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UNUSUAL REPRODUCTIVE ASSOCIATIONS OF *ISCHNURA ELEGANS* (VANDER LINDEN) MALES (ZYGOPTERA: COENAGRIONIDAE)

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Abstract – *I. elegans* ♂♂ were seen in unusual associations with conspecific ♀♀. In a triple connection a ♂ was in tandem with a ♀ that had genital contact with another ♂. Another association involved a copula in which the ♀ was still in the wheel position, but the ♂ had ceased to hold the ♀ at her collum for more than half an hour. Several mixed tandems of ♂ *I. elegans* with ♀ *Lestes sponsa* were observed in natural and experimental conditions; also one brief ♂-♂ conspecific tandem. The reduced discrimination by males which leads to these associations may be adaptive to low density populations. This may invalidate the sexual cannibalism hypothesis of C. UTZERI (1980, *Notul. odonatol.* 1: 100-102). It is suggested that sex-biased cannibalism within the genus *Ischnura* is mainly the result of a combination of a female's higher energy demand combined with a high level of female aggression.

Introduction

Sperm competition plays a crucial role in shaping the reproductive behaviour in Zygoptera (WAAGE, 1984, 1986). A common behaviour in damselflies to prevent sperm manipulation by rivals is post-copula mate guarding (WAAGE, 1984). The members of the genus *Ischnura*, particularly *I. elegans*, are in many respects behaviourally very distinct from other damselflies. Adult female zygopterans normally do not visit the water except for reproduction (e.g. WAAGE, 1980), but adult *I. elegans* females are frequently seen at the water (e.g. PARR & PALMER, 1971; PARR, 1973). In addition, they have extremely long copula durations, and females always oviposit alone (e.g. KRIEGER & KRIEGER-LOIBL, 1958; ROBERT, 1958; MILLER, 1987a, 1987b). MILLER (1987b) demonstrated sperm competition in this species and suggested that long copula durations probably replace postcopula guarding (MILLER, 1987a; see also CORDERO, 1990).

Within the genus, and especially in *I. elegans*, there are several reports of females eating adult males (e.g. MÜLLER, 1972; MARTENS, 1978; UTZERI 1980; CORDERO, 1992). UTZERI (1980) called this phenomenon "sexual cannibalism" and hypothesized that only females do this because the male is not recognized as conspecific, while males do recognize females as conspecific and as a result do not eat them (see also CORDERO, 1992).

We report here on some unusual reproductive associations in male *I. elegans*. We will discuss these in the light of sperm competition and sexual cannibalism, thereby trying to extend our understanding of the unusual behavioural ecology of the species.

Study area and methods

The study site was a small pond (perimeter 124 m) near the University of Antwerp (Belgium). It is part of a park landscape, dominated by bushes and pastures. The oviposition places are discrete patches. We visited the pond daily from 17 July until 11 August 1994. During this period, a low density population of *I. elegans* was present. Some observations were made during an experiment with attached females of *Lestes sponsa* (Hans.). These experiments were carried out on 11 and 13 July. There were three types of tethered *Lestes* females: one pinned in oviposition posture, one pinned with the abdomen parallel to a stem, and another attached to a long piece of elastic, restricting its mobility.

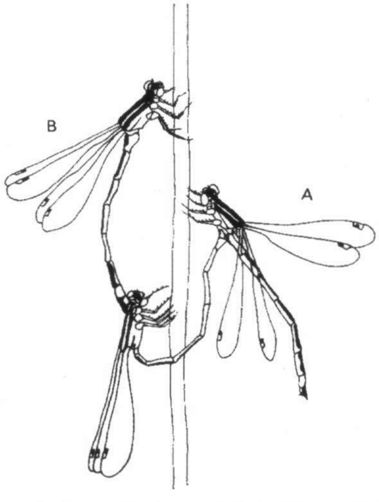

Fig. 1. *I. elegans*: triple association with two males.

Behavioural observations

On 31 July at 13:10 h, a triple association was seen, involving two males and one female *I. elegans* on a sedge stem at the waterside (Fig. 1). All three animals held the stem with their legs. Male B grasped the female in the typical tandem link. The female, while attached to male B at her collum, had the abdomen twisted so that her valves made contact with the accessory genitalia of male A. She hung rather passively with wings closed. Male A had his wings opened and had the last abdominal segments curved downwards. After some time, male B was able to dislodge the link between male A and the female and flew away with her. The couple disappeared from sight.

On 2 August (14:17 h) another unusual male-female association was observed, this time with only one male involved. Both male and female clung to a sedge stem (Fig. 2). The female was in the copula position with her valves still attached to the male's genitalia. The male, however, did not hold the female at the collum with his anal appendages, but had bent his abdominal segments in a position similar to the oviposition posture of a female. They stayed in this position for more than half an hour.

On several occasions during the study period we saw mixed tandems of a male *I. elegans* with a female *L. sponsa*. On 2 August (11:52 h), such a tandem sat in a patch of *Phalaris arundinacea* and then flew away along the pond edge. In flight, the tandem displayed an erratic zigzag course. Although the female *L. sponsa* was much larger, and clearly tried to free herself, she was unable to dislodge the tandem link.

During the experiment with tethered females *L. sponsa* we observed five cases of tandem formation by *I. elegans* males (three on 11 July and two on 13 July). One of these males was responsible for four mixed tandems. In all these cases the male *I. elegans* chose the female that was pinned with the abdomen parallel to the stem. On two of these

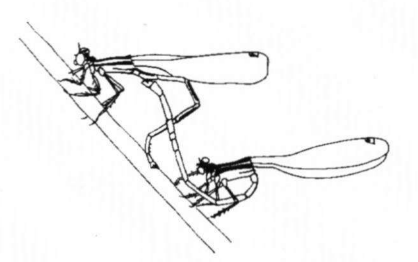

Fig. 2. *I. elegans*: unusual male-female association, with genital contact only.

occasions, the male showed intra-male sperm transfer while in tandem.

Finally, on June 8 a male fell into the water and was seized by another male. The second male was able to fly away with the male in tandem and to land on a perch. After one minute they separated.

Discussion

The observed triple association is of type O as described by EDA (1970). This differs from the other three types of triple connections he distinguished, in that both males are linked with the female. Although we did not observe the formation of the triple association, a plausible scenario is that male A first mated with the female. During copula, the collum link was broken and a rival male B took the opportunity to clasp the female at her collum. While the female was still connected with her valves to male A, male B formed a tandem with her and partly pulled the female away from male A. The female abdomen became twisted during this action. The observation of the double association on 2 August can be seen as a precursor for the triple connection. The copula link in *I. elegans* is extremely strong. MILLER (1987c) even reported that a wire can be threaded through a pair in copula and used to lift them off their perch (see also KRIEGER & KRIEGER-LOIBL, 1958; PFAU, 1971; MILLER 1987a). The strength of the link was also shown during the successful tandem of an *I. elegans* male with a much larger and heavier *L. sponsa* female. Together with the observed 'precursor' association, this makes the possibility of a forced removal of the tandem grip by a rival male highly improbable. EDA (1970; see also UTZERI & BELFIORE, 1990) is the only one to report on the formation of a triple connection. He saw a rival anisopteran male to remove the caudal appendages of the other male before mating with the female himself.

The reason why a male ends the collum grip long before the female terminates genital contact is puzzling. This is especially unexpected in *I. elegans* where copula takes a very long time (up to 7 hours) and is interpreted as a form of mate guarding (MILLER, 1987a, 1987b; see also FINCKE, 1987; CORDERO, 1990). Moreover, males are thought to control the duration of copulation in this species (MILLER, 1987b). However, many copulations of *I. elegans* start between 8:00 h and 8:30 h and the mean copula duration is ca 5 hours and a half (MILLER, 1987a), and thus the observed associations probably were formed at the end of a normal copula. In *I. elegans*, mate guarding occurs in the second stage of the copula (MILLER, 1987b; see also CORDERO, 1990). This means that males guard females after having partly removed the rival's sperm and introduced their own. Sperm manipulation seems rather moderate in this species, with males only replacing about 26% of the rival's sperm within the female (MILLER, 1987b). However, if females use bursal sperm first, the last male may be able to fertilise most of the eggs of the next batch (MILLER, 1987b). Because male B was able to fly away with the female, he had the opportunity to mate with her and to remove male A's sperm. The probable cost for male A was therefore a reduced paternity. This cost may be high, given the long copula duration and the short adult lifespan of males (approx. 10 days; see HINNEKINT, 1987).

Compared with the data given by MOORE (1991) and HINNEKINT (1987), the population density at the pond was very low, with a highest steady density of about 10 males per 100 m stretch of pond margin. HINNEKINT (1987; see also MILLER,1987b) stated that interactions of individuals and aggression are negligible at low population densities. In this situation a male may relax his copula grip, especially at the end of the copula, without a great risk of a takeover. Therefore this kind of double association may only occur in low density populations and hence be very rare. Because most matings in *I. elegans* occur away from the water (PARR & PALMER, 1971; PARR, 1973; VAN NOORDWIJK, 1978), this is difficult to confirm. There is only one other report describing this type of association in *I. elegans* (UTZERI & BELFIORE, 1990).

Mixed tandems in natural conditions are rare in *Ischnura* (BICK & BICK, 1981). There is one report of a mixed tandem between an *I. elegans* male and a *Coenagrion puella* female (UTZERI & BELFIORE, 1990) and the current observations provide only the second record of a Coenagrionidae-Lestidae inter-family pairing (BICK & BICK, 1981). Homosexual conspecific tandems have not been reported for *I. elegans* (UTZERI & BELFIORE, 1990) except in a fieldcage situation (KRIEGER & KRIEGER-LOIBL, 1958). However, male mating readiness in this situation is indicated since the males twice showed intra-male sperm transfer. The great size and colour difference between female *I. elegans* and *L. sponsa* suggests that males have low mate recognition capacity (see also FRANTSEVICH & MOKRUSHOV, 1990; MOKRUSHOV, 1992). KRIEGER & KRIEGER-LOIBL (1958), however, showed that males preferred dummy females of their own species. The forming of mixed tandems in our low-density population might be adaptive because, in such circumstances, female arrivals are highly unpredictable. The cost in time and energy of forming wrong tandems may be lower than the benefit of gaining a higher probability of seizing one of the few conspecific receptive females at the pond on a given day (UTZERI & BELFIORE, 1990).

In any event, males are not always able to recognize conspecific females immediately. This may invalidate UTZERI's (1980) sexual cannibalism hypothesis, because it is based on the assumption that females do not recognise conspecific males, whereas males do recognise conspecific females. However, based on our results, one would also expect males to eat females. Therefore, the prime reason for this sex-biased cannibalism may be a combination of energy demand and female aggression. Moreover, the energy gain from eating a conspecific is more important in females because the maturing of a clutch of eggs is highly energy demanding (e.g. LAWRENCE, 1992). Indeed, females of the genus *Ischnura* show very developed aggression and refusal display behaviour patterns (BICK, 1966; ROWE, 1978; ROBERTSON, 1985). This may even reduce harassment of unreceptive females by males at the water, and may explain the presence of unreceptive females at the pond, as suggested by PARR & PALMER (1971; see also FINCKE, 1987). HINNEKINT (1987) even states that older males are forced to leave a population following aggression from younger males, while older females can stay longer in the population. In an extreme form, female aggression, together with the high energy demand, may result in cannibalism (FINCKE, 1987). ROBERTSON (1985) observed a female *I. ramburi* that was repeatedly chased and grasped by a male, finally grasping him and eating his thorax. There are also reports of *I. elegans* females in copula with an adult male while eating a teneral male (MÜLLER, 1972; CORDERO, 1992). The cryptic oviposition behaviour of *I. elegans* later in the day, when most males have left the pond (KRIEGER & KRIEGER-LOIBL, 1958; VAN NOORDWIJK, 1978; HINNEKINT, 1987), does not invalidate our hypothesis. When ovipositing they are less able to defend themselves.

It is clear from this discussion that, despite our knowledge of population parameters (e.g. PARR & PALMER, 1971; PARR, 1973; VAN NOORDWIJK, 1978; HINNEKINT, 1987) and the mechanism of sperm competition (MILLER, 1987b), there is still a great need for basic behavioural data for *Ischnura elegans*.

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