

EGG RELEASE RATES WITH TEMPERATURE AND BODY SIZE IN LIBELLULID DRAGONFLIES (ANISOPTERA)

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Egg release rates at different abdomen temperatures were determined for 2 populations of *Erythemis simplicicollis* (Say) by submerging females' abdomens in vials of water of known temperature and timing the durations of egg flow. The log of flow rate increased linearly with increasing abdomen temperature in both New York and Florida (N=29 and N=62 respectively) from 18 to approximately 38° C above which flow rates decreased or ceased. Significant differences were found in the slopes and elevations of the regression of log egg flow on temperature for the two populations, the N.Y. females releasing eggs from 67% to 8% faster than the Florida females between 20 and 38° C respectively. The Q_{10} of flow rate with temperature was 1.8 for the N.Y. females, and 2.2 for the Florida population. Comparing 10 spp. in the Libellulidae, egg flow rate at a given temperature increased significantly with increasing body size.

INTRODUCTION

Behavioral and physiological attributes of animal populations can be both constrained by phylogeny and moulded by natural selection. Some characteristics are invariant within higher taxonomic categories, such as endophytic oviposition in the suborder Zygoptera. Others can vary both between and within species, either as a consequence of covariance with characteristics shaped in detail by natural selection or in direct response to selective pressures. Damselflies with endophytic oviposition have far slower egg deposition rates than some exophytically ovipositing libellulid dragonflies. BICK et al. (1976), reviewing 5 zygopteran species, found rates ranging from 1.3-2.8 eggs/min for *Lestes unguiculatus* (Hag.) to 5.4-5.5 eggs/min in *Chromagrion conditum* (Hag.). Using fresh plant material, WAAGE (1978) found rates ranging from 3.4 to 17.3 eggs/min for the damselfly *Calopteryx maculata* (P. de Beauv.), averaging

7-10 eggs/min for four common plant species. The maximum duration of oviposition observed, 75 min in a single day, could have resulted in the release of 525 to 750 eggs. In contrast to these rates, investigators collecting clutches from a variety of libellulids have obtained from a few hundred to a few thousand eggs in under 5 min (cf. CORBET, 1962, 1980 for references). The endophytic oviposition habit probably constrains zygopterans to slower release rates than libellulids (CORBET, 1962; WAAGE, 1978), but variation of egg release rate within either group or within a single species must depend on other factors.

This study investigates egg flow rates in libellulid dragonflies, one aspect of reproductive physiology to date largely unexamined in this family or in the suborder Anisoptera. In libellulids which oviposit exophytically eggs flow steadily from the vulva. Females fly over a water surface, tapping their abdomens to the surface so that the eggs which have accumulated on the vulva since the last dip are washed off, although some *Sympetrum* species drop their eggs from a height of several centimeters or more (CORBET, 1962). Egg release rates were expected to depend on abdomen temperature with a Q_{10} approximating 2.0 to 2.5 (PROSSER, 1973; TRIBE & BOWLER, 1968) unless special adaptations existed to liberate flow rates from physico-chemical phenomena. Differences in release rates between species were expected possibly as a result of covariance with body size or egg size. The possibility that egg release rates might be directly shaped by selective pressures was also considered. How the flow rates determined in this paper relate to natural, free-flying egg release rates is not discussed.

METHODS

Egg release rates were obtained from 10 libellulid species in one or both of two areas. One was a series of ponds within the Austin Cary Memorial Forest of the University of Florida, 8 miles NE of Gainesville, Florida (FL) (Lat. 29.7° N, Long 82.4° W), in 1978, '79, the other Tyrrel Lake in Millbrook, New York (NY) (Lat. 41.8° N, Long 74.2° W), in 1983. Females were captured during or immediately after copulation when they usually extruded eggs freely whether touching water or not. To control a female's abdomen temperature, the terminal 6 or 7 segments were submerged vertically in a vial of water for 15 seconds prior to moving the female to a second vial of water matched for temperature for 60 seconds or until egg flow slowed, whichever came first. Egg release rate then equalled the total eggs in the second vial divided by the time interval between removing the female from the first and from the second vial. Watching the egg flow of female *E. simplicicollis* inserted in water around 10° C cooler than ambient and thus at least 10° C cooler than their bodies revealed that at most 12 to 15 sec passed before egg flow stabilized at a slower rate. The temperatures of both vials were recorded immediately with YSI thermister probe # 427 and the female hind wing length measured (FL only). All determinations were made in the shade; those shorter than 30 sec were discarded.

Complete clutches for *E. simplicicollis* and *Plathemis lydia* (Dru.) were estimated in 1978 in FL by collecting all eggs released by females captured before 11.00 hr. Dissections of some females afterwards revealed that all mature ova appeared to be released into the vials. Free females of both species were paint marked individually and timed while ovipositing. To estimate the maximum duration of a single oviposition bout, only data from undisturbed females which terminated the bout of their own accord were used. Clutch size and oviposition durations were measured for *P. lydia*

between 25 June and 15 July 1978 and for *E. simplicicollis* between 20 July and 15 August 1978.

In NY, male *E. simplicicollis* were captured, placed in small sealed tupperware containers on ice and weighed to the nearest mg within 4 to 8 hrs. Analyses of Variance were used to test for the significance of regressions and the significance of the difference between regression slopes.

RESULTS

The log of egg release rate for female *Erythemis simplicicollis* increased linearly with increasing temperature between 18 and 38° C (Figs 1, 2). Temperatures cooler than 18° C were not attempted. At temperatures higher than approximately 38° C, however, slower flow rates were obtained than expected on the basis of lower temperature determinations (Figs 1, 2). Females whose abdomens were submerged in water of 39° C or more flexed their abdomens repeatedly as though trying to escape the water. Four females submerged in water of 41 to 43° C ceased to release eggs within a few seconds, yet minutes later released eggs in a vial of cooler water. These data suggest that high temperatures inhibit egg flow. Thus only determinations in water of 38° C or less were used for the regression analysis. 40° C or less might also have been appropriate.

The flow rates of female *E. simplicicollis* from Florida increased from a mean of 6.0 eggs/sec at 28° C to 13.0 eggs/sec at 38° C, a Q_{10} of 2.2, while those from N.Y. increased from 8.3 to 14.5 eggs/sec over the same temperature range, a Q_{10} of 1.8. These differences in Q_{10} , or slope, of the regressions were significant ($F_s = 4.15$, $df = [1, 87]$, $p < 0.05$). The elevations of the regressions were also significantly different ($t = 19.7$, $df = 84$, $p < 0.001$), although converging at the higher temperatures. Thus between 20 and 38° C, *E. simplicicollis* released eggs on average between 67% and 8% faster, respectively, in NY than in FL.

Variability was high in both populations, and the variance was not significantly

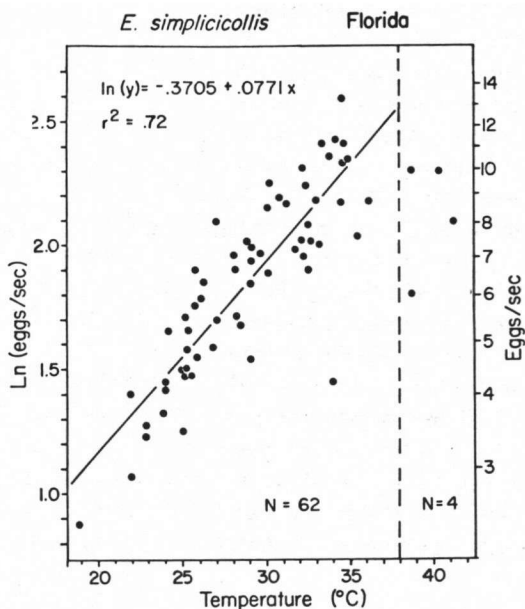


Fig. 1. Egg flow rate with abdomen temperature for *Erythemis simplicicollis* in Gainesville, Florida, 1979, as Ln (log to the base e) transform of flow rates (eggs/sec) against vial water temperature. Regression analysis for temperatures less than 38° C only; $F_s = 153.6$, $df = [1, 60]$, $p < 0.001$.

different between the two (F test, $p > 0.10$). Within this species there was no suggestion that female body size influenced the direction or degree of deviation in egg flow rate from the regression line ($p > 0.45$, $N = 62$, FL). Experimenter error could have only accounted for a small fraction of the variance. Repeated counts of the same clutch yielded the same value $\pm 2\%$ maximum disagreement ($N = 5$ trials on 2 clutches). Errors in handling the female and stopwatch should have been more severe for the shorter determinations, but the absolute deviations of determinations shorter than the mean determination were no different from those longer. Most of the variability around the predicted rates for a given temperature must have resulted from characteristics of the females as yet undetermined.

Comparing 10 species of Libellulidae, egg flow rate ranged from a low of 1.3 eggs/sec for *Sympetrum rubicundulum* (Say) to 28 eggs/sec (maximum of 12 females) for *Plathemis lydia*

between 30 and 34° C (Fig. 3). Only one or two determinations were made for 8 of the species. As expected, egg flow rates did covary significantly with body size as measured by abdomen length and/or total weight (Table I, Spearman Rank Correlation, $r_s = 0.85$, $p < 0.01$, $N = 10$ species). One or two determinations for several species leaves a large margin of error for the true mean flow rate at a given temperature. If the variance in release rate with temperature for these libellulids was similar to or larger than that found for *E. simplicicollis* FL, then the 95% confidence limits for the true mean flow rate at approximately 32° C given only 1 determination would be at least ± 0.20 log units and for the true mean given the average of only two determinations at the same temperature would be at least ± 0.15 log units (SOKAL & ROHLF, 1969). This error in measurement of mean flow rates should tend to obscure any relationship between species' body size and

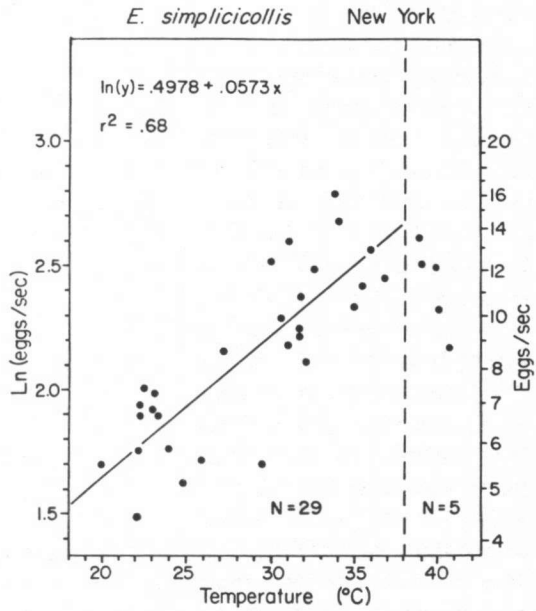


Fig. 2. Egg flow rate with abdomen temperature for *Erythemis simplicicollis* in Millbrook, New York, 1983. Regression analysis for temperatures less than 38° C only; $F_s = 57.47$, $df = [1, 27]$, $p < 0.001$.

flow rates. Thus the Spearman Rank Correlation based on one or two determinations per species is a conservative estimate of the true degree of correlation.

Notable departures from the correlation were *S. rubicundulum* with the slowest egg flow although ranked only 4th smallest and *P. lydia* with the fastest release rates although not as large as *Libellula luctuosa* (Burm.) or *Orthetrum ferruginea* (Fab.). *S. rubicundulum* was exceptional also in having large spherical eggs at least 3x the volume of the eggs of the remaining species which were difficult to distinguish from each other (except *Erythrodiplax minuscula* Ramb. with somewhat smaller eggs than the rest). *Plathemis lydia* was exceptional in having the shortest duration copulation, 3-4 sec (CAMPANELLA & WOLF, 1974; pers. obs.), compared to 10 to 20 sec or more for *Libellula luctuosa* (CAMPANELLA, 1975), *Pachydiplax longipennis* (Burm.) (pers. obs.), and *Erythemis simplicicollis* (pers. obs.), the other fast maters of the group.

The fact that females of libellulid species can vary as much as perhaps 20 fold in egg release rates at a given abdomen temperature suggests that clutch size for free-flying libellulids cannot be guessed from the duration of oviposition. For example, while the longest undisturbed ovipositions for *E. simplicicollis* (mean = 119 sec, s.d. = 52, N = longest 20 out of 98 total) were 3.3 times as long as those of *P. lydia* (mean = 34 sec, s.d. = 8.1, N = longest 19 out of 100 total), the total clutches collected from females before 11.00 hr were indistinguishable (*E.*

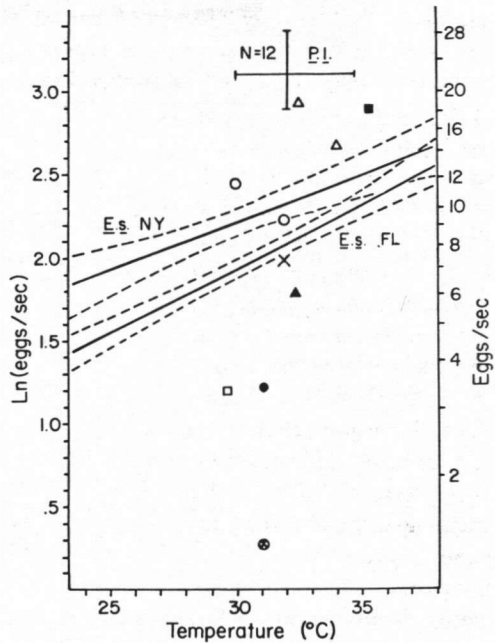


Fig. 3. Comparison of egg flow rates with temperature for 9 libellulids in addition to two populations of *E. simplicicollis*. See Table I for species' identification symbols. Each point represents a single determination with one female. The crossed bars at the top represent the total range of 12 determinations for *Plathemis lydia* in Gainesville, Florida, in 1978; temperatures of individual vials of water were unknown in these cases, but the possible range of temperatures was determined by comparison to matched vials used for *E. simplicicollis*. The mean of the 12 observations was 22.8 eggs/sec, s.d. = 3.6. Dashed lines represent the 95% confidence limits of the mean value of egg release rate for each temperature for the two populations of *E. simplicicollis*.

Table I
Libellulid egg flow rate and body size

Symbol, Species	Origin	Flow rate eggs/sec ¹	N	Rank rate	Abdomen length (mm) ²	Rank size ³	
⊗ <i>Sympetrum rubicundulum</i>	NY	1.3	1	1	21-23	4	
□ <i>Erythrodiplax minuscula</i>	FL	3.3	1	3	14-17	2	
● <i>Perithemis tenera</i>	NY	3.4	1	2	12-13	1	
▲ <i>Celithemis eponina</i>	NY	6.0	1	4	23-28	5	
× <i>Sympetrum vicinum</i>	NY	7.3	1	5	21-22	3	
	<i>Erythemis simplicicollis</i>	FL	8.0 ⁴	62	6	24-30	7
	<i>Erythemis simplicicollis</i>	NY	10.5 ⁴	29	6	24-30	7
○ <i>Pachydiplax longipennis</i>	NY	9.1-11.7	2	7	23-35	6	
△ <i>Libellula luctuosa</i>	NY	14.4-18.8	2	8.5	28-31	9	
■ <i>Orthemis ferruginea</i>	FL	18.0	1	8.5	36-39	10	
	<i>Plathemis lydia</i>	FL	18.0-28.8	12	10	25-37	8

¹ Egg flow rate at $32 \pm 3.0^\circ$ C, cf. Fig. 3.

² Lengths from NEEDHAM & WESTFALL (1955), includes males and females.

³ The range of abdomen lengths of *P. longipennis* and *E. simplicicollis* overlap totally. I therefore used the mean masses of the two species as reported by MAY (1976) to rank the species on size (mean = 175 mg, N = 104 and mean = 270 mg, N = 90 respectively for males from FL).

⁴ Mean

simplicicollis, mean = 899 eggs, s.d. = 441, N = 10 females, *P. lydia*, mean = 973 eggs, s.d. = 336, N = 10 females). This means that free-flying *P. lydia* females must have been releasing eggs approximately 3.3 times as fast. The difference in egg flow rates shown in Figure 3 is consistent with this conclusion.

DISCUSSION

In contrast to zygopterans which may lay between 3 to 10 eggs/min, libellulid dragonflies of moderate to large size can lay between 600 and 1200 eggs/min depending on the species. Presumably they are capable of fertilizing eggs with stored sperm at these rates as well. Hatching success for eggs obtained from *E. simplicicollis* and held at room temperature on petri plates averaged 91% (N = 2723 eggs, McVEY & SMITTLE, 1984) which means that fertilization was 97% or better. Hatching success of eggs of the other species was not systematically investigated.

The rate at which *Erythemis simplicicollis* release eggs is dependent on their abdomen temperature, the log rate increasing linearly with temperature as do many enzymatic reaction rates (PROSSER, 1973). Furthermore, the Q_{10} 's and elevations of egg release rate with temperature of two populations separated by 12° latitude were significantly different from each other, although neither Q_{10} was significantly different from 2.0, a value common for insect general metabolism and muscle specifically (PROSSER, 1973). Egg release declined sharply after 38

to 40° C, although lethal body temperatures for this species appear to exceed 46° C (MAY, 1976). The maximum body temperature endured voluntarily, however, is about 40° C (MAY, 1976). It is possible that temperatures higher than 38 to 40° C increased the viscosity of fluids which facilitated egg flow or incapacitated muscles involved in egg release.

Egg flow rates did correlate with body size over the set of 10 species sampled (all available species at both study sites). Higher flow rates with larger body size might have resulted from covariance of oviduct diameter with body size while egg size remained for the most part independent of body size. It is also possible that larger species produce larger clutches, egg size being roughly the same, and selection has shaped the characteristics which determine egg flow rates to allow the release of larger clutches in a period of time similar to that for smaller species. Comparisons of *E. simplicicollis* with *P. lydia* contradict this latter idea, however. *P. lydia* released clutches similar in size to those of *E. simplicicollis* but in a substantially shorter time. *Sympetrum rubicundulum* exhibited the slowest egg release rate probably as a consequence of its exceptionally large eggs which provide for the embryos' long diapause period (CORBET, 1962). Thus, perhaps a substantial amount of the variation in egg flow rate among libellulids is a consequence of covariance of flow rate with body and egg size which in turn have been acted upon strongly by natural selection.

Nonetheless, body size and egg size cannot be the only parameters which have influenced the evolution of egg flow rates with abdomen temperature. For example, the NY population of *E. simplicicollis* was slightly though not significantly smaller in body size than the FL population (mean hind wing length = 30.5 mm, s.d. = 0.9, N = 43, for NY and 30.9 mm, s.d. = 1.4, N = 669, for FL, mean body weight = 227 mg, N = 46 for NY, this study, and 270 mg, N = 90 for FL from MAY, 1976, males only), yet the NY population of females released eggs significantly faster than the FL population. Furthermore, *Plathemis lydia* females released eggs faster than the larger *Libellula luctuosa* and *Orthemis ferruginea*. This might have resulted from more intense selection for rapid oviposition in *P. lydia* than in the other two. The idea is appealing because *P. lydia* also copulate in the air in a remarkably short period of time, about 3 seconds, and female arrival at the ponds is far more restricted to solar noon under sunny skies than it is for *L. luctuosa* (CAMPANELLA & WOLF, 1974; CAMPANELLA, 1975) or *O. ferruginea* (pers. obs.). Both factors suggest that the duration of time in which female *P. lydia* can visit the pond is more seriously limited by other factors than in the other two. Faster oviposition allows the release of a clutch in a shorter period of time, and hence a shorter exposure to the risks of predation or male-male competition while visiting the pond.

Although females of most libellulid species must be exposed to more or less risk of predation and male disturbance during oviposition, one factor which might select for less than maximal egg release rates for a given body size could be egg

spacing. Females of some species including *E. simplicicollis*, *L. luctuosa*, and *Celithemis eponina* (Dru.), seldom tap their abdomens more than a few times in the same spot (pers. obs.). Female *E. simplicicollis* often wander over 6 m² of floating vegetation in a single oviposition bout (McVEY, 1981). Faster rates would result in more egg clumping and perhaps decreased egg survival. For example, JACOBS (1955) has shown that severe clustering of eggs which can result from communal oviposition by female *Perithemis tenera* (Say) at a single site can prevent many of them from hatching.

If egg spacing is important, fine tuning of flow rate with temperature might occur. For example, the NY *E. simplicicollis* population might experience cooler abdomen temperatures on average than the FL one. With faster egg release rates they might compensate for this and achieve similar egg spacing in both locations. Serious consideration of factors shaping egg release rates in libellulids must await data on more species and how these rates relate to natural oviposition by free-flying females.

In conclusion, egg flow rates at a given abdomen temperature in libellulids can differ not only between species, but also between populations of the same species. The difference can be both in mean flow rate for a given temperature and the Q_{10} of the relationship.

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