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HETEROSPECIFIC TANDEM FORMATION IN *SYMPETRUM DEPRESSIUSCULUM* (SÉLYS) (ANISOPTERA: LIBELLULIDAE)

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At the roosting sites 26 tandem formations of males with individuals of 7 other Anisoptera spp. were observed in the morning. Males are active before sunrise and fly low in the vegetation searching for females. They approach other dragonflies which perch motionless at the roosting sites and show no refusal displays. Males grasp them and form tandems, but there were no heterospecific copulations. With increasing morning temperature the other Anisoptera spp. became active and the tandems separated. Towards the end of the breeding season of *S. depressiusculum* the proportion of the other spp. of Anisoptera in the roosting community and the number of heterospecific tandem formations increased.

INTRODUCTION

There are numerous reports in the literature of dragonfly pairs in tandem, or even in copulation, involving individuals of two closely related species, especially in the two Anisoptera genera *Sympetrum* and *Gomphus* (e.g. JURZITZA, 1966; BICK & BICK, 1981; ISHIKAWA, 1982; UBUKATA, 1984). But heterospecific tandem formations involving two genera or even two different families have also been reported (BICK & BICK, 1981). Formation of mixed pairs can be prevented through the form of the male's appendices and through specific mechanisms of recognition. Most of the males grasp a heterospecific female only with the appendages, but without genitalic contact. They may persist in making attempts to copulate but normally females of the wrong species do not cooperate. The pattern of tactile sense organs on the thorax may allow the female to identify a male of her species (ROBERTSON & PATERSON, 1982).

Thus males show less discrimination and it is the female that uses tactile

mechanisms to identify her partner at close range. However, we know little about the behavioural mechanisms of heterospecific tandem formation. During studies of the reproductive behaviour of the libellulid dragonfly *Sympetrum depressiusculum* (Sél.) a strikingly large number of heterospecific tandems between males and individuals of other Anisoptera species was observed. Adults and immatures aggregate in large numbers at common roosting sites (ROBERT, 1958; MILLER et al., 1984). MILLER et al. (1984) have pointed out that male *S. depressiusculum* form tandems with *Orthetrum cancellatum* (L.) and *Crocothemis erythraea* (Brullé). A male *S. depressiusculum* remained perched in tandem with an immature *O. cancellatum* for 2-3 h (MILLER, 1987). In this paper behaviour that causes heterospecific tandem formation of *S. depressiusculum* is presented and discussed.

MATERIAL AND METHODS

The observations were made near Arles in southern France (48° 24' north, 3° 45' east, Dept. Bouche-du-Rhône) in July, 1989, July, 1990 and in June/July, 1991. Most dragonflies roosted in the grass and reeds of small meadows between rice fields bordered by sporadic bushes and trees.

The daily observation period started at 0530 (European Summer Time) and the beginning of flight activity, the time of the first tandem formations and copulations of *S. depressiusculum* were noted. The flight activity of the males was recorded on video. Each of the observed heterospecific tandem formations was noted.

At 3-day-intervals between 2.VII and 22.VII.1990 between 0600 to 0800 the Anisoptera occurring at the roosting site were randomly captured and the proportion of *S. depressiusculum* and of other Anisoptera species determined. The density of the roosting dragonflies was recorded by counts after sunset on 5 areas of 1 m^2 in the centre and at the edge of the community. The pre-copulatory--guarding of male *S. depressiusculum* and their daily rhythm of activity are described by MILLER et al. (1984).

RESULTS

Altogether 26 heterospecific tandems were observed. There were tandems of adult males of *Sympetrum depressiusculum* with males and females of 7 other Anisoptera species (Tab. I), including 2 between members of different families, 16 between different genera and 8 between different species of the same genus. Mixed pairs were observed exclusively in the morning hours between 6.15 h and 9.25 h (Fig. 1).

The number of heterospecific tandems was related to the specific daily activity rhythm and the flight activity of adult males of *S. depressiusculum* searching for females. Adult males were already active before sunrise. The temperature at the beginning of *S. depressiusculum*'s daily activity at 0540 was between 11.2°C and 14.5°C. Males flew low among vegetation and grasped females perching motionless at their roosting site. The tandems remained perching on grass. With increasing temperature after sunrise (0610-0615) females and immatures of *S. depressiusculum* also left their roosting sites. They perched on higher tips of

Table I

Heterospecific tandem formation of male *Sympetrum depressiusculum* at roosting sites (1989-1991)

Species	Male		Female	
	immature	adult	immature	adult
Libellulidae				
Crocothemis erythraea (Brullé)	1	1	2	8
Sympetrum fonscolombei (Sél.)		1	1	6
Orthetrum cancellatum (L.)	1			1
O. albistylum (Sél.)				1
Libellula fulva (Müll.)				1
Gomphidae				
Onychogomphus uncatus (Charp.)				1
Corduliidae				
Oxygastra curtisii (Dale)		1		

grass and on surrounding small trees. After 0800 tandem formation scarcely occurred and the flight activity of males was low. It did not increase before 0845 when the tandems flew to the reproductive sites. First copulations were observed at 0915.

The other Anisoptera species were not observed in flight before 0745. Until this time they perched motionless in the vegetation. Males of *S. depressiusculum* approached and formed a tandem (e.g. 1 observation with female *Orthetrum cancellatum* at 0650, with adult male *Crocothemis erythraea* at 0700, with female *Libellula fulva* Müll. at 0715). All mixed pairs remained at the site of tandem formation. Separation of a tandem with *O. cancellatum* was noticed after 85 min and with *L. fulva* after 41 min when the large Anisoptera flew off. But tandems with the smaller Anisoptera *C. erythraea* and *Sympetrum fonscolombei* (Sél.) were observed at a later time of day. A flying tandem with a female *S. fonscolombei* was still seen at 0925. Copulations or attempted copulations of male *S. depressiusculum* with individuals of other species were not observed.

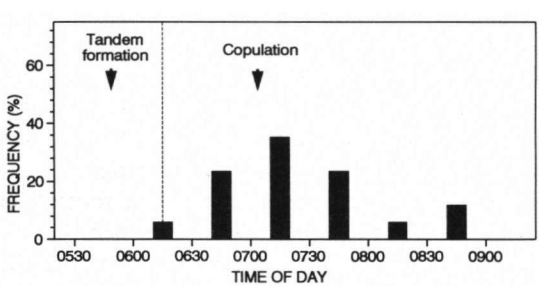

Fig. 1. Heterospecific tandem formation of male *Sympetrum depressiusculum* during course of the day (n = 17). – [The arrows indicate the first daily tandem formations of male *S. depressiusculum* and the first daily copulations. The broken line indicates sunrise].

The density of roosting *S. depressiusculum* in the centre of the site decreased during the breeding period from 2.VII to 22.VII.1990. During the same period the

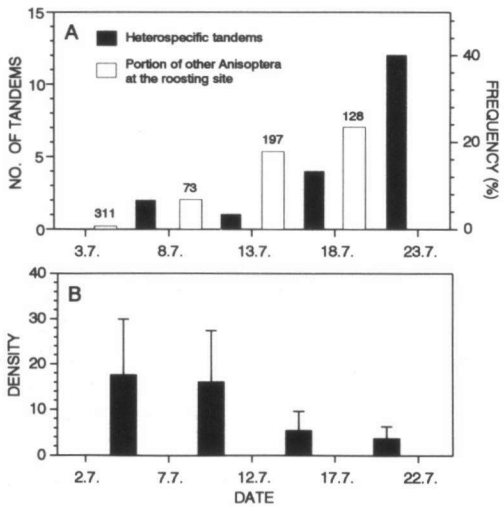

Fig. 2. *Sympetrum depressiusculum*: (A) heterospecific tandem formation of male (n = 18) and the proportion of *Crocothemis erythraea* and *Sympetrum fonscolombei* at the roosting community during the flight season, 1990 (the numbers give the sample size); – (B) density of roosting *S. depressiusculum* (mean ± 95% conf. limits Ind./m^2) in the centre of the site.

proportion of other Anisoptera species in the roosting community and the frequency of heterospecific tandem formation increased distinctly towards the end of July (Fig. 2).

DISCUSSION

The formation of heterospecific tandems in *Sympetrum depressiusculum* at the roosting sites can be attributed to the specific behaviour of the males in search of females and after tandem formation to the subsequent precopulatory guarding (MILLER et al., 1984). The beginning of daily activity of the males was essentially earlier than in other Anisoptera. While males of *S. depressiusculum* are able to warm up by wing-whirring when the temperature is low (VOGT & HEINRICH, 1983; MILLER et al., 1984), giving them possible advantages in the search for females, other Anisoptera remain motionless in the vegetation during the low morning temperatures. Because other Anisoptera species do not show any displays to repel approaching *S. depressiusculum* males they can be grasped. This happens regardless of the sex or size of the other species.

Males may recognize flying females by their characteristic flight movements (UBUKATA, 1983), but tandem formation at the roosting sites shows the unspecific recognition pattern of perching conspecifics in male *S. depressiusculum*. Only in *Anax parthenope* Sél., which weighs 8-9 times more than *S. depressiusculum*, males did not form tandems. All other species occurring at the roosting site were seen in mixed pairs. Most of the heterospecific tandems were found much later than the time when tandems of *S. depressiusculum* pairs first formed. This is possibly due to the spatial distribution of the other Anisoptera species at the roosting site. They mainly perched at the edge of the roosting community, so that the probability of a male grasping a heterospecific individual was lower.

Males which had grasped males or females of another species showed a form of precopulatory guarding, while the tandem perched in the vegetation sometimes for several hours, as do tandems with conspecific females. But in no case it was

observed that the males made attempts to copulate. As soon as the temperature increased and the other Anisoptera became active, most of the tandems separated. In mixed pairs with species such as *Orthetrum cancellatum* and *Onychogomphus uncatus* (Charp.), which are several times the weight of male *S. depressiusculum*, the larger Anisoptera flew off with the male releasing them or being torn off. Already few minutes after separation of the tandem *O. cancellatum* appeared as predator of *S. depressiusculum* (REHFELDT, unpubl. data). Merely the smaller Anisoptera such as *C. erythraea* and especially *S. fonscolombei* were held longer by the males, and with these two species flight in tandem was also observed.

The frequency of the heterospecific tandem formation depends on the probability of males encountering another dragonfly on their search for a female in the early morning hours. The probability increases with the drop in density of *S. depressiusculum* towards the end of July, when the proportion of other species, especially of *Crocothemis erythraea* and *Sympetrum fonscolombei*, increases in the roosting community.

Also in the other non-territorial *Sympetrum*-species, where heterospecific tandem formation is known (JURZITZA, 1966; BICK & BICK, 1981), tandem formation is thought to take place while males are searching for females. However, in these species large roosting communities and precopulatory-guarding are not known. These species occur at common habitats (WATANABE & TAGUCHI, 1988; MICHIELS & DHONDT, 1987) and at the reproductive site during the daily reproductive period males may accidentally grasp individuals of another species.

Sympetrum sanguineum (Müll.) males paired with females of three other *Sympetrum* species that inhabit similar reproductive sites (JURZITZA, 1966; REHFELDT & HADRYS, 1988). In *S. depressiusculum* no heterospecific tandem formation was observed at the reproductive sites (rice fields). Here, the sympatric *S. fonscolombei* occurs only in low numbers. This species weighs more than male *S. depressiusculum* and during the daily reproductive period it may effectively repel approaching male *S. depressiusculum*.

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