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REVIEW

Updates and perspectives on reproductive behavior of South American wolf spiders

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Abstract. The family Lycosidae is one of the spider families with the greatest diversity of species and with varied and striking strategies. Studies on Neotropical wolf spiders have contributed new and valuable information to the field of sexual selection for several decades, having discovered cases that differ markedly from previously known patterns, not only for the family but for spiders in general. Here we provide a review of studies on reproductive biology of South American wolf spiders in recent decades, focusing on the subfamilies Lycosinae, Allocosinae and Sossipinae. The promising possibilities of the spiders of this family to test fundamental hypotheses in sexual selection and reproductive biology are highlighted, and we outline areas of particular interest for future studies. We hope that this review will inspire further studies on a broader range of wolf spider species in the Neotropics.

Keywords: Lycosidae, courtship, copulation, sexual strategies, reproductive strategies.

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Ever since the inception of studies of reproductive biology, spiders have had a prominent place (Darwin 1871). Their patterns of sexual dimorphism, courtship, and copulation have been explored with particular interest in foundational work on sexual biology (Peckham & Peckham 1889, 1890; Gerhardt 1923, 1924). Depending on each group of spiders, their sexual behaviors exhibit a rich universe of visual, acoustic, chemical, and tactile signals (Foelix 2011). The type of sperm transfer, added to the risk of sexual cannibalism, invites a detailed examination of sexual selection at pre-copulatory and copulatory levels (Huber 2005). Indeed, there are many examples of studies using spiders to investigate mate choice, cryptic female choice, sperm competition and sexual conflict (Austad 1984; Elgar 1998; Schneider & Lubin 1998; Eberhard & Huber 2010; Schneider & Andrade 2011; Peretti & Aisenberg 2014).

The family Lycosidae is one of the most speciose spider families, with 2440 species (World Spider Catalog 2022) in 11 subfamilies (Piacentini & Ramírez 2019). Elegant experimental studies on mate choice, sperm transfer and multimodal communication in wolf spiders (e.g., Rovner 1967, 1975; Tietjen 1979; Tietjen & Rovner 1982; Stratton et al. 1996; Rypstra et al. 2003) laid the foundation for later work that tested hypotheses about sexual cannibalism and sexual selection (Huber 2005; Hebets 2008).

Most wolf spiders are wanderers throughout almost their entire lives (Foelix 2011). In general, they do not build webs to capture their prey, but actively hunt them, either by following or ambushing them. The eyes, with the exception of the anterior median ones, have a crystalline layer called a tapetum that reflects light (Barth 2002). Therefore, these spiders have relatively efficient vision even in low light conditions, which affects their hunting strategies and sexual behavior. Courtship is markedly "multimodal", which means that individuals of both sexes combine chemical, visual, tactile and vibratory signals during the encounter (Table 1A) (Costa 1975; Costa & Capocasale 1984; Hebets 2005, 2008; Elias et al. 2006; Hebets et al. 2013; González et al. 2013; Aisenberg 2014; Uetz et al. 2016). During the reproductive season, the female releases contact sexual pheromones that she deposits on her silk threads (Hedgekar & Dondale 1969; Baruffaldi & Costa 2010). The male detects these signals and initiates courtship (Rovner 1967; Costa 1975; Vaccaro et al. 2010). In some species, the female responds to male courtship by shaking her front legs and orienting herself towards the male (Rovner 1967; Costa 1975; Vaccaro et al. 2010; González et al. 2013; Aisenberg 2014). The copulatory position in this family is with the male placed on top of the female facing opposite directions (Fig. 1), a position considered derived for wandering spiders (Foelix 2011). Copulations are of variable duration and patterns depending on the species and the location of copulation, which can range from an open field to a burrow (at the entrance or inside it), or on a web (Table 1B) (Capocasale 1982; Costa & Sotelo 1994; Stratton et al. 1996).

Since the early 1900s, most reports about reproductive behavior for the family have focused on North American and European species (Stratton et al. 1996). In iconic genera such as *Pardosa* CL Koch,1847 and *Rabidosa* Roewer, 1960, male courtship includes pedipalpal drumming, foreleg elevation and shaking, and abdominal vibrations; copulation occurs on the ground with one ejaculation per pedipalpal insertion, and females remain cataleptic after the male dismounts (Montgomery 1903; Rovner 1968, 1972; Rypstra et al. 2003). In South America, this kind of research began with studies performed between the mid-1970s and the 1990s (e.g., Capocasale & Costa 1975; Costa 1975, 1979, 1991, 1995, 1998; Capocasale 1982, 1990; Costa & Capocasale 1984; Costa

Table 1A.—List of pre-copulatory behaviors of selected South American Lycosidae species, with their corresponding references and their presumed associated signaling modalities: vibratory (Vib), visual (Vis).

	PRE-COPULATORY					
	Tremulation	Web tensioning	Legs elevation (legs I)	Stride walking	Substrate touch with legs I	Pedipalpal drumming
LYCOSINAE						
Lycosa poliostoma (CL Koch, 1847)	no	no		no	no	yes (Vib)
Lycosa erythrognatha Lucas, 1836	no	no	yes	no	no	yes (Vib)
Hogna gumia (Petrunkevitch, 1911)	no	no	yes	no	no	yes (?)
Schizocosa malitiosa (Tullgren, 1905)	no	no	yes	no	no	yes (Vib)
Pavocosa gallopavo (Mello-Leitão, 1941)	no	no	yes, eventually of legs II	no	no	yes (Vib)
Hogna bivittata (Mello-Leitáo, 1939)	yes	no	no	no	yes (Vib)	yes (Vib)
Hogna sp.	no	no	no	no	no	yes (Vib)
Lycosa carbonelli Costa & Capocasale, 1984	no	no	yes	no	?	yes (Vib)
Tropicosa thorelli (Keyserling, 1877)	no	no	yes	no	yes (Vib)	yes (Vib)
Lycosa inornata Blackwall, 1862	no	no	yes	no	yes (Vib)	yes (Vib)
ALLOCOSINAE						
Allocosa senex (Mello-Leitão, 1945)	no	no	no	no	yes (Vib)	yes (Vib)
Allocosa marindia Simó, Lise, Pompozzi & Laborda, 2017	no	no	no	no	yes (Vib)	yes (Vib)
SOSIPPINAE						
Aglaoctenus lagotis (Form I) (Holmberg, 1876)	yes (Vib)	yes (Vib)	yes (Vis)	yes (Vib)	no	no
Aglaoctenus lagotis (Form II) (Holmberg, 1876)	no	yes (Vib)	no	no	yes (Vib / Vis)	no
Aglaoctenus oblongus (CL Koch, 1847)	no	no	yes (Vis)	no	yes (Vib / Vis)	yes (Vib)
Diapontia uruguayensis Keyserling, 1877	?	no	no	no	yes	yes (Vib)

& Sotelo 1994). These studies allowed the advance into more specific questions on reproductive and evolutionary biology in this family. Studies on Neotropical species have contributed new and valuable information to the field of sexual selection (Macedo & Machado 2013), with cases that differ markedly from previously known patterns, not only for the family but for spiders in general (Costa et al. 2000; González et al. 2013; Aisenberg 2014; Toscano-Gadea & Costa 2016; Costa-Schmidt et al. 2017).

Here we review recent work (since the 1970s) on reproductive biology in South American wolf spiders, focusing on the subfamilies for which we have the most information: Lycosinae, Allocosinae and Sosippinae. According to the most recent phylogeny of the family, based on molecular data

Table 1A.—Extended.

PRE-COPULATORY					
Waving (of legs I in the air)	Leg scratching	Abdominal vibration	Calling ♀ (movement of legs I or II)	Presence of ornaments on legs (tufts or colour)	References
			LYCOSINAE		
yes, eventually of II (Vis)	yes	yes (Vib)	yes, eventually abdomen rotation (Vis)	no	Fernández-Montraveta & Simó (2002);Toscano-Gadea & González (2020a)
yes (Vis)	yes, intense	yes, scarce (Vib)	yes, eventually abdomen rotation (Vis)	no	Toscano-Gadea & González (2020b)
yes	?	no	yes (Vis)	no	Schwerdt et al. (2015)
yes (Vis)	no	yes (Vib)	yes (Vis)	no	Costa (1975, 1979); Fernández-Montraveta & Simó (2002)
yes, eventually of II (Vis)	yes	no	yes, and abdomen rotation (Vis)	yes, dorsal face legs I & II	Toscano-Gadea & Costa (2016)
no	no	yes (Vib)	no	no	Costa & González (2015)
yes (Vis)	no	yes, scarce (Vib)	no	yes	Costa & González (2015)
yes (Vis)	no	yes (Vib)	yes (Vis)	no	Costa & Capocasale (1984)
yes (Vis)	yes	yes (Vib)	no	no	Costa & Capocasale (1984)
yes, in an angle from 45 to 60 ° (Vis)	yes	no	yes, and abdomen rotation (Vis)	yes, coxae legs I & II, chelicerae & pedipalps	Toscano-Gadea & González (2019)
			ALLOCOSINAE		
yes	no	yes (Vib)	yes (Vib)	no	Aisenberg et al. (2007; 2009; 2010); Garcia-Diaz et al. (2015)
yes	no	yes (Vib)	yes (Vib)	no	Aisenberg et al. (2007; 2009; 2011a)
			SOSIPPINAE		
no	yes	yes (Vib)	yes (Vib/Vis)	no	Capocasale (1982); Fernández-Montraveta & Simó (2002); Stefani et al. (2011); González et al. (2013)
no	yes	yes (Vib)	yes (Vib/Vis)	no	Sordi (1996); Fernández-Montraveta & Simó (2002); Stefani et al. (2011); González et al. (2013)
yes (Vib/Vis)	no	no	yes (Vib/Vis)	yes	González & Toscano-Gadea (2020)
yes (Vib/Vis)	no	yes (Vib)	?	no	Piacentini et al. (2017), González & Toscano-Gadea pers. obs.

(Piacentini & Ramirez 2019), Lycosinae and Allocosinae are closely related, whereas Sosippinae appears to be distantly related to them, with a more ancestral position in the family. The promising possibilities presented by wolf spiders for testing hypotheses of sexual selection and areas for future research are highlighted for each subfamily and for the family as a whole in the final section of the paper.

1. Typical wolf spiders: the Lycosinae

Lycosinae is the most diverse subfamily of wolf spiders with approximately 1502 species, representing 62% of the species described for this family (World Spider Catalog 2022). They comprise the wandering wolf spiders present in a great variety of habitats, both natural (grasslands, mountains, sandy areas)

Table 1B.—List of copulatory and post-copulatory behaviors of selected South American Lycosidae species, with their corresponding references and their presumed associated signaling modality: vibratory (Vib).

	COPULATORY/POST-COPULATORY			
	Place of copulation	N° of mounts	N° of ejaculations per insertion	Body shaking
	LYCOSINAE			
Lycosa poliostoma (CL Koch, 1847)	ground	once	once	no
Lycosa erythrognatha Lucas, 1836	ground	once	once	no
Hogna gumia (Petrunkevitch, 1911)	ground	once	various	no
Schizocosa malitiosa (Tullgren, 1905)	ground	once	once	no
Pavocosa gallopavo (Mello-Leitão, 1941)	ground	once, sometimes twice	once	yes (?)
Hogna bivittata (Mello-Leitáo, 1939)	ground	once	various	yes (?)
Hogna sp.	ground	once	various	no
Lycosa carbonelli Costa & Capocasale, 1984	ground	once	various	no
Tropicosa thorelli (Keyserling, 1877)	ground	once	various	no
Lycosa inornata Blackwall, 1862	ground	once	once, and rarely twice	no
	ALLOCOSINAE			
Allocosa senex (Mello-Leitão, 1945)	burrow	various	various	yes (Vib)
Allocosa marindia Simó, Lise, Pompozzi & Laborda, 2017	burrow	various	various	yes (Vib)
	SOSIPPINAE			
Aglaoctenus lagotis - (Form I) (Holmberg, 1876)	web	once	various	yes
Aglaoctenus lagotis - (Form II) (Holmberg, 1876)	web	once	various	yes
Aglaoctenus oblongus (CL Koch, 1847)	ground/web	once	once	no
Diapontia uruguayensis Keyserling, 1877	web	once	various	no

and synanthropic (associated with human constructions) (Castro O'Neil 2010). Body size is also variable within the group, ranging from body lengths between 9 and 15 mm for species such as *Tropicosa thorelli* (Keyserling, 1877) (formerly *Lycosa thorelli*) (Costa & Capocasale 1984) and *Lycosa inornata* Blackwall, 1862 (Aisenberg et al. 2011a), to body lengths of about 30 mm for species such as *Lycosa poliostoma* (CL Koch, 1847) and *L. erythrognatha* Lucas, 1836 (Aisenberg et al. 2011a).

Sexual behavior in this subfamily has been widely studied (Stratton et al. 1996). In fact, the historical reference species for the entire family (*Rabidosa rabida* (Walckenaer, 1837) and *Schizocosa ocreata* (Hentz, 1844)) belong to this subfamily (Rovner 1967, 1968, 1972; Uetz et al. 2016). Typically, male courtship in this subfamily includes pedipalpal drumming, foreleg shaking, and abdominal vibrations (Rovner 1967; Hebets 2005; Hebets et al. 2008; Rundus et al. 2010), and there are even species in which males have ornaments on different segments of the front legs, exposed to females during courtship (*Schizocosa ocreata*) (Uetz & Denterlein 1979). Copulatory durations are highly variable within this subfamily, ranging from copulations of several seconds (*Arctosa littoralis* (Hentz, 1844)) to several hours (*S. ocreata*) (Stratton et al. 1996). Copulatory patterns also differ between species, both in the number of ejaculations per insertion (one or more), as well as in the number of insertions prior to making the pedipalpal side change (alternating an insertion with each pedipalp or performing a series of insertions with each of them) (Stratton et al. 1996; Brown 2006; Dolejs et al. 2012).

Although there are multiple studies on the reproductive biology and sexual selection in South American lycosines, these have focused on only a few species (see Tables 1 and 2). For example, in Uruguay the sexual behavior has been described in detail for only seven species out of a total of 31 species described so far for this country (Castro O'Neil 2010; Costa & González 2015). *Schizocosa malitiosa* (Tullgren, 1905) is one of the most studied South American wolf spiders, having proved to be an excellent model for studies of sexual behavior (Costa 1998; Aisenberg & Costa 2005; Useta et al. 2007; Coelho et al. 2010; Costa et al. 2011) (Fig. 1). First, *S. malitiosa* is one of the few spider species (Baruffaldi et al. 2010), along with the ctenid *Cupiennius salei* (Keyserling, 1877) (Schulz & Papke 2000) and the agelenid *Agenelopsis aperta* (Gertsch, 1934) (Papke et al. 2001), for which we know

Table 1B.—Extended.

COPULATORY/POST-COPULATORY				
Movement similar to chewing with pedipalps	Copulation duration (min)	Sexual cannibalism	Catalepsy	References
		LYCOSINAE		
yes	102.3 ± 44.3	low	yes	Fernández-Montraveta & Simó (2002); Toscano-Gadea & González (2020a)
yes	86.4 ± 29.7	low	yes	Toscano-Gadea & González (2020b)
?	125.3 ± 36.2	?	yes	Schwerdt et al. (2015)
yes	98.7 ± 29.3	no	yes	Costa (1975, 1979); Fernández-Montraveta & Simó (2002)
no	5.4 ± 4.2	yes, moderate	no	Toscano-Gadea & Costa (2016)
no	8.1 ± 3.3	no	no	Costa & González (2015)
yes	124.3 ± 35.5	?	yes	Costa & González (2015)
no	36.2 ± 10.4	no	yes	Costa & Capocasale (1984)
?	57.1 ± 17.7	no	yes	Costa & Capocasale (1984)
yes	52.0 ± 10.3	low	yes	Toscano-Gadea & González (2019)
		ALLOCOSINAE		
no	33.6 ± 16.9	yes, the male can attack the female	no	Aisenberg et al. (2007; 2009; 2010); Garcia-Diaz et al. (2015)
no	21.1 ± 5.9	no	no	Aisenberg et al. (2007; 2009; 2011a)
		SOSIPPINAE		
no	60.9 ± 55.5	no	no	Capocasale (1982); Fernández-Montraveta & Simó (2002); Stefani et al. (2011); González et al. (2013)
no	7.8 ± 3.5	no	no	Sordi (1996); Fernández-Montraveta & Simó (2002); Stefani et al. (2011); González et al. (2013)
yes	255.3 ± 58.7	no	yes	González & Toscano-Gadea (2020)
yes	200.7	no	yes	Piacentini et al. (2017), González & Toscano-Gadea pers. obs.

the composition of chemical substances involved in sexual communication and intra-species recognition. Baruffaldi et al. (2010) determined the chemical composition of the *S. malitiosa* pheromones and found that male courtship is more intense in response to silk from a virgin female compared to silk from a mated female. According to this study, the chemical signal on the silk persists for approximately three days under natural conditions (Baruffaldi et al. 2010).

Copulation in *S. malitiosa* is long and complex, and it consists of two pedipalpal mating patterns (Costa 1979). During the first copulatory pattern (of shorter duration), the male first makes a series of insertions with one pedipalp, then changes sides and makes a series of insertions with the other pedipalp, and so on. This pattern comprises 80% of the total insertions of the entire copulation. In the second pedipalpal pattern (of longer duration) the male inserts each pedipalp once, alternately (Costa 1979). This clear differentiation in pedipalpal patterns is not frequent in the other South American lycosines, nor in those of the North (Stratton et al. 1996). The reasons underlying long copulations and complicated patterns, and their functions (insemination, stimulatory, and/or other), have been studied in Uruguay from 1975 to the present. Costa & Toscano-Gadea (2003) mechanically interrupted copulations at the beginning of the second copulatory pattern and allowed the male to court and copulate with a second female. Surprisingly, both copulatory patterns generated numerous offspring, only with a small numerical superiority of the first pattern —the one with the shortest duration but with the greatest number of pedipalpal insertions. Additionally, Aisenberg & Costa (2005) tested whether copulations with artificially sterilized *S. malitiosa* males, which performed normal pedipalpal insertion patterns but were prevented from transferring sperm, generated sexual reluctance in females. These authors confirmed that sperm transfer and/or associated substances were necessary to cause a decrease in post-copulatory sexual receptivity in the females of this species. Later, Estramil & Costa (2007), González & Costa (2008) and Aisenberg et al. (2009) observed that female sexual reluctance occurs almost immediately after the end of copulation and persists for at least one month. This decrease in female sexual receptivity could be related to receptivity inhibiting substances that might be transferred jointly with the sperm (Useta et al. 2007; Michalik et al. 2012) (Table 2).

Subsequent studies suggest that the phenology and distribution of wolf spiders that live in grasslands of southern Uruguay indicate the existence of sympatry and synchrony

Figure 1.—Copulation of *Schizocosa malitiosa*. The black arrow points to one of the erect spines on the rear legs of the male, when the pedipalp hematodoca also expands (indicated by the white arrow), and ejaculation occurs. Photo: M. González and C. A. Toscano-Gadea.

between the wolf spiders *S. malitiosa* and *L. poliostoma* (Toscano Gadea & Gonzalez in prep). These studies determined that males of both species have a very similar courtship (Table 1A), mainly consisting of shaking the first and second pair of legs, pedipalpal drumming on the substrate and abdominal vibrations. These observations raised the following questions: how can *L. poliostoma* males avoid confusion when detecting the pheromones occurring in *S. malitiosa* silk? How do females discriminate the courtship carried out by the males of their own species? Recent studies allowed us to hypothesize about a differential distribution in microenvironments: we predict that *S. malitiosa* prefers areas with high plant coverage, while *L. poliostoma* prefers open landscapes with low vegetation coverage (Toscano-Gadea & González 2020a). In this way, the possibility of interspecific encounters between *L. poliostoma* and *S. malitiosa* would decrease, minimizing identification errors and avoiding the occurrence of interspecific cannibalism. However, under laboratory conditions there are males of *L. poliostoma* (a small percentage) capable of performing some (but not all) courtship units when exposed to silk deposited by *S. malitiosa* females. This does not occur in the opposite direction (i.e., *S. malitiosa* males do not recognize pheromones of *L. poliostoma* females). More studies are necessary to disentangle the sexual communication patterns between these two species.

Another Lycosinae that shares the same reproductive period and the same environment as *S. malitiosa* and *L. poliostoma* is *Lycosa inornata* Blackwall, 1862 (Toscano-Gadea & González 2019). Males of this species shake their first pair of legs in the air, but with the legs extended forward at an angle of approximately 45 to 60 degrees to the substrate (Table 1A). Females react to male courtship by rushing towards them and striking them with their bodies. If the male continues with the courtship, the female usually presses her entire body against the substrate, making lateral movements with the abdomen, a signal that allows the male to mount and start pedipalpal insertions. Similar to what was observed in *S. malitiosa, L. inornata* has two successive copulatory patterns. The first pattern presents the shortest duration but the greatest number of pedipalpal insertions (Toscano-Gadea & González 2019). Ongoing studies seek to determine whether male courtship behavior, less conspicuous than that observed in other Lycosinae species, is related to the grassland environment they inhabit and/or to the risk of being preyed upon by other, larger lycosids.

Pavocosa Roewer, 1960 and *Hogna* Simon, 1885 are other genera of Lycosinae present in South America. So far, only five species have been reported for the genus *Pavocosa*, and of these, only *Pavocosa gallopavo* (Mello-Leitão, 1941) is present in Argentina, Brazil and Uruguay. The males of this species perform similar courtship to that of other Lycosinae previously mentioned, but the most striking behavior is that of females, which seem to be much more selective than those of other species (Toscano-Gadea & Costa 2016). While males court, the females raise the first and sometimes the second pair of their front legs in the air and ostentatiously open the

Figure 2.—Adult male of *Allocosa senex* inside its burrow. Photo: M. Casacuberta.

chelicerae facing the males. If males continue with courtship, the females can advance and hit them with their body while males extend the first pair of legs seeking to separate the front legs of the females and achieve the mount. Even when males are successful in mounting, the females can make a sudden movement, which can provoke male dismount before pedipalpal insertions. This female behavior could be related to the higher rate of precopulatory sexual cannibalism in *P. gallopavo* compared to the species mentioned above (Toscano-Gadea & Costa 2016). Finally, recent studies on the sexual behavior of South American *Hogna* indicate that, similar to what has been observed in the North American species *Schizocosa ocreata* (Scheffer et al. 1996; Stratton 2005), males display dark hair tufts located at the end of their forelegs and jerk the legs vigorously during courtship (Costa & González 2015) (Table 1A). These outstanding characteristics related to visual communication used during male courtship make the genera *Pavocosa* and *Hogna* promising models for studies of sexual selection.

The remarkably active *P. gallopavo* females provide a valuable opportunity to discover and understand mate choice. This female behavior could be related to strong selection on males and/or control over the copulation duration by females. What happens if active behaviors of the females are artificially prevented? Studies in progress, with anesthetized females, seek to shed light on these topics. Moreover, more studies are needed to understand sexual cannibalism in this species. Under laboratory conditions *P. gallopavo* seems to have a higher rate of sexual cannibalism compared to other South American lycosines (Toscano-Gadea & Costa 2016). The absence of catalepsy at the end of copulation would expose the male to possible attacks when dismounting. Is the sexual cannibalism observed in this species related to the absence of catalepsy in the female? Are females exerting extreme mate choice on potential sexual partners? All these questions remain to be investigated.

2. Rule-breaking wolf spiders: the Allocosinae

The Allocosinae subfamily, considered endemic to America, includes two representatives of the genus *Allocosa* that have been models in numerous studies of sexual selection: *Allocosa senex* (Mello-Leitão, 1945) and *A. marindia* Simó et al., 2017. *Allocosa senex* inhabits sandy fluvial and oceanic coasts in Uruguay, Brazil and Argentina, while *A. marindia* inhabits coastal Uruguay and southern Brazil (Capocasale 1990; Simó et al. 2017). Individuals of both species build burrows on the sand with silk lined walls (Costa 1995) (Fig. 2). These burrows are their refuges during the day and in the coldest months of the year; they will emerge at night for foraging or to search for sexual mates during the summer (Costa 1995; Aisenberg 2014). Contrary to what has been reported in typical wolf spiders from the northern hemisphere and most spiders, both species show atypical sexual size dimorphism and sexual patterns (Aisenberg et al. 2007; Aisenberg & Costa 2008; Aisenberg 2014). Males are larger than females and females are the ones who actively seek mates; the females detect the presence of volatile pheromones emitted by males, who remain inside their burrows (Aisenberg et al. 2007; Aisenberg & Costa 2008; Aisenberg et al. 2010; Aisenberg 2014). Once the male burrow is detected, the female begins the courtship by waving legs I and II and vibrating the abdomen up and down, while the

Table 2.—Contribution of South American lycosids to the knowledge of diverse aspects of sexual selection. The acronyms indicate which of the cited characteristics are (without a question mark), or could be (followed by a question mark), linked to different contexts of sexual selection. MC = Mate Choice, IC = Intrasexual Competition, NG = Nuptial Gift, ART = Alternative Reproductive Tactics, SeC = Sexual Conflict, CC = Copulatory Courtship, CFC = Cryptic Female Choice, SD = Sperm Dumping (particular case of CFC), SC = Sperm Competition, OSR = Operational Sex Ratio.

	Contexts and stages of intersexual interactions		
		Mating Stage	
Model species	Reproductive ecology of premating	*Precopulatory*	*Copulatory*
Schizocosa malitiosa (Lycosinae)	OSR 1:1[1] Mobile females and males. Abundant females all year round, abundant males in autumn[1].	Female pheromones associated with silk are present while moving in order to promote male courtship[2,3].	Long copulation, with two copulatory patterns: Pattern 1 with an approximate duration of 40 minutes and 80% of the total insertions. Pattern 2, 60 minutes and 20% of total insertions[4,5,6].
Allocosa senex (Allocosinae)	OSR 1:1[1] Mobile females, sedentary males*[2]. Males build burrows in order to mate[2]. Males emit volatile pheromones[3]. Temporal monogamy *[4]. * see **Reproductive ecology of postmating**	Females prefer to copulate with males that offer deeper burrows[2]. **MC** Males prefer virgin females and in good body condition[2]. **MC** Males perform sexual cannibalism[5]. **MC**	Females perform body shaking in demand of more ejaculations[6]. **CC? MC?**
Allocosa marindia (Allocosinae)	OSR<1[1] (more females than males) Males build burrows to mate[2]. Males emit volatile attraction pheromones[3].		
Aglaoctenus lagotis (Sossipinae)			
Form I	OSR 1:1[1] Low population density[2]. Mobile males (abandon web), sedentary females[1,3]. Phenology: Autumn sexual period (Mar-May). Egg sac and hatchling laying, spring (Sep-Nov). Females spend the winter copulated; males die[1].	Female pheromones associated with web that promote courtship[6]. Males court copulated females for longer and with less intensity[2]. **MC?** Female pheromones associated with web in order to promote courtship[4]. Contact? Volatile? Males court females copulated for a longer time. **MC?** Copulated females prefer males in better body condition[2]. **MC**	Rupture of copulating bulbs in rematings[5]. Females perform female jerks[6]. **CC/CFC?** Whitish remains in epiginum, with encapsulated spermatozoa[7]. **SD?** Females perform female jerks during copulation[6]. More in copulations with males in worse body condition[8] **CC/CFC?** Whitish remains in epigynum, with encapsulated spermatozoa[7] **SD?** Cannibalism in copulation, frequent after the third remating. Cannibalized males transfer the least sperm[8]. **SeC?**
Form II	OSR 1:1[1] High population density[2]. Mobile males (abandon web), sedentary females[1,3]. Phenology: Continuous sexual, and egg sac and offspring period (August-January)[1].		

male responds by vibrating his abdomen from within the burrow and approaching the female (Aisenberg et al. 2007). This pattern of behavior is repeated many times while the male guides the female towards the end of the burrow, at which point a change of positions occurs, with the female moving towards the bottom of the burrow and the male towards the entrance of the burrow (Aisenberg et al. 2007).

Copulation in both species of *Allocosa* occurs in the typical lycosid copulatory position but within male burrows, and consists of numerous and successive mounts and dismounts, a

Table 2.—Extended

Contexts and stages of intersexual interactions		
Mating Stage		
Postcopulatory	Reproductive ecology of postmating	References
Existence of quiescent females after copulation (catalepsy). Females copulate few times (1 or 2)[7,8]. Possible transfer of RIS during Pattern 1 generating reluctance to remate in females[9,10]. **SC?**	Females build silk tubes during egg sac development[11]. Long-lived females build 4 egg sacs[8,12] and possibly live through 2 reproductive periods. Extensive egg sac care[13].	[1] Costa (1991) [2] Costa (1975) [3] Baruffaldi et al. (2010) [4] Costa (1979) [5] Costa & Sotelo (1984) [6] Bardier et al. (2015) [7] Aisenberg & Costa (2005) [8] González & Costa (2008) [9] Estramil & Costa (2007) [10] Aisenberg et al. (2009) [11] Capocasale & Costa (1975) [12] Capocasale et al. (1984) [13] Pintos et al. (2021)
Male donates burrow to female[2]. **NG?** Collaborative burrow closure[2]. **IC?**	Females can remate[7]. **SC/CFC?** Some males show the strategy of locating and courting females inside burrows from other males[7]. **ART?**	[1] Aisenberg et al. (2011c) [2] Aisenberg et al. (2007) [3] Aisenberg et al. (2010) [4] Aisenberg (2014) [5] Aisenberg et al. (2011b) [6] García-Díaz et al. (2015) [7] Bollatti (2020)
		[1] Aisenberg & Costa (2008) [2] Aisenberg & González (2011) [3] Aisenberg et al. (2010)
Females and males copulate few times, monogamous tendency[2,5]. Females and males copulate many times, a polygamous tendency[2,8] **SC/CFC?**	Offspring remains in the maternal web for more than a week. They eat prey captured by female[9]. Females die shortly after the hatchlings hatch[9]. Offspring remain in maternal web for more than a week. They eat prey captured by female. Trophalaxis?[4]	[1] González et al. (2014) [2] González et al. (2019) [3] Sordi (1996) [4] Stefani et al. (2011) [5] González (2018) [6] González et al. (2013) [7] González (2015) [8] Abregú et al (2019) [9] González & Toscano, obs pers.

characteristic not widespread in Lycosidae (see Table 1B; Aisenberg et al. 2007; Aisenberg & Costa 2008; García-Díaz et al. 2015). Once copulation is complete, the male leaves his burrow and blocks the entrance with sand while the female deposits silk from the inside (Aisenberg et al. 2007). Thus, the female will remain inside the burrow and there she will build her egg sac, emerging once the young are ready to disperse (Aisenberg et al. 2007; Aisenberg & Costa 2008; Postiglioni et al. 2008). Males and females of both species are selective during mating; males prefer to copulate with virgin females,

while females prefer to copulate with males that build deeper burrows (Aisenberg et al. 2007; Aisenberg & Costa 2008; Aisenberg & González 2011). Postiglioni et al. (2008) reported that females of both species can lay up to four successive egg sacs after copulation during a reproductive period, with the first egg sac being the most successful in terms of number of eggs. According to Aisenberg et al. (2007), the mating system of these species is sequential monogamy, where the females mate again after the dispersal of the progeny.

Though these two *Allocosa* species have many similarities in their life history traits, there are also several differences between them. *Allocosa senex*, for instance, is a longer-lived species, which can survive for two reproductive seasons as adults (Aisenberg & Costa 2008). In turn, it shows a wider distribution that includes very different environments such as freshwater fluvial beaches with coarse sand and marine coasts with brackish water and fine sand beaches (Bollatti et al. 2017). Individuals living in two geographically distant locations (one in Uruguay and the other in Central Argentina) show marked differences in their sexual repertoire. Couples from Central Argentina engage in a greater number of ejaculations, male abdominal vibrations, and male touches on the female cephalothorax. Females of *A. senex* from Central Argentina exhibit shorter latencies between copulation and the construction of the egg sac (as early as 24 hours after copulation, in contrast to females from Uruguay, which require approximately one month before the construction of the egg sac) (Bollatti 2020). These reports suggest that this species can alter the expression of a trait depending on environmental conditions.

Another essential characteristic of *A. senex* is high male selectivity in mating decisions (Table 2). Males not only prefer to copulate with virgin females, but also with those who have good body condition, and they can reject and even cannibalize non-preferred females (Aisenberg et al. 2009, 2011b). This extreme male selectivity makes sense considering that males need to rebuild a burrow to obtain refuge and generate new mating opportunities with virgin females, a process that reduces their mating opportunities compared to other polygynous wolf spiders (Aisenberg 2014). Furthermore, De Simone et al. (2019) reported that the construction of a burrow has negative repercussions on the weight of males; therefore, the donation of the burrow is an energy-costly investment. It has been reported that males from central Argentina may vary their reproductive tactics depending on the context; they are able to locate, court and copulate with females that are still housed within the burrows of their previous sexual partners (Bollatti et al. 2022). These observations suggest that males could evade the costs of building and donating their burrow, revealing, in turn, that females from the same locality remate with males that do not offer burrows (Bollatti et al. 2022).

The selective pressure exerted by female mate preferences could have both morphological and behavioral repercussions on males. According to Albín et al. (2018), *A. senex* males have more silk glands related to the production of attachment discs that give stability to burrows, compared to females and juveniles. On the other hand, Carballo et al. (2017) found that, after being rejected by a female in her first exposure, males lengthen their burrows more frequently than those who were not exposed to potential mates and show a more intense response after being rejected by a virgin female. This indicates that *A. senex* males have plasticity in their burrowing behavior and respond according to the availability and choosiness of the females, to ensure success in future matings (Carballo et al. 2017). However, the females of this species are not only demanding during courtship; García-Díaz et al. (2015) found that during copulation, females perform body shakes that act as signals for the male to make more frequent ejaculations, suggesting the occurrence of copulatory communication between the sexes. Furthermore, Bollatti (2020) reported that females perform a greater number of body shakes when males have better body condition.

In contrast, *A. marindia* males survive for only a single reproductive period and, although they are selective when making reproductive decisions, sexual cannibalism of females is absent or very rare (Table 2) (Aisenberg & Costa 2008; Aisenberg & González 2011). Lerette et al. (2015) reported the occurrence of *Wolbachia*, an endosymbiont bacterium that is capable of manipulating the reproduction of its hosts, favoring the reproduction and survival of infected females in order to increase its own transmission (Charlat et al. 2003; Duron et al. 2008; Goodacre & Martin 2013), in a population of *A. marindia*. One of the consequences of infection with *Wolbachia* is a female-biased sex ratio in some populations, something that has been observed in the population of *A. marindia* from Marindia, Canelones, Uruguay (Aisenberg & Costa 2008). Ongoing studies are trying to determine if the bias towards *A. marindia* females found in the field and after rearing of clutches in the laboratory (Aisenberg & Costa 2008) occurs due to infection with this bacterium.

The research thus far leads to several new lines of inquiry. Investigating whether other species in the subfamily Allocosinae exhibit reversal in sex roles will allow us to determine at what point in their phylogenetic history this mating system arose and what factors drive the maintenance of these atypical sexual behaviors in *A. senex* and *A. marindia*. We wonder if there is also geographical variation in other *A. senex* characteristics such as density of individuals, variation in operational sex ratios, and behavioral traits such as female remating rates. In addition, we wonder whether the alternative reproductive tactic (ART) of mating with a female without providing a new burrow is unique to *A. senex* males from the central Argentina population, and whether this tactic is also used by *A. marindia* males. Since ARTs have been reported to be fixed or dynamic depending on the stability of the physical and social environment (Oliveira et al. 2008), it would be interesting to study if they are fixed or dynamic in *A. senex*. Moreover, it would be a challenge to unveil the signal or cue that the non-donor males detect to locate potential mates, since pheromones have been reported only for males in both species. Another intriguing question is whether ARTs can affect male paternity, or if females can exercise cryptic choice in this context. We are also interested in determining how commonly ARTs and female remating occur under natural conditions in *A. senex*.

3. Web-building wolf spiders: the Sosippinae

With four genera (*Aglaoctenus* Tullgren, 1905, *Diapontia* Keyserling, 1877 , *Hipasella* Mello-Leitão, 1944 and *Sosippus*

Figure 3.—Male of *Aglaoctenus lagotis* (Form II) pulling the female web during courtship. Photo: Carlos A. Toscano-Gadea.

Simon, 1888) and 20 species, the Sosippinae subfamily is one of the smallest within the wolf spiders (World Spider Catalog 2022). Although web-building species have also recently been found within Venoniinae, Piratinae and Lycosinae (Murphy et al. 2006), less than 1% of the lycosids are reported to be web-builders (González et al. 2015a), and Sosippinae is the only subfamily which has confirmed members that live their whole lives in webs (Brady 1962; Dondale 1986). Being sedentary and constructing webs are exceptional traits for a family characterized by wandering (Foelix 2011) and places the few web-building species in a central position to reveal if this ecological habit is ancestral or derived in the family and to determine the factors shaping its origin.

The reproductive biology of the Sosippinae is almost unknown (see Tables 1A, 1B). There is some data about maternal care in *Sosippus floridanus* Simon, 1898 (Brach 1976), about courtship and copulation in *Diapontia uruguayensis* Keyserling, 1877 (Aisenberg et al. 2011b; Piacentini et al. 2017), and *Aglaoctenus* (South American) is the most-studied genus from this subfamily. Although there is still only fragmentary data on *Aglaoctenus oblongus* (CL Koch, 1847) (González & Toscano-Gadea 2020), there are several studies on *Aglaoctenus lagotis* (Holmberg, 1876) (Capocasale 1982; Sordi 1996; Santos & Brescovit 2001; Stefani & Del-Claro 2011; Stefani et al. 2011; González et al. 2013, 2014, 2015a,b, 2019; González 2018; Abregú et al. 2019).

*Aglaoctenus lagoti*s (Fig. 3) is an annual species with a unique reproductive period (Santos & Brescovit 2001; González et al. 2014). Sexual encounters occur in the funnel-webs of the female. Male courtship occurs on the platform (or sheet) of the funnel and mainly consists of web stretching and jerking (Table 1A). To date, this is the only wolf spider reported to display behavioral units commonly attributed to typical web-building spiders (González et al. 2013). Similar behaviors are common in Araneidae, Theridiidae and Agelenidae families (Ross & Smith 1979; Robinson & Robinson 1980; Singer et al. 2000; Galasso 2012; Bosco & Chuang 2018) and differ from the leg waving and pedipalpal drumming typically displayed by courting male wolf spiders (Costa 1975; Chiarle et al. 2013; Uetz et al. 2016). Considering these web-based behaviors and the apparent absence of male ornaments functioning as visual signals, the courtship of *A. lagotis* seems to involve mainly vibratory signals (Table 1A), although no studies have focused on these communication channels. About chemical signals, there is only one study that indicates the occurrence of female pheromones (based on behavioral evidence) involved in mate localization and triggering courtship, although it is not clear whether these are only contact chemical signals or also volatile ones (Stefani et al. 2011).

Copulation in *Aglaoctenus lagoti*s (in the typical position of Lycosidae, Fig. 1) occurs at the entrance of the funnel tube and consists of multiple ejaculations (expansions of the hematodocha) per insertion (González et al. 2013) (Table 2), which is considered ancestral to the family (Stratton et al. 1996). The couple shakes repeatedly during mounting, and the dismount occurs during or immediately after one of these movements, when the male leaps backwards out from the funnel tube and rapidly escapes through the platform of the web (Stefani et al. 2011; González et al. 2013). Females never become cataleptic (González et al. 2013) and after some copulations, they show whitish remains with encapsulated spermatozoa in their epigynes (González 2015) (Table 2). Each female remains in the same web throughout the period she carries her single egg sac and the spiderlings (González et al. 2014).

This species has two distinct "forms" that have been postulated to be different species (González et al. 2015b; González et al. 2022), with strong differences between their reproductive biology and sexual behavior (González et al.

2015b). The southern form (Form I) shows lower population density, shorter sexual period, more synchronous female and male phenology and significantly longer copulations than the northern form (Form II) (González et al. 2013, 2014) (Table 1B). Moreover, although females and males can remate under laboratory conditions, their mating system appears essentially monogamous under natural conditions (González 2015; González 2018; González et al. 2019; González & Toscano-Gadea, in prep.), with males suffering explosions of their hematodochae that irreversibly prevent future copulations (González 2018). In the northern form (Form II), on the contrary, females and males remate repeatedly (Abregú et al. 2019; González et al. 2019) (Table 1B).

Aglaoctenus oblongus (CL Koch, 1847) is the other species of the subfamily in which studies of its reproductive biology are in progress. This species is found in webs during some stages of its life, such as during the development of the egg sac (in dense silk tubes with smaller platforms and closer to the ground than *A. lagotis*) and during molting events, but it maintains a wandering habit the rest of the time (Piacentini 2011; González & Toscano-Gadea, unpublished data). This mixed habit seems to be reflected in their reproductive traits as well. Thus, although it remains unknown where copulations occur in the field, in the laboratory sexual encounters can occur in or out of the web (González & Toscano-Gadea, unpublished data). Courtship behavior is different from that observed in *A. lagoti*s (González & Toscano-Gadea 2020). Instead, leg waving is common (Table 1A), and males display dark hair clusters on the first pair of legs (González & Toscano-Gadea pers. obs.) implying visual signaling. Copulations last several hours, and males perform a single ejaculation per insertion and chew their pedipalps between each insertion (Table 1B). Females sometimes move and walk with males mounted on top of them, but they can remain cataleptic after mating (González & Toscano-Gadea, pers. obs.) similarly to reports for other wolf spiders (e.g., Costa 1979; Toscano-Gadea & González 2019; González & Toscano-Gadea 2020).

Although the information is preliminary, the phenology of this species suggests overlapping generations, with females building several egg sacs throughout their lives. This is in contrast to the single egg sac produced by *A. lagotis* (Santos & Brescovit 2001; González et al. 2014) but is a common scenario in many other wolf spiders (Capocasale & Costa 1975; Fernández-Montraveta & Ortega 1990; Pintos et al. 2021). The females remain in the silk tube, a structure that resembles brood chambers that many typical lycosids build during the period when they carry their egg sacs (Capocasale & Costa 1975; Costa & Simó 2014), and which they abandon for offspring dispersal (González & Toscano-Gadea, unpublished data).

Finally, Piacentini et al. (2017) report copulations of *Diapontia uruguayensis* in the absence of web and with durations of several hours, under laboratory conditions. The females usually move with the male on top of them and might become cataleptic after dismounting. The courtship behavior reported is dissimilar to those observed in *A. lagotis,* but females and sub-adults are found in small webs in the field. González & Toscano-Gadea (pers. obs.) working with individuals in webs, have observed behaviors during courtship that resemble those of *A. lagotis*.

Many questions related to reproductive biology and sexual selection remain to be answered in this group of lycosids. Increasing knowledge of sosippines from other latitudes and trying to encompass the different degrees of web dependency present in this subfamily, as well as studying communication channels involved during sexual encounters, will shed light on the origin and evolutionary loss of webs in wolf spiders. Interestingly, it has been recently reported that typically wandering lycosids (*Lycosa erythrognatha*, *L. poliostoma* and *Schizocosa malitiosa*) invade the webs of *Aglaoctenus lagotis* under natural conditions and evict the owners (sometimes adult females) (González & Toscano-Gadea 2021). How frequent are these evictions? How do they affect the reproductive lives of the females removed from their webs? These are some of the questions we are currently working on. Field studies, while challenging, will be particularly important for determining natural dynamics of sexual encounters and mating decisions in these species with both sedentary sexes. At the same time, testing the factors underlying the appearance of whitish remains covering female epigynum (possibly mating plugs?) after certain copulations in *A. lagotis* (the first case as far as we know in lycosids), as well as why couples from different species shake their bodies during copulation, would be very valuable for learning about possible mechanisms of mate choice in the group. The shakes during copulation, probably initiated by females, have not been commonly reported, but this scenario is changing for some species now being studied in South America. This and other traits involved in sexual interactions that do not have clear functions (such as catalepsy and chewing of pedipalps), also provide opportunities to understand reproductive processes and selective forces shaping the sexual strategies reported for this family.

4. Conclusions and perspectives for future studies

Although Lycosidae has been one of the most studied spider families in terms of sexual behavior, research to date has mainly focused on very few species and therefore there is still much to learn about this very abundant and speciose family. In fact, if we consider South America, as far as we know, studies about the reproductive biology of species belonging to the Artoriinae, Zoicinae and Pardosinae subfamilies are scarce or absent. Although it exceeds the scope of this work, comparative phylogenetic analyses and studies of phylogenetic inertia will undoubtedly led to great contributions in this taxonomically chaotic family. Until now, and with the most recent phylogeny of Lycosidae (Piacentini & Ramírez 2019), fewer than half of the species addressed in this study have been included in the phylogenetic analysis of the family. So, much more work is needed to advance our understanding of the systematics of this family.

The information in this review shows the promising characteristics of this group for studies of reproductive biology and sexual selection, due to its very good response to the experimental conditions of laboratory rearing and maintenance, and the innumerable possibilities of elegant manipulations for testing hypotheses related to female choice, sperm competition and sexual conflict (Eberhard 2004). However, studies that test the mating systems of wolf spiders under natural conditions are still very scarce. The technology to which we now have access allows us, for example, through

fixed cameras that film in high quality, to monitor the activity of individuals in the field and record the number of visits by potential partners. Also, the application of capture-mark-recapture studies, spatial mapping and radiotelemetry techniques—still scarcely used for wolf spiders but applied to other arachnids (Janowski-Bell & Horner 1999; Nørgaard 2005; Hamilton 2008; Gaffin & Curry 2020)—could provide valuable information about mobility and navigation patterns to help understand the diversity and dynamics of mating strategies described in this group.

Other traits that have still been little explored are the variations in female attraction throughout the reproductive cycle, and how consecutive and numerous matings influence female and male receptivity. Likewise, there are very few studies in wolf spiders that link genital morphology with the sexual behavior of the species. An exception is the study by Poy et al. (2019), which focused on the copulatory mechanics of *Agalenocosa pirity* Piacentini, 2014. Detailed studies of genital morphology and sections of frozen in-copula couples facilitated analyses of the sexual behaviors present in this species. These kinds of studies, combined with experimental manipulations of certain traits, may shed light on the selective forces shaping sexual behaviors. A promising idea is that of artificial insemination, which would make it possible to separate the effects of insemination per se from other variables such as the stimulation received by the female during copulation.

Likewise, behavioral plasticity, learning, and animal personalities are topics of great current debate among evolutionary biologists and would be interesting to explore further in spiders (Schneider & Andrade 2011). The few examples in this group come mostly from studies of predatory or anti-predatory behavior (Jakob et al. 2011; Jackson & Nelson 2011). However, reproductive behaviors offer very fertile scenarios to test hypotheses related to these topics and there is a recent explosion of work on these issues that could be extrapolated to South American wolf spiders. In particular, species with widespread distributions offer excellent opportunities to test how geographic variation can shape morphological and behavioral traits associated with reproduction.

The Neotropics show a heterogeneous mix of fragmented climates shaped by its location between two oceans with contrasting temperatures and altitudes (Macías-Ordóñez et al. 2013). It has been widely reported that selection on sexual characteristics can vary spatially and temporarily according to environmental heterogeneity (Ryan et al. 1990; Ishikawa et al. 2006; Briceño et al. 2007; Amezquita et al. 2009; Olivero et al. 2015). As the Neotropical region is the most diverse in the world (Macías-Ordóñez et al. 2013), we expect to find a richer range of reproductive adaptations among the wolf spiders inhabiting this wide region compared to those inhabiting temperate zones of the Northern Hemisphere. This situation places wolf spiders in an ideal position for comparative studies to understand the evolution of the diverse and fascinating reproductive tactics reported for this group.

This review is not intended to be an exhaustive report on existing studies of the reproductive biology of South American wolf spiders. Our goal has been to highlight models that exemplify the wide range of possibilities that the different species of wolf spiders in the Neotropical zone can represent, with very diverse and striking strategies, in an effort to inspire future studies on these issues in reference to the family.

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