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Weight-associated male mating success in the swarming caddis fly, *Mystacides azureus* L.

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Mating behaviour and mate choice were studied in *Mystacides azureus* L. (Trichoptera, Leptoceridae). Males formed swarms over the water surface and chased approaching females. One male grasped a female and a tandem was formed. Males in tandem flight and newly emerged males had, on average, a greater wing load and dry/wet weight ratio than swarming males. This might indicate that younger males had a higher mating success than older males. In addition, males have larger eyes than females, which suggests that male mating success is due to their ability in detecting females as well. The mating system of *M. azureus* is driven primarily by scramble competition among males, since it seems unlikely that females actively choose among males; a receptive female always accepted the male which first caught up with her. More than half of the females in tandem flight were found to be inseminated and also to carry fewer eggs than unmated females.

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1. Introduction

Many male insects aggregate at sites in the environment where the chances of encountering receptive females are highest. These sites almost always belong to one of four types: zone of emergence, foraging area, oviposition site, or some distinctive landmark (Parker 1978, Thornhill & Alcock 1983). Since the function of these aggregations is mating, some form of mate selection may be involved, either by female choice or male-male competition, or both (c.f. Bradbury & Gibson 1983). Mating aggregations often provide good opportunities for observing mating behaviour and mate selection.

The family Leptoceridae (Trichoptera) consists of 29 species in Fennoscandia (Svensson & Tjeder 1975). In more than half the number of the species males have been reported to aggregate in swarms, usually at dawn and dusk. The males choose species-specific swarm sites (Mori & Matubani 1953, Gruhl 1960, Statzner 1978) and, when swarming, exhibit a species-specific flight behaviour (Solem 1978, 1984). Females frequently enter the swarming sites, and several studies have reported pair formation taking place in the swarms (e.g. Wesenberg-Lund 1943, Hickin 1953, Tozer et. al. 1981). Usually the male grasps the female around the abdomen with his maxillary palps. Copulation may occur either on the riverside herbage as in *Mystacides niger* L. (Hickin 1953), or in the air as in *Nectopsyche albida* (Walker) (Tozer et. al. 1981). The objective of this paper is to present information on mating behaviour and mate choice in *Mystacides azureus* Linneus 1761.

2. Material and methods

The study was carried out at a mesotrophic lake (Lake Erken) in southern Sweden (N 59°50', E 18°40'). The swarms were observed from the shore, sometimes with a pair of binoculars. Swarming males were sampled on seven occasions from 16 June to 29 August 1984 and on four occasions in 1985. Pairs in tandem flight were collected during the same periods. All specimens were caught with a sweep-net. Newly emerged males (max. 9 h old, ready to fly) were caught by use of floating traps, in July and August 1985 and 1986.

The collected pairs were killed before copulation had started. Females were killed mechanically and dissected immediately in a 0.9% saline solution to investigate the presence of sperm and number of eggs in the genital tract. All other specimens were deep frozen, and their wet weight was measured two or three days later on a Cahn electrobalance. The right fore wing was cut off and the length was measured to the nearest 0.04 mm using an ocular micrometer.

To investigate whether a certain position in the swarm is superior to others, the number of pair formations in different parts of swarms were counted. For each observed pair formation I estimated where it occurred in the area the swarm covered at that moment. The swarms were divided into five parts (seen from the shore): (1) the outer part, (2) the inner part, (3) the left part, (4) the right part, and (5) the centre part. The observations were made at two swarm sites, both from the shore and from a boat, "beside" the swarm. This part of the study was made in July 1987.

Outline drawings of the right wing of thirty-two males were made with the aid of a drawtube, and wing areas were measured with a digitizer table. The linear regression of a square of fore wing length on wing area subsequently was used to calculate the wing areas for all collected males. This model explained most of the total variation in wing area (F=637.1, P<0.001, r^2=0.95). Wing load was measured as wet weight/total wing area. Dry weight (24 h in 60°C) was also determined for a number of males. Weight ratio was calculated as dry weight/wet weight. Since caddis flies generally do not feed as adults (Richards & Davies 1977), but loose weight successively during their adult lifetime (Svensson 1972), then high wing load and weight ratio indicate low age. This indirect measurement of age was necessary since earlier mark–release–recapture experiments had failed due to extremely low recapture frequency (0.28%).

Some measured variables (fore wing length, dry weight, and dry/wet weight ratio) changed significantly during the observation season 1984 and these variables were analysed by an Analysis of Covariance (Snedecor 1966). Other variables were analysed by Student's t test or Mann-Whitney U-test.

The terminology of the internal female genitalia follows Unzicker (1968). Identification was made by use of Macan (1973). Nomenclature follows Svensson & Tjeder (1975).

3. Results

3.1. Mating behaviour

Swarming occurred primarily at dusk. Males formed dense swarms 5–10 cm above the water surface and at a 2–5 m distance from the shore. Male flight behaviour consisted of varying horizontal and vertical zig zag patterns. The amplitude of the horizontal zig zags was 25–50 cm and the vertical 5–10 cm. Males changed position repeatedly within the swarm, causing the centre of the swarm to move over the swarming area and for the swarm to disperse and reform, over and over again. Females approached the swarm from above, probably from their resting places on the shore vegetation. Swarming males first discovered an approaching female at a distance of less than half a metre above the swarm. Sometimes, usually in swarms of low male density, a female could fly into the swarm before she was discovered. When the female was discovered, one or several males left the swarm and started to fly towards or after her. The female then flew upwards, away from the swarm, chased by males. When a male reached a female, he grasped her and the "tandem" then flew to the shore and settled on the vegetation, 1–4 m above the ground, and copulated in an end-to-end position. Grasping usually occurred within a few seconds after detection. When the pair settled, it was possible to observe that the male held the female around her abdomen with his maxillary palps and sometimes also with his forelegs. A very high proportion (64 of 65) of the pairs in tandem flight copulated. The number of pair formations in different parts of the swarms did not differ significantly (Table 1).

Table 1. Number of pair formations in five different parts of *Mystacides azureus* swarms. The positions are seen from the shore. Data from 1987. χ^2 = 3.29, df = 8, N.S.. Numbers in brackets are the total number of observation hours at each swarming site.

Part:		outer	inner	left	right	centre	Total
Site 1	(6.0)	38	29	35	22	31	155
Site 2	(10.5)	78	70	69	70	85	372

3.2. Remating of females

Sperm was found in the prespermathecal diverticulum and/or the spermatheca in 59% of the tandem females (n = 113). Mean egg number was 164.8 in the unmated females and 59.2 in the inseminated ones, (χ^2 = 76.66, P < 0.001) (Fig. 1). Unmated and inseminated females did not differ with regard to fore wing length (mean wing length for unmated = 7.28±0.29 mm and inseminated 7.36±0.31 mm; t = 1.393, P > 0.15).

3.3 Mate choice

Males caught in tandem or swarming flight did not differ with regard to fore wing length, dry weight, wet weight or thorax width (Table 2). However males in tandem flight had a higher dry/wet weight ratio than swarming males, and this effect also caused a greater wing load in males caught in tandem flight. Newly emerged males also showed higher weight ratio and wing load than swarming males (Table 3).

Table 2. Comparison between males of *Mystacides azureus* in tandem and swarming flight. Variables showing correlation with the date were analysed by an Analysis of Covariance, others by Student's *t* test. Data from 1984.

Variable	“type of males”	*n*	adjusted mean±SD	
Weight ratio	tandem	76	0.296±0.032	*P*<0.004
	swarming	124	0.282±0.033	
Forewing length (mm)	tandem	130	7.40±0.25	N.S.
	swarming	178	7.41±0.24	
Dry weight (mg)	tandem	76	0.882±0.113	N.S.
	swarming	124	0.877±0.189	
Wet weight (mg)	tandem	130	3.93±0.44	N.S.
	swarming	178	3.84±0.49	
Thorax width (mm)	tandem	129	0.991±0.043	N.S.
	swarming	177	0.985±0.048	
Wing load (N/mm^2)	tandem	130	0.090±0.007	*P*<0.015
	swarming	178	0.088±0.010	

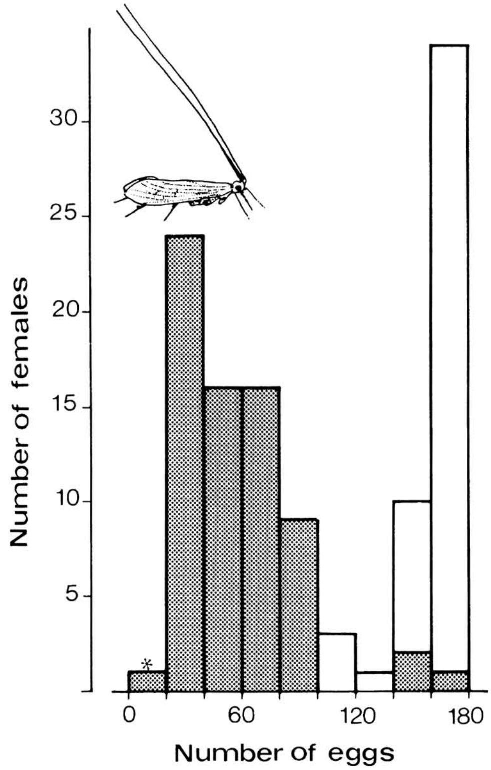

Fig. 1. Frequency of number of eggs per female in unmated (open areas) and inseminated (shaded areas) tandem females in *Mystacides azureus*. The female marked with an asterisk was found to be infected by a nematode and is therefore excluded from the statistical analysis.

Table 3. Comparison between newly emerged and swarming males of *Mystacides azureus*. Statistical test: Mann-Whitney U-test. Data from 1985 and 1986.

Variable	“type of males”	*n*	mean±SD	
Weight ratio	newly emerged	24	0.269±0.014	*P*<0.011
	swarming	427	0.260±0.020	
Wing load (N/mm^2)	newly emerged	24	0.090±0.011	*P*<0.004
	swarming	427	0.088±0.009	

4. Discussion

Except for the swarming pattern, the swarms of *M. azureus* are similar to those of the leptocerid *Nectopsyche albida*, described by Tozer et. al. (1981). Both species form swarms just above the water surface, and swarms consist almost entirely of males. However, there appear to be important differences in the process of mate choice. In *N. albida* females successively inspect several male displays until a male is chosen. A female of *M. azureus*, on the other hand, most often did not reach the swarm before she was discovered and intercepted by males. The swarms of *M. azureus* often consisted of hundreds or thousands of males, and males from all positions in the swarms were observed to achieve pair formation. It, therefore, seems unlikely that a general, certain position within a swarm was superior to an other. Swarming males appeared to be scanning the swarming area for females, trying to outrace rivals to mates.

The eyes of *Mystacides* males are larger than those of females (Esben-Petersen 1916, Petersson &

Solem 1987). This property is rather common among insects, occurring for example in Ephemeroptera, Spheridae and Empididae, and might be seen as an adaptation for mate finding (Thornhill & Alcock 1983). This sexually dimorphic character and the flight behaviour in *M. azureus*, render it likely that swarming males may compete for arriving females. The competition apparently consists of a "race" from swarming position to the approaching female, which is grasped by the first male that reached her.

More than half the number of the dissected tandem females were already inseminated. These females carried significantly fewer eggs than unmated females. Fig. 1 shows that the distribution of egg number in tandem females was clearly bimodal. Lifetime fecundity of *M. azureus* is not known. However, females of *M. longicornis* L. lay 218–257 eggs (Hanna 1964), and females of *M. azureus* probably are able to lay slightly more than 200. Females probably copulate soon after emergence and lay about two thirds of their eggs, and then copulate with a second male before the remaining eggs are laid. As females initiated the mating process by approaching the male swarms and rematings were very frequent, the second copulation apparently has some adaptive value to females. Polyandry among insects has been divided into four functional categories (genetic benefit, convenience, material-benefit, and sperm-replenishment polyandry (Thornhill & Alcock 1983)). Convenience polyandry is unlikely, since females initiate mating by approaching a swarm of males. Males of *M. azureus* do not transfer spermatophores (Khalifa 1949) and the spermatheca is medium-sized (Unzicker 1968), therefore also material-benefit polyandry seems unlikely. However, more data are needed before it can be stated which type applies to *M. azureus*.

The results show that males in tandem flight have higher wing load than did swarming males. This extra weight was dry substance, because the dry/wet weight ratio was higher for males that flew in tandem. Even newly emerged males had higher wing load and dry/wet weight ratio than swarming males. This indicates that in *M. azureus*, mating males on average were younger than non-mating males. Adult caddis flies have rarely been observed feeding; their mouthparts are reduced, but are still useful for licking fluids (Richards & Davies 1977). A low food intake results in a successive weight loss during their adult lifetime (Svensson 1972). Age-associated decline in flight performance as measured by total duration of sustained flight until exhaustion, has been described in several species (e.g. Wigglesworth 1948, Pringle 1965, Rowley & Graham 1968). In *Musca domestica* L. (Diptera), for example, such reduction in flight capacity has been shown to be associated with morphological and cytolytical changes in the flight muscles (Sohal 1976). This might explain why, in *M. azureus*, younger males were more successful than older males in pair formation.

Thus, male copulatory success should be functions of individual differences in flight capacity, female detection ability, and, indirectly, age.

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