Animal Behaviour 79 (2010) 1031–1036

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Nuptial gift-giving behaviour and male mating effort in the Neotropical spider *Paratrechalea ornata* (Trechaleidae)

María J. Albo*, Fernando G. Costa

Laboratorio de Etología, Ecología y Evolución, Instituto de Investigaciones Biológicas Clemente Estable

A R T I C L E I N F O

Article history:
Received 7 October 2009
Initial acceptance 25 November 2009
Final acceptance 22 January 2010
Available online 12 March 2010
MS. number: 09-00623

Keywords:
male mating effort
oviposition acceleration
Paratrechalea ornata
sexual selection
spider nuptial gift

The occurrence of nuptial gifts is rare in spiders, being well known only for a single species, *Pisaura mirabilis* (Pisauridae), whose males offer females a prey wrapped in silk during courtship. Although some males can mate without offering a prey, the gift in this species is thought to represent male mating effort. Male gift offering has been recently described in *Paratrechalea ornata*, a Neotropical spider belonging to another family, Trechaleidae. We investigated the function of the gift in this species by testing the mating effort hypothesis and two other nonexclusive hypotheses, sexual cannibalism avoidance and paternal investment. Two groups of males were exposed to virgin females: 23 males with no prey (NP group) and 21 males carrying a prey (CP group). Mating success, courtship, copulation and first oviposition were recorded. Males from group CP had better mating success, longer copulations and longer palpal insertions than those from NP. Longer copulations were associated with earlier eggsac construction and oviposition. Some unmated males from NP wrapped prey carrion when they returned to their breeding jars after the trial. Our findings suggest that nuptial gift giving represents male mating effort for *P. ornata*. Nuptial gifts would allow males to control copulation duration and to accelerate female oviposition, improving sperm supply and paternity, and minimizing possible costs of remating with polyandrous females.

Nuptial gifts are common in invertebrates and have been intensively studied in insects (Boggs 1995; Vahed 2007; Gwynne 2008). In general, gifts could be prey, carrion or plants, regurgitations, salivary and glandular secretions, specialized male body parts and ejaculated substances (Vahed 1998, 2007). Historically, nuptial gifts were defined as potentially nutritive substances donated by males to females during mating (Boggs 1995). Such gifts can supply the female with nutrients and so function as paternal investment (Thornhill 1976a; Gwynne 1984; Simmons & Parker 1989). In some insects the nuptial gift has a positive effect on female fecundity and can also increase female longevity (Wiklund et al. 1993; Karlsson 1998; Lewis & Cratsley 2008). However, because there is limited knowledge of the nutritional value of gifts, and there is evidence that some nuptial gifts improve male reproductive success but do not provide direct (nutritious) benefits for females, sexual conflict between the sexes could be operating (Vahed 1998, 2007; but see Gwynne 2008). By providing such gifts, males can manipulate the time of copulation, thus promoting the production of large ejaculates, inducing a female refractory period, accelerating oviposition and maximizing their reproductive success (mating effort hypothesis: Thornhill 1976b; Simmons & Gwynne 1991; Eberhard 1996; Wolfner 1997; Heifetz et al. 2001; Arnqvist & Rowe 2005; Sakaluk et al. 2006).

Two other hypotheses can explain the adaptive significance of nuptial gifts, beyond the paternal investment and mating effort: avoidance of sexual cannibalism and sensory exploitation (Vahed 1998, 2007). Cannibalism avoidance was proposed by Bristowe (1958) and Kessel (1955) as a tactic to prevent female attacks, but has limited empirical support. Sensory exploitation assumes males manipulate females by offering gifts that exploit pre-existing female sensory biases, without necessarily implying costs for females (intersexual conflict). A good example is the donation of spermatophores in crickets, which provide the gustatory stimuli that females prefer (Sakaluk 2000; Vahed 2007). These hypotheses are not mutually exclusive.

The occurrence of nuptial gifts is rare in spiders; in fact the Palaearctic *Pisaura mirabilis* (Pisauridae) has been the only well-studied species, particularly in the context of sexual selection (Austad & Thornhill 1986; Lang 1996; Drengsgaard & Toft 1999; Stålhandske 2001, 2002; Bruun et al. 2003; Prokop 2006; Bilde et al. 2006, 2007; Andersen et al. 2008; Hansen et al. 2008; Prokop & Maxwell 2009). Males of this species offer females a prey wrapped in silk during courtship, which is bitten and consumed by the female during mating. Stålhandske (2001) observed that in a Scandinavian population, males lacking

---

* Correspondence: M. J. Albo, Laboratorio de Etología, Ecología y Evolución, Instituto de Investigaciones Biológicas Clemente Estable, Av. Italia 3318, 11600 Montevideo, Uruguay.
E-mail address: mjalbo@iibce.edu.uy (M.J. Albo).

0003-3472/$38.00 © 2010 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
doi:10.1016/j.anbehav.2010.01.018

a donation can also mate without risk of cannibalism. She suggested that the gift facilitates the copulation position, and keeps the female occupied handling it during mating. Larger gifts result in longer copulations and more fertilized eggs (Austad & Thornhill 1986; Stålhandske 2001). In *P. mirabilis* the gift functions as male mating effort to facilitate copulations, and the silk wrapping provides direct benefits to males in the form of increased control over mating and longer copulations (Lang 1996; Stålhandske 2001; Bilde et al. 2007; Andersen et al. 2008).

Recently, Costa-Schmidt et al. (2008) described that in *Paratrechalea ornata*, a Neotropical spider that belongs to the family Trechaleidae, males also construct and donate nuptial gifts during courtship and copulation. *Paratrechalea ornata* is found in southern Brazil, northern Argentina, Paraguay and Uruguay (Carico 2005) and, like other trechaleids, inhabit semiaquatic environments, especially the borders of streams and rivers. Females carry the eggsac attached to the spinnerets, similar to the wolf spiders (Lycosidae). In Uruguay *P. ornata* co-occurs with other larger trechaleid species such as *Trechalea bucculenta* and *Trechaleoides biocellata* (M. J. Albo & F. G. Costa, unpublished data). As was found in the pisaurid *P. mirabilis*, males of *P. ornata* may present either a wrapped or an unwrapped nuptial prey gift (Albo et al. 2009). Prey wrapping seems to be triggered by perception of cues on the female's silk and increases in frequency according to the male's age (Albo et al. 2009).

In the present study we tested the function of the nuptial gift in *P. ornata* by comparing the sexual behaviour and the reproductive success of pairs in both the presence and the absence of a nuptial gift. Under the male mating effort hypothesis, males presenting a nuptial gift are predicted to experience briefer courtship, higher mating success and longer mating than males without a gift. Under the paternal investment hypothesis, females that received a nuptial gift are predicted to produce more or larger offspring than those that did not. Under the sexual cannibalism avoidance hypothesis, males without a gift are more likely to be cannibalized by females than males carrying a gift. The experimental design did not allow us to test the sensory exploitation hypothesis. We compared our findings with those from *P. mirabilis* to discuss the function and evolution of this conspicuous behaviour.

METHODS

We collected subadult individuals of *P. ornata* in February and May 2007, and in April, August and September 2008, from riparian areas of Yerbal Chico Stream, Quebrada de los Cuervos, Treinta y Tres Province (32°55′30.50′S, 54°27′33.10′W) and Santa Lucía River, Paso del Molino, Arequita, Lavalleja Province (34°16′40.10′S, 55°14′00.80′W), Uruguay. In the laboratory, the spiders were kept in individual glass jars (8 cm internal diameter and 11 cm height) and raised until adulthood. We noted the dates of moults during this time. Spiders were fed weekly with a mixed diet of termite workers (*Nasutitermes* sp.), flies, *Musca domestica*, and pieces of mealworms, *Tenebrio molitor*, and wet cotton wool was provided daily for water. Juvenile and penultimate spiders were raised in a climate room (mean ± SD = 24.4 ± 1.8 °C) to accelerate their development, while adults were maintained at ambient temperature conditions (20.4 ± 2.3 °C). All females and males used in the experiments were virgins. Adult individuals were experimentally used 20 days after the final moult. Because these spiders are nocturnal, experimental observations were carried out after sunset under laboratory conditions, from 28 September to 9 December 2007 and from 25 April to 27 October 2008. The experimental cages were glass terraria of 30 × 14 cm base and 20 cm height. The base was covered by a thick layer of pebbles, simulating natural riparian conditions, with a fitted petri dish of 14 cm diameter with water (Fig. 1). The ambient temperature during the experimental period was 20.4 ± 2.3 °C.

To investigate the function of the nuptial gift in courtship and mating, we exposed 23 females to a male with no prey (group NP) and 25 females to a male carrying a prey (group CP). One day before the experimental trial, a female was placed into the experimental cage allowing silk deposition and habituation, whereas an adult male was placed in a petri dish and fed with a fruit fly (*Drosophila* sp.) to prevent starvation. For the mating trials, each male of the CP group received a large living fruit fly (*Drosophila funebris*) and was transferred to the female experimental cage immediately after he captured the prey. In both treatments the trials consisted of two steps. First, we exposed the male to the female silk, isolated from the female by an opaque glass barrier. Second, after 15 min we carefully removed the barrier, allowing male–female encounter. This time period is enough for males to wrap the prey in silk (Albo et al. 2009). If a male did not wrap the prey, we allowed the male to encounter the female carrying the unwrapped prey. Therefore, males from the CP treatment could encounter females carrying either a wrapped or an unwrapped prey. If the male courted a female with a prey but mated without donating it (maintaining the prey in his chelicerae), we included these data in CP for the courtship analyses, but considered them as a separate group (no donation, ND) for the mating analyses.

Individuals were not reused, except for three females that were first used in NP and did not mate, and were subsequently reused in CP. To avoid possible effects of previous experience, we excluded their data from the courtship analysis, but we included them in the mating analysis because of their virgin condition. Each trial was stopped when the mating ended, or after 30 min when no interactions were observed. Behaviours and interactions between individuals were timed and recorded. We noted the occurrence of prey wrapping, male courtship, female sexual receptivity, gift acceptance and mating (see Costa-Schmidt et al. 2008). Male courtship consisted of nonlinear locomotion (searching behaviour) and foreleg vibrations towards the female. Female sexual receptivity consisted of hyperflexion of forelegs and active behaviour towards the male; female acceptance was when the female grasped the gift and accepted the mount (CP) or directly accepted the mount (NP). The copulatory position involved the male climbing over the prosoma of the female (as in the wolf spider posture), where the male turned towards one side of her abdomen, while the female twisted it, permitting one palpal insertion. Afterwards, the male returned to the face-to-face posture, biting the gift. Typically, mating involved four palpal insertions (Costa-Schmidt et al. 2008). Total copulation duration included the entire period between first mount and final dismount. Insertion duration was measured from palpal insertion until palpal disengagement. The interval between two consecutive insertions included the face-to-face posture. Both total insertion duration and total interval

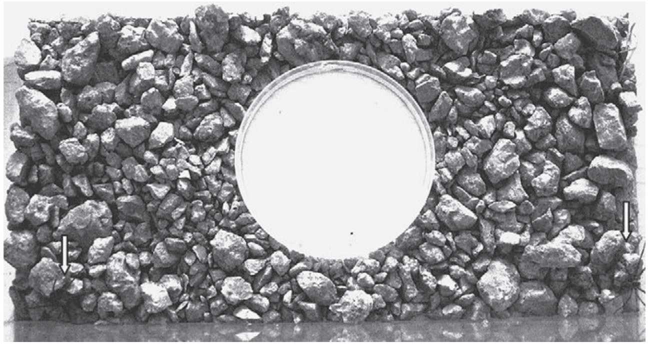

Figure 1. Experimental terrarium containing a dish with water surrounded by pebbles, simulating riparian conditions. The two spiders are indicated by arrows. Photo: M. Trillo.

between insertions were obtained by adding data corresponding to each copulation. Each mated female was individually raised and we recorded the period until first eggsac construction (latency to oviposit) and the number of emerged spiderlings. Voucher males, females and spiderlings were deposited in the arachnological collection of the Facultad de Ciencias, Montevideo, Uruguay.

We used the Past statistical package (Hammer et al. 2003) and JMP 7 package (SAS Institute, Inc., Cary, NC, U.S.A.). We tested normality and homogeneity of variances with Shapiro–Wilk and Levene tests, respectively. For comparing mean values, we used the Mann–Whitney *U* test and the Student's *t* test for two independent samples, and the Fisher's exact probability test to compare frequencies. To perform ANCOVA, we log transformed solely the data samples involved. We also performed linear regression and correlation analyses. All the tests were two tailed.

RESULTS

Courtship and Male Mating Success

All males and females found each other in both treatment groups. The first male–female encounter occurred significantly sooner, after a mean ± SD of 12.1 ± 7.7 min, in NP than in CP (8.7 ± 7.3 min; Mann–Whitney test: $U = 184$, $N_1 = 23$, $N_2 = 25$, $P = 0.03$). In NP, four males did not court and 19 courted the females, whereas all 25 males courted in CP (Fisher's exact test: $P = 0.045$). Courtship duration appeared briefer in NP (8.4 ± 7.7 min) than in CP (14.4 ± 15.6 min), but this was not statistically significant (Mann–Whitney test: $U = 195.5$, $N_1 = 19$, $N_2 = 25$, $P = 0.33$). In CP, 11 males first found the females when they were carrying the prey wrapped in silk, whereas the other 14 males found the females when carrying unwrapped prey.

Nine of the 23 pairs mated in NP. In CP, 15 males mated after donating the prey, six did not mate, and four males mated without donating the prey (maintaining it in the chelicerae) during the entire copulation. These last cases were considered separately in the following analyses (see Methods). Males with a prey were more likely to mate than males without prey (Fisher's exact test: $P = 0.039$). In CP, six males carrying a wrapped prey courted females and five of them mated; nine males with an unwrapped prey courted females and three mated. No significant differences were found in the frequency of mating between groups (Fisher's exact test: $P = 0.12$). Males that failed to mate carrying an unwrapped (six cases) or a wrapped prey (one case) immediately wrapped or rewrapped it, and successfully mated afterwards. After trials and once returned to their breeding jars, five unmated and two mated males from the NP group immediately constructed nuptial gifts by packing mealworm carrion in silk.

Copulation Duration and First Oviposition

The CP group showed longer copulations, more and longer insertions, and longer intervals between insertions than NP (Table 1). We also compared these groups with ND (the group of four males that mated without donating the prey). This last group showed the following mean ± SD values: copulation duration: 3.4 ± 3.1 min; insertion duration: 0.8 ± 0.3 min; interval between insertions: 2.6 ± 3.3 min; number of insertions: 1.8 ± 0.5 min. We found no differences in copulation duration (with NP: $U = 7$, $N_1 = 4$, $N_2 = 9$, $P = 0.11$; with CP: $U = 22.5$, $N_1 = 4$, $N_2 = 17$, $P = 0.32$), insertion duration (with NP: $U = 9.5$, $N_1 = 4$, $N_2 = 9$, $P = 0.21$; with CP: $U = 22.5$, $N_1 = 4$, $N_2 = 17$, $P = 0.32$), interval between insertions (with NP: $U = 7$, $N_1 = 4$, $N_2 = 9$, $P = 0.09$; with CP: $U = 23$, $N_1 = 4$, $N_2 = 17$, $P = 0.35$) or number of insertions (with NP: $U = 14$, $N_1 = 4$, $N_2 = 9$, $P = 0.55$; with CP: $U = 20$, $N_1 = 4$, $N_2 = 17$, $P = 0.21$).

Table 1

Mean total values ± SD of copulation duration, number and duration of palpal insertions and interval between insertions (min) during mating in groups with males carrying no prey (NP) and prey (CP)

	Treatment NP (*N*=9)	Treatment CP (*N*=17)	*U*	*P*
Total copulation duration	2.0±3.3	6.5±6.7	32.0	0.018
Insertion duration	0.6±0.2	1.2±0.8	39.0	0.046
Interval between insertions	1.4±3.1	5.3±6.3	35.5	0.028
Number of insertions	1.6±0.7	2.7±1.4	38.0	0.034

All statistical comparisons were performed using the Mann–Whitney *U* test. Three unmated females used in NP were reused and mated in CP and their data were considered in the analysis of CP. Data from a single mating from CP were not included because of a recording failure.

The occurrence of the first oviposition was similar in both treatments: eight of nine mated females constructed an eggsac in NP and 12 of 18 females in CP (data from three unmated females used in NP were included in CP; see Methods). We found no statistical differences between these frequencies (Fisher's exact test: $P = 0.36$). None of the 14 unmated females constructed an eggsac. The latency of oviposition (period between mating and first eggsac construction) was longer in NP (24.6 ± 9.9 days) than in CP (14.5 ± 10.1 days; Mann–Whitney test: $U = 18.5$, $N_1 = 8$, $N_2 = 12$, $P = 0.03$). We found a significant relationship between copulation duration and latency of female oviposition (ANCOVA: $F_{1,1} = 13.35$, $P = 0.002$); CP showed a significant (inverse) linear relationship ($r_{11} = -0.76$, $P = 0.006$), while NP did not show a significant relationship ($r_8 = 0.09$, $P = 0.82$; Fig. 2a). Similar relationships were found between insertion duration and latency of oviposition (ANCOVA: $F_{1,1} = 9.79$, $P = 0.006$; in CP: $r_{11} = -0.63$, $P = 0.04$; in NP: $r_8 = -0.017$, $P = 0.96$; Fig. 2b). We also tested whether female age and room temperature affected oviposition latencies. We found no significant relationship (ANCOVA: $F_{1,2} = 0.031$, $P = 0.99$). Spiderling emergence was observed only from three eggsacs in NP and from five eggsacs in CP, with a mean ± SD of 44.3 ± 34.5 and 34.8 ± 25.8 spiderlings, respectively, showing no significant difference (Student's *t* test: $t_1 = 0.45$, $P = 0.66$).

Female Receptivity

Sixteen females from NP were receptive towards the courting males, adopting the hyperflexion posture; however, seven of them did not mate. In this group, three other females were reluctant, evading male contact, and the remaining four females were not courted. Seventeen females from CP were receptive (showing hyperflexion), but two of them did not mate. All 21 females from CP were courted but four of them were reluctant. When we compared the occurrence of mating between the receptive females of NP and CP, CP showed a near significantly higher female receptiveness (Fisher's exact test: $P = 0.057$). Eight females in NP and eight females in CP initially 'attacked' males, performing fast jumping, which was avoided by males. After an attack, the male and female remained face-to-face until the male started or continued courting while the female stayed motionless. In CP we observed a single case of sexual cannibalism after mating when the male left after a single insertion, but maintaining the gift grasped by the third pair of legs. The female attacked immediately, trying to bite the gift and simultaneously captured and ate the male. In the no-donation male group (ND) the four females were receptive; two of them attacked males and all four mated.

Copulation Description

In comparison with the Brazilian population studied by Costa-Schmidt et al. (2008), where a nuptial gift is obligatory for mating

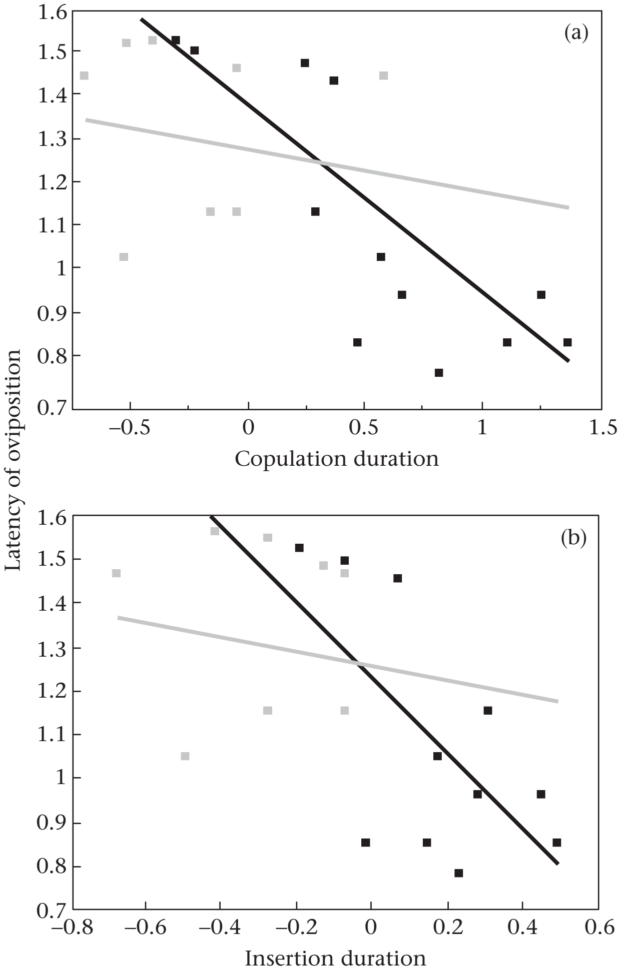

Figure 2. Linear relationship between latency of oviposition and (a) total copulation duration and (b) insertion duration. Latency is expressed as log-transformed days and copulation and insertion durations as log-transformed minutes. Grey lines and squares indicate data from group NP and black ones those from group CP.

success, in the Uruguayan population studied here males succeeded in mating also without a gift. We here briefly redescribe the mating with particular emphasis in cases when the gift is not present. Mating consisted of phases of palpal insertion alternated with the face-to-face position, in which both the male and the female grasped the gift (Fig. 3). Before palpal insertion, the male clasped the gift with the claws of the third pair of legs and mounted the female, attempting to insert the pedipalp; afterwards, he returned to the face-to-face position and unclasped the claws. When no donation was present (NP group), we observed that the male behaviour was similar, and the tarsi of the third legs of the male clasped the female's mouthparts during insertions, but we did not observe direct contact between male and female mouthparts once the insertion finished. When males kept the gift in the chelicerae (ND group), the mating pattern was similar to that observed in NP. These males retained the prey in the face-to-face position and they did not appear to have any difficulties inserting their palps.

DISCUSSION

The presence of nuptial gifts in *P. ornata* enhanced male mating success and increased copulation duration, in agreement with reports for gift-giving insect species (Sakaluk 1984; Thornhill 1976b; Simmons & Gwynne 1991; Vahed 2007). Our findings support the hypothesis that the maintenance of the nuptial gift in *P. ornata* is mediated by male mating effort, improving the male's chances of mating and possibly providing advantages in sperm competition. These functions of the nuptial gift have received empirical support in the gift-giving spider *P. mirabilis* (Drengsgaard & Toft 1999; Bilde et al. 2007), including evidence that the gift can improve mating position and facilitate palpal insertion (Stålhandske 2001). The absence of a nuptial gift did not increase the occurrence of sexual cannibalism, and the one case where the female attacked and cannibalized the male was in the presence of a gift. Therefore, the hypothesis that the gift could be used by males to avoid being eaten by females in this species may be discarded. Finally, we did not find evidence of more offspring associated with gift occurrence, giving no support to the hypothesis of paternal investment in *P. ornata*, as was reported for insects (Thornhill 1976a; Gwynne 1984; Simmons & Parker 1989; Boggs 1995). However, we cannot discard this nonexclusive hypothesis because of the small sample sizes of the hatched spiderlings.

Figure 3. Female (left) and male (right) in the face-to-face position grasping the gift, during mating. Photo: M.J. Albo.

Our results showed that males carrying a nuptial gift (wrapped or unwrapped prey) actively searched for females, and found them before males without a gift. Our results also suggest that the former had higher motivation for searching, displaying courtship more frequently and being more successful in achieving copulations. Even though they perceived the female's cues, males lacking a gift actively kept exploring the substrate as if they were searching for a nuptial prey, avoiding, in some cases, any mounting attempt. To carry a gift prior to female encounter could benefit males by facilitating mating and securing longer copulations. The latter is likely to benefit males under sperm competition (Drengsgaard & Toft 1999), and these benefits might also compensate for costs to males of capturing prey without feeding on it, releasing large amounts of silk, losing time and energy without the certainty of meeting the female, and risking predation while wrapping and carrying the gift (see Albo et al. 2009).

Our results for *P. ornata* suggest that males carrying a wrapped prey increase their probability of mating in the first sexual encounter compared with those presenting unwrapped gifts, but with no statistical support possibly because of the small samples. Wrapping prey seemed to be important for male mating success, because most of the males carrying unwrapped prey initiated prey wrapping after coming into contact with the female, and all these males mated after offering a wrapped prey. In addition, half of the males from the NP group did not mate despite females apparently being receptive. Receptive females were also active and performed many ritualized attacks, suggesting that these 'attacks' could be a signal of receptiveness, or alternatively the female was searching for a nuptial gift. Both results indicate the importance of carrying a gift for males. These males wrapped prey carrion later in their breeding jars, carrying 'symbolic' or non-nutritious donations. 'Symbolic' donations were also observed in the field in *P. ornata* populations, containing dry prey or even a seed (M. J. Albo & F. G. Costa, unpublished data). In *P. mirabilis*, males obtain a similar mating success with wrapped and unwrapped prey (Bilde et al. 2007), but Andersen et al. (2008) suggested that silk wrapping increases the male's control over mating. 'Symbolic' donations were also reported in *P. mirabilis* under both laboratory (Nitzsche 1999; G. Winther & M. J. Albo, unpublished data) and field conditions (Bristowe 1958; Nitzsche 1988; Stålhandske 2002).

The nuptial gift by itself could directly advance oviposition through the action of unknown chemical substances or other gift properties. However, our findings suggest that increased copulation duration of *P. ornata* caused by gift presence seemed to accelerate the female's first oviposition. Longer copulations implied more insertions and longer intervals between insertions. The effect of copulation duration could arise from increased sperm transfer and even from associated substances in the ejaculate, affecting female oviposition rate and fecundity (Heifetz et al. 2001; Vahed 2006; Gwynne 2008). By promoting longer copulations males could ensure the rapid use of their sperm, maximizing sperm supply and egg fertilization, and siring most of the offspring (Gwynne 2008). *Paratrechalea ornata* females are polyandrous (M. J. Albo, unpublished data) and males would benefit from accelerating oviposition by minimizing sperm competition, but this effect could negatively affect the female's interests, as was reported for some insects (Simmons & Gwynne 1991; Sakaluk et al. 2006). Then, male manipulation and conflict of interests could be involved. However, early oviposition in *P. ornata* could also be advantageous for females because they can then rapidly produce offspring before they become too old, by maximizing clutch number during the breeding season (up to four eggsacs; M. J. Albo, unpublished data). From the female's perspective, the occurrence of numerous and longer insertions after gift donation could be explained in a scenario of cryptic female choice, where females choose the sperm of males with costly copulatory courtship (Eberhard 1996). Moreover, the female may be evaluating male quality during the long face-to-face intervals between insertions. Further research is needed to elucidate these hypotheses.

In summary, our results suggest that male nuptial gifts evolve as mating effort to increase the male's chances of obtaining a long mating, ensuring the paternity in a polyandrous context with high levels of sperm competition. Further research is particularly needed on the role of 'symbolic' donations, the nutritional value of nuptial gifts and prey-wrapping behaviour in female choice in *P. ornata* and in other gift-giving spider species.

Acknowledgments

We thank Anita Aisenberg, Soledad Ghione, Alicia Postiglioni, Rodrigo Postiglioni and Carlos Toscano-Gadea for their help in the collection of spiders; Maria. J. Ferreiro, Santiago Ruiz and Rafael Cantera from the Department of Biología del Neurodesarrollo from IIBCE for kindly providing *Drosophila* spp; Trine Bilde, Søren Toft and William Eberhard for constructive discussions; and Luiz Ernesto Costa-Schmidt, Trine Bilde, Estefanía Stanley and two anonymous referees for valuable comments on the manuscript.

References

Albo, M. J., Costa-Schmidt, L. E. & Costa, F. G. 2009. To feed or to wrap? Female silk cues elicit male nuptial gift construction in the spider *Paratrechalea ornata* (Trechaleidae). *Journal of Zoology*, **277**, 284–290.

Andersen, T., Bollerup, K., Toft, S. & Bilde, T. 2008. Why do males of the spider *Pisaura mirabilis* wrap their nuptial gifts in silk: female preference or male control? *Ethology*, **114**, 775–781.

Arnqvist, G. & Rowe, L. 2005. *Sexual Conflict*. Princeton, New Jersey: Princeton University Press.

Austad, S. N. & Thornhill, R. 1986. Female reproductive variation in a nuptial-feeding spider, *Pisaura mirabilis*. *Bulletin of the British Arachnological Society*, **7**, 48–52.

Bilde, T., Tuni, C., Elsayed, R., Pekar, S. & Toft, S. 2006. Death feigning in the face of sexual cannibalism. *Biological Letters*, **2**, 23–35.

Bilde, T., Tuni, C., Elsayed, R., Pekar, S. & Toft, S. 2007. Nuptial gifts of male spiders: sensory exploitation of female's maternal care instinct or foraging motivation? *Animal Behaviour*, **73**, 267–273.

Boggs, C. L. 1995. Male nuptial gifts: phenotypic consequences and evolutionary implications. In: *Insect Reproduction* (Ed. by S. R. Leather & J. Hardie), pp. 215–242. Boca Raton, Florida: CRC Press.

Bristowe, W. S. 1958. *The World of Spiders*. London: Collins.

Bruun, L. E., Michaelsen, K. R., Sørensen, A., Nielsen, M. H. & Toft, S. 2003. Mating duration of *Pisaura mirabilis* (Araneae: Pisauridae) depends on size of the nuptial gift and not on male size. *Proceedings of the 21st European Colloquium of Arachnology, St Petersburg*, **1**, 35–39.

Carico, J. E. 2005. Descriptions of two new spider genera of Trechaleidae (Araneae, Lycosoidea) from South America. *Journal of Arachnology*, **33**, 797–812.

Costa-Schmidt, L. E., Carico, J. E. & Araújo, A. M. 2008. Nuptial gifts and sexual behaviour in two species of spider (Araneae, Trechaleidae, *Paratrechalea*). *Naturwissenschaften*, **95**, 731–739.

Drengsgaard, I. L. & Toft, S. 1999. Sperm competition in a nuptial feeding spider, *Pisaura mirabilis*. *Behaviour*, **136**, 877–897.

Eberhard, W. G. 1996. *Female Control: Sexual Selection by Cryptic Female Choice*. Princeton, New Jersey: Princeton University Press.

Gwynne, D. T. 1984. Courtship feeding increases female reproductive success in bushcrickets. *Nature*, **307**, 361–363.

Gwynne, D. T. 2008. Sexual conflict over nuptial gift in insects. *Annual Review of Entomology*, **53**, 83–101.

Hammer, Ø., Harper, D. A. T. & Ryan, P. D. 2003. PAST: palaeontological statistics software package for education and data analysis. Version 1.18. http://folk.uio.no/ohammer/past.

Hansen, L. S., Fernández González, S., Toft, S. & Bilde, T. 2008. Thanatosis as an adaptive male mating strategy in the nuptial gift-giving spider *Pisaura mirabilis*. *Behavioral Ecology*, **19**, 546–551.

Heifetz, Y., Tram, U. & Wolfner, M. F. 2001. Male contributions to egg production: the role of accessory gland products and sperm in *Drosophila melanogaster*. *Proceedings of the Royal Society B*, **268**, 905–908.

Karlsson, B. 1998. Nuptial gifts, resource budgets, and reproductive output in a polyandrous butterfly. *Ecology*, **78**, 2931–2940.

Kessel, E. L. 1955. The mating activities of balloon flies. *Systematic Zoology*, **4**, 97–104.

Lang, A. 1996. Silk investments in gifts by males of the nuptial feeding spider *Pisaura mirabilis* (Araneae: Pisauridae). *Behaviour*, **133**, 697–716.

Lewis, S. M. & Cratsley, C. K. 2008. Flash signalling, mate choice, and predation in fireflies. *Annual Review of Entomology*, **53**, 293–321.

Nitzsche, R. 1988. 'Brautgeschenk' und Umspinnen der Beute bei *Pisaura mirabilis*, *Dolomedes fimbriatus* und *Thaumasia uncata* (Arachnida, Araneida, Pisauridae). *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg*, **30**, 353–393.

Nitzsche, R. 1999. *Das Brautgeschenk der Spinne*. Kaiserslautern: Rainar Nitzsche Verlag.

Prokop, P. 2006. Insemination does not affect female mate choice in a nuptial feeding spider. *Italian Journal of Zoology*, **73**, 197–201.

Prokop, P. & Maxwell, M. R. 2009. Female feeding and polyandry in the nuptially feeding nursery web spider, *Pisaura mirabilis*. *Naturwissenschaften*, **96**, 259–265.

Sakaluk, S. K. 1984. Male crickets feed females to ensure complete sperm transfer. *Science*, **223**, 609–610.

Sakaluk, S. K. 2000. Sensory exploitation as an evolutionary origin to nuptial food gifts in insects. *Proceedings of the Royal Society B*, **267**, 339–343.

Sakaluk, S. K., Avery, R. L. & Weddle, C. B. 2006. Cryptic sexual conflict in gift-giving insects: chasing the chase away. *American Naturalist*, **167**, 94–104.

Simmons, L. W. & Gwynne, D. T. 1991. The refractory period of female katydids (Orthoptera: Tettigoniidae): sexual conflict over the mating interval? *Behavioral Ecology*, **12**, 691–697.

Simmons, L. W. & Parker, G. A. 1989. Nuptial feeding in insects: mating effort versus paternal investment. *Ethology*, **81**, 332–343.

Stålhandske, P. 2001. Nuptial gift in the spider *Pisaura mirabilis* maintained by sexual selection. *Behavioral Ecology*, **6**, 691–697.

Stålhandske, P. 2002. Nuptial gifts of male spiders function as sensory traps. *Proceedings of the Royal Society B*, **269**, 905–908.

Thornhill, R. 1976a. Sexual selection and parental investment in insects. *American Naturalist*, **110**, 153–163.

Thornhill, R. 1976b. Sexual selection and nuptial feeding behavior in *Bittacus apicalis*. *American Naturalist*, **110**, 529–548.

Vahed, K. 1998. The function of nuptial feeding in insects: a review of empirical studies. *Biological Reviews*, **73**, 43–78.

Vahed, K. 2006. Larger ejaculate volumes are associated with lower degree of polyandry across bushcricket taxa. *Proceedings of the Royal Society B*, **273**, 2387–2394.

Vahed, K. 2007. All that glisters is not gold: sensory bias, sexual conflict and nuptial feeding in insects and spiders. *Ethology*, **113**, 105–127.

Wiklund, C., Kaitala, A. & Wedell, N. 1993. Decoupling of reproductive rates and parental expenditure in a polyandrous butterfly. *Behavioral Ecology*, **9**, 20–25.

Wolfner, M. F. 1997. Tokens of love: functions and regulation of *Drosophila* male accessory gland products. *Insect Biochemistry and Molecular Biology*, **27**, 179–192.