BioOne COMPLETE

A REVIEW OF LEG ORNAMENTATION IN MALE WOLF SPIDERS, WITH THE DESCRIPTION OF A NEW SPECIES FROM AUSTRALIA, ARTORIA SCHIZOCOIDES (ARANEAE, LYCOSIDAE)

Authors: Framenau, Volker W., and Hebets, Eileen A.

Source: The Journal of Arachnology, 35(1) : 89-101

Published By: American Arachnological Society

URL: https://doi.org/10.1636/ST06-15.1

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/The-Journal-of-Arachnology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

2007. The Journal of Arachnology 35:89–101

A REVIEW OF LEG ORNAMENTATION IN MALE WOLF SPIDERS, WITH THE DESCRIPTION OF A NEW SPECIES FROM AUSTRALIA, *ARTORIA SCHIZOCOIDES* (ARANEAE, LYCOSIDAE)

Volker W. Framenau: Department of Terrestrial Invertebrates, Western Australian Museum, Locked Bag 49, Welshpool DC, Western Australia 6986, Australia. E-mail: volker.framenau@museum.wa.gov.au

Eileen A. Hebets: School of Biological Sciences, University of Nebraska, 348 Manter Hall, Lincoln, Nebraska 68588 USA.

ABSTRACT. Morphological modifications of the first pair of legs in addition to widespread color variations of these legs among males of closely related species have been reported in a variety of spiders. Here, the evidence for sexual dimorphism in male foreleg morphology within wolf spiders (family Lycosidae) is reviewed and shown to occur in a number of species belonging to at least seven genera in five subfamilies: *Alopecosa*, *Hogna*, *Schizocosa* (all Lycosinae) *Pirata* (Piratinae), *Evippa*, (Evippinae), *Pardosa* (Pardosinae) and *Artoria* (Artoriinae). These modifications, often in combination with distinct dark pigmentation, can be divided into three major groups: leg elongation, segment swelling and exaggerated setation (''brushes''). The latter two occur mainly on the tibial segment of the first leg. The function of these foreleg modifications has been studied most extensively in the genus *Schizocosa*. Since the courtship displays of all male *Schizocosa* incorporate a seismic component, foreleg ornamentation (namely pigmentation and associated ''brushes'') composes only one part of a multimodal courtship display. The function of this foreleg ornamentation appears to vary across closely related *Schizocosa* species and in some instances involves an interaction with the seismic signaling component. In most instances it appears to play a role in female mate choice and/or mate choice learning. In addition to reviewing lycosid foreleg modifications, we describe a new species of wolf spider, *Artoria schizocoides* from southwestern Western Australia that possesses sexually dimorphic modifications of the tibia of the first leg. Unique within the Artoriinae, males of this species carry spatulate setae on the ventral side of the tibia of the first leg that differ morphologically from other leg modifications in wolf spiders.

Keywords: Courtship display, sexual dimorphism, sexual selection, secondary sexual traits

Two main evolutionary processes that work independently or in combination are thought to explain sexual dimorphism or the morphological differences between males and females. One category relates morphological differences between males and females to a reduction in intersexual competition for resources (ecological niche partitioning) (Shine 1989; Fairbairn 1997). The second explains sexual dimorphism by differences between the sexes in the relationship between a particular trait and reproductive fitness (sexual selection or differences in reproductive roles) (e.g., Selander 1972; Hedrick & Temeles 1989; Reynolds & Harvey 1994). Sexual selection arises through competition between members of one sex for reproduction with the other sex. Here, dimorphic structures may either be used in direct aggressive encounters with members of the same sex (generally males; intrasexual selection), or used by members of the opposite sex to assess mate quality (generally females; intersexual selection) (Darwin 1871; Andersson 1994).

In wolf spiders, sexual dimorphism is evident in a multitude of forms and most differences between males and females are attributed to differences in reproductive roles. With a few exceptions (e.g., *Donacosa merlini* Alderweireldt & Jocqué 1991) females are larger than males. In most ground dwelling species, these size differences are mainly explained by a fecundity advantage of larger females (Prenter et al. 1997, 1998, 1999). Sexual dimorphism also exists with respect to differences in trophic morphology (i.e., the sizes of che-

Downloaded From: https://bioone.org/journals/The-Journal-of-Arachnology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

licerae and venom glands); these differences have been ascribed to the increased importance of foraging for females rather than an avoidance of intersexual competition for food (Walker & Rypstra 2001, 2002). Across many wolf spider species, especially those with sedentary females, males also possess comparatively longer legs than females. This leg dimorphism is thought to have evolved through an advantage of more mobile males to encounter females occupying permanent burrows (Framenau 2005a). While the above forms of dimorphism refer mainly to differences in body shape or size, dimorphic color patterns to augment body size and condition have also been argued to play an important role in the mating behavior of wolf spiders (Moya-Laraño et al. 2003).

Dimorphic patterns of foreleg pigmentation appear to be one of the most widespread and conspicuous form of sexual dimorphism among wolf spiders (Framenau, pers. obs.) and these differences in foreleg ornamentation appear to be driven mostly by sexual selection. Male foreleg ornamentation commonly involves extremely dark pigmentation or very distinct light coloration on individual foreleg segments or covering the entire front pair of legs. In some species, males possess an exaggerated form of foreleg ornamentation involving morphological modifications of the first pair of legs. These morphological modifications occur in a variety of forms in most currently recognized subfamilies of wolf spiders. Our study aims to review the evidence for sexual foreleg dimorphism within the spider family Lycosidae by compiling morphological information from the taxonomic literature. In addition, we describe a species with a novel form of male tibial ornamentation—ventral spatulate modified setae. This species, *Artoria schizocoides* n. sp., belongs to the Australasian/Pacific subfamily Artoriinae and is the only species within this subfamily known to the authors with excessive setation on the first pair of legs.

MORPHOLOGICAL MODIFICATIONS IN THE FIRST LEG OF WOLF SPIDERS

Morphological modifications of the first pair of legs in male wolf spiders belong to three major categories: (1) elongation, (2) swelling and (3) exaggerated setation, the latter two of which are most prevalent on the tibial segment (Table 1).

Elongation.—An elongation of the front pair of legs can be either subtle (e.g., *Alopecosa cuneata* (Clerck 1757) (Kronestedt 1990) or very conspicuous (e.g., *Artoria flavimana* Simon 1909) (Framenau 2002). For example, in the Palaearctic *Alopecosa cuneata*, the ratio of the length of tibia I to tibia IV is higher than in a related species of similar size, *A. pulverulenta* (Clerck 1758) (Kronestedt 1990). This elongation of the forelegs has been related to male courtship displays (Kronestedt 1990), as there is direct contact between the forelegs of a male and female *A. cuneata* in the form of the female grasping the swollen tibial segment of the male with her chelicerae (Kronestedt 1990, for more detail see below). Male *Alopecosa taeniata* (C. L. Koch 1835) also have longer legs as compared to the closely related *A. aculeata* (Clerck 1758) (Kronestedt 1990). In this case however, the elongation is not restricted to the forelegs and increased species-specific mobility of males during courtship is suggested to explain this pattern (Kronestedt 1990), although there is currently no experimental evidence to support this hypothesis.

In almost all wolf spiders the fourth pair of legs is the longest, followed by leg I, and then II and III, or less commonly III and II (expressed in the ''leg formula'': IV > I > II > III or IV > I > III > II). However, in males of the Australian *A. flavimana* mentioned above, the front pair of legs is extremely elongated and much longer than the fourth pair of legs. In females of *A. flavimana* the fourth leg is the longest, similar to both sexes of all other species in this genus (Framenau 2002, 2004, 2005b, also this study). The elongation is not restricted to a single segment as in *A. cuneata* but concerns all segments. The behavioral mating sequence of *A. flavimana* is not known and therefore the function of this morphological modification remains unclear. In male orb-weaving spiders, an elongation of the first pair of legs has been argued to be beneficial to avoid sexual cannibalism (Elgar et al. 1990).

Swelling.—The tibia of the first leg of male *A. cuneata* is not only elongated (see above) but also distinctly swollen (Fig. 1). The swollen segment does not appear to purely serve to exaggerate a visual signal during male

Downloaded From: https://bioone.org/journals/The-Journal-of-Arachnology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

courtship since the cuticle around the tibia is equipped with numerous pores (Kronestedt 1986, 1990; Dahlem et al. 1987). The pores correspond to exocrine glandular units which are composed of a large adenocyte, a long sinuous epicuticular ductile and a canal cell among supporting epidermal cells (Juberthie-Jupeau et al. 1990). During courtship, the female has to actively grasp one tibia of the male with her chelicerae before he can mount her. During this grasping it is possible that females are able to assess secretions from the male's gland tissue (Dahlem et al. 1987). A swelling of the tibia of the first leg is also evident in *Pirata cantralli* Wallace & Exline 1978 and *Pardosa vancouveri* Emerton 1917 (Dondale & Redner 1990), and described as ''slight'' for *A. pulverulenta* (see Dahlem et al. 1987), suggesting a similar morphology and function (Table 1). Scattered pores have also been found on legs of other lycosids, e.g., in *Pardosa* C. L. Koch 1847, *Trochosa* C. L. Koch 1847 (Kronestedt 1986), and *Acantholycosa* Dahl 1908 (Kronestedt & Marusik 2002) and in *Xerolycosa miniata* (C. L. Koch 1834) (Juberthie-Jupeau et al. 1990).

Color dimorphism and excessive setation (''brushes'').—The most conspicuous sexual dimorphism in wolf spiders involves differences in foreleg pigmentation between the sexes, with males possessing dark pigmentation on particular foreleg segments. In some species this pigmentation is accompanied by the addition of dense brushes of specialized setae. Male pigmentation/brushes are often referred to as secondary sexual ornamentation and are thought to play an important role in reproductive behavior. The function of male foreleg ornamentation has received a great deal of attention within the Nearctic species of the genus *Schizocosa* where 14 of the 24 described species in North America display foreleg dimorphisms (Stratton 2005). The dimorphisms of some species are considered ''slight'' (Stratton 2005) and original species descriptions state that the ''general structure and color'' of females is ''essentially as in males'' (*S. floridana* Bryant 1934, *S. maxima* Dondale & Redner 1978, *S. saltatrix* (Hentz 1844)). Without considering these species, four North American species remain that possess foreleg pigmentation only: one species with pigmentation on the tibia (*S. uetzi* Stratton 1997) and three species with pigmentation on the femur (*S. cespitum* Dondale & Redner 1978, *S. communis* (Emerton 1885), *S. retrorsa* (Banks 1911)) (Stratton 2005). Seven North American species are described as having brushes on their foreleg tibia: four species with tibia I brushes and pigmentation (*S. aulonia* Dondale 1969, *S. bilineata* (Emerton 1885), *S. salsa* Barnes 1953, *S. segregata* Gertsch & Wallace 1937; Table 1) and three species complexes with tibia I brushes and pigmentation in addition to femur I pigmentation (*S. crassipes* (Walckenaer 1837) (Fig. 2), *S. ocreata* (Hentz 1844), *S. stridulans* (Stratton 1984; Table 1) (Stratton 2005). Based upon a morphological phylogeny of the North American species, male foreleg ornamentation is suggested to have evolved independently five to six times and to have been subsequently lost two or three times (Stratton 2005).

All known *Schizocosa* species possess a seismic component to their courtship display and seismic signaling is believed to be ancestral in this genus (Stratton 2005). A survey across wolf spiders found male foreleg ornamentation to be associated with the presence of active leg-waving displays, resulting in the suggestion that all ornamented species possess multimodal courtship signaling (seismic and visual) (Hebets & Uetz 2000). In signal isolation experiments across numerous *Schizocosa* species, which vary in presence or absence and type of foreleg ornamentation, females of only brush-legged species responded to isolated conspecific visual signals while females from all species responded strongly to conspecific male seismic signals (three monomorphic species: *S. duplex* Chamberlin 1925 (Hebets & Uetz 1999); *S. rovneri* Uetz & Dondale 1979 (Scheffer et al. 1996); *S. saltatrix* (Uetz & Roberts 2002); one pigmentation only species: *S. uetzi* (Hebets & Uetz 1999); and three brush-legged species: *S. crassipes*, *S. stridulans* (Hebets & Uetz 1999), and *S. ocreata* (Scheffer et al. 1996); summarized in Uetz & Roberts 2002; Hebets & Papaj 2005). These results suggest that while seismic signaling is important across all species, visual signaling is putatively important in species with strong sexual foreleg dimorphism.

The foreleg brushes in *S. ocreata* are known to be condition-dependent (Uetz et al. 2002) and in the absence of seismic signals,

Downloaded From: https://bioone.org/journals/The-Journal-of-Arachnology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Table 1.—Morphological modifications of legs in male wolf spiders. Abbreviations: pt = patella; tb = tibia; t = tarsus, mt = metatarsus. Roman numbers refer to leg (e.g., I = leg 1).

Species	Distribution (Platnick 2006)	Morphological modification of legs	Reference
Piratinae (sensu Zyuzin 1993)			
Acantholycosa solituda (Levi & Levi 1951)	Nearctic (Rocky Mountains)	tb and mt I and II with dense cover of lanate pubescence of long, light, curved, fine setae	Kronestedt & Marusik (2002, fig. 14)
A. sterneri (Marusik 1993)	Palaearctic (Mongolia, Sth Siberia)	tb and mt I and II with dense cover of lanate pubescence of long, light, curved, fine setae	Kronestedt & Marusik (2002, figs 15, 16)
Pirata canadensis Dondale & Redner 1981	Canada	t of leg I curved	Dondale & Redner (1990, fig. 371)
P. cantralli Wallace & Exline 1978	USA, Canada	tb I & mt I swollen, mt I with many long curly setae ventrally	Dondale & Redner (1990, fig. 375)
Lycosinae (sensu Dondale 1986)			
Alopecosa cuneata (Clerck 1757)	Palaearctic	pt I & II slightly swollen, tb I extremely swollen and slightly elongated, tb II slightly swollen	Fig. 1; Dahlem et al. (1987, figs. 1c, 3, 4), Kronestedt (1986, fig. 1), Kronestedt (1990, fig. 13H)
A. pulverulenta (Clerck 1757)	Holarctic	pt & tb I & II slightly swollen	Dahlem et al. (1987, fig. 1b) (doubtful as per T. Kronestedt, pers. comm.)
A. barbipes (Sundevall 1833)	Palaearctic	tb and mt I with ventral brushes	Dahlem et al. (1987, fig. 1d)
Camptocosa parallela (Banks 1898)	Southern USA, Mexico	tb and basal half of mt I with long dense black setae	Dondale et al. (2005)
C. texana Dondale, Jiménez & Nieto 2005	Texas (USA)	tb and basal half of mt I with brush of long dark setae, more dense dorsally and ventrally	Dondale et al. (2005)
Hogna crispipes (L. Koch 1876), *H. kuyani* Framenau, Gotch & Austin 2006, *H. diyari* Framenau, Gotch & Austin 2006	Australia, Pacific	mt I with thin, hair-like setae around whole circumference	Framenau et al. (2006)
Schizocosa aulonia Dondale 1969	USA	tb I with brushy setae	Dondale (1969), Stratton (2005, fig. 23)
S. bilineata (Emerton 1885)	Nearctic	tb I with brush of erect black setae	Dondale & Redner (1990), Stratton (2005, fig. 25)
S. crassipes (Walckenaer 1837)	USA	tb I with brush of erect black setae	Fig. 2; Stratton (2005, fig. 27)

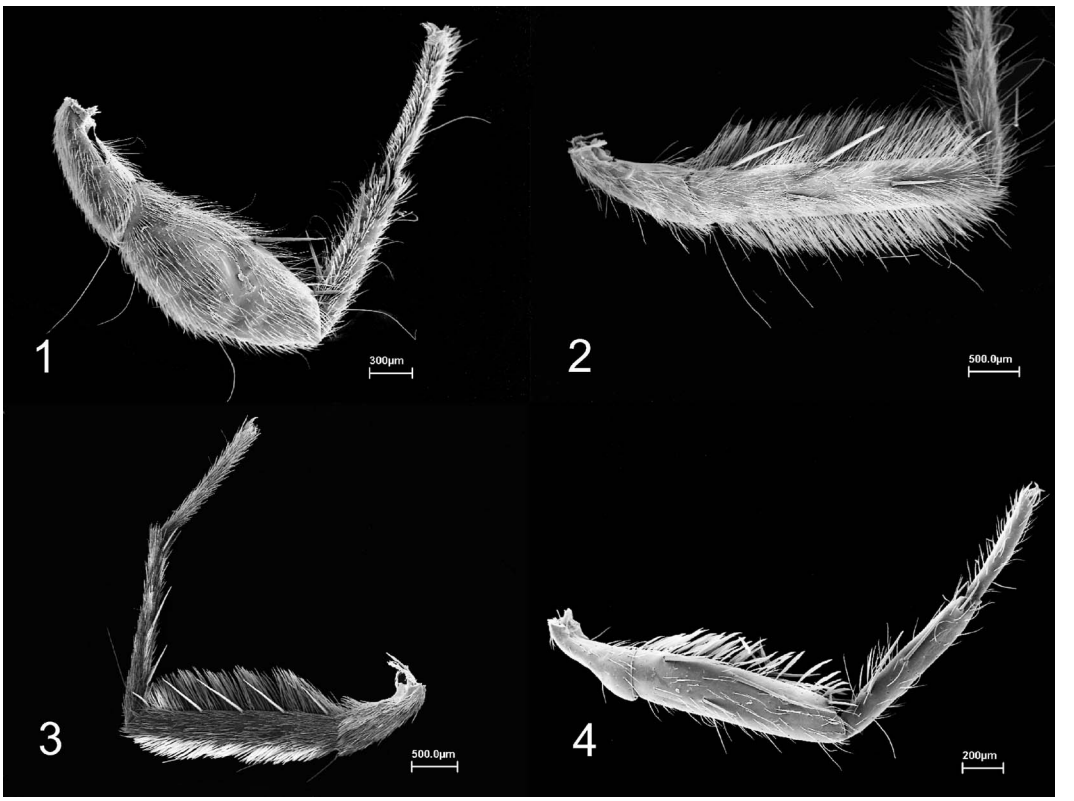
Downloaded From: https://bioone.org/journals/The-Journal-of-Arachnology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Table 1.—Continued.

Species	Distribution (Platnick 2006)	Morphological modification of legs	Reference
S. ocreata (Hentz 1844) (varying morphospecies differentiated in Stratton (2005)	Nearctic	tb I with brush of erect black setae	Dondale & Redner (1978, fig. 5), Dondale & Redner (1990, fig. 50), Stratton (1991, fig. 11; 2005, fig. 29–31)
S. salsa Barnes, 1953	USA	tb I with apical brush of erect black setae	Stratton (2005, fig. 24)
S. segregata Gertsch and Wallace 1937	USA	tb I with brushy setae mainly ventrally	Stratton (2005, fig. 26)
S. stridulans Stratton, 1984	USA	tb I with brushy setae	Stratton (1991, fig. 13; 2005, fig. 28)
Pardosinae (sensu Dondale 1986)			
Pardosa agrestis purbeckensis F.O. P.-Cambridge 1895	Western & Central Europe	t, mt & apical part of tib I with long, rigid, straight setae	Tongiorgi (1966b, fig. 21), Heimer & Nentwig (1991, fig. 860.2)
P. astrigera L. Koch 1878	Palaearctic	tb and mt I with many long, straight setae	Tanaka (1993)
P. ilguensis Nosek 1905	Turkey	tb & mt I & II slightly swollen and covered with short setae, scopulous ventrally	Tongiorgi (1966b, fig. 20)
P. mixta (Kulczyn'ski 1887)	Palaearctic	t, mt & apical part of tb I with very long lateral and forwardly directed setae	Tongiorgi (1966a, fig. 106; 1966b, fig. 23); Heimer & Nentwig (1991, fig. 859.5)
P. plumipes (Thorell 1875)	Palaearctic	tb & mt I with very long hair-like setae	Tongiorgi (1966b, fig. 22)
P. vancouveri Emerton 1917	USA, Canada	mt & t I swollen	Vogel (2004, fig. 127)
P. vittata (Keyserling 1863)	Europe to Georgia	mt II with ventrally with long setae	Tongiorgi (1966a, fig. 6)
Evippinae (sensu Zyuzin 1985)			
Evippomma plumipes (Lessert 1936)	Africa	tb I with plumose setae, mt I densely covered with white setae	Alderweireldt (1992)
E. squamulatum (Simon 1898)	Africa	tb I with plumose setae	Fig. 3; Alderweireldt (1992, fig. 1d)
Artoriinae (sensu Framenau 2007)			
Artoria flavimana Simon 1909	Australia	extremely elongated front leg	Framenau (2002)
A. schizocoides **n. sp.**	Western Australia (this study)	ventral brush of spatulate setae	Fig. 4

females have decreased receptivity to males with shaved versus intact brushes (Scheffer et al. 1996) as well as to males with smaller brushes (McClintock & Uetz 1996). Curiously, female receptivity did not vary with male ornamentation in experiments using the video playback technique, with courtship sequences involving manipulated male ornamentation (''control'' video *vs* ''no ornamentation'' video *vs* ''enhanced brushes'' video; McClintock

Downloaded From: https://bioone.org/journals/The-Journal-of-Arachnology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use



Figures 1–4.—Photographs of ornamented tibia on the first pair of legs in male wolf spiders. 1. Tibial swelling in male *Alopecosa cuneata* from Marburg, Germany (WAM T56440). 2. Tibial setae in male *Schizocosa cf.* crassipes from Oxford Campus, University of Mississippi, USA (WAM T56106). 3. Tibial setae in male *Evippomma squamulatum* from Tuinplaas, Springbokvlakte, South Africa (WAM T56480). 4. Tibial setae in male *Artoria schizocoides* from Jarrahdale, Western Australia (WAM 97/584).

& Uetz 1996). Live trials involving males with shaved brushes versus intact brushes also did not result in mating frequency differences (Scheffer et al. 1996). Ultimately, tibia I brushes in *S. ocreata* are thought to increase courtship signal efficacy in a seismically unpredictable, heterogeneous signaling environment (Scheffer et al. 1996). A pre-existing bias in females for foreleg brushes was previously suggested to have played a role in the evolution of *S. ocreata* foreleg ornamentation (McClintock & Uetz 1996); however a recent morphological phylogeny suggests that the formerly observed preference of females from a non-ornamented species (*S. rovneri*, McClintock & Uetz (1996)) for males with brushes is a retained behavioral trait (Stratton 2005).

In experiments using the video playback technique in the absence of seismic signals, females of a second brush-legged species, *S. crassipes* showed a marginally significant preference for pigmented males over non-ornamented males (Hebets & Uetz 2000), suggesting a role of brushes in female mate choice. Females of a third brush-legged species, *S. stridulans*, were significantly more receptive to video playbacks of males with enhanced brushes as compared to males with pigmentation removed (Hebets & Uetz 2000), clearly demonstrating a role of foreleg ornamentation in female mate choice. However, in a follow-up study using the same video playbacks in conjunction with seismic courtship signals from live males, female *S. stridulans* did not distinguish among visual stimuli (Hebets unpublished data), suggesting that visual signals are important only in the absence of seismic information for *S. stridulans*. Interestingly, the exact opposite pattern was ob-

Downloaded From: https://bioone.org/journals/The-Journal-of-Arachnology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

served in a pigmentation only species (*S. uetzi*), where females did not distinguish among visual stimuli using video playbacks in the absence of a seismic signal (Hebets & Uetz 2000). However, with the addition of a conspecific seismic signal, females preferred males with exaggerated ornamentation (''brushes added'' vs ''no ornamentation'' video, Hebets 2005). Follow-up experiments with *S. uetzi* suggest that the seismic and visual signals interact such that the seismic signal alters a female's visual attention (Hebets 2005). A recent study using live manipulated males questions the significance of this intersignal interaction for inexperienced females (Hebets et al. 2006) but suggests that the pigmentation observed in *S. uetzi* may be important in female mate choice learning. The importance of early experience on adult mate choice was previously demonstrated in *S. uetzi* as females were more likely to mate with a male of a familiar versus unfamiliar foreleg pattern (Hebets 2003). In the same study, females were more likely to cannibalize males possessing an unfamiliar foreleg pattern, suggesting strong selection on male ornamentation, maturation time, and/or male behavior (Hebets 2003).

While the tibia I brushes of many *Schizocosa* species have attracted much scientific attention, such morphological modifications are also found in other genera within the subfamily Lycosinae Sundevall 1833 (sensu Dondale 1986) (Table 1). *Alopecosa barbipes* (Sundevall 1833), for example, was listed as junior synonym of *A. accentuata* (Latreille 1817) by Lugetti & Tongiorgi (1969), and the presence (*A. barbipes*) or absence (*A. accentuata*) of tibial brushes was previously regarded as intraspecific variation. Subsequently, *A. barbipes* was removed from this synonymy based on morphological, behavioral and ecological differences (Dahlem et al. 1987; Cordes & Helversen 1990) and recent molecular studies confirmed the identity of *A. barbipes* as a separate species (Vink & Mitchell 2002). Bushy setae on the first tibia of males can also be found in other subfamilies of wolf spiders (Table 1). Two species of *Evippomma* Roewer 1959, *E. plumipes* (Lessert 1936) and *E. squamulatum* (Simon 1898), carry a striking fringe of black setae on the ventral and dorsal side of the first tibia (Fig. 3; also Alderweireldt 1992). The males of *Artoria schizocoides* n. sp. carry unique spatulate setae on the ventral side of their first tibia (Fig. 4; see also below). Other segments in addition to the tibiae may carry conspicuous modified setae. The males of *Pirata cantralli* Wallace & Exline 1978 have long curly setae on the metatarsi of the front legs (Dondale & Redner 1990). Some species of *Pardosa* C.L. Koch 1847 have conspicuous setae on the tarsi, metatarsi and tibia (Tongiorgi 1966a, b). Although a similar function as in *Schizocosa* is likely, there is no experimental evidence on the significance of these structures in these species.

The excessive setation observed in some wolf spider species may not function solely in a reproductive context. For example, in some Australian species currently listed in *Hogna* Simon 1885 males possess very fine, long setae around the whole circumference of the front tibia (Table 1; also Framenau et al. 2006). In contrast to the setation in *Alopecosa*, *Schizocosa*, *Evippomma*, *Pardosa* and *Artoria*, these setae are less conspicuous in live specimens and thus a role in visual signaling appears doubtful. When disturbed, males run with their front legs raised high in the air, suggesting a putative role in sensory perception and information gathering (Framenau pers. obs.). However, there is currently no experimental evidence for this function and detailed studies of setae structure may elucidate a putative role in sensory perception.

In summary, morphological modifications of the front legs in wolf spiders can be found in most of the currently recognized subfamilies (Dondale 1986; Zyuzin 1993; Framenau 2007). They are generally absent in the larger, burrowing and mainly nocturnal species, for example in the genera *Lycosa* Latreille 1804 (Palaearctic) (e.g., Orta-Orcaña et al. 1996), *Geolycosa* Montgomery 1904 (Nearctic, Palaearctic), *Tasmanicosa* Roewer 1959 and *Venatrix* Roewer 1960 (e.g., Cutler 2002) (both Australian). It appears that foreleg modifications are more common in smaller, diurnal species, which strengthens their putative function in visual signaling. Although numerous *Schizocosa* species have been the focus of elegant studies regarding female mate choice and the evolution of male foreleg dimorphism/ornamentation, much remains to be learned. Foreleg ornamentation appears to function in different ways even among closely related *Schizocosa* species, suggesting that it may be

Downloaded From: https://bioone.org/journals/The-Journal-of-Arachnology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

difficult to make broad generalizations about the evolution of sexual dimorphisms in wolf spiders. However, studies of similar morphological modifications in other wolf spider taxa are needed and will certainly add to our general understanding of the evolution of sexual foreleg dimorphism.

TAXONOMY

Artoria is an Australasian genus, currently with 23 representatives from the Philippines in the North to New Zealand in the South (Framenau 2002, 2004, 2005b; Framenau et al. 2006). However, a large number of unnamed species have been found in Australian and Pacific collections and the genus is believed to include more than 80 species in Australia alone (Framenau, personal observation). *Artoria* is characterized by a male pedipalp with a bifurcate or spoon-shaped apically directed tegular (= median) apophysis with a narrow base (Framenau 2002). Recent molecular studies suggest that *Artoria* as currently defined may not represent a monophyletic group (Murphy et al. 2006), however all currently described *Artoria* species belong to the Australasian/Pacific subfamily Artoriinae that received very good nodal support (Vink et al. 2002; Murphy et al. 2006). This subfamily can easily be identified by the presence of a basoembolic apophysis in the male pedipalp (Framenau 2007). Other genera within this clade include *Anoteropsis* L. Koch 1877 and *Notocosa* Vink 2002 (Vink 2002), *Tetralycosa* Roewer 1960 (Framenau et al. 2006) and *Diahogna* Roewer 1960 (Framenau 2006).

METHODS

Descriptions are based on specimens preserved in 70% EtOH. A female epigynum was prepared for examination by submersion in lactic acid for 24 h. Scanning electron microscope (SEM) images were taken with a Carl Zeiss Leo 1420VP (Oberkochen, Germany) after fixing the respective spider parts in Karnovsky's fixative (Sheehan & Hrapchak 1980) and osmic acid. For clarity, the illustrations of genitalia omit the setae. The morphological nomenclature follows Framenau (2002). All material investigated is lodged at the Western Australian Museum, Perth, Australia (WAM).

Abbreviations.—Measurements are in mm: total body length (TL), carapace length (CL) and width (CW), abdomen length (AL) and width (AW). Eyes: anterior row of eyes (AE), anterior median (AME), anterior lateral (ALE), posterior row of eyes (PE), posterior median (PME), posterior lateral (PLE).

Artoria schizocoides new species
Figs. 4–11

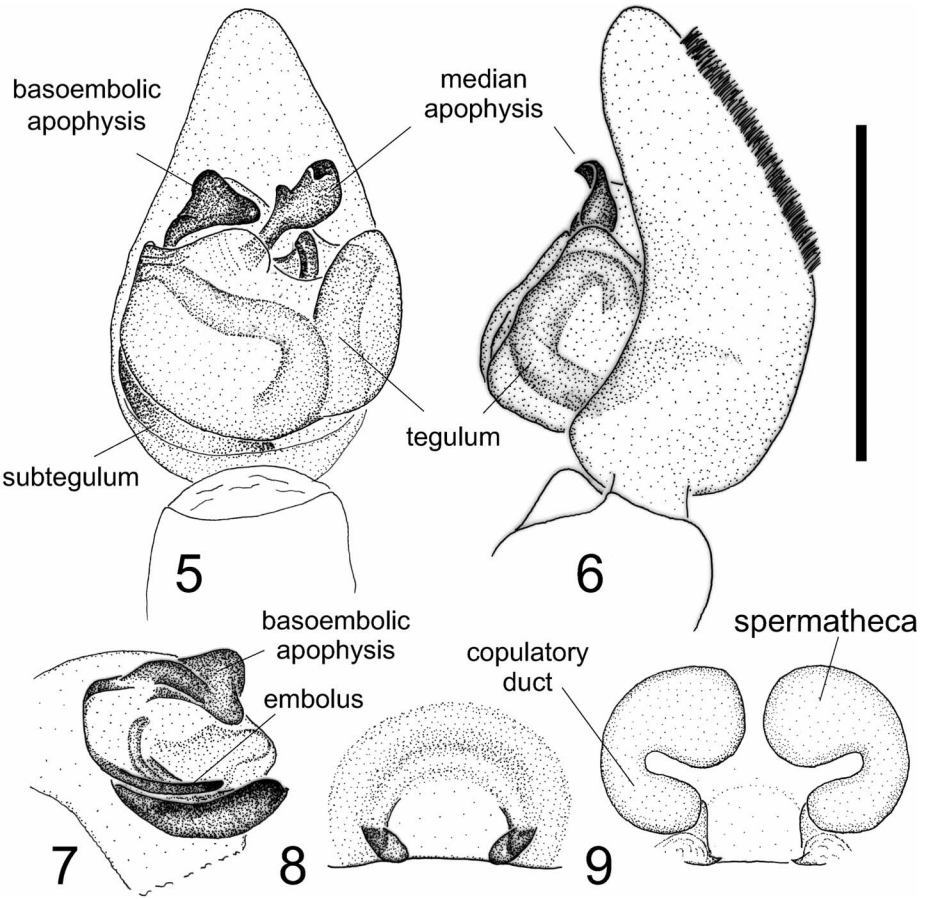
Types examined.—Holotype male, Australia, Western Australia: Bluff Knoll, Stirling Range National Park, 34°23′S, 118°15′E, 19 March 1996, S. Barrett, site 230, wet pitfall trap (WAM T53800). Paratypes: 1 male, 4 females, Bluff Knoll, Stirling Range National Park, Western Australia, Australia (34°22′56″S, 118°14′55″E), 7 September 1995, S. Barrett, site 214, 900m, pitfall traps (WAM T53799, T53875).

Other material examined.—AUSTRALIA: *Western Australia*: 1 ♂, 1 ♀, Alcoa mine, NE Jarrahdale, 32°17′S, 116°08′E (WAM T44717); 2 ♂, Alcoa mine site & forest, N and NW Jarrahdale, 34°54′S, 117°55′E (WAM 97/583–4); 51 ♂, 10 ♀, Dwellingup, 32°43′S, 116°04′E (WAM T42134, T53762–76); 1 ♂, Forth River, 45 km SE Northcliffe, 34°50′S, 116°26′E (WAM T65102); 1 ♂, 1 ♀, Jarrahdale, 32°20′S, 116°03′E (WAM T55764–5); 7 ♂, 2 ♀, Manjimup, 32°15′S, 116°09′E (WAM T53777–9); 15 ♂, 4 ♀, Mt. Cooke, 32°25′S, 116°18′E (WAM 98/2168, T53780–2, T62483, T65097; T65595); 60 ♂, 3 ♀, Mt. Lindesay, 34°50′30″S, 117°18′21″E (WAM T53807–10); 3 ♂, 1 ♀, Porongurup National Park, 34°40′56″S, 117°51′59″E (WAM T53805); 1 ♂, Quinninup, nearby, 34°26′S, 116°15′E (WAM T65093); 21 ♂, 4 ♀, Stirling Range National Park, Bluff Knoll, 34°23′S, 118°15′E (WAM T53799, 53801-3); 3 ♀, 4 juv., Stirling Range National Park, 12 km S Bluff Knoll, 34°29′S, 116°15′E (WAM T55578); 1 ♂, Stirling Range National Park, Mondurup Peak, 34°24′18″S, 117°48′44″E (WAM T53804); 29 ♂, 14 ♀, 7 juveniles, Stirling Range National Park, S face of Pyongurup Peak, 34°22′17″S, 118°19′20″E (WAM T53761); 1 ♂, 1 ♀, Stirling Range National Park, The Cascades, 34°22′29″S, 118°14′17″E (WAM T53832); 1 ♂, Sues Bridge, 50 km SW Nannup, 34°05′S, 115°40′E (WAM T65136).

Etymology.—The specific name is an adjective in apposition and refers to the wolf spider genus *Schizocosa*, the best studied genus in relation to the behavioral significance of brushed front legs in males.

Diagnosis.—*Artoria schizocoides* is the

Downloaded From: https://bioone.org/journals/The-Journal-of-Arachnology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use



Figures 5–9.—*Artoria schizocoides*; male holotype (WAM T53800) and female paratype (WAMT53875), both from Bluff Knoll, Stirling Range National Park, Western Australia. 5. Left male pedipalp, ventral view; 6. Left male pedipalp, retrolateral view; 7. Left male pedipalp, apical part of bulb; 8. Epigynum, ventral view; 9. Epigynum, dorsal view. Scale bar: 5, 6 = 0.41 mm; 7 = 0.34 mm; 8, 9 = 0.55 mm.

only *Artoria* species known to the authors of which males have spatulate setae on the ventral side of the tibia of the first leg. The epigynum of females remotely resembles that of *A. cingulipes*, however, *A. schizocoides* is much smaller and darker in colorations.

Description.—*Male* (holotype WAM T53800): Carapace: dorsal line straight in lateral view, head flanks vertical; carapace very dark brown; brown median band, as wide as PLE anteriorly but narrowing and brightening posteriorly, distinctly yellow behind fovea; indistinct brown submarginal bands; head region very dark brown, base of eyes black; dark gray radial pattern; scarce cover of short white setae, slightly denser in head region; few longer bristles in head region; one very long bristle between AME, two long bristles between ALE; AE strongly procurved. Sternum: yellow; gray pigmentation; sparsely covered with brown bristles, which are longer towards margins. Labium: brown, front end truncated and white. Chelicerae: dark brown, falces yellow; few long bristles in basal half; three retromarginal teeth, with the basal smallest, three promarginal teeth, with the medium largest. Pedipalp (Figs. 5–7, 10): cymbium dorsally with scopulate setae in apical half; apical tip of tegular apophysis bent ventrally, small protrusion on its apical edge; embolus reaches to about three quarters length of sclerotized groove of terminal apophysis (Fig. 7). Abdomen: dark olive gray; indistinct brown lanceolate heart mark in anterior half; mottled

Downloaded From: https://bioone.org/journals/The-Journal-of-Arachnology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

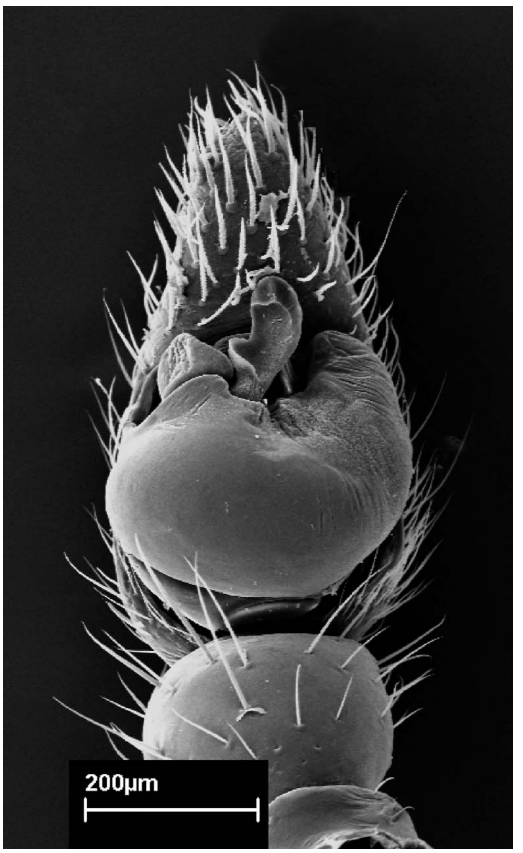


Figure 10.—*Artoria schizocoides*; pedipalp of male from Alcoa mine site and forest, N and NW of Jarrahdale, Western Australia (WAM 97/584) in ventral view (SEM).

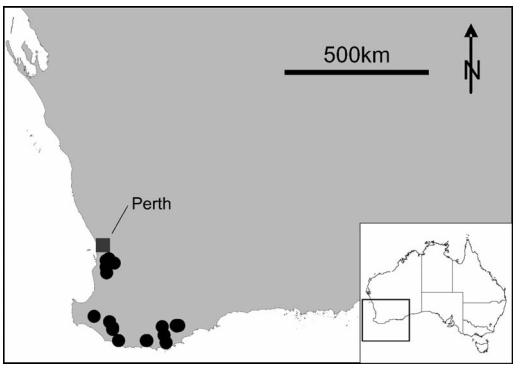


Figure 11.—Records of *Artoria schizocoides* in Western Australia.

with brown spots; sparsely covered with white and, less dense, black setae; venter yellowish gray; three indistinct gray longitudinal bands; spinnerets with brown pigmentation. Legs: leg formula IV > I > III > II; femur I dark gray, femora II–IV dorsally brown with three indistinct dark annulations, ventrally yellow; tibia I black, ventrally with dense brush of spatulate setae (Fig. 4), tibiae II–IV light brown with indistinct annulations; metatarsus I yellow with contrasting black base, metatarsi II–IV brown with indistinct annulations; tarsus I yellow, tarsi II–IV brown; spination of leg I: Femur: 3 dorsal, 1 apicoprolateral; tibia: 3 ventral pairs, 2 prolateral; metatarsus: 3 ventral pairs; 1 apicoventral.

Female (based on paratype WAM T53875): Carapace and sternum: coloration and setae arrangement as male but carapace slightly lighter; AE strongly procurved. Labium: brown, front end truncated and white. Chelicerae: light brown, claws dark brown, brown bristles medially; dentition as male. Abdomen: dorsally uniformly olive-gray; indistinct lighter heartmark in anterior half and two light patches in posterior half; covered with short brown setae; venter olive-gray with irregular small yellow spots laterally and in two longitudinal lines medially; spinnerets yellow. Epigynum, ventral view (Fig. 8): Simple and round sclerotized ring, white centrally. Epigynum, dorsal view (Fig. 9): Large kidney-shaped complex of spermathecae and copulatory ducts. Legs: Leg formula IV > II > I > III; all segments light brown with distinct annulations; spination of leg I: Femur: 3 dorsal, 1 apicoprolateral; tibia: 2 ventral pairs, 1 apicoprolateral; metatarsus: 3 ventral pairs.

Measurements: male holotype WAM T53800 (female paratype WAM T53875): TL 3.24 (5.43), CL 1.88 (2.11), CW 1.30 (1.53). Eyes: AME 0.06 (0.06), ALE 0.06 (0.06), PME 0.26 (0.26), PLE 0.20 (0.20). Row of eyes: AE 0.35 (0.43), PME 0.69 (0.75), PLE 0.75 (0.87). Sternum (length/width) 0.87/0.81 (0.93/0.81). Labium (length/width) 0.23/0.20 (0.35/0.29). AL 1.56 (3.04), AW 0.98 (2.31). Legs: Lengths of segments (femur + patella/tibia + metatarsus + tarsus = total length): Pedipalp 0.69 + 0.61 + – + 0.66 = 1.96, I 1.36 + 1.62 + 0.95 + 0.58 = 4.51, II 1.27 + 1.45 + 0.95 + 0.58 = 4.25, III 1.19 + 1.30 + 1.13 + 0.66 = 4.28, IV 1.59 + 1.82 + 1.88 + 1.13 = 6.42 (Pedipalp 0.67 + 0.75 + – + 0.52 = 1.94, I 1.30 + 1.59 + 0.93 + 0.58 = 4.40, II 1.27 + 1.50 + 1.01 + 0.55 = 4.33,

Downloaded From: https://bioone.org/journals/The-Journal-of-Arachnology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

III 1.24 + 1.45 + 1.16 + 0.61 = 4.46, IV 1.53 + 2.11 + 1.88 + 0.81 = 6.33).

Variation: males (females) (range, mean ± s.d.): TL 3.32–3.90, 3.49 ± 0.22; CL 1.73–1.96, 1.79 ± 0.09; CW 1.21–1.39, 1.28 ± 0.05; $n = 10$ (TL 3.90–5.64, 4.64 ± 0.53; CL 1.79–2.17, 1.99 ± 0.17; CW 1.27–1.50, 1.36 ± 0.09; $n = 10$).

Distribution.—Southwest Western Australia (Fig. 11).

Natural history.—*Artoria schizocoides* appears to mature in winter. Most records of adult females and males are from a period between June and September, with occasional reports from October and November. The species seems to prefer dry to moderately moist forests in mountainous regions.

ACKNOWLEDGMENTS

We are indebted to Gail Stratton and Ansie Dippenaar-Schoeman who provided material for this study. Young-Bo Lee and An-Ja Ko (National Institute of Agricultural Science, Seoul, Korea) took the SEM photographs. Torbjörn Kronestedt provided helpful and constructive comments on an earlier draft of this manuscript. Julianne Waldock initially directed the senior author's attention to the small brush-legged *A. schizocoides* in the collection of the WAM. This investigation forms part of a revision of Australian wolf spiders funded by the Australian Biological Resources Study (ABRS) to Mark Harvey (Western Australian Museum) and Andy Austin (University of Adelaide).

LITERATURE CITED

Alderweireldt, M. 1992. A taxonomic revision of the African wolf spider genus *Evippomma* Roewer, 1959 (Araneae, Lycosidae). Journal of African Zoology 106:153–167.

Alderweireldt, M. & R. Joqué. 1991. A remarkable new genus of wolf spiders from southwestern Spain (Araneae, Lycosidae). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie 61:103–111.

Andersson, M. 1994. Sexual Selection. Princeton University Press, Princeton, New Jersey. 624 pp.

Cordes, D. & O.v. Helversen. 1990. Indications for the existence of *Alopecosa barbipes* (Sundevall 1832) as a sibling species to *Alopecosa accentuata* (Latreille 1817). Results of morphological, ethological and biogeographical studies. Bulletin de la Société Européenne d'Arachnologie, hors serie 1:70–74.

Cutler, A.R. 2002. Courtship in the wolf spider *Venatrix lapidosa* (Araneae: Lycosidae). Honours Thesis, The University of Melbourne, Australia.

Dahlem, B., C. Gack & J. Martens. 1987. Balzverhalten von Wolfspinnen der Gattung *Alopecosa*. Zoologische Beträge (N.F.) 31:151–164.

Darwin, C. 1871. The Descent of Man, and Selection in Relation to Sex. J. Murray, London. 797 pp.

Dondale, C.D. 1969. Two new species of the spider genus *Schizocosa* (Araneida: Lycosidae) from the Great Lakes region. Canadian Journal of Zoology 47:751–758.

Dondale, C.D. 1986. The subfamilies of wolf spiders (Araneae: *Lycosidae*). Pp. 327–332. *In* Actas X Congreso Internacional de Aracnología, Jaca, España (J.A. Barrientos, ed.). Volume 1.

Dondale, C.D. & J.H. Redner 1990. The Insects and Arachnids of Canada, Part 17. The Wolf Spiders, Nursery Web Spiders, and Lynx Spiders of Canada and Alaska (Araneae: Lycosidae, Pisauridae, and Oxyopidae). Biosystematics Research Centre, Ottawa, Ontario, Canada. 383 pp.

Dondale, C.D., M.L. Jiménez & G. Nieto. 2005. A new genus of wolf spiders from Mexico and southern United States, with description of a new species from Texas (Araneae: Lycosidae). Revista Mexicana de Biodiversidad 76:41–44.

Elgar, M.A., N. Ghaffar & A.F. Read. 1990. Sexual dimorphism in leg length among orb-weaving spiders: a possible role for sexual cannibalism. Journal of Zoology, London 222:455–470.

Fairbairn, D.J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. Annual Review of Ecology and Systematics 28:659–687.

Framenau, V.W. 2002. Review of the wolf spider genus *Artoria* Thorell (Araneae, *Lycosidae*). Invertebrate Systematics 16:209–235.

Framenau, V.W. 2004 [imprint date 2003]. Two alpine wolf spiders of Australia: *Artoria alta* sp. nov., and the male of *Lycosa musgravei* McKay, 1974 (Araneae, Lycosidae). Proceedings of the Royal Society of Victoria 115:27–34.

Framenau, V.W. 2005a. Gender specific differences in activity and home range reflect morphological dimorphism in wolf spiders (Araneae, Lycosidae). Journal of Arachnology 33:334–346.

Framenau, V.W. 2005b. The wolf spider genus *Artoria* Thorell (Araneae, Lycosidae) in Australia: new synonymies and generic transfers. Records of the Western Australian Museum 22:265–292.

Framenau, V.W. 2006. Revision of the wolf spider genus *Diahogna* Roewer, 1960 (Araneae, Lycosidae). Journal of Natural History 40:273–292.

Framenau, V.W. 2007. Revision of the new Australian genus *Artoriopsis* in a new subfamily of wolf spiders, Artoriinae (Araneae: Lycosidae). Zootaxa 1391:1–34.

Framenau, V.W., T.B. Gotch & A.D. Austin. 2006.

Downloaded From: https://bioone.org/journals/The-Journal-of-Arachnology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

The wolf spiders of artesian springs in arid South Australia, with a revalidation of *Tetralycosa* (Araneae, Lycosidae). Journal of Arachnology 34:1–36.

Hebets, E.A. 2003. Subadult experience influences adult mate choice in an arthropod: exposed female wolf spiders prefer males of a familiar phenotype. Proceedings of the National Academy of Science USA 100:13390–13395.

Hebets, E.A. 2005. Attention-altering interactions among signals in multimodal wolf spider courtship displays. Behavioral Ecology 16:75–82.

Hebets, E.A. & D.R. Papaj. 2005. Complex signal function: developing a framework of testable hypotheses. Behavioral Ecology and Sociobiology 57:197–214.

Hebets, E.A. & G.W. Uetz. 1999. Female responses to isolated signals from multi-modal male courtship displays in the wolf spider genus *Schizocosa* (Araneae: Lycosidae). Animal Behaviour 57: 865–872.

Hebets, E.A. & G.W. Uetz. 2000. Leg ornamentation and the efficacy of courtship display in four species of wolf spider (Araneae: Lycosidae). Behavioral Ecology and Sociobiology 47:280–286.

Hebets, E.A., K. Cuasay & P.K. Rivlin. 2006. The role of visual ornamentation in female choice of a multimodal male courtship display. Ethology 112:1062–1070.

Hedrick, A.V. & E.J. Temeles. 1989. The evolution of sexual dimorphism in animals: hypotheses and tests. Trends in Ecology & Evolution 4:136–138.

Heimer, S. & W. Nentwig. 1991. Spinnen Mitteleuropas. Paul Parey, Stuttgart, Germany. 543 pp.

Juberthie-Jupeau, L., A. Lopez & T. Kronestedt. 1990. Structure et ultrastructure de la glande tibiale chez le mâle d'*Alopecosa cuneata* (Clerck) (Araneae, Lycosidae). Revue Arachnologique 9: 63–77.

Kronestedt, T. 1986. A presumptive pheromone-emitting structure in wolf spiders (Araneae, Lycosidae). Psyche 93:127–131.

Kronestedt, T. 1990. Separation of two species standing as *Alopecosa aculeata* (Clerck) by morphological, behavioural and ecological characters, with remarks on related species in the pulverulenta group. Zoologica Scripta 19:203–225.

Kronestedt, T. & Y.M. Marusik. 2002. On *Acantholycosa solituda* (Levi & Levi) and *A. sterneri* (Marusik) (Araneae: Lycosidae), a pair of geographically distant allied species. Acta Arachnologica 51:63–71.

Lugetti, G. & P. Tongiorgi. 1969. Ricerche sul genere *Alopecosa* Simon (Araneae-Lycosidae). Atti de la Società Toscana di Scienze Naturali (B) 76: 1–100.

McClintock, W.J. & G.W. Uetz. 1996. Female choice and pre-existing bias: visual cues during courtship in two *Schizocosa* wolf spiders. Animal Behaviour 52:167–181.

Moya-Laraño, J., P.W. Taylor & C. Fernandez-Montraveta. 2003. Body patterns as potential amplifiers of size and condition in a territorial spider. Biological Journal of the Linnean Society 78: 355–364.

Murphy, N.P., V.W. Framenau, S.C. Donellan, M.S. Harvey, Y.-C. Park & A.D. Austin. 2006. Phylogenetic reconstruction of the wolf spiders (Araneae: Lycosidae) using sequences from the 12S rRNA, 28 rRNA and NADH1 genes: implications for classification, biogeography and the evolution of web building behavior. Molecular Phylogenetics and Evolution 38:583–602.

Orta-Orcaña, J.M., J. Moya-Laraño & J.A. Barrientos. 1996. Precopulatory male ethograms of three species of *Lycosa* Latreille 1804 (Araneae: Lycosidae) of the Iberian peninsula. Revue Suisse de Zoologie, volume hors série II:515–522.

Prenter, J., W.I. Montgomery & R.W. Elwood. 1997. Sexual dimorphism in northern temperate spiders: implications for the differential mortality model. Journal of Zoology, London 243:341–349.

Prenter, J., R.W. Elwood & W.I. Montgomery. 1998. No association between sexual size dimorphism and life histories in spiders. Proceedings of the Royal Society of London, Series B 265: 57–62.

Prenter, J., R.W. Elwood & W.I. Montgomery. 1999. Sexual size dimorphism and reproductive investment by female spiders: a comparative analysis. Evolution 53:1987–1994.

Reynolds, J.D. & P.H. Harvey. 1994. Sexual selection and the evolution of sex differences. Pp. 53–70. *In* The Differences Between the Sexes (R.V. Short & E. Balaban, eds.). Cambridge University Press, Cambridge, UK.

Scheffer, S.J., G.W. Uetz & G.E. Stratton. 1996. Sexual selection, male morphology, and the efficacy of courtship signalling in two wolf spiders (Araneae: Lycosidae). Behavioral Ecology and Sociobiology 38:17–23.

Selander, R.K. 1972. Sexual selection and dimorphism in birds. Pp. 180–230. *In* Sexual Selection and the Descent of Man, 1871–1971 (D.C. Campbell, ed.). Aldine, Chicago, Illinois.

Sheehan, D. & B. Hrapchak. 1980. Theory and Practice of Histotechnology. Second edition. Battelle Press, Ohio. 480 pp.

Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Quarterly Review of Biology 64:419–461.

Stratton, G.E. 1991. A new species of wolf spider, *Schizocosa stridulans* (Araneae, Lycosidae). Journal of Arachnology 19:29–39.

Stratton, G.E. 2005. Evolution of ornamentation and courtship behaviour in *Schizocosa*: insights

Downloaded From: https://bioone.org/journals/The-Journal-of-Arachnology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

from a phylogeny based on morphology (Araneae, Lycosidae). Journal of Arachnology 33: 347–377.

Tanaka, H. 1993. Lycosid spiders of Japan XI. The genus *Pardosa* C.L. Koch—*paludicola*-group. Acta Arachnologica Tokyo 42:159–171.

Tongiorgi, P. 1966a. Italian wolf spiders of the genus *Pardosa* (Araneae, Lycosidae). Bulletin of the Museum of Comparative Zoology 134:275–334.

Tongiorgi, P. 1966b. Wolf spiders of the *Pardosa monticola* group (Araneae, Lycosidae). Bulletin of the Museum of Comparative Zoology 134: 335–359.

Uetz, G.W. & J.A. Roberts. 2002. Multi-sensory cues and multi-modal communication in spiders: insights from video/audio playback studies. Brain, Behavior & Evolution 59:222–230.

Uetz, G.W., R. Papke & B. Kilinc. 2002. Influence of feeding regime on body size, body condition and male secondary sexual character in *Schizocosa ocreata* wolf spiders (Araneae, Lycosidae): condition-dependence in a visual signalling trait. Journal of Arachnology 30:461–469.

Vink, C.J. 2002. Lycosidae (Arachnida: Araneae). Fauna of New Zealand 44:1–94.

Vink, C.J. & A.D. Mitchell. 2002. 12S DNA sequence data confirms the separation of *Alopecosa barbipes* and *Alopecosa accentuata* (Araneae: Lycosidae). Bulletin of the British Arachnological Society 12:242–244.

Vink, C.J., A.D. Mitchell & A.M. Paterson. 2002. A preliminary molecular analysis of phylogenetic relationships of Australasian wolf spider genera (Araneae, Lycosidae). Journal of Arachnology 30:227–237.

Vogel, B.R. 2004. A review of the spider genera *Pardosa* and *Acantholycosa* (Araneae, Lycosidae) of the 48 contiguous United States. Journal of Arachnology 32:55–108.

Walker, S.E. & A.L. Rypstra. 2001. Sexual dimorphism in functional response and trophic morphology in *Rabidosa rabida* (Araneae: Lycosidae). American Midland Naturalist 146:161–170.

Walker, S.E. & A.L. Rypstra. 2002. Sexual dimorphism in trophic morphology and feeding behavior of wolf spiders (Araneae: Lycosidae) as a result of differences in reproductive roles. Canadian Journal of Zoology 80:679–688.

Zyuzin, A.A. 1993. Studies on the wolf spiders (Araneae: Lycosidae). I. A new genus and species from Kazakhstan, with comments on the Lycosinae. Memoirs of the Queensland Museum 33: 693–700.

Manuscript received 2 April 2006, revised 17 September 2006.

Downloaded From: https://bioone.org/journals/The-Journal-of-Arachnology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use