SHORT COMMUNICATIONS

LARVAL GROWTH IN *NASIAESCHNA PENTACANTHA* (RAMBUR) (ANISOPTERA: AESHNIDAE)*

S.W. DUNKLE[1]

Department of Entomology and Nematology, University of Florida,
Gainesville, Florida 32611, United States

N. pentacantha was reared in the laboratory from egg to adult in one year, and had 14 or 15 larval instars. Instar 2 differs from all other Nearctic Aeshnidae by having 2 pairs of horns on the head. Instars 3-15 differ from all other Nearctic Aeshnidae by having mid-dorsal abdominal spines on at least segments 8 and 9. Stadia duration decreases from instars 2 to 4, then increases to 7, then decreases at 8, then increases to possible diapause in late instars. Male larvae died at a faster rate than females (p <0.01), so that by instar 15 only 37.5% of the survivors were males. Growth rates for both head width and total body length varied cyclically, with maxima at instars 4, 9, and 15 and minima at instars 2, 6, and 12. Certain morphological changes between instars are described.

INTRODUCTION

The larva of the monotypic dragonfly *Nasiaeschna pentacantha* (Rambur) was first described in detail simultaneously by NEEDHAM (1901) and by NEEDHAM & HART (1901). All of the published descriptions and keys from 1901 to the present apply only to the later instars. This study gives selected growth changes for all the instars of *N. pentacantha* and characterizes the rate of development.

S.W. Dunkle

METHODS

Several mature female *N. pentacantha* were placed in containers floored with paper toweling moistened with aged tap water, but only one female, collected near Gainesville, Florida, laid eggs. The eggs were laid on 25 Aug. 1979 and began hatching in 16 days after incubation at room temperature. Thirty second instar larvae were placed into separate 4 dram vials, each with a twig for a perch, and were fed newly hatched *Aedes* larvae. The mosquito larvae were not only active food organisms, but helped to prevent deoxygenation of the culture water, since they breathe air and feed on bacteria which use dissolved oxygen. As the dragonflies grew, they were placed in successively larger jars and fed enchytraeid worms as well as *Aedes*. Food was kept with the larvae constantly, so that this study records maximum growth rate at room temperature. Measurements of dimensions less than 4.8 mm were made with an ocular micrometer in a dissecting microscope; larger structures were measured with a metric ruler. Measurements of total length were taken from exuviae, measured in dorsal view from the proximal edge of the labrum to the distal tip of the epiproct. The caudal appendages are divergent in exuviae; thus the epiproct is foreshortened in dorsal view, and the actual length is slightly more than the length I recorded. The head width was measured in dorsal view across the widest part of the eyes.

Analysis of variance was performed as described by SCHEFLER (1969); growth ratios were transformed to arcsin values before analysis.

RESULTS

The eggs of *N. pentacantha* are similar to those of other Aeshnidae that have been described, except for *Anax* which has a hatching cone at the anterior pole (cf. CORBET, 1963). The eggs are pale yellow, 0.30-0.35 x 1.46-1.58 mm.

Table I

Growth of the head in instars 2-15 of *Nasiaeschna pentacantha* — (Measurements are in mm, ranges in parentheses. Growth factors were obtained by dividing the head width of instar Y by the head width of instar Y-I. Growth factors are different among instars at p <0.01)

Instar	$\overline{X}$	Head width	N	$\overline{X}$	Growth factors	N
2	0.73	(0.69-0.79)	28			
3	0.89	(0.82-0.96)	27	1.22	(1.11-1.37)	23
4	1.08	(0.98-1.16)	20	1.21	(1.15-1.27)	19
5	1.32	(1.22-1.44)	18	1.23	(1.11-1.32)	18
6	1.61	(1.44-1.78)	16	1.22	(1.09-1.34)	16
7	1.91	(1.80-2.08)	18	1.18	(1.11-1.38)	14
8	2.26	(1.96-2.72)	17	1.19	(1.07-1.32)	16
9	2.77	(2.52-3.04)	14	1.22	(1.12-1.35)	14
10	3.34	(3.04-3.80)	14	1.21	(1.13-1.28)	14
11	3.97	(3.80-4.20)	12	1.20	(1.14-1.25)	12
12	4.66	(4.32-4.96)	11	1.17	(1.05-1.24)	9
13	5.15	(4.80-5.80)	8	1.11	(1.02-1.24)	6
14	6.31	(6.00-6.70)	7	1.25	(1.15-1.34)	7
15	8.00	(7.70-8.30)	7	1.27	(1.19-1.33)	7
				1.21		175

Table II
Total length, taken from exuviae, of instars 2-15 in *Nasiaeschna pentacantha* — (Measurements are in mm, ranges are in parentheses. Growth factors were obtained by dividing the length of instar Y by the length of instar Y-1. Growth factors are different among instars at p <0.01)

Instar	$\overline{X}$	Total length	N	$\overline{X}$ Growth factor		N
2	2.16	(2.00- 2.30)	24			
3	2.58	(2.32- 2.78)	17	1.19	(1.05-1.36)	10
4	3.20	(2.92- 3.52)	19	1.24	(1.14-1.32)	17
5	4.08	(3.80- 4.64)	17	1.29	(1.17-1.37)	16
6	4.89	(4.60- 5.50)	16	1.20	(1.14-1.30)	16
7	6.13	(5.50- 7.00)	16	1.25	(1.12-1.38)	12
8	7.87	(7.20- 8.80)	13	1.28	(1.15-1.37)	12
9	10.19	(9.00-11.80)	14	1.29	(1.02-1.37)	13
10	13.38	(12.30-14.30)	12	1.32	(1.20-1.43)	12
11	17.13	(16.00-18.00)	11	1.29	(1.24-1.38)	11
12	21.91	(20.50-22.80)	8	1.29	(1.26-1.32)	6
13	27.87	(26.50-29.00)	7	1.27	(1.19-1.36)	5
14	35.39	(31.80-38.00)	7	1.27	(1.14-1.36)	7
15	41.30		1	1.30		1
				1.26		138

The first instar, also called the prolarva, probably lasts only a few minutes. The hydrophobic exuviae of this instar were seen floating on the water of the hatching jar, but are not described.

Of the 30 larvae I attempted to rear, 7 reached full growth in 15 instars. One male developed in 14 instars, apparently by skipping instar 12 or 13. Data from the latter male are generally not included in the following discussion. The head width and total exuvial length of each instar are listed in Tables I & II. No consistent difference in size was noted between male and female larvae.

Total lengths taken from whole larvae were not used in this study, but I compared them with exuvial lengths of equivalent instars. The total length of a whole larva usually fell within the predicted length range for its instar. The predicted range was obtained by multiplying the length of the previous instar's exuviae by the minimum and maximum growth factors (Tab. II) observed between the instars involved. The 6 whole larvae (in alcohol) which fell outside the length ranges predicted from exuviae were 23% shorter to 1% longer, $\overline{X} = 9.7\%$ shorter, than predicted. Final instar larvae are not included in the above calculations because only 1 final instar exuviae was available for comparison. To summarize, the total lengths of wild-caught larvae preserved in alcohol can probably be compared directly to the total lengths observed in this study, or if the reader wishes, can be increased by 9.7% before comparison.

The larvae are mostly dark brown with abdominal segments 1-3 or 4 pale until about instar 9. Such disruptive coloration of aeshnid early instars was thought by CORBET (1963, p. 83-84) to possibly help prevent cannibalism.

The antennae are 3-segmented in probably all odonate second instars. In *N. pentacantha,* the antennae become 4-segmented at instar 4 or 5, 5-segmented at instar 7 or 8, and 6-segmented at instar 9 or 10. WALKER (1958) stated that the antennae are 7-segmented, but all the last instars in the Florida State Collection of Arthropods, from Florida, Louisiana, and Oklahoma, have 6-segmented antennae. The antennal segments develop as described by MIYAKAWA (1977) for other aeshnids. New segments are added by the division of the basal segment of the flagellum.

Two pairs of spines or horns are present on the head, a short vertical pair on the vertex and a long lateral pair on the occiput. In the second instar the lateral horns extend beyond the level of the eyes and are curved slightly anteriorly (Fig. 1a). MÜNCHBERG (1930) shows similar but straighter lateral horns in second instars of the European *Brachytron pratense* (Müller). Second instar *Basiaeschna janata* (Say) have curved horns like those of *N. pentacantha,* but the horns of *B. janata* project dorso-laterally, and the vertex has a transverse ridge instead of another pair of horns. The lateral horns in *N. pentacantha* become proportionately shorter with age, so that they are bumps as wide as high by instar 8 or 9. Both pairs of horns remain as prominent bumps to and including the final instar.

The wings appear as separate bumps at instar 6, 7, or 8. They become progressively longer until the hindwing extends over segment 3 or 4 of the abdomen in the final instar.

The tarsi are 1-segmented in the second instar, become 2-segmented in the third instar, and become 3-segmented at instar 10, 11, or 12.

Fig. 1. *Nasiaeschna pentacantha:* (a) Head of second instar larva in dorsal view; — (b) Metafemur of seventh instar larva in dorsal view, showing distal spine.

The joint between segments 2 and 3 appears as a deep groove one instar before the joint actually forms.

A curious feature of the legs is a femoral spine which projects anteriorly to the femoro-tibial joint (Fig. 1b). The femoral spine is interesting because it is present only in the middle instars. It develops at instar 3 and remains prominent to instar 9 or 10, and is reduced to a bump thereafter.

Lateral abdominal spines are present on segments 6 or 7-9 in the second instar. A lateral spine on segment 5 develops in instar 4, 5, or 6. Thus lateral spines are present on segments 5-9 from at least instar 6 to the final instar.

Dorsal abdominal spines develop on segments 8 and 9 at instar 3. A dorsal spine is usually present on segment 7 from instar 4 onwards; it did not develop until instar 5 in one specimen. Additional dorsal spines develop on segments 5-6
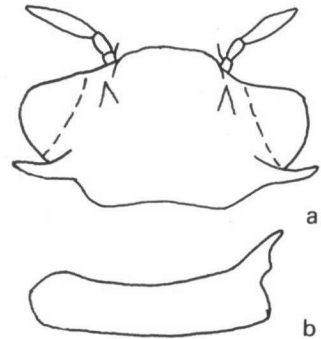
in some individuals in the middle instars, but these decrease in relative size in late instars, so that the final instar normally has dorsal spines only on segments 7-9.

The cerci or lateral abdominal appendages appear as a small triangular sclerite at instar 4, 5, or 6, and become progressively longer to the final instar. The cerci of the final instar are about 38% of the length of the epiproct in males, 30-34% in females. The epiproct becomes longer in proportion to the paraprocts until the epiproct is subequal to the paraprocts by instar 9 or 10. A long paraproct tip seta present in instar 2 is lost in subsequent instars.

Small spines projecting anteriorly from tergite 10 within the intersegmental membrane begin development at instar 6, 7, or 8. One such spine is present on each side at the level of the cercus; the purpose of the spines is apparently to strengthen the articulation between tergites 9 and 10. The spines increase to about 14% of the length of tergite 10 at the level of the spine in the final instar.

The sex of the larvae cannot be distinguished morphologically until instar 7 or 8, when the anterior gonapophyses of the female ovipositor appear on the posterior margin of sternite 8. The male primary genitalia are confined to sternite 9, but appear at the same instars as in the female. The male secondary genitalia begin development on sternite 3 at instar 11, and the ante-apical tubercle of the epiproct can be seen at instar 11 or 12.

The life cycle of *N. pentacantha* in the laboratory is one year. One male which was allowed to transform became adult 323 days after oviposition. The time spent in each instar is given in Table III; the mean times are significantly different among instars at $p < 0.01$ even if just instars 2-10 are considered. Stadia length increases

Table III

Days spent per instar, and sex ratio of survivors, in instars 2-15 of *Nasiaeschna pentacantha* — (Differences in both time of development and in sex ratio are significant at $p < 0.01$. Ranges of development times are given in parentheses)

Instar	$\overline{X}$	Days	N	% Male	N
2	16.4	(13-31)	18	47.4	19
3	13.8	(6-21)	9	47.4	19
4	7.4	(5-14)	10	47.4	19
5	9.6	(5-20)	9	47.4	19
6	14.9	(8-34)	9	47.4	19
7	17.3	(3-37)	7	47.4	19
8	11.6	(5-14)	5	50.0	18
9	16.8	(11-22)	5	40.0	15
10	19.8	(10-31)	4	40.0	15
11	32.7	(15-48)	3	38.5	13
12	48.5	(32-65)	2	33.3	12
13	82.0	(25-139)	2	33.3	9
14	63.1	(31-146)	7	37.5	8
15	46.0		1	37.5	8

notably at instars 11-15, and probably diapause occurs during one or more of these instars. Stadia duration does not simply increase with successive instars, rather the pattern seems to be a decrease in duration from instars 2 to 4, followed by an increase to instar 7, then another decrease at instar 8, followed by an increase to possible diapause in late instars. However, there was a great amount of individual variation, and some individuals did not closely follow this pattern.

N. pentacantha larvae have a strong positive thigmotaxis and remain clinging to a support as it is pulled from the water. The labium strike is notably slower than in other Aeshnidae I have observed.

DISCUSSION

Since *N. pentacantha* can develop with either 14 or 15 larval instars, and because of the great amount of variation in the instar when larval structures begin development, I found construction of a key to the larval instars impractical. Second instars differ from other instars by having no mid-dorsal abdominal spines and 1-segmented tarsi. Final instars have the hindwing extending to the mid-length of abdominal segment 3 or beyond, and the ovipositor of the female extends the full length of sternite 9. Penultimate instars have the hindwing extending to between the anterior and posterior edges of abdominal segment 2, and the ovipositor of the female extends about 3/5 the length of sternite 9. Instars 3-12 or 13 overlap in their characteristics; head width is as good a way as any to assign wild-caught larvae in these instars to instar classes.

Male larvae die at a faster rate than females, as shown by the highly significant decline in sex ratio in Table III. The percentage of males was probably higher during instars 2-6, but is not known because some individuals died before external evidence of sex appeared. I expect that the natural environment would be harsher than laboratory conditions, causing an even greater proportional mortality of males in the wild. But conversely, it is possible that some factor such as accumulation of toxic metabolites in the culture water caused higher mortality of the males than would be usual in nature. Male Anisoptera larvae probably do die at a faster rate than females in the wild. In all 9 species of Anisoptera listed by CORBET (1963), only 41.1-49.3% of the emerging adults were male. The probable cause of reduced male viability is the XO or XY chromosome condition of the males.

Growth rates calculated from both head width and total length are given in Tables I & II. The average increase in head width between instars was 21%, and in total length 26%, both close to the Przibram Growth Factor of 26% discussed by CALVERT (1929). The average growth rate of total body length was greater than for head width between all instars except between 2 and 3, and 5 and 6. However, the growth rates among instars in the present study were significantly different at $p < 0.01$ for both head width and total body length. The pattern for changing

growth rates of both head width and total length seems to be an increase to instar 4, a decrease to instar 6, an increase to instar 9, followed by a decrease to instar 12, and finally an increase to instar 15. Thus the growth rate changes cyclically, with a longer period as growth proceeds. So far as I am aware, rhythmic changes of growth rate have not been reported previously in Anisoptera.

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