Megalepthyphantes n.	3	dc	a	b	d		d	~15–30″
Microlinyphia p.	?	dc	a	b		a2		1.5′
Neriene c.	?	dc	a	b		a2		~2′
Neriene m.	3	dc	a	b		a2	d	1–2.5′
Erigone d.	?	dc	b	b				
Erigone l.	4	dc	b	b	d			~30″
Gongylidium r.	1	dc	b	b	d	a2	d	~1′
Nephila i.m.	20				d		d	~1′
Pachygnatha l.	1		b	b	d	s	s	16′
Tetragnatha e.	1	~65′	b	b	d	s	s	3′
Tetragnatha m.	1	~1h	b	b	d	s	s	7.5′
Tetragnatha n.	2	~12′	b	b	d	s	s	
Aculepeira c.	1							~3′
Agalenatea r.	1	~30′				a		3′
Araneus a.	1	~2h				a2	d	5′

Table 3: *Continued*

Species	N	when occurs[1]	deposit position[2]	uptake position[3]	dir./ indir.[4]	alt./ sim.[5]	drop contact[6]	duration[7]
Araneus d.	4	~30–50′				a2	d	7–11.5′
Araniella c.	2	30′,53′	b	b	d	a2		4′,5′
Cyclosa c.	1	~10′	b	b	d	a2	d	9′
Larinioides s.	?	50′, ~1h	b	b		a		
Nuctenea u.	?	hrs?						
Zilla d.	1?	~15′	b	b	d	a2	d	2′
Zygiella a.	1	~45′	b	b		a2	d	~4′
Zygiella x-n.	5	mins?	b					~3′
Alopecosa a.	1	15′				a2		
Pisaura m.	2	40′,46′	a	a	i	a	d	−15′
Oxyopes r.	1			b	i	a2	s(~20″)	19′?
Agelena l.	2	90′	a	a	i		d	21′,24′
Histopona t.	1		a	a	i	a2	s(~10″)	17′
Tegenaria a.	1	52′			i		d	13′
Tegenaria d.	1						d	~10′
Tegenaria p.	1	~45′	a	a	i	a	d	10′
Argyroneta a.	2					a2	d	~2′
Dictyna a.	2	~30′	b?	b?	d	a2	s(2–3′)	>30′
Dictyna u.	2	~30′	b	b	d	a2	s(~40″)	~14′,18′
Nigma w.	2	73′, ~2h	b	b	d	a2	s	6′;13′
Cheiracanthium sp.	1	hrs		b	i	a	d	3′
Clubiona p.	1			b	i			
Drassodes l.	1	>2h	a	a	i	a	d	17′
Gnaphosa m.	1	~2h	a	a	i	a	d	28′
Philodromus f.	1		b	b	d	a2	d	~6′
Misumena v.	1	16′	b	b		a	d	~5′
Xysticus c.	1	>3h	b	b	d	a	d	6′

least one species with apparent copulatory courtship (the respective numbers in Eberhard's literature survey were 34% and 43%).

Eberhard (1994) demonstrated that previous accounts were strongly biased towards underestimating the frequency of copulatory courtship. When biases caused by the difficulty of observing behavioural details and lack of attention to male behaviour during copulation were overcome, the percentage of species performing apparent copulatory courtship jumped from 36% to 81%. While lack of attention to male behaviour is apparently not a major problem in Gerhardt's observations, his data may still represent underestimates. As noticed above, his sample sizes were often very small. Thus, copulatory courtship was noted in 25% of species of which only one pair was observed, but in 36% of species of which 5 or more copulations were observed. In addition, genitalic movements were not counted as courtship, because they might be involved in sperm transfer *per se* or in sperm removal rather than in copulatory courtship. If they were also counted as copulatory courtship (the latter function is supported by circumstantial evidence — Huber & Eberhard, 1997), the percentage of species performing copulatory courtship would jump from 32% to 64% (and to 67% of the genera and 82% of the families).

Concluding, Gerhardt's data support the idea that, as in insects (Eberhard, 1991, 1994), copulatory courtship is common in spiders and that sexual selection by cryptic female choice has been an important factor in the evolution of spiders.

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