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OVIPOSITION DURATION AND EGG DEPOSITION RATES IN *CALOPTERYX MACULATA* (P. DE BEAUVOIS) (ZYGOPTERA: CALOPTERYGIDAE)

J.K. WAAGE
Division of Biology and Medicine, Box G, Brown University, Providence,
Rhode Island 02912, United States

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Using fresh plant material at simulated oviposition sites, egg deposition rates for *C. maculata* females were found to average 7-10 eggs/min for four common plant species. Significant differences in mean duration of oviposition were found among females ovipositing: 1) alone (2.4 min), 2) while guarded by a mate (13.4 min), and 3) while guarded by a non-mate (9.8 min). Maximum duration of oviposition per day was 75 min (525-750 eggs) and over a 17 day period was 181 min (1,267-1,810 eggs). Females mated on about one half of the days present in the study area and up to five times ($\bar{x} = 2.04$) on a single day. The adaptive significance of post-copulatory guarding is discussed.

INTRODUCTION

Our knowledge of odonate reproductive behavior reveals considerable interspecific variation in (1) the expression of territorial behavior, (2) the complexity of pair-forming displays, (3) the location and duration of copulation, (4) the interaction between mates during oviposition, (5) the location and duration of oviposition and (6) the frequency of mating. As this knowledge increases certain phylogenetic patterns are beginning to emerge. For example, classifications of oviposition behavior have been presented by EDA (1960), HEYMER (1972) and SCHMIDT (1965, 1975) and general patterns of reproductive behavior have been discussed by BICK (1972) and SAKAGAMI et al. (1974). Likewise, considerable attention has been given to the nature and function of territorial behavior (see JOHNSON, 1964, and WAAGE, 1973 for references and CAMPANELLA, 1975, KAISER, 1974 and UBUKATA, 1975 for recent work).

In addition to identifying these phylogenetic patterns of species specific behavior, considerable attention should be given to the adaptive significance of behavioral variations within species. Studies of intraspecific variations and of the ecological factors which influence them are necessary to provide a clear understanding of the processes by which the phylogenetic patterns have arisen. Ideally, such studies will attempt to measure the significance of variations in behavior among individuals in terms of differential reproductive success.

Such a duality in the study of odonate behavior reflects the modern synthesis of evolutionary and ecological approaches to studying behavior. This synthesis recognizes that most of the behavioral repertoire of an organism represents a set of interacting adaptations which is best understood in the context of both the phylogenetic events from which the behaviors are derived and the more recent and environmental states in which they are continually tested by natural selection.

The primary purposes of this paper are to present a methodological approach to obtaining data on female reproductive output and the results of a study on egg deposition rate, oviposition duration and maximal egg output for *Calopteryx maculata* females. Natural oviposition sites are simulated by placing plant material, having no eggs from a previous oviposition, in places where none exists or in place of existing vegetation. This method provides a means for (1) estimating egg deposition rates, (2) estimating the fertility of eggs deposited and (3) examining the effects of manipulation of the kind, density and dispersion of oviposition sites in an area on male and female reproductive behavior. Only deposition rates are presented here.

The genus *Calopteryx* provides a good opportunity for quantitative, manipulative and comparative behavioral studies. Previous work on European *Calopteryx* species (e.g. BUCHHOLTZ, 1951; HEYMER, 1972, 1973; KLOTZLI, 1971; PAJUNEN, 1966b) and on one of the five North American species, *C. maculata* (JOHNSON, 1962; WAAGE, 1972, 1973) has revealed considerable variation in territorial and reproductive behavior among and within species. An example of the potential of *C. maculata* for quantitative behavioral studies is my observation of 1,647 male/female encounters resulting in 272 copulations and post-copulatory events in only 17 days (60 hr) along a 12 m section of stream (with 6-15 territorial males).

METHODS

The data that follow were collected from a population of *C. maculata* on the Palmer River, south of Route 44 in Rehoboth, Massachusetts. This is a gravel and sand bottom stream, 3-10 m wide, and 0.25-1.5 m deep. In the area studied it flows through deciduous woods (maple and oak) and is lined with dogwood (*Cornus* spp.) and viburnum (*Viburnum* spp.) bushes, grass and sensitive fern

(*Onoclea sensibilis*). Population density of *C. maculata* was 0-20 males per 15 m of shore.

Egg deposition rates were estimated using simulated oviposition sites made by attaching fresh vegetation to sticks anchored in the stream bottom. The vegetation used was sensitive fern (*Onoclea sensibilis*), bur reed (*Sparganium* sp.), buttercup (*Ranunculus aquatilis*) and water arrowhead (*Sagittaria* sp.). Fresh material was collected for each observation period and checked for previous oviposition before use. *Sparganium, Ranunculus* and *Sagittaria* leaves were usually collected from plants well below the water surface and not accessible to *Calopteryx* species in the area.

Once established each artificial oviposition site was watched continuously and the duration of oviposition for each *C. maculata* female was recorded to the nearest 0.01 min. One or more females were allowed to oviposit, usually until they left spontaneously, before the vegetation was collected and placed in plastic bags for transport to the laboratory. Eggs were counted under the 6-20 power magnification of a dissecting microscope. Most of the plants were translucent allowing each egg to be seen within the leaf tissues. *Ranunculus* stems were opaque and egg counts were based on the number of punctures. Dissections revealed one egg per puncture. Counting was aided by letting the material remain 24-48 hours at room temperature during which time the distal end of the egg turned brown and the plant material became more translucent.

The egg deposition rate was calculated by dividing the total number of eggs found in the plant material at a site by the total number of female minutes of oviposition observed there. Thirty-two oviposition sites were used; and 7,872 eggs deposited by 84 females were counted.

Data on oviposition duration and reproductive activity of marked females were recorded between 30 June and 23 July during 60 hours of observation at one 12 x 6 m section of stream. Oviposition was timed to the nearest 0.01 min from initial contact of the abdomen with plant material at an oviposition site until departure of the female. Both marked and unmarked females were timed. Individually marked females provided the data on frequency of mating, duration of oviposition and egg production.

Results are expressed in the text as mean ± standard error unless otherwise noted.

RESULTS

EGG DEPOSITION RATES

The four plants used as simulated oviposition sites were commonly used by *C. maculata* at the Palmer River study area. They were chosen on the basis of ease of locating and counting eggs and variation in leaf and stem size, shape and penetrability. An analysis of variance of the data presented in Table I reveals no significant differences in egg deposition rate among the four plants ($F = 2.143$ $p > 0.10$). However, there is a marked trend in the data that may relate to differential suitability of these plants for oviposition. *Ranunculus aquatilis* and the sensitive fern (*Onoclea sensibilis*) tend to have lower rates of egg deposition than do *Sagittaria* and *Sparganium*. *Onoclea* leaves that have bent or been forced into the water or that are submerged after heavy rains provide sites for oviposition close to shore. These leaves, while providing large and stable perching sites in flowing water, are more leathery than the flat, thinwalled *Sparganium* and *Sagittaria*. Oviposition into *Ranunculus* was confined to the stems and leaf axils and females observed at close range seemed to spend more time probing with their abdomens while locating stems. *Sagittaria* and *Sparganium* have flat, ribbon-like floating leaves that provide both a stable perch and easily accessible plant material for oviposition. Eggs were deposited only in submerged (1-10 mm) or damp portions of these plants.

Table I

Egg deposition rates for *Calopteryx maculata* females utilizing four plant substrates

Plant species	No. trials	No. ♀♀	No. eggs	No. eggs/min (range)*
Ranunculus aquatilis	10	36	2,160	6.63 ± 1.89 (3.4-10.7)
Onoclea sensiblis	10	14	1,653	7.01 ± 1.05 (4.1-9.8)
Sagittaria spp.	6	19	2,194	8.72 ± 2.52 (6.3-12.8)
Sparganium spp.	6	15	1,865	9.74 ± 4.23 (5.1-17.3)

* Expressed as mean ± 95% confidence limits.

Simultaneous or successive oviposition by several females often resulted in the utilization of the same regions of a plant, but no direct contact between eggs or obvious puncturing of previously laid eggs was observed. Simultaneous oviposition by several females on the same plant material is common and no attempt to prevent it was made during egg deposition studies. The large variances associated with several of the plants may have been partly due to (1) eggs overlooked in counting, (2) eggs already present, but unnoticed before the material was used for oviposition and (3) the lack of distinction between probing and actual oviposition while timing events. As a rough approximation, *C. maculata* in this population deposits 7-10 eggs/min of oviposition.

DURATION OF OVIPOSITION

Table II presents the results of timed oviposition sequences for three classes of females:

Table II

Duration of oviposition for guarded and non-guarded *Calopteryx maculata* females

Duration (min)	Alone	Ovipositional status *Guarded mate*	 *Guarded non-mate*
<1	75	3	2
1-4.9	20	28	25
5-9.9	6	34	33
10-14.9	1	30	18
15-19.9	–	18	13
20-24.9	2*	20	8
25-29.9	1*	9	1
30-34.9	–	6	1
35-39.9	–	2	
40-44.9	–	1	
45-49.9	–	1	
50-54.9	–	1	
55-60	1*		
Total No. ♀♀	*106*	*156*	*101*
Mean duration ± S.E.	*2.4 ± .7*	*13.4 ± .8*	*9.8 ± .7*

Analysis of variance for oviposition duration

Source of variation	df	MS	F
Among groups	2	3,802.04	54.94**
1. alone vs guarded	1	6,814.23	98.46**
2. mate vs non-mate	1	789.86	11.41**
Within groups	358	69.21	
Total	*360*	*3,871.25*	

* Submerged oviposition, female not accessible to males. Excluding these females mean ± S.E. = 1.4 ± .3.

** Significant at the $p < 0.001$ level.

(1) Alone – Females ovipositing either in the territory of a male with whom they have not mated and who is not guarding previous mates, or at an oviposition site not in a male's territory.

(2) Guarded Mate – Females ovipositing within the territory of a male they have just mated with and who is guarding them.

(3) Guarded Non-Mate: Females ovipositing within territory of a male they have not mated with, but who is guarding them and previous mates of his own. Guarding refers to the aggressive behavior of a male towards other males and centered around one or more ovipositing females at an oviposition site in his

territory. This behavior can be distinguished from territory defense (WAAGE, 1973) by the close association between the guarding male and the guarded females. Approaching males are displayed to and chased, but these chases are short when compared with territorial defensive chases occurring when no ovipositing females are present.

It is obvious from Table II that unguarded females rarely are able to oviposit for more than a few minutes ($\bar{x} = 2.42$ min) before they are discovered and courted or pursued by a male. Only those few females who became submerged during oviposition were able to escape courtship and tandem attempts by males. Submerged oviposition in *C. maculata* is rare (3 of 363 observed ovipositions in Table II) and usually seems to result from movement of vegetation the females are ovipositing into rather than active movement by the female.

If the three submerged ovipositions are excluded, females alone average 1.49 min of oviposition with 75% of the durations less than 1 min and only 7% exceeding 5 min. At a 7-10 eggs/min deposition rate this means only 10-15 eggs per bout of oviposition.

Females who oviposit in their mate's territory will be guarded by him against other males and will be able to oviposit significantly longer. Their average duration is 13.35 min with 98% of them ovipositing for periods exceeding 1 min and 80% exceeding 5 min. The termination of guarded oviposition appears largely due to the female, although resumed mating activity of the guarding male and a male's failure to protect all females ovipositing in his territory also result in termination of oviposition. At 7-10 eggs/min, guarded mates lay about 93-134 eggs per bout of oviposition.

Males guarding a previous mate will often guard additional females they have not mated with who attempt oviposition when the male's mate is present (WAAGE, 1973). These females may have mated with other territorial males and subsequently left oviposition sites in their territories, or they may have mated with non-territorial males. Table II shows that the duration of oviposition for these females approaches that of guarded mates (mean = 9.82 min or 69-98 eggs per bout of oviposition) with 98% of the females exceeding 1 min of oviposition and 73% exceeding 5 min.

An analysis of variance for the data in Table II reveals significant differences ($p < 0.001$) between guarded and unguarded (= alone) oviposition and between guarded mates and guarded non-mates.

Several factors may account for the differences between guarded mates and non-mates: (1) non-mates may have already oviposited elsewhere, (2) non-mates must arrive after an ovipositing mate is already present in order to be guarded by the male, thus mates get a head start on oviposition, and (3) non-mates may represent a class of females who tend to oviposit in more than one location per mating event.

MATING FREQUENCY AND EGG PRODUCTION

Between 30 June and 23 July, 88 females were marked for detailed observation of mating and oviposition. Only 36 of these were subsequently observed in reproductive activity. The following data are presented for 29 females seen on two or more days in the study area. These females were involved in mating and oviposition an average of one-half to two-thirds of the days they were known to be present in the area. The maximum number of copulations for a female on any given day was 1-5 ($\bar{x} = 2.04 \pm 0.20$, $n = 27$). Over the same time period 15 territorial males present for 4 or more days copulated a maximum of 1-9 times per day ($\bar{x} = 4.73 \pm 0.50$, $n = 15$).

Total observed oviposition time over all days a given female was present was 2-181 min ($\bar{x} = 55.25 \pm 8.41$, $n = 28$). The daily maximum durations for the same females were 2-75 min ($\bar{x} = 32.8 \pm 3.6$, $n = 28$). Ten of these females oviposited a total of 60 min over all days present while 10 exceeded 40 min in one day. It appears that *C. maculata* females are capable of laying as many as 525-750 eggs per day and 1,267-1,810 eggs over a 4-14 day period (7-10 eggs/min for 75 and 181 min).

The above summary of the data does not give a full impression of the variation among females in reproductive activity. For example, one female was present on seven consecutive days, copulated twelve times (including five times in one day) and was observed ovipositing for only 3 min. Most of her matings were with the same territorial male. At the opposite extreme, another female was present on five consecutive days, absent three days, and active on five of the following six days. She copulated six times (three in one day) and oviposited a total of 181 min (74 in one day). Since observations were confined to one area and females of *C. maculata* are known to be mobile (WAAGE, 1972), even these "maximum" estimates may omit additional activity in other areas along the stream or on days when observations were not made.

Maximum observed oviposition for a single mating on one day can be estimated by data from 11 females who oviposited for 28-60 min. This represents a potential 196-600 eggs per mating, but the presence of sperm from previous matings or fertility of the eggs produced were not known. Attempts at capturing females after mating and isolating them for complete oviposition were not successful.

DISCUSSION

SIMULATED OVIPOSITION SITES

By using vegetation free of previous oviposition and simulated oviposition sites, one can readily obtain egg deposition rates for endophytically ovipositing species and for a variety of commonly used plants. Once these rates are known relative reproductive success of individuals, approximated by number of eggs produced, can be estimated by timing the duration of oviposition into each plant type. In addition, the fertility of the eggs produced by a given mating can be determined by laboratory culture. This latter approach was used by JACOBS (1955) to determine the ability of *Plathemis lydia* and *Perithemis tenera* males to inseminate a large number of females over short periods of time. Data collected under these conditions can be used at two levels: (1) comparatively among species and (2) as an index of the relative reproductive success of individuals within a population.

In addition to its utility in obtaining estimates of egg deposition rates, simulated oviposition sites can be used to collect a variety of data on oviposition behavior, habitat selection, and determinants of male territorial behavior. For example, it can be used to change the quantity and distribution of oviposition sites in an area in order to examine the effects of these variables on size and distribution of male territories. Oviposition activity and preferences for certain territories or plant species can be assessed even without continual observation by setting up oviposition sites with fresh plant material each day and collecting this material later for examination of eggs (assuming the eggs for all species in the area can be identified). Finally, the question of what attracts a female to a particular oviposition site (chance, the male, the plants, or the presence of other females) can only be answered if oviposition sites can be altered and manipulated.

EGG PRODUCTION

Few quantitative data are available for comparing egg deposition rates, oviposition duration, and potential egg production among odonates. BICK et al. (1976) reviewed known egg deposition rates of five zygopteran species. These rates ranged from 1.3-2.8/min for *Lestes unguiculatus* to 5.4-5.5/min in *Chromagrion conditum*. The estimates of 120-180/min by ROBERT (1958) for *Sympecma fusca* seem exceedingly high. The comparison of these rates at present is difficult since work to date has revealed considerable variation in deposition rate within a species. Given the remarkable variation in duration of copulations (3 sec to more than 5 hr – see CORBET, 1962) among odonates, it is desirable to get a firm idea of reproductive output for the same species in order to determine the degree to which these variations represent phylogenetic accidents or different reproductive tactics related to specific conditions of density and habitat structure. For example, do small coenagrionids with long copulation times mate only once or twice and lay large numbers of eggs per mating while some libellulids mate often and briefly, laying a relatively small proportion of total potential egg production after each mating? The copulation times for *Calopteryx* are among the shortest for zygopterans (e.g. 1-5 min in *C. maculata*, WAAGE, 1973) and the frequency of mating per individual seems far greater than for other zygopterans for which such data are available. This and their elaborate territorial behavior suggest a pattern of reproductive behavior strongly convergent to that of some libellulids with short copulation times, frequent matings, and strongly developed territorial behavior. The actual reasons for this convergence may be discovered in the examination of how the interrelationships between behavior and environment affect reproductive success.

While guarded *C. maculata* females lay an estimated average 93-134 eggs in a single bout of oviposition, multiple bouts observed for marked females show that an average of 230-328 eggs may be laid per day (7-10/min in 32.8 min/day) with a potential production of 750 eggs or more per day and 1,810 or more in a lifetime. Again, these figures are not greatly different from previous estimates for other Zygoptera (see BICK et al., 1976; GRIEVE, 1937), but the significance of such comparisons with the limited amount of data at hand is difficult to evaluate. In general, one would expect odonates, like most other organisms, to be capable of producing far more zygotes than actually result in adults and that this potential zygote production would be roughly correlated with body size. For example, the number of eggs oviposited in single batches varies as expected both between Zygoptera and Anisoptera and within Anisoptera (see Table II in CORBET, 1962) when the reduced rate of oviposition imposed on a species by endophytic oviposition is considered.

I was unable to get *C. maculata* to oviposit in cages or the laboratory and cannot determine if a single mating is sufficient to fertilize all the eggs produced by a female in her lifetime as appears true for *Ischnura verticalis* (GRIEVE, 1937). Specimens have been collected for dissections of ovaries and sperm storage vesicles in order to explore this problem further.

THE ADAPTIVE SIGNIFICANCE OF POST-COPULATORY GUARDING

A question more directly related to the adaptive significance of different patterns of oviposition behavior and post-copulatory associations is the relation within a species between behavioral variations and reproductive output. Since eggs are fertilized as they are laid, a male's investment in reproduction via a given mate is not realized until oviposition. Delays between mating and oviposition may result in female mortality and, perhaps more significantly, in subsequent matings by the female resulting in dilution or displacement of the first male's sperm. PARKER (1970) noted that the phenomenon of dilution or displacement of sperm by successive mates results in sperm competition among males. He argued that it may have been an important factor in selecting for male behaviors that assure a substantial period of oviposition by a mate prior to her subsequent matings. A moment's thought about post-copulatory interactions between odonate males and females reveals a variety of behaviors that could lessen sperm competition: submerged oviposition, tandem oviposition, and guarding of ovipositing females by males.

The difference in average oviposition duration for guarded versus non-guarded *C. maculata* females reported in this study certainly supports the hypothesis that post-copulatory guarding enhances the reproductive success of both male and female. However, males that guard non-mates appear to be aiding the reproduction of other males in the population while decreasing their own potential reproduction by diverting their attention from mates and by not attempting to mate with all females arriving in their territories. While appearing altruistic, this phenomenon may instead reflect a combination of circumstances that essentially force males into this behavior. These circumstances include: (1) an inability to distinguish between mates and non-mates, (2) the high probability of losing previous mates to other males while attempting matings with ovipositing non-mates and (3) a tendency for females to aggregate in territories of males who are effective guarders.

BUCHHOLTZ (1951) noted that *C. splendens* males did not court or mate with females arriving while a previous mate was still ovipositing. PAJUNEN (1966b) observed similar behavior in *C. virgo* and noted that several non-mates might oviposit in a male's territory along with his mate. HEYMER (1973) observed guarding of multiple females in several *Calopteryx* species. However, he noted that most of these females were mates of the guarding male and that the presence of previous mates did not seem to inhibit further matings by a guarding male. The significance of these variations in post-copulatory behavior and an evolutionary explanation for guarding of non-mates will be presented in another paper (WAAGE, in prep.). For purposes of the present paper I primarily want to point out the new dimensions added to behavioral studies of odonates by considering: (1) the measurement of reproductive success and its variation among individuals and (2) the phenomenon of sperm competition and its consequences.

One can view the process of reproduction as an optimalization, shaped by sexual and natural selection, of the investment of time and energy in reproduction balanced against the success, expressed as relative fitness, of that reproduction. This suggests that variations in reproductive behavior among and within species represent alternative patterns of finding and investing in mates. The essential factors in such an optimalization are predictable and measurable. They include the probability of locating mates, the number of fertilized eggs laid per unit of time, and the probability that an unprotected female will be mated by another male. For example, female behavior in this system should reflect an optimal compromise among the number of eggs laid with a given mate, the number of different mates (variability among offspring), and the suitability of oviposition sites. This requires no conscious behavior of foresight by individuals, only that those types which from generation to generation happen upon optimal combinations relative to current selective factors will tend to increase in frequency relative to those that do not. Viewed in this way, one can make and test predictions about male and female behavior under differing conditions of density and habitat structure. Recent work by CAMPANELLA & WOLF (1974) and CAMPANELLA (1975) have emphasized this general approach to odonate behavior. To a large degree previous work by JACOBS (1955) and PAJUNEN (1962, 1963, 1964, 1966a) have also sought to examine behavioral variation in relation to varying environmental conditions.

Further efforts in this direction can easily move the study of odonate behavior into a position of making extremely valuable contributions to the general field of behavioral and evolutionary ecology, an area now dominated by literature on birds, mammals and social insects.

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