Effect of Photoperiod and Temperature upon the Growth Rate of the Later Instars of *Erythemis simplicicollis* (Say) (Odonata; Libellulidae)

B. ELWOOD MONTGOMERY
Purdue University,
West Lafayette, Indiana 47907

During the period of 1961 to 1968 over 9,000 Odonata naiads were collected in the field and introduced into photoperiod-temperature studies in our laboratory. Records of several experiments have been published (6, 7, 9, 10, 11, 12). However, many other experiments have never been analyzed and published because of preoccupation with studies in other areas. An attempt is being made now to summarize and analyze these and to publish results that seem significant.

Erythemis simplicicollis (Say), sometimes called the "green jacket," is a very common libellulid dragonfly of wide distribution. It occurs from southern Canada into Mexico and the Antilles. In Indiana it is virtually ubiquitous around ponds and lakes. It has a flight period in the state from early May into October, being most abundant from mid-June to late August (8) (Table 1.). Bick (1) from published data by Davis and Fluno (2) and his own observations gave the flight period in Florida and the Gulf States from March 4 to November 2, and noted oviposition "continuous" from April 10 to September 4. In more southern areas it may be found in flight throughout the year.

The life history of this species at New Orleans was worked out by Bick (1) who reported an incubation period of 10-16 days, with an average of 11.6 days, and a duration of 113 days for the one individual which survived to emergence and an average of 109.3 days for the 11 individuals in his study (Table 2). No conditions of temperature or day length were cited, except that the eggs were placed "under a bell jar above which a desk lamp was kept burning throughout the incubation period." The rearing apparently was carried out under "room conditions" and

TABLE. 1 *Relative seasonal abundance of adults and different instars of Erythimis simplicicollis (Say).*

	April	May	June	July	Aug.	Sept.	Oct.
Index of adult abundance[1]		-1-5	5-15-10	16-15-23	15-13-12	10-2-1	
Number	73	47			380	165	45
Octult					2%		
Septult					8%		2%
Septult					21%	1%	4%
Quintult		2%			29%	8%	13%
Quintult	4%	6%			26%	14%	24%
Tertult	33%	13%			11%	19%	33%
Penult	33%	30%			4%	35%	13%
Ult	30%	49%			2%	23%	9%

[1]Based upon data from Montgomery (1945); the index of relative abundance was compiled by tabulating the number of collections, or sightings, over a 40 year period, by thirds of months.

[2]Based upon data from Montgomery (1971); compiled from analysis of collections of maiads made for temperature-photoperiod studies.

TABLE 2. *Duration of development stages of Erythemis simplicicallis (Say). Comparison of Louisiana and Indiana material. Minimum, maximum and average in days.*

Instar	Egg	1	2	3	4	5	6	7	8	9	10	11	12	13	Total Naiad Stage
	10-16	1-7	3-6	2-4	2-4	2-4	3-6	4-6	5-7	3-9	4-9	5-12	14-18		
La	11.6	4.5	3.5	2.7	2.4	3.3	4.0	5.1	5.9	6.1	6.2	9.2	15.3	40	109.3
		11-22	2-15	13-14				12-16	11-14	11-40	11-23	24.47	50-111	80-142	
21°/16	14	14.9	8.3	13.5	17	15	10	14.7	13.0	25.3	15.3	27.0	85.3	116.8	357.7
ratio		11.0-3.1	0.7-2.5	6.5-3.5	8.5-4.3	7.5-3.8	3.3-1.7	3.0-2.7	2.2-2.0	3.7-4.4	2.8-2.6	4.8-3.9	3.8-6.2	2.0-3.6	
Ind/La		3.0	2.8	5.0	7.1	4.5	2.5	2.9	2.2	4.1	2.5	2.9	5.6	2.9	3.4
		15-27	9-19												
18°/16		21.9	15.8	11	37										
		4-6	10-27	6-7											
24°/16		5.1	18.5	6.5	12	10									

natural day length. The natural day length at New Orleans (30°N latitude) at the time of hatching (June 18-24) was 14 hours 4 minutes, the longest days of the year at this latitude. This gradually decreased (ca ½ to 2 minutes per day) to 11 hours 40 minutes on October 9, the date of the emergence of the naiad which completed development.

A collection of naiads, in the nontult to quintult instars, was obtained August 9 from a lake in an old strip mine pit at Ashboro, Clay County, Indiana. These were separated into individual culture dishes during the following two days and reared through the remaining instars in our laboratory. Ten naiads were placed in each of 15 "climate" cabinets with different regimes of temperature and photoperiod. These were selected to measure the effects of temperature and photoperiod upon development, especially to determine if there is a definite division between "long day" and "short day" environments for this species, and to compare the length of time required for a complete life cycle with that reported by Bick (1) in Louisiana.

The day length at the time the naiads were collected and removed from the natural environment (40° N latitude) was approximately 14 hours, decreasing about two minutes per day.

A mated pair of *E. simplicicollis* was collected July 10, 1967 at a pond on the Purdue Forage Farm in Dubois County, Indiana. A clutch of eggs was obtained by grasping the female by the wings folded above the body and dipping the tip of the abdomen against the surface of water in a small container. The eggs were returned to the laboratory, which was air conditioned to 21°C, and incubated under natural light conditions (day length of 14 hours, 50 minutes to 14 hours, 30 minutes). A number of eggs hatched in 14 days and naiads were isolated into 2″ culture dishes. Lots of 10 were placed in cabinets at three different temperatures, 18°C, 21°C and 24°C, all with a 16-hour photoperiod. Most of the naiads survived through the first instar, many through the second, a few through the fourth at 18°C, and the fifth at 21°C and 24°C. The data from the 21°C rearings were combined with those of the August 9 material of the same temperature to give a complete life history from the Indiana population. This furnishes a base for comparison with Bick's life history data based upon a Louisiana population (Table 2).

Naiads hatched from eggs in the laboratory and those of the size of the Ashboro material (2-5 mm in length) were started in 2″ culture dishes, transferred to 4-¼″ dishes when they became conspicuously larger (7-9 mm in length) and to 1-or 1-½ pint fruit jars when the ultimate instar was attained. Inverted U-shaped strips of ¼″ screen wire were provided as supports for emergence. All dishes and jars were examined daily for molts and to supply food. It may be noted that those environments indicated as 0 hours photoperiod were thus exposed to light for 5 to 10 minutes daily for this examination. Food consisted of protozoa and other organisms from "hay infusions" and/or nematodes for small naiads and "white worms" (Enchytraeidae) for all others. The worms remained alive and active from one feeding to the next so that it is believed that food was always available. The instar of naiads which did not survive to emergence was determined by the length of the wing pads of the dead insects, which were preserved with all exuvia until checked. However, this character could not be employed to identify the instar of naiads before the septult as the pads are not present until this instar and are too small to be reliable in this and the following instar. Furthermore, neither this nor any other instar. characteristic can be examined without danger of injury in living naiads.

Upon the assumption that all naiads develop in 13 instars the octult of our material has been equated with the sixth instar of Bick's study. There appears to be some variation from the instar characteristics given by Bick but a more thorough study of our extensive material is needed to determine if there are differences between the two populations, or if the number of instars may vary between individuals, as was found in Anax (6). The photoperiods in our studies were constant as the cabinets were light proof and all examinations were made during light periods. However, the length of the effective photoperiod in nature may be questioned as there appears to be no definitive evidence on the threshold of optical stimulation of Odonata naiads. There is a little experimental evidence that this threshold, in some species at least, may be below the level of moonlight (5). This series of experiments shows very definite effects of photoperiod as well as temperature upon the development, or the duration of instars (TABLES 2-5).

The survival rate of Odonata naiads in laboratory rearings is very low. Bick had one naiad of 11 reach emergence (9%) with two others reaching the ultimate instar but dying after 1 and 15 days respectively. In most of our experiments, especially with Anisoptera, the rate of survival to adult emergence was about the

TABLE 3. *Duration of instars in several regimes of temperature/photoperiod.*

Temperature/ photoperiod	Naiad Number	Instar 6	7	8	9	10	11	12	13
	3297	1	14	8	17	17	21	49	56
27°/	3288	8	7	10	21	20	12*		
16 hrs	3295			11	12	43	37	52	33
	3291			17	8	15	17	15*	
	3292			8	28	17	19	70*	
	3324	1	25	8	11	28	22	39	117
	3320		8	9	37	14	22	35	58
	3322			15	16	12	21	27	72
	3323			15	21	21	33*		
27°/	3325			17	9	17	21	8*	
13½ hrs	3326			15	16	12	19*		
	3318				8	23	14	28	209
	3319				15	32	14	30	82
	3321				11	23	28	35	134
	3327				15	39	18	43*	
	3376	12	58	23	15	16	21	70	115
27°/	3368			8	116	43	92	64	92
9 hrs	3372			43	96	32	21	62	62
	3375			26	105	24	29	34	35
	3373				108	21	52	75	80
	3359		19	7	31	67	26	25	43
27°/3x3 hrs	3362			46	11	10	20	30	67
	3355	22	13	128	0*				
27°/0 hrs	3357			19	143	71	37	0*	
	3348				19	120	55	101	64
	3349				25	102	49	77	59
	3354				8	121	50	71	100
	3434	30	184	42	34	142	103	50	142
21°/0 hrs	3437			24	173	39	41	121	146

TABLE 4. *Effects of temperature and photoperiod upon the rate of development of Odonata naiads; duration of instars-range (minimum and maximum) and average in days.*

Temperature (°C) Photoperiod (hours)	Instars 5	6	7	8	9	10	11	12	13	6-13	7-13
"Natural"	2.4	3.6	4-6	5-7	3-9	4-9	5-12	14-18			
Bick's data	3.3	3.9	5.1	5.9	6.8	6.2	9.2	15.3	40	92.4	88.5
27°/16 hrs			7-14	8-17	8-28	11-43	11-54	15-71	33-56		
			10.5	11.3	18.2	23.4	30.5	46.3	44.5		184.7
27°/14.5 hrs	17	14	8-14	9-41	8-26	15-52	7-49	15-50	33-40		
	17.0	14.0	10.0	20.0	10.8	27.2	23.5	31.0	36.0	172.5	155.5
27°/14 hrs			17	8-17	8-37	11-35	26-52	27-107	28-103		
			17.0	10.3	14.5	18.9	33.7	46.7	67.1		208.7
27°/13.5 hrs			8-25	8-17	9-37	12-39	14-33	27-43	72-209		
			17.5	13.2	15.9	22.5	21.2	33.9	112.0		236.2
27°/13 hrs		8	8	3-11	4-9	6-16	10-35	15-43	32-62		
		8.0	8.0	7.5	7.0	10.3	18.0	23.3	50.0	132.0	124.0
27°/12 hrs		15	16	8-15	25-76	22-41	42-85				
		15.0	16.0	11.3	42.7	33.7	68.7			187.4	(7-12)
27°/9 hrs		12	58	23-43	15-116	16-43	21-92	34-75	35-115		
		12.0	58.0	30.7	88.0	25.8	47.0	61.0	76.8	399.3	387.3
27°/3x3 hrs		22-101	5-19	7-46	11-86	10-84	20-37	30-68	43-67		
		64.5	12.5	22.3	42.7	58.0	28.8	41.0	58.3	328.5	264.0
27°/0 hrs		22	13-120	128	19-143	72-121	37-58	71-124	60-100		
		22.0	66.5	128.0	62.3	103.5	48.5	93.2	76.3	600.4	578.4
21°/16 hrs		10	12-16	11-14	11-40	11-23	24-47	50-111	86-142		
		10.0	14.7	13.0	25.3	15.3	27.0	85.3	116.8	306.7	296.7
21°/9 hrs		3		16-22	22-194	43-134	23-79	48-103	60-92		
				19.0	117.3	76.3	47.0	72.0	71.7	403.3	(8-13)
21°/0 hrs		30	184	24-42	34-173	36-142	41-103	50-121	142-146		
		30.0	184.0	33.0	103.6	90.0	72.0	85.5	144.0	742.1	712.1

TABLE 5. *Relative duration of instars of Ashboro material to that of Louisiana life history; ratios of minimums, maximums and averages.*

Temperature/	Instars									
photoperiod	5	6	7	8	9	10	11	12	13	6-13	7.13
27°/16 hrs			1.8-2.3	1.6-2.4	2.7-3.1	2.8-4.8	2.8-4.5	1.0-3.9	0.8-1.4		
			2.0	2.9	2.7	3.8	3.3	3.0	1.1		2.1
27°/14.5	8.5-4.3	4.7-2.3	2.0-2.3	1.8-5.9	2.7-2.9	3.8-5.8	1.4-4.1	1.0-2.8	0.8-1.0		
	5.2	3.6	2.0	3.4	1.6	4.4	3.0	2.0	0.9	1.9	1.8
27°/14			4.3-2.8	1.6-2.4	2.7-4.5	2.8-3.9	5.2-4.3	1.9-5.9	0.7-2.6		
			5.2	1.7	2.1	3.0	3.7	3.0	0.9		2.4
27°/13.5			2.0-4.2	1.6-2.4	3.0-4.1	3.0-4.3	2.8-2.8	1.9-2.4	1.8-5.2		
			3.4	2.2	2.3	3.6	2.3	2.2	2.8		2.8
27°/13		2.7-1.3	2.0-1.3	0.6-1.6	1.3-1.0	1.5-1.8	2.0-2.9	1.0-2.4	0.8-1.6		
		2.0	1.6	1.0	1.7	2.0	1.5	1.5	1.3	1.4	1.4
27°/12			3.8-2.5	3.2-2.8	2.7-1.7	6.3-8.4	4.4-3.4	3.0-4.7			
			2.9	2.7	1.7	6.9	3.7	4.5		3.7 (7-12)	
27°/9		4.0-2.0	14.5-9.7	4.6-6.1	5.0-12.9	4.0-4.8	4.2-9.7	2.4-4.2	0.9-2.9		
		3.2	11.4	5.2	13.0	4.2	5.1	4.0	1.9	4.3	4.4
27°/3x3		7.3-16.8	1.3-3.2	1.4-6.6	3.7-9.6	2.5-9.3	4.0-3.1	2.1-3.8	1.1-1.7		
		15.3	2.5	3.8	6.3	9.4	1.3	2.7	1.5	3.6	3.0
27°/0		7.3-3.7	3.3-20.0	25.6-18.3	6.3-13.7	17.8-13.4	9.4-4.8	5.1-6.9	1.5-2.5		
		5.6	13.0	21.7	9.2	16.6	5.3	6.1	1.9	6.4	6.5
21°/16		3.3-1.7	3.0-2.7	2.2-2.0	3.7-4.4	2.8-2.6	4.8-3.9	3.6-6.2	2.2-3.6		
		2.6	2.9	2.2	3.7	2.5	2.9	5.6	2.9	3.3	3.6
21°/9				3.2-3.1	7.3-21.6	10.8-14.9	4.6-6.6	3.8-5.7	1.7-3.6		
				3.2	17.3	12.3	5.1	4.7	1.8	4.8	(8-13)
21°/0		10.0-5.0	46.0-30.7	4.8-6.0	11.3-19.2	9.0-15.8	8.2-8.6	3.6-6.7	3.6-3.6		
		7.7	36.0	7.1	15.2	14.5	7.8	5.9	3.6	8.0	8.0

same. However, in these experiments, probably because the tests were started with naiads instead of eggs, the rate is somewhat higher. The rate of survival to emergence in nature must be very low as the eggs produced per female are numbered in the hundreds and thousands (2). We counted 250 and 990, respectively, in two clutches of eggs in this species (13) and it appears likely that each female may oviposit several times. Jacobs (4) reported another libellulid, *Plathemis lydia* (Drury) as ovipositing seven times at the same pond in a period of 22 days; we found one clutch of *P. lydia* eggs to number 1429.

The "climates" in which the lots of naiads of the August 9 collection were reared included nine photoperiods at 27°C (80°F), and three each at 21°C (70°F) and 34°C (90°F). These were selected to measure the effects of temperature and photoperiod especially to determine if there is a definite division in photoperiod lengths upon the rate of development. At 34°C only three naiads survived beyond the initial instar (that in which collected), all of these were collected in the quintult, the remaining 27 were collected in the septult or younger rendering instar identification impossible. All 10 naiads in the nine hour cabinet died without molting. Two quintult naiads in the 0-light cabinet survived into the tertult (in 57, 56, and 16 days) and into the ult (18, 25, 17 and 16 days) respectively. The one in the 16-hour environment reached the adult in 2, 28, 17, 21 and 68 days.

The data on development in the 21°C and 27°C environments, expressed in duration of instars (minimum, maximum and average) are given in Table 4. The average length of time required for completion of development through the last seven instars (7-13) varied from 124 to 236.2 days for the photoperiods of 13 hours and longer. However, this variation is not at all correlated with the length of photoperiod as the shortest period was at 13 hours and the longest at 13½ hours. In view of the variation of duration in all instars for individuals these differences are probably not significant. However, the 12-hour period appears to be less favorable, although the data are incomplete, as four died in the initial instar and two surviving into the ult both died after a few days. The 9-hour period showed a considerably longer time for this development but when the nine hours were divided into three equal periods distributed at equal intervals throughout the day the time required was reduced. At 21°C the period for completion of the life cycle was lengthened, although at 16 hours of light it was less than those of the 27°C/9- and 3x3-hour periods.

In all regimes the duration of instars was greater than the periods reported by Bick for Louisiana; the ratios for the averages as shown in Table 5, varied from 0.9 (only two cases) to 36.0 times those in Bick's rearings. In all except the 27°C/13 hour there were one or more naiads with three times or more instar lengths than the maximums of the Louisiana material. These "long" periods were found in all instars included in the experiment (5-13), and showed some correlation with temperature and photoperiod. The percentages of "long" periods of all naiads in all instars for the 27°C groups were: 16h.—18%, 14-½h.—12%, 14h.—16%, 13-½h.—13%, 12h.—40%, 9h.—53%, 3x3h.—29%, and 0h.—52% and for 21°C groups: 16h.—21%, 9h.—59% and 0h.—93%. The effects of 16 hours of light at 21°C and the 3x3 photoperiod at 27°C in decreasing the number of such long periods is evident. The ability of naiads of this species to complete development with only 5-10 minutes of light in each 24-hours, with repeated very long instars resulting in 6.4 and 8.0 times the period required under "natural" conditions is most interesting. The universal occurrence of these long periods must be an adaptation to survival over winter. The very definite difference in the effects of the 13-and 12-hour photoperiods correlates very well with the flight period in the Indiana season, mid-May through September. A day length of 13 hours or more, beginning about April 10 would seem to stimulate emergence of some individuals within a month and a day length of 12 hours and less beginning September 1 would tend to inhibit the emergence of most individuals until the combination of lower temperatures and shorter day lengths would end all emergences for the season.

E. simplicicollis appears to have only one generation a year and to pass the winter in all instars as young as the octult, possibly younger as we have no data on either the "long" instars earlier or any occurrence of the earlier instars in the spring or autumn (Tables 1-3). There are no definite broods, ovipositing continuing through most of the flight period as observed by Bick (1), and development being lengthened or interrupted, by the lower temperatures and shorter day lengths of winter in any instar. However, it seems possible that a few individuals might complete the life cycle during a single season and that others might go through two winters. Furthermore, it is very likely that the shorter developmental period in the Louisiana population with a longer season of favorable growth may result in a partial second generation and that in more southern areas there could be two generations a year. In the northern portion of the range with opposite conditions it is probable that more than a year is regularly required for a generation.

Literature Cited

1. BICK, GEORGE H. 1941. Life-history of the dragonfly *Erythemis simplicicollis* (Say). Ann. Ent. Soc. Amer., 34:215-230.
2. CORBET, PHILIP S. 1963. A biology of dragonflies. Chicago, Triangle Books. xvi + 247 pp.
3. DAVIS, E. M. & J. A. FLUNO. 1938. Odonata at Winter Park, Florida, Ent. News, 49:44-47.
4. JACOBS, M. E. 1955. Studies on territorialism and sexual selection in dragonflies. Ecology, 36:566-586.
5. JENNER, CHARLES E. & PAUL E. LUTZ. 1963. (Discussions during Colloquium on the Odonata.) Pr. N. centr. Br., ent. Soc. Amer., 18:101-156.
6. MACKLIN, JERRY M. 1964. Notes on the life history of *Anax junius* (Drury) (Odonata: Aeshnidae). Pr. Ind. Acad. Sci., 72:154-163.
7. ____ & B. ELWOOD MONTGOMERY. 1962. Further notes on the rates of development of naiads of *Neotetrum pulchellum* (Drury) (Odonata: Libellulidae). Pr. Ind. Acad. Sci., 2:158-160.
8. MONTGOMERY, B. ELWOOD. 1945. The distribution and seasonal abundance of the Indiana species of Corduliidae and Libellulidae. Pr. Ind. Acad. Sci., 54:217-224.
9. ____ 1963. Effects of photoperiod and temperature on rate of development in naiads of *Ischnura verticalis* (Say). Pr. N. centr. Br., ent. Soc. Amer., 18:140-146.
10. ____ 1971. Records and observations of Indiana odonata. Pr. Ind. Acad. Sci., 80:253-263.
11. ____ & JERRY M. MACKLIN. 1962. Rate of development of the later instars of *Neotetrum pulchellum* (Drury) (Odonata: Libellulidae). Pr. N. centr. Br., ent. Soc. Amer., 17:21-23.
12. ____ 1966. Photoperiod studies on the Odonata. Pr. N. centr. Br., ent. Soc. Amer., 21:30-31.
13. ZEHRING, CONNIE SUE, ARCHIE ALEXANDER & B. ELWOOD MONTGOMERY. 1962. Studies of the eggs of Odonata. Pr. Ind. Acad. Sci., 72:150-153.