ADULT SEX RATIOS AND FEMALE REPRODUCTIVE POTENTIAL IN *CALOPTERYX* (ZYGOPTERA: CALOPTERYGIDAE)

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Census data suggest that population sex ratios of adult *C. maculata* (P. de Beauv.) and *C. dimidiata* Burm. are 1:1 despite an excess of males (significant in *C. maculata* only) at the water. The adult sex ratios of both species, however, were strongly influenced by where censuses were made and the differences found appeared to reflect different activity patterns of males and females and not true distortions of the population sex ratios.

Reproductive potential of *C. maculata* females was estimated from egg counts and sperm volume indices of dissected females. Those females collected along the stream prior to the daily (1300-1500 hrs) peak in reproductive activity and those collected immediately before or after copulation carried maximum numbers of eggs (averages = 267-272). There was a steady decrease in egg number per female during the day. Females collected after 10-15 min of oviposition and those collected in woods adjacent to the stream carried the fewest eggs (averages = 155 and 177). Sperm volume indices also decreased during the day in samples of females at the water. Maximum sperm volumes were found in postcopula females. However, females collected in tandem prior to copulation had 83% of the maximum and females collected after 10-15 min of oviposition had 90% of the maximum sperm index. Females collected in the woods still carried 65% of the maximum. The substantial sperm volumes carried by females prior to mating and after oviposition suggest that many matings may occur primarily to provide access to specific oviposition sites and guarding males. The variations found in female reproductive potential are consistent with predicted female activity patterns that would result in an excess of males at the water.

INTRODUCTION

Although there is considerable variation in the juvenile (larval and exuvial) sex ratios of Zygoptera (LAWTON, 1972), the general tendency is

toward the 1:1 ratio expected from the XX/XO sex determination mechanism of odonates. In contrast, males make up 60-90% of adult damselflies censused at breeding and oviposition sites (see discussion). It is generally assumed that this male excess at the water reflects differential activity by males and females and not the true adult population sex ratio. Odonate females mature and oviposit a number of clutches of eggs during their lifetime (CORBET, 1962). Presumably they periodically come to oviposition areas at the water to mate and oviposit, remaining away from the water and male activity between clutches. Males are most likely to obtain mates at or near oviposition sites and thus tend to aggregate in these areas throughout the breeding season.

While the above generally reflects what is known about zygopteran reproductive behavior, it rests on two assumptions that have rarely been tested:
(1) Female activity and distribution patterns reflect their reproductive potential.
(2) The total population sex ratio is 1:1, or at least not as distorted as that found in samples taken at the water.

This paper examines adult sex ratios for *Calopteryx maculata* (P. de Beauvois) at and away from the water and the correlations between the quantities of eggs and sperm carried by *C. maculata* females and their distribution and activity. In addition, census data are presented for *C. dimidiata* Burmeister which reveal a 1:1 adult sex ratio at the water.

METHODS

Sex Ratios

Periodic censuses of 30 and 400m sections of Fleming Creek and the edge of a nearby, planted pine woods in the University of Michigan Botanical Gardens, Washtenaw Co. Michigan (cf. WAAGE, 1971) in 1968-72 provided data on adult *C. maculata* sex ratios at and away from the water. Periodic censuses of a 250m section of the Palmer River in Rehoboth, Massachusetts during 1976 and 1977 provided additional data on adult sex ratios for both *C. maculata* and *C. dimidiata*. These censuses were made between 1200 and 1500 hrs on clear or partly cloudy days when adult activity was maximal (cf. Fig. 1). Where census data were pooled for several samples, recounts of the same individuals may have occurred, thereby biasing the estimated sex ratios slightly toward males (cf. PARR & PARR, 1979). A collection (n = 247) of nymphs of *C. maculata* from Fleming Creek in 1968-70 provided an estimate of the juvenile sex ratio. Nymphs were sexed using abdominal characters described by MARTIN (1939).

Eggs and Sperm

Reproductive potential was assessed from eggs and sperm carried by *C. maculata* females collected in different contexts at and away from the water. Collections were made on the Flat River above Stepstone Falls, Escoheag, Rhode Island and the Palmer River, Rehoboth, Massachusetts in 1978. Females were collected in seven contexts:

(a)   Woods — in a pine woods 20-200m from the stream (1000-1500 hrs)
(b)   On stream early — at the water 1000-1200 hrs
(c)   On stream middle — at the water 1200-1500 hrs
(d)   On stream late — at the water 1500-1700 hrs
(e)   In tandem — in tandem but before copulation
(f)   Postcopula — after copulation but before oviposition
(g)   Postoviposition — after 10-15 min of oviposition

Collected females were kept in a portable cooler in the field, and were transferred to a refrigerator (4°C) for 1-3 days or frozen (-20°C) until dissection. Dissection, in 70% ethanol, involved removing both ovaries and the sperm storage organs (bursa copulatrix, spermatheca and vagina) with fine-tipped dissecting forceps. The genitalia were easily removed by taking off the ventral sclerite of abdominal segment 8 and then pulling on the ovipositor valves. Under a dissecting microscope, the ovaries were teased apart and mature eggs (clear) were separated from immatures (opaque) and counted.

The vagina and sperm storage organs are sheathed in muscle and fatty tissues that obscure the transparent bursa copulatrix, and spermatheca. These tissues were teased off with dissecting forceps after they had first soaked for a minute in a 1:1 mixture of acetic acid and 70% ethanol. In this species the genitalia and the sperm in them were not visibly altered by this treatment. However, this may not be true for all odonates. Sperm of *Celithemis elisa* contracts into a granular form, unrecognizable as sperm, if exposed to even dilute acetic acid.

Once the surrounding tissues are removed, the sperm mass can be easily seen within the bursa copulatrix and spermatheca. Since *Calopteryx* sperm is clumped and virtually impossible to separate, I did not attempt to estimate the number of sperm per female. Instead, the volume of sperm contained in the bursa and spermatheca was estimated by measuring the dimensions of the sperm mass within them using an ocular scale at 40X. An index of sperm volume was then calculated and is presented without units of measure in tables and text. Sample sizes for sperm volume estimates are smaller than for egg number estimates because many of the females used for egg numbers were also used in tethering experiments involving matings with males (WAAGE, 1978, 1979), thereby making them inappropriate for sperm volume estimates in the context in which they were originally collected.

The significance of differences in sex ratios from 1:1 was assessed using the G statistic (SOKAL & ROHLF, 1969). The significance of differences in egg number and sperm volume was assessed by analysis of variance. These data are presented in text and tables as mean ± standard error.

RESULTS

SEX RATIOS

While I have no estimate of the sex ratio at emergence, a sample of late instar nymphs from the Fleming Creek population revealed a 1:1 ratio (121 male:126 female, G=0.06, p>0.1). Mark-recapture estimates of survivorship for *C. maculata* (WAAGE, 1972) do not reveal a differential in male and female longevity. Assuming this holds for other populations, adult sex ratios should largely reflect differential activity and habitat preferences of the sexes.

Stream censuses on Fleming Creek, 1968-71 (Tab. IA) and the Palmer River, 1976-77 (Tab. II, *C. maculata*) revealed a variable but significant

Table I

Pooled sex ratios from censuses (N>30) of *Calopteryx maculata* at and away from
Fleming Creek - Michigan, 1968-72. (N = sample size, (n) = number of censuses pooled,
% ♂ = percent of males in pooled sample, and * = significant (p<0.05) deviation from
1:1 sex ratio by G-test)

A. Fleming Creek - at the water

Sample period	1968 N (n)	% ♂	1969 N (n)	% ♂	1970 N (n)	% ♂	1971 N (n)	% ♂
1-15 June	48 (1)	65*	36 (1)	53	583 (2)	62*	201 (2)	61*
16-30 June	237 (3)	58*	72 (1)	81*	503 (1)	62*	569 (2)	62*
1-15 July	—		404 (2)	62*	828 (2)	60*	1053 (2)	64*
16-31 July	241 (6)	68*	—		522 (2)	57*	979 (3)	62*
1-15 August	36 (1)	75*	259 (1)	67*	667 (3)	54*	196 (2)	59*
16-31 August	—		41 (1)	44	91 (1)	55	—	

B. Pine Woods - inland

Sample period	1970 N (n)	% ♂	1971 N (n)	% ♂	1972 N (n)	% ♂
16-31 May	—		—		32 (1)	59
1-15 June	—		326 (3)	46	420 (5)	39*
16-30 June	402 (3)	28*	443 (3)	38*	191 (5)	36*
1-15 July	358 (3)	41*	647 (5)	32*	—	
16-31 July	80 (2)	33*	81 (2)	27*	—	

Table II

Pooled sex ratios from censuses (N>30) of *Calopteryx maculata* and *C. dimidiata*
on the Palmer River - Massachusetts, 1976-77. (N, (n), % ♂ and * as in Table I)

Sample period	1976 maculata N (n)	% ♂	dimidiata N (n)	% ♂	1977 maculata N (n)	% ♂	dimidiata N (n)	% ♂
16-30 June	455 (2)	56*	206 (2)	52	185 (2)	63*	45 (1)	47
1-15 July	729 (4)	62*	566 (4)	57*	247 (2)	57*	126 (2)	49
16-31 July	580 (4)	52*	239 (4)	53	430 (2)	56*	163 (2)	54
1-15 August	—		—		130 (1)	51	—	

excess of males at the water for most sampling periods. The exceptions were samples from early (Tab. IA, 1969) and late (Tab. IA, 1969 and 1970; Tab. II, 1977) in the flying season. Males outnumbered females at the water in 51 of the 56 individual samples pooled in Tables IA and II, and this excess was significant in 37 samples. The Fleming Creek censuses averaged 61.6% males and the Palmer River ones, 57% males.

Censuses of a pine woods, 90m from Fleming Creek, in 1970-72 revealed an excess of females in 30 of 32 samples (pooled in Tab. IB). This female excess was significant in 20 of the samples occurring generally during peak densities in the woods. Across the three years female averaged 63.6% of the pine woods population. As in the stream censuses, samples early or late in the flying season were most likely to have sex ratios not significantly different from 1:1.

In contrast to *C. maculata*, sex ratios at the water for *C. dimidiata* rarely deviated significantly from 1:1 (3 of the 15 samples pooled in Tab. II). Over two years, males averaged 54.1% of the population. Teneral individuals of both sexes of *C. dimidiata* were commonly observed along the stream, while

Table III

Sex ratios of *Calopteryx maculata* and *C. dimidiata* on open and shrubby sections of the Palmer River - Massachusetts, 1976-77. (Open sections were sunny and had numerous oviposition sites. Shrubby sections were less sunny and had few oviposition sites. N, % ♂, and * as in Table I)

| | | Open sections (75m) | | | | Shrubby sections (60m) | | | |
| | | *maculata* | | *dimidiata* | | *maculata* | | *dimidiata* | |
	Data	N	% ♂	N	% ♂	N	% ♂	N	% ♂
A. 1976:	26 June	29	55	—	—	33	45	—	—
	28 June	85	66*	44	59	52	56	46	57
	2 July	74	72*	55	51	62	45	51	59
	6 July	80	69*	49	51	55	47	44	57
	8 July	72	71*	52	62	20	50	64	55
	11 July	61	79	60	62	44	50	64	55
	19 July	54	54	35	54	68	59	41	46
	22 July	50	66*	24	67	66	50	28	36
	23 July	59	58	21	57	49	43	34	53
	26 July	44	66*	12	67	50	42	27	59
B. 1977:	20 June	62	56*	13	46	35	43	17	53
	3 July	30	77*	3	—	35	31*	12	50
	10 July	83	61*	41	56	38	45	35	37
	28 July	101	58	33	64	60	42	7	—
	6 August	41	61	—	—	44	39	—	—

C. maculata tenerals were seen only at emergence. I have not found *C. dimidiata* more than 10-20 meters away from the water. Thus the segregation of sexes and immatures does not appear as marked in *C. dimidiata* as it is in *C. maculata*.

Along the Palmer River, there were spatial variations in *C. maculata* and *C. dimidiata* sex ratios (Tab. III). Two 30m sections of the stream, thickly lined with shrubs and with few oviposition sites, were compared to five 15m sections that were more open and had numerous oviposition sites. Sex ratios for both species were 1:1 in the shrubby sections, except on July 3, 1977 when a significant excess of females was found. The yearly averages were 49 and 40% males for *C. maculata* and 52 and 53% males for *C. dimidiata*. In contrast, the five open sections of the stream had male biased sex ratios in *C. maculata* (yearly average = 66 and 63%). The male excess was significant in 10 of 15 samples. While *C. dimidiata* males outnumbered females in all but one of the samples (yearly average = 59 and 55%), none of the samples had a sex ratio significantly different from 1:1. Thus at two levels of scale (whole stream and subsections) *C. maculata* shows a marked differential in male and female distributions while *C. dimidiata* does not.
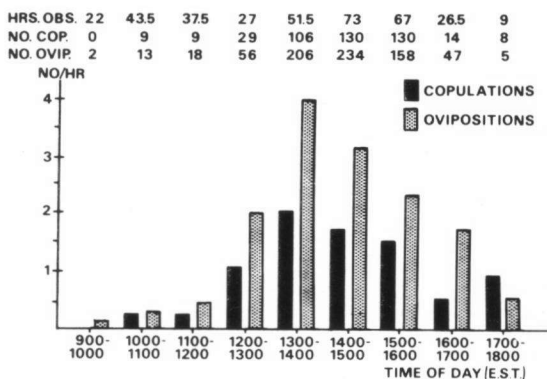

Fig. 1   Number of copulations (solid bars) and ovipositions (stippled bars) seen per hour of observation of *Calopteryx maculata* versus time of day. Data are from Fleming Creek and the Palmer River. For each time interval, the figures above the graph are: total hours of observation, number of copulations seen and number of ovipositions seen.

DAILY REPRODUCTIVE PATTERN

In *C. maculata*, the frequency of copulation and oviposition varies with time of day. Despite the marked effects of temperature and light intensity on the daily pattern in any one place, a general activity pattern can be obtained by pooling observational data from several years and habitats. Figure 1 reveals this pattern for 360 hours of observation on Fleming Creek and the Palmer River. Because the duration of oviposition is longer than that for

copulation, the same ovipositing female may have been included in two successive observation periods. This explains much of the excess of ovipositions over copulations for each time period. In addition, some females may have oviposited several times per mating and females may have oviposited in the observation area after mating with males in another area. These data for 408 copulations and 739 ovipositions reveal a well-defined peak of reproductive activity between 1200 and 1600 hrs.

FEMALE REPRODUCTIVE POTENTIAL

The relationship of female reproductive potential to the daily pattern of reproductive activity was examined by dividing females collected on the stream into three categories: (1) early — collected before 1300 hrs; (2) middle — collected between 1300 and 1600 hrs; (3) late — collected after 1600 hrs. The estimates of egg number and relative sperm volume from the 1978 dissections are presented in Figures 2 and 3. The patterns revealed in these figures are generally similar except for females collected after 10-15 min of oviposition. The significance of differences among means for egg numbers is illustrated by the following array where
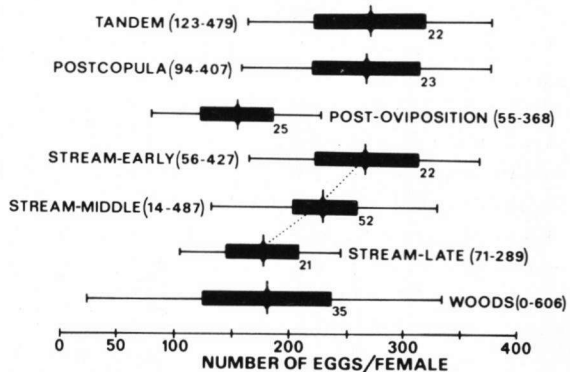

Fig. 2. Number of eggs per female *Calopteryx maculata* collected in seven different contexts (cf. text). Vertical line, solid box and horizontal line are respectively, mean, 95% confidence limits and one standard deviation. Sample sizes are given below each diagram. Numbers in parentheses are ranges.

lines underscore means that do not differ significantly (p>0.05, Student-Newman-Keuls procedure, SOKAL & ROHLF, 1969):

Tandem	Post-copula	Stream early	Stream middle	Stream late	Woods	Post-oviposition

The maximum number of eggs was carried by females captured in tandem before copulation ($\bar{x} = 272.3 \pm 22.6$). However, this mean did not differ significantly from those for postcopula ($\bar{x} = 268.9 \pm 22.5$) and on the stream early ($\bar{x} = 267.2 \pm 21.5$) males. The fewest eggs were carried by females taken

after 10-15 min of oviposition ($\bar{x} = 155.4 \pm 15.1$), on the stream late ($\bar{x} = 176.6 \pm 15.4$) and in the woods ($\bar{x} = 177.0 \pm 26.1$). These last three means were not significantly different, but did differ significantly from the first group ($F = 27.8$, $p < 0.001$). Intermediate between these groups were females collected on stream in mid-afternoon ($\bar{x} = 231.2 \pm 13.7$). Females from the woods had the lowest (0) and highest (606) number of eggs, suggesting they were in various stages of the egg maturation cycle. The pattern among females on the stream is thus one of steady decrease in egg numbers during the day. The overall pattern is consistent with the hypothesis that females come to the stream with a clutch of eggs, mate, oviposit and return to the woods late in the day.

The significance of differences between means of the sperm volume index (Student-Newman-Keuls procedure, as above) is as follows:

The maximum sperm volume index was from post-copula females ($\bar{x} = 4.20 \pm 0.27$). However, between 90 and 77% of this maximum was found in post-oviposition ($\bar{x} = 3.77 \pm 0.19$), on stream-early ($\bar{x} = 3.71 \pm 0.29$), in tandem ($\bar{x} = 3.49 \pm 0.35$) and on stream-middle ($\bar{x} = 3.22 \pm 0.08$) females. These five means did not differ significantly. The lowest sperm volume indices, 65-48% of postcopula, were from woods ($\bar{x} = 2.71 \pm 0.22$) and on stream-late ($\bar{x} = 2.00 \pm 0.37$) females. These means did not differ significantly but were significantly lower than those of the first group ($F = 33.87$, $p < 0.001$).
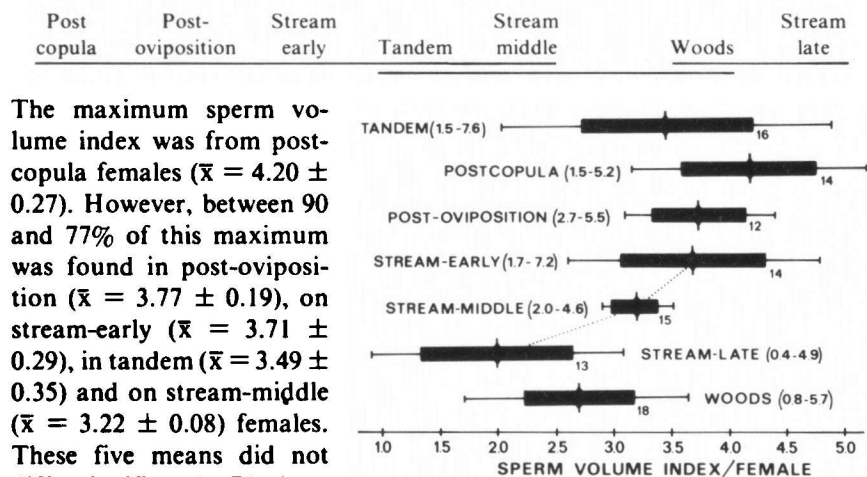
Fig. 3. Sperm volume indices for female *Calopteryx maculata* collected in seven different contexts (cf. text). Diagrams give mean, 95% confidence limits and one standard deviation (cf. Fig. 2).

DISCUSSION

SEX RATIO

There is considerable variation in larval and exuvial sex ratios within and among zygopteran species (Tab. IV). However, in 12 of 18 species studied

Table IV

Larval and exuvial sex ratios for Zygoptera. Data for species not cited by LAWTON, 1972 (L) are for studies with sample sizes (N) greater than 100. N, % ♂ and * as in Table I.

Species	N	% ♂	Sample	Reference
Argia plana	218	50.5	exuviae	BICK & BICK, 1968
Coenagrion puella	1352	54.4*	larvae	LAWTON, 1972 (L)
	659	56.9*	exuviae	PARR & PALMER, 1971 (L)
	136	52.2	exuviae	VAN NOORDWIJK, 1978
C. pulchellum	305	60.3*	exuviae	VAN NOORDWIJK, 1978
Enallagma aspersum	804	50.2	exuviae	INGRAM & JENNER, 1976
E. cyathigerum	1889	49.9	exuviae	PARR & PALMER, 1971 (L)
E. ebrium	209	44.0	exuviae	KORMONDY & GOWER, 1965 (L)
E. hageni	626	51.9	exuviae	INGRAM & JENNER, 1976
E. praevarum	194	43.3	larvae	JOHNSON, 1964 b
Erythromma najas	332	46.7	exuviae	VAN NOORDWIJK, 1978
E. viridulum	224	46.9	exuviae	VAN NOORDWIJK, 1978
Ischnura damula	675	43.7*	larvae	JOHNSON, 1964 b
I. elegans	1404	51.4	larvae	PARR & PALMER, 1971 (L)
	630	52.2	exuviae	VAN NOORDWIJK, 1978
I. verticalis	189	34.4*	exuviae	KORMONDY & GOWER, 1965 (L)
	344	52.6	exuviae	KORMONDY & GOWER, 1965 (L)
Pyrrhosoma nymphula	2450	52.0*	larvae	LAWTON, 1972 (L)
	753	53.7*	exuviae	CORBET, 1962 (L)
	97	63.0*	exuviae	CORBET, 1962 (L)
Lestes eurinus	783	48.2	larvae	LUTZ, 1968 (L)
	296	52.0	exuviae	LUTZ, 1968 (L)
L. rectangularis	104	29.8*	exuviae	GOWER & KORMONDY, 1963 (L)
L. vigilax	252	46.1	exuviae	INGRAM, 1976
Calopteryx maculata	247	48.9	larvae	this study

there was no significant deviation from a 1:1 sex ratio. Of the remaining six species, three had a significant excess of females and three a significant excess of males. In contrast to this general tendency toward an equal sex ratio at emergence, zygopteran adult sex ratios appear to be strongly male biased when censuses are taken at the water: *Ischnura elegans* (57.5-82.1%; PARR, 1965; PARR & PALMER, 1971), *Ceriagrion tenellum* (69-81%; PARR & PARR, 1979), *Argia plana* (75%; BICK & BICK, 1968), *Coenagrion puella* (70-89.6%; PARR & PALMER, 1971), *Pyrrhosoma nymphula* (81.5%; CORBET, 1952), *Enallagma civile* (82%; BICK & BICK, 1963), *Lestes disjunctus australis* (86%; BICK & BICK, 1961), *Enallagma cyathigerum* (90.2%; PARR & PALMER, 1971) and the anisozygopteran *Epiophlebia superstes* (99.7%; OKAZAWA & UBUKATA, 1978). Besides *Calopteryx dimidiata* (this study), the exceptions to this trend are *Enallagma praevarum* (JOHNSON, 1964a) where males were estimated to comprise 21-43% of the

adult population and *Agriolestes amabilis* (TILLYARD, 1917) where 195 of 196 individuals collected at the water were females, the males apparently occupying tree tops far above the stream. BORROR (1934) indicated an approximately equal sex ratio at the water for *Argia moesta*. However, his estimates for all samples, two-thirds of which were away from the water, were 31-33% males.

Given the tendency toward an equal juvenile sex ratio, the excess of males at the water can be explained by either differential mortality or differential behavior of the sexes. Differential mortality is difficult to isolate since survival rate or longevity estimates are derived from capture-recapture methods which are themselves potentially biased by differential mobility or behavior patterns of males and females. In *Argia apicalis* (BICK & BICK, 1965), *A. plana* (BICK & BICK, 1968) and *Ischnura elegans* (PARR, 1965) longevity estimates for males were one to three days greater than for females. In *Enallagma civile* (BICK & BICK, 1963), *E. praevarum* (JOHNSON, 1964a) and *Lestes disjunctus australis* (BICK & BICK, 1961) male and female longevity rates were within one day of each other. In *Calopteryx maculata* (WAAGE, 1972) female longevity estimates were approximately two days higher than for males. Male survival rates were slightly higher than female rates in VAN NOORDWIJK's (1978) estimates for *Platycnemis pennipes*, *Coenagrion puella*, *C. pulchellum* and *Ischnura elegans*. Thus there is little evidence for consistently higher female adult mortality that might account for the general male excess observed.

PARR (1965), PARR & PALMER (1971) and PARR & PARR (1979) presented capture-recapture estimates and other arguments suggesting that male excess at the water in *Ischnura elegans*, *Coenagrion puella*, *Ceriagrion tenellum* and *Enallagma cyathigerum* did not reflect the true adult sex ratio. Instead they argued that differences in behavior during maturation and pair formation could account for differences among species in the degree to which adult sex ratios at the water approximated population sex ratios predicted from exuvial counts.

My census data for *Calopteryx maculata* also provide a variety of evidence for a 1:1 adult population sex ratio. First the excess of *C. maculata* males on Fleming Creek (61.6%) seemed to be balanced by an excess of females (63.6%) in the adjacent pine woods. Second, equal *C. maculata* sex ratios did occur at the water early and late in the flying season (Tabs. I, II) on both streams. Third, there were equal *C. maculata* sex ratios on the Palmer River in areas of low male activity and few oviposition sites (Tab. III). *C. dimidiata* had an equal adult sex ratio at the water (Tabs II, III) which, while unusual among Zygoptera, conforms to the expectations for a species in which males and females mature at the water and remain there during their adult life. Since both *Calopteryx* species occur on the same streams and

utilize the same oviposition sites (although *C. dimidiata* oviposits while submerged), their marked differences in sex ratios at the water suggest differences in reproductive behavior which allow *C. dimidiata* females to remain at the water between bouts of oviposition. My preliminary studies of *C. dimidiata* suggest that females are rarely approached by males unless they fly within a meter of a male's oviposition site and that refusal displays (wing spreading) by perched *C. dimidiata* females are more effective in deterring courting males than are *C. maculata* refusal displays.

FEMALE REPRODUCTIVE POTENTIAL AND ACTIVITY PATTERNS

The data on eggs and sperm carried by *C. maculata* females at different times and in different contexts (Figs. 2, 3) conform to expectations for odonate behavior in general: females visit oviposition areas to mate and oviposit their current clutch of mature eggs and then leave these areas of male activity (and interference) to feed and mature another clutch of eggs. Males are likely to remain at or near oviposition areas where receptive females with full clutches of mature eggs are most likely to be encountered. This reproductive pattern seemed to underlie the distribution of sexes discussed above.

The steady decrease in female egg numbers and sperm volume index during the day (Figs. 2, 3; on stream early to late) corresponds to the peak of reproductive activity during early afternoon (Fig. 1). Females collected before the peak (on stream-early) had essentially equal numbers of eggs and volumes of sperm to those in the process of mating (tandem and postcopula) and may comprise the primary mating pool each day. The similarity of egg numbers for females after oviposition, on stream-late and in the woods, supports the idea that females return to the woods (inland) following mating and oviposition. The largest range (and variance) in egg numbers was for females from the woods. This is expected since females in the woods represent recent ovipositers, females maturing a new clutch of eggs and females about to move to the water to mate. The difference in mean egg number (approx. 100 eggs) between precopula and postoviposition females corresponds to approximately 10-14 min of oviposition at the egg deposition rates found by WAAGE (1978). This equals the average duration of oviposition by guarded females found by WAAGE (1978). Maximum duration of oviposition by one female during one day in the 1978 study was 75 min which would result in 500-750 eggs. The maximum number of eggs per female found in the present study was 598 in a postcopula female and 606 in a female from the woods. Thus there is good agreement between estimates on oviposition potential (WAAGE, 1978) and the dissections reported here.

The sperm volume data revealed two striking patterns. First, females at the water before and during the daily reproductive peak carried 77-88 percent as

much sperm by volume as females who had just mated. If odonate sperm is viable for several days as suggested by the studies of GRIEVE (1937) and JACOBS (1955), then why would these females mate again as is evidenced by the fact that females in tandem carried 83 percent as much sperm as postcopula females? Two answers are possible. First, the sperm may be several days old and less viable than fresh sperm that would be obtained by remating. Second, mating with a territorial male may be the primary means for a female to gain access to an oviposition site and be guarded by the male (WAAGE, 1978, 1979). Thus it may be advantageous for her to mate again even if she has viable sperm.

The second striking pattern revealed by the sperm data is that females collected after an average of 10-15 min of oviposition still had a sperm volume index 90 percent of that for postcopula (preoviposition) females. This finding is hard to interpret since females in the woods and on stream late in the day carried only 48-65 percent of the postcopula volume. One possibility is that many of the females on the stream late in the day or in the woods have oviposited two or more times with sperm received from one mating and stored while maturing new clutches of eggs. This explanation does not completely agree with the suggestion above that mating may be required to gain access to oviposition sites, but is consistent with the observation that males will occasionally guard non-mates while mates are present (WAAGE, 1979). The sperm-volume decrease could also reflect a compacting of the sperm mass within the female's storage organs during the day. ·

A significant, but unanswered question is why females receive more sperm than is needed for oviposition of one clutch of eggs. Is this a relic of an evolutionary state in which a single mating provided a female with a sufficient store of viable sperm for a lifetime of oviposition as is indicated by GRIEVE's (1937) findings for *Ischnura verticalis*? Does it indicate that males provide females with more sperm than needed as a potential investment in future fertilization if by chance the female oviposits a new clutch of eggs without remating? Or does it indicate that the sperm is not used by the female exclusively for fertilization but at least in part as a source of nutrition as appears to be true in some Lepidoptera and Orthoptera (BOGGS & GILBERT, 1979; FRIEDEL & GILLOT, 1977)?

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