

**THE DURATION OF THE STAGES OF COPULATION IN  
*ENALLAGMA CYATHIGERUM* (CHARPENTIER)  
(ZYGOPTERA: COENAGRIONIDAE)**

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*Received January 15, 1991 / Accepted February 18, 1991*

Copulation in *E. cyathigerum* can be divided into 3 stages. Stage I, which is correlated with the removal of rival sperm from the female's storage organs, shows a greater degree of variability of duration than later stages. Such variability is dependent in part on the time of day: copulations occurring late in the day are significantly shorter. The number of rhythmic movements occurring during stage I is positively correlated with the duration of the stage whereas their frequency is negatively correlated. In stage II, during which the ejaculate is transferred to the female, the number of rhythmic movements remains more or less constant at about 20 and their frequency is negatively correlated with the overall duration of the stage. In stage III no movement occurs but the duration is positively correlated with that of stage I. Some of the factors which may account for the variability of copulation are considered.

**INTRODUCTION**

The duration of copulation varies widely in different species of Odonata (CORBET, 1962). It can be as brief as 3-5 seconds in the aerial copulations of some libellulids or it may last for many hours in some *Ischnura* spp. (ROBERTSON, 1985; MILLER, 1987; CORDERO, 1990).

MILLER & MILLER (1981) divided the copulations of *Enallagma cyathigerum* into three stages. In stage I the male's abdomen is held in a curved position and rhythmical swaying of the whole abdomen occurs at 10-60 cycles min<sup>-1</sup> as a result of active flexions of the 2nd and 3rd segments. Stage I may be periodically interrupted by temporary disengagements of the genitalia when short flights and

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changes of perch may occur. In the much shorter stage II, the male's abdomen is held more or less straight except for the terminal segments which are sharply bent, and a slower type of rhythmical movement appears at 9-22 cycles  $\text{min}^{-1}$ . Finally in stage III the male's abdomen is again curved as in stage I but there is no detectable movement.

Stage I is associated with the removal of sperm from the female's bursa, while during stage II and possibly continuing in stage III the male transfers his own sperm to the female. A comparable pattern of activity has been observed during the copulation of several other zygopterans including *Ischnura* spp. (MILLER, 1987; CORDERO, 1990), *Mnais p. pruinosa* (SIVA-JOTHY & TSUBAKI, 1989), *Erythromma viridulum*, *Coenagrion puella*, *Ceriagrion coromandelianum*, *Lestes sponsa* and *Pyrrhosoma nymphula* (P.L.M. unpubl.), although the form of the movements is not identical in all these species. Detailed observations on the durations of each stage have been made in *Ischnura graellsii* by CORDERO (1990). Nearly all the variability of copulation duration occurs in stage I in that species and it can be correlated with the time of day, the population density and with the previous history of the female. We have made observations on the copulation of *E. cyathigerum* which show that although the overall duration is less than in *Ischnura* spp., most of the variability also occurs within stage I. We have examined the occurrence and frequency of rhythmic abdominal movements which occur during stages I and II, and relate these to the overall duration of the stage.

## METHODS

The activity of *E. cyathigerum* was observed at a large gravel pit about 3 miles north of the centre of Oxford during July and August, 1988. The weather during this period was variable with many cloudy, wet days when no reproductive activity was observed. The study sites were all within 15 m of the water among low vegetation. Copulatory stages were observed with the help of a close-focusing monocular. Ambient shade temperatures were 18-26°C. Sixty-six copulations were studied closely and of these 54 were selected for analysis.

Eighteen pairs were caught at the end of stage I and preserved immediately in 70% ethanol. The males' sperm vesicles and the females' bursae and spermathecae were dissected under a binocular microscope and the volume of sperm each contained was estimated on a 3-point scale.

## RESULTS

Copulations were observed at all times between 10:00 and 16:30 h, but there was an increase in their frequency between 11:00 and 14:30 h on sunny days (Fig. 1). The mean durations of copulation and its component stages are shown in Tab. I.

Stage I, with a mean gross duration of about 23 min, normally occupied about 80% of the total copulation. Gross values include the time occupied by "breaks"

when the genitalia were temporarily disengaged but the tandem clasp was maintained, and when the pair sometimes took off and flew a short distance to a new perch. The maximal duration observed for stage I was 65 min. Activity usually started with a few fast rhythmic movements whose form resembled those occurring in stage II, but the normal

movements of this stage were soon established and they continued throughout at  $0.2-1.0 \text{ s}^{-1}$ . The values approximate to a Poisson distribution, but when the duration of breaks was subtracted the resulting net values suggested a normal distribution.

Some factors which might be responsible for the variability of stage I have been examined. No correlation of the net duration was found with the time during the season, the distance of the copulatory site from the water, or with the number or frequency of interferences by other males. Surprisingly, no correlation with temperature was found. The gross duration was negatively correlated ( $P < 0.05$ )

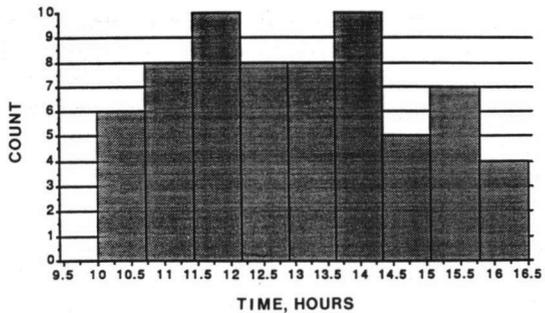


Fig. 1. Histogram of the frequency of occurrence of copulations at different times of the day in sunny conditions.

Table I  
The duration of the stages of copulation of *E. cyathigerum*

	MEAN (seconds)	S.E.	Variance $\times 10^{-3}$	N
Total copulation (Gross)	1954	1186		30
Total copulation (Net)	1500	783		30
Stage I (gross)	1421	135	987.6	54
Stage I (net)	1040	86	400.5	54
Stage II	79	7	1.7	30
Stage III	286	21	13.4	30

with the time of day (Fig. 2), stage I being shorter towards the end of the day. A comparable reduction in the duration of copulation was found by MICHIELS & DHONDT (1988) in *Sympetrum danae* and by CORDERO (1990) in *Ichnura graellsii*. Both the gross and the net durations were positively correlated with the number and frequency of breaks of the genitalia ( $P < 0.001$ ) (Fig. 3), so that in longer copulations there were more breaks and these occurred at a higher frequency than in short copulations.

The number of rhythmic movements increased significantly with the net duration of stage I (Fig. 4), in agreement with the results of SIVA-JOTHY & TSUBAKI (1989) from *Mnais p. pruinosa*. This occurred despite the fact that there was a fall in the frequency of movements as the net duration increased (Fig. 5). During breaks the penis was withdrawn from the female but it remained extended. The mean durations of stages II and III are given in Table I, and these stages accounted for approximately 4% and 15% respectively of the total duration

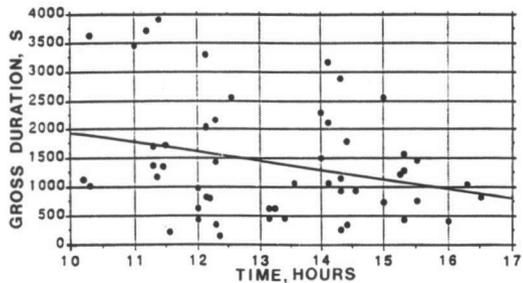


Fig. 2. The gross durations of stage I of copulation (i.e. including time of "breaks") plotted against time of day. — (s = seconds) — [Regression equation  $Y = -160.716x + 3543.103$ ;  $R^2 = 0.072$ ;  $P = 0.0491$ ].

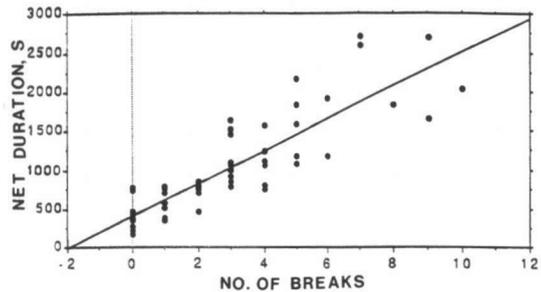


Fig. 3. The net durations of stage I of copulations (i.e. excluding time of "breaks") plotted against the number of breaks. — (s = seconds) — [Regression equation  $Y = 210.593x + 408.444$ ;  $R^2 = 0.744$ ;  $P = 0.0001$ ].

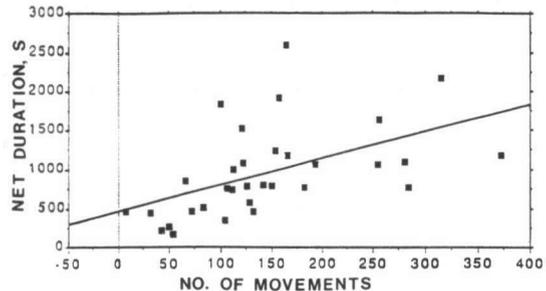


Fig. 4. The net durations of stage I (i.e. excluding the time of "breaks") of copulation plotted against the total number of rhythmic movements. — (s = seconds) — [Regression equation  $Y = 3.431x + 462.609$ ;  $R^2 = 0.263$ ;  $P = 0.0027$ ].

of copulation. During stage II, whose duration varied much less, a new type of rhythmic movement appeared at a mean frequency of  $0.25 \text{ s}^{-1}$  whereas during stage III no movement could be detected. The duration of both stages was significantly and negatively correlated with temperature ( $P < 0.001$ ) while the duration of stage II was negatively correlated with the frequency of rhythmic movements, as in stage I (Fig. 6). As a result the number of cycles of movement in this stage remained approximately constant at 20. Breaks occurred in stages II and III only when a pair was disturbed.

No correlation was found between the durations of stages I and II, but there was a positive correlation between the durations of stages I and III ( $P < 0.005$ ).

The volume of sperm in the seminal vesicles of 17 males, caught upon the completion of stage I and immediately preserved, was examined. In 16 the vesicle was full or almost full, but in one it was empty. Capture may occasionally cause sperm release by the male which perhaps accounts for the one empty male. The results show that sperm are not normally released during stage I, in agreement with an earlier report (MILLER & MILLER, 1981).

Of 18 females caught in stage I, 12 had empty bursae while in 6 the bursae were approximately half-filled. In all females the spermathecae were full. These results suggest that males remove sperm from the bursa but not from the spermatheca during copulation. Sperm may be added to the spermathecae during copulation (WAAGE, 1986).

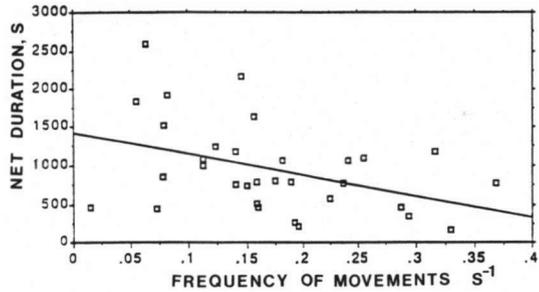


Fig. 5. The net durations of stage I of copulation plotted against the frequency of rhythmic movements per second (s). The movements are faster in shorter copulations. — [Regression equation  $Y = -2740.849x + 1429.22$ ;  $R^2 = 0.167$ ;  $P = 0.0204$ ].

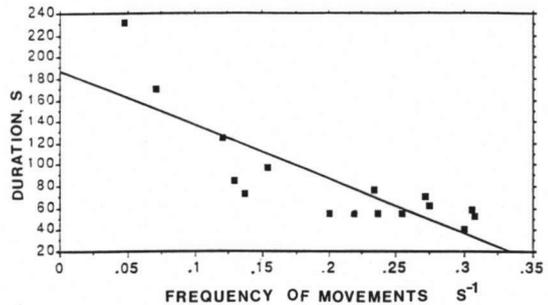


Fig. 6. The durations of stage II of copulation plotted against the frequency of rhythmic movements. — (s = seconds) — [Regression equation  $Y = -502.102x + 187.35$ ;  $R^2 = 0.693$ ;  $P = 0.0001$ ].

## DISCUSSION

MICHIELS & DHONDT (1988) have concluded that the duration of copulation in *Sympetrum danae* is negatively correlated with temperature, time of day and with the number of previous copulations a male has experienced on the same day. CORDERO (1990) found that in *Ischnura graellsii* almost all the variability of duration occurs within stage I, such variability being correlated with the time of day and the population density, with shorter copulations occurring later in the day, particularly at high population densities. In addition he was able to show that copulations were longer with previously mated females than with virgins, the effect being greatest at low densities, implying that males can distinguish non-virgins from virgins. He also found that the age of each partner affected the duration.

In the 54 timed copulations of *E. cyathigerum*, the male was observed to start copulation either immediately after seizing a female or after flying towards the water in tandem. In some of the latter cases it is possible that copulation had commenced previously and that what was observed was a re-introduction of the penis after a break. If so, this would give rise to an underestimation of the true duration of stage I.

Most of the variability of copulation duration was found within stage I, a time when rival sperm are removed from the bursa of the female. Correspondingly almost all of the small sample of females caught in stage I and dissected had empty or half-empty bursae but filled spermathecae. No copulation with a virgin female was identified, and we do not know therefore if such matings differ in duration, as in *I. graellsii* (CORDERO, 1990).

The duration of copulation did not appear to be affected by population density unlike the situation in *I. elegans* (MILLER, 1987) and *I. graellsii* (CORDERO, 1990), nor was it affected by the number of approaches made by rival males. Copulations which occurred late in the day were shorter and some of these may have been with females after their rescue at the water surface following a period of submerged oviposition (cf. MILLER, 1990). Such females would have been of little value to males unless they contained some mature eggs in the lateral oviducts and were likely to oviposit again before encountering another male, but whether males can distinguish such females is unknown. Moreover few females were observed to commence oviposition after about 17.00 h.

Breaks in which the genitalia were disengaged but the tandem clasp was maintained were normal occurrences during stage I in most copulations of *E. cyathigerum*. Sometimes they were accompanied by a short flight of < 1 min duration to a new perch. Such breaks, which did not occur in response to harassment by other males, may allow the penis to pull out rival sperm from the female's tract, the sperm then drying and flaking off before the penis is re-inserted. The occurrence of long-duration stages I was correlated with a greater

number and frequency of such breaks, which suggests that more rival sperm might be removed when stage I was of long duration, as described by SIVA-JOTHY & TSUBAKI (1989) in *Mnais p. pruinosa*. It is not clear why the duration of stage I should be correlated with that of stage III, but if a long stage I does permit more rival sperm to be removed from the female, then it may take correspondingly longer to package the new sperm into the increased space available in the storage organs.

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