THE INFLUENCE OF CERTAIN CONSTANT TEMPERATURES UPON THE RATE OF EMBRYONIC DEVELOPMENT OF anisopterous dragonflies Perithemis tenera (SAY) and Plathemis lydia (DRURY) (ODONATA: LIBELLULINAE)

EVELYN SANDERS CALDWELL

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An Abstract

Presented to

the Graduate Council of

Austin Peay State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Arts

in Education

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by

Evelyn Sanders Caldwell

1972

Abstract

The rate of development of eggs of Perithemis tenera and Plathemis lydia individually cultured at 5, 10, 15 20, 25, and 30° is described. Rate of development was found to be proportional to temperature at 20, 25, and 30° C. Eggs at 15° C had not completed development at the end of 60 days. Eggs at 5° C and 10° C showed little or no development.

Studies of hatching time alone do not give a complete analysis of rate of development. The study suggests that temperature has different effects at various morphological stages of development.

Morphogenesis is outlined and discussed briefly.

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1972

To the Graduate Council:

I am submitting herewith a Thesis written by Evelyn Sanders Caldwell entitled "The Influence of Certain Constant Temperatures upon the Rate of Embryonic Development of anisopterous dragonflies Perithemis tenera (Say) and Plathemis lydia (Drury)." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Arts in Education, with a major in biology.

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Major Professor by E. A. Boehme

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ACKNOWLEDGMENTS

The author wishes to express thanks to Dr. Charles Boehms, Vice President for Student Affairs for his help in designing the problem and his constructive criticisms throughout the study. Gratefulness is also expressed for the use of his library and his dissertation which was cited frequently. Most sincere thanks are expressed for the manner in which he gave freely of his time.

Thanks are also given to Dr. Floyd Ford for his criticism of the paper.

Sincere thanks are due my husband, Nick for his assistance with the calculations and his encouragement and help in every way while the paper was being written.

Much appreciation is given my parents, especially my mother for caring for our son, making it possible to devote time to the writing of the paper and for their usual encouragement.

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I. INTRODUCTION

The rate of embryonic development of poikilothermic animals in relation to the temperature of their environment has been of considerable interest to investigators. According to Kume and Dan (1968) temperature is the environmental factor which exerts the most important influence on embryonic development in poikilothermic animals. Between the low and high threshold temperatures the rate of development varies considerably. Differences occur in the rate of development between species. Within species the rate of embryonic development of morphological stages differs.

Many studies have been conducted to determine the influence of temperature upon the rate of embryonic development of insects. Howe's (1965) review of the literature lists sixteen extensive studies showing the response of hatching to various constant temperatures.

Studies of stages of embryonic development of insects have been less numerous. Slifer (1932) showed that the majority of a pod of grasshopper eggs incubated at a definite temperature for a definite period of time reached the same stage of development. A certain percentage lagged behind or more rarely were in advance of the rest. Burdick (1937) did extensive work on the effects of low temperature exposure on grasshopper eggs concluding that environmental factors acting before the eggs were laid influenced their rate of development.

Specific work on the influence of temperature upon the rate of embryonic development of dragonflies has been limited. The determination of the duration of the egg stages of several species of dragonflies has been made by Gardner, Corbet, Longfield and MacNeill (Corbet, Longfield, and Moore, 1960). Extensive work has been done by Corbet (1960) on the influence of temperature upon the egg stage of Anax imperator (Leach) and Lestes sponsa (Hausmann) (Corbet, Longfield, and Moore, 1960). Boehms (1971) has done an extensive study of the dragonfly Sympetrum vicinum with reference to the influence of

constant temperatures on morphological stages and total hatching time.

As a general rule the results of experiments to determine the rates of embryonic development of insects at various constant temperatures are expressed as the means of the periods between two recognizable events (Howe, 1965). Further statistical analysis has been the subject of much controversy. Messenger and Flitters (1959) plotted curves of the rate of embryonic development of three species of fruit flies with reference to over twenty temperatures. Few studies have so many points of reference, thus predictions of the influence of temperature are extrapolated from curves mathematically equated to fit experimental data. Browning (1952) applied the x^2 goodness of fit test to logistic curves based on the work of Birch, Davidson and Prosner on three widely separated orders of insects and concluded that it was unlikely that the observed trend in rate of development with temperature could be expressed by means of a logistic curve. He suggested however, that it remains a useful tool for

predicting rate of development despite slight inaccuracies. Boehms (1971) suggested a polynomial regression equation to describe the rate of embryonic development and total hatching time of Sympetrum vicinum.

No previous study has been done on the influence of temperature upon the direct embryonic development of Perithemis tenera and Plathemis lydia. The present study was undertaken (1) to establish morphological stages in the embryonic development of Perithemis tenera and Plathemis lydia and (2) to determine the influence of certain constant temperatures upon morphological stages of embryonic development and total hatching time.

II. NOTES ON *Perithemis tenera* and *Plathemis lydia*

Plathemis lydia, one of the so called "white tail" dragonflies is a medium sized dragonfly which is approxmately twice as large as the little amber winged *Perithemis tenera*. According to Needham and Westfall (1960), *Plathemis lydia* ranges further north in the United States and into Canada. *Plathemis lydia* also has a wider range in the southwestern United States than *Perithemis tenera*. *Perithemis tenera* has been reported in Mexico, whereas *Plathemis lydia* has not.

Both species are exophytic or display superficial oviposition releasing their eggs into the water. Like all Odonata, the eggs require submersion in water for hatching to take place.

The eggs of both *Perithemis tenera* and *Plathemis lydia* are ellipsoidal ovoid. According to Ando (1962) species with superficial oviposition produce ellipsoidal eggs without exception which are of two distinct types, elongate and ovoid.

Both Perithemis tenera and Plathemis lydia were found on the wing and mature from early spring until early fall.

The initial and terminal daily flight time of Perithemis tenera and Plathemis lydia were observed in a study of a community of adult Odonata in North Carolina. According to Lutz and Pittman (1970) these two species were considered to belong to the late morning group in that they began their daily flight period between 0700 and 1200 hours. The daily flight period extended until late afternoon. Perithemis tenera began and ended flight at essentially the same light intensity. Plathemis lydia stopped flying at a much lower light intensity than they began. (Lutz and Pittman, 1970)

Corbet (1960) proposed an ecological classification of two types of British dragonflies. The first type was called a "spring" species. These fly early in the year and have a well synchronized emergence with an early peak. "Synchronized" alludes to length of the flight season,

i.e., a highly synchronized species has a short flight season. The second type was called a "summer" species. It is represented by species which emerge later in the year and do not show a close synchronization.

Corbet's (1960) hypothesis that North Temperate Zone Odonata can be categorized into "spring" or "summer" species was based on two criteria (1) the predominant overwintering instar classes and, (2) the time and duration of the seasonal flight period. In fifty-three species observed in North Carolina by Paulson and Jenner (1971) as a group the Libellulids were found to overwinter in a great spread of instar classes. While results are inconclusive this study suggests that Perithemis tenera and Plathemis lydia are both "summer" species.

III. MATERIALS AND METHODS

During the spring and summer of 1967, gravid female dragonflies of the family Libellulidae, subfamily Libellulinae, Perithemis tenera and Plathemis lydia were collected by net as they were ovipositing in ponds and small streams. Both species are common and abundant in the Montgomery County, Tennessee and Todd County, Kentucky area where they were collected.

Eggs were collected at the site by grasping the wings of the female between the thumb and forefinger and dipping the tip of the abdomen into vials of pond water. Eggs of Plathemis lydia were released in a steady stream while those of Perithemis tenera were released more slowly requiring several dippings of the abdomen into the water.

A gelatinous and adhesive layer was present on the eggs. It was thin just after oviposition, but absorbed water and became thick within approximately forty-five minutes. The vials of eggs were taken to the laboratory where the eggs were forcibly separated with streams of water from a micro pipette. Using the pipette, one egg

was placed in each of 20 individual cylinders containing approximately 1 cc. of filtered pond water. Each unit of 20 eggs was placed in a fingerbowl so that water just covered the tops of the individual containers. Petri dishes were used as loosely fitting covers to help prevent rapid evaporation.

Units of 20 eggs were incubated at constant temperatures of 5, 10, 15, 20, 25, and 30° C. A total of 120 eggs was thus used from eggs collected from each female. A total of 960 eggs was used for the study. Temperatures were selected to fall within the ambient water temperatures excluding extreme weather variations.

Temperatures of 5 to 20° C were obtained in commercial refrigerators. Temperatures of 25 and 30° C were obtained by placing the fingerbowls on racks in water baths with controlled heat and constant stirring. Temperatures were found to be accurate within $\pm \frac{1}{2}$° C.

Eggs were observed daily until hatching or for the periods indicated. Eggs at 30° C were selected for determining the stages of development. A representative drawing was made each day until hatching. The similarity of the

two species was such that one set of drawings was sufficient. The development of eggs at 30° C for the duration of one day represented a morphological stage. All drawings were made with the Abbe camera lucida using various available University laboratory microscopes at 100X.

Mean values of development and total hatching time were determined by the equation:

$M = fx/n$ where:

M = mean

x = total days (until hatching or passing to the next stage)

f = number of eggs (hatching or passing to the next stage)

n = total number of eggs incubated at a particular temperature

The standard deviation was calculated according to the equation:

$\sigma = fx^2/n$ where:

σ = standard deviation

f = number of eggs

x = total days

n = total number of eggs incubated at a particular temperature.

The standard error was calculated according to the equation:

$M = \sigma/\sqrt{n-1}$ where:

σ = standard deviation

M = mean

n = total number of eggs incubated at a particular temperature

Percent development per day was plotted using the temperature as the abscissae and the reciprocal of the duration of total development 1/y times 100 as the ordinate.

The logistic equation $1/y = K/1 + e^{a-bx}$ (Andrewartha and Birch, 1954) was found to describe the relationship of development time with temperature at the range studied in which development proceeded directly to hatching. y represents total development time. a, b, and K are constants. K defines the upper asymptote toward which the

curve is trending; b defines the slope of the curve; and a relative to b fixes its position along the x axis.

IV. EXPERIMENTS AND RESULTS

The influence of temperature upon the morphological stages of the developing embryo and total hatching time was observed in eggs of Perithemis tenera and Plathemis lydia. Eggs were individually cultured at temperatures of 5, 10, 15, 20, 25, and 30° C.

Readily identifiable morphological structures served as guides for the determination of stages. The development which occurred in one day in eggs of Plathemis lydia cultured at 30° C met the criteria for staging. Little difference was found in embryonic development in eggs of Perithemis tenera and Plathemis lydia, therefore only one set of diagrams was made. Terminology for the description of stages was derived from Ando (1962) and Boehms (1971).

IVa. Morphological stages in embryonic development (Figure 1)

Stage 1. The first stage immediately following oviposition was characterized by homogeneity of the components of the cytoplasm. The yolk (y.) was evenly distributed throughout the egg. The chorion (ch.) was trans-

parent and surrounded by the gelatinous membrane (g.m.). A nipple shaped pedicel (p.) was present on the anterior pole of the egg.

Stage 2. The second stage was an early cleavage stage in which the nuclei now invested with cytoplasm and a cell membrane migrated forming a thick ventral plate (v.p.) in the aconal region of the egg. The homogeneous yolk was now divided into large yolk spherules (y.s.).

Stage 3. The ventral plate or germ disc continued to grow by cell multiplication and differentiation giving rise to surface partioning. This was evidenced by the presence of cephalic lobes (c.lb.), thoracic (th.) and abdominal segments (ab.seg.).

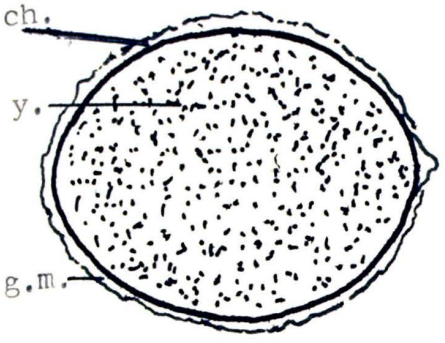
Stage 4. The fourth stage was defined by development of the appendages (app.) in the aconal region. The proctodeal region (proct.) was clearly identifiable by mesodermal cell masses. The cephalic lobe (c.lb.) was well established. The yolk sac showed shrinkage and the amnionic cavity (a.c.) was in evidence.

Stage 5. The ommatidia were clearly visible defining the relative position of the eye. Thoracic appen-

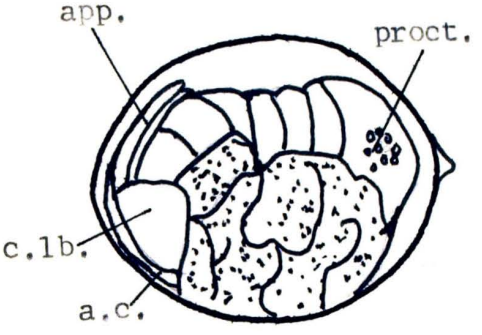
dages (th.app.) had lengthened considerably. Proctodeal (proct.) development was evidenced by an increase in the mass of mesodermal cells.

Stage 6. The embryo having completed blastokinesis, a 180^{o} rotation along a sagittal plane of the egg, resulted in the head now lying in the conal end of the egg. The embryo was now in the hatching position. Sufficient ommatidia had been formed to give the eye its shape. The stomodeum (stom.) and proctodeum (proct.) were well defined.

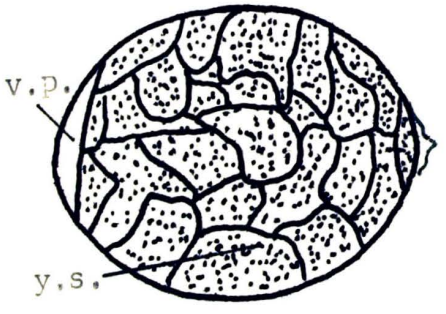
Figure 1. Morphological stages in the embryonic development of Perithemis tenera and Plathemis lydia. Species were so similar in morphological structure that one set of drawings sufficed. Key to abbreviations: a.c., amnionic cavity; ab.seg., abdominal segments; app., appendages; c.lb., cephalic lobe; ch., chorion; g.m., gelatinous membrane; p., pedicel; proct., proctodeum; stom., stomodeum; th., thorax; th.app., thoracic appendages; v.p., ventral plate; y., yolk; y.s., yolk spherules.



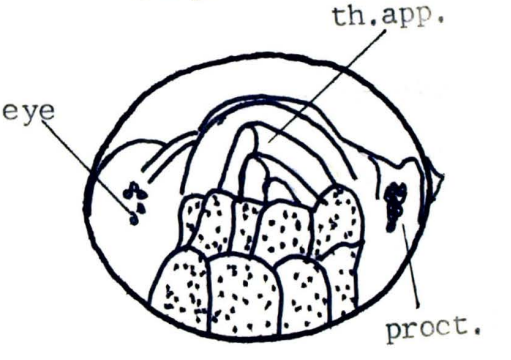
Stage 1



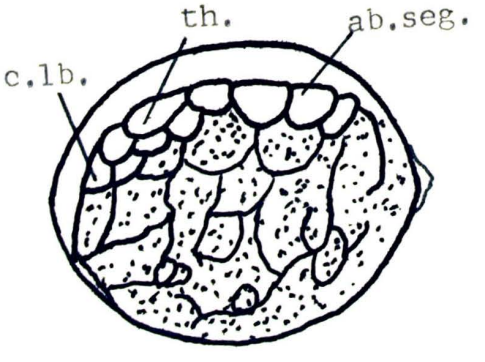
Stage 4



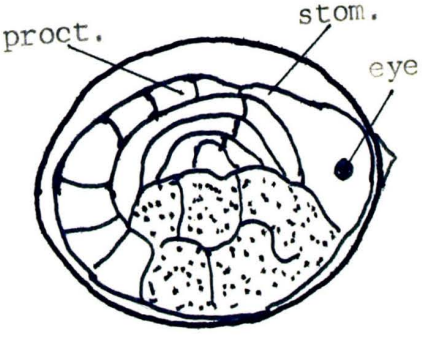
Stage 2



Stage 5



Stage 3



Stage 6

IVb. Influence of temperature on duration of stages

Mean development time of stages, standard deviations, and standard errors of the mean at the 1% confidence level calculated for directly developing eggs at 20, 25, and 30° C are shown in Tables 1 and 2.

Eggs of both species incubated at 5 and 10° C showed little or no development throughout the 60 day period of the study. Many eggs died. At 15° C eggs of Perithemis tenera completed Stage 2 after a mean time of 28.2 days, Eggs of Plathemis lydia at the same temperature completed Stage 1 after a mean period of 25.8 days, but did not progress beyond the second stage after 60 days. At 20° C development in Stages 1, 2, and 3 was at a relatively constant rate requiring approximately 2 days for each stage. Stages 5 and 6 required the longest developmental period in both species. Development in Stages 1, 2, and 3 required approximately twice as long in eggs cultured at 20° C than in those cultured at 30° C. In Stages 5 and 6 development time was increased by 3 to 4 times. At 30° C development required approximately 1 day for completion of each stage

Table 1

Mean development time of embryonic stages (M), standard deviations (σ), and standard errors (σ_M) at the 1% confidence interval of eggs individually cultured at 5, 10, 15, 20, 25, and 30° C.

Perithemis tenera

	Stage 1			Stage 2		
°C	M	σ	σ_M	M	σ	σ_M
5	-	-	-	-	-	-
10	-	-	-	-	-	-
15	6.1	(See text)		22.1	-	-
20	2.0	0	0	2.0	0	0
25	2.0	0	0	1.0	0	0
30	1.0	0	0	1.0	0	0
	Stage 3			Stage 4		
5	-	-	-	-	-	-
10	-	-	-	-	-	-
15	-	-	-	-	-	-
20	2,0	0	0	3.0	0.459	0.006
25	2.0	0	0	1.0	0	0
30	1.0	0	0	1.0	0	0
	Stage 5			Stage 6		
5	-	-	-	-	-	-
10	-	-	-	-	-	-
15	-	-	-	-	-	-
20	3.84	0.475	0.006	3.16	0.364	0.005
25	1.2	0.4	0.004	1.0	0	0
30	1.0	0	0	1.0	0	0

Table 2

Mean development time of embryonic stages (M), standard deviations (σ), and standard errors (σM) at the 1% confidence interval of eggs individually cultured at 5, 10, 15, 20, 25, and 30° C.

Plathemis lydia

°C	M	σ	σM	M	σ	σM
	Stage 1			Stage 2		
5	-	-	-	-	-	-
10	-	-	-	-	-	-
15	25.8 (See text)		-	-	-	-
20	2.0	0	0	2.0	0	0
25	1.0	0	0	1.0	0	0
30	1.0	0	0	1.0	0	0
	Stage 3			Stage 4		
5	-	-	-	-	-	-
10	-	-	-	-	-	-
15	-	-	-	-	-	-
20	1.6	0.580	0.011	1.4	0.537	0.009
25	1.0	0	0	1.0	0	0
30	1.0	0	0	1.0	0	0
	Stage 5			Stage 6		
5	-	-	-	-	-	-
10	-	-	-	-	-	-
15	-	-	-	-	-	-
20	4.5	1.025	0.019	3.7	1.4	0.025
25	2.9	0.277	0.005	2.1	0.863	0.014
30	1.08	0.343	0.004	1.0	0	0

in both species.

IVc. Influence of temperature on total hatching time

The mean total development time, standard deviation, and standard error at the 1% confidence level were calculated for directly developing eggs at 20, 25, and 30^{o} C as shown in Table 3.

The means were found to be significantly different at all temperatures at the 1% confidence level.

Percent development per day versus temperature is shown in Figure 2. Percent development per day of eggs of Perithemis tenera varies with temperature according to the equation: $1/y = 0.195/\ 1 + e^{5.813 - (0.253)(x)}$. (See appendix). Percent development per day of eggs of Plathemis lydia varies with temperature according to the equation $1/y = 0.288/1 + e^{4.240 - (151)(x)}$.

Boehms (1971) suggests a polynomial regression equation to describe the rate of development of eggs of Sympetrum vicinum. Andrewartha and Birch (1954) suggest that the logistic equation $1/y = K/1 + e^{a-bx}$ gives a realistic easily comprehended picture of the trend of speed of development at different constant temperatures.

Table 3

Mean development time (M), standard deviation (σ), and standard error of the mean (σM), of eggs cultured individually at 20, 25, and 30° C.

Perithemis tenera

°C Temp.	M	σ	σM
20	16.0	1.102	0.127
25	8.2	0.362	0.036
30	6.0	0	0

Plathemis lydia

°C Temp.	M	σ	σM
20	15.22	2.690	0.448
25	9.0	0	0
30	6.075	0.109	0.011

Figure 2. Percent development per day of individually cultured eggs of A. Perithemis tenera and B. Plathemis lydia versus temperature at 20, 25, and 30°C. Percent development, 100/y where y = incubation period in days is the ordinate. The abscissae is temperature in °C.

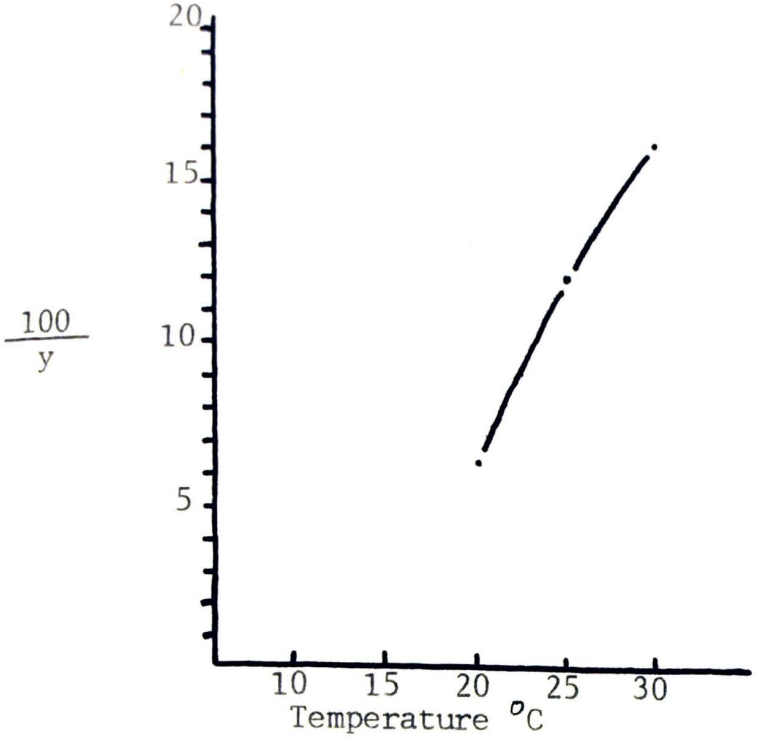


Figure 2A. Perithemis tenera

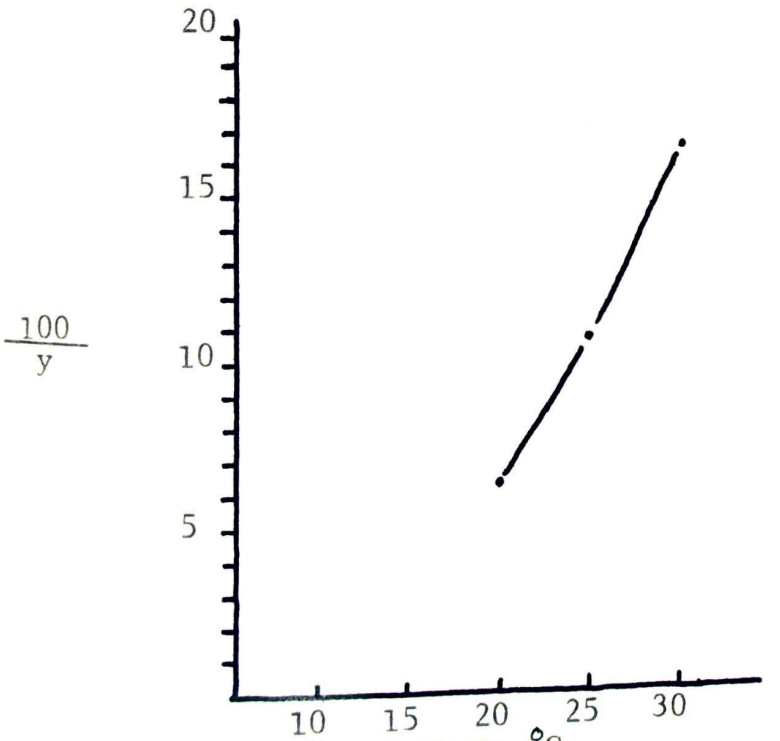


Figure 2B. Plathemis lydia

This simpler equation was found to be adequate for the description of the duration of hatching of directly developing eggs of Perithemis tenera and Plathemis lydia at the range of temperatures studied.

V. DISCUSSION

Previous studies on the influence of temperature upon the rate of embryonic development in Odonata eggs have been restricted to species demonstrating diapause. Boehms' work (1971) provided the first attempt at establishing thermal coefficients for different stages of morphological development. That study indicated that during prediapause and postdiapause a positive relationship was exhibited between the rate of development and an increase in temperature. Development during the diapause stage demonstrated a negative thermal relationship.

The present study is the first to determine thermal coefficients for direct developing eggs of temperate zone anisopterous odonates. It was established in Perithemis tenera and Plathemis lydia that a positive thermal relationship existed in all stages of development. As the temperature to which the eggs were exposed was increased the rate of development increased in the six morphological stages from oviposition to eclosion.

The rate of development varied over the range of temperatures: 5, 10, 15, 20, 25, and 30° C. No development occurred at 5 and 10° C indicating these temperatures were below the threshold of development. At 15° C eggs of Perithemis tenera required a mean duration of 28.2 days to develop through Stage 2, but did not develop further throughout the course of the study. Eggs of Plathemis lydia required 25.8 days to complete Stage 1 and remained in Stage 2 throughout the study period. With an increase in temperature of 10° C from 20° to 30° C, Stages 1, 2, and 3 doubled in rate of development in both species. Stages 5 and 6 of Plathemis lydia and 4, 5, and 6 of Perithemis tenera increased in rate of development three and fourfold.

The logistic curve $1/y = K/1 + e^{a-bx}$ was found to describe the rate of embryonic development of both species at the temperatures studied.

From the data presented in this study direct developing eggs exhibit similar thermal characteristics to the prediapause and postdiapause stages in delayed developing eggs. The range of temperatures studied corresponded to the ambient water temperatures. This suggests that Perithemis

tenera and *Plathemis lydia* may be classified as "summer" species. It is believed that further study will reveal that they are multivoltine.

VI. SUMMARY

Eggs of Perithemis tenera and Plathemis lydia incubated at constant temperatures of 20, 25, and 30° C developed rapidly and hatched. Percent development per day of eggs of Perithemis tenera varies with temperature according to the equation: $1/y = 0.195/1 + e^{5.813 - (0.253)(x)}$. For Plathemis lydia this relationship was described by the equation: $1/y = 0.288 + e^{4.240 - (0.151)(x)}$.

Eggs at 15° C showed some development, but did not hatch.

Eggs at 5° C and 10° C showed little or no development.

A detailed study was made of the embryonic development of Perithemis tenera and Plathemis lydia prior to the experiment. Six morphological stages were established. The appearance of and changes in gross morphological structures were used as indicators of the influence of temperature upon their rate of development.

Stages of embryonic development were observed at 15, 20, 25, and 30° C. At 15° C the eggs of Perithemis

tenera had completed Stage 2, but were still in the third stage at the end of 60 days. Eggs of Plathemis lydia had completed the first stage, but were still in the second stage of development at the end of the study. A more pronounced influence was observed on the developmental rates of Stages 5 and 6 of Plathemis lydia and 4, 5, and 6 of Perithemis tenera between the eggs cultured at 20° C and 30° C than on the beginning stages. The first three stages of development doubled in rate with an increase of 10° C from 20° C to 30° C. A three to fourfold increase was observed in the remaining stages of development. No delayed development occurred at temperatures suitable for development to occur.

Results of the study indicate that Perithemis tenera and Plathemis lydia may be classified as multivoltine "summer" species.

APPENDIX

Sample calculation: Finding the value of the constants K, a, and b, in the equation $1/y = K/1 + e^{a-bx}$ by the trial and error method.

A value for the constant K is first assumed. Then using experimental values for x and y at 20^{o} C, the equation is solved for a in terms of b

$$1/y = K/(1 + e^{a-bx})$$

Rearranging terms (1) $e^{a-bx} = Ky - 1$

Assume K = 0.300 $e^{a-b20} = (0.300)(15.22) - 1$

$$e^{a-b20} = 3.566$$

$$a-b(20) = 1.273$$

(2) $$a = 1.273 + 20\ b$$

Using the same assumed K value and experimental values for x and y at 25^{o} C equation (1) is again solved for a in terms of b.

$$e^{a-b25} = (0.300)(9.00) - 1$$

$$e^{a-b25} = 1.700$$

$$a-b25 = 0.531$$

(3) $$a = 0.531 + 25b$$

Substituting equation (2) into equation (3) and solving for b.

$$1.273 + 20b = 0.531 + 25b$$

$$0.742 = 5b$$

$$0.1484 = b$$

therefore: solving for a

$$a = 1.273 + 20b$$

$$a = 1.273 + (20)(0.1484)$$

$$a = 4.241$$

Using these calculated values for a and b and experimental values for x and y at 30^{o} C, the equation (1) is then solved for K.

$$4.241 - (0.1484)(30) = K(6.075) - 1$$

$$e^{-0.211} = (6.075)\ K - 1$$

$$1/e^{-0.211} = 6.075\ K$$

$$1.810 = 6.075\ K$$

$$0.298 = K$$

K is then assumed to be 0.298 and the above equation repeated until the assumed K is the same as the calculated K.

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