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Diurnal and seasonal variations in swarming and mating behaviour of the dance fly *Empis borealis* (Diptera; Empididae)

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In the dance fly species *Empis borealis* (L.) (Diptera, Empididae), females (1–40) gather to swarm at landmarks and males carrying an insect prey visit these swarms for mating. Sun exposure was necessary for swarming and windy conditions abrupted swarming totally. Under favourable climatic conditions, swarming persisted for most of the day, starting at 08.00 and continuing until 19.00–20.00 (local time), at temperatures ranging from 8 to 21°C. Swarming activity during the day showed no major variation. The mean number of swarming females at the swarm-sites and the number of swarm-sites used declined during the flight period. During female swarming activity, male visiting rate and mating frequency were independent of temperature. The number of males visiting swarm-sites, mating frequency and male visiting frequency calculated per female (used as a measurement of the operational sex ratio) declined during the flight period. The male visiting frequency declined more rapidly than the number of swarming females, indicating that males may have a higher mortality rate than the females. The proportion of visiting males which mated in swarms was independent of date although prey availability and female mating status varied. Thus, the male degree of choosiness was similar throughout the flight period. Swarming behaviour in the female sex is an adaptive behaviour in *E. borealis* and does not seem to be influenced by resource availability, habitat quality, mating frequencies, sex ratios, or abiotic factors.

1. Introduction

Insect mating systems might vary or change between years and during the breeding season (e.g. Kon 1987; Larsson 1989). Thus, the view one might get of the mating system may depend on when and where the studies have been performed (time of day, time during the breeding season, year, and sites studied). To better understand mating systems in insects, examination of the temporal variation of the activities of the species concerned and identification of factors causing this variation is therefore necessary.

For several years, we have studied the mating system and behaviour of the swarming, courtship role-reversed dance fly species *Empis borealis* (L.) (Diptera: Empididae) (Svensson & Petersson 1987, 1988, 1992, 1994, Svensson et al. 1989, 1990). This species is distributed in north and central Europe, eastwards to the Ural mountains (Chvála & Wagner 1989). Females are commonly found swarming in damp spruce forests in early spring (April–June) and the mating system can be summarized briefly as follows (Howlett 1907, Gruhl 1924, Tuomikoski 1938, 1939, Svensson & Petersson 1987, 1988, 1992, 1994., Svensson et al. 1989, 1990). Females gather to swarm at landmarks and males carrying an insect prey item visit these swarms for mating. Usually a single male with a prey item approaches a swarm and he either mates with one of the females or leaves, still with his prey item, for another swarm. Males also visit swarm-sites temporarily without females. Males hunt for prey which are presented to females at mating, whereas females do not hunt and only consume prey received from males. Females are polyandrous. The number of individuals in insect swarms is generally high, often several thousands (Sullivan 1981). The number of swarming females in swarms of *E. borealis* is low. Median swarm size is about 4 (Svensson & Petersson 1994) and therefore more easily studied than most other swarming insects. Swarm-sites remain the same during the whole flight period and may persist over several years. Males mated more frequently with the larger females in each swarm.

We have experienced that the number of swarming females, as well as the number of males visiting the swarms, seems to vary during the day and over the season. For example, we observed that few males visited the swarms late in the season when females still did swarm in abundance. In this paper we report on the temporal variations in swarming and mating activities during the flight period in the dance fly *E. borealis*. We also asked; does the probability of females being mated at different parts of the flight period or different times of the day change?

2. Materials and methods

This study is based on two data sets. In the first one, 55 swarms from 1984, 1985 and 1987, includes the number of swarming females, the number of males and the number of copulations per minute (cf. Svensson & Petersson 1992). The second one (cf. Svensson & Petersson 1994) was originally collected to estimate the variation of number of swarming females at swarm-sites. To do so, 69 swarm-sites were marked with numbered tags at the beginning of the swarming season. These swarm-sites were then observed about once a day, and the number of swarming females and whether or not they were shaded was noted. Temperature and estimated wind velocity were also recorded. When appropriate, these two data sets were pooled.

In most cases the values in the data sets have been adjusted for variation due to one or several abiotic variables. For example, if the variation during the day was evaluated, the variations due to temperature, wind, year, and day of the swarming season were held constant. The adjustments have been done by using the residuals from multivariate linear regressions and by standardizing the mean of ordinal or nominal classes to the value of the overall mean for the studied variable. Calculations were made using SAS software (SAS Inst. 1987).

3. Results

3.1. Female swarming activity

Females were observed swarming at temperatures from + 8 to + 21°C and within this temperature range no correlations to swarming activity was found. At temperatures lower than +10°C, however, the average swarm size was about half the smallest one at temperatures above +10°C.

683 observations from 69 swarm-sites revealed that females preferred to swarm at sun-exposed sites. At 373 of these observations, when females were present only 13 included swarm-markers in the shade (Fishers exact test, $p < 0.001$). The number of observations with no females swarming at swarm-sites was 222/88 (shade/sun).

Females started to swarm in the morning soon after the sun reached over the trees, about 08.00 local time, and continued to 18.00 (Fig. 1), occasionally until 20.00. During this time period, no apparent activity pattern was seen. The activity was about the same during the day but the swarm sizes tended to be built up before noon, increasing from about three females at 08.00 hours to about five females at 11.00 hours. In the afternoon, at 16.00 hours, there was a marked increase.

The mean number of swarming females at each swarm-site declined over the flight period ($r = -0.53$, $p < 0.007$; date log-transformed)

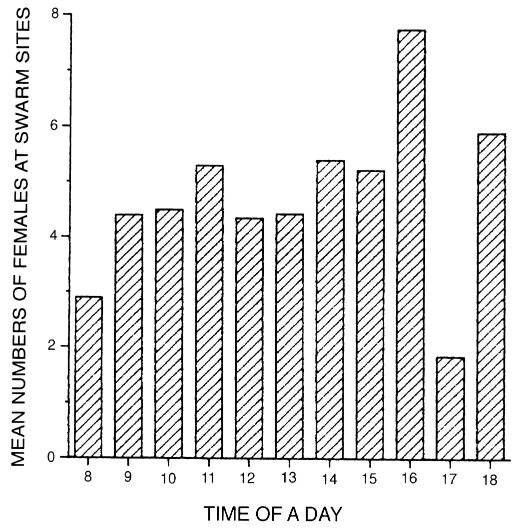

Fig. 1. Diurnal swarming activity of *Empis borealis* females.

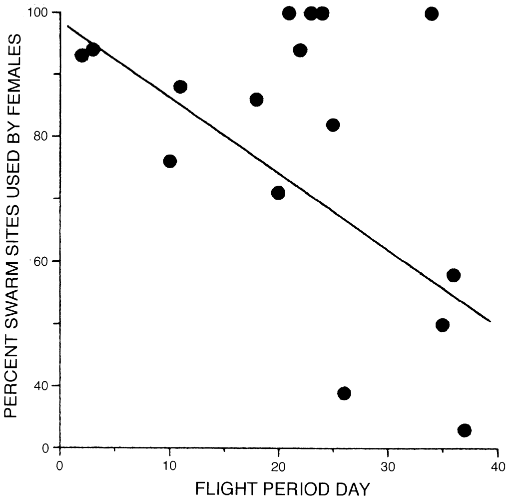

Fig. 3. Percent of swarm-sites used by *Empis borealis* females during the flight period. $Y = 98.71 - 1.19x$, $r^2 = 0.49$, $F = 13.2$, $p < 0.003$. Weight variable = number of swarm-sites observed each day.

(Fig. 2). There was also a tendency for fewer swarm-sites being used by the females late in the swarming season (Fig. 3). The proportion of used swarm-sites varied from 33.3% to 100%, with the four lowest values recorded during the second half of the swarming season. However, the variation both within and between days was very large.

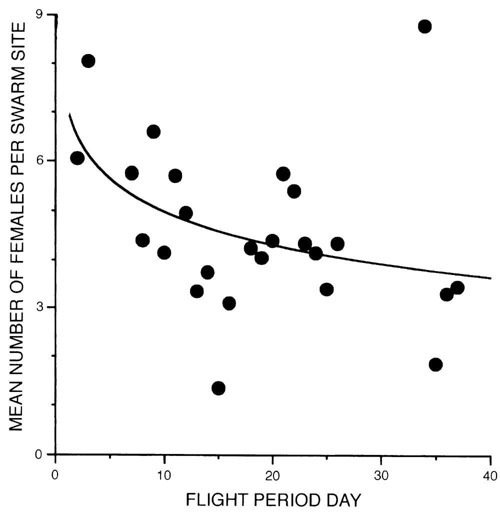

Fig. 2. Mean number of swarming *Empis borealis* females per swarm-site during the flight period. $Y = 8.02 - 2.70\log(x+1)$, $r^2 = 0.28$, $F = 8.91$, $p < 0.007$. Weight variable = number of swarm-sites observed each day.

3.2. Male visiting frequency at swarms

During female swarming activity the number of males visiting the swarm-sites per minute was independent of temperature and time of day, and the pattern of these two relationships was very similar to those of number of swarming females. However, the number of visiting males declined during the flight period ($r = -0.63$, $p < 0.003$; date log-transformed), (Fig. 4).

3.3. Operational sex ratio

As a measurement of the operational sex ratio (OSR) over the season, we calculated male visiting frequency per female. This gives an estimate of how many males per female there were in the swarms. Male visiting frequency per female declined during the swarming season ($r = -0.73$, $p < 0.001$; date log-transformed) (Fig. 5), indicating that the number of males in the population declined faster than the number of females. For the data collected in 1988, when both number of swarming females and male visiting frequency were recorded, the number of

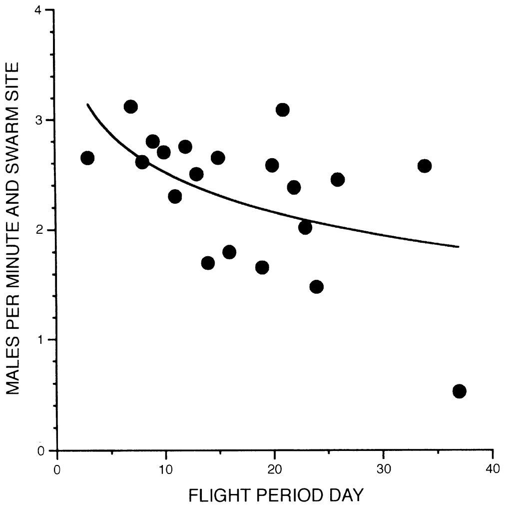

Fig. 4. Mean number of *Empis borealis* males per minute visiting female swarms during the flight period. $Y = 4.26 - 1.62\log(x+1)$, $r^2 = 0.40$, $F = 12.1$, $p < 0.003$. Weight variable = number of swarm-sites observed each day.

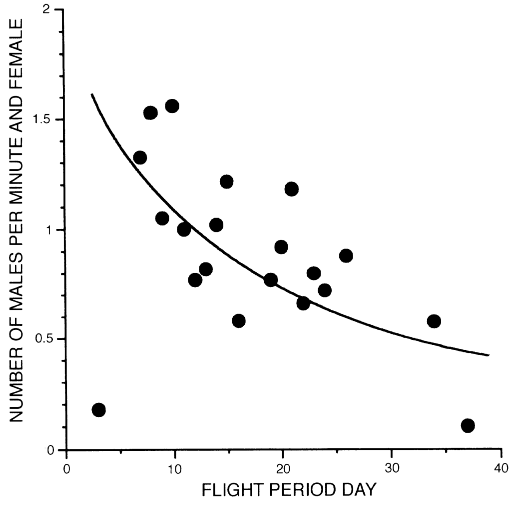

Fig. 5. Mean number of *Empis borealis* males per minute and female visiting female swarms during the flight period. $Y = 2.45 - 1.28\log(x+1)$, $r^2 = 0.53$, $F = 20.4$, $p < 0.001$. Weight variable = number of swarm-sites observed each day.

females was almost constant during the season, probably an effect of that very few observations were made during the last third of the swarming season that year. Male visiting frequency, however, declined during the swarming season 1988, and the two slopes differed significantly ($F = 35.58$, $p < 0.001$, homogeneity of slopes model). Male visiting frequency per female was not altered by temperature or time of day.

3.4. Mating frequency

Mating was observed at temperatures from + 10.5°C to + 21°C and mating frequency was not correlated with temperature. The number of matings in swarms per minute was rather constant until 15.00, when a marked decrease was observed. Mating frequency during the flight-period was negatively correlated with date ($r = -0.54$, $p < 0.02$; both variables log-transformed) (Fig. 6). No correlations were found for mating frequency per female with temperature or time of day. However, the diurnal mating frequency pattern was similar to that of the number of swarming females. During the flight period, the mating frequency per female decreased significantly ($r = -0.63$, $p < 0.005$; mating frequency per female log-transformed) (Fig. 7).

The proportion of visiting males that mated was not correlated with temperature, time of day or flight period day. However, the proportion of visiting males which mated, as well as the mating frequency (see above) seem to be different during the first two or three days of the swarming season. During these days, the proportion of virgin females was much larger than later on, for example, after four to six days almost 90% of the swarming females were inseminated (Svensson & Petersson 1987). The males might then be predicted to be less choosy very early during the swarming season, especially if the first male mating with a female fertilizes most of her eggs. The present data, however, did not confirm such a pattern that male choosiness varies with date.

4. Discussion

Swarming activity in insects is usually confined to the light hours of the day (Sullivan 1981; but see

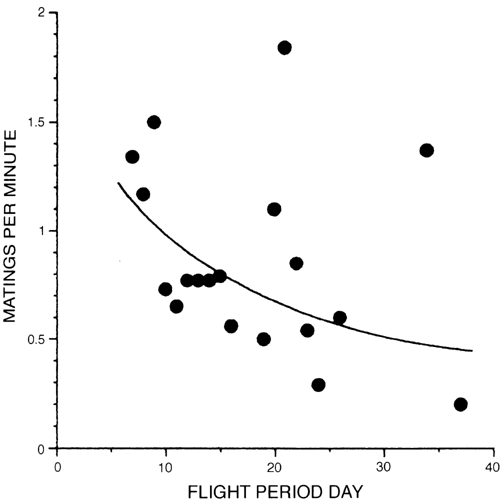

Fig. 6. Mean number of matings per minute in *Empis boralis* swarms during the flight period. $\log(Y) = 0.54 - 0-55\log(x+1)$, $r^2 = 0.29$, $F = 7.1$, $p < 0.02$. Weight variable = number of swarm-sites observed each day.

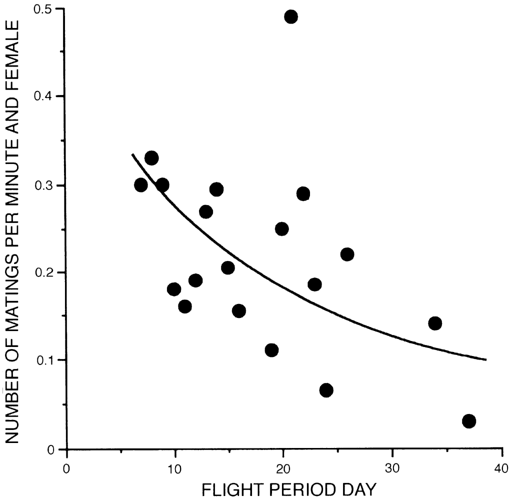

Fig. 7. Mean number of matings per minute and female in *Empis borealis* swarms during the flight period. $\log(Y) = -0.97 - 0.042x$, $r^2 = 0.39$, $F = 10.9$, $p < 0.005$. Weight variable = number of swarm-sites observed each day.

Savolainen & Syrjämäki (1971) for "night-swarming") and hence, it is generally regarded as a visually guided type of mating behaviour. Swarming activity and behaviour often differ between closely related species in the same area (Downes 1955, Haddow & Corbet 1961, Lindeberg 1964, Savolainen 1978). Concerning *E. borealis,* there are no other species present to compare with at that time of the year and few data are available for the timing of swarming in closely related empidids. The daily duration of swarming activity is very variable among species. Some swarm for just a short period of the day (Downes 1955, 1969, Forrest 1985, Blackwell et al. 1992), during crepuscular or full daylight, yet others swarm for most of the day (Savolainen 1978). Swarming behaviour of females in *E. borealis* is exhibited all day and hence falls into the latter assembly of species. Furthermore, female swarming in *E. borealis* is constant both temporarily and geographically (Scotland, Howlett 1907; Germany, Gruhl 1924; Finland, Tuomikoski 1939; Sweden, Svensson & Petersson 1987). No alternative mating systems have been found and many swarm-sites in our study area have been used for more than 10 years.

Temperature, illumination and other climatic factors have been shown to have large effects on swarming activity in insects (Haddow & Corbet 1961, Savolainen 1978, Yuval & Bouskila 1993). In *E. borealis,* females are very much dependent on direct sunshine and calm weather (Howlett 1907; Gruhl 1924; Tuomikoski 1939; Svensson & Petersson 1987). Under basic climatic conditions, temperature did not affect swarming in *E. borealis*, but at higher temperatures more females were found in swarms.

Gwynne & Simmons (1990) found that resource availability had a major impact on the mating system in a cricket species. For *E. borealis,* prey availability varies during the flight period, which might give rise to variations in the degree of male choosiness. Two opposing factors, availability of prey and non-mated females, may create a male mate choice selectivity during the flight period. Firstly, the species is one of the earliest empidids to emerge in the spring and the prey availability, both in terms of abundance and body size, is much lower at the beginning of the flight period of *E. borealis* (mainly emerging winter diapause insects as prey) than at the end (abundance of emerging spring insects). A large prey item caught early in the flight period might be of greater importance than later on, since females only mate with males providing a prey, and since copulation duration also increases with prey volume (Svensson et al. 1990). Therefore, males should be predicted to be more choosy early in the flight period than late. Secondly, males should benefit from mating with virgin females, but all females in the population are mated within the first week of the flight period and hence, males may be predicted to be more choosy late in the flight period. We have previously found that males are unable to discriminate between virgin and non-virgin females in swarms (Svensson & Petersson 1992). Thus, female mating status might not affect male degree of choosiness. We found that the proportion of visiting *E. borealis* males which mated was independent of the flight period. Thus, male degree of choosiness seems to be constant throughout the flight period.

Swarming in *E. borealis* is most often exhibited in direct sunshine. When adults emerge in early spring, the deciduous trees are still without leaves. As leafing time continues some swarm-sites become shaded all day and will be unsuitable for swarming. Therefore, the proportion of swarm-sites used declines with date. The position of swarms at the swarm markers also changes during the day in relation to the position of the sun.

Although female mating expectancy in swarms diminished with date, females still swarm in abundance late in the flight period. This may be regarded as an expression of the high value of prey gifts by males, not merely for acquiring mates for fertilization of eggs, but also for survival, since females probably are not predatory themselves. The fact that male visiting frequency calculated per female declines more rapidly than the number of swarming females probably reflects that the males died off faster than the females. The shorter life span of males might be due to them using a substantial amount of energy in hunting prey and travelling between different swarm-sites. Hunting males may also be more exposed to injuries and predation than the swarming females.

To conclude, it is our view that swarming behaviour of the female sex in *E. borealis* is an adaptive and persistant behaviour and not seem to be influenced by to resource availability (prey), habitat quality (geographical areas), mating frequencies, sex ratios, or abiotic factors. There are still several questions to be answered for a more complete understanding of the mating system of *E. borealis*: Why do females swarm? What causes the sex ratio changes during the flight period? Further field studies have to be made on this and related species to be able to make a comparative analysis. Furthermore, the phylogeny of the genus *Empis* and other dance fly species has to be reconstructed to be able to answer these questions.

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