

## Notes on bridal veil construction in *Oxyopes schenkeli* Lessert, 1927 (Araneae: Oxyopidae) in Uganda

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### Summary

Sexual behaviour in *Oxyopes schenkeli* is described under natural conditions during daytime in Uganda. After a brief tactile courtship by the male, the female drops on a dragline where the male wraps her in a bridal veil of silk. None of the courtship episodes observed ended in copulation, with one male being cannibalised by the female, probably because egg-laying was imminent. Bridal veil construction while suspended from a dragline is also seen in the pisaurid *Pisaurina mira*, while *Oxyopes heterophthalmus* mates on a dragline but without the addition of a bridal veil.

### Introduction

Most oxyopids are sit-and-wait cursorial hunters and do not build a prey-catching web. Courtship can therefore be expected to consist of olfactory, visual and tactile elements, as in *Oxyopes heterophthalmus* Latreille in which the male lowers and raises his palps, vibrates his abdomen and raises his vibrating front legs steeply in the air (Gerhardt, 1933). In at least four tropical species of oxyopids the egg-sac is attached to vegetation and the female stands on guard (pers. obs). This paper is the first to describe in the Oxyopidae the male behaviour of laying down silk (bridal veil) around the female's body.

### Material and methods

Observations were carried out over several days during the last two weeks in November 1995. *Oxyopes schenkeli* Lessert was abundant in a small grassy clearing beside the main track (the Royal Mile) leading into Budongo forest reserve north of Masindi, Uganda. Numerous adults of both sexes could easily be found resting in the open some 60–90 cm above the ground on grasses and small bushes in the clearing, and on a tangle of vines and other secondary vegetation on the forest margin beside the track. During the period of study the females were heavily gravid, and were therefore larger than the males, but a few weeks earlier there would have been only minimal size disparity in favour of the females. Two other unidentified *Oxyopes* spp. were also present but were less abundant. None of the three species could be found in dense shaded forest nearby.

Observations and the precise timing of events took second place to accurate recording of what was happening via 35 mm colour photography. All timings are therefore estimates, but a comprehensive colour record of events is now available.

### Results

Courtship activity was observed only between 1100 and 1400h in bright overcast conditions. At other times

the spiders were present, but did not appear to engage in sexual activity, which was never observed when the grassy clearing was exposed to hot afternoon sunshine. In all observed courtships the males approached females which were resting statically on the upper surface of a large tough-leaved grass. The blades of this grass arched upwards and over to provide a more or less horizontal or slightly sloping platform towards the apex, and it was here that the females often sat. The male approached up the underside of the blade, advancing gradually until he was almost beneath the female, which remained motionless throughout. At no time during the entire approach was the male able to see the female. No particular jerking or vibrating of the male's body, such as could indicate vibratory substrate-transmitted courtship, was noted throughout this approach.

The male then slowly eased his way on to the upper-side of the blade, a few cm behind the female. Edging forwards he began tapping the leaf with legs I, which he then used to caress the female from behind (Fig. 1). Then he mounted the rear of the female's abdomen, while gently stroking her with legs I and II. Up until this point no female was seen to react to the male's approach and no aggressive reactions were noted. In every observed instance the female reacted to the male's "mounting" and stroking behaviour by walking away and dropping from the blade on a dragline.

The female became suspended head-downwards some 6–9 cm below the blade. The male descended her dragline to the female which, although unmoving, did not hunch in her legs as seen in some female spiders presumed to be in a cataleptic state following the male's courtship, e.g. *Agelena labyrinthica* (Clerck) (pers. obs.). Next he twirled her round and round while wrapping her in silk, alternating "twirling" with running round and round her while trailing silk (Figs. 2, 3). These "bonds" were concentrated around legs I to III of the female, and took the male 1–2 minutes to complete, involving numerous "twirlings" and "run-arounds".

The male then tried to insert a palp. In all observed instances, except one, it was at this juncture that the female instantly shrugged off her "bonds" and returned to her original position on the blade. One male repeated his courtship efforts several times, with the female responding quickly each time by dropping off the blade, only to break free every time at the last moment before palp insertion. In the last observed courtship the female (which had already responded to several courtship overtures by dropping on her dragline) finally pierced the male with her fangs as he tried to insert a palp. He appeared to die instantly and without a struggle. One female on a grass blade was also seen feeding on a male, but it is not known whether he was captured during courtship or mating.

During the next few days the females began to construct their "nests" throughout the grassy area. These consist of a fresh green leaf suspended some 30–60 cm above the ground in a scaffold of threads. The female encloses the egg-sac within the leaf, which is folded over slightly, and then stands guard on top. It is not known whether the female cuts a section of leaf off a living

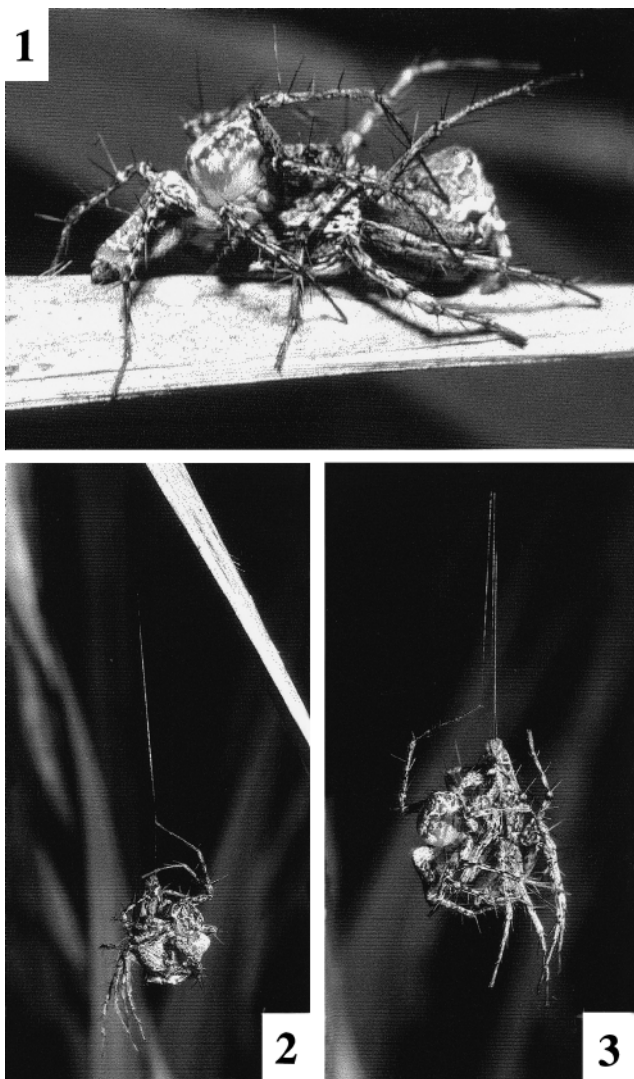
plant, or whether she manages to find a correctly sized section lying on the ground or on vegetation (the latter eventualities seem unlikely). No nest-making activity was seen during the day, so presumably it takes place at night. Over the next few days the leaves gradually turn brown and become less conspicuous, as does the drably coloured female in her exposed position on top. The female remains until the young emerge, but it was not observed how long she remains with them. Similar nesting habits were noted in at least one of the other *Oxyopes* spp. in the area.

### Discussion

Several points about the sexual behaviour of this species are of interest. The ability of the males to orient accurately to the underside of a grass blade immediately below a female which they are unable to see at any time before or after they begin their approach indicates the

use of some olfactory means for locating the females. An alternative explanation, that the male sees the female's silhouette from beneath the blade is ruled out by the blade's thickness and the fact that courtship does not take place in bright sunlight. The combination of mating on a dragline and construction of a bridal veil seems to be unique among members of the Oxyopidae studied so far. It thus adds a new family to those in which bridal veil construction is normally a part of the sexual process. This was first described in the thomisid *Xysticus cristatus* (Clerck), in which the male "ties" the female down to the substrate (Bristowe, 1958). In the Neotropical pisaurid *Ancylometes bogotensis* (Keyserling) the male wraps the female's legs in silk but does not tether her to the substrate (Merrett, 1988). Procedures in another pisaurid, *Pisaurina mira* (Walckenaer), are remarkably similar to the procedures described above for *O. schenkeli*, and likewise include bridal-wrapping while suspended on a dragline (Bruce & Carico, 1988). Males of this species also "twirl" the females, but only 3–5 times, not the numerous (20 or more) times seen in *O. schenkeli*. Mating on a dragline is also known in the oxyopids *O. heterophthalmus* (Gerhardt, 1933), and *Peucetia viridans* (Hentz) (Whitcomb & Eason, 1965), but these do not construct a bridal veil. Males of *Nephila maculata* (Fabricius) do not construct a bridal veil as such, but spend considerable amounts of time laying down a latticework of fine silk across the females' bodies (Robinson & Robinson, 1973; pers. obs.), almost identical to the behaviour reported in *Argiope aemula* (Walckenaer) (Robinson & Robinson, 1980). The latter paper also reported the placing of a few threads across the female's body in another araneid, *Herennia ornatis-sima* (Doleschall). Males are also reported as silking lightly across females in *Latrodectus tredecimguttatus* (Rossi) (Theridiidae; Stern & Kullmann, 1981), *Latrodectus hesperus* Chamberlin & Ivie (Ross & Smith, 1979), *Dictyna volucripes* (Keyserling) (Dictynidae; Starr, 1988) and *Tibellus oblongus* (Walckenaer) (Philodromidae; Stern & Kullmann, 1981), although Bristowe (1958) did not mention this in his description of mating in *T. oblongus*.

There has been much discussion about the function of such "bridal veils" in spiders, with no conclusive outcome. A possible reduction of predation by females on their mates has been the most consistent suggestion in the popular biological press and elsewhere (e.g. Bruce & Carico, 1988), but with little concrete support from the present paper. The instant ease with which the female *O. schenkeli* breaks free of her "bonds" lends scant support for the theory that the "bonds" could restrict—even for a vital instant—the female's ability to pierce the male with her fangs at the vulnerable moment of palpal insertion, as shown by the female reported above. What is particularly notable from the present study is the fact that several females which were very close to laying eggs should have shown any positive response *at all* to courtship. In most spiders so far studied, females which are close to egg-laying either respond aggressively to further male courtship or, in cursorial spiders such as *Pisaura mirabilis* (Clerck), simply run away when approached



Figs. 1–3: Courtship behaviour of *Oxyopes schenkeli*. **1** Male (left) approaching female from behind and stroking her with his legs I and II, just before she jumped off the grass blade; **2** Male (right) walking around the female as he wraps her in silk, showing the length of the silken line on which she has dropped; **3** Male (left) twirling the female as he lays down silk, some of which is visible between the female's legs I and II.

(pers. obs.). Some female *O. schenkeli* gave the appropriate response to courtship and jumped off the grass blade on their draglines several times in 40–50 minutes. This demonstrates that the instinct to react positively to a suitor is very strong in this species, even up to the last days before egg-laying commences. It also seems unlikely that the females would fail to detect the approach of the male up the grass blade towards them, and the lack of any aggression by the female at this stage also reinforces the idea that they are generally very co-operative. The single act of sexual cannibalism observed took place only after the female had responded several times to the male's courtship and jumped off on her dragline. It seems that only after several abortive attempts at copulation did the female's instinct to treat the male as a meal overcome her instinct to submit to him.

Female oxyopids exhibit an entelegyne style of reproductive morphology, with separate insemination and fertilisation ducts for the sperm-storage organ or spermatheca (Foelix, 1982). Such "conduit" morphology should favour a pattern of first-male sperm priority, in which the sperm of the first male to mate with a female should gain prior access to the eggs on a first-in-first-out basis (Austad, 1984). Given the behaviour of the males of *O. schenkeli* it seems likely that such first-male advantage is absent, and even "final call" matings could gain a substantial reproductive benefit, as found in *Agelena limbata* Thorell, in which second males were able to fertilise 62.9% of the eggs (Masumoto, 1993). The males themselves would therefore have nothing to lose and much to gain by attempting such last-minute mating efforts, as receptive females will shortly cease to be available once egg-laying commences. However, the males of *O. schenkeli* do not appear to exhibit the "kamikaze" tactics of abandoning courtship finesse altogether, typical of "final call" mating attempts by *Agelena labyrinthica* males (Preston-Mafham & Preston-Mafham, 1993: 27). Although it had not been observed in the field, examination of the three different males in the photographs taken of *O. schenkeli* (two engaging in courtship, one as prey of a female) showed that all three had only a single palp. Presumably the other palp had been lost in earlier (presumably successful) mating attempts. Although the ratio of males to females in the study population of *O. schenkeli* was not censused, it seems likely from the author's recollection that although females certainly outnumbered males, it was not by a degree that would indicate that substantial cannibalism had taken place (in a sexual context) shortly after the females became adult, when they would probably have quickly been first mated.

Robinson & Robinson (1973) were convinced that the laying down of silk by males of *Nephila maculata* served to stimulate the female, and it is possible that this is the main function of so-called bridal veils in all species which use them. Courtship procedures are quite rudimentary in all these species, at least when compared with many species which do not utilise silk during mating, so it seems likely that the silk, impregnated with male pheromones, serves to bring about important changes in the female. These changes could be behavioural

(maintenance of a state of semi-catalepsy) and/or physiological (internal changes to the epigyne, preparing the way for palpal insertion). In this context it is perhaps significant that in one pisaurid, *Pisaurina mira*, the male's pheromones could be transmitted via the silk of the bridal veil, while in another, *Pisaura mirabilis*, the means of transmission could be via the dense shroud of silk enveloping the nuptial gift that the male presents to the female, and on which she feeds during a lengthy copulation (pers. obs.). In the latter species it seems highly significant that the males do not wrap prey intended for their own consumption, but only that intended for a sexual role. As silk is a protein, its production is expensive, and considerable quantities are used in wrapping the "gift". The advantages in producing the wrapping must therefore be considerable, otherwise the behaviour would not have become fixed. The silk must therefore play a central role, and its function as a pheromone-bearing "badge of identity" preparing the female physiologically and behaviourally for copulation seems highly likely.

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