

**AN EXPERIMENTAL STUDY OF THE REFUSAL DISPLAY
IN THE DAMSELFLY *PLATYCNEMIS PENNIPES* (PALL.)
(ZYGOPTERA: PLATYCNEMIDIDAE)**

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Females in tandem or having been in tandem, single females laying eggs and juvenile females can demonstrate refusal display to conspecific males and those of certain closely related spp. Refusal display has some successive states depending on the male's persistence. The responses of *P. pennipes* males to the refusal display by females were studied by means of 11 models. These differed in the presence and position of the abdomen. Female models with abdomens that rise at angles of 45° and 90° obtained the largest number of negative reactions. At an extreme state of refusal display (abdomen rises to maximal angle) the number of positive reactions by a male rose, but seizure of the female in tandem was hampered. Males demonstrate a threat display that is similar to female refusal display. In the natural environment threat display probably decreases the frequency of homosexual contacts, whereas refusal display of females leads to an economy of male time and energy.

INTRODUCTION

Communication of Odonata imago is characterized by a variety of key visual stimuli. They can be divided into two alternative groups: one of positive reactions of individuals (attracting) and another of negative reactions (repelling). The first group of stimuli takes part in the recognition of sexual partners, for marking places of oviposition (MARTENS, 1989) and in roosting. The second group serves for giving signals indicating occupied territory, refusal to pair etc. Such stimuli can be purely morphological [i.e. the general body position (UBUKATA, 1983) or the coloration of abdomen and wings (FRANTSEVICH & MOKRUSHOV, 1984) or behavioural [e.g. wing clapping of Calopterygidae (BICK & BICK, 1978)]. The majority of Zygoptera (BUCHHOLTZ, 1956; PAJUNEN, 1963;

UTZERI, 1988) and some Libellulidae (PAJUNEN, 1964; ROBBEY, 1975) hold the abdomen elevated while perching. This position is observed among individuals of both sexes. For the female it is a display of refusal to pair (UTZERI, 1988). This is well demonstrated by females, especially juvenile ones, when conspecific individuals and/or individuals of closely related species appear. The same occurs in females resting after oviposition, in cold individuals in the early morning and in females in tandem. The response of intruding males to the refusal display can be different (ranging from a pairing attempt to an escape or attack). Some Lepidoptera and Coleoptera have a comparable refusal display in their sexual behaviour (males and females of the butterfly *Thymelicus lineola* (Hesperiidae) (PIVNIK & McNEIL, 1985), females of the ladybird beetle *Harmonia axyridis* (OBATA, 1988). Experimental studies of key visual stimuli, that excite refusal display for pairing in *Pieris rapae crucivora* (Lepidoptera, Pieridae) females were carried out by OBARA (1984). A similar investigation of the release of attack by a territorial male *Sympetrum* was carried out by FRANTSEVICH & MOKRUSHOV (1984).

MATERIAL AND METHODS

Field observations and experiments were carried out at the Vorskla River near the village Nizhniye Mliny (5 km from Poltava City) in summer 1990. Observations were recorded in a field journal and on film.

EXPERIMENTS WITH MODELS. — Freshly killed specimens were penetrated by a straw that passed into the thorax and abdomen and was fixed to a holder (BUCHHOLTZ, 1956). The following 11 variants of models were made (the models are shown with the histograms in Figs 7-17): (1) intact ♀, straight abdomen (0°); — (2) ♀, three last abdomen segments curved at an angle of 45°; — (3) ♀, caudal half of abdomen curved at an angle of 45°; — (4) ♀, abdomen curved at an angle of 45°; — (5) ♀, abdomen curved at an angle of 90°; — (6) ♀, abdomen thrown back over thorax at an angle of 135°; — (7) ♀, without abdomen; — (8) ♀, abdomen turned down at an angle of 45°; — (9) intact ♂, abdomen straight (0°); — (10) ♂, caudal half of abdomen curved at an angle of 45°; — (11) ♂, abdomen curved at an angle of 45°. Wings of models were intact.

Prepared models were used during no more than 1-2 days (they were kept in a refrigerator because they dried and lost their natural colouration over a longer period of use). Models were shown to males perched not more than 1.5 m from the edge of the water. Observations were carried out between 11.00 and 16.00 h. Such males await females at the perches and thus they demonstrate high sexual activity. Models were presented in one way only (in profile), because a "face to face" presentation usually evoked an aggressive reaction (attack, escape). After 10-15 presentations models were changed. Due to this, temporal changes in male activity had only a slight influence upon the relationships of the various responses. This thesis was checked by summing all the male responses recorded for five days at a particular time interval. The mean male responses were then compared for every time period. Every model was shown to every male only once. Registration was carried out according to FRANTSEVICH & MOKRUSHOV (1984). Behavioural male responses were registered as one of five reactions:

- (1) tandem (t): ♂ settles upon the model and seizes its prothorax with the anal appendages;
- (2) survey (s): ♂ flies around the model and settles upon it without attempting to pair;
- (3) indifference (i): ♂ continues to perch, sometimes demonstrating a threat display;
- (4) escape (e): ♂ rapidly moves to another perch, usually in an opposite direction from the model;

(5) attack (a): ♂ suddenly rushes at the model, usually "face to face".

Altogether 1415 reactions (an average of 130 belonging to each model) were registered.

In separate experiments models Nos 9, 10, 11 were shown to perching females.

RESULTS AND DISCUSSION

FEMALE REFUSAL DISPLAY

At the bank of the river single females and females in tandem were often exposed to assaults by conspecific males and by coenagrionid males (*Coenagrion puella*, *C. pulchellum*, *Erythromma viridulum*). Juvenile females usually fell into the grass in these cases. Juvenile females, females that had been in tandem, and single females during oviposition (Fig. 1) demonstrated refusal display. *Platycnemis pennipes* has an extreme



Figs 1-5. *Platycnemis pennipes* (Pall.) different successive conditions of female refusal display: (1) in tandem; - (2) perching, straight abdomen; - (3) curving up last 2-3 abdominal segments; - (4) female raises abdomen at base at an angle of 45°, slightly moves wings apart and with the help of jerky movements folds and opens them; - (5) throwing back abdomen over thorax, rising on her hind legs.



variant of this behaviour (as shown by the work of BUCHHOLTZ (1956)), and there are some discrete variants that the female demonstrates depending on male persistence and the distance between them (Figs 2-5): (a) perching female curves up last 2-3 abdominal segments (Fig. 3); - (b) female raises the abdomen up to an angle of 45°, slightly moves the wings apart and with jerky movements, folds and opens them (Fig. 4); - (c) female throws the abdomen back over the thorax, rising on the hind legs (Fig. 5).

Refusal display can be demonstrated by the female during the flight. She curves up the abdomen and performs jerky movements up and down (Fig. 6).

Females demonstrated refusal displays when male models approached from the

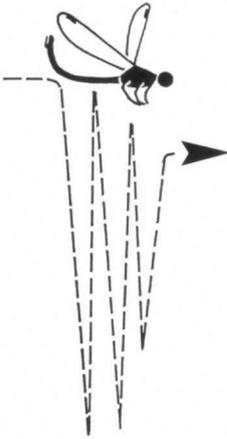


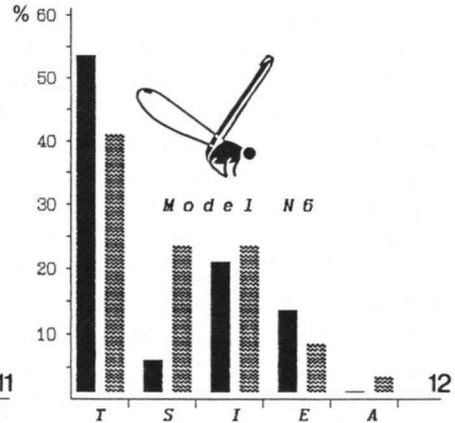
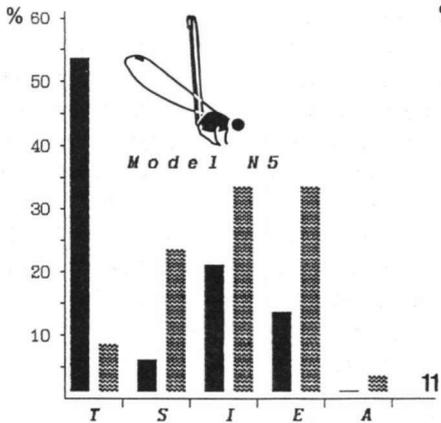
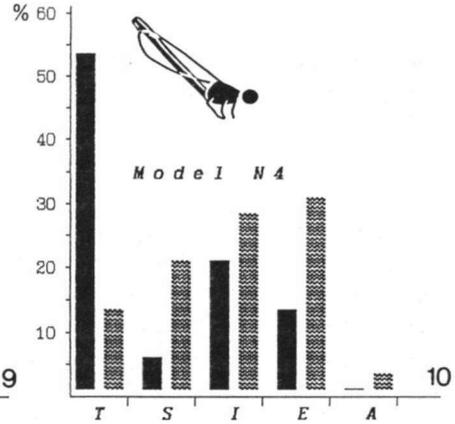
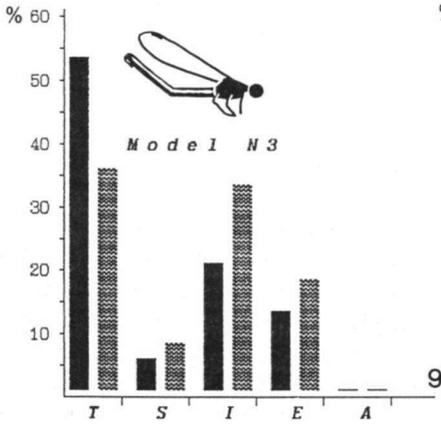
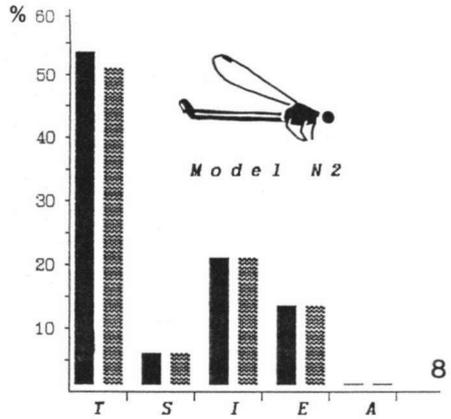
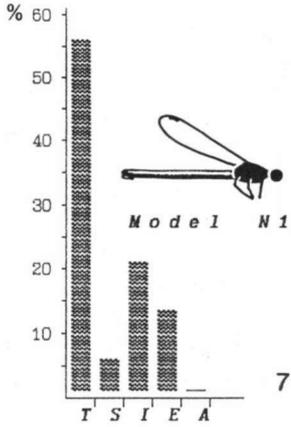
Fig. 6. *Platynemesis pennipes* (Pall.): female demonstrating refusal display in flight.

front or from one side. The display was especially vigorous when the models were placed 3-4 cm above her. We did not observe any escape reaction. The female responds by raising the abdomen and spreading her wings. The duration of presentation of the male model did not change the female position. Tactile contact intensified the effect of visual stimuli. The female raised the abdomen vertically and threw it forwards over the thorax only in response to tactile contact with the model. Sometimes in this case the female demonstrated escape and refusal display together. Females do not react if male models are presented from behind.

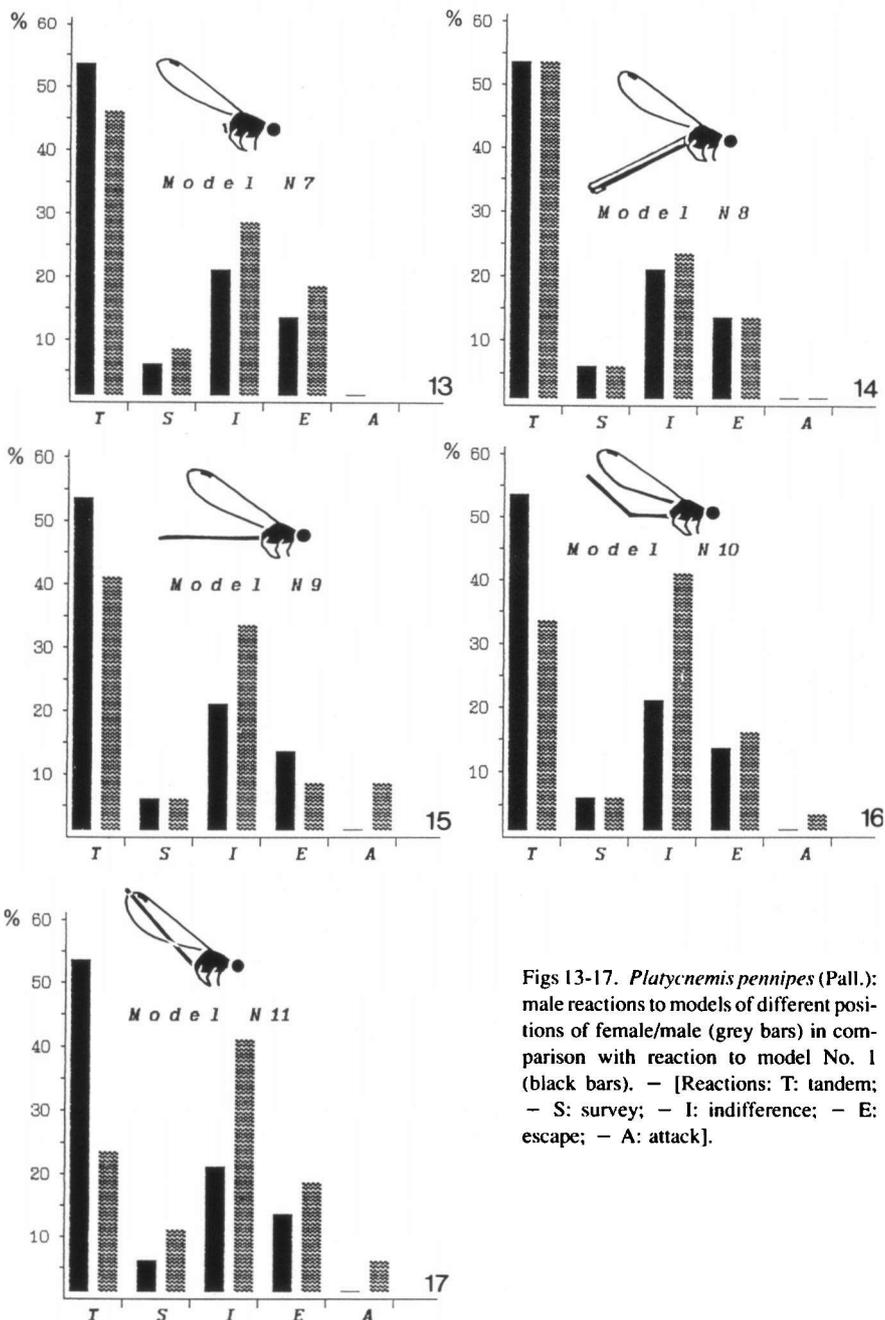
MALE THREAT DISPLAY

Wing movements by Zygoptera females and males in refusal/threat display were observed by UTZERI (1988). He supposed that this behaviour of females comes from intraspecific imitation of aggressive males by the females. Males demonstrate such behaviour as a threat display towards other males, or as a response to females' refusal display. Males can also demonstrate threat display by abdomen movements. To designate the aggressive behaviour of males, UTZERI proposed the term: "threat display" and for such behaviour in females the term "refusal display". We use these terms in this paper.

Males that perch near the river react by attack to the approach of other males. After this they perform the "face to face" behaviour. Then, if the intruder flies away, the resident pursues him usually for a distance of 10-15 cm, after which he returns to the perch or to a place not far from it (3-15 cm). Sometimes perching males demonstrate a behaviour that corresponds to female refusal display. It occurs when the intruder attempts to pair with the resident. This may take place in the morning and in the evening when the sexual activity of some individuals is lower. During the daytime homosexual attempts are rather rare, but in experiments with models they are seen more frequently. This can possibly be due to the fact that male models correspond to males only in outward appearance. Model immobility, the showing of any model in profile and the absence of aggressive behaviour reduced the attack reaction of a resident (Figs 15-17) and led to indifference reactions. In this case we did not distinguish such a reaction from refusal display.



Figs 7-12. For caption see Figs 13-17.



Figs 13-17. *Platycnemis pennipes* (Pall.): male reactions to models of different positions of female/male (grey bars) in comparison with reaction to model No. 1 (black bars). — [Reactions: T: tandem; — S: survey; — I: indifference; — E: escape; — A: attack].

Some males can fly 10-20 m along the edge of the water during their time of maximum activity (12.00-15.00 h.), often with neck elevated abdomens. Such flights are also performed by females from broken tandems (the same refusal display). In this way the individual indicates to the surrounding males her repeal of tandem formation.

MALE REACTIONS TO DIFFERENT POSITIONS OF FEMALE

Results of experiments with female models are presented in histograms (Figs 7-14). From model 1 to model 6 the percentage of positive reactions (tandem, survey) decreases while the percentage of negative reactions (indifference, escape, attack) rises (Fig. 18). Models 5 and 6 were the most effective for causing negative reactions of males.

Females without an abdomen (7) and with an abdomen turned down (8) evoked reactions that differed slightly from those to intact models (only by percentage of indifference). After vertically raising the female abdomen and curling it, the proportion of positive reactions rises. This position hampers the access of the male to the female and tandem formation is difficult. In this case males do as follows: fly to the model from behind, seize the thorax with the legs and try to seize the prothorax with the anal appendages. Such attempts are usually unsuccessful, whereas attempts to seize the thorax of a female from the front sometimes lead to success. Due to this, this model (6) has a comparati-

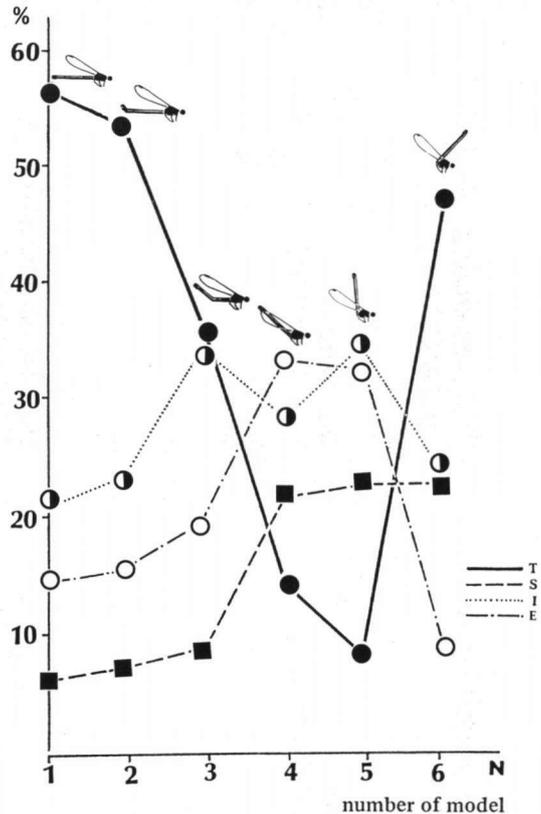


Fig. 18. *Platycnemis pennipes* (Pall.): dependence of male responses on abdomen angles of female models. In row of models Nos 1-6 abdomen angles increase. — [Reactions: T: tandem; — S: survey; - I: indifference; - E: escape].

vely high percentage of survey reactions. Seizure from one side (from above the prothorax) led to tandem in more cases. More persistent males had success in this female position also.

MALE REACTIONS TO DIFFERENT POSITIONS OF MALE

Only 3 models (9, 10, 11) were used in this experiment. In the line of these models we can also see some displacement to negative reactions (Figs 15-17). A high percentage of homosexual contacts in the experiment does not correspond to the situation in nature where they are rare, because there are key visual stimuli connected with behaviour that serve for male recognition. When the resident flies from the perch, the intruder demonstrates its aggressive behaviour by rushing at the resident flying at him "face to face". If this does not happen, the resident may mistake the individual for a female. We often saw this in our experiments. Threat displays, between resident and intruder males result in a considerable lowering of homosexual contacts in *P. pennipes*.

CONCLUSION

The refusal display is a dynamical behavioural act. It is evoked by a key visual stimulus — appearance of conspecific and coenagrionid males, that display to the resident one of two reactions: attack or attempt to pair. Experiments with models cannot reflect the whole spectrum of communicative possibilities of refusal display because in species with little sexual dimorphism (*Coenagrion*, *Ischnura elegans*, *P. pennipes*) the recognition of a female is connected more with reciprocal behavioural reactions of both sexes than with morphological signs.

Males do not react or react only slightly when females display refusal because they are not ready for pairing. As these females are in a zone of many active mature males, their behaviour economises male time and energy.

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