

**TERRITORIAL AND REPRODUCTIVE BEHAVIOUR
OF *CALOPTERYX AEQUABILIS* SAY
(ODONATA : CALOPTERYGIDAE)
IN NOVA SCOTIA, CANADA**

K. F. CONRAD¹ and T. B. HERMAN²

¹ Department of Biology, University of Calgary
2500 University Dr. N.W., Calgary,
Alberta, T2N 1N4, Canada

² Department of Biology, Acadia University
Wolfville BOP 1X0, Nova Scotia

Territorial and reproductive behaviours of marked *Calopteryx aequabilis* individuals were recorded along a small first-order stream in Nova Scotia, Canada, from May 29 to August 13, 1983. Prominent agonistic behavioural sequences, such as "challenge", "chase and escape", "escort flight", "circular battle" and "reverse threat", as well as the reproductive sequences "cross display", "courtship arc", "mounting", "grasping" and copulation, were described and catalogued to provide a basis for further ecological studies of *Calopteryx* species in the area.

INTRODUCTION

The elaborate territorial and reproductive behaviour of *Calopteryx* spp. has been the subject of many behavioural studies in Europe, Asia and North America. An extensive catalogue of the behaviour patterns of many *Calopteryx* species already exists.

Calopteryx aequabilis, the northern-most North American representative of the genus, has received little attention, with the exception of work by WAAGE (1973) who compared the mating behaviour of *C. aequabilis* to *C. maculata*, the principal species of his study.

We undertake here to describe and catalogue the territorial and reproductive behaviour of *C. aequabilis* from a low density population in Nova Scotia.

MATERIAL AND METHODS

C. aequabilis adults were captured with aerial insect nets along a small, heavily vegetated first-order stream which flows through grain fields into the Canard River, Kings County, Nova Scotia (45°07'N, 64°29'E) (Fig. 1). Each damselfly was individually marked with waterproof ink. A total of 678 damselflies were marked over 59 study days from May 29 to August 13, 1983. Based on simple enumeration, the peak density of *C. aequabilis* reached approximately 1 adult male per 10 m along the 635 m section of stream sampled. Behavioural observation was limited to about one hour daily from 13.00 to 14.00 hrs, because the study was primarily concerned with demographics of the population.

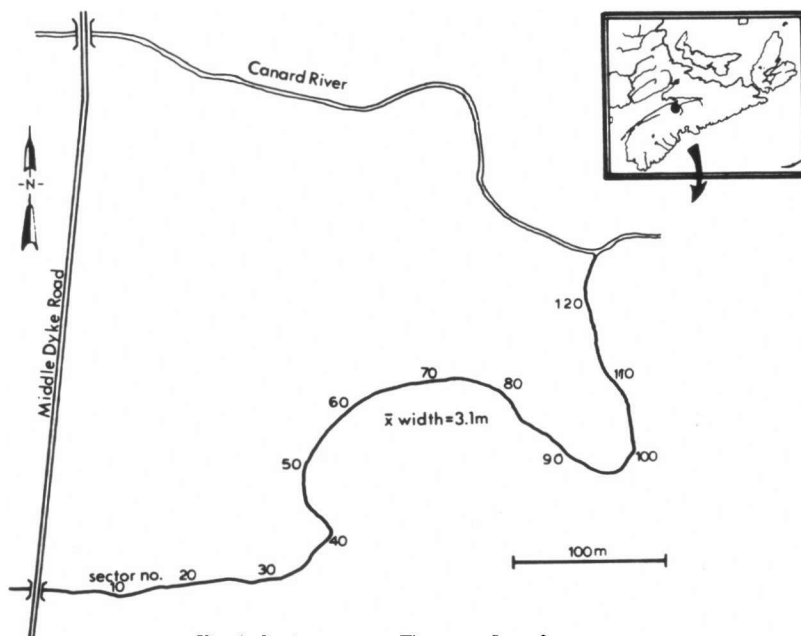


Fig. 1. Study area map. The water flows from west to east.

OBSERVATIONS

FLIGHT AND PERCHING POSTURES

Adult male *C. aequabilis* have two basic flight postures, a butterfly-like "NORMAL flight" and a more maneuverable "CROSS-WING flight", which both appear similar to the corresponding flight postures described for *C. virgo* by

PAJUNEN (1966). Males may return repeatedly to a "home perch" in their territory ("defended area), often over a number of days.

While perching, *C. aequabilis* holds its wings in two basic positions with respect to its abdomen :

LINEAR (low or high) – The anterior margin of the wings is held roughly parallel to the abdomen, and the abdomen is held either parallel to the substrate (low) or at an angle, usually $> 30^\circ$, to the substrate (high) (Fig. 2).

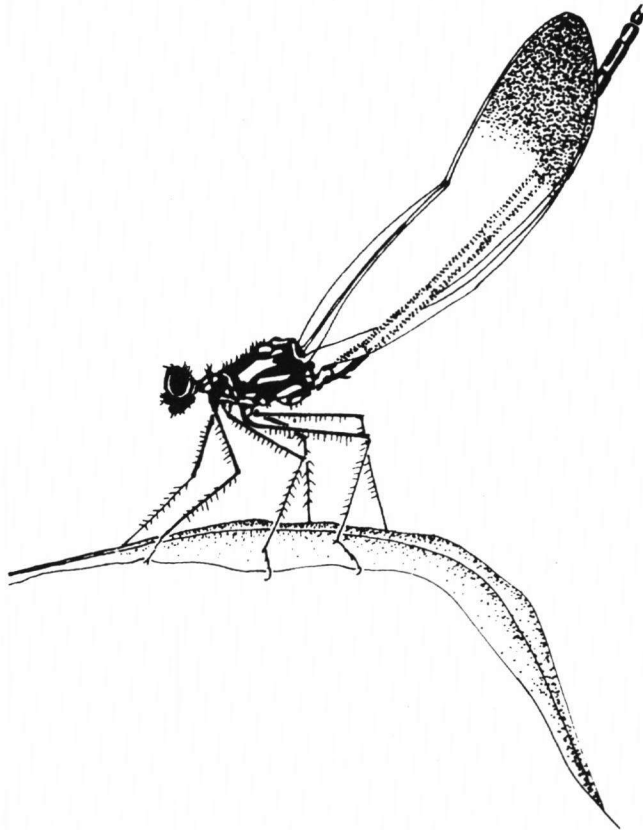


Fig. 2. "Linear high" perching posture. (Drawings by A. Woolaver.)

ANGULAR – The wings are held at an angle, usually $> 30^\circ$, with respect to the abdomen, which is roughly parallel to the substrate.

SPLAYED-WING postures, with the abdomen slightly raised, the posterior wings rotated slightly and nearly horizontal, and the anterior wings parted slightly, were also observed, most commonly in recently emerged teneral

and in some imagos on cool, cloudy days. No preference for orientation to the sun was noted. Males perching on or near the water surface often hooked abdominal segments 9 and 10 sharply upward.

WING CLAPPING (BICK & BICK, 1978), in which the wings are usually opened only halfway, was frequently observed, especially in solitary individuals immediately after brief flights. WING WARNING, as in *C. virgo* (PAJUNEN, 1966) and *C. maculata* (WAAGE, 1973) occurs in response to an intruder and may be accompanied by bobbing of the entire body. The resident male briefly splays its wings and raises its abdomen between them.

AGGRESSIVE INTERACTIONS

Aggressive interactions occurred over water, usually less than one meter above the surface.

CHASE AND ESCAPE — Flight is NORMAL and of almost any speed ; the distance between combatants varies. The chase continues until the intruder leaves the territory (Fig. 3).

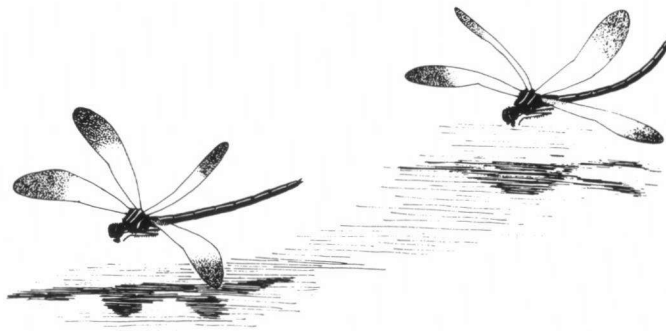


Fig. 3. "Chase and escape" aggressive encounter. The "resident" appears on the right and has an upcurved abdomen.

ESCORT FLIGHT — The resident flies beside, slightly below and usually 30-35 cm from the intruder until the intruder reaches the territory boundary.

CIRCULAR BATTLE — In this intense mutual circular chase, males may physically clash (twice both combatants fell to the water) (Fig. 4). Flight is NORMAL but rapid. The battle usually begins near a territory boundary or other contested area and may follow a CHASE AND ESCAPE OR ESCORT FLIGHT if the intruder turns back toward the resident's territory.

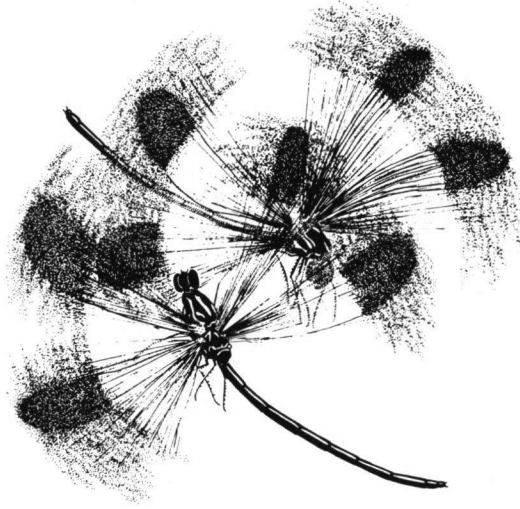


Fig. 4. "Circular battle".

REVERSE THREAT — This is a short-lived (< 10 sec) response, in which an intruder, upon re-entering his territory, faces away from his pursuer, and with little forward movement flies from side to side in an arc of approximately 30 cm (Fig. 5). This distinctly defines territory borders.

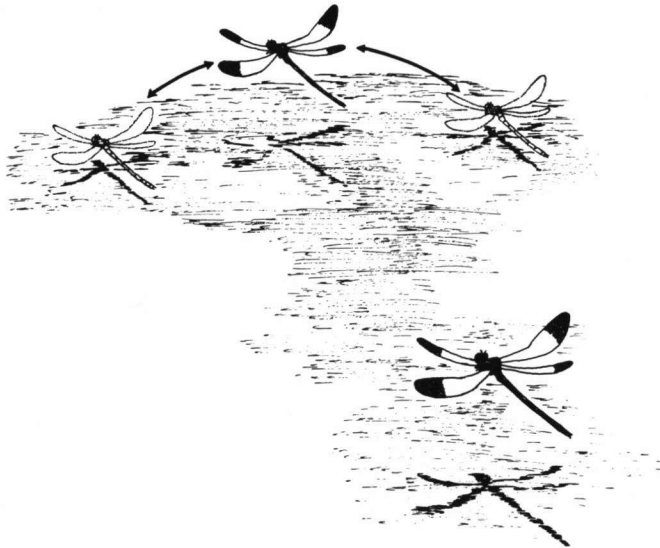


Fig. 5. "Reverse threat". The "resident" (lower right) has reached the territorial boundary of the male it is following.

REPRODUCTIVE BEHAVIOUR

CROSS DISPLAY — In the cross display the male flies toward an approaching female in the **CROSS-WING** posture (Fig. 6). His ninth and tenth segments are sharply upturned. The male always faces the female and usually his hindwings nearly or barely touch the water. Often there is some forward and backward movement with respect to the female.



Fig. 6. "Cross display". The male's wingtips barely touch the water. The female may hover briefly.

The cross display always occurs in the vicinity of the prospective oviposition site. Males rarely appear to "lead" (WAAGE, 1973) the female back to the oviposition site.

DIVE DISPLAY — The male dives to the water and spreads its hind wings flatly on the surface. Its abdomen is raised approximately 45° , with abdominal segments 9 and 10 sharply upturned. This display is brief and was infrequently observed (Fig. 7).

Only *flying* females are shown **CROSS** and **DIVE DISPLAYS**. Perching or ovipositing females are harassed until they fly and are then displayed to.

COURTSHIP ARC — If the female perches in response to the cross display the male will continue to fly in his **CROSS-WING** posture but begins bobbing between 5 and 10 cm up and down while moving in an arc around her, 20 to 30 cm from her and facing her at all times (Fig. 8). The female may offer a refusal display as described for *C. maculata* (WAAGE, 1973), but as long as she does not fly, the male will continue to slowly approach her.

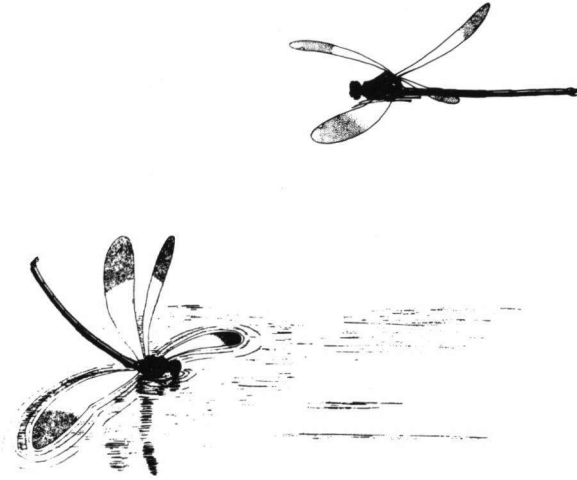


Fig. 7. "Dive display"; this display was brief and was observed infrequently.

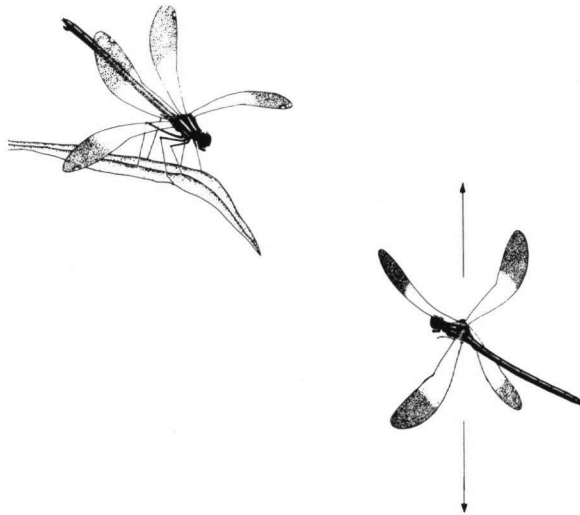


Fig. 8. "Courtship arc". The male begins bobbing up and down while moving in an arc around the perched female. The female is shown "wing-warning", regarded as a refusal display by WAAGE (1973).

COPULATION AND OVIPOSITION

The male lands on the proximal end of the female's wings and walks forward on her prothorax. Sperm translocation immediately follows tandem formation. If the pair is disturbed after tandem formation they may clumsily fly a short distance in tandem and copulate elsewhere. Copulation takes place in the vicinity of the male's territory, usually on vegetation within a meter of the water.

As soon as the "wheel" of copulation is broken the male returns to his "home perch". As in *C. maculata* (WAAGE, 1973 ; JOHNSON, 1962) the female remains perched near the site momentarily. Rather than flying directly to the oviposition site she may leave the area briefly.

The returning female is greeted by the male with a slow CROSS-WING flight. No mate recognition signal was recognized, although the female sometimes holds her abdomen upcurved. After hovering briefly the female lands on the aquatic vegetation selected for oviposition and begins probing beneath the surface of the water with the tip of her abdomen. Oviposition is endophytic. Usually only the tip of the abdomen is submerged if the available plants are suitable. Occasionally the female submerges entirely by slowly backing down the vegetation, probing and ovipositing as she goes, sometimes to depths exceeding 20 cm.

GUARDING

Typically, the male remains near the ovipositing female and guards against intruding conspecific adult males. Intruding adult females are usually courted or pursued from the territory.

Sometimes females are able to oviposit in a territory of a male with whom they have not mated. This may occur when the male is guarding another female, awaiting the arrival of a recent mate from the copulation site, or is engaged in an aggressive encounter with another male.

Twice, males that discovered "extra" females ovipositing in their territories chased away their own mates instead of the intruder, but permitted them to return without copulation. On five occasions males mated with additional females while their mates were still ovipositing. One male was seen guarding five females, some of which may have mated with other males.

Males that discover unguarded females hover over the female's wings bumping and appearing to nip at the wingtips repeatedly until a guarding male chases them or the female leaves. She may submerge or fly away. If the

female flies the male will pursue her to shore and begin a courtship arc when she perches. Attempts to forcibly take females in tandem (*C. maculata*, WAAGE, 1973) were not observed.

TIMING OF SEQUENCES

Forty-three observed cross displays led to six courtship arcs, which resulted in just two copulations. Of 14 observed copulations, 11 were discovered at the beginning of "wheel" formation or while in progress. Based on 11 timed observations, copulation time (the time spent in the "wheel") ranged from 73 to 356 seconds ($\bar{x} = 169$ s). Twelve of the observed copulations led to oviposition. Thirty ovipositions, timed to the nearest minute ranged from 1 to 24 minutes ($\bar{x} = 8.5$ min). Of 49 observed ovipositions, 13 (26%) were unguarded. Nine of the guarded females submerged, as did two of the unguarded females. There was no significant tendency for unguarded females to submerge ($G = 0.038$, $P \geq 0.5$). WAAGE (1978) reported 34 (21%) unguarded ovipositions in 162 observed ovipositions.

FEMALE OVIPOSITION TACTICS

Territorial males control access to oviposition sites and "trade" copulations for the right to oviposit in the territory (ALCOCK, 1979 ; WAAGE, 1979a). The strategy is effective for males, at least in *C. maculata*, because males have evolved a mechanism to remove and replace a previous competitor's sperm (WAAGE, 1979b).

After copulation, the male returns quickly to his territory, leaving his mate at the copulation site to follow on her own. But the female doesn't always follow her mate to "his" oviposition site. Even if she does fly promptly to her mate she does not always select the vegetation originally displayed to her by the male or deposit a large number of eggs there.

It is unlikely that a male is always able to identify his most recent mate and since unguarded oviposition seems to occur frequently in *Calopteryx*, even under high density situations (13 males per 10 m of stream, WAAGE, 1978) it does not seem that males are able to control access to *all* oviposition sites.

A female who has mated with a territorial male has several options available for her "oviposition strategy". She may oviposit in the territory of her mate under his protection, she may seek out another guarding male and try to sneak on to "his" oviposition site, or she may find a non-territorial site

and oviposit unguarded. If she is harassed by males she may choose to submerge, flee, or accept the harasser as a mate, having the store of sperm from her previous mate replaced. One female *C. aequabilis* that was followed for nearly two hours oviposited in her mate's territory, two unguarded sites and attempted to oviposit in two other male's territories.

ACKNOWLEDGEMENTS

We wish to thank Anne Woolaver for providing the illustrations of behaviours ; Mark Pulsifer and Doug Bamford for assistance in the field ; Gordon Pritchard for travel support for KFC and comments on a previous draft ; and J. K. Waage for comments on the manuscript. Financial support was provided by NSERC operating grant A7737 to TBH and an Acadia University Beardsley Summer Fellowship to KFC.

REFERENCES

- ALCOCK, J., 1979. Multiple mating in *Calopteryx maculata* (Odonata : Calopterygidae) and the advantage of non-contact guarding by males. *J. nat. Hist.* 13 : 439-446.
- JOHNSON, C., 1962. Breeding behavior and oviposition in *Calopteryx maculatum* (Beauvois) (Odonata : Calopterygidae). *Amer. Midl. Nat.* 68 : 242-247.
- PAJUNEN, V. I., 1966. Aggressive behavior and territoriality in a population of *Calopteryx virgo* L. (Odonata : Calopterygidae). *Ann. zool. fenn.* 3 : 201-214.
- WAAGE, J. K., 1973. Reproductive behavior and its relation to territoriality in *Calopteryx maculata* (Beauvois) (Odonata : Calopterygidae). *Behaviour* 47 : 240-256.
- WAAGE, J. K., 1978. Oviposition duration and egg deposition rates in *Calopteryx maculata* (P. de Beauvois) (Zygoptera : Calopterygidae). *Odonatologica* 7 : 77-88.
- WAAGE, J. K., 1979a. Adaptive significance of postcopulatory guarding of mates and nonmates by male *Calopteryx maculata* (Odonata). *Behav. Ecol. Sociobiol.* 6 : 147-154.
- WAAGE, J. K., 1979b. Dual function of the damselfly penis : sperm removal and transfer. *Science* 203 : 916-918.