Ann. Zool. Fennici 24:323–334. 1987

Sex-role reversed courtship behaviour, sexual dimorphism and nuptial gifts in the dance fly, *Empis borealis* (L.)

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Svensson, B. G. & Petersson, E. 1987: Sex-role reversed courtship behaviour, sexual dimorphism and nuptial gifts in the dance fly, *Empis borealis* (L.). — Ann. Zool. Fennici 24:323–334.

Dance fly swarms usually consisted of five to ten females (range 1–40). Females moved between swarm-sites, which were the same during the whole flight-period and over several years. Usually a single male with a nuptial gift approached a swarm. He either mated with one of the females or left, still with his gift, for another swarm. Males coming to swarm sites activated females resting at the swarm-marker to swarm. At the end of the flight-period males were very few, while females still swarmed.

Males hunted for prey, which were presented to the females prior to mating. Females did not hunt and were only seen to consume prey received from males. The most frequent nuptial gifts were Diptera, including conspecifics.

Females, and presumably males, mate several times. Swarming females had no mature eggs. The number of mated females in the population rose rapidly to 80% during the first six days of the flight-period, and on day 20 all females were mated. No sexual difference was found regarding wet-weight, but wings were longer and broader in the females, whose wing-area on average was about 60% larger than in males. Femur I was about 20% longer in males than in females.

We suggest that the sex-role reversed courtship behaviour, the offering of nuptial gifts and the sexual size dimorphism in *E. borealis* have evolved because males limit female reproductive success, and males therefore should become choosy and females should compete for mates.

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1. Introduction

Empidid flies are commonly called dance flies or balloon flies, with reference to their swarming behaviour, and to the habit of males in some species of wrapping up a nuptial gift in silky threads, so that it looks like a balloon, before offering it to a female prior to mating (Kessel 1955). In many species, however, males offer the female a prey without wrapping it up, while in other species the female is offerred an empty balloon. Male dance flies, mainly of the genera *Empis*, *Hilara* and *Rhamphomyia*, after capturing a prey often gather and form swarms which females join for mating (Gruhl 1924, 1955, 1963, Tuomikoski 1939, Hobby & Smith 1961, 1962, Alcock 1973, Chvála 1976, 1980, 1983, Downes 1970, Alcock et al. 1979). In a few species, like *Empis borealis* and a few other *Empis*, *Rhamphomyia* and *Hilara* species, females have been reported to form swarms to which prey-carrying males come for mating (Howlett 1907, Hamm 1908, Gruhl 1924, 1963, Tuomikoski 1939, Chvála 1976).

Sex-role reversal in relation to the usual male and female reproductive behaviour, is an important evolutionary phenomenon (Ridley 1978, Zeh & Smith 1985). Since females normally contribute more to each offspring than males, females exhibit mate choice, whereas males compete for females (Bateman 1948, Williams 1966, Trivers 1972). But if male parental investment exceeds female investment, theory accordingly predicts a reversal in the behavioural patterns. Also, if males monopolize resources of critical importance for female reproductive success, a sex-role reversal is expected to evolve (Thornhill & Alcock 1983, Gwynne 1986a).

Sex-role reversal in reproductive behaviour has been found in widely separate animal groups, for example, birds (Oring 1982, Petrie 1983), fishes

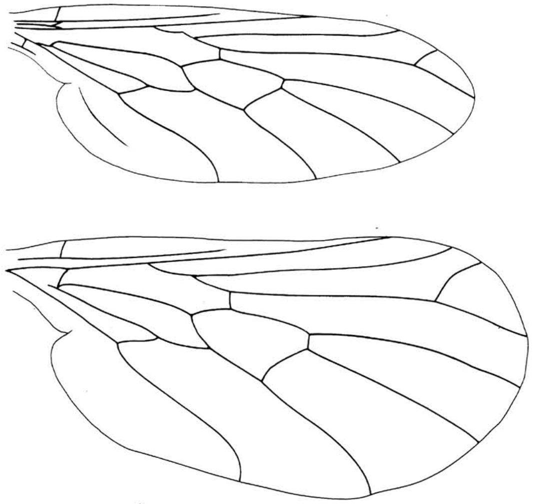

Fig. 1. Wing-shape in *Empis borealis* females and males.

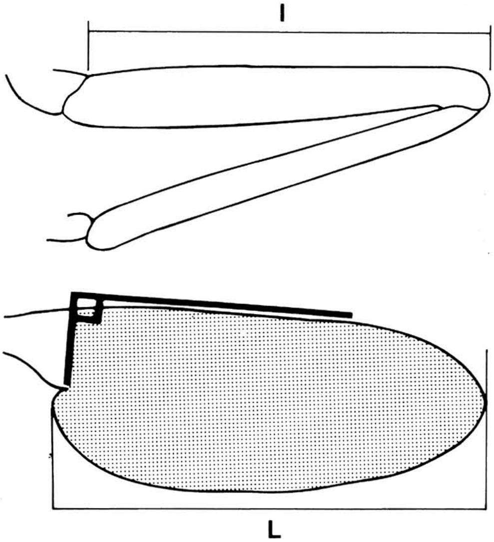

Fig. 2. Standard for femur I length (l), wing-length (L) and wing-area (hatched) measurements in *Empis borealis*.

(Fiedler 1954, Berglund et al. 1986a, b), frogs (Wells 1981) and arthropods (Hatziolos & Caldwell 1983, Thornhill & Alcock 1983, Zeh & Smith 1985). In insects the best documented sex-role reversed mating systems are found in the giant water bug family Belostomatidae (Smith 1980) and in katydid crickets (Gwynne 1984b).

This study reports on the swarming and mating behaviour, sexual dimorphism, foraging, and fecundity in the sex-role reversed dance-fly species *Empis borealis* (L.). The purpose of this paper is to provide a basis for our studies on the mating system and sexual selection of this species.

2. Material and methods

2.1. Identification of the species and sexes

Empis borealis is 6–8 mm long with dark brownish wings (see, Lundbeck 1910, Engel & Frey 1956, or Collin 1961, for a detailed description of the species). Species identification in the field is made easy as no other similar empidid species are present in May (Tuomikoski 1938, 1952). Sex identification in the field is made by the shape of the wings—narrow in males and very broad in females (Fig. 1)—and by the shape of the abdomen tip—pointed in females and enlarged with a hypopygium in males.

2.2. Study areas

The main study area during 1982–1986 was situated in a wooded area 3 km southwest of Uppsala, Sweden (N 59°48', E 17°40'). The area is covered by a coniferous forest, with scattered deciduous trees. Wet and boggy areas are common. Additional behavioural observations were made at Fågelsundet, 100 km north of Uppsala (N 60°36', E 17°57').

2.3. Body parts measured and male and female weight

The wing-length was measured to the nearest 0.05 mm, as the greatest distance from the tip of the wing to the tip of the anal lobe (Fig. 2), using a stereo-microscope equipped with an ocular micrometer. Wing-area was measured by first mounting the wing between slides and then drawing from a camera lucida, and the area was then calculated to the nearest 1/10 mm^2 (Fig. 2). Length of femur I was measured as shown in Fig. 2. Wet-weight of males and females was measured on a Cahn electrobalance to the nearest 0.001 mg, after the flies had been killed by freezing. Wing-load was measured as wet-weight per total wing-area (mg/mm^2).

2.4. Fecundity, egg size and female mating frequency

In the first week of the flight period in 1984 23 females were collected, and the number of ovarioles was counted. The size of the largest egg in the ovarioles was compared to the size of the spermatheca. As mature eggs were not found in *E. borealis* females, a comparison was made with other empidid species to estimate the size of mature eggs.

During different parts of the flight period in 1984, 1985 and 1986 168 swarming females were collected to investigate the female population mating frequency by presence of sperm in the spermatheca. The position of the single spherical spermatheca is in the 5th abdominal segment.

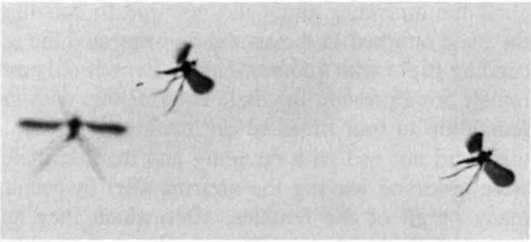

Fig. 3. Posture of swarming *Empis borealis* females.

3. Results

3.1. Female swarming behaviour

Female swarming behaviour took place near landmarks (bushes or trees) along tracks, in glades or edges of mires (Fig. 3), from about 08.00 h to 19.30 h. Swarming activity was highly dependent on the weather. Windy and cloudy weather diminished or stopped the swarming, and females rested at the land-marks. As the weather improved, one female would start swarming and was soon followed by the others.

Usually five to ten females swarmed together, but occasionally 30–40 females could be observed in a single swarm. Single "swarming" females were also often found. Some swarm-sites seemed to be more attractive, and they were generally occupied by a larger number of females than others. There was a continuous exchange of swarming and resting females at each swarm site. Thus, the number of females using one particular site may be considerably larger than the number actually observed swarming at a given time, as several females may be resting on the landmark.

The diameter of swarms was in the order of 0.5–1.5 m with the vertical axis being more extended, and the bottom of the swarms being from 0.5 to 6 m above the ground.

Along a path, over a distance of 200 m, 14 swarms were established by 11.00 h. The shortest distance between swarm sites was 3–4 m. Swarm-sites were abandoned when they became shaded and new, sunny swarm-sites were established close-by. The position of swarms thus varied during the day. The same landmarks were used during the whole flight period and also for several years. Of 18 landmarks marked in 1982, all were used in 1983 and most of them also in the subsequent four years.

Females were observed to move between swarm sites. This was easily observed along tracks where individual females could be followed. This swarm "turnover" is illustrated by the number of females caught (resting and swarming) at 10 min intervals at one swarm site. The number of females initially was five, in two hours 53 females were caught there, and at another swarm site, 26 females were captured in one hour.

The flight pattern of swarming females when no male was present, was a slow, horizontal cruising or hovering flight with sudden up and down movements. The second and third legs hung below females in flight and the first pair was often directed forwards (Fig. 3). When a male entered a swarm the flight of the females became erratic and involved more rapid movements; female flight behaviour observed from a distance clearly announced the presence of males in the swarm. When a male with prey arrived to a swarm, the number of swarming females increased; resting female flies took off from the landmark. If a male arrived at a swarm site with only resting females, they most often took off and started to swarm. If the females did not start, the male made a couple of rapid turns around twigs where females were resting, which often succeeded in provoking them to swarm. On a few occasions this male behaviour was observed although no females at all were present at the land-mark. This flight-inducing behaviour was repeated a couple of times before the male left the swarm site. Provoked swarming was also induced by other species of insects (*Callophrys rubi* L., Lepidoptera, Lycaenidae; *Laphria* sp., Diptera, Asilidae) and by any small object thrown into the "swarm-volume".

When males were not present in swarms, no aggressive behaviour was observed between females at the beginning of the flight period, but later in the flight-period (when males occasionally visited swarms), females often darted at each other. However, when males were present in swarms, physical interactions were never observed between females. Instead, females were sometimes observed to pounce on males from below, while the male was performing ascending flights with another female.

Males were never observed to swarm.

3.2. Mating behaviour

Usually a single male, with a nuptial gift, approached the female swarm and started circling around within. The behaviour leading to mating most often started with one male flying in below one of the females at a distance of 0.1–0.2 m. They then as-

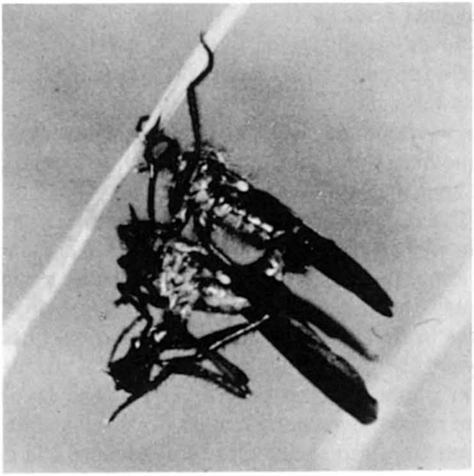

Fig. 4. Mating in *Empis borealis*. The male supports the couple with his front legs on a grass straw. The female is held by the male's second and third pair of legs, and by genitalia contact. The female feeds on a nuptial prey, holding it with all her legs. Note that male hind legs also secure the nuptial gift.

cended, closer together, up to 1–2 m above the swarm, and after very rapid coupling lost height for a moment. The male was then above the female and held her with his legs. Prey was handed over to the female and the pair flew down to the vegetation where mating was completed. This general precopulatory sequence, from the time the male entered the swarm to coupling together, took about 5 sec. We did not observe when genitalic contact was established, which is related to male presentation of the prey to the female. However, pairs which were netted at ground level, were found to be copulating, immediately after coupling.

Mating was completed while the pair were hanging on a grass-straw or twig (Fig. 4). The male supported himself and the female using only his front legs. His second legs held the female thorax and the third pair her abdomen, supporting the nuptial gift beneath her proboscis. The female used all her legs to handle the prey. Mating lasted from 6 to 40 min (mean = 20.5, *SD* = 9.3, *n* = 32) (Frisk & Svensson, unpubl.).

From time to time the pair flew away, to distances from a few up to 50 metres. Such postnuptial flights were usually performed about 3–4 times by each copulating pair and were more frequent when it was windy. Conspecifics did not disturb copulating pairs, and pairs that parted because they were disturbed did not attempt to re-engage.

If the ascending flight did not lead to coupling, the male returned to the swarm and repeated the ascending flight with another female. Even if only one female were present, the male could fly up with the female up to four times before mating. Often male visits did not end with coupling and mating; males were observed leaving the swarms after inspecting many or all of the females, after which they approached another swarm. These males were carrying prey and behaved similarly to males who obtained mates. In large swarms (30–40 females) a male could inspect many females in a minute. Males and females sometimes ascended and coupled, but uncoupled at once. Both individuals then returned to the swarm—the female to swarm and the male, still with the prey, to inspect females. In a few cases coupling took place at once within the swarm without ascending flight. Such behaviour was only observed in the first days of the flight-period.

Usually single males visited female swarms one at a time, although occasionally two or more males were present simultaneously. Thus, the sex ratio in swarms was in general highly female biased, rarely a one to one ratio and never male biased. If two males visited a swarm, both could ascend with only one female. The lower male was observed trying to couple with the male above him. They at once uncoupled and then proceeded to inspect other females in the swarm. No aggression was observed between males in swarms.

Under favourable conditions the number of males visiting swarms on average was 25 per hour, with a maximum of 46 per hour (mean value for about nine hours of observations). Towards the end of the flight-period, however, males rarely visited swarms. During 4 h of observations, at that time, only nine males visited swarms.

3.3. Sexual dimorphism

Wing-length on average was about one millimetre shorter in males than in females. Whilst male wing-length was constant over the years, female wing-length showed small variations (Table 1). The size of males and females (wing-length) collected early (first half of the flight period) did not differ from those captured late (second half of the flight period).

Wet-weight did not differ between the sexes, but both sexes were significantly heavier in 1985 than in 1984 (Table 2). Males and females collected early and late in the flight-period 1984 did not differ in weight. Slopes of regressions between wet-weight

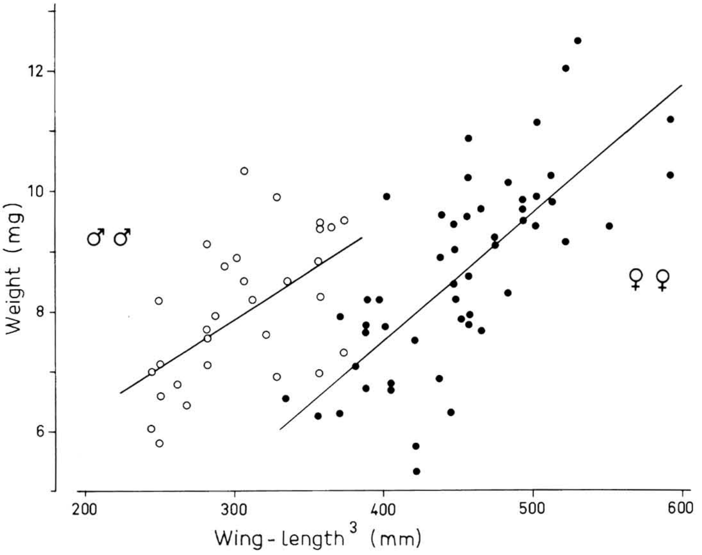

Fig. 5. The relation between body weight and wing-length³ in male and female *Empis borealis* in 1984. (females: $Y = 0.021\ X^3 - 1.016$, $r^2 = 0.57$, $P < 0.0001$, $n = 51$; males: $Y = 0.016\ X^3 + 3.195$, $r^2 = 0.32$, $P < 0.0011$, $n = 29$).

Table 1. Male and female *Empis borealis* wing-lengths in 1982–1985. Sample sizes in parentheses. Means indicated (mean ± *SD*) by the same letters were not statistically different at the 5% level (Duncans multiple range test).

Year	Males	Females
1982	6.55±0.24 (41) a	7.69±0.32 (112) b
1983	6.54±0.25 (56) a	7.44±0.34 (116) c
1984	6.62±0.45 (97) a	7.62±0.33 (122) b
1985	6.54±0.19 (25) a	7.51±0.27 (79) c

Table 2. Male and female *Empis borealis* weights in (mean ± *SD*) 1984 and 1985. Sample size in parentheses.

	Males	Females	*t*
1984	8.01±1.21 (30)	8.67±1.59 (52)	1.98 N.S.
1985	9.40±0.87 (20)	9.38±1.35 (68)	0.06 N.S.
	t=4.48, P<0.001	t=2.62, P<0.02	

and wing-length³ are similar between years and sexes, and are shown for the 1984 material in Fig. 5.

Sexes differed markedly in terms of wing shape and area, female wings being longer and much broader than male wings, and the average wing-area was about 60% larger in females than in males. The correlation between wing-area and wing-length was highly significant in both sexes (female wing-area = $1.22 \times (\text{wing-length})^2 - 8.68$, $n = 21$, $r^2 = 0.98$, $P < 0.001$; male wing-area = $0.79 \times (\text{wing-length})^2 + 2.08$, $n = 13$, $r^2 = 0.95$, $P < 0.001$).

Accordingly, there was a clear difference between male and female wing-load. Male wing-load on average was 67% greater than female wing-load. In males wing-load was independent of size but larger females, having a greater wing-load, were relatively heavier than smaller ones (Fig. 6).

The femur I length was measured in all wing-length classes of males and females which showed that femur I in males was about 20% longer and also much hairier than in female femur I. Accordingly, the relationship between size (wing-length) and femur I length showed a strong correlation in both sexes (males: $r = 0.96$, $n = 18$, $P < 0.001$; females: $r = 0.94$, $n = 18$, $P < 0.001$).

3.4. Flight period

There was a difference between years regarding the start of the flight period. In 1982 it started on 12 May, in 1983 2 May, in 1984 28 April, in 1985 2 May and in 1986 30 April. Both males and females appeared on the first day of the flight period in all years. The flight period lasted for four to five weeks. Its end varied among the years, with males rarely being found late in the flight-period, while the females were still common. At the end only females were present.

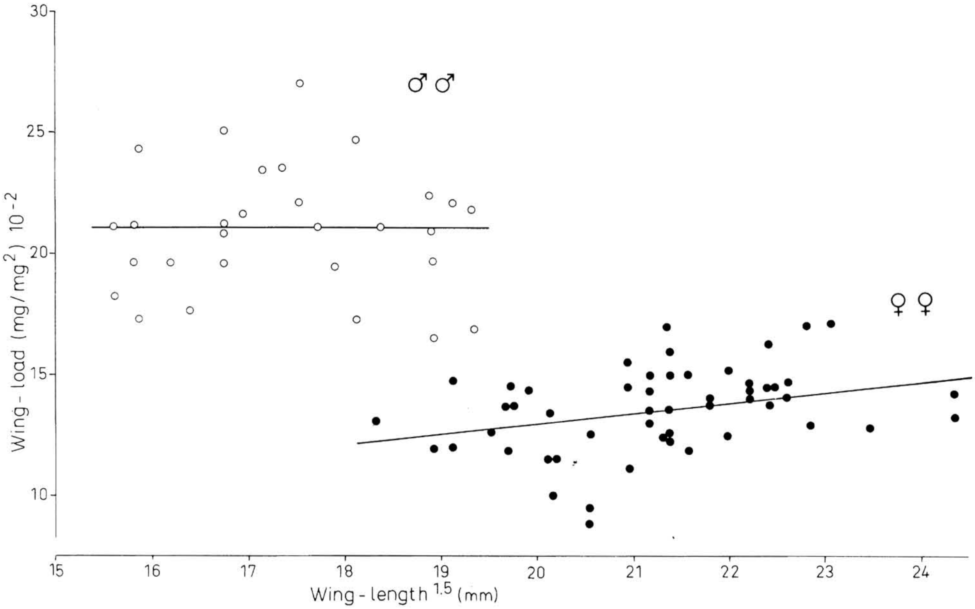

Fig. 6. Wing-load in male and female *Empis borealis* in relation to wing-length$^{3/2}$. (Males: $Y = 0.013\ X^{3/2} \times 10^{-3} + 0.211$, $r^2 = 0$, N.S., $n = 29$; females: $Y = 4.658\ X^{2/3} \times 10^{-3} + 0.0360$, $r^2 = 0.123$, $P < 0.011$, $n = 51$).

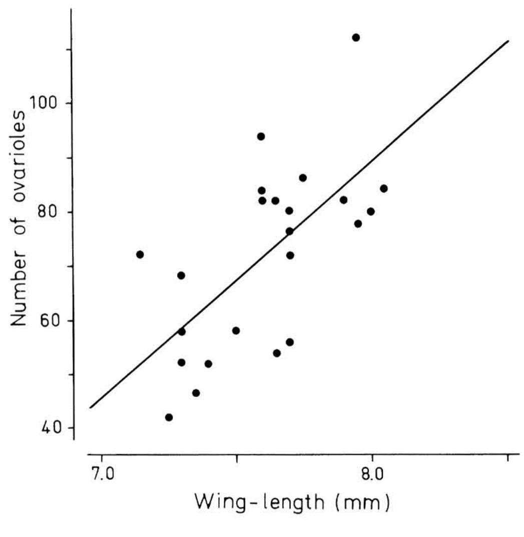

Fig. 7. Number of ovarioles in *Empis borealis* females of different size (wing-length).

3.5. Fecundity, egg development and oviposition

The number of developing eggs observed in each ovariole was four to five and the number of ovarioles ranged from 42 to 112. Fecundity correlated positively with both wet-weight ($r = 0.54$; $P < 0.01$) and wing-length ($r = 0.65$; $P < 0.01$; $n = 23$) (Fig. 7).

None of the 250 females dissected was found to have fully developed eggs in its ovarioles. These females were collected while they were swarming or resting at swarm sites. The largest developing egg in the ovarioles usually was about the size of the spermatheca, about 0.3 to 0.4 mm in diameter, presumably less than 1/4 of a mature egg. Oviposition was not observed.

3.6. Polyandry and female population mating frequency

54 pairs were collected at the very moment a male grasped a female in the air for mating. 48 of these females were found to have sperm in the spermatheca, showing that they had mated earlier.

The number of mated females in the population were found to increase rapidly (more than 80%) during the first six days of the flight period (Fig. 8). From day 11 to 17 there was a slight further increase, and on day 20 or after all females collected were mated. The female mating frequency pattern was similar between years.

3.7. The feeding behaviour of males and females

Both females and males were found to visit flower heads of *Salix* spp. (both male and female plants).

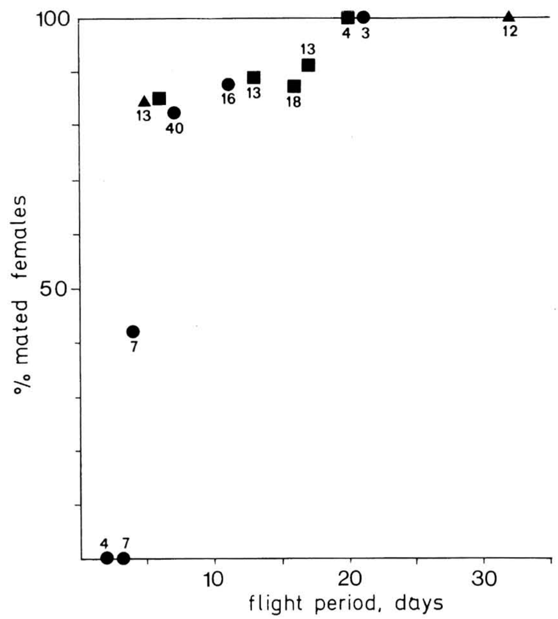

Fig. 8. Frequency of mated *Empis borealis* females in the population at different times during the flight period in 1984–1986. Symbols represent; squares: 1984 (*n*=66), circles: 185 (*n*=77) and triangles: 1986 (*n*=25). Sample size on each occasion is also shown.

Willows were in some areas scattered, so that nectar and/or pollen (both sexes of *Salix* spp. produce nectar) could not be utilized as food without long flights. However, dissected females showed no trace of pollen in their guts although pollen was often found on the body surface. Other available flowering plants (*Caltha palustris, Tussilago farfara, Hepatica nobilis* and *Anemone nemorosa*) were not utilized.

Ten water-traps (yellow, blue or red) were put out for the whole flight period, in both study areas, in 1984. No *E. borealis* specimen was caught although females were found swarming in the vicinity of the traps.

Males were sometimes found perching on twigs, apparently waiting for prey. They were also found consuming prey. Females were only seen consuming prey during mating. Males preyed mainly upon soft-bodied insects from several orders (Table 3). Gall midges were the smallest prey and conspecifics and stone-flies the largest. In some species of flies (Simuliidae, Empididae and Phoridae), male individuals were mainly taken (Table 3).

Males were observed to prey on conspecifics and in 10 cases the predator and its prey (five males and five females) were collected. The relative sizes of predator and prey were calculated (weight/wing-length relationship, Fig. 6), which showed that the predator in all cases was bigger than, or of the same size (one case) as, its conspecific prey. In 1982 and 1986 no intraspecific predation was observed. Cannibalism was observed throughout the flight-period with no apparent temporal peak and the size of the predators (wing-length) was represented by all size classes within the male population. From the 213 prey items collected from mating pairs in 1984 five were conspecifics.

Prey volume (length × height × breadth) in 1984 varied between 0.01 and 10 mm^3 (n = 181), and weight in 1984 and 1985 between 0.06 and 2.87 mg (n = 49). The weight of *Triphleba opaca* males presented females at mating showed a larger variation than volume (Weight: CV = 62.4; Volume: CV = 37.5). Weight of a conspecific prey was only 1.2 mg. Larger prey was taken as the flight-period advanced ($r = 0.21$, $n = 148$, $P < 0.009$).

4. Discussion

4.1. Female swarming in *E. borealis*

The swarming and mating behaviour of *E. borealis* has been described by Howlett (1907), Gruhl (1924) and Tuomikoski (1939), and our observations agree in most respects with theirs. However, Tuomikoski (1939) reported that males sometimes swarm, whereas we only occasionally saw males alone at female swarm sites; in fact, these males were not swarming but searching for females. The number of females at swarm sites was almost always much greater than that of males. Regular female swarming behaviour has also been reported for a few other *Empis* (*E. nitida* Meigen, *E. livida* L., *E. pennipes* L.) (Hamm 1908, Gruhl 1924, Tuomikoski 1939), *Rhamphomyia* (*R. geniculata* Meigen, *R. anfractuosa* Bezzi, *R. vesiculosa* Fallén, *R. spinipes* Fallén) (Gruhl 1963) and *Hilara* species (*H. nigrina* Fallén, *H. morata* Collin, and *H. clavipes* Harris) (Chvála 1976). Although the mating system is known for only a few species of these genera, female swarming and sex-role reversal in courtship are probably not uncommon in these genera.

In *E. borealis*, the weight of the sexes was similar but wing-area was highly dimorphic — the female wing-area being much larger. In empidid flies such a great sexual difference is very rare. In northern Europe, the species *Rhamphomyia marginata* F. is

Table 3. Male nuptial gifts offered *Empis borealis* females 1982–1986. The number of individuals is given for each taxa and the percentages (italics) for the main taxonomical groups. In some prey species the sex ratio (males/females) is shown.

	1982	1983	1984	1985	Total
PLECOPTERA	*21*	*0*	*4*	*5*	*5.3*
Nemoura cinerea Retz.	8	–	8	1	17
HOMOPTERA	*5*	*23*	*10*	*5*	*11.2*
Cicadellidae, *Balclutha punctata* Fabr.	–	1	–	–	1
Cicadellidae, *Colladonus torneellus* Zett.	–	–	1	–	1
Cicadellidae, *Macropsinae* sp. (nymph)	–	–	1	–	1
Psyllidae, *Psylla ?klapaleki* Sulc	1	10	18	1	30
Triozidae, *Trioza* sp.	–	–	2	–	2
Liviidae, *Livia juncorum* Latr.	1	–	–	–	1
HYMENOPTERA SYMPHYTA	*8*	*4*	*3*	*5*	*4.0*
Xyelidae, *Xyela julii* Breb.	3	2	7	–	12
Xyelidae, *Xyela longula* Dalm.	–	–	–	1	1
HYMENOPTERA PARASITICA	0	0	0	0	
Braconidae, *Lysaphidius* sp.	–	–	–	–	1
NEUROPTERA	*3*	*2*	*1*	*0*	*1.6*
Hemerobiidae, *Hemerobius stigma* Steph.	1	–	2	–	3
Crysopidae, *Crysopa carnea* Steph.	–	1	1	–	2
LEPIDOPTERA	*8*	*10*	*15*	*9*	*12.8*
Incurvariidae, *Adela cuprella* Den & Schiff	–	–	1	–	1
Eriocraniidae, *Eriocrania haworthi* Brad.	3	4	22	2	31
Eriocraniidae, *Eriocrania ?semipurpurella* Steph.	–	–	7	–	7
Tortricidae, ?*Lyda strobiella* L.	–	–	1	–	1
Yponomeutidae, *Plutella xylostella* L.	–	1	–	–	1
COLEOPTERA	*0*	*0*	*0.5*	–	*0.3*
Curculionidae, *Brachonyx pineti* Payk.	–	–	1	–	1
DIPTERA, NEMATOCERA	*29*	*14*	*21.5*	*24*	*21.5*
Nematocera spp.	4	1	15	4	24
Chironomidae spp.	–	–	2	–	2
Simuliidae spp.	3	–	12/0	–	15
Cecidomyiidae spp.	2	5	17	1	25
Sciaridae spp.	2	1	–	–	3
DIPTERA BRACHYCERA/CYCLORRHAPHA	*26*	*47*	*44*	*52*	*42.7*
Empididae, *Empis borealis* L.	–	2/3	3/2	–	10
Empididae, *Rhamphomyia caudata* Zett.	–	–	4/0	–	4
Empididae, *Rhamphomyia nitidula* Zett.	1	1	10/4	–	16
Empididae, *Iteaphila macquarti* Zett.	–	–	1/1	–	2
Empididae, spp.	–	–	4/1	–	5
Phoridae, *Triphleba opaca* Meig.	–	8	28/4	6/2	48
Phoridae, *Phora dubia* Zett.	–	–	5/3	2/0	10
Phoridae, *Megaselia* sp.	–	1	–	–	1
Chamaemyiidae, *Leucopsis* sp.	–	–	1	–	1
Sciomyzidae, *Hydromya dorsalis* Fabr.	–	–	1	–	1
Lonchaeidae, *Earomyia lonchaeoides* Zett.	–	3	–	–	3
Lonchaeidae, *Earomyia nigra* Meig.	–	–	1	–	1
Sphaeroceridae, *Copromyza freyi* Hackman	–	–	1	–	1
Chloropidae, *Elachiptera cornuta* Fall.	–	–	1	–	1
Tachinidae, *Lypha dubia* Fall.	1	–	–	–	1
Scatophagidae, *Gonatherus planiceps* Fall.	8	–	1	–	9
Anthomyiidae, *Egle* spp.	–	4	8/5	1/0	18

	1982	1983	1984	1985	Total
Anthomyiidae, *Phorbia ?curvicauda* Zett.	–	1	–	–	1
Fannidae, *Fannia limbata* Tiens.	–	–	1	–	1
Muscidae, *Lispocephala alma* Meig.	–	–	1	–	1
ARANAE	*0*	*0*	*0.5*	–	*0.3*
Aranae sp.	–	–	1	–	1
SEED FRAGMENT	*0*	*0*	*0.5*	–	*0.3*
	–	–	1	–	1
TOTAL	38	49	213	21	321

known to exhibit such a great dimorphism. Females of this species also swarm (Svensson, unpubl.). Thus, it seems very likely that enlarged female wing-area and female swarming behaviour are correlated (Gruhl 1963). The narrow wing in the predatory *E. borealis* males may be adapted for rapid flight and greater manoeuvrability. The enlarged wing in the non-predatory females presumably allows them to fly slowly, exhibit themselves, and possibly to swarm for longer periods of time, thus enhancing their chance to obtain a mate and his gift.

Table 4. Comparison of prey groups used as nuptial gifts by *Empis borealis* from four studies.

	This study (*n* = 321)	Howlett (1907) (*n* = 25)	Gruhl (1924) (*n* = 9)	Tuomikoski (1939) (*n* = 61)
Plecoptera	5	64	33	68
Ephemeroptera	–	20	–	–
Homoptera	11	–	–	2
Hymenoptera	4	–	–	–
Neuroptera	2	–	–	–
Lepidoptera	13	–	22	2
Tricoptera	–	–	12	–
Coleoptera	x	–	–	–
Diptera	64	16	33	26
Aranae	x	–	–	–
Seed fragment	x	–	–	–
Without prey	x	–	–	–

4.2. Do *E. borealis* males limit female reproductive success?

Our results show that the prey choice in *E. borealis* males varied between years and also during the season (Table 3). Other studies (Table 4) have also shown a very broad spectrum of choice of prey. All data on *E. borealis* support the idea that the species is a generalized predator. Males have a longer femur I than females, which is likely to be an adaptation to their predatory habits (Nentwig & Wissel 1986).

E. borealis males were found to prey on males of swarming insect species, "swarm-feeding", as do other empidids (Downes 1970). However, in *E. borealis* both sexes of conspecifics were equally often taken, although conspecific females should be more easily located. Probably males, in some way, are inhibited to prey on conspecific females at swarming-sites. Gruhl (1924) and Tuomikoski (1939) also observed cannibalism in *E. borealis*.

The fact, that, sometimes, no prey was found with newly coupled pairs is no proof that males may cheat females because small prey may have been lost. A seed offered as a nuptial gift was also observed. However, wind-borne seeds have mistakenly been taken as "prey" (Hobby 1932, Hobby & Smith 1962), and probably "seed-predation" is unintended (males hunt only for flying prey; Tuomikoski 1939). If cheating exists it is an exceptional behaviour.

E. borealis males and females only visit *Salix* flowers (Tuomikoski 1952). Since no pollen was found in the guts of dissected flies, probably nothing but nectar was consumed. Furthermore, no flies were caught in the water-traps which usually attract flower-visiting insects. *E. borealis* is probably not primarily adapted for foraging on plants. Thus, males use both prey and nectar, while virgin females only take nectar. Females obtaining mates will, in addition, ingest nuptial gifts presented by males, which enhance egg production (Gwynne 1984a). Males therefore may limit female reproductive success.

Towards the end of the flight period males were scarce, while females still swarmed frequently. The decline in male numbers may be a result of higher mortality in the males than in the females, or of males being initially scarce and subsequent mortality being equal in both sexes. However, as in most insect species, males and females in *E. borealis* presumably emerge in equal proportions (Wigglesworth 1972). We suppose that *E. borealis* males are exposed to a greater mortality risk while hunting dangerous prey (12 %, mainly empidid flies, Table 3) and traveling between hunting and swarming sites, while females generally are more stationary and were not observed to be predated when swarming. We, therefore, suggest that males suffer a higher mortality than do females. The sex ratio will then turn female biased and males will constitute a scarce resource.

No sperm was transferred to the female in the short interval between a male grasping a female in the air and their being caught (Petersson & Svensson, unpubl.). Hence, the frequent presence of sperm in the spermatheca of females collected in that way indicates that multiple mating is prevalent in females. Another indication of this is the rapid increase in the proportion of mated females in the swarming period. This increase was not met by a corresponding decrease in mating frequency. At the end of the flight-period all females were mated. Multiple mating by females provides them with an additional nuptial gift, as well as more sperm, which should promote egg production and also supply energy for swarming further after mating. We hypothesize that *E. borealis* females mate with several males, until they have received sufficient nutrients for maturing their eggs. The load of developing eggs might then inhibit successful swarming and, as a result, females leave swarms to mature their eggs and oviposit. Later they may rejoin swarms and participate in more matings.

4.3. Why do *E. borealis* males offer females a nuptial gift?

Several explanations for nuptial prey feeding in insects have been suggested (Thornhill & Alcock 1983). Courtship feeding in Diptera has been reported from several families, with both predatory and non-predatory species (Berg & Valley 1985, Steele 1986a, b). Hence, male courtship feeding in Diptera is not generally associated with predatory habits. In *E. borealis*, females were not predatory at all, and therefore nuptial gift offering by males can not be regarded as a way of safeguarding against sexual cannibalism (Buskirk et al. 1984).

Offering, especially large prey, may ensure complete sperm transfer. Thornhill (1980) showed for the mecopteran, *Hylobittacus apicalis* (Bittacidae), that the duration of mating was positively correlated with prey size and also with the number of sperms transferred. In *E. borealis* mating time increased with size of prey (Svensson et al., unpubl.) and there was, thus, more time to transfer sperm.

Nuptial feeding has been discussed in terms of mating and parental efforts, respectively (Low 1978). No general explanation is available to distinguish between these two reproductive effort components (Alexander & Borgia 1979, Gwynne 1984b, 1986a, b, Wickler 1985, 1986, Sakaluk 1986). A proximate reason for courtship feeding in *E. borealis* may be mating effort, but as an ultimate explanation, parental effort may be more important. In ordinary mating systems, where males have no resources except gametes to invest or monopolize, females are thought to be a resource limiting male fitness. If males monopolize resources critically needed for production of female gametes, those resources should limit female reproductive success and be worth competing for. Males should, in such cases, be the choosing sex. In *E. borealis*, males seem to invest more in reproduction than females, and accordingly, males should choose among females and females should compete for males.

Acknowledgements. We thank Mr. B. Karlsson and Mr. M. Frisk for skillful field assistance; Dr. S. Jonsson, Dr. L. Hedström and Mr. N. Ryrholm for identification of often badly damaged prey; Dr. B. W. Svensson, Prof. S. Ulfstrand and the two reviewers for constructive and valuable comments on the manuscript. Financial support was given by the Swedish Natural Science Research Council.

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Received 19.II.1987
Printed 23.XII.1987