

**FEEDING-RELATED BEHAVIOUR IN LARVAE OF *ENALLAGMA  
CYATHIGERUM* (CHARPENTIER) (ZYGOPTERA: COENAGRIONIDAE)**

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Larvae of *E. cyathigerum*, even when densely aggregated, exhibit no evident spacing or agonistic behaviour. Cannibalism is rare or non-existent among healthy larvae, even after they have been denied food for several days and are exhibiting heightened feeding activity. When exposed to high densities of prey, larvae show no detectable sign of "wasteful killing" (sensu JOHNSON et al., 1975, *Ecology* 56: 1081-1093). The feeding-related behaviour of larvae of *E. cyathigerum*, as exhibited in the laboratory, differs markedly from that of *Pyrrosoma nymphula* and *Lestes sponsa* (which themselves differ *inter se*) in some respects and resembles it in others.

**INTRODUCTION**

The ways in which dragonfly larvae interact with conspecifics and prey has important applied and theoretical implications. Such feeding-related behaviour is liable to influence the feasibility of large-scale rearing for biological-control programmes (cf. SEBASTIAN et al., 1980); and its ecological effects may include the modification of developmental rate (MACAN, 1977; BAKER, 1980) and enhancement of mating success among males (HARVEY & CORBET, 1985).

Since Macan's suggestion (1977) that a form of territoriality exists among larvae of *Pyrrosoma nymphula* (Sulz.), and the subsequent demonstration that this and other species do indeed defend space against conspecifics (MACHADO, 1977; ROWE, 1980; BAKER, 1981; HARVEY & CORBET, 1985, 1986) attention is being focused on the extent to which such behaviour is present in different taxa of Odonata. It is becoming clear from preliminary studies that some, perhaps most, species are not territorial as larvae (e.g. *Cordulegaster boltonii* [Don.], PRODON, 1976; *Lestes sponsa* [Hans.], HARVEY, 1985) and this

suggests that it may be useful to identify contrasting types of feeding-related behaviour as a step towards inferring their ecological significance.

Forms of behaviour which are candidates for early consideration in this regard are:

- territorial behaviour among conspecifics (i.e. spacing and defence of space mediated by agonistic behaviour) versus the absence of such behaviour;
- sedentary feeding by ambush versus searching and pursuit of prey;
- cannibalism, usually as a sequel to enforced abstinence from feeding versus the absence of cannibalism; and
- killing, but not consumption, of prey present at high density and excess to immediate nutritional requirements (i.e. "wasteful killing" sensu JOHNSON et al., 1975) versus the absence of such killing.

As examples of Zygoptera whose positions on this matrix are known from laboratory studies, we have *Pyrrhosoma nymphula* and *Lestes sponsa*. The former is territorial (HARVEY & CORBET, 1985, 1986), feeds by ambush, seldom exhibits cannibalism (but see MACAN, 1964, p. 329) and engages in wasteful killing (CORBET et al., 1989). The latter differs from *P. nymphula* in all respects except the last (HARVEY, 1985). Here we report observations on another zygopteran, *Enallagma cyathigerum* (Charp.), which occupies yet another position on the matrix. In doing so, we hope to stimulate interest in characterising other species so that the day will come nearer when the feeding-related behaviour of different dragonflies can be correlated with their taxonomic affinity or ecological role.

#### MATERIAL AND METHODS

Larvae of *Enallagma cyathigerum* were collected by handnet on 6 October 1986 from Rohallion Loch, Perthshire (56°32'N, 3°32'W; NO 048 387). They were identified according to the characters described by CHOWDHURY & CORBET (1987).

Spacing and cannibalism. — Larvae were divided into 2 batches, each comprising 5 larvae in each of 6 size groups (body length in mm, excluding antennae and caudal lamellae: 7-8.9, 9-10.9, 11-12.9, 13-14.9, 15-16 and 16.1 and over). Each batch, comprising 30 larvae, was housed in a white, translucent, plastic carton (20x14 cm; height 15 cm) containing 1 litre of tap water (depth 4 cm). The water had stood overnight in each carton to bring it to laboratory temperature (18-21°C) and to permit dechlorination. In each carton were floated 3 pieces (each 4.5x3.5 cm) of black, plastic "Netlon" — a grid of coated wires intersecting at right angles to enclose a rectangular space (5x6 mm).

Because these were the only perches provided, the larvae on them sustained severe competition for space, some larvae being obliged to cling to other larvae, and a few being excluded altogether. Living larvae (3-5 days old, comprising instars III and IV) of the mosquito, *Aedes aegypti* (L.), were provided as food, in excess of a day's requirements, at intervals of 1, 2, 4 or 7 days according to the food-denial regime required. Larvae of *E. cyathigerum* were observed 3 or 4 times each day, during daylight, including the time of feeding. Observations continued for 30 days.

Wasteful killing. — Larvae of 2 size groups (9-10.9 mm and 15-16 mm) were each placed in a white, plastic tub (diameter 8.5 cm, height 5.5 cm) containing 100 ml of tap water (depth 2.5 cm). Each larva was denied food for 1, 2 or 4 days and then offered 10, 20 or 50 prey larvae (mixed instars III and IV) and observed continuously for 1 hour. Each combination of size group of predator and duration of food denial was replicated 9 times.

## RESULTS

Unless qualified otherwise, the word "larva" refers to *E. cyathigerum*.

**SPACING.** — Larvae, except for a few apparently unable to secure perching space, clung to the Netlon grid or to each other in dense aggregations. No movements or postures associated with agonistic display in other dragonfly species were ever observed. On 8 occasions a single mosquito larva was grasped simultaneously by 2 larvae and in the resulting tug-of-war was torn into two fragments; but even under such conditions nothing resembling threat or attack behaviour was witnessed.

**CANNIBALISM.** — The effect of withholding food from larvae for 2, 4 or 7 days was to increase their rate of grasping and consuming prey when eventually it was provided, but not to induce cannibalism. On 2 occasions a larva which had been injured during handling in the course of another experiment was placed in each container and lay on the bottom, wriggling but unable to swim. One of these injured larvae was grasped and partly eaten by a healthy larva. Apart from this, and despite the variation in size among the larvae, no cannibalism was detected. All larvae survived for the duration of the experiment (i.e. 30 days).

**WASTEFUL KILLING.** — In no experiment designed to detect it was wasteful killing observed. Larvae grasped and (completely) consumed prey larvae in rapid succession for 7-12 minutes after being provided with them and then, apparently satiated, remained inactive and seldom responded to prey swimming around them. At such times, when prey larvae touched a dragonfly larva or browsed on the latter's head, antennae or legs, the dragonfly would sometimes jerk the affected part of its body or move away; but it was never seen to attack the mosquito larva.

## DISCUSSION

The larva of *E. cyathigerum*, though by preference thigmotactic, is able to tolerate very high densities of conspecifics without exhibiting agonistic or spacing behaviour, or cannibalism. The fact that the sole instance of cannibalism involved an injured larva suggests that it may normally be averted by recognition between larvae of species-specific signs or signals. The behaviour detected in these experiments may or may not be consistent with the occupation in nature by *E. cyathigerum* larvae, at what appears to be high density, of *Littorella uniflora* (L.) Aschers carpeting the bottom in shallow water as a thick sward a few centimetres high. In its behaviour when exposed to a high density of conspecifics, it is the antithesis of *Pyrrhosoma nymphula* in all the respects we have identified except that it feeds by ambush.

So little is known of how dragonfly larvae behave in nature that it is premature to speculate on the adaptive correlates of the behavioural types that are evident from laboratory studies. A useful way forward would be to confine larvae of

species with contrasting behaviour, and which coexist in nature, such as *E. cyathigerum*, *L. sponsa* and *P. nymphula*, in aquaria containing different types of perches, such as *Littorella* and *Potamogeton natans* L., and to see how the larvae distribute and conduct themselves.

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