

Heterospecific copulation with subsequent oviposition in Libellulidae (Odonata)

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Abstract

Two cases of heterospecific mating in two different genera of Libellulidae were documented photographically from pair formation to subsequent oviposition. The pairs consisted of male *Orthetrum trinacria* x female *O. cancellatum* and of male *Sympetrum danae* x female *S. striolatum*. Copulation and oviposition took place in the genus specific manner. Due to the rare observation of these events the full course of the behaviour is described and the possible reproductive success of heterospecific pairing is discussed.

Zusammenfassung

Heterospezifische Paarung mit anschließender Eiablage bei Libelluliden (Odonata) – Zwei Fälle von Paarungen zwischen unterschiedlichen Arten innerhalb jeweils derselben Gattung konnten von der Paarbildung bis zur anschließenden Eiablage fotografisch dokumentiert werden. Die Paare bildeten sich aus *Orthetrum trinacria* ♂ x *O. cancellatum* ♀ und *Sympetrum danae* ♂ x *S. striolatum* ♀. Paarung und Eiablage erfolgten jeweils in gattungstypischer Weise. Da solches Verhalten bisher nur selten beobachtet worden ist, werden die beiden Fälle im Detail beschrieben und im Hinblick auf den möglichen Fortpflanzungserfolg diskutiert.

Introduction

Within anomalous pair connections in Odonata, heterospecific tandems are observed and documented rather often. CORBET (1999: 490 ff) reviews 175 recorded cases, 60 % of them intrageneric. MILLER & FINCKE (2004) list 101 examples of documented interspecific couples only among Zygoptera. These records split into 52 intrageneric, 29 intergeneric, 18 within different families and even two between Zygoptera and Anisoptera. The frequency of apparent copulation within heterospecific tandems lies between 20 and 29 %, less often documented in Zygoptera (except Calopterygids) than in Anisoptera (CORBET 1999: 491). Calopterygids and libellulids are seen in anomalous copulation most often (BICK & BICK 1981).

Oviposition subsequent to a heterospecific copula is a very rarely documented behaviour within the Odonata. BICK & BICK (1981) observed a male *Argia plana* with a female *A. moesta* ovipositing normally, but they did not see if this tandem had been in copula before. In their review about heterospecific pairing in odonates, they present only one other example: copula with apparent oviposition of a male *Calopteryx aequabilis* with a female *C. maculata* (WAAGE 1971 in BICK & BICK 1981). CORBET (1999: 492) refers only to these two published interactions.

Offspring have only rarely been recorded as a result of heterospecific pairing (e.g. ASAHINA 1974; MAUERSBERGER 1994; OLIAS et al. 2007; TYNKKYNEN et al. 2008).

Recently the complete sequence of reproductive behaviour in two cases of heterospecific mating from tandem formation to oviposition could be followed and documented photographically.

Methods

The observations documented here were only made by chance. Fortunately, the activities of both heterospecific pairs started in midair while I was taking photographs of dragonflies. By continuous shooting (up to 8 fps) with a digital DSLR camera (Nikon D300, D700) with tele-macro lens (180 mm, 270 mm equivalent in DX), releasing the shutter at any change of action and disregarding focusing, the behavioural sequence could be reconstructed by the exact time given in the exif-metafile data of the pictures. Usable voucher photographs of these rarely observed events resulted.

Observations

(1) Whilst travelling during Pentecost 2009, at a stop at Sardinia's largest natural water body, Lago Baratz (NE Sardinia, Italy: 40.68°N, 8.22°E), the following observations were made. On 29-v-2009, a stretch of ca 100 m of the southwestern shore was investigated between 10:30 and 14:00 h CEST mainly for collecting exuviae and taking pictures. It was a sunny day with ca 25°C air temperature and very windy.

- 13:21:44 h Picture taken of perched male *Orthetrum trinacria*
- 13:27:09 h Male takes off and grasps female *O. cancellatum*, which was flying during oviposition ca 5 m distant from the males' perch.
- 13:28:41 h First pictures taken of the flying tandem (Fig. 1a)
- 13:28:48 h Copulation starts and lasts a little more than 1 s; four photos are made (Fig. 1b)

- 13:28:57 h Release of the female *O. cancellatum*, which immediately starts to oviposit, non-contact guarded by the male
- 13:29:44 h The male is involved in contest with conspecific males; the female uses this instance for a quick escape.

Total time of event: 8 min

Total time of copula: 1-2 s.

Total time of oviposition: 47 s

Among the 15 species of Odonata recorded on that day at Lago Baratz, *O. cancellatum* was the most frequent anisopteran. Conspecific pairing and oviposition was repeatedly noticed. In contrast, only males of *O. trinacria* were observed.

(2) On 19-ix-2010 the pond 'Heimatsee' (NE Wurttemberg, Germany: 49.36°N, 10.03°E) was visited. This water body was created in September 2006 in order to promote threatened odonate species like *Lestes dryas* and *L. virens*. The habitat was checked two to four times per year for efficiency control.

Altogether 13 odonate species were on the wing on that sunny but cold day (air temperature 14°C) with only little wind. *Sympetrum danae* was seen that day for the first time at this locality, and only males were observed. This species has be-

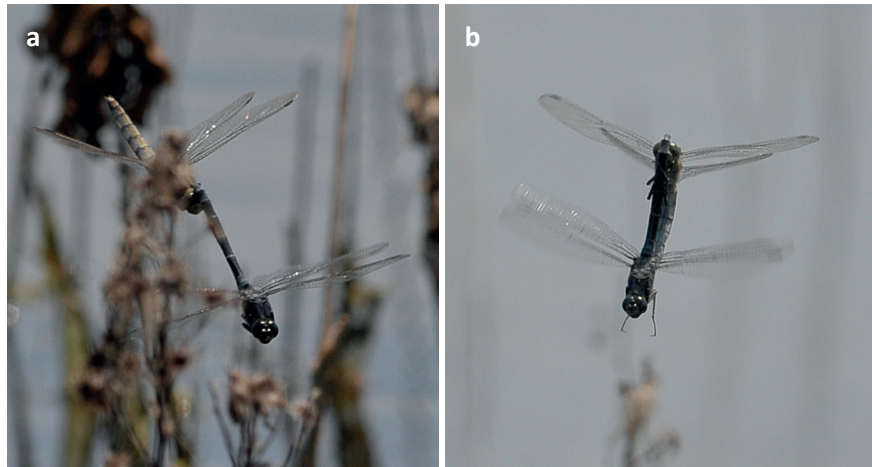


Figure 1: Heterospecific pairing in the genus *Orthetrum*: (a) tandem and (b) copula of *O. trinacria* male and *O. cancellatum* female. Lago Baratz, Sardinia, Italy, 29-v-2009. —
Abbildung 1: Heterospezifische Verbindungen innerhalb der Gattung *Orthetrum*: (a) Tandem und (b) Kopula von *O. trinacria*-Männchen und *O. cancellatum*-Weibchen. Lago Baratz, Sardinien, Italien, 29.05.2009.

come very rare in the region over the past ten years. It was only the second observation of *S. danae* in 2010. Three more *Sympetrum* species were reproductively active on that day: *S. sanguineum*, *S. striolatum* and *S. vulgatum*.

- 14:20:08 Photos are taken of a conspecific tandem of *Sympetrum striolatum* at oviposition in flight.
- 14:21:17 *S. striolatum* tandem disconnects; the female perches on the ground.
- 14:25:12 Male *S. danae* grasps female *S. striolatum* directly from the ground; copulation wheel is formed in midair without any resistance from the female.
- 14:25:40 The pair alights on a dry stem ca 40 cm above ground (Fig. 2a), ca 8 m from the shoreline.
- 14:31:50 Copulation terminates in flight and the tandem heads immediately to the shoreline. Again no resistance from the female is noted.
- 14:33:09 The tandem starts oviposition over open shallow water near the shore.
- 14:33:29 The tandem moves to a more vegetated area and continues oviposition.
- 14:34:23 Frequency of oviposition movements is about one per second (Fig. 2b).
- 14:34:56 Male releases female that flies straight up in the air for approximately 10-12 m and then descends towards a forest. Male perches again close to the shoreline.

Total time of action: 14:48 min.

Total time of copula: 6:10 min (\pm maximal 10 s).

Total time of oviposition: 3:06 min.

Discussion

Interspecific matings are obviously the result of an error. Could we take them as normal within the range of reproductive behaviour in libellulids? Without any question, libellulids do show the most dynamic and quickest pair building behaviour in odonates (CORBET 1999: 523 ff).

The non-territorial *Sympetrum danae* shows a high degree of post-copulatory mate guarding and the males are able to inseminate a female at an average of 95 %, irrespective of any previous mating (MICHIELS & DHONDT 1988). The males normally seize females beside the water and 77 % of the matings occur before solar noon. Males remate the same day up to six times, 39 % at least once a day.

Within a six-day study in a large enclosure, 30 % of the males failed to copulate and 35 % of the copulations were conducted by only 5 % of the males (MICHIELS & DHONDT 1991). In *S. danae* copulation lasts between 6 and >100 minutes, with an average of 16 minutes (STERNBERG & HUNGER 2000). The heterospecific copula between *S. danae* and *S. striolatum* lasted 6:10 minutes and happened well after solar noon. Oviposition in *S. danae* starts normally in tandem, and after disconnection it is continued by the female being non-contact guarded by the male for a while. Duration of oviposition depends on the density of males, the remaining stock of eggs in the female and the temperature (STERNBERG & HUNGER 2000). The observed 3:06 minutes seem to be short, but the *S. striolatum* female had started oviposition before it was seized by the male *S. danae*. Furthermore, it was late on a relatively cold day.

For *Orthetrum trinacria* I was unable to find detailed information about mating and oviposition behaviour. ASKEW (1988) only states that ovipositing females are male-guarded. In *Orthetrum* copulation can be completed in less than 10 seconds.



Figure 2: Heterospecific pairing in the genus *Sympetrum*: (a) copula and (b) oviposition of *S. danae* male and *S. striolatum* female. Heimatsee, northeastern Württemberg, Germany, 19-ix-2010. — Abbildung 2: Heterospezifische Verbindung innerhalb der Gattung *Sympetrum*: (a) Paarung und (b) Eiablage von *S. danae*-Männchen und *S. striolatum*-Weibchen. Heimatsee, NO-Württemberg, Deutschland, 19.09.2010.

But the duration of copulation can vary widely within the genus and within a species (CORBET 1999: 526). There is a strong correlation between copulation duration and removal of sperm. Copulations that exceed 5 minutes in *O. cancellatum* lead to a nearly 100 % removal, copulations under 4 minutes were highly variable between 0 – 100 % removal (CORBET 1999: 526). Copulations with only 1 or 2 seconds are considered to follow the 'last in, first out' mechanism, which can be effective too and is observed in some species. MICHELS & DHONDT (1988) examined females during the first oviposition bout of *S. danae* after mating and found no evidence for sperm mixing. But WOLF et al. (1989) showed that the average paternity expectation was higher for long than for short copulations in *Leucorhina intacta*.

After mating, a female *O. cancellatum* either disappears from the vicinity of the water body or immediately starts oviposition, being non-contact guarded for a short time (STERNBERG 2000). This was also observed with the female at Lago Baratz in Sardinia. However, there is no evidence whether the females observed in this study actually laid eggs after the heterospecific copulation. They may have shown only ovipositing behaviour, as exoephytic oviposition is hard to substantiate in the field.

Hundreds of heterospecific tandem possibilities within Zygoptera and Anisoptera have been reported so far (e.g. BICK & BICK 1981; MILLER & FINCKE 2004). But the number of reported copulae is much smaller, and the documented number of heterospecific pairs subsequently ovipositing is only four, including this study. From all these anomalous connections we learned that some males have the possibility to grasp nearly any female of all species they can reach. Such males may benefit from seizing any dragonfly that broadly resembles a conspecific female instead of waiting upon detailed determination (CORBET 1999: 491).

Are hybrids an inevitable result of such actions or does nature have more clues than morphological traits to defend this? Genitalia are often species-specific and are more divergent among closely related species than any other taxonomically relevant trait (EBERHARD 2010). In many species a 'lock and key' mechanism has evolved that anticipates any attempt to copulate with heterospecific congeners. But in some odonate species we can find a universal key and an intelligent lock (EBERHARD 2010). Whilst the male appendages are able to grab even males of different genera, most females seem to recognize if they are involved in a one-way connection. According to TYNKKYNNEN et al. (2008) the male's role in hybridization should no longer be neglected. CORBET (1999: 492) indicates that, even if heterospecific copulation with insemination takes place, postcopulatory reproductive isolation mechanisms could still prevent hybridization. The scarcity of real hybrids discloses that most species of Odonata are effectively isolated. Hybrids of highly related species are defined mostly by phenotypical traits only (e.g. MAUERSBERGER 1994; OLIAS et al. 2007). But TYNKKYNNEN et al. (2008) demonstrate by mitochondrial DNA analyses the true existence of F1 hybrids between *Calopteryx splendens* and *C. virgo* in the wild. In any case, the two *Calopteryx* taxa examined by TYNKKYNNEN et al. (2008) are undoubtedly distinct taxa (MISOFF et al.

2000; WEEKERS et al. 2001). This suggests that hybridization may lead to genetic incompatibilities.

Heterospecific connections seem to happen more often in the Nearctic region than in Neotropical, Ethiopian or Australian regions (BICK & BICK 1981), possibly because the opportunities for sexual contacts also depend on weather conditions in the Nearctic. During both cases of heterospecific interactions presented in this study the weather was not ideal. Moreover, they occurred after solar noon and specific females were not available. These factors may lead the males to overcome normal inhibitions in the choice of their females. Normally a female urgently rejects any heterospecific male after having recognized him (LOIBL 1958). So why did these two observed females show no resistance? The scarcity of observations may be a result of the real scarcity of this kind of behaviour. We should regard this as an error by the male, caused by multiple factors like low temperature, late time of day, and a poor availability of females.

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