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THE UPRIGHT MALE POSITION DURING OVIPOSITION AS AN ANTI-PREDATOR RESPONSE IN *COENAGRION PUELLA* (L.) (ZYGOPTERA: COENAGRIONIDAE)

G.E. REHFELDT

Zoologisches Institut der Technischen Universität, Pockelsstrasse 10a, D-3300 Braunschweig, Federal Republic of Germany

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In *C. puella* tandem pairs oviposit with the male positioned rigidly upright on the prothorax of the female. At the oviposition site during windy weather males may spontaneously settle in a horizontal position in front of the female. In this situation predation risk from approaching predators (green frogs) was greatly increased. Disturbance experiments with groups of pairs with both types of male positions show that tandems with male upright make a speedier escape than pairs with males horizontal. In pairs of the latter kind males have to take up an inclined or upright position before take off, so that the pair remains longer within range of an approaching predator.

INTRODUCTION

Most Zygoptera, and also many Anisoptera oviposit in tandem (WESENBERG-LUND, 1913; SCHMIDT, 1975; CORBET, 1962; WAAGE, 1984). The male grasps the female prothorax with his appendices. During oviposition into floating water plants the male may perch horizontally in front of the female or, as in most species of the family Coenagrionidae, may take up a rigidly upright position with straight abdomen, supported only by the prothorax of the female; the legs of the male are then pressed firmly against his thorax and his wings are held more or less tightly together. This position is the "Agrion"-type described by WESENBERG-LUND (1913) and BUCHHOLZ (1950).

Many studies have demonstrated the significance of guarding by the male in tandem so as to protect the female against interference from rival males UÉDA, 1979; CORBET, 1980; SHERMAN, 1983; WAAGE, 1984; CONVEY, 1989). It is the most secure type of guarding. For *Argia moesta* RÜPPELL et al. (1987)

suggested that groups of tandems with upright perching males ovipositing close together may prevent the females from being attacked by solitary males. However, most zygopteran species show a scattered distribution during oviposition and in these the significance of the upright carriage of the male has not been studied.

Adult dragonflies are prone to attack from various predators at the oviposition site and have evolved fast visual responses to escape (JACOBS, 1955; CORBET, 1962; WAAGE, 1984). Zygopteran tandems which oviposit at small, shallow waters are often exposed to a high pressure from predators hunting on the water surface such as spiders or frogs (BICK & BICK, 1965; REHFELDT, 1990). In this situation the upright position of males during tandem oviposition may reduce the predation risk by allowing a speedy escape steeply upwards.

The damselfly *Coenagrion puella* oviposits into floating stalks and leaves of various water plants of the bank vegetation of standing waters (WESENBERG-LUND, 1913; ROBERT, 1959; BANKS & THOMPSON, 1985, 1987; THOMPSON & BANKS, 1989). The male is usually upright above the female, but he may also grasp vertical or sloping stems of water plants with his legs and then show an inclined position.

At sites with floating water plants during windy weather or during breaks in oviposition (ROBERT, 1959) the male may also settle horizontally on the oviposition site. I used this situation to test the hypothesis that the position of the guarding male during oviposition influences predation risk. The success of green frogs preying on pairs ovipositing with the male upright (UMP) was compared with that on pairs ovipositing with the male horizontal (HMP). The escape behaviour of both types of pairs after sudden disturbance was tested during field experiments.

STUDY AREA AND METHOD

Observations and experiments were performed in May/June 1989 at small, shallow ponds near Brunswick (Lower Saxony, 52°21′ N, 10°35′ E). The banks were covered with reeds, mainly *Typha* and *Juncus*, the water surface (> 80%) with floating *Lemna minor* and *Potamogeton natans*. The flight period of *Coenagrion puella* ranged from the end of May to mid July. The observations were made on 16 days during sunny weather and temperatures of 21-27° C. Wind speed varied from zero to gusty from west/southwest with a force of four to five (Beaufort scale).

At two ponds three areas of study were marked out with floating wooden frames each enclosing an area of 2.56 m² (1.6x1.6 m). After landing within these areas pairs changed their oviposition locations (floating water plants) frequently. The duration of stay of tandems within a frame and at the various oviposition sites, and the males' position (UMP or HMP) were noted. In the analysis I included only oviposition periods longer than 10 s, which indicated successful egg laying.

At the study sites one to five frogs (*Rana esculenta*-complex) approached ovipositing tandems by stalking or leaping. The number of successful and unsuccessful attacks on, and kills of, solitary pairs with UMP or HMP, and in groups of tandems showing both types of male position, was noted. From video recordings I determined the distance between frog and the sighted tandem when it escaped.

To determine the responsiveness of tandems with one or the other type of male position to sudden disturbance I conducted field experiments by disturbing mixed groups of ovipositing pairs to induce the escape response. Before disturbing a group of tandems they were fanned with a ventilator from a distance of about 1 m until in at least one pair the male settled on the floating water plants. After 10 s the tandems were disturbed with a dummy frog approaching evenly and quickly on the water surface. From video recordings I determined with single-frame analysis the time difference between takeoff of the first and the last pair of a group.

Data are expressed as means ± 1 SE unless otherwise stated. Any non-significant results ($P > 0.05$) are denoted as NS in the text and tables.

RESULTS

OVIPOSITIONS WITH HMP

The number of ovipositing tandems in a frame varied from one to 25. During good weather *Coenagrion puella* tandems performed ovipositions almost exclusively with rigidly upright males (165/2). Pairs moved from one oviposition site to another after 60.8 ± 8.2 s (N=60) continuing oviposition into another water plant. During windy weather conditions the number of tandems with HMP increased. On 24.5.1989 during strong gusts, in 18 out of 67 pairs (26.9%) the males settled periodically on the oviposition site. During a gust most males started to sway, moving to an inclined position with wings whirring before settling on the floating water plants at the oviposition site. However, sudden strong gusts sometimes simply overturned the male to a horizontal position. Before taking off and changing to a new oviposition site in tandems with HMP, the male took up an upright position. The female lifted her bent abdomen out of the water and then the pair flew off in a more or less inclined flight path, usually landing and continuing oviposition with the male upright (22/23).

As strong gusts occur randomly, a guarding male may settle horizontally at various times during ovipositing. The duration of oviposition with HMP was extremely variable (16 - 460 s) and lasted 10.9 - 96.8% of the duration of stay at one oviposition location. The duration of ovipositing at a certain site for pairs with HMP lasted longer (145 ± 29.6 s) than for pairs with UMP ($t = 2.75$, $dF = 22$, $P < 0.02$).

RISK OF PREDATION

Under windy weather conditions the risk of predation to solitary pairs with HMP was significantly higher than for tandems with UMP (0.44 vs 0.13, $\chi^2=4.63$, $P<0.05$, Fig. 1). In mixed groups with UMP and HMP pairs, in HMP pairs disturbed by an approaching frog 2 out of 17 flew off last. Their risk of being caught was higher than for UMP pairs in groups (0.25 vs 0, Fig. 1) and was similar to the risk of solitary tandems with UMP (0.14). However, there was no difference in the distance between the frog and the sighted tandem at the onset of the

escape response between pairs with UMP (18.5 ± 1.89 cm, N = 23) and pairs with HMP (14.7 ± 1.58 cm, N = 15, U = 131.5, NS).

DISTURBANCE EXPERIMENTS

The responsiveness of pairs with variable male positions was tested in disturbance experiments during windless weather. After disturbance of groups of 2 pairs with both types of male position, the HMP pair was significantly slower in escaping than the UMP pair (Tab. I). In HMP pairs taking off was delayed by 0.51 ± 0.08 s compared to UMP pairs. In all tests the male first took up an inclined or upright position before taking off steeply upwards. Also in mixed groups with other proportions of guarding male positions (up to five UMP tandems) the HMP tandem took off significantly later.

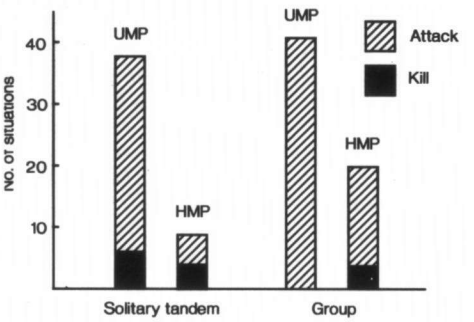

Fig. 1. Disturbance by green frogs of *Coenagrion puella* tandems during oviposition. Oviposition occurs singly (N=53) or in mixed groups (N=18), with pairs showing the male guarding upright (UMP) and horizontal (HMP).

Table I
Disturbance experiments of groups of *Coenagrion puella* tandems with a variable proportion of pairs ovipositing with upright guarding male (UMP) and with males perching on the oviposition substrate (HMP) (data in brackets give the expected values)

UMP/HMP	HMP tandems take off first	HMP tandems take off last	χ^2
1 : 1	2 (6.5)	11 (6.5)	6.23*
>1 : 1	2 (8.57)	10 (3.43)	17.62***

* $P < 0.02$, *** $P < 0.001$

DISCUSSION

In most species of Coenagrionidae tandem males guard their ovipositing mates in an upright position (CORBET, 1962; SCHMIDT, 1975). In *Coenagrion puella* tandems ovipositing into floating water plants during good weather, males only exceptionally settled horizontally in front of the female. However, windy weather may lead to a high proportion of ovipositions of tandems with HMP because males cannot maintain the upright position without being blown over. In species where HMP tandem oviposition is frequent, such as *Ceriagrion*,

Enallagma or *Erythromma,* oviposition occurs more frequently at sites with deep or flowing water with dense vegetation and into vertical structures above or below the water surface (BUCHHOLZ, 1950; ROBERT, 1959; SCHMIDT, 1975).

Oviposition with UMP may have evolved to reduce the risk of predation at the oviposition sites. Observations and experiments indicate that in HMP pairs responsiveness to disturbance is reduced compared to UMP pairs. In HMP pairs the male has to take up an upright position before take off, thus causing delay; so the period the pair remains within range of the leaping frog is extended and the predator thus has a better chance of catching HMP pairs. In contrast, UMP tandems take off steeply upwards with less loss of time. When taking off they are more agile and so have an increased chance of escaping from the leaping frog.

BANKS & THOMPSON (1985) observed in *C. puella* aggressive flights of rival males towards ovipositing tandems, which induced the tandems to take off and leave the oviposition site. However, tandem splitting was not observed. The significance of male position for reducing harassment from rival males may be low, and the grasp of the male on the female's prothorax, regardless of his position, may be sufficient to prevent the female from being taken over.

As tandems are sensitive to wind during flight (RÜPPELL, 1989), they may reduce their exposure to such unfavourable weather conditions by reducing the frequency with which they change oviposition site location. This probably also reduces the chances of their being noticed by a predator owing to increased movements of the body and wings of the guarding male during windy weather conditions.

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