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EQUATIONS RELATING COMMONLY USED MORPHOLOGICAL MEASUREMENTS OF *ANAX JUNIUS* (DRURY) (ANISOPTERA: AESHNIDAE), INCLUDING AN ALLOMETRIC ANALYSIS OF SIZE

T.C. FOLSOM
Department of Zoology, Erindale College, University of Toronto, Mississauga, Ontario, L5L 1C6, Canada

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The prediction equations for conversion between head width, labium length, body length, and wet and dry weight along with the statistical information required for estimating errors and confidence limits are provided. All of the prediction equations (regression analysis) explain greater than 95% of the total variance. — A study of intra-instar variation in 3 morphological parameters suggests that head width is the least variable and generally most practical parameter to measure. — A study of allometric growth was concentrated on the thorax, trying to detect deviations from simple allometry for late instar larvae. No deviations were found, including the lack of a "mature" stage of larval growth which has been reported for a synchronously emerging mayfly sp. (H.F. CLIFFORD, 1970, *Can. J. Zool.* 48: 305-316). As the mature stage mayflies could apparently emerge regardless of body length, Clifford hypothesized that the mature stage aided in synchronizing emergence. The lack of such a stage in *A. junius* is consistent with the hypothesis because this sp. does not emerge synchronously.

INTRODUCTION

Researchers intending to describe or compare larval odonate sizes choose from a variety of possible morphological parameters to measure. In the case of *Anax junius*, ROSS (1967, 1971) measured labium length, KIME (1974) measured head capsule width, and both TROTTIER (1970, 1971) and BEESLEY (1972) measured total body length. Obviously comparison of data between such studies is difficult without a means of converting the different parameters of interest into comparable measurements. One purpose of this paper is to provide prediction equations for converting measurements of one larval structure into another or to dry weight. Also, variability in measurement data was examined for an indication of which morphological parameter would be best for routine use by most investigators.

The other purpose of this paper is to examine how larvae change in form with change in size using the allometric method. CLIFFORD (1970) found deviations from simple allometry in a mayfly species that was particularly striking in those larval body parts that would reflect the development of adult structures such as flight muscles. He proposed that larvae of a certain body length pass into a "mature stage" from which they are ready to emerge regardless of size and that this promotes synchronous emergence. As both Odonata and Ephemeroptera are paleopteran insects with an inability to fold the wings parallel to the body, the odonate larval thorax and wing pad development may be similar to the pattern CLIFFORD (1970) detected. Consequently an allometric analysis of the *Anax* thorax was undertaken.

METHODS

The 71 larvae measured for the prediction equations were collected from several sites in southern Ontario, Canada, and preserved in Kahle's solution (ethanol, water, formalin, acetic acid; 15:30:6:1 parts) after collection. Size measurements (head width, labium length, body length) were made to within .01 mm with an ocular micrometer equipped dissecting microscope. Larvae whose body length exceeded the microscope's capacity (>32 mm long) were measured to within .5 mm in a petri dish put over 1 mm graph paper. The head width size range of larvae used was 0.78-9.90 mm for the prediction equations and 1.80-8.95 mm for the allometry equations.

Head width was measured at the widest point across the eyes. Labium length was measured from the anterior cleft to the prominent arc-like suture at the base, as per ROSS (1967). Body length was measured from the most anterior part of the head to the end of the paraprocts, as per TROTTIER (1970).

Larval dry weight was obtained by drying at 75°C for 24 hours. The data for the relationship between larval wet weight and head width were read from figure 7 in KIME's (1974) thesis. She measured 10 starved *A. junius* larvae and obtained their wet weights according to MOENS' (1973) method, which accounts for the water held in the rectum.

An additional 66 larvae were measured for the allometry analysis. The head width and body length were measured as above. The width of the mesonotum was measured at its anterior end where it joined the pronotum. The distance from the posterior edge of the pronotum to the beginning of the abdomen, measured on the side of the body below the wingpads, was called the mesometanotum length.

Least squares regression analysis with one Y value per X value generated the prediction equations and allometric equations. A common logarithmic transformation was performed on all data to remove the exponential character of the data. All equations were of the form log Y = a+b (log X).

The relative variability of three measurements (head width, labium length, and body length) was analyzed in 25 ultimate instar *A. junius* for an indication of which parameter varies least within an instar and would be best for routine measurement by most investigators. These larvae were determined to be ultimate instar independently of body size by the high degree of pigment development of the eyes.

RESULTS AND DISCUSSION

THE PREDICTION EQUATIONS

Correlations among the size parameters and dry weight were all greater than 0.97 (Tab. I) showing almost perfect correlation between the pairs of parameters. The means and sums of squares for these parameters and KIME's (1974) data concerning larval wet weight are presented (Tab. II) as well as the residual variance (Tab. IIIA) as they will be necessary for anyone computing standard errors and confidence intervals of predicted values.

Table I

Product-moment correlation coefficients for all combinations of the four parameters measured (l = length; — wd = width; — wt = weight).

	Labium l	Body l	Dry wt
Head wd	0.982	0.986	0.981
Labium l		0.977	0.976
Body l			0.975

The three easily measured parameters (head width, labium length, and body length) were regressed as independent variables against dry weight and each other (Tab. IIIA). For all cases the slope (b) was very significantly different from zero ($F_{(1,69)} > 1320$; $p < .001$). The coefficient of determination (R^2) showed that the regression accounts for at least 95% of the total variance in all cases so precise predictions can be readily made with these equations.

The equations for wet and dry weight versus head width can be used to estimate the expected loss in larval weight upon drying. As the slopes were virtually identical, it was only necessary to compare the intercepts (Tab. IIIA). Comparing the antilogs of the intercepts showed that dry weight would be about 10% of wet weight.

Table II

A: Means ($\bar{x}$), and sums of squares (Σx^2) for four mesurements made on 71 *Anax junius* larvae; — **B**: The same information from 10 larvae measured by KIME 1974, fig. 7).

Parameter	$\bar{x}$	Σx^2
A.		
Head wd (log mm)	0.526	5.898
Labium l (log mm)	0.456	9.103
Body l (log mm)	1.154	9.221
Dry wt (log mg)	0.572	78.583
B.		
Head wd (log mm)	0.788	0.057
Wet wt (log mg)	2.410	0.625

THE VARIATION STUDY

Head width, labium length, and body length were measured for 25 ultimate instar larvae, and coefficients of variation (standard deviation/mean x 100) were calculated (Tab. IV). The head width coefficient of 1.8% was the lowest suggesting that this structure varies the least within the instar. Labium length was somewhat more variable and body length still more so.

For establishing instar number or population size structure head width seems to be the best body structure to measure because it was least variable. Head width also has a slightly higher R^2 for predicting dry weight than does either other parameter (Tab. IIIA). A further advantage is that it is relatively easy to measure head width on living larvae which usually object to being held upside down for labium measurements. The full size range of head widths can be accommodated by dissecting microscopes but *Anax* body length may exceed the microscope's capacity. Then a second means of measurement would be needed for the large specimens, adding another component of measurement error. For these reasons, head width is clearly the best parameter for describing the size of *Anax* larvae for most purposes.

THE ALLOMETRY STUDY

If two structures grow at the same rate, they exhibit isometric growth and the slope (b) of the allometric equation $\log Y = a + b(\log X)$, should equal one (SIMPSON et al., 1960). Larvae change in form as they grow if the slope is greater than one (positive allometry) or less than one (negative allometry).

Table III

A: Prediction equations for dependent variables from independent variables. Least squares regression equations are of the form log Y = a + b (log X) where a is the Y intercept and b the slope or regression coefficient. Also given are standard errors for b (SE b), residual variance (s^2), and the coefficient of determination (R^2). (N = 71 larvae). The regression of head width and wet weight (N = 10 larvae) was based on data of KIME (1974). — B: Allometry equations of the same form as the prediction equations. (N = 66 larvae).

Independent variable (X)	Dependent variable (Y)	a	b	SE b	Residual s^2	R^2 (%)
A.						
Head wd	Labium l	-0.186	1.220	0.0281	0.00465	96
Head wd	Body l	0.505	1.233	0.0248	0.00362	97
Head wd	Dry wt	-1.313	3.581	0.0854	0.04305	96
Labium l	Head wd	0.166	0.790	0.0182	0.00301	96
Labium l	Body l	0.706	0.984	0.0256	0.00597	96
Labium l	Dry wt	-0.737	2.869	0.0762	0.05279	95
Body l	Head wd	-0.384	0.789	0.0158	0.00231	97
Body l	Labium l	-0.665	0.971	0.0253	0.00590	96
Body l	Dry wt	-2.713	2.846	0.0783	0.05657	95
Head wd	Wet wt	-0.336	3.486	0.1520	0.00117	98
B.						
Head wd	Mesonotum wd	-0.468	1.294	0.0159	0.00070	99
Head wd	Meso-metanotum l	-0.884	1.809	0.0187	0.00097	99
Body l	Mesonotum wd	-0.896	0.988	0.0258	0.00304	96
Body l	Meso-metanotum l	-1.486	1.383	0.0337	0.00521	96

Changes in form of *Anax* larvae were examined with respect to head width, labium length, body length, mesonotum width, and meso-metanotum (MMN) length. The 95% confidence intervals for the regression coefficients were calculated.

The slopes of labium length (1.220) and body length (1.253) versus head width (Tab. IIIA) were greater than one (95% CI ±0.056 and ±0.049 respectively), indicating that the head in young larvae is larger, compared to the feeding apparatus and overall body, than it is in later instars. Perhaps a relatively large brain and eyes are necessary for the complex processes of prey capture.

Comparing mesonotum width and MMN length to head width (Tab. IIIB) showed that both were growing much faster than head width (b = 1.294 ± CI 0.031 and b = 1.809 ± CI 0.037 respectively). Obviously as larvae approached the ultimate instar the structures responsible for adult flight were becoming more important in the larval body. When compared to body length the mesonotum width was isometric (b = 0.988 ± CI 0.051), but MMN length was again positively allometric (b = 1.383 ± 0.067).

Deviations from simple allometry caused by a change in relative growth rate between structures can be detected by plotting the difference between observed and predicted Y values against the associated X values (SIMPSON et al., 1960). If there is a methodical trend to the positive and negative deviations, such a change in the growth rates is indicated. In *Anax*, no methodical trends were detected in either notum measurement against both head width and body length. Thus there was no evidence for changes in growth rate of *Anax* leading to the mature stage CLIFFORD (1970) detected in a mayfly. Indeed, the high values of the coefficients of determination (Tab. IIIB) show that the simple regression did a very good job of accounting for the variation in the data.

Table IV

Head width, labium length, and body length for 25 ultimate instar larvae showing the mean and coefficient of variation (CV)

	Mean (mm)	CV %
Head wd	8.67	1.8
Labium l	7.46	3.4
Body l	44.24	7.1

CLIFFORD (1970) measured many morphological parameters of the mayfly *Leptophlebia cupida* and derived allometry equations based on total body length. Striking negative deviations from simple allometry were apparent for measurements of mesonotum length, mesonotum width, pronotum width (females), abdomen width (females), and forceps length (males). These structures reflect the development of adult structures like wings, flight muscles, eggs, and accessory male genitalia. The deviations for these measurements began at about 7 mm body length and resulted in generally slower growth of the thorax, abdomen (females), and forceps (males) relative to body length. CLIFFORD (1970) proposed that the mayflies passed from an "immature" stage to a "mature" stage when they were about 7-9 mm in total length. In the mature stage the larvae were ready to emerge regardless of size. Thus when environmental conditions for emergence are proper, all mature stage larvae could emerge and emergence will tend to be synchronous.

This allometry analysis of *Anax* was concentrated on the thorax to see if a similar mature stage with respect to the flight structures could be detected, but apparently there is no such stage. This absence is probably due to the lack of synchronous emergence in *A. junius*. Both the summer and winter generation of *Anax* in southern Ontario have emergence periods over a month long and it takes two weeks for 50% of *Anax* to emerge (TROTTIER, 1971). The lack of a mature stage in this non-synchronously emerging species therefore is consistent with CLIFFORD's (1970) hypothesis that the stage is important in promoting synchronous emergence. The hypothesis predicts that a mature stage would be found in the synchronously emerging spring species of Odonata.

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