

**TERRITORIAL BEHAVIOUR OF A LARVAL DRAGONFLY
XANTHOCNEMIS ZEALANDICA (McLACHLAN) (ZYGOPTERA:
COENAGRIONIDAE)**

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Territorial behaviour is shown to exist in the weed-dwelling larvae of *X. zealandica*. Caudal swinging, usually interpreted as a ventilation movement, was found to be an intraspecific threat display. In the laboratory, a uniform spatial distribution of larvae was obtained. This result has implications for resource partitioning by predators in the littoral zone.

INTRODUCTION

Territorial behaviour is widespread among animal species and plays an important role in dispersion, resource utilisation and intraspecific competition among reproductives. In adult insects it has been recorded in many orders generally in association with courting and mating. Hitherto (BROWN & ORIAN, 1970; CORBET, 1962; LIN, 1978) it has apparently not been shown to exist in larval insects (which of course do not directly partake in reproductive activity). While BENKE & BENKE (1975) considered territorial behaviour to be rare among aquatic insects, MACAN (1977) speculated on the biological significance of spacing in larval aquatic insects and postulated that some form of territorial behaviour might help to account for the observed larval population structure of *Pyrhosoma nymphula* (Sulzer) (Zygoptera: Coenagrionidae). MACHADO (1977) found agonistic behaviour and displacement in late-instar larvae of the leaf-axil-dwelling *Roppaneura beckeri* (Santos) (Zygoptera: Protoneuridae). PRODON (1976) was unable to detect territorial behaviour in *Cordulegaster boltoni* (Donovan) (Anisoptera: Cordulegasteridae).

While studying hunting site selection by larvae of the New Zealand damselfly *Xanthocnemis zealandica*, I found that the larvae took up positions on stems and defended these positions from conspecifics. Caudal swinging, formerly held to be a ventilatory movement (CORBET, 1962), seemed to function as an intraspecific threat display. Caudal swinging differs from the generalised threat display (raising the tip of the abdomen so the caudal lamellae are above the head) reported in other Zygoptera (CORBET, 1962; NEEDHAM, 1930) and some Anisoptera (HEYMER, 1970).

MATERIAL AND METHODS

Apparatus used in the study of site selection consisted of three aquaria (25 x 40 x 10 cm deep) each containing eight colour-coded larvae (ROWE, 1979), in the ultimate (F) and penultimate (F-1) instars, and eight wire-stiffened polythene tube "stems" held by a wire frame above each aquarium. Agonistic behaviour was observed in these aquaria and in smaller (4 x 10 x 10 cm) aquaria each containing two larvae. The investigation was conducted at $15 \pm 1^\circ\text{C}$ and a photoperiod of 16 h L: 8 h D, a regime designed to avert metamorphosis by the diapausing larvae used. Larvae were given oligochaetes (*Lumbriculus variegatus*) as food.

Because the thrust of the main investigation was to examine hunting site selection the larvae were allowed to initiate their own movement and were provided with surplus food to minimise unnatural behaviour patterns occasioned by further stress. The observations have been repeated with non-diapausing larvae with cladoceran prey and results consistent with the original investigation were obtained.

More than 150 separate episodes of threat display and response have now been observed.

AGONISTIC BEHAVIOUR

A walking *X. zealandica* larva holds its body away from and parallel to the substrate with the tips of the caudal lamellae slightly separated. When a larva climbs onto a stem a characteristic and conspicuous behaviour occurs: the animal swings its abdomen slowly from side to side, and the spread caudal lamellae describe an arc with an amplitude of about three body widths and a period of ca 0.5-1.0 sec. As it advances, the larva pauses every few centimetres or so and vigorously swings its abdomen at a higher frequency and with a greater amplitude than is observed when it is also walking. Such a bout of "static caudal swinging" (SCS) can last 2-3 min before the larva moves forward again. Unless disturbed, a larva soon moves to the bottom of the stem and remains there head downwards with its body close to the stem, and its caudal lamella pressed together. Several larvae remained each on its individual stem (and if undisturbed, at the bottom of the stem) for more than 50 days.

THREAT BEHAVIOUR

If approached by another larva walking over the bottom of the aquarium, the occupant of a stem will raise its body from the stem, spread its caudal lamellae and raise the tip of its abdomen (Fig. 1). If approached closely, it will also embark on a bout of SCS. An approaching larva encountering such activity almost invariably alters course within seconds to avoid the occupied stem. If a second larva should arrive on a occupied stem by swimming through mid-water, by crossing from another stem, or by climbing past the occupant, a clash occurs.

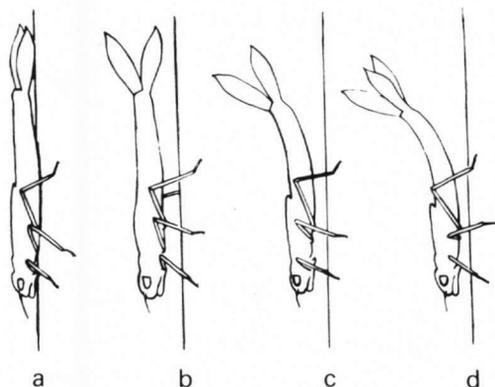


Fig. 1. Sequential reaction to an approaching conspecific: (a) normal resting position; — (b) alert posture also adopted before feeding; — (c) response to a closer approach; — (d) caudal swinging commences. — For threat behaviour the tip of the abdomen is raised further than in (d) and there is no caudal swinging. After (d) the tip is lowered and normal SCS begins. (From a single series of photographs.)

A clash is usually initiated when the intruder turns to face the bottom and moves down the stem towards the occupant. On a few occasions (4 observations) the occupant was seen to turn, follow the intruder up the stem and initiate the clash. Clashes typically proceed through a series of stages (Fig. 2). The advancing animal (usually the intruder) moves slowly towards its opponent with its lamella spread and swinging continuously. Frequently it pauses and performs SCS. As the swinging loses intensity towards the end of a bout the approached animal, which is usually facing

away from the advancing animal, responds with a bout of SCS. Both larvae may remain stationary for up to 10 min, alternately engaging in bouts of SCS. The intruder normally terminates this activity by turning and retreating, leaving the stem, or by continuing the advance. When the advancing larva comes within range of its opponent's spread caudal lamellae, it strikes with its labium, whereupon the larva struck turns and faces the attacker. Both larvae perform SCS, either alternately or simultaneously. If neither animal retreats at this stage one will strike at the other with its labium. Usually the intruder then retreats; but on four occasions larvae stood and exchanged alternate labium strikes for 4 to 20 s; during such fights the larvae were

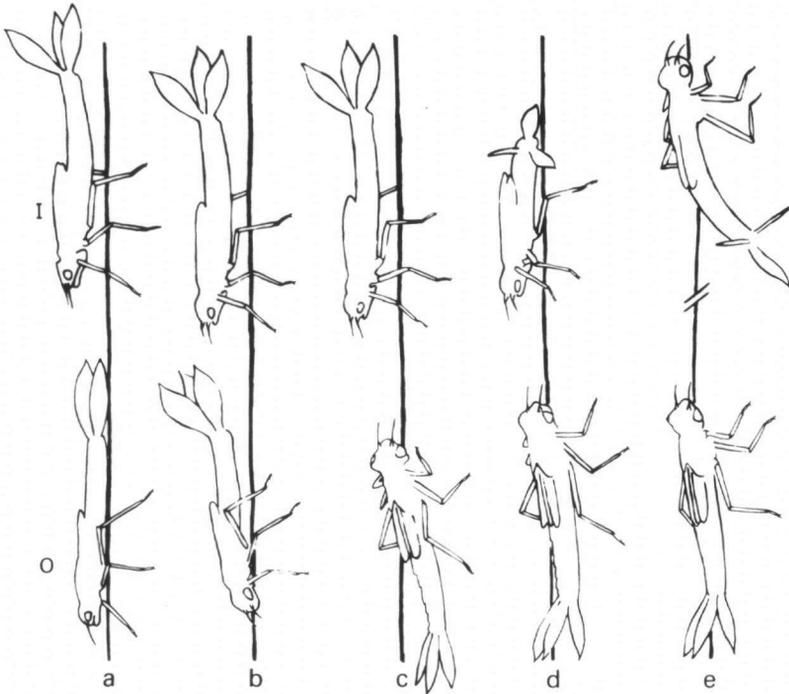


Fig. 2. A clash: (a) occupant (O) at base responds to SCS of intruder (I); — (b) occupant turns in response to intruder's labium strike at caudal lamellae; — (c) alternate SCS followed by exchange of labium strikes; — (d) intruder curves abdomen, turns and retreats; — (e) occupant makes intermittent labium strikes as the intruder retreats, abdomen still bent (not swinging); separation of three body lengths. — (From a series of photographs of a single conflict.)

separated by too great a distance to allow physical contact. An animal retreating after SCS or a fight holds its abdomen curved perpendicularly to the sagittal plane. The victor remains in position. After fights the victor frequently continues to make labium strikes; retreating animals which have paused resume their movement away from the victor after such a strike. This signal elicits further retreat up to six body lengths from the victor.

RESULTS OF CONTESTS

Of 18 contests observed in the large aquaria, 14 were won by the occupant ($P < 0.016$, binomial). On two of the occasions when the occupant lost, it had been subject to two almost simultaneous invasions and was displaced by the second intruder.

NON-CONSPECIFICS

The intraspecific displays differ markedly from the reactions of *X. zealandica* larvae to other approaching objects of similar size: stem-occupying larvae did not react detectably to stem-climbing caddis larvae (Trichoptera: Conoesucidae) or to bottom-crawling Ephemeroptera. *X. zealandica* larvae usually sidled around the stem when the conoesucid larvae began to climb over them; however, on two observed occasions the dragonfly larva remained immobile while being climbed over. Stem-occupying larvae responded to the approach of a probe, pencil or finger by lifting the caudal lamellae over the head, a threat reaction described previously for other zygopteran larvae (CORBET, 1962).

DISTRIBUTION

The types of intraspecific agonistic behaviour described for *X. zealandica* provide a mechanism which may bring about the observed regular distribution of larvae over stems. Comparison of the random colonisation predictions (FULLER, 1957) and the observed frequencies (Tab. I) indicates a highly skewed distribution, as did other data from distributions when only seven larvae were on stems. Within each class (defined by the greatest number of larvae on any one stem) of the distribution, the ratio of observed to expected frequencies is ordered according to the greatest number of singly occupied stems.

DISCUSSION

Caudal swinging, including SCS, has previously been interpreted only as a ventilatory movement which increases the rate of respiration (CORBET, 1962; LAWTON, 1971). That this should be the only interpretation is inconsistent with my observations of *X. zealandica*: climbing larvae showed caudal swinging only when on stems, and mainly initially, while interacting and thus determining their localisation on stems; it became rarer thereafter except when two larvae were on the same stem.

In *X. zealandica* caudal swinging in well oxygenated water is associated with intraspecific displays. Displays and fights occur when more than one larva is on the same stem. The outcome of such displays and fights is usually the displacement of the intruder. The distribution of larvae on stems is consistent with such territorial behaviour. In many ways the course of larval clashes parallels that observed in adult dragonflies (PAJUNEN, 1962) but with the temporal scale slowed perhaps a thousandfold.

FOX (1975) has discussed the significance of cannibalism as a population

Table I
Larval spacing on stems

Distribution of larvae among 8 stems	f(th)	f (obs)	f(obs)/f(th)
2,1,1,1,1,1,1,0	25	97	3.88
2,2,1,1,1,1,0,0	95	143	1.50
2,2,2,1,1,0,0,0	63	31	0.49
3,1,1,1,1,1,0,0	25	29	1.16
3,2,1,1,1,0,0,0	84	53	0.63
3,3,1,1,0,0,0,0	10	3	0.28
3,2,2,1,0,0,0,0	32	6	0.19
4,1,1,1,1,0,0,0	10	10	1.0
4,2,1,1,0,0,0,0	16	0	0
all others	15	5	0.3

The frequency distribution 2,1,1,1,1,1,1,0 denotes one stem with two larvae, six stems each with one larva and one empty stem. The theoretical frequencies, $f(\text{th})$ are based on the assumption that colonisation is random. $f(\text{obs})$ are the observed frequencies. There were 377 observations made at regular intervals over a period of two months during which time the larvae moved freely. For reasons discussed in the text it was impracticable to disturb the system to produce quasi independent observations and thus this result is not amenable to statistical testing. The time covered by the series of observations is far greater than the average length of stem occupancy (ca 7 days) and the very strongly skewed result obtained is highly indicative of a mechanism driving the system towards a uniform distribution.

regulator in arthropod predators. Examination of prey items from field-caught coenagrionid larvae (CHUTTER, 1961; MACAN, 1964; PEARLSTONE, 1973) has shown the incidence of cannibalism to be extremely low, despite the high larval densities at the sampling sites. Stark (pers. comm.) found no cannibalism in approximately 200 faecal pellets from *X. zealandica*. *X. zealandica* is usually semivoltine in most habitats where it has been studied (DEACON, 1979) and it is perhaps significant that SCS is used by *X. zealandica* against conspecifics of similar size at least as early as the F-5 instar, a year prior to emergence. It is possible that territorial behaviour will prove to be widespread among the larvae of the Coenagrionidae and this may in some way account for their abundance in the littoral zone. Two possible mechanisms would be the reduction of cannibalism because of the ritualized threat display and the dispersal of the larvae throughout the available microhabitat, thus allowing better food resource utilization.

The question arises: what limiting resource produced the evolutionary pressure towards larval territorial behaviour in *X. zealandica*? This is particularly interesting in view of the extremely heavy mortality expected

between entering metamorphosis and returning to the water to breed (e.g. BENKE & BENKE, 1975; PARR, 1973). A comparison between *X. zealandica* and *Austrolestes colenisonis* (White) (Lestidae), a species, which is found in the same places, produces an intriguing dichotomy. In *X. zealandica* the larvae are normally semivoltine and territorial, while on the other hand the adult males maintain only a defended "personal distance" of ca 5 cm. In *A. colenisonis* the larvae are normally univoltine and not territorial, while the males strongly defend territories extending 1-2 m from their perching sites. The factors behind such dichotomies merit investigation.

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Since the preparation of this material R.L. BAKER (1980, *Can. J. Zool.* 58: 1060-1065) has shown that in *Coenagrion resolutum* the larvae move about until they find a "hunting site" that provides a food source. In *X. zealandica*, on the other hand, larvae which had been starved for a week prior to being placed with stems immediately took up positions on the stems and showed no greater propensity to change site than did unstarved, fed larvae despite being held without food for a further 168 hours while under observation.