Notes on the Life History of *Anax junius* (Drury) (Odonata: Aeshnidae)[1,2,3]

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Many authors have suggested the important effects of environmental factors on the growth of Odonata. Photoperiod and temperature were the two factors considered of primary importance in the study reported here.

Anax is a cosmopolitan genus of the 35 to 40 species which are distributed in the temperature and tropical zones. Four species are known from North America, but the range of only one, *A. junius*, enters Canada (28). Furthermore, the genus has been studied by several authors. *A. junius* was selected for this particular experiment because of its wide distribution in America, and because Calvert (5, 6) had previously described its life history and growth rate.

Tillyard (1915a, 1915b, and 1916) reported on the physiological and morphological changes in the early stages of *Anax;* Portman (1921) who was probably the first worker to publish a complete life history for a species of this genus, reared *A. imperator* Leach from egg to adult in a little less than seven months. Later, Calvert (5, 6) reared *A. junius* from egg to adult. More recently, some excellent studies were conducted on *A. imperator* both in the field and laboratory by Corbet (8, 9, 10, 11).

As far as known, Calvert is the only other worker who has published a complete life history for this species. Because he has given an excellent detailed account of the color changes and growth rates which he found and since these observations are similar to his, a detailed description of each instar has been omitted in this paper.

Calvert (6) was able to rear one male from the egg to the adult stage. Using the data obtained from this individual, he assigned various other naiads and exuvia to corresponding instars. In this way he was able to study the growth rates and characters of three short incomplete ontogenetic groups of exuvia loaned to him by Dr. Kennedy as well as many other exuvia and naiads. He concluded that *A. junius* had either 12 or 13 instars, not counting the pronaiad. The individual which he reared moulted 13 times in addition to the pronaiadal moult or 14 times in all. He listed the duration of the immature stage as being 322 to 328 days. He stated, however, that there was no basis for asserting that this naiad presented the normal or typical development of this species. "Its eminence and its usefulness rests entirely on the chance of its having been reared to maturity." Calvert (6).

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1. Purdue University Agricultural Experiment Station Journal Paper 2304.
2. Research from the Entomology Environment Laboratory.
3. Material in this paper formed a portion of a thesis prepared under the direction of Prof. B. Elwood Montgomery and presented in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Purdue University, August, 1961.

Laboratory Rearing Experiments

On June 24, 1960 a female *A. junius* was seen ovipositing alone at a small gravel pit about one mile south of the Purdue University campus. She was captured and taken to the laboratory alive, where she was induced to oviposit a few eggs. Her wings were placed between pieces of cork board and stiff paper, in a manner similar to that used for spreading freshly-killed dragonflies for display purposes. The body was supported by the wings, however, because there was no center board. This simple apparatus was then placed over a dish of water containing a soft water-soaked piece of wood. The legs and abdomen of the female were allowed to come in contact with the wood, and about an hour later, she was seen ovipositing in a more or less normal manner. About thirty eggs were secured in this way. This method is similar to that suggested by Gardner and MacNeill (13) for securing eggs of species which oviposit exophytically.

The eggs were kept at a room temperature of 68°-80°F. On July 5, 1960, 20 second instar naiads were found in the dish.

Rearing studies were then started in a controlled environment chamber described by Macklin (20). The temperature was maintained at 80°F. and the day length was set at 17 hours continuous light in each 24 hour period. These specific conditions were selected in an effort to determine if a diapause could be initiated in this species as it was in *A. imperator* by Corbet (10).

The naiads were separated into individual culture dishes and 10 were placed in a constant environment chamber, the others were placed in similar dishes outside. The culture dishes, 4½" in diameter and 1½" deep, were filled with water to which protozoa cultures were added to supply the naiads with food. The dishes were covered with glass plates to prevent evaporation.

All of the naiads outside and one naiad inside the chamber died within the next three days. The death of the naiads outside the chamber may represent the normal mortality rate, or it may have been caused by the relatively high room temperature, which was nearly 95°F. during part of this period.

Five of the surviving naiads were placed outside the chamber, but none of these survived the third instar. Of the four remaining naiads kept inside the chamber, only one, a male (#606), reached maturity. This individual moulted only 11 times, counting the pronaiadal moult as the first, and completed immature growth in 111 days including the egg stage (Table 1). Although it is unfortunate that no other naiads matured from these eggs, the data for naiad #606, can be compared with Calvert's data and with the data from other partial rearings carried out in the constant environment chamber. The principal value of these rearing experiments lies in the fact that they show considerable deviation from the study made by Calvert, and also answer some of the questions which his study raised.

TABLE 1

Comparative data for two A. *junius* naiads reared from egg to adults, developing in 111 days in 11 instars, and 341 days in 14 instars.

Instars	Moult Date[a] (Macklin) #606	Moult Date[a] (Calvert) #3	Days of Duration #606	Days of Duration #3	Number of Segments Tarsi #606	Number of Segments Tarsi #3	Number of Segments Antennae #606	Number of Segments Antennae #3	Length in mm. #606	Length in mm. #3	Head Width in mm. #606	Head Width in mm. #3	Length of rear wing-sheaths in mm. #606	Length of rear wing-sheaths in mm. #3
Egg[b]	6-24	7	11	18										
1[c]	7- 5		few minutes											
2	7- 9	8	4	8+	1	1	3	3	2.6	2.45	1.0	.73		
3	7-15	8	6	14	2	2	3	4	4.4	2.82	1.6	.9		
4	7-18	9	3	15	2	2	4	4	5.3	3.35	1.7	1.23		
5	7-20	9	2	3	2	2	4	4	8.9	3.68	2.5	1.39		
6	7-25	9	5	11	2	2	lost	5	11.5	7.36	2.8	1.92	0.4	.14
7	7-30	9	5	4	3	3	5	5	14.5	10.14	3.5	2.49	0.6	.22
8	8-10	9	11	9	3	3	6	5	20.1	14.0	4.2	3.03	1.09	.33
9	8-20	10	10	14	3	3	7	6	27.7	18.0	5.3	3.76	1.7	.57
10	9-13	2	2	131	3	3	7	7	35.0	22.5	6.7	4.62	3.8	1.06
11	10-13	3	30	23	3	3	7	7	36.0	29.5	8.2	5.56	8.4	1.72
12		4		28		3		7		38.0		6.54		2.74
13		5		21		3		7		44.0		7.61		5.24
14		6		42		3		7		47.0		8.5		10.39
Total			111	341										

a. month and day for #606, month only for #3.
b. deposited by female in laboratory.
c. pronaiad counted as 1st instar, not observed.

Comparison of Immature Stages

By comparing the characteristics of naiad #3 of Calvert (6) with naiad #606, it was found that the latter appears to skip certain instars and combine the characteristics of some others (Table 1).

Considering the time duration found for the instars as shown by Table 1, much variation is evident. The longest (10th) instar of Calvert's naiad #3 required 131 days to complete. This period from October to February is "the winter diapause, spent in a moderately heated room and during which the larva fed. At other times of the year this instar may be reduced to twelve days,—" (Calvert 6).

By comparing the total length of naiad #606 with the lengths listed by Calvert, it would appear that transformation took place when this naiad reached a size equal to the 11th larval stadium or the 12th instar of his naiad #3. If instars two to 11 for naiad #606 are compared with instars two to 12 for Calvert's naiad #3, and if the minimum number of days (12) cited by Calvert is substituted for the 131 day period of this 10th instar of #3, then it will be found that the two naiads made about the same growth in total length,—38 mm. (#3) and 36 mm. (#606) in 141 days and 96 days respectively.

Other Rearing Experiments

Seven naiads were collected from the same gravel pit at which the ovipositing female of *A. junius* was taken. Two of these naiads were collected in January, four in June, and one in August, 1960. Because these naiads were selected on the basis of size, they do not represent the average sample from the pit during these periods. The smallest naiads found during each collecting trip were placed in the constant environment chamber for rearing.

The number of days each of these naiads spent in the various instars as compared with naiad #606 is shown in Table 2. Of the seven naiads collected in nature, six were reared to the adult stage. One of these moulted eight times, four moulted seven times, one moulted two times, and one died during transformation to the adult stage after four moults.

The penultimate and ultimate instars tend to be longer than the earlier instars. It also appears that the naiads which were collected in the latter instars, such as the quintult and tertult, had a longer ultimate instar than those which were placed in the chamber at an earlier stage. In general, it would seem that *A. junius* naiads living in similar conditions, such as the warm shallow water near the shores of a pond, and having at least ten to 15 hours of daylight each day could be expected to mature quite rapidly. Naiad #634 completed its last seven instars in 104 days and naiad #606 made its total growth, eleven instars, in only 100 days. Because the naiads which were placed in the constant environment chamber in the earlier instars developed much more rapidly than the naiad reared by Calvert, it is assumed that the conditions inside the chamber were favorable.

The extreme variation found between the number of days required for the different naiads to complete the same instar may be attributed partly to the time of year when they were collected.

TABLE 2

Number of Days in Each Instar for Eight *A. junius* Naiads Reared in a Constant Environment Chamber

Specimen Number	Sex	Instar										
		Decimult	Novult	Octult	Septult	Sextult	Quintult	Quartult	Terbult	Penult	Ult	Total
469	M			7[a]	30	7	7	17	20	26	24	138
470	F			9[a]	23	11	5	16	16	29	24	133
570	F		3[a]	3	4	1	4	7	18	26	41	107
572	F						2[a]	8	23	31	47[b]	111
573	F								8[a]	30	69	107
574	F			2[a]	4	2	5	12	20	31	36	112
606	M	4	6	3	2	5	5	11	10	24	30	100
634	M			8[a]	5	5	5	5	14	15	24	81
Average		4	6	3	11.33	5.17	5.17	10.86	17.29	26.50	36.88	

a. Naiad required this number of days to complete the instar in the chamber, but the total duration of the instar is not known.

b. Died in transformation.

Average number of days includes only naiads in the chamber during the complete instar.

F—Female.

M—Male.

Compared with naiad #606, the growth rate of naiad #634, which was collected August 28, 1960, was quite rapid. Although the octultimate and septultimate instars of #634 were somewhat longer than these same instars for #606, it is interesting to note that #634 completed the last seven instars in only 73 days as compared to 87 days for #606. Naiads #570 and #574 which were collected on June 20, 1960, matured more slowly in the last three instars than did naiads #606 and #634. Although an accurate comparison cannot be made because of the different photoperiods, it may be noticed that the naiads collected in midwinter required a much longer time in the first instar following their collection than did the others; naiad #469 and #470 which were collected on January 3, 1960, spent 30 days and 23 days respectively in the septultimate instar as compared to two to five days for the others. If it is assumed that growth is nearly stopped during the winter, it would only be natural for these individuals to be somewhat slow in starting to grow after having been taken from this cold natural environment where the air temperature was 27°F. and the surface water temperature was 32.5°F. They were collected from bottom debris about four feet below the surface and 15 feet from the south edge of the pond.

Naiads #572 and #573 which were collected in the quintultimate and terultimate instars developed more slowly in the final instar than did the other naiads collected on June 20, 1960. In fact, these two naiads required more time in the penultimate and ultimate instars than did the naiad reported by Calvert. This naiad spent only 21 days in the penult instar and 42 days in the ult compared with 30 and 31, and 47 and 69, respectively, for these instars in #572 and #573. The growth rates of these naiads in nature were probably not altered very much by the constant environment. There is, of course, the possibility that other factors caused these naiads to mature more slowly in the final instar. Grieve (15), for example, found that parasites lengthened the growth period of *Ischnura verticalis* Say. However, one should not overlook the possibility that this variation in growth rate may occur commonly in this species.

Variations in Size of Reared Naiads

The naiads reared in the constant environment chamber show a rather wide range of variation in size, but it does not appear to be much different from the finding of Calvert for this species, and it is much less than the differences cited in the literature by other authors. The ultimate instar exuvia of the eight naiads which were placed in the constant environment chamber ranged from 36.0 mm. to 46.9 mm. in total length, and from about 8.2 mm. to 8.9 mm. in head width. Cabot (3) listed a total length of 40-52 mm. for this species. Needham and Hart (22) gave the total length as 39 mm. and the head width as 8 mm. Garman (14) listed the total length of mature naiads as 50 mm. Needham and Westfall (23) referred to the length of the naiads in terms of the genus only; they gave the total length as 40 mm. to 62 mm. Walker (28) listed 43.5 mm. to 47.0 mm. for the total length. Corbet (10) found that mature *A. imperator* naiads varied from 44 mm. to 56 mm. in length. The males were usually about one millimeter shorter than the females.

The length of the front margin of the rear wing-sheaths of the naiads reared in the constant environment chamber ranged from 8.2 mm. to 10.4 mm. Naiad #574 measured 39.7 mm. in length but the rear wing-sheaths were only 8.2 mm. long. In addition, the sizes of the adults did not vary in direct proportion to the ultimate exuvia. Naiad #634 which measured 46.7 mm. in length was much longer than naiad #606 which was only 36.0 mm. long, but the abdomen of the adults of naiads #634 and #606 measure 52 mm. and 49.2 mm., respectively. The naiad of the only other male placed in the chamber, #469, was 45.1 mm. long and the abdomen of the adult emerging from this exuvia was 51.6 mm. in length.

Discussion and Conclusions

In order to clarify some of the points raised by Calvert (6), it is necessary to discuss the seasonal distribution of *A. junius*. Montgomery (21) studied the distribution and relative seasonal abundance of this species over a 41-year period from 1900 to 1940 inclusive (Figure 1). According to his findings, adults of *A. junius* are found on the wing from the first third of March to the last third of October in Indiana. No population peaks which would indicate a synchronized emergence are shown. Whedon (29) observed this species ovipositing in Minnesota (44° North Latitude) as early as the 5th of March. He stated that, "Undoubtedly this large dragonfly is to be found very commonly over the entire state from April to November." Naturally, one would expect to find them flying earlier in the south. Blatchley (1) reported them at Sarasota, Florida, on February 17, 1911, and Calvert (4) stated that Skinner took a male at Guantanomo, Cuba, February 13, 1914.

The long flight period and consequently, the extended mating season as well as some unique field observations have led other authors to believe that *A. junius* matures in a comparatively short period of time. Paul Fischer (12) wrote: "In Franklin Park, in this city (Columbus, O.) a small lake was dug last winter in a place which was before entirely dry and well-drained, and during the last of April and the first of May this lake was filled with water from the city waterworks' pipes, which I am sure contain no dragon fly nymphs; and on the 30th day of August last, the shores of this artificial lake were literally lined with the exuvia of *Anax junius* nymphs; so they could not have been older than four months at the utmost."

Kellicott (18) interpreted Fischer's observation as appearing "to show that in this species, at least, imagoes mature from eggs laid the same season." Needham and Hart (22), referred to Kellicott and drew the conclusion that this indicated "the occurrence of two broods in a year. This is confirmed by one of our experiments, half-grown larvae were placed by Mr. Hart in a breeding-cage June 16 reaching the imago stage August 4." Brimley (2) also made an interesting observation. He stated "During the late summer of 1902, the water in Green's rock quarry (North Carolina) dried completely up, and remained so for at least two months. Unfortunately, I did not notice the dates when the pool dried and when it filled up again. On July 22 and August 10, 1903, I found in the quarry exuviae of recently transformed *Anax junius;* on Sep-

tember 5, 1903, of *Tramea carolina;* on August 10, of *Lestes forcipatus;* on August 10 and 18, of *Pachydiplax longipennis;* thus apparently showing that these four species had in this case completed their transformation in less than six months. The quarry had not had any water in it in the previous fall before late November at the earliest; thus, the eggs of these species must have apparently been deposited in the spring of 1903."

Based on the fact that 341 days were required to rear naiad #3, Calvert (6) concluded that: 1. Hart's experiment may possibly have speeded up the growth rate owing to food, the higher temperatures of June and July and other laboratory condition," 2. in Brimley's case, eggs were probably laid in November of the previous year; and, 3. in Fischer's case, partly grown naiads were introduced into these waters by artificial means. Calvert suggested that "in spite of his (Fischer's) assurance to the contrary, larvae of the eighth instar of younger, of a body length of 14 mm. or less, were introduced by the water pipes or otherwise."

Kennedy (19) who mentioned only *junius* in the genus stated that "*Anax* has speeded up its life cycle to three months." Wilson (30) said "Some species of *Anax, Tramea,* and *Aeschna* may have two broods during the year."

Calvert (6) summed up his observations as follows: "The existing breeding evidence does not admit of the occurrence of two successive generations within a year in temperate North America. Under continued high temperature of both water and air, either in nature or in the laboratory, two generations per year may be possible, but this has yet to be demonstrated."

The rearing experiments described in this paper have now demonstrated this possibility and tend to support the field observation made by Fischer and Brimley.

We are now faced with the question of whether *A. junius* has a winter dormancy or diapause as was suggested by Calvert which would delay development until late spring or early summer and therefore, prevent the occurrence of two generations in a single year. Jenner (16) stated, "there is no evidence at the present time to indicate that low temperature promotes diapause in any nymph of any species of Odonata." However, Corbet (11) found what appeared to be a diapause in *A. imperator* which was induced by changing the photoperiod.

The threshold of optical stimulation of naiads is another question to be considered. It has been suggested that the threshold of activity for the Odonata is below the intensity of moonlight (17).

The fact that naiads #469 and #470 had moved out into newly filled parts of the gravel pit on January 3, 1960 even though ice was covering most of the pit, indicates that they were not completely dormant. Therefore, it seems probably on February 27 that growth, if stopped, during the winter, starts quite early in the spring. Water temperature at the four foot depth from which these naiads were taken, was 45°F.

A. junius unlike *A. imperator,* matures in relatively large numbers throughout the season (Figure 1). This would indicate that it does not

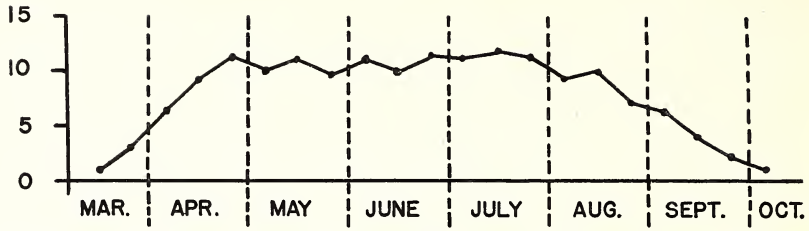

Figure 1. Flight season range and relative seasonal abundance of *A. junius* Drury in Indiana. Numbers are tabulated by thirds of months plotted as the "moving average" (average of three successive periods plotted at the midpoint) of collections or observations made during the period 1900-1940 inclusive. (Modified from Montgomery, 1947.)

have a diapause which synchronizes emergence. A long day-length of 17 hours employed in these rearing experiments was selected because Corbet (10) found that a constant long photoperiod of 15 hours and 20 minutes appeared to induce a diapause in *A. imperator*. No such diapause seems to be present in *A. junius*.

Even if *A. junius* were subject to a control mechanism which would induce a diapause such as is known for *A. imperator*, the day length and water temperature both increase under normal conditions in this area until the latter part of June.

Using nautical twilight at the 40° latitude (the approximate latitude of Lafayette, Indiana) it may be found that a 17 hour day occurs as early as April 21, and using astronomical twilight, this day length is encountered at this latitude on March 27.

If adults of *A. junius* emerged on March 15 and required two weeks to become sexually mature, they could lay eggs by the first of April. These eggs would have about 90 days in which to hatch and mature before the day lengths began to shorten. It is possible, of course, that the eggs in nature would not hatch as quickly as they did in the laboratory. Nevertheless, the naiads from these eggs could be in the penultimate or ultimate instar by the first of July. They would still have more than a hundred days, in some years, in which to complete their growth before the end of the flight period.

In view of these rearing experiments and the field observations indicated, it would appear that adults of *A. junius* emerging in March and April could lay eggs that would become adults during the same season in this area and, therefore, give rise to a second generation the same year.

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