# MOVEMENT PATTERNS AND BEHAVIOR OF *CALOPTERYX AEQUABILIS* SAY (ZYGOPTERA : CALOPTERYGIDAE) IN NOVA SCOTIA, CANADA

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A population of individually marked *Calopteryx aequabilis* was monitored daily during summer 1982 along a 630 m section of stream draining agricultural fields in the Canard Valley, Kings County, N.S. Among adults, resident males were more site-specific than experimentally introduced males or resident females. After emergence, tenerals remained near the stream. Teneral males became significantly more site-specific and were subject to increased mortality and/or dispersal as they matured. Oviposition was usually attended by males, and occurred both at the surface and when females were fully submerged.

## INTRODUCTION

The genus *Calopteryx* has proved ideal for behavioral, ecological, and evolutionary studies in Europe, North America and Japan. Although extensive data on other *Calopteryx* spp. are available, relatively little is known of *C. aequabilis* Say, the northernmost representative of the genus in North America.

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In our initial observations of this species we were intrigued by the distribution of different sex/age classes, by the behavioral interactions involved in spacing and/or dispersal, and by the effect of microhabitat on distribution.

We present here results of the first segment of an experimental study of demography and behavior in *C. aequabilis*. We examine abundance, residency time, patterns of movement, and some aspects of reproductive and territorial behavior.

## STUDY AREA

Damselflies were observed along a small tributary of Canard River in King's County, N.S. (45°07'N, 64°29'E). This area is part of a dyke-land reclaimed from salt marsh within the last 200 years. The substrate is fine and unconsolidated (ROLAND, 1982). The stream is bordered by hay and grain fields. A grassy strip ($\cong$ 5 m in width) above the banks of the creek was mowed several times during the summer, separating the stream vegetation from that of the fields. Dominant plants along the stream included: *Nasturtium officinale* R. Br., *Sparganium eurycarpum* Engelm., *Scirpus atrovirens* Willd., *Scirpus rubrotinctus* Fern., *Juncus effusus* L., *Spartina pectinata* Link, and *Typha latifolia* L. Among odonates *Calopteryx aequabilis*, *Calopteryx maculata* Beauvois, *Ischnura verticalis* (Say), *Enallagma hageni* (Walsh), *Sympetrum internum* Montgomery and *Anax junius* Drury were abundant.

## METHODS

A 630 m transect was flagged at 5 m intervals along the creek during June 1982. These 5 m sectors were numbered consecutively downstream. Three sections within this transect (A: sectors 1-35, B: 36-70, C: 91-125) were delimited for comparative purposes.

All *C. aequabilis* captured on the transect were numbered with indelible ink on the right forewing. When first captured, damselflies were classed as teneral or adult. Tenerals were characterized by soft, amber-coloured wings, soft bodies and, in males, less discrete banding on the wings. "Recaptures" were made with minimal disturbance with the aid of binoculars, with which marks could normally be read from distances of at least 10 m.

On 14 July 25 adult male *C. aequabilis* were captured at Habitant River (45°09'N, 64°26'E), approximately 7.5 km from the study area, transported to the study area, and released at dusk in sector 54. Their initial movements were observed from the following dawn.

The population was censused initially on 9, 18, 19, 28 June and daily in early afternoon from 1 July to 15 August. The location (sector number) of each sighting and any behavioral observations were recorded.

Height of aquatic vegetation was examined, and in each sector was assigned to one of two categories: tall (≥ 50% of cover exceeding 1 m) or short (> 50% of cover not exceeding 1 m).

G-tests for heterogeneity and independence, Mann-Whitney U-tests, and Kolmogorov-Smirnov two-sample tests were used for statistical analyses where appropriate. In U-tests where $n_1 > 20$, t-values corrected for ties were computed (SOKAL & ROHLF, 1969).

## RESULTS

### *Abundance*

*C. aequabilis* were first observed on the study area on 6 June, and by mid-June were abundant, but the population was not systematically sampled until 1 July. The last sighting of the season occurred on 13 August. Throughout the season, 300 individuals were marked.

Over the entire transect, after 30 June, male *C. aequabilis* significantly outnumbered females ($U = 1167$; $t_{(cor)} = 2.56$, $p < 0.02$), even without inclusion of the experimentally introduced males. However, sex ratio of tenerals at first capture was nearly 1:1 (45♀♀; 50♂♂). Oscillations in numbers of the two sexes did not always appear to be synchronous. Abundance of females began to decline slightly earlier than that of males.

Temporal patterns of abundance differed along different sections of the transect. In section C, where the creek was relatively narrow and shallow, numbers fell more sharply than in other parts of the transect after mid-July. Dry weather and encroachment of vegetation on patches of open water, required for reproductive behavior in *C. aequabilis*, may have been responsible.

After the introduction of adult males to section B on July 14, densities of resident males and females in section 3 continued a decline that, for females at least, had been in effect before the introduction. However, a temporary increase in numbers of males and females occurred in other sections (Fig. 1).

### *Duration of Residency*

Males first captured as tenerals either emigrated or died in relatively higher numbers than other classes from 3-5 days after initial capture (Fig. 2). However, overall, the duration of residency on transect of males first captured as tenerals did not differ significantly from that of males first captured as adults ($U = 451$; $t_{(cor)} = 0.02$, $p > 0.5$) or from that of females first captured as tenerals ($U = 483.5$; $t_{(cor)} = 0.52$, $p > 0.5$) (Table I).

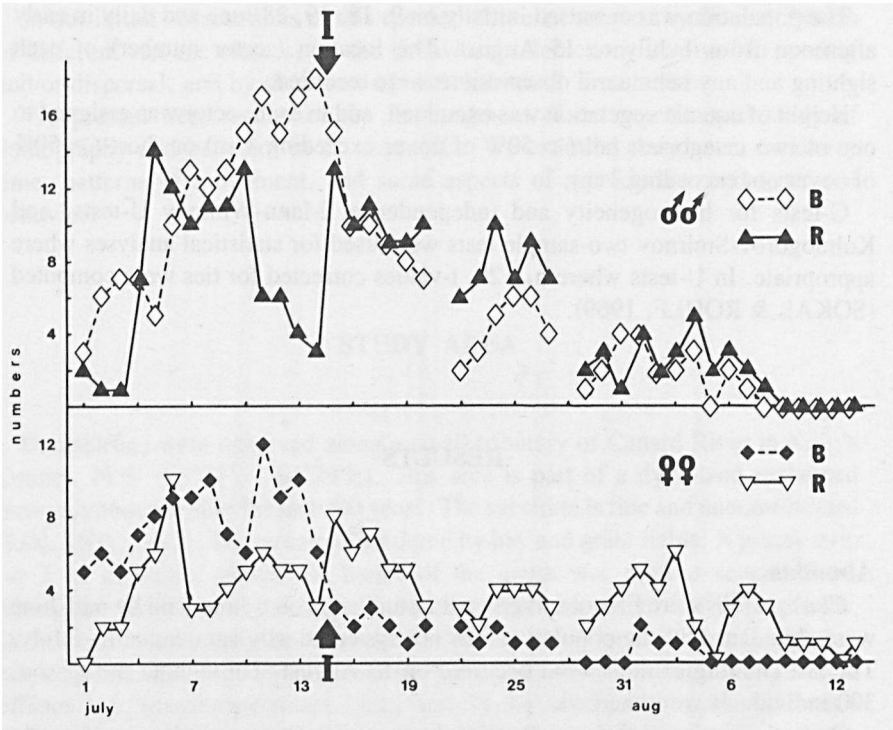


Fig. 1. Daily censuses of local males and females in area of introduction (Section B) and in remainder (R) of study area.

Table I
Duration of residency in study area for different classes of *C. aequabilis* (days).

| Class | n | $\bar{x}$ | Median | Maximum |
|---|---|---|---|---|
| "Local" males marked as adults | 45 | 7.29 | 4 | 28 |
| "Local" females marked as adults | 24 | 5.96 | 4.5 | 19 |
| "Local" males marked as tenerals | 50 | 6.92 | 5 | 30 |
| "Local" females marked as tenerals | 45 | 5.62 | 3 | 29 |
| Experimentally introduced males (adult) | 25 | 4.28 | 2 | 20 |

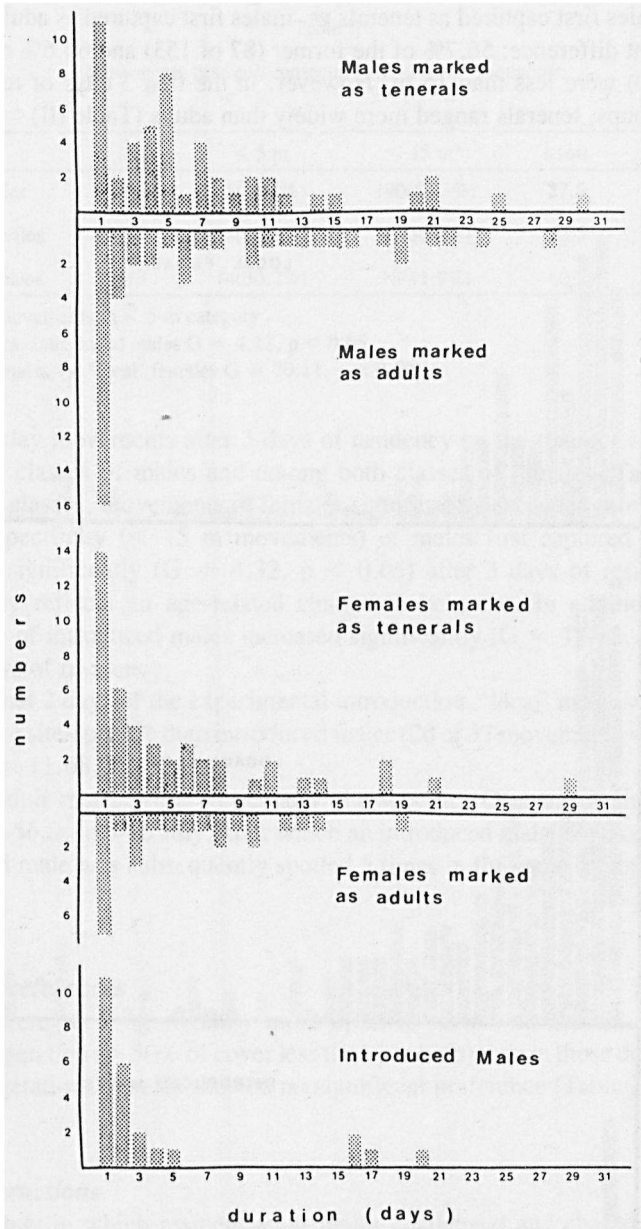


Fig. 2. Duration of residency on transect of "local" males marked as tenerals (above) and adults (below), of "local" females marked as tenerals (above), and adults (below), and of introduced males.

### *Movements*

Distributions of movements by "local" males differed significantly from those of introduced males or "local" females (Kolmogorov-Smirnov, $p < 0.01$; Fig. 3). "Local" males were more site-specific than the other 2 groups (Table II). A comparison of movements between consecutive days over the entire residency

time of males first captured as tenerals vs. males first captured as adults revealed no apparent difference: 56.7% of the former (87 of 153) and 60.6% of the latter (97 of 160) were less than 15 m. However, in the first 3 days of residency of these 2 groups, tenerals ranged more widely than adults (Table III).

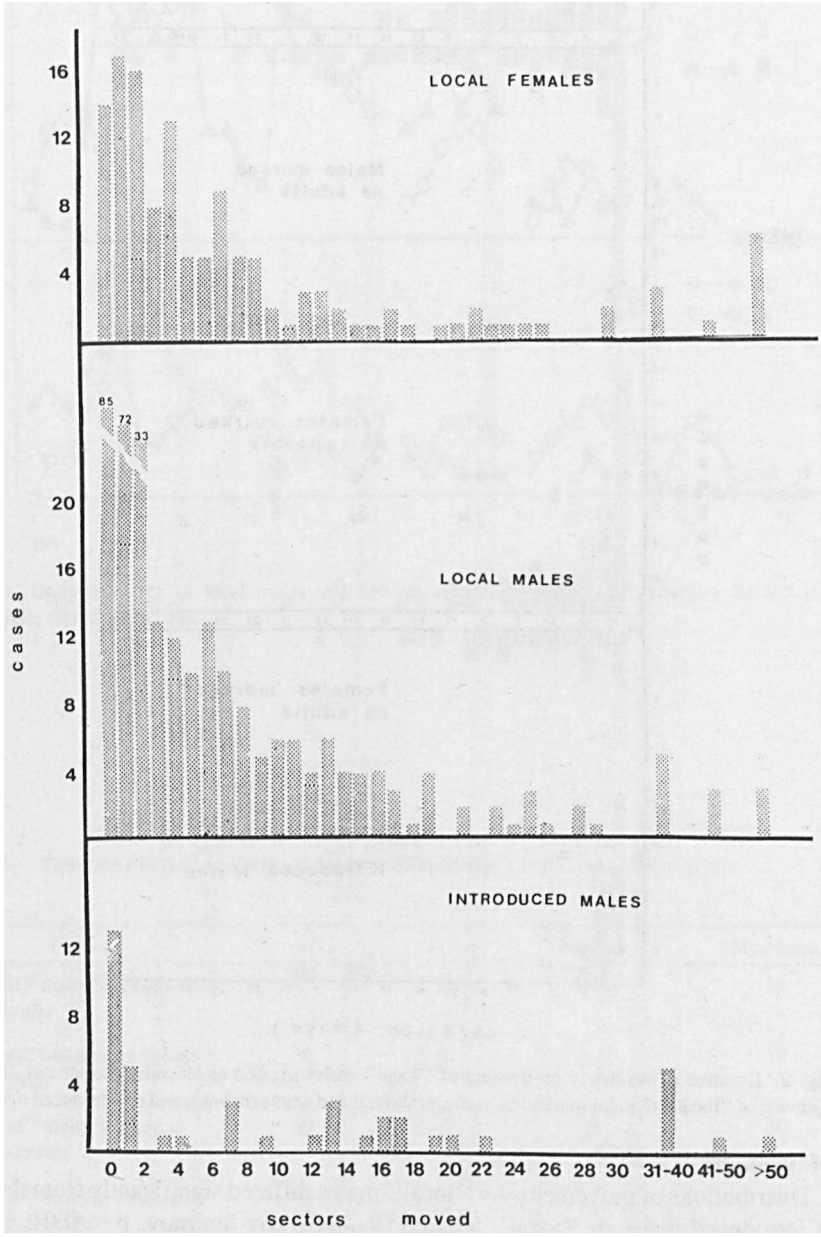


Fig. 3. Distance moved between consecutive days by "local" males, introduced males, and "local" females.

Table II

Movements between consecutive days by *C. aequabilis*.

| Class | n | < 5 m | < 15 m* | $\bar{x}$ (m) | Median (m) |
|---|---|---|---|---|---|
| "Local" males | 326 | 85(26.1%) | 190(58.3%) | 27.5 | 10 |
| "Local" females | 133 | 14(10.5%) | 47(36.1%) | 52.5 | 20 |
| Introduced males | 43 | 14(30.2%) | 18(41.9%) | 60.2 | 35 |

* Includes movements in < 5 m category
"Local" vs. introduced males $G = 4.12$, $p < 0.05$
"Local" males vs. 'local' females $G = 20.11$, $p < 0.001$

Day to day movements after 3 days of residency on the transect were similar among all classes of males and among both classes of females (Table III). In both local classes, movements of females significantly exceeded those of males. The site-specificity (< 15 m movements) of males first captured as tenerals increased significantly ($G = 4.32$, $p < 0.05$) after 3 days of residency; this presumably reflects an age-related change in behavior. In addition, the site specificity of introduced males increased significantly ($G = 12.42$, $p < 0.005$) after 3 days of residency.

In the first 2 days of the experimental introduction, 'local' males were significantly more site-specific than introduced males (20 of 37 movements < 15 m vs. 1 of 16; $G = 11.68$, $p < 0.001$).

Some adult males were particularly site-specific. One was seen 9 times in sectors 55-56 from 8-16 July, after which an introduced male displaced him. The introduced male was subsequently spotted 5 times in the same sectors.

### *Habitat Preferences*

Males were seen significantly more often in sectors dominated by "short" aquatic vegetation (> 50% of cover less than 1 m high) than in those dominated by "tall" vegetation; females showed no significant preference (Table IV).

### *Male Interactions*

Encounters in which resident adult males challenged and chased adult male intruders were common. Simple chases in which residents flew to meet intruders and then followed several cm behind predominated, while intense whirling encounters, in which wings of the two combatants audibly struck, occurred less frequently. The latter were observed only over patches of open water. In nearly all encounters residents successfully retained territories (= defended areas). On the day of the introduction both types of male-male interactions increased noticeably. Territorial males were tolerant of teneral males and allowed them to perch within a few cm.

Table III

Movements between consecutive days by *C. aequabilis* during individuals' first 3 days (≤ 3) vs. after 3 days (> 3) on transect. Mann-Whitney U-statistics from comparisons among classes shown below.

| | | Movements | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | n | | < 15 m (%) | | $\bar{x}$ (m) | | median (m) | |
| | Class | ≤ 3 | > 3 | ≤ 3 | > 3 | ≤ 3 | > 3 | ≤ 3 | > 3 |
| A. | "Local" males marked as adults | 36 | 125 | 61.0 | 60.0 | 24.6 | 28.3 | 10 | 5 |
| B. | "Local" females marked as adults | 13 | 29 | 38.5 | 31.0 | 26.9 | 66.6 | 17.5 | 35 |
| C. | "Local" males marked as tenerals | 49 | 106 | 42.9 | 62.3 | 38.3 | 29.4 | 17.5 | 5 |
| D. | "Local" females marked as tenerals | 37 | 53 | 35.1 | 35.8 | 43.4 | 46.5 | 20 | 25 |
| E. | Introduced adult males | 16 | 27 | 6.3 | 63.0 | 105.0 | 32.8 | 85 | 5 |

| | | |
|---|---|---|
| ≤ 3 | A vs. C | $U = 1113$ ; $t_{(cor)} = 2.07$, $p < 0.01$ |
| | A vs. E | $U = 547$, $p < 0.01$ |
| | B vs. D, A vs. B, C vs. D | not significant |
| > 3 | A vs. B | $U = 2543.5$; $t_{(cor)} = 3.24$, $p < 0.01$ |
| | C vs. D | $U = 3557.5$; $t_{(cor)} = 2.76$, $p < 0.01$ |
| | A vs. C, A vs. E, B vs. D | not significant. |

Table IV

Number of sightings of *C. aequabilis* in relation to dominant height of aquatic vegetation (see Methods).

| | Vegetation Height | |
|---|---|---|
| | 'Short' | 'Tall' |
| Number of sectors | 89 | 37 |
| Sightings of males | 418 | 85 |
| Male sightings/sector | 4.69 | 2.30 |
| Sightings of females | 226 | 60 |
| Female sightings/sector | 2.54 | 1.62 |
| Males: "tall" vs. "short" | $G = 9.27, p < 0.005$ | |
| Females: "tall" vs. "short" | $G = 3.27, 0.10 > p > 0.05$ | |

### *Reproduction*

Reproductive behavior was observed only on warm days (daily max: 25-33°C), under either cloudy or sunny and either windy or calm conditions. All observed copulations followed courtship and involved territorial males. Seven timed copulations ranged from 120-300 seconds. Females sometimes oviposited at the surface with only the tips of their abdomens submerged. At other times they descended below the surface to oviposit. Complete submersion was witnessed in 7 of 17 oviposition sequences. Submersion time varied from 7 to > 50 min. In only 3 cases did females oviposit in the absence of males.

## DISCUSSION

The data on abundance must be interpreted cautiously. Values include tenerals and non-territorial adult males that may have been transient. However, the vast majority (≥ 65%) of individuals in all classes were recaptured at least once (HENDERSON, 1983).

Do behavioral interactions help to maintain densities of adult males at or below some threshold? The introduction experiment did not increase densities of males above former levels for long. Unfortunately, numbers had begun to decline on at least parts of the transect by the beginning of the introduction. Thus the results of the introduction must remain inconclusive.

Initially, introduced males appeared to be at a disadvantage in territorial disputes. Resident males became no less site specific on the 3 days following the introduction, whereas introduced males were highly mobile at this time. In fact, 11 introduced males were never seen again after the release date. Similar fates of introduced males of other dragonfly species have been reported (ST. QUENTIN, 1934; MOORE, 1953).

Tenerals remained at the stream during maturation. Territorial males appeared to tolerate teneral males until they matured; this would explain the relatively high rate of disappearance of males marked as tenerals 3-5 days after initial capture. In other odonates, young mature males are often inferior competitors (CORBET, 1980).

However, factors other than territorial or aggressive behavior undoubtedly also influenced daily abundance. High winds on 1-3 July appeared to reduce abundance substantially, and numbers of both sexes were lower than in June censuses. In part these reductions reflected changes in activity and thus "trappability". Some individuals were discovered in mid-day taking shelter beneath leaves; thus the likelihood that some were overlooked increased in windy weather.

The overall predominance of males in census samples, despite nearly even sex ratios of tenerals at first capture, suggests differential emigration/immigration, mortality, or trappability between sexes. Females were somewhat less conspicuous and may have escaped notice more frequently than males. We have no reason to suspect that females left the transect more often than males, particularly since extensive clearing from agricultural activity on either side of the stream provided little cover away from water. Based on the larger number of males (45) than females (24) first captured as adults, immigration of adult males appeared to exceed that of adult females.

Males spent significantly more time in open areas than in tall vegetation, whereas females did not. Males must display in order to attract potential mates and maximize their fitness whereas females need only expose themselves for brief bouts of reproductive activity. WAAGE (1980) found a similar pattern in *C. maculata*, which he attributed to the availability of oviposition sites.

Site specificity did not apparently weaken as the season progressed. In places where there were clear landmarks, males appeared to have more limited territories. A similar pattern was observed by PAJUNEN (1966) in *Leucorrhinia rubicunda*.

In the present study *C. aequabilis* males and females displayed patterns of movement similar to those observed by WAAGE (1972) in *C. maculata*. Females on average were less site specific and ranged farther each day than males. Males were usually highly localized, but also composed the majority of adult immigrants. This suggests a bimodal pattern of male movements, due to occasional long distance dispersal.

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