

REPRODUCTIVE BEHAVIOUR OF *LEUCORRHINIA ALBIFRONS* (BURMEISTER) IN A NON-TERRITORIAL SITUATION (ANISOPTERA: LIBELLULIDAE)

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The reproductive behaviour in a high-density situation of the sp. was investigated in northern Poland in 1993 and 1995. Because of their high density, males were non-territorial. After a very brief tandem flight, copulations took place either on the ground or in the surrounding pine trees and lasted, on average, 640 s. Afterwards the male guarded the female while she was on post-copulatory rest (PCR). During PCR (which occurred in 11 out of 13 observed cases), the male bent his abdomen tip up to the basal segments after a mean time of 81 s. This behaviour was interpreted as intra-male sperm translocation (ST). Oviposition took place over open water. During mating time, from 10:00 h to about 17:00 CEST, almost none of the observed ovipositions was completed undisturbed. Outside this time, half of the ovipositions observed was completed undisturbed. The latter lasted 34 s, in which the female had an average frequency of 0.6 to 1.9 dips per s. Eleven hand-held ovipositions revealed a mean egg number of 327 eggs per female and a mean egg flow rate of 4.6 eggs s⁻¹. It is concluded that the mating system of *L. albifrons* is best described as a combination of resource limitation and female control. Some known effects of high male density on the reproductive behaviour of the Libellulidae are discussed.

INTRODUCTION

Libellulid dragonflies are among the best studied animals in regard to their reproductive biology, including species recognition (SINGER, 1990), mate recognition (PAJUNEN, 1964a), territorial behaviour (PARR, 1983; WOLF & WALTZ, 1988), alternative mating behaviour (WALTZ & WOLF, 1984; CONVEY, 1989; WOLF et al., 1989; WOLF & WALTZ, 1993), sperm competition (SIVA-JOTHY, 1984; MICHIELS & DHONDT, 1988), genital morphology (MILLER, 1991) and underlying factors of oviposition site selection (WOLF & WALTZ, 1988). Many of the investigations were carried out in the genus *Leucorrhinia*. General descriptions

of the mating behaviour have been made for *L. rubicunda* (MUNCHBERG, 1931; PAJUNEN, 1963; PAJUNEN, 1966; RÜPPELL, 1990), *L. dubia* (MUNCHBERG, 1931; STEINER, 1948; SCHIEMENZ, 1954; PAJUNEN, 1962a, 1964a), *L. pectoralis* (KIAUTA, 1964) and *L. hudsonica* (HILTON, 1984). Detailed information on aggressive interactions between males are available for *L. caudalis* (PAJUNEN, 1964b) and *L. dubia* (PAJUNEN, 1962b). PAJUNEN (1964a) and SINGER (1990) showed that species recognition is not perfect within the sympatric *Leucorrhinia* species *L. dubia* and *L. rubicunda*, and within *L. intacta*, *L. frigida* and *L. proxima*, respectively. All species studied so far have been shown to defend territories, either from perches (PAJUNEN, 1966), by patrolling, or by both tactics (WOLF & WALTZ, 1984, 1993). Perching might be costly. First, SMITH & COOK (1991) showed that territorial males of *L. frigida* have higher loads of the parasitic water mite *Limnochares americana*. Second, in high-density populations of *L. dubia* (PAJUNEN, 1962a, 1962b), *L. caudalis* (PAJUNEN, 1964b) and *L. rubicunda* (PAJUNEN, 1966), the territorial system is too costly and breaks down. The aim of the present paper is to describe aspects of the reproductive behaviour of the hitherto unstudied species *L. albifrons* in such a high density situation.

MATERIAL AND METHODS

The study was undertaken at one peat bog pond in a chain of four in the Kaszub Lake District, 18 km northeast of Chojnice, northeastern Poland (53°46' N, 17°42' E, approx. 200 m alt.). The pond's diameter was about 100 m. Floating *Sphagnum* mosses, leaves of the waterlilies *Nuphar* and *Nymphaea*, and stems of *Peucedanum palustre* were the dominant vegetation. The moss vegetation extended all around the banks and at a water depth of about 3 m was a thick layer of mud. The pH of the water was 5.5. The study site and its close surroundings harbour a rich dragonfly fauna that is detailed elsewhere (BROCKHAUS, 1990; ŁABĘDZKI, 1994; REINHARDT, 1994). The study was conducted between 18-VI and 1-VII, 1993 and between 29-VII and 4-VIII, 1995 when daily observations took place. The weather was rather changeable in the 1993 observation period and warm and sunny in 1995.

Individuals were observed unaided or by binoculars and as many variables as possible were measured to the nearest second according to the following protocol: the duration of tandem, copula and intra-male sperm translocation (ST), the time of ST after copula and duration of post-copulatory rest (PCR- time from copula to the onset of oviposition flight by the female). Furthermore, the number of copulation attempts by the male, location of copulation, the duration of oviposition and whether or not mate-guarding took place by the male were noted. During oviposition, the number of dips, disturbances by males and the distance from the pond margin were also noted. In total, 27 data sets could be used from the 1993 season and 34 from the 1995 season. Additional data were derived from 12 incomplete video sequences. For all events, date and time of day were noted. Eleven females were caught for hand-held ovipositions (STEINER, 1948; McVEY, 1984) and their duration was measured in eight females. They were defined as being finished when no eggs were laid for 60 s. Each female's eggs were stored separately and were counted in the laboratory.

At a certain stage very shortly after copulation the male bent his abdomen tip up to the basal segments (see Results), exactly as has been described for the intra-male sperm translocation (ST, see UTZERI, 1985; UTZERI & OTTOLENGHI, 1992). To determine if this was ST (which usually occurs before copulation, UTZERI, 1985; UTZERI & OTTOLENGHI, 1992) or served, for instance to clean penis of his own or foreign sperm, twelve males (three in copula, two after ST, and seven in an

unknown stage) were captured in 1995. They were dried and later investigated for the presence of a sperm crust on the penis. If penis cleaning occurred during this abdomen bending, one would expect to find no sperm crust at the penis of those males that were captured in an unknown stage, or at least not in those males captured immediately after they showed this abdomen bending.

In order to describe the temporal pattern of male and female arrival, one pond bank about 50 m long was searched for males, females and copulation wheels. Counts were made in 15 min intervals and the respective ambient temperature was measured in the shade to the nearest 1°C. Altogether, 34 counts were carried out in 1993 and 64 in 1995. Data were then pooled for hours and an average values given.

Within-year data are compared by non-parametric statistics using the statistic programme SPSS 6.0.1. In the following, means \pm 1 S.D. with the range and sample sizes in brackets are given.

RESULTS

MATING ACTIVITY

Under the warm weather conditions of 1995, no distinct diel mating pattern was detected. In the more changeable period of 1993, mating seemed to peak around 13:00 CEST (Fig.1). At the mating site, there was usually a 2.5 to 5 fold bias towards males with a total of approximately 10 males per 50 m shoreline (Fig.1). However, there is also a strong correlation of male and female presence at the water. At maximum male activity, nearly all females observed were in copula. The percentage of solitary females was higher only in early morning and late evening.

DESCRIPTION OF THE REPRODUCTIVE BEHAVIOUR

From the parameters measured, only wheel perching

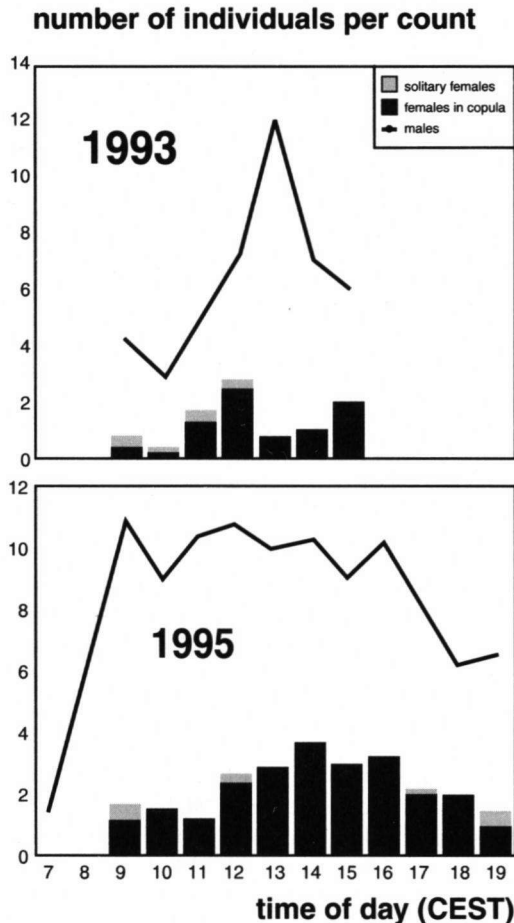


Fig. 1. Presence of males and females at one bank (length: approximately 50 m) of the oviposition pond. The percentage of females in copula is also given. Data are based on single counts (at least 15 min apart) and are pooled for 4 days each in both 1993 and 1995. Weather situations in 1993 prevented further observations. See Methods for further explanation.

height, oviposition duration and the number of dips per second differed between the two years. Thus, all other variables are combined.

The male grasped the female usually during the first or second attempt although third attempts were also observed. The tandem position did not last longer than 1 s if mating occurred. No ST could be detected during this short tandem time. If copulation was refused after the tandem attempt, tandem durations of up to 40 s were observed. In 1993, copulation took place at heights of 0 to 10 cm ($n=19$) but were observed at heights of 0 to 400 cm (average 114 ± 120 cm, $n=22$) in 1995. Matings, on average, lasted for 640 ± 426 s (73 - 1827 s, $n=19$). If two extraordinarily short copulations of 73 and 80 s are excluded, the mean would be 706.5 ± 400.0 s. Abdomen pumping, during which rival sperm is removed from the female bursa copulatrix, was only recorded 3 times. In these cases it ended after 326 s (copulation duration: 511 s), after 246 s (copulation duration 663 s), and after 117 s (copulation duration 291 s). During mating, the pair changed its site 0 to 5 times ($n=25$). These flights, which were usually over short distances only, occurred sporadically or were induced by approaching ants or other insects. When other males of *L. albifrons*, Lepidoptera or asilid flies approached a copulating pair the copulating male briefly opened his wings, resulting in a retreat of the disturbing individual in all cases. During copulation both sexes groomed the head with the front legs. Usually, the female used all three pairs of legs to hold the male's abdomen. After the end of copulation, when males and females separated, both sexes rested on the ground, close to each other (on average 50 ± 44 cm, 15 to 120 cm, $n=13$). In one case the termination of copulation was preceded by a strong vibration of the whole female body including the wings. During PCR, the male bent his abdomen tip to the basal segments. This occurred after 81 ± 71 s (range 18 to 279 s) and lasted for 2 to 3 s ($n=12$), in one case for 6 s. Twice, this abdomen bending was not observed until the male escaped after 300 s and 376 s.

Of the twelve males captured to investigate the purpose of the abdomen bending behaviour, only one (in an unknown stage) did not have a sperm crust at the penis head. All others, including the two males captured immediately after abdomen bending had sperm crusts.

PCR occurred in 11 of 13 cases. In the two other cases, the pair flew in copulation wheel to the open water. Both times the females were grasped by other males immediately after being released by the first male. After an average time of 152 ± 98 s (27 - 376 s, $n=11$) of PCR, females flew to oviposit. In three out of these eleven cases the male tried to initiate oviposition by flying in front of the female. Occasionally, females left the site of PCR and flew to the surrounding forest. There was no relation between copulation duration and PCR duration ($r_s=0.429$, $p=0.397$, $n=11$, N.S.). In the hours from 10:00 h to 17:00 h CEST, only two undisturbed ovipositions were observed (out of some hundred observed). Before or after this time, (8:00 h to 10:00 h and 17:00 h to 20:30 h CEST), 7 out of 14 (50%) were undisturbed. They lasted, on average, 34.4 ± 16.6 s (14 to 53 s, $n=5$) in 1995 but

were significantly longer in 1993 (Mann-Whitney U- test, $U= 1.0$, $p= 0.010$) when they lasted for 91.8 ± 49.8 s (range 51 - 180 s, $n= 6$). I several times observed a male remating with the same female immediately after a copulation. When females arriving at the oviposition site were disturbed they were chased by up to seven males.

In 1993, during single undisturbed oviposition bouts, females dipped 82 ± 49 times (range 26 to 154, $n= 5$) on the water surface but 42 ± 25 times (range 14-69, $n= 6$) in 1995. In contrast, there was also a difference in the dipping frequency between the two years. In 1993, a mean of 0.82 ± 0.23 dips per s (range 0.6 to 1.12, $n= 6$) was observed but in 1995, the observed mean was 1.41 ± 0.31 (range 0.6 to 1.90, $n= 13$). The difference between the two years was statistically significant (Mann-Whitney- U- test, $U= 7.5$, $p= 0.003$). In 1995, five completed ovipositions had the same dip frequency as ten disturbed ones, where only the first part of the dipping sequence could be observed (Mann- Whitney U- test, $U= 14.5$, $p= 0.196$, N.S.). The complete sequences show a positive correlation of dipping frequency with temperature ($r_s= 0.900$, $p= 0.037$, $n=5$). No such relationship was evident in 1995 ($r_s= -0.041$, $p= 0.889$, $n=14$). The eggs were laid in open water, usually at least 5 to 10 m from the bank. Oviposition flights were carried out in long loops. The other *Leucorrhinia* species present, *L. dubia*, always laid its eggs within two m of the margin.

HAND-HELD OVIPOSITIONS

Egg flow during hand-held ovipositions at air temperatures of 24 - 28°C lasted 69.2 ± 20 s (range 36 - 100 s, $n= 8$), whereby 326 ± 146 eggs (range 184 to 723 eggs, $n= 11$) were laid. From these data, a mean egg flow rate of 4.6 ± 2.5 eggs per s (range 2.3 to 9.9 eggs per s, $n= 8$) can be derived. No ambient temperature dependent egg release rate occurred ($r_s= -0.156$, $p= 0.711$, $n= 8$). However, hand-held ovipositions lasted longer than undisturbed ones (Mann- Whitney U- test, $U= 2.0$, $p= 0.008$), indicating some sort of unnatural pattern during hand-held oviposition in this species, resulting in an underestimation of the egg flow rate.

DISCUSSION

OVIPOSITION

Given an abdomen length of 24 - 27 mm in *L. albifrons* (SCHIEMENZ, 1981) an egg flow rate of 6 - 11 eggs per s would have been expected at $32 \pm 3^\circ\text{C}$ (McVEY, 1984). I found no difference in the dipping frequency between undisturbed and disturbed ovipositions, indicating that it is fairly constant within one oviposition bout. During hand-held ovipositions, *L. albifrons* females caught during or shortly

after copulation laid 327 eggs. Given a mean of 82 dips per undisturbed oviposition in 1995, approximately 4 eggs were laid per dip. This is, however, a very rough estimate as little is known about the egg flow pattern with increasing dip number. REHFELDT (1991) found that undisturbed ovipositions were carried out with higher dip rate than disturbed ones in *Crocothemis erythraea* at one of two sites investigated. However, another important factor in egg release rate, the female's present egg load (WATANABE & HIGASHI, 1993), has rarely been investigated and might interfere with such results.

Table I
Effects of high male density on aspects of the reproductive behaviour of libellulid dragonflies

Behaviour aspect	Effect	Species	Reference	
number of ovipositing females territoriality	decreasing	<i>Leucorrhinia intacta</i>	Wolf & Waltz, 1988	
	increasing	<i>Libellula julia</i>	Hilton, 1984	
		<i>Libellula luctuosa</i>	Moore, 1987	
		<i>Nesiothemis nigeriensis</i>	Parr, 1983	
		<i>Acisoma panorpoides</i>	Hassan, 1978	
	decreasing	<i>Libellula saturata</i>	DeBano, 1993	
		<i>Leucorrhinia rubicunda</i>	Pajunen, 1966	
		<i>Leucorrhinia dubia</i>	Pajunen, 1962a	
		<i>Leucorrhinia caudalis</i>	Pajunen, 1964a	
		<i>Leucorrhinia albifrons</i>	this study	
individual male mating success	decreasing	<i>Libellula luctuosa</i>	Moore, 1989	
	increasing	<i>Pachydiplax longipennis</i>	McKinnon & May, 1994	
female rejection rate	decreasing	<i>Libellula luctuosa</i>	Moore, 1989	
copulation duration	no change	<i>Libellula luctuosa</i>	Moore, 1989	
mate guarding	less likely	<i>Libellula luctuosa</i>	Moore, 1989	
	increasing	<i>Sympetrum parvulum</i>	Ueda, 1979	
		<i>Pachydiplax longipennis</i>	Sherman, 1983	
oviposition duration	decreasing	<i>Libellula luctuosa</i>	Moore, 1989	
oviposition frequency	decreasing	<i>Pachydiplax longipennis</i>	McKinnon & May, 1994	
operational sex ratio	male biased	<i>Libellula luctuosa</i>	Moore, 1989	
undisturbed ovipositions	decreasing	<i>Leucorrhinia rubicunda</i>	Rüppell, 1990	
			Pajunen, 1966	
			<i>Pachydiplax longipennis</i>	Robey, 1975
			<i>Leucorrhinia albifrons</i>	this study
			<i>Leucorrhinia rubicunda</i>	Rüppell, 1990
female arrival in copulation wheel	increasing	<i>Leucorrhinia rubicunda</i>	Rüppell, 1990	
sitting oviposition	occurring	<i>Leucorrhinia rubicunda</i>	Rüppell, 1990	
male perching time	decreasing	<i>Leucorrhinia rubicunda</i>	Rüppell, 1990	
heterospecific tandem formation	increasing	<i>Leucorrhinia rubicunda</i>	Rüppell, 1990	
		<i>Sympetrum depressiusculum</i>	Rehfeldt, 1993	
male interaction duration	increasing	<i>Libellula saturata</i>	DeBano, 1993	
satellite male behaviour	increasing	<i>Libellula quadrimaculata</i>	Convey, 1989	

MATING SYSTEM

The differences between the two years with a more distinct male activity peak in the cooler 1993 season support a temperature dependent mating activity rather than a dependence on the time of day. It is interesting that maximum density in 1993 (12 males per 50 m of shore) was close to the plateau reached in 1995 (9 to 11 males per 50 m of shore) indicating that this was the maximum density.

The high density of males resulted in a high percentage of disturbed ovipositions. Therefore, very few mating sequences could be observed completely. Nevertheless, the mating pattern observed in *Leucorrhinia albifrons* corresponds well with other findings within the genus (PAJUNEN, 1962a, 1962b, 1963, 1964a, 1964b, 1966; KIAUTA, 1964; HILTON, 1984; WALTZ & WOLF, 1984; WOLF & WALTZ, 1984, 1988, 1993), including the lack of courtship, the duration of copulation, repeated mating in both sexes, temperature dependence of mating peaks, common occurrence of PCR, high percentage of interrupted ovipositions when densities are high, dipping frequency, egg number, and egg flow rate. The present investigation showed for both years that males do not defend territories. This is in contrast to casual observations of intra- and inter-specific male aggression at neighbouring ponds and at different localities in eastern Germany where densities were low (less than three males per 50 m of shore, unpubl. data). In contrast to PAJUNEN (1962a) I observed a male to pair with the same female several times. This possibly was a result of the high population density and the male's inability to recognize the previous mate. Other types of libellulid reproductive behaviour associated with high density are shown in Table I, indicating that there is no typical libellulid response. Another behaviour most likely connected with high densities was the occurrence of ST just after copulation. Up to now, this has been reported for only one other dragonfly species, i.e. *Pachydiplax longipennis* (ROBEY, 1975). Neither PAJUNEN (1963) from film sequence analyses of *L. dubia* and *L. rubicunda* nor KIAUTA (1964) in *L. pectoralis* and HILTON (1984) in *L. hudsonica* did observe ST behaviour and concluded that sperm transfer in *Leucorrhinia* is generally not immediately followed by copulation. At least in PAJUNEN's (1963) study, the species showed similar high densities as does *L. albifrons* in the present study. I therefore assume that ST immediately after copulation is an advantage for a male in high density populations. It enables him to be immediately ready for further copulations. Maximizing his mating bouts would increase his paternity chances. ST immediately after copulation would then be adaptive.

PCR has been observed in many libellulids (e.g. PRENN, 1930; PAJUNEN, 1963; MILLER, 1983; MILLER & MILLER, 1989; REHFELDT, 1989; LEE, 1994; WILDERMUTH, 1994). Although listing only a few of them and incorrectly citing MILLER & MILLER's (1989) observations on the proportion of *Orthetrum coerulescens* copulations with PCR, LINDEBOOM (1996) concluded that PCR nearly always occurs. REHFELDT (1989) observed that only 86 % of the copulations

were followed by PCR, and also PRENN (1930) mentions copulations both with and without PCR in *L. dubia*. MILLER & MILLER (1989) and REHFELDT (1989) summarized possible functions of PCR for the females: testing the male's guarding quality, avoiding male interference, assessing predation pressure by awaiting other ovipositing females, preparing eggs for deposition, or sperm handling. While MILLER & MILLER's (1989) data favour the sperm handling hypothesis, REHFELDT's (1989) data indicate a significant influence of the presence of other males, bank vegetation, and disturbance (see however LEE, 1994). For the Calopterygidae LINDEBOOM (1996) clearly confirmed a sperm handling function and assumed that the sperm expelled is that from the previous male. If this holds true also for the Libellulidae, only copulations with virgin females or those with insufficient sperm reserves should be expected without PCR. However, the lack of PCR could also be a result of contact-mate guarding. This was the case in the present study where 2 out of 13 observed copulations were without PCR due to contact-guarding. Thus, the behaviour pattern described above can also be seen as a consequence of a sexual conflict between male and female. If the male controls the termination of copulation he should fly in wheel position with his mate to the oviposition site. In the case of female control she should have the choice of whether to initiate PCR (for whatever reason) or to escape and later return to the oviposition site. In both cases, however, the male's control of paternity decreases. In this situation it would be advantageous for a male to be ready for copulation with other females and to perform ST while "waiting" for the female's decision (to leave or to oviposit) or by stimulating her to oviposit e.g. by fluttering in front of her (MILLER & MILLER, 1989; this study).

The frequent male-female encounters, the partial ability of males to control oviposition sites, the occurrence of guarded and unguarded ovipositions, and multiple matings per day by the two sexes lead to the acceptance of one of the two resource-based mating systems (*sensu* CONRAD & PRITCHARD, 1992) for *L. albifrons*. Outside the main mating activity, females are able to oviposit uninterrupted, clearly indicating that males cannot completely control oviposition sites. Thus, for *L. albifrons* the resource-limitation mating system (CONRAD & PRITCHARD, 1992) applies. The long copulation duration in *L. albifrons* (up to 30 min, mean 11 min in this study) and the genus *Leucorrhinia* in general (15-40 min in *L. dubia*, PAJUNEN, 1962a; 20-30 min in *L. caudalis*, PAJUNEN, 1964b; 15-25 min in *L. pectoralis*, KIAUTA, 1964; approx. 15 min in *L. hudsonica*, HILTON, 1984), the absence of courtship display, and the occurrence of contact-guarding favours the assumption of a non-resource-based mating system (see CONRAD & PRITCHARD, 1992). Thus, the mating system could at best be described as a combination of the resource-limitation and female-control systems. A combination of two systems rather than one pure strategy was previously described for *Lestes sponsa* (STOKS et al., 1996). However, the lack of reliable information on the mating behaviour of *L. albifrons* at lower density remains a problem in identifying the mating system of *L. albifrons*.

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