

**LONGEVITY AND MOBILITY OF ADULT *CALOPTERYX MACULATA*
(BEAUVOIS, 1805) (ZYGOPTERA: CALOPTERYGIDAE)**

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Average adult life span including an 11 day teneral period was 16-20 days for males and females, with a maximum of 47 days. Longevity estimates were not significantly altered by increasing the area censused for marked adults from 30 m to 1,128 m, indicating that dispersal was not affecting the estimation of longevity. Most males were territorial, many remaining in the same place up to eight days. Females were rarely found in the same place on consecutive days and their average mobility was greater than that of most males. Maximum movement between days was 122 m for females and 536 m for males. Non-territorial males in some populations of *Calopteryx* are probably individuals unable to acquire territories when there are more males in an area than territory sites. In *C. maculata* these males quickly occupy oviposition sites added to an area and become territorial at them.

INTRODUCTION

In this paper I present the results of two mark-recapture studies on adult *Calopteryx maculata* (Beauvois). The studies provide information on male-female differences in longevity and mobility, and offer estimates of these parameters for comparison with those of other odonates, especially other *Calopteryx*.

These large, conspicuous damselflies are well suited for this type of study. They are easily captured and marked, and resume normal activity at the water within minutes after release. The marks are easily seen at a distance against their dark body and wing coloration. Both sexes spend much of their time perching in the open on vegetation along streams. Their dispersal is primarily along these streams, making it easy to census an area for marked individuals.

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METHODS

The ecology of *C. maculata* was studied along Fleming Creek in The University of Michigan Matthaei Botanical Gardens. This creek drains an area of farm and pasture land northeast of Ann Arbor, Michigan. Approximately 400 m of creek north of and including a 30 m primary marking area and 730 m south of it were censused during mark-recapture studies in the summers of 1968 and 1970.

Adults were marked on the thorax, wings, or abdomen with dots of enamel paint such that several hundred of each sex could be individually distinguished. Most marking was done at the water, but during 1970 a number of individuals were marked in pine woods 90 m from the stream. Periodic censuses involved wading along the stream or walking around the pine woods, counting unmarked individuals and plotting the locations of marked individuals on maps of the census areas. Recapture of individuals during a census was rarely necessary because their marks could be seen at a distance of several meters. Occasionally surveys were repeated at different times of the same day.

The longevity and mobility data are both non-normally distributed, and were analyzed with the Mann-Whitney U-statistic, and the Chi-square 2 X 2 contingency test for independence. The level of significance was $p = 0.05$. Both means and medians are presented in the tables even though the means are biased upward by a positive skew of the longevity and mobility distributions.

LONGEVITY

Here longevity is an estimate based on the length of time between marking and last recapture of individuals returning to the stream following a teneral period of about 11 days (WAAGE, 1971). Combining the two marking studies (Table I), the mean longevity was 6.2 days for males (median = 5 days) and 8.6 days for females (median = 5 days). The difference between sexes was not significant ($U = 13929.0$, $n_1 = 215$, $n_2 = 143$, $p = 0.066$). Combining the 11 day

Table I
Results of marking studies on *Calopteryx maculata*

	1968		1970	
	♂♂	♀♀	♂♂	♀♀
No. Marked	212	160	148	138
No. Recaptured	140	79	75	64
Mean Longevity (days)	5.5	7.7	7.7	9.6
Median Longevity (days)	4.4	4.5	6.0	5.5
Maximum Longevity (days)	32	37	37	35

teneral period with the 4-6 day longevity estimates, the average adult life span of *C. maculata* is 15-17 days.

Although estimates of average adult life span for four *Calopteryx* species agree (Table II), variations exist in the estimations of the teneral period and mean longevity. These variations may result from: (1) species differences; (2) differences in criteria used to determine limits of the teneral period; (3) temperature differences, which BUCHHOLTZ (1951) has shown to affect the maturation rate; and (4) differences in age at marking.

Table II
Longevity estimates for different species of the genus *Calopteryx*

Species	Sex	Number of days as:			Life span
		Teneral Mean	Adult Mean	Adult Maximum	
<i>maculata</i> (1)	♂ + ♀	11	4-6	37	15-17
<i>splendens</i> (2)	♂ + ♀	1-4	12	—	13-16
<i>virgo</i> (3)	♂	1-3	10-12	41	11-15
<i>haemorrhoidalis</i> (4)	♂	10	—	19?	—

(1) Present study; (2) BUCHHOLTZ (1951) (8 ♂♂, 2 ♀♀); (3) KLÖTZLI (1971) (46 & 68 ♂♂); and (4) HEYMER (1971).

Similar estimates for average adult life are available for several other Zygoptera: about 23 days for *Lestes disjunctus australis* (BICK & BICK, 1961); 21 days for *Argia moesta* (BORROR, 1934); about 22 days for *Pyrhosoma nymphula* (CORBET, 1952, 1963); and less than 25 days for *Hetaerina americana* (JOHNSON, 1962b). None of these authors noted a significant difference between the sexes in longevity.

Effect of Mobility on Estimates of Longevity

A major assumption in the estimation of longevity by the mark-recapture method is that the disappearance of marked individuals is due to death and not to emigration from the census area. To determine if emigration affected the estimation of longevity in this study, longevity was recalculated for five lengths of stream surveyed: 30 m, 396 m, 655 m, 762 m, and 1,128 m (Table III). Only individuals marked in the primary marking area were included. There was no significant increase in longevity for males ($U = 3017.5$, $p = 0.096$) or females ($U = 1023.0$, $p = 0.086$) between the 30 m and 1,128 m survey distances, suggesting that the loss of marked adults in this study was due to death and not to dispersal along the stream.

Table III
 Estimations of longevity of *Calopteryx maculata*, using
 five different lengths of stream surveyed

Length of stream surveyed (meters)	Sex	N	Longevity (days)		
			Median	Mean	Std. dev.
30	♂♂	64	4.0	4.66	3.56
	♀♀	42	3.0	6.57	7.86
396	♂♂	82	4.0	5.02	4.06
	♀♀	50	4.0	8.26	8.61
655	♂♂	96	4.0	5.06	3.82
	♀♀	55	4.0	7.42	7.89
762	♂♂	103	4.0	5.21	4.02
	♀♀	58	4.0	8.35	8.42
1,128	♂♂	107	5.0	5.68	4.48
	♀♀	58	4.0	8.81	8.65

Sources of Mortality

During 1968-71, 31 males and 7 females were either found dead or observed being eaten. The excess of males probably reflects a greater portion of observation time at the water where males were more common. Four males and one female were found dead but uneaten in the water.

Spiders, including *Tetragnathidae*, *Lycosidae*, *Pisauridae*, *Araneidae*, and *Theridiidae* preyed upon 11 males and 5 females at or within a few meters of the water. One male perched near an ovipositing female was taken by a green frog (*Rana clamitans*). The dragonfly, *Boyeria vinosa*, often patrolled areas of stream where *C. maculata* was present, but only one predation (a male) was observed.

The wings of 14 males found along the shore and in the pine woods were assumed to be remains left by birds (spiders would also leave some exoskeleton). A redwinged blackbird (*Agelaius phoeniceus*) took one female. Other birds whose activities indicated they were potential predators included: cedar wax-wings (*Bombycillia cedrorum*), eastern kingbirds (*Tyrannus tyrannus*) and bronze grackles (*Quiscalus versicolor*).

MOBILITY

Males and females were concentrated along sections of the stream where emergent vegetation and debris accumulated on fallen branches provided numerous oviposition sites. Males comprised 54-63% of the population at the

water, but only 27-43% of that in the nearby pine woods. The pine woods population consisted mainly of teneral of both sexes and mature females. Along the creek densities ranged from less than 1 to 30 individuals/10 m.

Distances between locations of marked individuals on successive days, measured on census maps, were used to estimate mobility. This estimate did not include movements to and from sleeping places on shore, which ZAHNER (1960) found to involve several meters for *C. splendens*. Movement was assumed to occur along the stream and not overland.

Male and female mobility differed in several respects (Fig. 1). A significantly

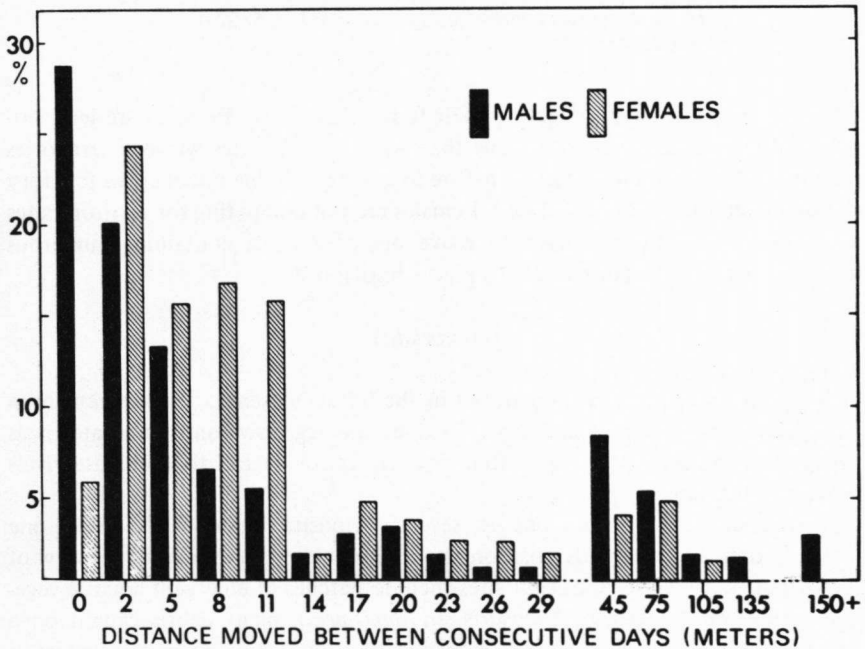


Fig. 1. Percent of males and females plotted against distance moved between consecutive days. Note division of the abscissa into 4 interval classes: 0 m, 1-30 m in 3 m increments, 31-150 m in 30 m increments, and greater than 150 m. The figure is based on 153 estimates for 77 males and 94 estimates for 41 females.

greater proportion of the males did not move between days (29% versus 5.5% of the estimates, $\chi^2 = 18.67$, $p < 0.001$). The mean distance moved by males was greater than that for females, reflecting a small number of extreme movements by some males, but females were significantly more mobile than males as expressed by their median movement (Table IV). A significantly greater proportion of the females moved less than 31 m/day (92% versus 82% of the estimates, $\chi^2 = 4.20$, $p < 0.05$).

These results suggest that males either localize strongly or move considerable

Table IV
Distance moved between consecutive days by males and females
of *Calopteryx maculata* in 1968 and 1970

Sex	N	Distance moved in m/day			
		Median	Mean	Std. dev.	Range
♂♂	153	3.4	25.0	62.4	0-536
♀♀	94	7.4	13.4	20.4	0-122

U-test: males versus females; distance moved: $U = 5852.0$,
 $p = 0.0068^{**}$

distances between days, reflecting their territorial nature. Females are less variable and in general are more mobile than most males. Males without territories may move considerable distances before locating a suitable unoccupied territory site or a male that can be displaced. Females are not competing for territory sites and would normally not have to move out of an area containing numerous oviposition sites to acquire mates or places to oviposit.

Territoriality

Males of *C. maculata* are territorial in the following sense: (1) they remain in or regularly return to a fixed area; (2) they are aggressive and dominate rivals within this area; (3) they are often not aggressive or fail to dominate rivals outside of this area.

Territories contain from one to several oviposition sites and at least one perch, within 2 m of the oviposition site and providing an unobstructed view of the oviposition area. Oviposition sites include patches of emergent aquatic vegetation (e.g. *Potamogeton*, *Anacharis*, or *Sagittaria*); plant debris caught on a fallen branch in the water or on a branch of a bush trailing in the water; or leaves, sticks, and grass that had fallen into the water. Males defend their territories against intruding conspecific males by displays and chasing.

Males occupied the same territory for periods of 1-8 days ($\bar{x} = 2.9$ days, $n = 43$). ZAHNER's (1960) estimates of permanence in a territory were 1-8 days and 1-13 days ($\bar{x} = 1.9$ and 2.4 days) for *C. splendens* and 1-13 days ($\bar{x} = 3.1$ days) for *C. virgo*. KLÖTZLI (1971) noted a maximum of 41 days for *C. virgo*, and HEYMER (1971) found a maximum of 19 days for *C. haemorrhoidalis*.

KLÖTZLI (1971) found that the frequency of territory change in *C. virgo* was significantly higher for the youngest and oldest males than for males in middle age groups, and that the territory stability of the younger males was even less at higher densities.

Nonterritorial Males

At high densities some males do not behave territorially. Such males may move about on shore, periodically interacting aggressively with territorial males, or several may simultaneously perch on a single clump of emergent vegetation representing a potential oviposition site. When oviposition sites are added to an area by placing sticks in the water and draping them with *Potamogeton*, previously nonterritorial males perch on them within a few minutes and become territorial.

Decreases in territory size, level of aggression, and territory stability, and increases in the proportion of nonterritorial males, have been correlated with increases in population density in *C. splendens* and *C. virgo* (BUCHHOLTZ, 1951, 1955; KLOTZLI, 1971; PAJUNEN 1966; and ZAHNER, 1960). Nonterritorial males have been found under a wide range of population densities: 18 males/10 m in *C. maculata* (present study); 30-60 males/10 m in *C. splendens* (ZAHNER, 1960); and 2 males/10 m and 47 males/10 m in *C. virgo* (KLÖTZLI, 1971; PAJUNEN, 1966). HEYMER (1971) and JOHNSON (1962a) did not report nonterritorial males in *C. haemorrhoidalis* and *C. maculata*.

BUCHHOLTZ (1955), PAJUNEN (1966), and WAAGE (in preparation) noted differences in the pair-forming and post-copulatory behaviour of territorial and nonterritorial males of *C. maculata*, *C. splendens*, and *C. virgo*. Nonterritorial males show no attachment to or defense of a specific area; they engage in a mobile pursuit-type of courtship or attempt to pair with ovipositing females or females perched on shore, and they show no attachment to females following mating.

At high male densities (an excess of males over territory sites), three alternatives are available for males unable to acquire a suitable territory in a particular area: (1) they can be territorial on less suitable sites in the area; (2) they can emigrate to another area; or (3) they can be nonterritorial. Understanding the merits of these various alternatives will involve estimating the relative fitness of territorial and nonterritorial males under varying densities and arrangements of oviposition sites. Using artificial oviposition sites as described above, one could vary the arrangement and number of potential territory sites in an area and record the changes in behavior and mating success of marked males of known age.

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