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REVIEW

Solifuge (camel spider) reproductive biology: an untapped taxon for exploring sexual selection

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Abstract. The exploration of new and diverse animal groups in the study of sexual selection is both necessary and important to help better understand broad patterns and test sexual selection hypotheses regarding the evolutionary origins and maintenance of reproductive tactics and associated traits. Solifuges are, in this matter, an exceptional group and very little explored from the sexual selection point of view. At first glance, mating is apparently quite simple and conserved within this arachnid order, but solifuge reproductive behavior is unique among arachnids and more diverse than previously thought. In particular, these voracious animals appear to exhibit high sexual conflict, as males need to avoid being eaten by their aggressive female partners and mating encounters in some species involve periods of apparently male-induced female inactivity during sperm transfer. The extent to which reproductive encounters are coercive versus collaborative, however, remains largely unknown. In this review, we begin with a historical perspective of sexual behavior research in solifuges. We then discuss precopulatory mating patterns, the role of the female and male during mating, sexual dimorphism, and the influence of sexual selection during different stages of mating. In addition, we explore cases of sexual cannibalism and provide an updated analysis of how postcopulatory sexual selection may be acting on these amazing arachnids. This review shows that there is much to be done in this extraordinary group of animals.

Keywords: Sexual selection, sexual conflict, cryptic female choice, sperm competition, Solifugae

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Traditionally, within the field of sexual selection, several groups of arthropods have been used as animal models for questions related to mate choice, sperm competition, cryptic female choice and sexual conflict (Darwin 1871; Andersson 1994; Eberhard 1996; Birkhead & Møller 1998; Arnqvist & Rowe 2005). For example, insects have been widely studied due to their small body size, easy collecting and laboratory maintenance, relatively short life cycle and often curious reproductive features (Thornhill & Alcock 1983; Shuker & Simmons 2014). In recent decades, however, we have begun to expand our arthropod taxa to include studies of mating, sperm transfer and sexual selection in arachnids (Weygoldt 1990; Choe & Crespi 1997; Herberstein 2011). Although the use of more traditional arthropod "models" (e.g., *Drosophila*) has been beneficial for the study of evolution and sexual selection, it is now vital to include new and different animal models. Exploring the variability observed between taxa is critical for understanding the evolution and function of different reproductive strategies, and the incorporation of additional taxa will help us to make much more accurate generalizations and comparisons (Zuk et al. 2014).

Initially, arachnid studies focusing on topics of sexual selection were mostly limited to spiders (order Araneae). This is due to their great diversity, wide distribution, easy access and, above all, the diversity of reproductive strategies and behavioral patterns exhibited before, during, and after copulation (Choe & Crespi 1997; Eberhard 2004; Huber 2005). Gradually, research has been extending to other arachnid groups – groups that also encompass great behavioral richness. Scorpions (order Scorpiones), for example, have attracted a fair amount of research on topics including the functional morphology of spermatophores, sperm competition, and the use of pheromones in reproductive interactions (Jacob et al. 2004; Peretti & Carrera 2005; Vrech et al. 2014; Romero-Lebrón et al. 2019). In opilionids, or harvestmen (order Opiliones), studies have been carried out on sexual dimorphism, mating systems, life history, and pheromones, among other aspects (e.g., Munguía-Steyer et al. 2012; Buzatto et al. 2014; Machado et al. 2015; Stanley et al. 2016).

In the search for relatively unexplored animal taxa that might contribute significantly to our understanding of sexual selection's role in evolution, solifuges (Order Solifugae) appear to be a promising group. Solifuges encompass a fairly diverse order that inhabits mainly arid and semi-arid zones (Maury 1980, 1998; Beron 2018). Similar to other arachnid groups mentioned previously, solifuges display a range of different mating strategies and have a number of interesting sexually dimorphic traits that make them attractive study organisms for both comparative and experimental purposes. They are oviparous and their method of sperm transfer is unique among arachnids, always mediated by male chelicerae (Punzo 1998a; Harvey 2003; Bird 2015) – the same powerful appendages that are used to shear apart their prey.

Like most arachnids, solifuges are solitary and often cannibals. In such cannibalistic taxa, it is often hypothesized that male courtship must be very elaborate, to entice receptive females and/or reduce a female's aggressive tendencies. Alternatively, however, males may engage in more coercive behavior to acquire matings. Such coercion sets the stage for potential conflicts between female and male reproductive interests. Indeed, numerous accounts of putatively coercive behavior have been documented in solifuges, yet the degree to which a particular behavior is coercive versus collaborative remains an open question.

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In an attempt to determine the extent to which solifuges may be a useful model for the study of sexual selection, sexual conflict, and the evolution of animal reproductive behavior, we review the literature on solifuge sexual behavior through the lens of sexual selection. We begin with a brief history of the study of solifuge sexual behavior. We then review solifuge sexual behavior in the context of sexual conflict and cooperation. We focus specifically on the following aspects: male courtship and associated female behavior, courtship (or persuasive behavior) and apparent coercion by males, sexual dimorphism (with special attention to chelicerae), and the potential for postcopulatory sexual selection. We also include a brief synthesis of the existence of sexual cannibalism in this group. We conclude with a discussion of how increased knowledge of solifuge mating systems can lend insight into our understanding of sexual conflict and cooperation and their role in the evolution of reproductive traits, including behavior.

Historical overview.—There are published data on mating behavior for 17 species belonging to only five out of 12 extant families of this fantastic group of arachnids (with more than 1000 described species in about 140 genera) (Prendini 2011; Bird 2015; Beron 2018): (i) Galeodidae Sundervall, 1833, (ii) Solpugidae Leach, 1815, (iii) Eremobatidae Kraepelin, 1901, (iv) Ammotrechidae Roewer, 1934, and (v) Daesiidae Kraepelin, 1899 (see Supplementary Table S1, online at https://doi.org/10.1636/JoA-S-20-037.s1). In the early 1900s, Heymons (1902) provided the first work on this group, on *Galeodes caspius* (*Galeodes caspius subfuscus* Birula, 1937). This early study, which characterized the general pattern of mating, importantly laid the foundation for future research. Heymons (1902) described how the male approaches the female and touches her with his pedipalps; and how she (if receptive) enters a torpor-like state (a total lack of movement). Following this, the male holds her body with his chelicerae (mouthparts), moving her around until she rests on one side so that she lies laterally. She remains immobile throughout. The male massages the predominantly inactive female's genital area with his chelicerae until the genital operculum is opened. He then deposits a sphere of sperm (spermatophore) on the soil, takes it with his chelicerae, and introduces it into the female genital opening. The male restarts the cheliceral massages and eventually withdraws. The female suddenly regains movement and moves away.

This first description, very detailed for the time, was only followed by new observations on other species 60 years later. The 1960s were the "golden age" of contributions in the mating of solifuges. Amitai et al. (1962) provided observations of *G. sulfuripes* Roewer, 1934, observing that the female inactivity (i.e., "torpor-like state" in the classic terminology) was coincident with the male's pedipalps touching those of the female, and remarked that the female regained movement gradually. The work of Cloudsley-Thompson (1961, 1967) on *G. granti* Pocock, 1903 is added to this period. The pattern of this latter species differs somewhat from that of other Galeodidae. Mainly, the female is not so inactive, as she can present some subtle movements during mating. Junqua (1962, 1966), as part of detailed work on the biology of another Galeodidae, *Othoes saharae* Panouse, 1960, provided even more details. He observed that the male performed bites to the female's body coincident with her entering the inactivity state. These "bites" were performed while he rotated her body with his front legs and touched her body with the pedipalps. In all reported cases, the female's abdomen is directed forward, or anterior over the prosoma, at an angle of ~135 degrees to the horizontal resting posture of the abdomen.

In this same decade, Muma appears on stage with his works on the mating behavior of some Eremobatidae (Muma1966a, 1967): *Eremobates palpisetulosus* Fichter, 1941, *E. nodularis* Muma, 1951 and *E. durangonus* Roewer, 1934. These contributions not only added information on a new solifuge family, but also offered terminologies for the phases of sexual interaction. Previous terms used such as "assault" (e.g., in Junqua 1966) inspired the first of the phases that Muma recognized—"attack." In this phase, the male touches the female for the first time, including gripping her body with the chelicerae. This is followed by a "contact" phase, which includes sperm transfer. Finally, Muma describes the "release" phase in which the couple separates and the female, if inactive, starts to regain mobility. In the Eremobatidae, Muma also noted a new, rocking behavior during attack phase—a forward and backward movement of both sexes, while seizing each other, in which they lift their bodies, resting on the last three pairs of legs on the ground (Muma 1966a). If the female is not receptive, she may attack the male or move away. An interesting observation also made by Muma (1966a) is that the male may increase what could be interpreted as courtship (i.e., touches of legs and pedipalps to the female's body) if the female tries to interrupt the mating before sperm transfer. However, males also continually manipulate the female's body with his legs and pedipalps regardless of female's movement.

Although the females studied through this period in the family Eremobatidae seem to adopt an inactive state similar to the one described in the Galeodidae, in Eremobatidae, this state sometimes may not be so pronounced, and the female can regain movement during the contact phase (Muma 1966a, see the following sections). Also, in contrast to the Galeodidae, which exhibit indirect sperm transfer aided with the chelicerae, eremobatid males pass the sperm directly from the male gonopore to the female gonopore, and empirical data shows that mating lasts longer in Eremobatidae than in Galeodidae (Eremobatidae mean: 9 ± 5.4 min.; Galeodidae mean: 4 min., see Supplementary Table S1). Muma (1966a) also cites the occurrence of cannibalism in *E. palpisetulosus*.

After the 1960s, new work was not published on solifuge mating until the end of the 1980s, with a study carried out by Wharton (1987). This new work focused on a species of another family, Solpugidae, *Metasolpuga picta* (Kraepelin, 1899) (Wharton 1987). The peculiarities of this work are that it is based on (i) a diurnal solifuge and (ii) field observations. This research raised the possibility of chemical signaling between mates, as males appeared able to locate female burrows without any visual cues. Vision in this group is very poor, they cannot form images and would only distinguish light and darkness (Klann 2009). Importantly, although female *M. picta* could exhibit aggressive displays, there was never cannibalism observed towards the male. Unlike the previous two families, *M. picta* males deposit the spermatophore over the female's body, precisely in the female's dorsum instead of the substrate (Galeodidae), or directly to the female genital opening (Eremobatidae). Similar to some other species studied, the torpor-like state of the female occurs only if she is receptive and is coincident with the male quickly touching the female prosoma and chelicerae with their pedipalps. However, the physiological nature of this state and what exactly triggers it is still a matter of debate.

In the late 1990s, Punzo (1997, 1998a, b) added more observations on the mating of eremobatids, particularly in *E. palpisetulosus* and *E. marathoni* Muma, 1951, which are quite similar to the pattern of the rest of the family, in particular, *E. durangonus*. His contributions lie in more quantitative data regarding the sequence of each of the phases of mating, as well as percentages of the areas grasped on the female body, among other aspects. Notably, Punzo did not observe cases of cannibalism.

Nearly ten years later, in the early 2000s, two works provided data for other families; published three years apart. Although data of sexual dimorphism, especially in chelicerae, were already noted before, both publications offer the first data on sexual dimorphism associated with courtship and grabbing behaviors, e.g., longer pedipalps and pedipalp spines in males to hold females. They also provided new approaches to assess other morphological differences between the sexes associated with mating. These traits were described in an Ammotrechidae, *Oltacola chacoensis* Roewer, 1934 (Peretti & Willemart 2007) and a Daesiidae, *Gluvia dorsalis* (Latreille, 1817) (Hrušková-Martišová et al. 2010). Also, in the latter, authors added new details to the mating of Galeodidae *G. caspius subfuscus*, initially described by Heymons (1902). Peretti & Willemart (2007) also gave evidence for the function of the flagellum as a sperm holding organ in *O. chacoensis*.

These previous works also included a novel sexual selection framework for solifuges, as the authors tried to interpret the patterns of sexual behavior observed during the mating. Terms such as "coercion", "forced copulation", "sexual conflict", among others, were introduced in connection with solifuges. The observed mating behavior led the authors to these terms since in both *O. chacoensis* and *G. dorsalis,* the rapid initial grasping of the female by the male chelicerae is not followed by a female torpor-like state. On the contrary, the female remains moving, shaking her body vigorously at times, even trying to bite the male. However, in both species, there is a short period of seconds of stillness when the male inserts the spermatophore into her genital opening. Also, in both species, copulatory courtship occurs, but this is explicitly highlighted only in *O. chacoensis* (Peretti & Willemart 2007). In the case of *G. caspius subfuscus,* the male grasps the female, chewing on her body, and, as in *G. dorsalis* and *O. chacoensis*, causes wounds to appear on her body. Indeed, female injuries are evidenced and presumed to be inflicted by spines of male pedipalps (in *O. chacoensis* and *G. caspius subfuscus*) or by male chelicerae (in *G. dorsali*s necrosis on the female legs was observed) (Peretti & Willemart 2007; Hrušková-Martišová et al. 2010).

Most recently, a Galeodidae species (presumably *Galeodes olivieri* Simon, 1879 but the species was not verified) was studied by Pandram & Sharma (2018). Its behavior appears similar to that reported by Hrušková-Martišová et al. (2010) in *G. caspius subfuscus*. In the study, Padram and Sharma noted that the chances of the male being able to copulate will depend on the female's positive response, e.g., whether she elevates her body to allow the male to hold her with chelicerae – suggesting the importance of female mate choice.

Finally, Rowsell & Cushing (2020) have reanalyzed the mating of the eremobatid *E. pallipes* (Say, 1823), offering an updated comparison with the rest of the species of the genus studied to date. The mating sequence of this species coincides quite well with what Muma (1966a) had already pointed out for other eremobatids, except for the observation now of the existence of male juddering (quick forward and backward vibration of the whole male body) and female revival (a three stage return to movement and awareness) following inactivity. Interestingly, they describe for the first time the use of the male's suctorial organs in mating. These organs, located at the tip of the pedipalps, are eversible and were previously associated with prey capture and smooth surface climbing (Cushing et al. 2005; Klann et al. 2008; Willemart et al. 2011). Rowsell & Cushing (2020) also find that unsuccessful matings coincide with males deviating from the usual sequence or failing in achieving the usual time range for a certain behavioral sequence. This could be linked with the description of Muma (1966a) of what could be described as copulatory courtship but was not analyzed extensively. In addition, Rowsell & Cushing (2020) were able to obtain some virgin individuals and observed that some of them were able to remate.

Sexual conflict in the mating of the solifuges.—In synthesizing our baseline knowledge about solifuge matings, particular patterns begin to emerge. Specifically, we can categorize mating interactions into three major types, each with varying degrees of potential male coercion, female resistance, male courtship and/or persuasion, and female facilitation (Table 1). Given the potential contribution of collaborative and coercive behavior across species, we suggest that solifuges are a promising group to study how reproductive behavior is balanced within the framework of mate choice and sexual conflict. In this next section, we discuss the potential roles of male courtship or persuasion, female responses, mating system and male coercion, and sexual dimorphism.

Male persuasion and/or coercion.—Even in species studied to date, the extent to which male behavior can, or should, be considered courtship and thus persuasive, or coercive and potentially reflective of sexual conflict, remains unclear (Table 1). Furthermore, male coercion does not necessarily exclude persuasion. Although in some species, the overall reproductive scenario may appear coercive (this can be clearly seen in the introductory descriptions made by Heymons in his work of 1902), males may also perform subtle behaviors of possible stimulating functions. Contact of the female by males, for example, are frequently observed in other arthropods and are often interpreted as male behavior that functions to persuade a female to mate (Eberhard 1996; Peretti & Aisenberg 2015). In solifuges, we observe similar behavior of males touching females in specific places and/or at specific moments of mating.

In *O. chacoensis*, the male performs what could be considered copulatory courtship immediately before and during sperm transfer (Peretti & Willemart 2007). Despite apparent behavior to restrain the female, males also tap the female with their pedipalps and legs throughout the entire mating sequence. Tapping seems to vary in intensity and is

Table 1.—Potential scenarios of sexual selection operating on solifuges according to the type of behavioral patterns mostly observed in females and males during mating. Female behavior during mating refers to the level of female quiescence during mating. The terms “low”, “high” and “medium”, are simply relative for purposes of comparison among the pool of species that have been studied to date in order to mention what might be expected for some possible patterns. Abbreviations: SD. Sexual dimorphism.

						Opportunities for:		
Female Behavior during Mating	Predicted Behavioral/ Morphological traits	Families Studied to Date	Precopulatory Courtship	Sexual Coercion	Copulatory Courtship	Precopulatory Female Choice	Cryptic Female Choice	Sperm Competition
Complete Inactivity	- Low SD in pedipalpal spines(1) - Low SD in chelicerae - Low female injury during mating(1) - Low potential sexual cannibalism/ female aggression?(1) - High Polyandry - Mixed patterns of sperm precedence(2)	Galeodidae Solpugidae Ammotrechidae(3) Eremobatidae	Yes Yes Yes(3)	No/Yes?(4) No No(3)	Yes? Yes? Yes(3)	Yes Yes Yes(3)	Yes? Yes? Yes(3)	Yes Yes Yes(3)
Partial Inactivity	- Medium SD in pedipalpal spines - Medium SD in chelicerae - Injury to females during mating - Potential sexual cannibalism/ female aggression? - Polyandry - First male sperm precedence	Eremobatidae	Yes	Yes?	Yes	Yes	Yes	Yes
Complete Activity	- High SD in pedipalpal spines - High SD in chelicerae - Injury to females during mating - High potential sexual cannibalism/ female aggression - Monogamy or low polyandry - Last male sperm precedence?	Daesiidae Ammotrechidae(3)	No Yes?(5)	Yes Yes	Yes Yes	Low? Low?(5)	No? Yes(6)	No? Yes(6)

(1) Except for *Galeodes caspius subfuscus*.
(2) Sperm precedence may be very variable according to species (See text and refer to Warren, 1939; Vachon, 1945; Klann, 2009).
(3) *Titanopuga salinarum*
(4) *G. caspius subfuscus*.
(5) *Oltacola chacoensis*.
(6) Cannot be ruled out in low polyandry species like *O. chacoensis*.

more intense just before sperm transfer. In addition to tapping, males also move their chelicerae (the chewing-like movements already mentioned) while in contact with the female's internal genital region. It has been suggested that these cheliceral movements may serve as genital stimulation (Peretti & Willemart 2007) and/or may facilitate sperm transfer (in *G. dorsalis*) (Hrušková-Martišová et al. 2010). Such functions, however, have not been confirmed yet. To test a putative stimulatory or attractive function of male movements during reproductive encounters, rigorous studies are needed to establish a relationship between the pattern of movements and female acceptance of males and/or male paternity patterns. Even following sperm transfer, for example, females may be able to skew paternity by cryptic female choice (Eberhard 1996).

When analyzing solifuge's general morphology, an interesting feature is chaetotaxy, the arrangement of setae or hairs on the exoskeleton. We observe setae all over the body, including on the chelicera. Along with many features in solifuge functional morphology, sexual dimorphism in the cheliceral setae is obvious, but remains unexplored. Extensive sexual dimorphism, for example, appears among the fixed finger cheliceral setae located dorsally and retrolaterally (see Bird 2015 for a precise description of positioning over the chelicerae). These setae are thought to take a part in mating. This zone of the chelicera meets the female genital area during mating (see Peretti & Willemart 2007; Hrušková-Martišová et al. 2010). This could result in stimulation of the female. For example, male solifuges may stimulate females with the series of thin long hair-like setae located on the dorsal surface of their peltidium (Solifuge prosoma). This hypothesis comes from the observations made in males from *O. chacoensis*, that show a denser area with longer thin hair-like setae compared to females (Peretti & Willemart 2007). During the contact phase of reproductive encounters, the female's body is notably positioned to rest over this region, coinciding with the presence of these sexually dimorphic hair-like setae. This peculiar positioning allows for the possibility that these hair-like setae stimulate the ventral part of the female's abdomen. Though this remains speculative, this function could be readily tested through manipulative studies that remove male hair-like setae and observe potential alterations in mating encounters. There are other hypotheses though, that do not relate to mating. Pocock (1895), for example, suggested that these setae may aid to protect the flagellum when resting, and Bird (2015) suggests that these setae may function in males as chemo or mechanoreceptors. The actual function of these setae is unknown and needs further analysis.

Ultimately, much of the previous research on solifuge reproduction has presented male behavior from a coercive perspective, commonly using terms such as "assault" or "attack" and focusing on the often-coincidental female inactivity. In fact, Heymons (1902) introduces the mating paragraph saying that the observer could not help feeling sorry for the female who endures such harsh treatment. Despite apparent superficially aggressive male behavior, however, there are numerous opportunities for males to simultaneously (or alternately) engage in behavior that may stimulate females. Such stimulation may be important for female mate choice.

In support of a prominent role of female mate choice in solifuges, fifty-four percent of the mating interactions in one study of *O. chacoensis* did not pass the contact phase due to intense female shaking – a behavior that seems likely to be indicative of female resistance to mating. Prior to this point in the reproductive encounter, males performed encircling and tapping; behavior that females may use to assess males. The intensity of female shaking (which influences a male's success) may thus be directly related to male tapping behavior. This possibility has not yet been examined in detail. Alternatively, or simultaneously, tapping may directly aid in increasing female inactivity, though whether females are cooperative in quiescence or not remains unknown. As suggested by Hrušková-Martišová et al. (2010), female resistance/quiescence may reflect female receptivity, but it also may reflect coercion or exploitation by males; or a combination of both. Further research is needed to fully disentangle the roles of male persuasion, female choice or complicity, and/or male coercion or conflict in solifuge reproductive behavior.

Mating patterns and female behavior: Across studied species, and based upon observable female behavior, there is variation in the amount of movement females exhibit after the first bodily contacts with the male. Specifically, there is a general gradient of female activity (at least for an observer). The degree of activity appears to be accompanied by a particular degree of male coercion. In this section, we categorize female activity levels into three distinct states. With available data, these states are known to occur in different species, i.e., with the few observations that have been made and published, it has not been observed that the same species exhibits more than one type (See Table 1).

Female exhibits a state of complete inactivity.—Descriptions of species that show this characteristic show that the female acquires a state of total stillness, which continues throughout the sexual interaction. This response appears to be initiated by a rapid contact from the male's pedipalps to the female's body and is followed, to varying degrees, by an intermittent gripping of her with his chelicerae. During the interaction, the male touches the female with his pedipalps and legs, and then rubs her external and internal genital area with his chelicerae using chewing-like movements. This first stage of cheliceral movements stops for an instant and the male deposits a drop of sperm. In general, the sperm is dropped on the ground in *Galeodes* species (e.g., Hrušková-Martišová et al. 2010), but it is placed on the body dorsum of the female in *M. picta* (e.g., Wharton 1987), and there is direct placement via gonopore-gonopore contact in Eremobatidae (Muma 1966). The male then pushes the sperm into the female's genital atrium. Immediately afterwards, the male restarts the chewing-like movements. After a short period of time, the male moves away and the female regains mobility, or as in the case of Eremobatidae, the male moves away after the female regains activity. In matings with almost complete female inactivity, males exhibit genital massaging, i.e., chewing-like movements inside the female's genital opening, pre- and post-sperm transfer (see Supplementary File Table S1).

It is difficult to know why this state of complete inactivity occurs in the female. It has been speculated that it is somehow produced by the sudden touch of legs of the male, cheliceral reinsertion into the female genital opening, pedipalp contact and the adherence of the male's suctorial organs, and/or cheliceral body grasping of the female, or a combination of these (e.g., Junqua 1966; Punzo 1998a; Hrušková-Martišová et al. 2010; Rowsell & Cushing 2020). In support of the cheliceral grasping hypothesis, several previous authors have noted that they were able to induce a state of complete inactivity in the female by suddenly and forcefully grasping a female with their fingers or forceps (Heymons 1902; Berland 1932; Junqua 1966; Wharton 1987). The mechanism underlying this observation is briefly hypothesized in Heymons (1902), and recently reviewed in Rowsell & Cushing (2020). However, this subject requires further study.

Another more profound question arises when dealing with the female's inactivity state in solifuges. What factors have led to the evolution of such a behavior? We could speculate various outcomes but will here suggest only two, one from the male's point of view and one from the female's. In the first case, males might benefit from inactive females, as sperm transfer would not be challenged, and the chance of sexual cannibalism would be reduced drastically. From the female's perspective, an inactive state might save energy or resources that might otherwise be used to avoid or challenge coercion or coercive behaviors and could reduce the risk of injury. Alternatively, or additionally, the capacity of the male to produce the state of inactivity in females could be a form of precopulatory evaluation, or female choice.

Almost complete inactivity is commonly observed in the already mentioned Galeodidae (with different details in the behavioral patterns; see Supplementary Table S1), some Eremobatidae (Rowsell & Cushing 2020), Solpugidae (Wharton 1987), and in Ammotrechidae in *Titanopuga salinarum* Iuri, 2021 (Peretti, unpub. data). Particularly in Galeodidae, *G. granti* seems to be a little different than *G. caspius* and *G. sulfuripes*. Cloudsley-Thompson (1967) is precise in showing that in *G. caspius* and *G. sulfuripes*, females become lethargic and "paralyzed" respectively. However, when the author describes this matter in *G. granti*, he is not as precise, and he just says that: "*the male merely touches the female with his pedipalps, in reply to which she lifts her abdomen and allows him to grasp her with his jaws* (Cloudsley-Thompson 1967)." It is not clear if the female enters a complete inactivity state or not. Accordingly, Punzo (1998a) talks about a reduced lethargic state, compared to what is seen in *G. caspius* and *G. sulfuripes*, giving the idea that the female may show some subtle movements during mating. What is interesting is that in these works, both authors agree that females of *G. granti* "awaken slowly", thus suggesting the actual presence of a female's inactivity state in this species.

In a recent description of mating in *E. pallipes*, Rowsell & Cushing (2020) suggest that the female enters an almost inactivity state but with subtle moves of pedipalps, legs, and chelicerae. The authors also say that the female begins to struggle immediately after the male reinserts the chelicerae. They observed the behavior "female intense struggle" and define it as "*apparent intense struggling by female to escape from the male*." Just as the case cited above of *G. granti*, in some other Eremobatidae females do not struggle, but they also do not show the characteristics of complete inactivity as described for most Galeodidae and this inactivity may be less pronounced.

Female exhibits a state of partial inactivity (intermediate state between complete inactivity and complete activity).—In this case, complete inactivity is not always present in the female. As previously described, males engage in a firm grasping of the female's body with their chelicerae. In fact, the female can move legs (2nd and 3rd pairs of walking legs), walk with the male in tandem, and move the chelicerae prior to the sperm transfer phase. This walking behavior is curious as the male behavior differs compared to the behavior of males in species that show complete female inactivity. In species where females enter complete inactivity, the males carry the females. This is in direct contrast to these cases in which the females cooperate, walking along with the male. What is more, the females do not curve their legs ventrally as they do in the complete inactivity species. The female's body position also seems to be slightly different, i.e., in complete inactivity, their bodies curve beyond a straight angle, while in species with partial inactivity, the body seems to rest in a right-angle position. Additionally, females in this latter group may continue body shaking but do not attempt to bite the male constantly. Overall, these females engage in significantly less movement than 'complete activity' females (see below).

This partial inactivity state has been observed in some old descriptions of the Eremobatidae family (Muma 1966a; Punzo 1998a, b), e.g., "Eremobates *females may submit or accept a male without prolonged quiescence; one was even observed to feed on termites while being mated*" (Muma 1966a pg. 349). We reviewed more recent videos available on the internet for this review (See Supplemental Table S2, online at https://doi.org/10.1636/JoA-S-20-037.s2) and our assessment is consistent with Muma and Punzo. Eremobatidae seems to be a complex and flexible family. In this family, the females show a wide array of behavior spanning complete to partial inactivity. This variation could indicate differences in mating behavior and strategies that may be related to phylogeny or may be an individual or an environmental-dependent trait. We now need more studies with increased sampling within species as well as across more families to be able to understand these patterns of variation.

Female exhibit a state of complete activity.—The pattern of 'complete activity' is one in which the observed female continues to move, even increasing body movement, intermittently shaking vigorously, and attempting to bite males. 'Complete activity' matings often appear quite aggressive, as males apparently struggle to hold the female due to her continual movements. Males usually hold females either by gripping them from behind or by clasping them with their pedipalps or forelegs.

In all "complete activity" matings recorded to date, the male places a sperm-drop on the substrate. He then collects it directly with his chelicerae or uses the tarsi of the forelegs to place it between the chelicerae. Males then rub and chew the female's genital region with their chelicerae after transferring sperm into her genital atrium (see Supplementary Table 1).

"Complete activity" is a female state characteristic of the ammotrechid *O. chacoensis* and the daesiid *G. dorsalis*. This state may often be accompanied by the existence of injuries in the female pleura, evident, e.g., in *G. dorsalis* (Hrušková-Martišová et al. 2010). These injuries are likely caused by the spines located on the male's pedipalps (Hrušková-Martišová et al. 2010). Indeed, injury to the female pleura caused by male pedipalpal spines has been observed in the ammotrechid *O. chacoensis* (Peretti & Willemart 2007), but the possibility exists that male chelicerae may also cause injury.

Our classification based upon the degree to which females remain active or inactive during mating is aimed to be a starting point for organizing and synthesizing observations of mating across years, authors, and different resolutions of study. It is not intended to be a static classification, as the analysis of mating behavior is not as developed as in other arthropods and many species of the families cited here either have not yet been analyzed, or need to be reanalyzed. In the future, it will be important to study how flexible these operational categories are across solifuge species. Studies exploring flexibility in male tactics and female response as they relate to each sex's mating history, population and micro-environmental conditions (e.g., type of substrate where mating occurs), are now imperative for generating a broad understanding of reproductive patterns within and across solifuge families.

Coercion, mate choice, and mating systems: Regardless of the female's behavioral response (completely inactive, partially inactive, completely active), all male solifuges studied to date grasp the females during mating. As such, at first glance solifuge mating could be described as coercive in a descriptive classical sense, that is, male grasping the female, with attempts by the female to get away from the male and/or to bite him (Arnqvist & Rowe 2005). Coercion is suggested to be highest in 'complete activity' species, where female-male interactions appear quite agonistic and dangerous. The degree to which coercion versus cooperation is present across solifuges, however, remains an open question (Table 1). For example, it is unclear how and why varying female states are achieved and whether these reflect male tactics to subdue females versus female choice to acquiesce. Furthermore, these seeming extremes—male coercion vs. female choice—are not mutually exclusive.

Interestingly, so far it has been observed that species which would be described as possessing a pronounced type of coercive mating (i.e., "complete activity" females) are characterized by females that would not tend to remate (*G. dorsalis*) (Hrušková-Martišová et al. 2010) or would mate at only a low rate (*O. chacoensis*) (Peretti & Willemart 2007). Such patterns would imply the presence of a monandric mating system. In such species, it has been suggested that if monandry exists, it may be a result of the costs the females might incur due to physical injuries inflicted—directly or indirectly—by males while holding them (Peretti & Willemart 2007; Hrušková-Martišová et al. 2010) or while kneading the female's opisthosoma during mating (Bird 2015). Alternatively, or simultaneously, it may be a result of pre-copulatory female choice. 'Complete activity' females, for example, may critically evaluate their suitors (e.g., how effective they are at overcoming female resistance) and set a high threshold of acceptance before insemination, thus reducing both costs and benefits of future matings (see Table 1).

In contrast, species in which females exhibit "complete inactivity" are characterized by females that may be willing to mate with multiple males (Junqua 1966; Wharton 1987; Punzo 1998a; Hrušková-Martišová et al. 2010; Rowsell & Cushing 2020; Peretti, A. V. unpub. data on *T. salinarum*. Observations of females remating with the same male have also been observed. Amitai et al. (1962), for example, describe remating in *G. sulfuripes*, and they claim that all observations were made on the same mating pair on subsequent mating events. Works posterior to Amitai et al. (1962) suggest that multiple matings of the same pair can be achieved in captivity but seem to be difficult to verify in the field.

Female multiple mating with different males is more in line with a polyandric mating system. Such a mating system may benefit females by increasing the chances of mating with high quality mates and may be a means by which females can overcome constraints on precopulatory mate choice. If, for example, 'complete inactivity' in females is a male-induced behavior, it might function to remove a female's ability to actively choose a mate. However, multiple matings, paired with cryptic female choice through selection on sperm use from the spermathecae, could enable females to regain mate choice. Unfortunately, nothing is currently known about sperm use or cryptic female choice in solifuges.

We hypothesize that there may be a strong relationship across solifuges between mating system and level of sexual coercion, where the level of initial coercion negatively reflects the degree to which females retain precopulatory mate choice (i.e., high coercion=low precopulatory choice; low coercion=high precopulatory choice) (Table 1). Similar relationships have been shown in other animals, such as water striders, some dragonflies and guppies (Arnqvist & Rowe 2005; Shuker & Simmons 2014).

Although these explanations fit better with more traditional perspectives on sexual conflict during mating, alternative options could be suggested. As mentioned, complete activity in females could allow females to critically evaluate their suitors ("how effective they are in overcoming female resistance"), this being a form of precopulatory choice by the female. In contrast, completely inactive females will not be able to continue choosing once they have adopted the inactive behavior. Therefore, inactive females will benefit from remating in the future and perhaps use cryptic female choice, while highly active females might use female choice during the first mating (at a high cost due to physical injury) and then refrain from re-mating.

Unfortunately, accurate or reliable data on female or male mating rates are lacking in many of the species and families studied to date and no data are available on patterns of sperm use. As such, more research on solifuges mating systems is needed to fully test these hypotheses.

Given the lifestyle of some solifuge species, it is also possible that 'mate choice' occurs prior to reproductive encounters. In *M. picta,* for example, a species with "complete inactivity", Wharton (1987) observed that although males can locate females on the ground surface by direct body contact, they can also detect them when females are buried inside their burrows. Interestingly, the male begins to dig and then the female leaves her burrow and comes up to the surface if she is receptive. In this same work Wharton states: "*Thus male digging may serve as a stimulus to the female rather than as an attempt to actually excavate her*". Mate location and digging ability may thus provide another avenue for female choice and another means by which females can overcome any potential mate choice constraint caused by male coercion. As suggested by Wharton, it would be worthwhile to examine in more detail female behavior associated with male digging attempts. Exploring such questions requires mainly fieldwork, as laboratory observations infrequently incorporate mate location strategies into the equation of reproductive behavior.

Thus far, we have considered scenarios where females might exert choice on males, but it is equally possible that males may exert mate choice on females. Male mate choice is a complex matter (reviewed in Edward & Chapman 2011). Male behavior may, for example, vary with female attributes such as body size. Clutch size in solifuges is apparently associated with the body size of females. Larger females typically lay more eggs (Muma 1966b; Wharton 1987; Punzo 1995, 1997). Male choice for female quality then, may be straightforward, as fecund females may be bigger. Male mate choice may also be important in solifuges because of potential costs of reproduction. These costs could be directly associated with sexual cannibalism and sperm production, but other costs such as mate acquisition should not be discarded as we do not know variables such as operational sex ratios and potential reproductive rates (Emlen & Oring 1977; Clutton-Brock & Vincent 1991; Clutton-Brock & Parker 1992). Future work should examine potential preferences among males for larger and/or heavier females and explore how such preferences might manifest (e.g., through tapping intensity?). Like research programs aimed at determining the relationship between the degree to which females can choose mating partners and/or accept male sperm and the degree to which male behavior is coercive (female choice vs. male coercion), this relationship would be interesting to explore across solifuge species with respect to male mate choice and degree of coercion (male choice vs. male coercion).

Sexual dimorphism, genitalia and their roles during mating.—Some types of sexual dimorphism (SD) found in solifuges may be closely linked to the type of matings described above. We can find that sexual dimorphism is expressed in the following sets of traits:

Non-genitalic sexual dimorphism.—In some solifuge families, such as Galeodidae and Ammotrechidae, males tend to have a more gracile aspect than females (Junqua 1966; Maury 1984). Such general body shape differences could be associated with locomotory performance. Male movement may experience stronger selective pressure since males are generally vagrant and are pushed to move greater distances searching for females. Additionally, males need to avoid predators during mate searching, and males that are able to avoid sexual cannibalism and escape more easily after mating may have an advantage (Wharton 1987; Punzo 1998a).

In line with the more gracile aspect, male legs tend to be thinner as well. Pedipalps may also be longer in males than in females in Galeodidae, Solpugidae and other families. Longer pedipalps likely offer the male more distance between himself and a female, perhaps enabling him to avoid being bitten by her when he performs precopulatory touches or tapping (Junqua 1966; Wharton 1987; Hrušková-Martišová et al. 2010). Females, in contrast, may experience selection for increased body size. As mentioned previously, in females a larger body size is usually associated with a larger body mass, which results in more eggs laid (Muma 1966b; Wharton 1987; Punzo 1998a).

The length of certain lateral spines of the pedipalps is also dimorphic in some solifuge species. In *O. chacoensis*, for example, male pedipalp spines are longer than female's spines and are used to laterally lock the female body during mating (Peretti & Willemart 2007). There are records of differences in setae covering the body between the sexes in some species. The meaning, however, of this type of sexual dimorphism remains unknown and open for study.

At the sensory level, there is sexual dimorphism in the racquet organs (malleoli). Racquet organs are structures for chemoreception (Brownell & Farley 1974; Sombke et al., 2019). Males have larger and more numerous racquet organs than females (Cloudsley-Thompson 1961; Punzo 1998a; Yiğit et al. 2012). A similar pattern is seen in other arachnids. For example, scorpion pectines are chemo- and mechanosensory appendages ventrally attached to the abdomen (Wolf 2017). Males present bigger pectines with more and bigger pectinal teeth compared to females (Hjelle 1990). In Solifugae, the role of racquet organs within a context of sexual interaction still needs to be studied in depth. Wharton (1987) suggested that males would use the racquet organs to detect chemical signals left by females, making it easier for them to find their burrows. However, so far there is no experimental evidence to support that possibility. The study of the existence of sexual pheromones is a totally unexplored field in solifuges.

Secondary genitalic sexual dimorphism.—Due to the simple fact that the males use their chelicerae to transfer the spermatozoa to the female, chelicerae and associated structures (e.g., the flagellum) presumably act in all solifuges as secondary genitalia. As mentioned above, chelicerae of male solifuges are forward-facing appendages used not only for food, burrowing, and defense but also for grasping the body of the female and sperm transfer during mating. These sexual functions possibly explain, in part at least, the sexual dimorphism in cheliceral size and shape.

The fixed finger of the male's chelicerae may be much "straighter" than that of the female, e.g., in Eremobatidae (Muma & Muma 1988; Brookhart & Cushing 2004; Bird et al. 2015), Daesiidae (Maury 1980; Hrušková-Martišová et al. 2010). Alternatively, the fixed and mobile fingers of the male may have a degree of curvature that allows them to cross, e.g., in Ammotrechidae (Maury 1984), in *O. chacoensis* (Peretti & Willemart 2007) (Fig. 1); this crossing does not appear in females of these species. Although in the order this crossing of fingertips is not restricted to males and seems to be widespread, in some species it seems to be linked to some reproductive behaviors. For example, the male's crossed cheliceral fingertips function in clasping the female and can result in piercing of the female's cuticle (Peretti & Willemart 2007). Thus, it is important to analyze finger crossing, not as a generality of sexual dimorphism in the order, but focally in some groups, such as those exhibiting coercive-like reproductive behaviors. It is important in the future to analyze the magnitude of this tip crossing and to determine to what extent this character may aid the male in holding the female in a coercive scenario and/or enhancing the embedding of the chelicera in the female genitalia during insemination.

Figures 1–2.—Example of unexplored traits in the flagellum. Presence of fine bristles on the border of the flagellum in *O. chacoensis*. 1. General view of chelicerae with spoon-like flagellum; 2. Detail of the flagellum. Arrows show the setae covered zones, larger and denser on the more distal area.

In Eremobatidae, the fixed finger is not likely related to sperm transfer *per se* as these groups transfer sperm directly gonopore to gonopore. The fixed finger is a stylet that tapers through the mucron (cheliceral tip). Eremobatidae is a perfect model to analyze the function and modifications of the fixed finger for functions other than sperm transfer, as precisely stated by Bird (2015): "*The fact that the chelicera is not used to pick up sperm in Eremobatidae may have freed the fingers for other purposes in this family*." Although they do not use it to capture sperm and insert it to the female as in other families, the fixed finger shows great variability in Eremobatidae. In fact, eremobatids include some of the most markedly sexually dimorphic species (Bird 2015; R. Jones, pers. comm.). Bird (2015) suggests that the tapering in the fixed finger may be an adaptation to reach the narrowing oviducts of females. If this is true, the male has access to the spermathecae of the females and may, in theory, be able to remove previous sperm, or enhance collocation of his own gametes in a sperm competition scenario. The fixed finger of males of some eremobatids show grooves (flagellar groove) and differences in the base of the finger (fondal notch and retrofrondal dentition) (Bird 2015; Ryan Jones personal communication.). In this matter, it is important that future analyses examine both the internal genital atrium of the female and the base of her genital opening, where this fondal notch may be hitting or rubbing, in order to understand how these characters may be interacting and evolving.

The movement of male chelicerae within the female gonopore is presumed to be related to these observable sexual dimorphisms in shape (Bird 2015). Heymons (1902) describes the male chewing the ventral part of the female where the spermathecae are and suggests that this massage may aid in moving previous stored sperm, serve to stimulate the female, or both. Massaging the genital opening after sperm introduction has been hypothesized to perform several functions, for example facilitating release of spermatozoa from the spermatophore (Muma 1966a; Punzo 1998a) or forcing the sperm into a storage area (Junqua 1966; Muma 1966a). In this sense, Thomas & Zeh (1984) pointed out that the insertion of the fixed finger of the male chelicerae into the female before sperm transfer could have the function of preparing the genital tract for sperm transfer, detecting if there is sperm from previous copulations, or displacing and/or removing sperm transferred by other males. The role of the cheliceral movement during and even after sperm transfer remains to be discovered, as it could be merely to place the sperm better (Hrušková-Martišová et al. 2010) and/or to perform sexual stimulation as an "internal courtship" (Eberhard 1994, 1996), for example by rubbing against the internal walls of the female genital atrium. It could even be linked to maintaining female quiescence and/or regaining female consciousness (Rowsell & Cushing 2020).

The most notable feature that distinguishes male from female chelicerae is the presence of a flagellum on each of the fixed fingers (on the inner dorsal face) of both male chelicerae. The shape and size of the flagellum differs among families (for a complete review of forms in each family see Bird et al. 2015). The function of this structure is not yet determined (Bird et al. 2015) and it may not be possible to give a single explanation for all of them. Mating was not affected after the flagellum was removed from males in *G. caspius* (Heymons 1902) and *O. saharae* (Junqua 1962). Accordingly, and under this premise, Cloudsley-Thompson (1961) in *Galeodes arabs* (*G. arabs* C.L. Koch, 1842) and Lawrence (1963, 1965) in African Solpugidae, agree that the flagellum is not related to reproductive success. These two statements are tricky because none of the authors talk about sperm transfer success in the case of flagellum removal experiments, or mating success in terms of, for example, fertilized eggs.

Previously, Sørensen (1914) emphasized that the flagellum was a structure that could collect (e.g., in the Rhagodidae *Rhagodes* Pocock, 1897) or retain the sperm drop (e.g., in *Galeodes* and *Solpuga* Lichtenstein, 1796) during the sperm transfer phase. Kaestner (1933), after having studied three families of solifuges, also suggested that the flagellum might participate in the transference of the sperm during mating.

Indeed, the concave, ovoid flagellum of Ammotrechidae that resembles a spoon (Figs. 1, 2) acts as the organ that holds the sperm, and facilitates its intromission inside the female genital atrium in *O. chacoensis* (Peretti & Willemart 2007; Bird 2015; A.V. Peretti unpub. data). Preliminary SEM analyses show that the flagellum has fine bristles on the edges (Fig. 2). The actual function of these bristles is not yet known. They could serve to better hold the sperm drop and/or to have a role inside the female genital atrium (especially those in the distal part of the flagellum, which are longer and denser). Bird (2015) supports this idea, suggesting that the apex of the flagellum may be used as a species recognition mechanism or may be used to exert cryptic female choice in this species. The author also noted that there are examples of modifications of flagellar microstructures concentrated at the distal end of the flagellar shaft. The author takes as an example the flagellum of Solpugidae and says that this diversity appears in the area where the flagellum comes into contact with the female reproductive tract, or is directly inserted in the female during the transfer of the sperm drop (Wharton 1987). The flagellar shaft may be inserted inside the female and is thought to reach deep into the female genital apparatus (Bird 2015). It is also suggested that the male may secrete fluid inside the oviductal chamber, but its function here still remains elusive. These examples show that the flexible shaft of the flagellum is inserted inside the female, perhaps aiding to open the genital opening for the sperm drop to be transferred smoothly, thus enhancing sperm transfer, or exerting cryptic female choice. It can also be related to sperm competition. Therefore, at least in these species of ammotrechids, solpugids as well as some galeodids, the flagellum might be intimately linked to sperm transfer.

In Eremobatidae, the flagellum is not membranous as described in most of the other groups. The flagellum in Eremobatidae is modified into a group of setae when present (Muma 1951; 1962; Cloudsley-Thompson 1977; Brookhart & Muma 1981; Muma & Brookhart 1988; Brookhart & Cushing 2004; Klann 2009; see Bird 2015 for more details). Interestingly, eremobatids transfer sperm directly from the male genital opening to the female genital opening. Assuming that the flagellum aids in sperm transfer, eremobatids would not need such a membranous structure due to its particular form of sperm transfer. Nevertheless, it would be interesting to study if the setae serve to exert some kind of copulatory courtship while the male is inserting its chelicerae during contact phase of mating.

Another explanation for the function of some types of flagella involves the possibility that this structure may secrete and store putative sexual pheromones. In this regard, Lamoral (1975) analyzed males from four species of Solpugidae (*Solpugema hostilis* (White, 1846), *Solpuga venator* (now *Zeria venator* (Pocock, 1897)), *Solpuga recta* (now *Zeria recta* (Hewitt, 1919)), and *Zeriassa furcicornis* Lawrence, 1929), suggesting that the hollow filamentous flagellum of the males might be associated with the emission of a pheromone. The author also indicated that males may use this pheromonal emission in territorial displays among males during reproductive season. However, this study did not provide experimental data to support these hypotheses. In the same line of speculation about trait functions, Cloudsley-Thompson (1977) added the idea that the racquet organs could be the structures that detect pheromone emission coming from the flagellum. Additionally, he suggested that the racquet organs may aid males to detect vibrations acting as mechanoreceptors.

Ubiquitous across all flagella is the close association with the insertion of the fixed fingers of the chelicerae (Thomas & Zeh 1984), suggesting an important role in sperm transfer or even sperm removal (Heymons 1902; Rowsell & Cushing 2020). It has been suggested that there could be hemolymphatic pressure from the chelicerae to the flagellum to facilitate its movement within the female (Bird et al. 2015). It would be interesting to study whether some flagella could serve to remove or displace previous sperm, improve the position of a male's own sperm within the female (Klann et al. 2009), stimulate the female (Warren 1939), e.g., as an internal courtship in a context of cryptic female choice, or combine functions that may not be mutually exclusive.

Moreover, it has not been studied whether there is a relationship between the type of flagellum and the type of mating (e.g., according to the degree of male coercion and female behavior). The type of flagellum is conserved in each family (Bird et al. 2015), at least in its general structure. For example, in Ammotrechidae, flagella are similar in their basic form between *T. salinarum* (without coercion) and *O. chacoensis* (with coercion). However, there are subtler differences between them. For example, there are differences in the type and length of the fine bristles around their edges and the degree of concavity of each flagellum (A.V. Peretti unpub. data) (see the example of *O. chacoensis* in Figs. 1, 2). Differences such as these and the global diversity of the flagella suggest that sexual selection has been strong and has potentially exerted a diversifying effect on their form and functions. We see determining the function of male flagella as critical to understanding solifuge reproduction and the role of sexual selection and sexual conflict in influencing reproductive morphology and behavior.

Primary genitalic sexual dimorphism.—As in other arachnid groups (e.g., amblypygids; Weygoldt 2000), the general shape of the female and male solifuge genital sternite (Punzo 1998a) differs, but little is known about the functional significance (if any) of this difference in the outer genitalia. Punzo (1998a) reviewed some of these shapes, which are always used as sexual difference in taxonomy (e.g., Maury 1980, 1984; Muma & Muma 1988; Gromov 2000; Brookhart & Cushing 2004). The female operculum can present grooves, hollows, furrows, and a general shape that is not present in that of the male in Ammotrechidae and Daesiidae (Maury 1980, 1984). One possibility is that this form is intimately linked to the shape of the male's chelicerae, especially the movable fingers. Variability in the movable finger is subtle but notable mainly towards the fingertip, which is more slender in males and curves in different angles (Bird 2015). It has been observed in some species, for example, that the tip of the male movable cheliceral finger fits into particular areas on the female genital sternite (e.g., in *O. chacoensis* and *Titanopuga salinarum*); Peretti & Willemart 2007; A.V. Peretti, personal observation). On the other hand, fine details of the morphology of the female genital atrium are still scarce (Warren 1939; Junqua 1966; Klann 2009) and more data are needed. Detailed studies of the external as well as corresponding internal morphology of the female's genitalia and its physical connection(s) with the male chelicerae—particularly the flagellum—during mating are much needed.

On the existence of sexual cannibalism.—Another aspect associated with the mating of solifuges is the possibility of sexual cannibalism. Among arachnids, female cannibalism of courting males is frequent in scorpions and spiders (e.g., Elgar 1992; Peretti et al. 1999). Knowing the extent of this risk across solifuges is essential, since the risk of sexual cannibalism could favor the appearance of counter-adaptations in the male during mating. For example, a high risk of sexual cannibalism could selectively favor opportunistic or coercive male copulations (Elgar 1992; Fromhage & Schneider 2005). The relative risk of sexual cannibalism for males then may provide insights into the function of observed variation in reproductive behavior across species.

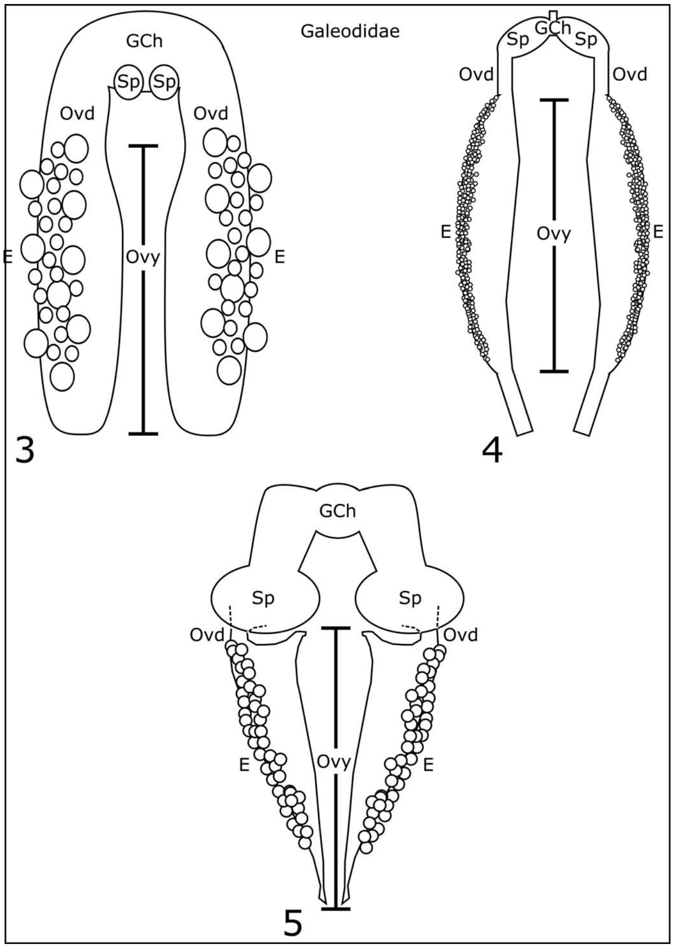
Regarding sexual cannibalism in solifuges, it has been observed that females in captivity commonly kill males before, during or after mating (reviewed in Punzo 1998a). In both the galeodid *G. caspius subfuscus*, and the daesiid *G. dorsalis,* cannibalism from female to male was observed at the first encounter (i.e., without mating) in about 38% of interactions (Hrušková-Martišová et al. 2010). In the ammotrechid *O. chacoensis,* out of 40 female-male encounters observed, 11 resulted in pre-copulatory cannibalism (against males in six cases). Post sperm transfer cannibalism was never observed. Male cannibalism to reluctant females has also been observed in some eremobatid species (Muma 1966a; but see Rowsell & Cushing 2020). It is not yet possible, however, to state whether these observed cannibalisms are a natural occurrence in female-male encounters or are instead promoted by captivity conditions. Wharton (1987), for example, never observed sexual cannibalism in his field observations of the solpugid *M. picta* and he warns that confinement in captivity may be a crucial factor in inducing the appearance of cannibalism between females and males. Undoubtedly, as suggested by Wharton (1987), more observations of matings in the field are necessary to corroborate laboratory observations.

Opportunities for postcopulatory sexual selection.—Besides what has already been commented on in some points about the potential for cryptic female choice, there are characteristics linked to sperm and its storage that may influence mechanisms of postcopulatory sexual selection. Spermatogenesis in solifugae males occurs just prior to the adult state (Alberti 1980, 2000; Klann et al. 2009). Indeed, the testes have degenerated once the male reaches adulthood, and the entire sperm supply is mostly stored in two large *vas deferens*. Adult males live a short time after mating (from one week to one month; Punzo 1998a) and have a limited stock of sperm throughout the entire reproductive season. Thus, males might be prone to sperm depletion (Boivin et al. 2005). This characteristic makes solifuges extremely attractive for studies focused on sperm allocation strategies and sperm competition. But what do we know about sperm and fertilization success in solifuges? Unfortunately, not much.

An unusual feature of the sperm of solifuges is that it is aflagellate (Alberti 1980, 2000). Sperm morphology has been characterized in Galeodidae, Eremobatidae, Ammotrechidae, Daesiidae, Solpugidae, Karschiidae Kraepelin, 1899 and Hexisopodidae Pocock, 1897 (Warren 1939; Alberti 2000; Klann 2009; Klann et al. 2005, 2009, 2011). Except in the case of Daesiidae, sperm morphology is not very variable among the species that have been studied inside each family (Klann, 2009). The aflagellate nature of all solifuge sperm thus far studied suggests that sperm competition itself may be limited, as sperm have no means to movement. Aflagellate sperm is taxonomically widespread and distributed in a wide variety of animal groups (Morrow 2004; Pitnick et al. 2009). It seems that selection may favor the loss of motility when sperm competition is absent and may open the door to other types of sexual selection such as cryptic female choice.

Sperm can compete, however, even without movement, for example through sheer numbers, strategic placement or chemicals inside the ejaculate. Thus, if sperm competition exists in solifuges, it seems possible that levels may vary across solifuge species that exhibit different mating systems. As mentioned previously, males are generally thought to mate multiply, but females of only some species may show the same behavior (Hrušková-Martišová et al. 2010). Furthermore, it has been suggested that due to a lack of spermatogenesis during adulthood, the amount of sperm that males transfer to females should be reduced over successive matings with different females as suggested for *G. caspius* (Heymons 1902; Berland 1932). This is similar to what is seen in other animal groups where males reduce their sperm supply with increased numbers of matings (reviewed in Dewsbury 1982; Engqvist & Reinhold 2007; Abe & Kamimura 2015; case studies in arthropods Nadel & Luck 1985 [Hymenoptera]; Watanabe et al. 1998 [Butterflies]; Rubolini et al. 2007 [Cray fish]; Vrech et al. 2019 [Scorpiones]). This pattern raises the question of whether males can strategically allocate sperm. For example, in many arthropods, males transfer more sperm to virgin females (Ball & Parker 2007), or according to risk or intensity of sperm competition (Engvist & Reinhold 2006). Might solifuge males do the same? For example, if there were an advantage to the first sperm transferred to a female's spermathecae (first male sperm precedence), then it would be advantageous for males to allocate a greater amount of sperm to virgin females. Such predictions could be easily tested by quantifying sperm transfer. Assuming sperm stratification, however, the physical form of the female spermathecae across families suggests that there could be differences in male sperm precedence (Figs. 3, 4, 5). Again, this is an excellent avenue for future studies.

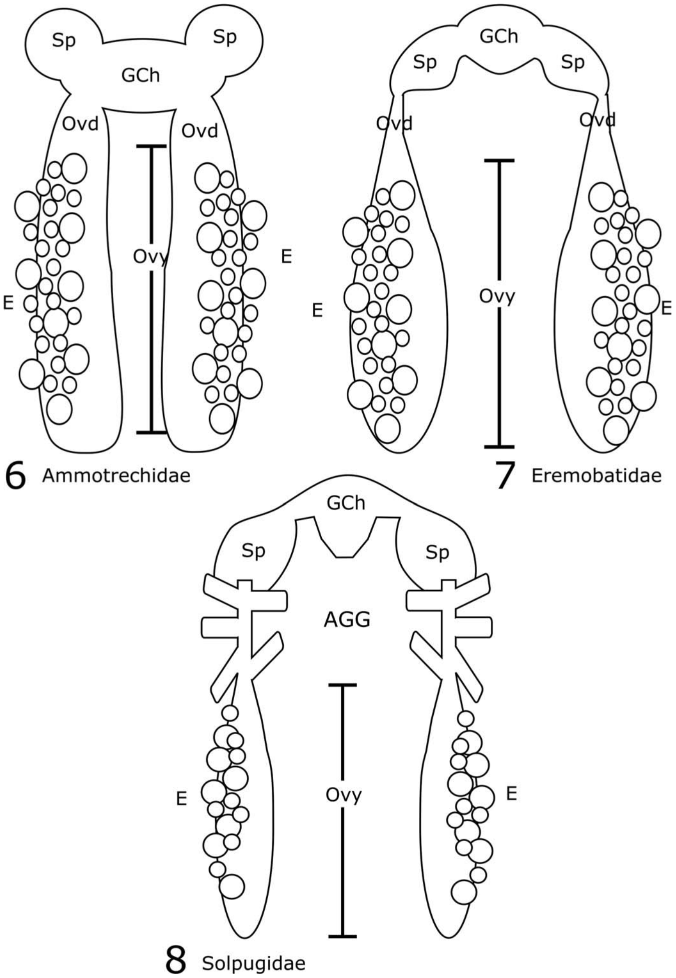
In spiders, Austad (1984) suggested a pattern of sperm precedence that we still invoke. Two types of general morphologies for spermathecae (= *receptacula seminis*) exist. First, cul-de-sac is precisely a sac-shaped spermatheca where the entrance of sperm for storage is the same as the exit for fertilization. With this spermathecal morphology, and assuming that there is not sperm mixing from different males, we predict last male sperm precedence. The last male to inseminate the female may have the advantage in fertilizing the eggs as his sperm will be the first to come out. Second, in a conduit type of spermathecae, the place of sperm entrance is different from the place of sperm exit and spermathecal openings are at opposite ends of the spermathecae (Uhl 2000). Again, in the absence of sperm mixing, we predict first male sperm precedence, as his sperm will be the first to come out.



Figures 3–5.—Types of female reproductive tracts in three species from Galeodidae 3. Represents *Galeodes araneoides* and *Galeodes caspius subfuscus*. *4*. *Galeodes barbarus*. *5*. *Oparbona simoni*. [4, 5. Redrawn from Vachon (1945); 3. Redrawn based on (Klann 2009). Note that the morphology of the reproductive tract may represent different types of sperm precedence Abbreviations: E: eggs, Gch: genital chamber, Ovy: ovary, Ovd: oviduct, Sp: spermatheca.

Uhl & Vollrath (1998) suggest that this last scenario is not always the case and that some females may show a conduit type of spermathecae functioning as a cul-de-sac. The spermatheca functions as a sac as the entrance and exit of sperm are located close to each other. In this case, although the morphology is conduit, the last male will have a reproductive advantage over the other males.

According to descriptions of spermathecal morphology and ultrastructure of the female's internal genitalia, we offer some suggestions of sperm precedence patterns. However, we emphasize that these suggestions are only exploratory because (1) they are based on the premise that there is no sperm mixing, which may not be true; (2) there is a great variability among families and even among species of the same genus (see for example Figs. 3–5), and (3) there are very few detailed descriptions of spermathecal internal morphology and ultrastructure. Vachon (1945) and Klann (2009) described the female internal genitalia of the galeodids *Galeodes araneoides* (Pallas, 1772) and *G. caspius subfuscus* respectively (represented here by Fig. 3). According to their description, two small



Figures 6–8.—Types of female reproductive tracts in three species from different families of Solifugae 6. Ammotrechidae. 7. Eremobatidae. [6, 7. redrawn from Klann (2009), 8 based on the ultrastructural descriptions of Warren (1939)]. Abbreviations: E: eggs, Gch: genital chamber, Ovy: ovary, Ovd: oviduct, Sp: spermatheca.

pouches are located at the base posterior to the genital chamber and are suggested as putative spermathecae. This disposition and sac morphology would suggest last male sperm preference. However, the description of Vachon (1945) of *Galeodes barbarus* Lucas, 1849 shows a different morphology. In this case, spermathecae appear as expansions of the oviductal tubes (Fig. 4). With this disposition and without any internal modification, we would predict first male sperm precedence. Lastly, Vachon (1945) also described the female's genital system of *Oparbona simoni* Roewer, 1934 (now *Oparbella flavescens* (C.L. Koch, 1842))." The Vachon study shows massive spermathecae that resemble the case reported by Uhl & Vollrath (1998) in spiders, where the conduit type of spermathecae may function more like a cul-de-sac because the insertion of the oviduct (Fig. 5) is not straight as seen in *G. barbarus* (Fig. 4). Among the scarce descriptions available in other species, Klann (2009) described the female genitalia of the ammotrechid *T. salinarum* and the eremobatid *Eremobates* sp.. In *T. salinarum*, the female's reproductive system shows two big lateral pouches with only one big aperture suggesting a last male sperm precedence (Fig. 6). Different is the case in the studied eremobatid, where there is an expansion towards the end of the oviduct in the zone of contact with the genital chamber, similar to what happens in *G. barbarous* but the expansion seems to be greater (Fig. 7). Again, as this is an expansion of one continuous duct, it has two ends, and sperm from the first male may be the first to reach the ovary.

According to Warren (1939) and his detailed ultrastructural study, Solpugidae may show a bit more complex genital system that may or may not fit with first sperm precedence. Unfortunately, this complexity makes it difficult to understand what could be happening with sperm inside. Internal morphology shows different ducts with different positioning and thickness (Warren 1939). It is remarkably interesting that the description in Warren (1939) mentions the presence of an accessory genital gland that is branched and appears to be attached between the spermathecae and the ovary (simplified in Fig. 8). The function of this gland and the presence of similar structures in other species remain an open question. Finally, we note that alongside these hypothesized sperm precedence patterns, we should also consider that males may be capable of removing sperm, as already mentioned in the section on secondary genitalia, and/or females might be able to manipulate sperm placement, making it more challenging to understand the patterns of male sperm precedence in solifugae.

In support of the notion that males may remove sperm, Heymons (1902) states that pre sperm transfer chewing may aid in sperm removal from previous matings. There has been repeated support for this hypothesized function of presperm transfer cheliceral chewing. For example, some authors such as Amitai et al. (1962), Muma (1966a), and Punzo (1998a), suggest that pre sperm transfer cheliceral insertion is deeper compared to the post sperm transfer cheliceral insertion. However, both Hrušková-Martišová et al. (2010) and Junqua (1966) state that the post transfer cheliceral insertion is deeper. Other authors like Peretti & Willemart (2007) do not note any difference in the relative level of cheliceral insertion.

If males make deeper pre sperm transfer cheliceral insertions, they may be stimulating females or may be removing sperm from previous matings. Shallow post transfer cheliceral insertions may aid in preventing sperm dumping or leaking as suggested by Heymons (1902). On the other hand, if pre sperm transfer cheliceral insertions are shallow, males may also be stimulating females. Furthermore, if post transfer cheliceral insertions are deep they may be ensuring that sperm is correctly delivered and maintain inside the female genital opening, or maybe help tear the sperm droplet. Ultimately, these hypotheses should be evaluated directly, and researchers should be open to the possibility that males from different species may show different strategies when coping with their own sperm and sperm from competitors.

Not only is solifuge sperm aflagellate, but the arrangement of sperm during transfer (and storage in the female?) is variable across species. Some species present single sperm cells, while others have sperm conjugation (sperm grouping; Pitnick et al. 2009) in the form of coenospermia or roleaux (Klann et al. 2009; Bird 2015). Sperm conjugation may be related to transferring a greater number of sperm in a more effective way; may help maintain greater viability by nurturing or protecting each other from the female's potentially harsh environment (Pitnick et al. 2009); may reduce sperm mixing (Warren 1939); or may have other functions. We do not have direct evidence, however, related to how such packaging may relate to sperm viability, sperm mixing, sperm competition and/or cryptic female choice.

Research addressing these basic gaps in knowledge is much needed. For example, similar approaches are being studied in other arachnids. In spiders, sperm is found coiled and inside a proteinaceous sheath (Alberti 1990; Michalik et al. 2004; Michalik 2007; Michalik & Ramírez 2014). Protected with this sheath, it reaches the female reproductive tract where it needs to shed the capsule and uncoil. The female may aid this process and thus may act in producing paternity bias by selectively activating stored sperm (Herberstein et al. 2011). Scorpions also bear conjugated sperm in the form of sperm packages (Michalik & Mercati 2010; Vrech et al. 2011). These spermatozoa are activated and separated inside the female genital tract shortly after sperm transfer (Peretti & Battán-Horenstein 2003). Similar information about solifuge sperm uncoiling is sorely needed.

The sperm masses described for species of solifuges seem to be formed by the ejaculate, i.e., sperm plus seminal fluids, and a viscous contention matrix or "emulsion" most probably coming from the seminal vesicles, as described for *S. hostilis* (Warren 1939). In fact, Junqua (1966) describes the sperm mass as mucus-agglomerated sperm. There seem to be differences in the consistency of the sperm mass. For example, the ammotrechid *T. salinarum* has a more compact sticky sperm drop compared to *O. chacoensis* that shows a more hyaline aqueous drop (A.V. Peretti, D.E. Vrech unpublished data). Maybe these differences in consistency and build could aid in stratification or differentiation of the different ejaculates of males inside the female spermathecae, giving a substrate to the occurrence of postcopulatory sexual selection. Some researchers agree that many of the moves the males do with the chelicerae inside the female genital opening before sperm transfer (see Suppl. Table), are meant to destroy or remove previous spermatophores or sperm masses already deposited inside the female genital tract (e.g., Heymons 1902; Wharton 1987; Bird 2015).

An additional mechanism for sperm competition, aside from sperm removal or sperm number and conjugation, may be the spermatophore (used with the general meaning of a male ejaculate packed into an autonomous unit ; Proctor 1998), which, in some species may aid to separate spermatozoa from different males. Although Heymons (1902) is one of the first to refer to this matter, he seems to have mistaken spermatophore and spermatozoa, as he describes the ejaculate as a viscous sticky sperm ball or sperm mass. Inside this sperm mass, he reports several small grains, as spermatophores, which he then describes as ellipsoidal in shape with spermatozoa inside. He mistakenly described sperm conjugation (Pitnick et al. 2009) in Solifugae as spermatophores (Klann et al. 2009; Bird 2015). After this, many researchers copied and mistranslated what he had said, but Warren (1939) is the only researcher that describes in detail the spermatophore of Galeodidae and how it is formed. He explains that the spermatophores are produced by a chitinous secretion generated by the epithelium of the seminal vesicles. The author shows that the spermatophores in these species consist of a thick external coat of chitin and an inner fibrous chitin matrix. Warren (1939) is the first to mention differences between species, describing the presence of spermatophores in *G. arabs* and *G. araneoides* (Pallas, 1772) but not in *Solpugema hostilis*, *Solpugopa chelicornis* (now *Solpuga chelicornis* Lichtenstein, 1796) and *Solpugiba lineata* (C.L. Koch, 1842). Further observations in other Solifugae agree with this observation, providing evidence that the presence of chitinous spermatophores are not common to all species e.g., Solpugidae (Warren 1939, but see Wharton 1987), Eremobatidae (Muma 1967; Muma & Muma 1988; Punzo 1998a), and Ammotrechidae (Peretti & Willemart 2007).

Despite limited evidence and numerous knowledge gaps, the simple observation that sperm plugs have been seen in females of some species blocking the gonopore after mating suggests that sperm competition may be important in some solifuge groups e.g., *O. sharae* (Junqua 1966) and *T. salinarum* (A.V. Peretti, personal observation). However, it is unknown whether these observations represent an excess of transferred sperm, a plug actively generated by the male (or female), or evidence of sperm dumping that the female selectively performed. Ultimately, sperm transfer and viability studies and associated assessment of potential mating plugs across species with different mating systems (monandry versus polyandry) would provide useful insight into the role of postcopulatory sexual selection in solifuge reproductive behavior.

Finally, in this framework of postcopulatory sexual selection, nothing is currently known about whether (and if so, how) females can influence sperm storage and/or egg fertilization. Female solifuges have large muscles surrounding the sperm storage area (Klann 2009), yet the function of these muscles remains unknown. For example, it is unknown if the female can actively contract these muscles to control and select sperm (Klann 2009), or if these muscles are simply used to help guide the fertilized eggs to the outside. If the former is true, this might have a role in a context of cryptic female choice in polyandrous species. It would be most worthwhile to first examine this in some Galeodidae, Solpugidae, Daesiidae, Ammotrechidae, and Eremobatidae in this regard, as published data on their respective mating behaviors are available. Experiments could be carried out with females that are anaesthetized before mating (in particular in those species where they are active during sperm transfer). This way they could not control the entry of sperm and researchers could see if this affected the positioning of the sperm within the reproductive tract and perhaps the fertilization of the eggs by the sperm of that male.

CONCLUSION

Provided that scientists can creatively design studies that enable detailed observations of the natural reproductive behavior of solifuges, this arachnid group could prove invaluable for increasing our understanding of the current balance as well as evolutionary dynamics between sexual conflict, mate choice, and post-copulatory sexual selection. The degree to which sexual conflict versus cryptic female choice, for example, plays a role in the evolution of reproductive traits (including behavior) is still very much debated (Lessells 2006; Peretti & Aisenberg 2015; Firman et al. 2017). Potentially cannibalistic predators such as solifuges, with their highly variable and seemingly aggressive repertoire of mating behaviors, are sure to provide valuable data to this ongoing discussion. Similarly, the variable mating systems across studied species sets the stage for different degrees of female/male mate choice and sperm competition, making solifuges a potentially powerful system to use in comparative studies of sperm dynamics, spermathecal morphology, and female and male roles in patterns of fertilization.

There is much in the way of low-hanging fruit with respect to solifuge sexual behavior. Perhaps surprisingly, there are no studies directly related to solifuge mating system dynamics or intensity of sexual selection. For most species, we lack knowledge regarding solifuge operational sex ratios, female and male mating rates in the field, and relationships between female or male quality and measurable traits such as fecundity, tapping behavior rate, etc. We also need basic natural history data on more species representing more families. In these new species, we need to answer many questions. What is the pattern of female and male activity? How are mates located? What is the range of a solifuge, and do they have territories? Do males engage in courtship and/or coercion? Is there courtship communication and if so, what does it look like? What sensory modalities are used? Do females and/or males mate multiply? Does sexual cannibalism appear to have a prominent role in their reproductive behavior?

Simultaneously, detailed focal-species studies should be directed at disentangling the degree to which particular behavioral patterns are coercive and/or collaborative, e.g., cheliceral grabbing and genital chewing. Research aiming to uncover the mechanism(s) underlying female "inactivity," for example, will likely be critical in determining the extent to which mating components such as female activity level are a result of sexual conflict and/or female mate choice. It will also be critical to ascertain the putative function of this torpor-like state. For example, does female lethargy reduce a male's likelihood of being cannibalized?

Similar to the state of complete inactivity adopted by females of some species of solifuges, situations of "catalepsy" have been observed in some spiders (Noureddine et al. 2000; Aisenberg & Costa 2005; Gónzalez & Costa 2008; Schneider & Andrade 2011; Abregú, D. pers. comm.). Also similar to solifuges, the function of female complete inactivity has yet to be rigorously determined. Does it protect the male from being attacked? Does it function as a means of copulatory control? Or does it benefit females in some manner? In addition to instances of female "catalepsy" during mating, males of some spider species, such as the nursery-web spider *Pisaurina mira* (Walckenaer, 1837) reduce their likelihood of being cannibalized by physically restraining their female partners with silk during sperm transfer (Anderson & Hebets 2018). A series of behavioral studies on this system have revealed a benefit to males of silk-wrapping as well as a lost opportunity cost for females (Anderson & Hebets 2016, 2017; Scott et al. 2018). What are the costs versus benefits of female inactivity in solifuges?

The degree to which female and male reproductive optima are aligned or divergent will be critical for understanding the evolution and function of distinct reproductive strategies across solifuge species. In exploring reproductive optima, more data are needed. For example, we require information about fitness outcomes of single, versus multiple, matings across species. We need to know sperm priority patterns, the likelihood of sperm mixing, and various strategies that either sex might have available to them to differentially utilize select sperm.

Finally, there is a dearth of information regarding the "semi" indirect sperm transfer of solifuges. Why do some species deposit the spermatophore on the ground? What is the role of the flagellum in spermatophore transfer and is this variable across species? What is the function of the cheliceral chewing? The list goes on and on.

In summary, similar to many unusual mating systems observed in spiders, the entire order of solifuges appears to offer a rich combination of extreme sexual behaviors, with ingredients such as cannibalism, coercion, possible induction of immobility states in one sex by the other, use of striking dimorphic traits, among other attributes. There is much low-hanging fruit in terms of research advances for this group and we encourage future research on solifuge reproductive biology, especially as it relates to our understanding of sexual selection, sexual conflict, and their role in trait and species divergence.

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SUPPLEMENTAL MATERIALS

Table S1.—Review of the patterns of sexual behavior during the mating sequence in the solifuges studied to date. Symbols and abbreviations: ♀, female; ♂, male; ✓, presence of the behavior; ×, absence of the behavior; ?, currently unknown or confusing data; 1, the female of some species is described to show some movements. Online at https://doi.org/10.1636/JoA-S-20-037.s1

Table S2.—List of videos files examined for this review. Online at https://doi.org/10.1636/JoA-S-20-037.s2

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