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FEMALE ARRIVAL AT THE OVIPOSITION SITE IN *PLATYCYPHA CALIGATA* (SELYS) : TEMPORAL PATTERNS AND RELATION TO MALE ACTIVITY (ZYGOPTERA : CHLOROCYPHIDAE)

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Females of the African *P. caligata* oviposit in streams on barkless driftwood and roots. The number of females landing on the oviposition sites correlates with the number of males and the number of ovipositing females. At noon with a high density of ovipositing females, 89% of the newly arriving females were nonmates. There were two arrival patterns of non-receptive females which decreased male interference. At sites with a high male density the temporal pattern of female arrivals was clumped. 66.1% of the approaching females landed within 30 s of other females. At small oviposition sites with two males present approaching females preferred situations where intensive territorial contests between the males occurred.

INTRODUCTION

In odonates the temporal availability of receptive females is an important factor determining the structure of mating systems (WAAGE, 1984 ; KAISER, 1985 ; POETHKE & KAISER, 1987 ; ALCOCK, 1987). Nonreceptive females should try to evade further copulations by decreasing their receptiveness to other males. Newly arriving females often prefer oviposition sites with other ovipositing females already present (WAAGE, 1987). In this way females of *Platycypha caligata* aggregate in large numbers on the oviposition substrate, thereby decreasing the probability of interference by males (MARTENS & REHFELDT, 1988). In these situations males guard mates and nonmates simultaneously (cf. WAAGE, 1979).

Here, I report on the influence of the timing of females arrivals on the interference of landing females by males in *P. caligata*. The reproductive behaviour of this stream dwelling damselfly has been described by CONSIGLIO (1974), ROBERTSON (1982) and MARTENS & REHFELDT (1988).

MATERIAL AND METHODS

The study was carried out on the Umzimkulwana River in Oribi Gorge (Natal, RSA; 30°42' S, 30°16' E) between 10 February and 9 March, 1987. The structure of the river bed is marked by large rocks causing various currents. Submerged vegetation is completely missing (see MARTENS & REHFELDT, 1988).

Observations were made between 10 a.m. and 4 p.m., Civil time, mainly at one site with two large pieces of driftwood (> 2.5 m) lying on the surface of the water longitudinally to the current, and at 6 small oviposition sites (driftwood length < 0.5 m). During the study the small sites were occupied at any one time by one to two males and two to five females and the large oviposition substrate by one to seven males and two to twenty-four females.

The data were collected at 30 s-intervals (N = 1060). The number of resident females as well as the number of perching and interacting males present were determined at the beginning of each interval. During the interval the number of landing females, of courting males, of females decamping the oviposition substrate after male interference and the number of copulations were noted. Data in the text are presented as mean ± standard error.

RESULTS

TEMPORAL PATTERN OF FEMALE ARRIVALS

Females in *Platycypha caligata* perch on stalks of the emergent vegetation or on rocks before they land on the oviposition site. Figure 1 shows the mean number of landing females per interval over the day at the large oviposition site. Product--moment correlations show a strong correlation between the number of males ($r = 0.27$, $p < 0.001$, $n = 1060$) and the number of ovipositing females ($r = 0.18$, $p < 0.001$, $n = 1060$). I observed copulations in 32 of 454 (7.1%) landing females. Between 10 00 and 11 00 h, and 15 00 and 16 00 h, civil time, the number of copulations was highest, involving up to 45% of the landing females. At noon most of the females (89%) were nonmates and they aggregated in large numbers on the oviposition substrate.

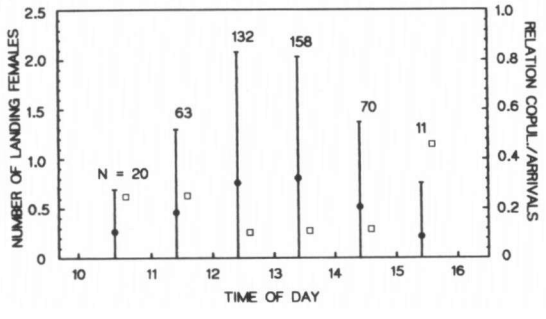

Fig. 1. Daily arrival pattern of females in *Platycypha caligata*. Black spots = number of landing females per 30 s (means ± SD.), open squares = ratio copulations/total number of landing females.

The temporal pattern of female arrivals changed within short periods. In 65.1% of all registration intervals no female landed. However, especially at noon with a high population density often several females started oviposition synchronously within one interval. Only 33.9% of all approaching females landed alone within 30 s : 24.2% landed together with one other female, and 41.9% with up to 7 other individuals.

Males usually courted approaching females unhesitatingly. Often they tried to approach very closely, attempting to land on the thorax of the female. With a larger number of synchronously landing females, courtship activity and the number of disturbed females increased, but this was much lower than expected in relation to singly landing females (Fig. 2). The number of copulations did not change.

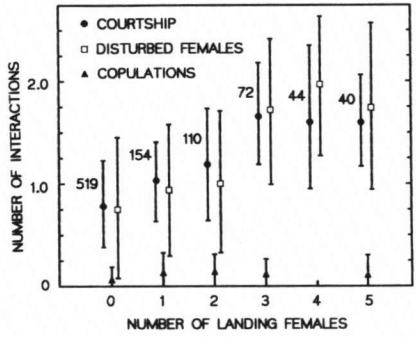

Fig. 2. Male-female interactions in relation to the number of landing females per 30 s in *Platycypha caligata*. Means ± SD.

MALE TERRITORIAL CONTEST AND FEMALE ARRIVALS

In small oviposition sites with one ovipositing female and one resident male present, 57.7% (n = 26) of the second-arriving females were forced to fly off. In contrast, in situations with two males present, no second-arriving female (n = 9) was interfered with by males in the same registration interval and such females started to oviposit. When resident males were present, territorial contests were significantly higher when females were landing (1.67 ± 0.33 vs 0.72 ± 0.16 interacting males in intervals without landing females, Mann-Whitney $U = 57$, $p < 0.05$, $n_1 = 36$, $n_2 = 6$). At the large oviposition site with higher male densities I could not find such differences. Here, in most registration intervals one or more males showed only little territorial interaction with the resident males and they perched near the oviposition site. They often immediately approached landing females and tried to court them.

DISCUSSION

Oviposition substrates in *Platycypha caligata* are strongly limited. During the investigation period nearly all potential oviposition sites were occupied by males.

Newly arriving females were attracted by ovipositing females, but the mating rate for males present did not increase. This observation corresponds with the results of WAAGE (1979) in *Calopteryx maculata* (Palisot de Beauvois). In this species three factors appear to reduce the mating frequencies of the male : (1) a lack of individual recognition, (2) the risk of losing a previous mate while copulating with an arriving female, and (3) a probable physiological limit to mating frequency. However, in my study, especially in situations with high male densities, these factors alone cannot explain the low frequencies of interference and mating in landing females.

The observations in *P. caligata* show that not only do males respond adaptively to female oviposition behaviour (WAAGE, 1984 ; ALCOCK, 1987), but also that females respond to the males' territorial behaviour. Females perch for long periods near the oviposition site before they start to oviposit. In *P. caligata* they may take advantage of favourable opportunities for landings.

In situations with one resident male nearly every newly arriving female is courted and interfered with. However, when two males are present, nonmates seem to prefer to land when territorial contests by the resident males occur. At oviposition sites with two resident males territorial disputes often escalated. These interactions lasted up to several hours and the males chased each other within a range of 5-10 m around the oviposition site (see ROBERTSON, 1982 ; WAAGE, 1988). Nonmates may then land unmolested on the oviposition substrate.

Synchronous females arrivals may have evolved to evade male interference if the male density in certain parts of the oviposition site is decreased for short periods by male-male or male-female interactions. This arrival pattern of females at the oviposition site has been described in other dragonfly species in high density situations as well (SIVA-JOTHY, 1984 ; HARVEY & HUBBARD, 1987).

In *P. caligata* with high male densities one or several males were usually not involved in territorial contests. These intruders perched near the oviposition site and they approached landing females. They tried to court them, mainly during territorial contests of the residents (see WAAGE, 1988 ; FORSYTH & MONTGOMERIE, 1987). At such times, the synchronous landings of several females on the oviposition site decreased the probability of interference by males. While the first female to land may be courted by males, the second and following females remained unmolested. In *P. caligata* the long duration of the courtship of often more than one minute (ROBERTSON, 1982) and the subsequent copulation near the oviposition site may promote the clumped temporal patterns of newly arriving, non-receptive females.

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