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Description of the courtship and copulation behaviours of the wall spider *Oecobius concinnus* (Oecobiidae)

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Abstract

Courtship and copulation behaviours are yet scantily described in many spider families, and this lack of information limits our understanding of the evolution of such behaviours within and across families. Here, we provide a detailed description of both courtship and copulation behaviour for *Oecobius concinnus* Simon, 1893. A striking characteristic of the male courtship is the construction of a tubular web (mating web) in which most courtship and copulation occurs. This web likely functions to restrain the female in a reduced space and as a substrate for male pheromones. The courtship consists of a complex web of interactions between both sexes, with some interactions being non-randomly performed.

Keywords: mating web • permutation analysis

Introduction

Spiders show a wide range of courtship behaviours that vary widely within and across taxa (Robinson 1982). But, despite the rapid accumulation of new information, knowledge on courtship behaviour is still fragmented and concentrated in a limited number of families, or a few species within some families (Robinson 1982; Aisenberg, Barrantes & Eberhard 2015). This limits the understanding of the evolution of courtship in this highly diverse group of arthropods.

The wall spider family (Oecobiidae) is one such group with large information gaps on the courtship behaviour of its species. Oecobiidae is a small family (122 species: World Spider Catalog 2021) with a worldwide distribution and several synanthropic species. Despite the ubiquity of the family, the courtship and copulation behaviours have been described only for *Oecobius annulipes* Lucas, 1846 (Glatz 1967), in which the male walks in the female's web, builds a mating web and courts the female with a series of body and leg movements (Glatz 1967). There is also some fragmented information on the courtship (e.g. pedipalp movements behaviour, number of insertions, and mating duration) of *Uroctea durandi* Latreille, 1809 (Gerhardt in Huber 1998), the copulation position in *Oecobius cellariorum* Dugès, 1836 (Gerhardt 1928), and incomplete and likely imprecise information for *Oecobius tembli* (or *O. tembili*) Camrage (Romeih, El-Erkosousy & Aiad 2013) [Note: this species is not listed in the World Spider Catalog 2021, but it might be *Oecobius templi* O. Pickard-Cambridge, 1876 based on its distribution]. For the last two species, the authors mentioned some behaviours performed by the male, and the mating posture of *O. cellariorum* (Gerhardt 1928), but did not include information on the mating web. Detailed quantifications of courtship and copulation behaviours have not been published for any Oecobiidae.

In this study we describe the courtship behaviour for both sexes of *Oecobius concinnus*. This is a species that occupies subtropical and tropical regions of the Americas, mainly associated with urban habitats (Santos & Gonzaga 2003), and is possibly introduced into Polynesia. Detailed information of the structure and construction of the web of *O. concinnus* was recently published by Solano-Brenes *et al.* (2022), but its courtship behaviour remains unknown.

Materials and methods

We collected 24 adult spiders with unknown mating history (13 females and 11 males) in Cartago (9°54′N 83°40′W) and San José (9°57′N 84°3′W), Costa Rica, between July and November 2016. We placed each spider in a Petri dish painted with black paint (following Solano-Brenes, Miranda & Barrantes 2018) and fed them with ants (*Crematogaster* sp.) and flies (*Drosophila* sp.) twice a week. We waited between three to seven days for females to build their webs before starting the trials.

We randomly assigned females and males to each trial and then placed the male in the female's Petri dish, near her web. When courtship did not occur or the female rejected the male (e.g. females walked away from their webs), we offered a second male to the female. Because we had fewer males than females, some males were used in more than one trial. We let those males used in more than one trial rest for three days between consecutive trials, to allow them to recover the energy invested in silk, courtship, and sperm from the previous trial.

To record the courtship and copulation, we simultaneously used a video camera (Sony HDR-SR11) and a Dino-Eye AM423X camera adapted to a stereomicroscope (Nikon SMZ645). We started the recording when the male touched a radial thread of the female web and finished when either the male or female abandoned the female web or both remained motionless for 15 min. We defined courtship as any behaviour that could potentially stimulate the opposite sex (e.g. seismic signals produced by web contact) and could increase the probability of copulation (Kodric-Brown 1993; Hebets *et al.* 2011). We defined copulation as when both female and male joined in a copulatory position and the

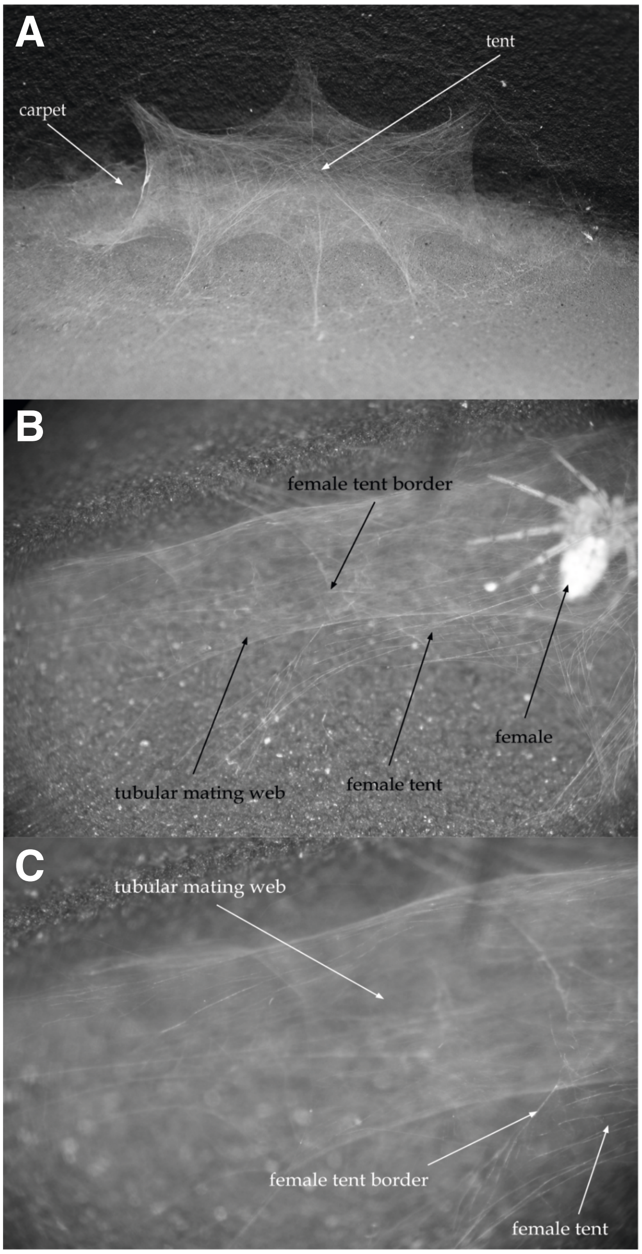

Fig. 1: *Oecobius concinnus*. **A** female retreat; **B–C** male mating web made between the carpet and the tent of the female retreat.

male pedipalp contacted the epigynum for at least two seconds; we used this definition because we were unable to observe the insertion of the conductor of the male pedipalp into the epigynum. If the male did not perform any behaviour within five minutes after contacting the female web, we gently touched the male with an entomology pin to make him move, which usually resulted in the initiation of courting. Using the video recordings, we described each behavioural unit during courtship and mating, following Glatz 1967; Aisenberg & Barrantes 2011; Segura-Hernández *et al.* 2020. To describe each behavioural unit of each sex, we played each video at slow motion (0.25×) using VLC media player 2.1.5 (https://www.videolan.org/vlc/releases/2.1.5.html).

Statistical analyses

To analyse the behavioural sequence among male and female behaviours, we used permutations to determine which transitions among behavioural units occurred non-randomly. The lack of detailed information on courtship behaviour of other Oecobiidae species prevent us from providing direct predictions on particular non-random transitions, but it is expected that an increase in non-random transitions between behaviours would reduce the variation in the courtship sequences (Slater 1973). To create the random scenarios, we mixed the observed behavioural units randomly (1000 simulations), creating random sequences. If the transition between two specific behaviours was not random, we expected that the number of observed events were more frequent than the transitions created randomly. We calculated the probability of an event happening randomly as the proportion of random scenarios in which the number of transitions were equal or greater than the number of observed transitions (details in Supplementary material at https://zenodo.org, doi: 10.5281/zenodo.7101820). This method provides an intuitive proxy of non-random transitions without following any specific error distribution. We excluded from the sequence analysis the behaviours observed in fewer than three couples, with fewer than two events per couple, or not related to courtship (e.g. grooming behaviours) (Table S1 in Supplementary material). We ran the analysis using the package stats (R Core Team. R, 2020) in the software R 4.0.3 (R Core Team. R, 2020).

Results

Courtship

We analysed the 11 pairs for which the courtship lasted on average 56 ± 19 min (mean ± standard deviation, SD). Since pairs mated more than one time, and the male continued courting the female between copulations, we added the periods of time when the male was courting the female to estimate the total courtship duration per trial. Male courtship began only after he walked into the female's retreat (Fig. 1A). When this occurred, the male started the construction of the mating web (see details below and Table 1). The male interrupted the mating web construction several times to perform different body movements, probably associated with seismic signals. Even after copulating multiple times with the female, males continued placing lines in the mating webs. All males (n = 8) constructed a mating web, and performed some body movements, but the sequence of the behaviours seemed non-stereotyped (see Behavioural transitions section).

We observed 26 behavioural units, 70% exclusively for males, 11% exclusively for females, and 19% shared by both sexes (Table 1 and Table S1 in Supplementary material). Moreover, nearly half of the behaviours (48%) were rare or not related with the courtship (Table S1 in Supplementary material). Most behavioural units performed by males during courtship involved body movements and leg

Behaviour	Pairs	Events	Period	Description
Abdominal lateral movement (♂)	8	25	Both	The male stood with the legs extended, moved slightly the abdomen laterally; no perceptible movements of the legs were seen during its performance.
Abdominal tapping (♂)	11	169	Both	The male moved its abdomen dorso-ventrally, tapping the web with its tip. These movements occurred individually or in a rapid sequence. On some occasions the male moved the body backward before tapping the web. The movement was produced by the legs I stretching forward. This body movement was fast and the spider waited a few seconds in this position, returning slowly to its initial position.
Abdominal dragging (♀)	7	26	After	After the pedipalp insertion, the female dragged the ventral area of the abdomen against either the mating web or the carpet of her own web. In some cases, after abdominal dragging, it was possible to see a trace of a whitish fluid on the web.
Approaches (♀, ♂)	10(♀) 9(♂)	139(♀) 62(♂)	Both	Either the male or female walked slowly or rapidly toward the other one. It excludes approaches during the mating web construction.
Contractions (♀, ♂)	5(♀) 11(♂)	68(♀) 409(♂)	Both	Rapid and repetitive movement of some segments of one or several pairs of legs, that made the body move up and down (similar to pushups in Ross and Smith 1979). This movement varied in amplitude.
Legs tapping (♂)	11	206	Both	The male tapped the mating web with legs I and II from the side closest to the female, which is either oriented toward or following the male orientation. When the male tapped with two legs (i.e. leg I and leg II) from the same side, both legs moved simultaneously and repeatedly. The tapping occurred when the male stood still or when moving toward the female.
Mating web construction (♂)	11	578	Both	It included the male attaching lines on the carpet and tent of the female web, and in the inner of the tubular mating web, after it was apparently finished. During attaching lines, the male moved forward as performing lateral abdominal movements, attaching the lines when the abdomen was near each fourth leg. Or the male rotated slightly on his transverse body plane while he moved laterally, attaching silk lines near the fourth leg to the side he rotated.
Move away (♀, ♂)	7(♀) 11(♂)	26(♀) 149(♂)	Both	When the female or male walked away from the other spider. The spider could abandon the female web or just move away a few millimetres on the web.
Pedipalp movements (♂)	10	143	After	Alternating up and down movements of male pedipalps.
Wide lateral abdominal movements (♂)	10	18	After	The male stood with all legs on the ground and slightly extended laterally, moved the abdomen widely laterally, between both fourth legs. The male flexed slightly the legs of the side he moved his abdomen, and stretched the opposite legs.
Abdominal tapping–Pedipalp movements (♂)	5	14	After	The male produced simultaneously "abdominal tapping" and "pedipalp movements".
Abdominal lateral movement–Contractions (♂)	4	6	Both	The male produced simultaneously "abdomen lateral movement" and "contraction".
Abdominal lateral movement–Leg tapping (♂)	3	5	After	The male produced simultaneously "abdomen lateral movement" and "leg tapping".
Contraction–Leg tapping (♂)	8	97	After	The male produced simultaneously the "contraction" and "leg tapping".
Contraction–Pedipalp movements (♂)	9	51	After	The male produced simultaneously "contraction" and "pedipalp tapping".
Pursuit (♀)	5	14	Before	The female pursued the male when he contacted her web.
Wrapping (♀)	1	1	Before	The female tried to wrap the male as wrapping prey, as reported by Glatz (1967).

Table 1: Description of behavioural units performed (agonistic behaviours and behaviours observed in more than three couples or with more than two events per couple) during the courtship by both males (♂) and females (♀) of *Oecobius concinnus* (n = 11 trials). We include the number of pairs for which behavioural units were recorded, the total number of events and the period in which the events occurred (After = after the first copulation, Before = before the first copulation, Both = before and after the first copulation).

tapping (Table 1). However, bouts of adding threads to the mating web was the most common behaviour performed by males (Table 1).

The mating web was a tubular structure constructed by the male between the tent and the carpet of the female sheet web (Fig. 1B–C). In most cases, one extreme of the mating web opened nearly at the centre of the carpet, inside the female web, and the other extreme opened outside the edge of the carpet of the female web. However, in some cases males built their entire tubular web inside the female's web (n = 3), but with the outer extreme positioned at the edge of the carpet of the female web. When the male constructed part of the tubular web beyond the edge of the female web, he first placed some threads between the wall and the floor of the Petri dish, which served as scaffolding for the external section of the mating web. Males always began constructing the mating web by placing threads on the carpet of the female web, then alternated with placing threads on the upper section of the tubular web, underneath the tent of the female web, while upside down. During construction, the male frequently tapped the web, alternating the tip of his palps. Males placed threads while performing two types of movements described in detail in Table 1 (Mating web construction behaviour).

Males also performed 16 behaviours possibly associated with seismic signals (e.g. leg contractions, leg and abdominal tapping, and lateral movements of the abdomen). Males often alternated these seismic signalling behaviours with mating web construction. Other behaviours related to pedipalp movements described by Glatz (1967), such as a sperm recharge of the pedipalps, were observed only after the first copulation.

Female behaviours included fewer body movements than the male, and they were related to attacking, escaping, or grooming (Table 1 and Table S1 in Supplementary material). However, abdominal dragging was one behaviour performed by seven (70%) of the females after copulation. In some cases, we observed a whitish liquid on the mating web after the female dragged her abdomen.

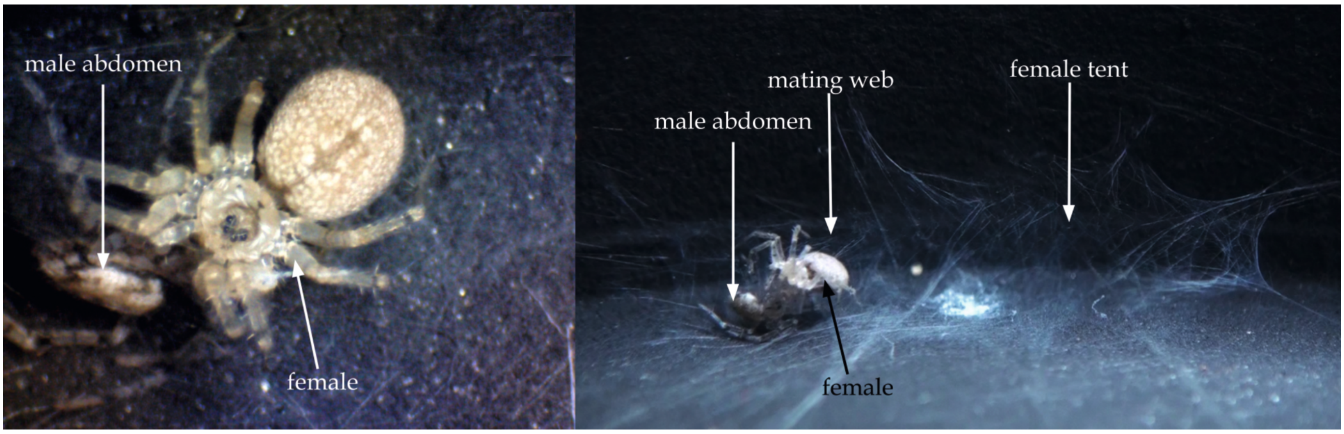

Fig. 2: One of the two possibilities of copulatory position of *Oecobius concinnus* in which males are positioned underneath the female.

Copulation description

We recorded 11 trials and, in 10 of them, we recorded at least one copulation. Only in one trial the female abandoned the web without copulating. In the pairs that copulated, the latency of the first copulation varied between 1.27 min to 21.92 min (8.65 ± 7.8 min, SD). We observed 37 matings with 2 to 11 matings per pair, with a mean duration of 13.43 s ± 13.08 s (SD). After copulation, males either continued courting or remained still. Thus, to have the total copulation duration of the pair, we summed the time of each mating period. The total copulation duration in *O. concinnus* ranged from 33 sec to 8 min. The time between copulations ranged from 0.53 min to 37.44 min.

In all cases when a pair mated, the female approached the male facing him, so that they faced opposite directions. We observed two copulatory positions. In one position, the female extended her legs and raised her cephalothorax while she flexed her abdomen ventrally until its tip touched (or nearly so) the web (Fig. 2). The male then moved partially underneath the female, such that the male's cephalothorax was underneath and nearly perpendicular to the female's cephalothorax. From this position, the male extended his pedipalp until its tip contacted the female's epigynum. We could not observe movements of the sclerites of the male pedipalp due to the small size of the spiders and because copulations occurred inside the mating web. In the second position, the female approached the male facing him, until both were side by side, facing opposite directions (Fig. 3). Both individuals, but mainly the female, raised their legs of the side closer to the male, so that the female exposed her epigynal area. From this position, the male extended his pedipalp closest to the female, until its tip contacted the female epigynum. In both copulatory positions, we observed the female's abdomen moving up and down rhythmically during copulation, as well as movements of the male's free pedipalp.

Behavioural transitions

We observed 171 transitions between behavioural units of the courtship and copulation, and 25% of them (n = 43) happened in a frequency higher than randomly expected (Fig. 4 and Table S1 in Supplementary material). Some transitions apparently occurred in response to the behaviour of either the female (e.g. males responded to females' approaches with leg tapping or they moved away) or the male (e.g. females responded to males' contractions with contractions).

Most transitions between behaviours had a frequency lower than 0.50. Other transitions such as Wide abdominal

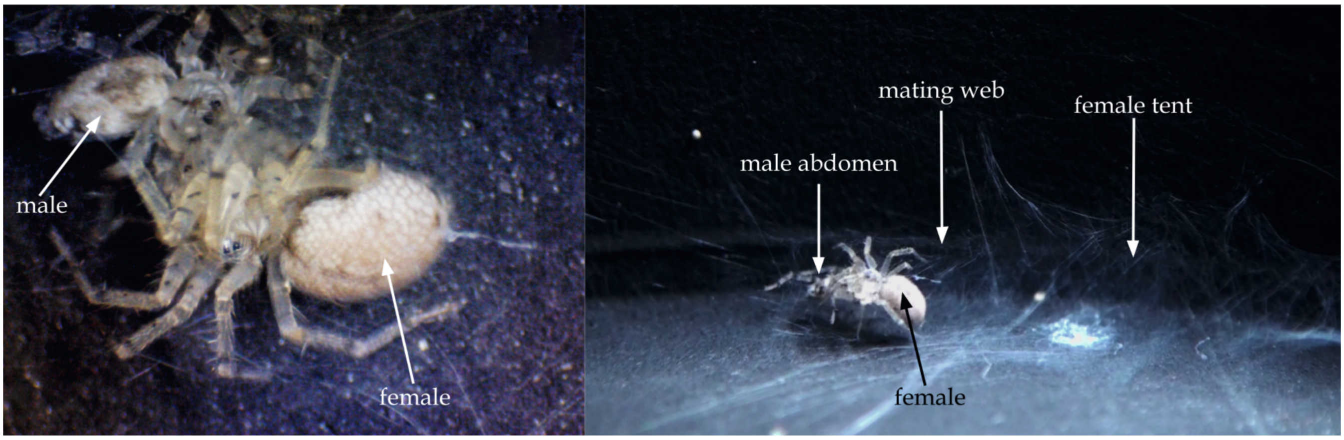

Fig. 3: One of the two possibilities of copulatory position of *Oecobius concinnus* in which males are positioned next to the female.

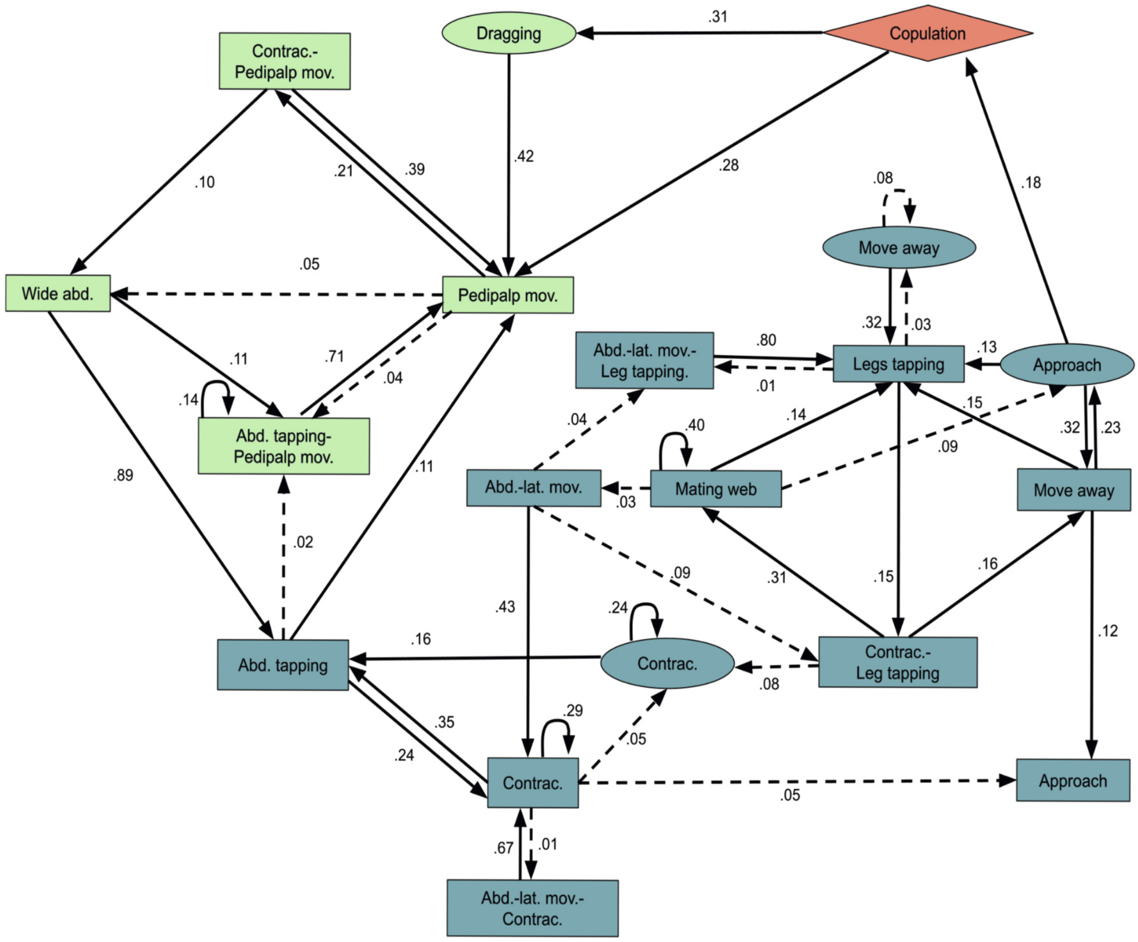

Fig. 4: Fluxogram of the more frequent behaviours during the sexual interaction in *Oecobius concinnus* from 11 mating trials. Ovals represent female behaviours and rectangles male behaviours. Blue figures are behaviours performed before and after the first pedipalp insertion, while green figures are behaviours performed only after pedipalp insertions. Arrows indicate transitions between behaviours with a probability lower than 0.05 to occur at random. The dashed arrows represent transitions with a frequency lower than 0.10. The number near each arrow is the observed frequency of the transition between the behaviours connected by the arrows.

movements to Abdominal tapping, and Legs tapping to Abdominal-pedicel movements–Legs tapping, occurred with frequencies higher than 0.50. Some behaviours occurred only after a particular behaviour was performed by the opposite sex. For example, copulations happened in all cases when the female approached the male, but not the other way around (Fig. 4). Also, other behaviours only occurred after pedipalp insertions such as male pedipalp movements and female abdominal dragging (Fig. 4).

Discussion

In many spider families, males construct silk structures in which the courtship and mating occur (Scott, Anderson & Andrade 2018). Frequently, the male places only a thread (i.e. mating thread), but in some species (e.g. *Steatoda*, Theridiidae), the male constructs a complex structure in the female web in which mating occurs (Knoflach 2004). However, it is unusual during the spider courtship that males construct a complex silk structure as the tubular mating web constructed by *O. annulipes* (Glatz 1967) and *O. concinnus*. A possible role for the mating web in *O. concinnus* is to serve as a pheromone substrate. Males of *O. concinnus* frequently interrupt seismic courtship signals to add new threads to the apparently finished mating web. Thus, with this behaviour males could refresh the pheromone supply. In several species, females use silk lines impregnated with pheromones to attract males (Gaskett 2007). The use of pheromones is less frequent in males, though there are at least seven spider species in which males use silk with pheromones in a sexual context (Scott, Anderson & Andrade 2018). It has also been suggested that the role of sex pheromones bound to silk lines produced by males reduce female aggressiveness, and likely increase receptivity in some spider species (Ross & Smith 1979; Aisenberg *et al.* 2008; Barrantes & Ramírez 2013). For instance, in *Kukulcania hibernalis* Hentz, 1842 males place abundant lines on the female web, which presumably contain pheromones and may have the function of reducing female aggressiveness (Barrantes & Ramírez 2013). Males of the genus *Latrodectus* Walckenaer, 1805 lay silk lines directly on the female (bridal veil), presumably to restrain her during copulation, though she can easily release herself. This suggests that pheromones bound to the bridal veil inhibit the female from moving (Ross & Smith 1979).

Another non-exclusive role that the mating web could play is to restrain female movements to avoid antagonistic behaviours. The mating web reduces the area in which the courtship is performed and this may prevent females to wrap or pursuit males as often occurs outside the mating web (Wrapping and Pursuit behaviours in Table 1). These webs could also offer an escape route to the male, as one exit of the mating web is at the edge or beyond the female retreat. In other species, males place a few silk lines between a nearby substrate and the female web, which allow males to either escape if females respond aggressively or to direct the vibrational signals towards a specific area of the female's web (Robinson 1982). In *Latrodectus mactans* (Fabricius, 1775) and *L. hesperus* (Chamberlin & Ivie, 1935) males cut down a large portion of the female web to presumably avoid females' attacks, though other possible functions for this behaviour have also been proposed (avoid female escaping, reduce web pheromone signals) (Breene & Sweet 1985; Ross & Smith 1979). However, in *O. concinnus* the functions of the mating web are speculative and need further testing.

The courtship in *O. concinnus* involves a large series of non-random interactive behaviours between the male and female (Fig. 4). Most of these behaviours involve body movements of males, which likely produce vibrational signals. Males produced these movements both before and after the first copulation. Vibrational signals during the courtship in spiders are thought to have different functions: 1) species recognition, 2) reducing female aggression, 3) female stimulation prior to copulation, 4) and/or honest male quality signals (Maklakov, Bilde & Lubin 2003). In *O. concinnus*, we do not have direct evidence supporting any of these possible functions. However, the frequent occurrence of these behaviours in all copulations, suggest that they may play an important role in sexual interactions: reducing female aggression, female stimulation, and/or signalling male quality.

Substrate vibration is ubiquitous in spiders (Robinson 1982; Eberhard 1994). A large number of vagrant and sheet web spider males perform pedipalp tapping and abdominal movements during courtship. For instance, in the genera *Cupiennius* Simon, 1891 (Trechaleidae) and *Schizocosa* Chamberlin, 1904 (Lycosidae), the males produce different vibrational patterns with their legs, pedipalps, and abdomen on different substrates (Barth 1993; Hebets *et al.* 2013; Hebets & McGinley 2019), and the male of *Tengella radiata* Kulczyński, 1909 (Zoropsidae) produces vibratory signals with the palps and abdomen on the female web (Barrantes 2008). Hence, it is likely that vibrations produced by *O. concinnus* males play an important role in male female sexual interactions.

Oecobius concinnus and *O. annulipes* share several behaviours, such as the construction of the mating web, as well as body and pedipalp movements (Glatz 1967). Contractions, before and after the first copula, were more frequent in males of *O. annulipes* than in those of *O. concinnus*, and the male pedipalp movements were performed only after the first copula. Glatz (1967) argued that pedipalp movements are related to recharging the pedipalps with sperm stored in the buccal cavity. This is an extremely rare behaviour among spiders, because males in other families charge their pedipalps directly on the sperm web. However, in *O. annulipes*, the males store the sperm in the mouth and then charge the pedipalps with it (Glatz 1967). We were not able to observe this sequence of behaviours in *O. concinnus*, but we observed pedipalp movements similar to those described by Glatz (1967) during pedipalp recharging, after the first copulation.

The number and duration of copulations in *O. concinnus* were similar to those reported for *O. annulipes* (Glatz 1967). Copulations are relatively short in *O. concinnus* and with only one pedipalp insertion during each copulation. As in other species, such as *Leucauge mariana* Taczanowski in Keyserling, 1881 (Tetragnathidae) and *Theridiosoma gemmosum* Koch, 1877 (Theridiosomatidae), there are multiple pedipalp insertions per copulation, often alternating pedipalps (Aisenberg & Barrantes 2011; Hajer, Hajer & Řeháková 2011; Segura-Hernández *et al.* 2020). The copulatory position changed frequently in the same pair, apparently depending on the position of the male in the mating web, but none of the two positions described for *O. concinnus* were similar to those reported for *O. annulipes* and *O. cellariorum* (Gerhardt 1928; Glatz 1967). In *O. cellariorum*, the copulatory position is similar to *O. concinnus* in Fig. 2, but male *O. cellariorum* maintains the body parallel to the female body rather than perpendicular (see fig. 6 in Gerhardt 1928). In *O. annulipes* the copulatory position is similar to the position of *O. concinnus* in Fig. 3, but male *O. annulipes* inserts the pedipalp more distant to the female body (i.e. if the female is on the right side of the male, the male uses the left pedipalp; see fig. 20 in Glatz 1967) rather than the closer, as in *O. concinnus*.

We found that only 25% of the transitions were different from the random expectations, and the majority occurred at low frequencies. These two characteristics suggest that the order in which behaviours are performed by *O. concinnus* is highly variable (Slater 1973). Several factors, such as male experience (Hoefler *et al.* 2010), male body condition (Eberhard, Machnis & Uhl 2020), male energy allocation in response to female quality (e.g. Solano-Brenes *et al.* 2021), and behaviour of the female during courtship (e.g. Sullivan-Beckers & Hebets 2014) could affect the frequency and order of behaviours during pre-copulatory courtship. The variation in courtship behaviour and copulation of *O. concinnus* could be influenced by the experience of males and females prior to the trials. A frequently used approach to control for previous experiences is to quantify the courtship behaviours on virgin spiders. This would be an interesting study in *O. concinnus* for comparing the performance of virgin with unknown mating history spiders. Although in some species (e.g. *Leucauge argyra*) the behaviour between mated and unmated females is basically the same (Aisenberg & Barrantes 2011).

In conclusion, the courtship performed by males of *O. concinnus* includes a series of different stimuli for the female, including the construction of a tubular web and different seismic vibrations. We suggest that the tubular mating web limit the females' attacks and provide a substrate for male pheromones. Additionally, this species changes the copulation position apparently as a response of the female to the male position inside the mating web.

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