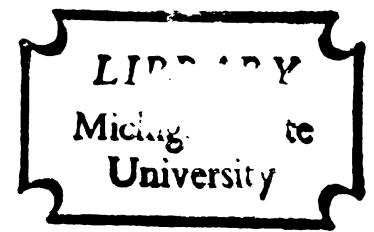


RESPIRATION IN ANAX JUNIUS DRURY
(ODONATA: AESHNIDAE)

Thesis for the Degree of M. S.
MICHIGAN STATE UNIVERSITY
MICHAEL F. PETITPREN

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THESIS



ABSTRACT

RESPIRATION IN ANAX JUNIUS DRURY (ODONATA: AESHNIDAE)

by Michael F. Petitpren

A Gilson differential respirometer was employed to evaluate the influence of time of day, season, sex, weight, temperature, and life stage upon the oxygen consumption of the dragonfly, Anax junius Drury.

The respiratory rate of twelve individual naiads monitored over a 24 hour period, six during the spring and six during the summer, showed no apparent diel or seasonal rhythm in metabolic rate.

The oxygen consumption of immature female dragonflies ($\mu\text{l/hr/individual}$) was significantly greater than that for the males at 13 and 20 C, but not significantly different at 27 and 34 C. Sex did not significantly influence the respiratory rate at 13, 20, 27, or 34 C when considered on a per gram basis.

The per cent of ash material increased proportionally with the growth of dragonfly naiads. Naiads weighing 4 mg (dry wt) contained approximately three per cent inert material while 13 per cent inert material was recorded for naiads weighing 300 mg (dry wt). Oxygen consumption

expressed either as a function of dry weight or ash free dry weight was not significantly different.

Respiration was related to dry body weight by coefficients of regression of 0.69, 0.79, 0.95, and 0.96 at 13, 20, 27, and 34 C, respectively. Respiration decreased significantly with increasing dry weight at 13 and 20 C, but increased directly with dry weight at 27 and 34 C.

Increasing water temperature resulted in increased oxygen consumption. Q_{10} increased with increasing dry weight, but decreased in the upper range of the temperatures evaluated.

It was not possible to delimit the specific instars for A. junius immatures. Respiratory rate decreased with growth at 13 and 20 C by coefficients of regression of 0.69 and 0.79, respectively. At 27 and 34 C the respiratory rate was not significantly altered during immature growth. Adult respiration was three times greater per unit gram weight when compared with naiad respiration at a comparable weight and temperature.

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(ODONATA: AESHNIDAE)

By

Michael F. ^{W. Kellogg}Petitpren

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INTRODUCTION

There is a wealth of information on the respiratory metabolism of economically important insects such as the cockroach, Periplaneta americana (L.); the flower beetle, Tribolium confusum Duval; the bee moth, Galleria mellonella (L.); and the honey bee, Apis mellifera L. In contrast, one is generally struck by the paucity of in depth studies on the respiratory rates of numerous common aquatic insects.

When the aquatic environment is degraded by pollutants such as human and industrial wastes, insecticides, and heated effluents, the survival of important animal life is greatly threatened. Such degradation of the environment is often reflected by changes in an organism's respiratory metabolism. Before the effects of pollutants on animal life can be assessed, it is first necessary to know the respiratory metabolism under "natural" environmental conditions.

Consequently, the common dragonfly, Anax junius Drury, was selected as an experimental animal for the following reasons: (1) to advance knowledge on the respiratory metabolism of an aquatic insect under the influence of certain modifying agents; (2) to establish

a base line of respiration upon which future studies on the effects of environmental modifiers of respiration might be ascertained; and (3) to contribute fundamental knowledge concerning the respiratory physiology of insects in general. As stated by Patton (1963):

The greatest deficiency in the study of biological activity of chemicals is lack of detailed fundamental knowledge concerning the normal physiology of insects in general and test species in particular. The pressure of meeting emergencies in the field has, in many cases, caused the research to be guided into a head-on approach without the devotion of necessary time (and money) to the solution of fundamental physiological problems that control the outcome of the experiments. This approach is analagous to starting the construction of a masonary arch with the keystone. Successful understanding of the problems of chemical-biological activity, resistance, and the ultimate goal of tailoring compounds to order will be achieved only after much time and effort have been expended on study of the fundamentals of the physiology and biochemistry of insects. There is no apparent shortcut to solution of the basic problems.

MATERIALS AND METHODS

Description of Study Areas

The animals employed in respiratory studies were collected from three ponds in the vicinity of the W. K. Kellogg Biological Station, Hickory Corners, Michigan during the spring and summer of 1966-67. The ponds were selected because of their proximity and availability of populations of A. junius.

Crum Park Pond (T2S R9W S6) has a surface area of 0.65 hectares. The pond has a water depth ranging from 0.5 to 1.5 m and is dominated by water lily, Nymphaea sp.; bladderwort, Utricularia sp.; and sedge, Carex sp. Approximately 25 per cent of the total 424 naiads tested were collected during 1966 among sedge along the pond's east shore.

Long Woods Pond (T1S R9W S8), with an area of 1.0 hectare and originally intended for waterfowl management, is located within the confines of the W. K. Kellogg Bird Sanctuary. A canal 3 to 5 m wide and 1 m deep has been dredged around the peripheral two-thirds of the pond's northern border. Nearly half of the total test animals were obtained from a dense stand of yellow waterlily (Nuphar sp.) occurring within the canal area.

The third collecting site, Marrow Pond, is located 100 meters NE of the W. K. Kellogg Biological Station and provided the only source of naiads during August and September, 1967. The pond is best described as a rather large (10 hectares) cattail-marsh with a central water lily region interspersed with areas of smartweed (Polygonum sp.) and purple-fringed riccia (Ricciocarpus sp.). In addition to naiads, the adults tested were obtained from laboratory-reared immatures collected from Marrow Pond.

Chemical and physical analyses of the pond waters were conducted periodically from 2 July through 4 September, 1966 and 28 July through 30 August, 1967. Water analyses were performed in accordance with the methods set forth in Standard Methods for the Examination of Water and Wastewater (American Public Health Association et al., 1965).

Air and water temperatures were measured with a mercury thermometer. Dissolved oxygen was ascertained by the Azide Modification of the Winkler Method using 0.0125 N sodium thiosulfate solution as a titrant. Hydrogen ion concentration was assessed with a Beckman pH meter (Model M-2). Alkalinity was determined by titration with 0.02 N H_2SO_4 , utilizing phenolphthalein and mixed bromcresol green-methyl red as indicators.

Field and Laboratory Methods

Naiads were collected by sweeping aquatic vegetation with a heavy-duty triangular dip net, and subsequently transported directly to the laboratory in a 10.4 liter polyethylene pail containing pond water and vegetation.

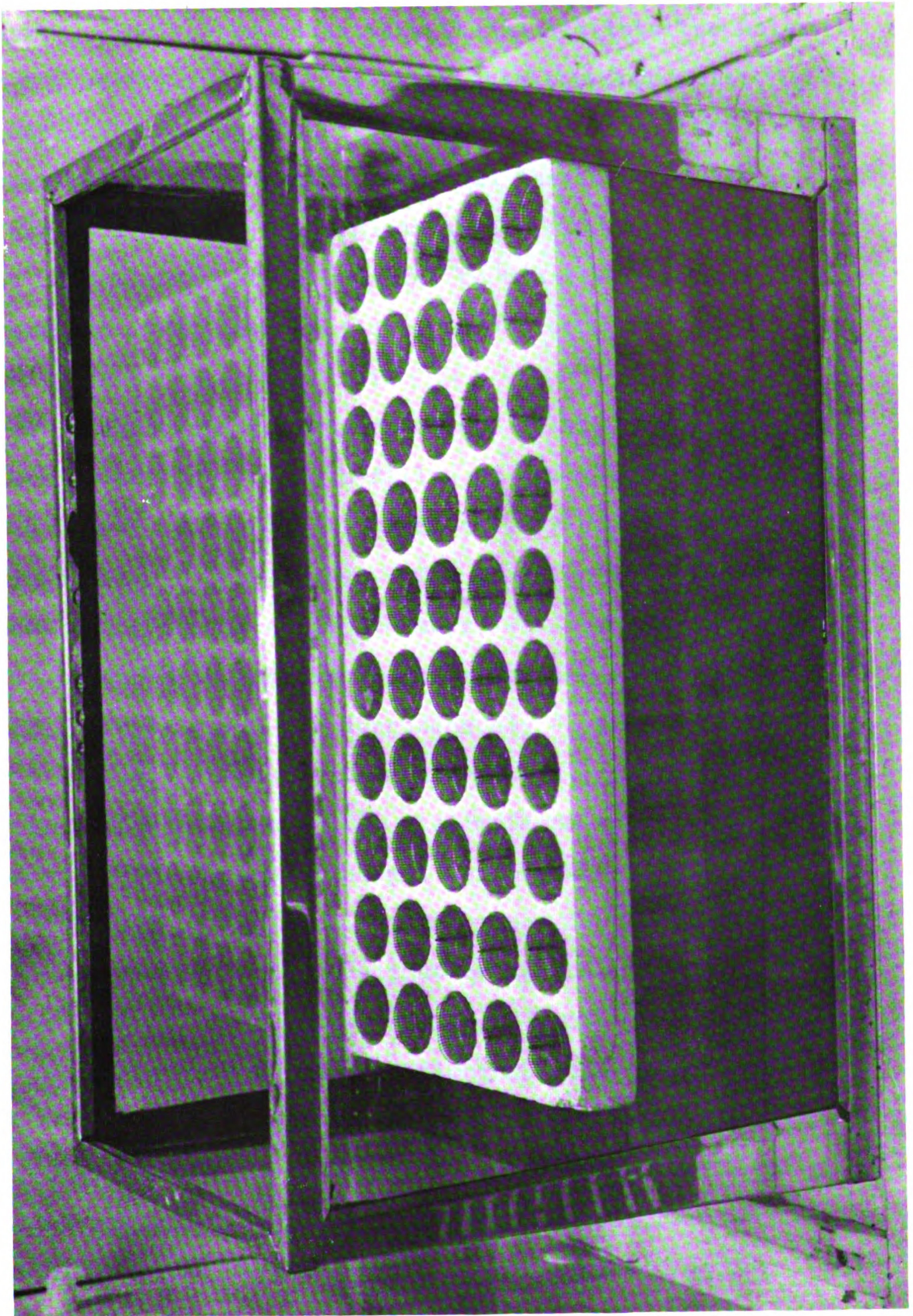
All animals were exposed to a similar pre-test history of 36 to 48 hours of starvation at a temperature (13, 20, 27, or 34 C) approximating that of the environment at the time of collecting. Each animal was evaluated only once at a single temperature for determination of oxygen consumption. Thus, all oxygen consumption observations were made independently.

Freshly collected, well aerated, filtered pond water was employed in the conditioning and evaluation of oxygen consumption. Handling of organisms was maintained at a minimum.

Since dragonfly naiads are highly cannibalistic under confined laboratory conditions, it was necessary to fabricate an acclimation apparatus for conditioning individual animals to experimental temperatures (Figure 1).

The apparatus was constructed by producing fifty holes (5 rows with 10 holes per row), 3.2 cm in diameter, into a piece of 40 cm x 20 cm x 3 cm styrofoam. Fiberglass screen (# 18 mesh) was weaved, using smooth wire (20 gauge), into tubes 3.2 cm in diameter and 7.0 cm in

Figure 1, Acclimation apparatus employed in conditioning Anax junius naiads to experimental temperatures.



length. The screen tubes were introduced into the holes in the styrofoam until the upper tube openings were flush with the upper surface of the styrofoam. The rough texture of the styrofoam held the screen tubes securely in place. Fiberglass screen (19 cm x 38 cm) was tied with monofilament line to the lower ends of the tubes. All materials used in the construction of the apparatus were non toxic.

The acclimation apparatus was floated in a 15 liter laboratory aquarium filled to one-third capacity with freshly collected filtered (filter paper No. V100, folded, size H) pond water. The aquarium and apparatus (containing one naiad per chamber) was transferred to an Ambi-Lo variable temperature chamber (pre-set to experimental temperature) for approximately 48 hours prior to initial oxygen consumption measurements. A thermostatic water bath was employed for acclimations above ambient temperature. Escape of naiads was prevented, during the conditioning period, by placing a piece of fiberglass screen over the entire acclimation apparatus. An air source with two air stones ensured continuous oxygenation of the water during the conditioning phase.

A Gilson Differential Respirometer (Gilson, 1963), Model No. GR 14, was employed in the evaluation of immature and adult dragonfly respiration. The manometric techniques used were those outlined by Umbreit et al. (1964).

The reaction flasks used in oxygen consumption measurements were provisioned with a substrate of boiled brick fragments, freshly filtered pond water (filter paper Munktells No. 8, size J), and accordion-folded filter paper wick saturated with 0.2 ml of 20 per cent KOH. Flasks of 7 ml, 15 ml, or 125 ml capacity were selected relative to the size of the naiads being tested. Adult respiration was measured in a specially constructed 1,250 ml reaction vessel containing a substrate of four or five sticks. The CO₂ absorbent (KOH) was contained in the side arm of the flask to prevent interference with the animal's well-being.

Each naiad, conditioned approximately 48 hours to the test temperature, was removed from the acclimation chamber and transferred to a flask containing filtered pond water. Precautions were taken to use flasks permitting liberal movement and complete emersion of test animals. End flasks (affixed to manometers 1 and 14) were controls measuring pressure changes not resulting from dragonfly respiration. Changes registered by the controls were averaged and either added or subtracted, at five minute intervals, from individual dragonfly respiration. Flasks of equal size were used concomitantly whenever possible to equalize sensitivity to pressure change.

After the flasks were lowered into the water bath, light was subdued by tapping a cloth securely over the respirometer. Flasks were oscillated slowly (84 cycles per minute) for 90 minutes before initiating measurements. The 90 minute period was necessary to equilibrate gas and liquid phases and permit animals to recover from handling and adjust to the experimental conditions.

The hydrogen ion concentration (pH) of the pond water was determined at various times before and after experimental evaluation. The changes in pH were in all cases considered negligible.

Oxygen consumption values were recorded at five minute intervals throughout a one-hour test period. Each test organism was subjected to four one-hour replicate oxygen consumption evaluations. The barometric pressure was noted at the beginning of each evaluation.

At the termination of an experiment the test organisms were removed from the flasks, killed in hot water, and placed in a drying oven for 24 hours at 104 C.

Organisms were transferred from the drying oven to a desiccator, containing CaCO_3 , for a two-hour period. Dry weights were determined to the nearest 0.1 mg.

Measurements of total body length, head capsule width, labium width and length, and meso-thoracic wing sheath length were determined to the nearest 0.1 mm utilizing a vernier caliper. Total body length was

measured from the distal end of the clypeus to the distal end of the epiproct; head capsule width from the most lateral points of the eyes; labium length from the distal points on the appressed moveable hooks of the lateral lobes to the proximal end of the mentum and labium width from the proximal ends of the opposite lateral lobes (labium terminology from Whedon, 1927); and wing sheath length from the mid-dorsal point of attachment to the most distal point of development. Whenever possible sex was determined by inspection of the ventral side of the ninth abdominal segment; females possessed ovipositors, males did not. See Appendix I for weight, linear measurement, and sex determinations.

Fifty-four oven dried specimens of various sizes were ashed to determine the relative percentage of ash material (cuticle, labium, endoskeleton, etc.) to oven dry body weight. Vycor tubes were washed, heated in a muffle oven approximately six hours at 520 C, removed, cooled, desiccated, and weighed to 0.1 mg accuracy on a Mettler balance. Tubes not deviating more than 0.1 mg from previous weights were provisioned with an oven dried specimen of known weight, placed in a muffle oven for one hour at 520 C, removed, cooled, desiccated, and reweighed to 0.1 mg accuracy. The weight of the ash subtracted from the dry weight of the organism equaled

the specimen's ash free dry weight. The percentage of ash free dry weight was determined by the equation:

$$P = (d-a/d) (100)$$

where P = per cent ash free dry weight; d = oven dry weight (mg); and a = weight of ash (mg).

Treatment and Calculation of Data

The oxygen consumption rates reported herein are representative of animals undergoing free, but moderate activity. The rates of oxygen consumption were computed utilizing various body weights as follows: (1) "Oxygen Consumption (μ l/hr/individual" or " O_2 consumption;" (2) "Oxygen Consumption (μ l/g dry wt/hr)" or " QO_2 ;" and (3) "Oxygen Consumption (μ l/g ash free dry wt/hr)" or "ash QO_2 ."

The values obtained in each oxygen consumption evaluation were plotted on arithmetic grid paper (10 mm to the cm), over a one-hour period, at five minute intervals. A line was fitted by inspection and the oxygen consumption rate computed for a 20 minute interval (between the 20 and 40 minute interval) and extrapolated on the basis of an hour. Micrometer readings of oxygen consumption were given digitally in microliters. To convert to standard conditions, corrections were made for the following:

1. Water bath temperature in degrees C = t.
2. Operating pressure (usually the same as barometric pressure) = P_b (3 is subtracted to compensate for the specific gravity of Hg at room temperature).
3. Pressure of water vapor = P_w .

The microliter readings were multiplied by the following to give microliters of dry gas at 760 millimeters Hg:

$$\text{multiplying factor} = \frac{(273) (P_b - 3 - P_w)}{(t + 273) (760)}$$

where: 273 = absolute zero 273° Kelvin

760 = standard barometric pressure (mm Hg)

t = water bath temperature in C

P_b = barometric pressure (in Hg x 25.4)

P_w = water vapor pressure at t.

Oxygen consumption evaluations were analyzed by the method of least squares, and met the following basic assumptions of parametric statistics (Li, 1964):

- a. the O_2 consumptions (y) of the animals of the same weights (x-arrays) follow a normal distribution,
- b. the relation between O_2 consumption and the average weight of different weight groups can be represented by a straight line, and
- c. the variances of the O_2 consumptions of all weight groups are the same.

Logarithmic transformation to the base 10 was performed on both dependent (y) and independent (x) variables to normalize the variances. Through logarithmic transformation, effects which are multiplicative on the original scale of measurement become additive on the logarithmic scale (Steel and Torrie, 1960).

The transformed oxygen consumption values were processed with an Olivetti Underwood Programma 101 Computer. Statistical results of processed data are given in Appendix II.

The relationship between respiration and body weight is expressed by the general linear regression equation:

$$\log y = a + b (\log x)$$

where y = predicted respiration; x = body weight; a = y intercept; and b = coefficient of regression indicating speed and direction of respiration as body weight increases.

Since over 400 independent observations were made, it was necessary to use statistical methods to test the hypotheses relevant to the data. The statistical methods employed were those set forth by Steel and Torrie (1960) and Snedecor (1956).

RESULTS

Field Methods

The results of physical and chemical analyses of the collection sites are given in Table 1.

Respirometry

Oxygen consumption by various animals is effected by intraspecific factors of sex, weight, and period in life cycle as well as by such environmental variables as time of day, season, and temperature (Prosser and Brown, 1961). These modifying factors were evaluated utilizing A. junius as the test organism.

Diel and Seasonal Effects

To determine the presence of either diel or seasonal oxygen consumption rhythms, respiration was monitored on two occasions over a 24 hour period at 20 C. No apparent diel changes in oxygen consumption were detected for twelve individuals evaluated in spring (April 28 through 29, 1967) and in summer (August 11 through 12, 1967) (Figure 2). Due to the apparent absence of diel and seasonal rhythms, no precautions in timing of oxygen consumption evaluations were considered necessary.

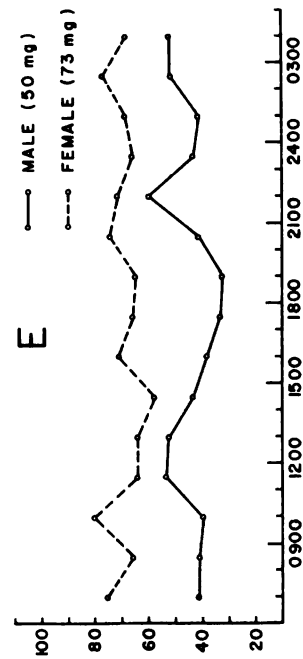
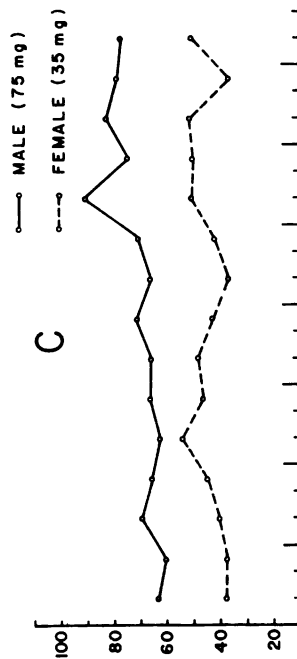
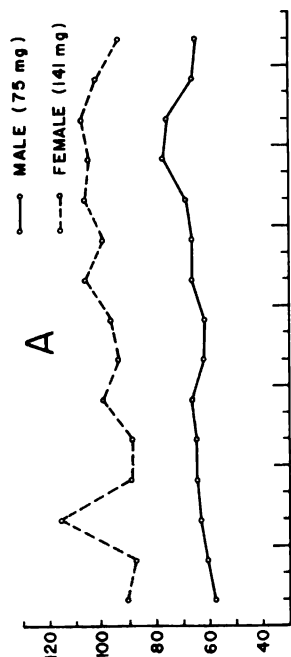
TABLE 1.--Chemical and physical determinations from Crum Park Pond (2 July to 4 September, 1966), Long Woods Pond (13 July to 4 September, 1966), and Marrow Pond (28 July to 30 August, 1967). Data were collected between 0800 and 1900.

Collecting Site	Temperature (C°)			Dissolved Oxygen (mg/l)	pH (mg/l)	Alkalinity (mgCaCO ₃ /l)					
	Air	Water				CO ₃	HCO ₃				
		Range	Range								
	$\bar{X}$	Range	$\bar{X}$	Range	Range	$\bar{X}$	Range	$\bar{X}$	Range		
Crum Park Pond	25.2 (8)*	20.0-28.5	25.4 (9)	21.6-29.0	5.4 (9)	2.0- 8.8	7.6-8.3 (7)	1.9 (9)	0.0- 9.0	137 (9)	100-173
Long Woods Pond	24.9 (8)	19.5-26.5	23.2 (8)	20.0-26.0	1.7 (8)	0.3- 3.6	5.6-7.1 (7)	0.0 (8)	0.0- 0.0	48.9 (8)	23-69
Marrow Pond	19.0 (2)	15.0-23.0	25.3 (4)	21.0-29.0	7.8 (2)	3.8-11.8	7.5- (1)	13.0 (2)	0.0-26.0	249.5 (2)	192-307

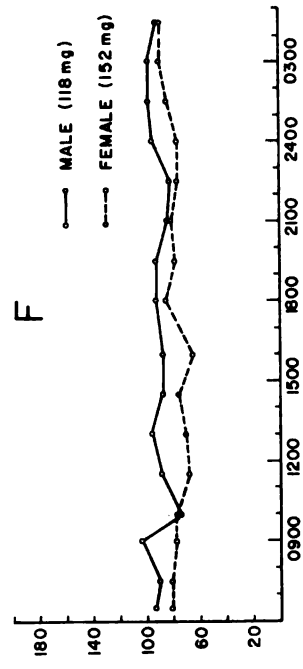
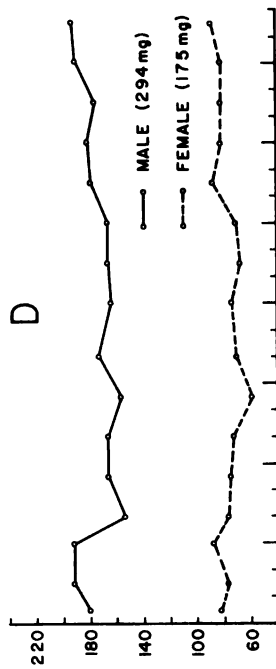
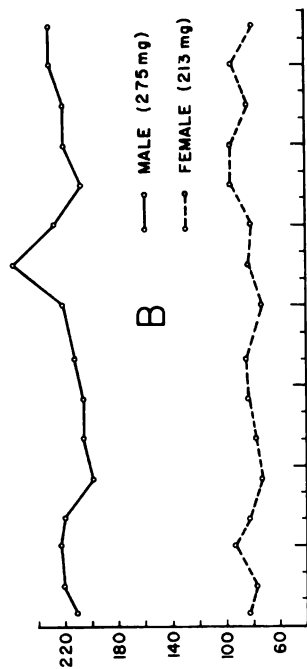
*The number in parentheses, (#), indicate number of days sampled.

Figure 2. Diel and seasonal oxygen consumption
of twelve individual Anax junius naiads
determined at 20 C.

SPRING



SUMMER



TIME (hr)

OXYGEN CONSUMPTION (µl/hr/individual)

Influence of Sex

The comparison of O_2 consumption and QO_2 between male and female dragonfly naiads was determined by testing the homogeneity of comparable coefficients of regression (b's) for males and females (Figure 3) (Steel and Torrie, 1960). Having met the assumption of a random sample drawn from a normal population, the level of significance was set at 5 per cent and the hypotheses tested:

$$(a) \quad H_0: \quad b_f - b_m = 0$$

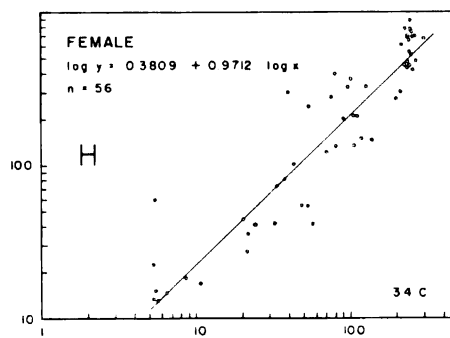
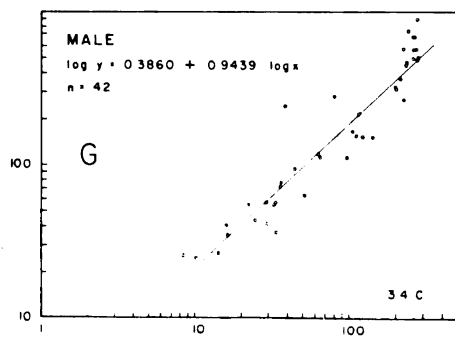
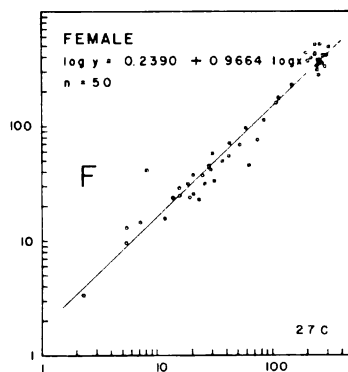
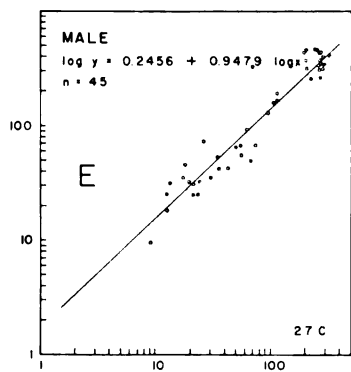
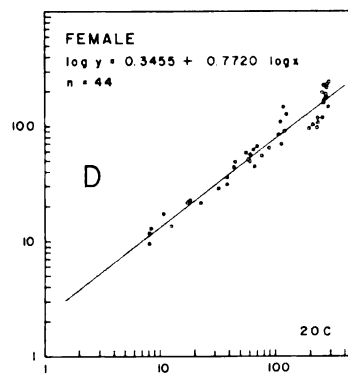
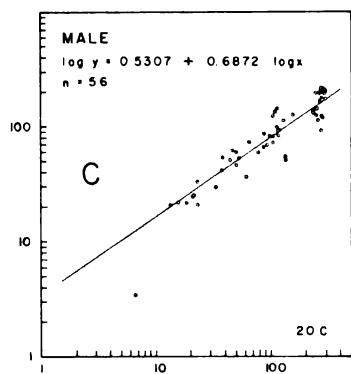
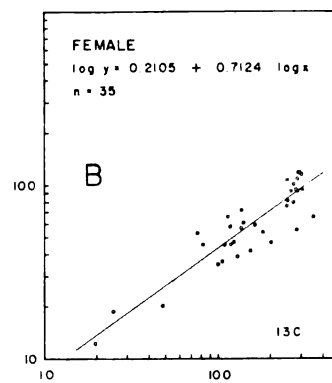
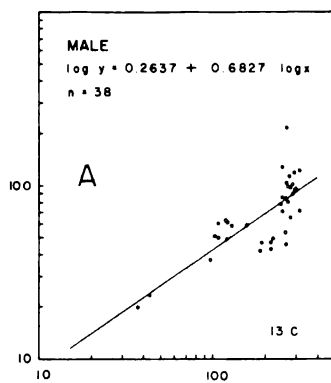
$$(b) \quad H_1: \quad b_f - b_m \neq 0$$

where b_m = male coefficient of regression; and b_f = female coefficient of regression.

Female dragonflies showed a significantly greater oxygen consumption rate (per individual) at 13 and 20 C, but O_2 consumption was not influenced by sex at 27 and 34 C (Figure 3 and Table 2). When oxygen consumption was expressed on the per unit weight basis, no sex difference was evident at any comparable temperature (Figure 4 and Table 3).

In general, male dragonflies (A. junius) tend to weigh more than females; however, the weight difference was not significant.

OXYGEN CONSUMPTION ($\mu\text{l/hr/individual}$)



DRY WEIGHT (mg)

TABLE 2.--Statistical analysis comparing log oxygen consumption between male and female Anax junius naiads at different temperatures.¹

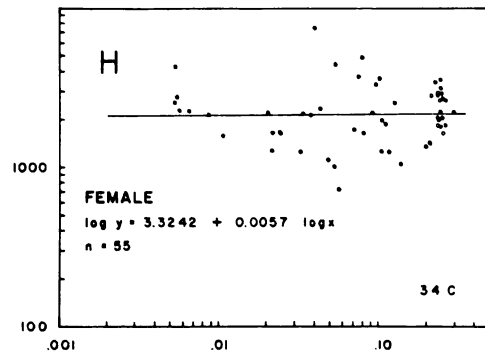
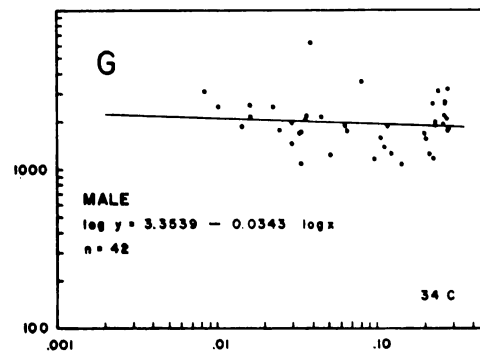
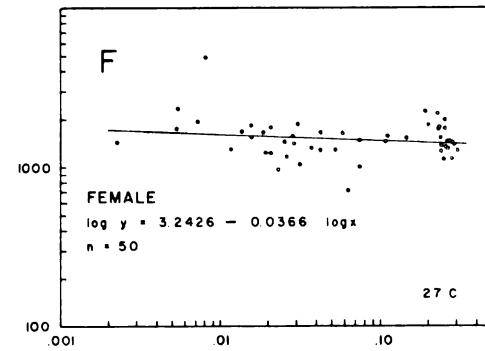
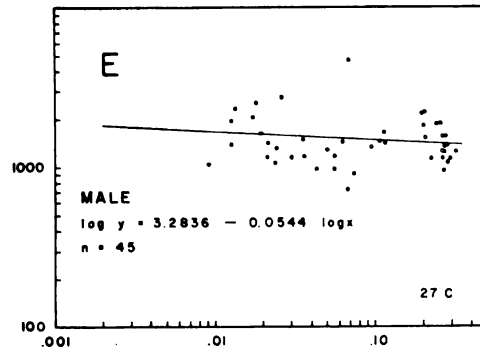
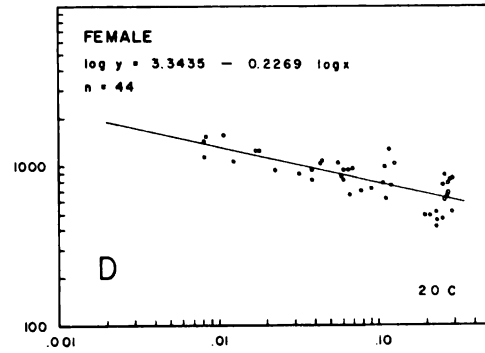
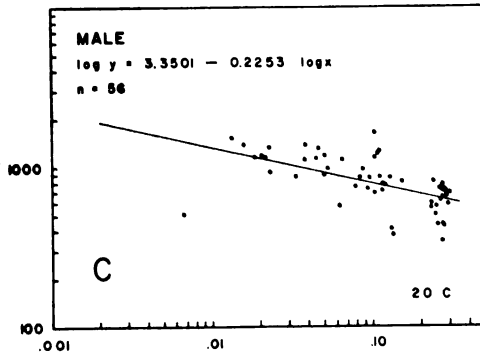
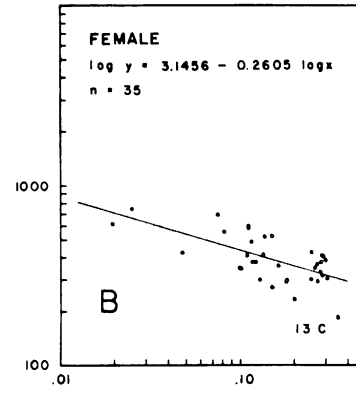
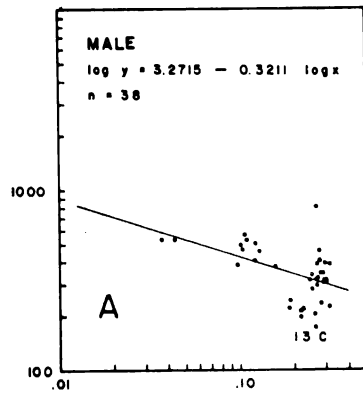
Expt. Temp. (C)	b_m	b_f	d.f.	s^2_p	t	$H_o: b_m - b_f = 0$
13	0.682	0.712	69	0.015	2.331*	rejected
20	0.687	0.772	96	0.033	4.631**	rejected
27	0.947	0.966	91	0.023	1.193	accepted
34	0.943	0.971	94	0.055	1.109	accepted

¹Accepted level of significance = 0.05 (two tailed test applied).

*Significant at the 0.05 level.

**Significant at the 0.005 level.

Figure 4. Comparison between male (A, C, E, and G) and female (B, D, F, and H) log oxygen consumption (per gram unit weight) for Anax junius naiads compared at 13, 20, 27, and 34 C, respectively.

OXYGEN CONSUMPTION ($\mu\text{l/g dry wt/hr}$)

DRY WEIGHT (g)

TABLE 3.--Statistical analysis comparing log oxygen consumption (per gram unit weight) between male and female Anax junius naiads at different temperatures.¹

Expt Temp (C)	b_m	b_f	d.f.	s^2_p	t	$H_0: b_m - b_f = 0$
13	0.321	0.260	69	0.016	-1.457	accepted
20	0.225	0.226	96	0.603	-0.021	accepted
27	0.054	0.036	91	0.953	-0.214	accepted
34	0.034	0.005	94	0.793	-0.304	accepted

¹Accepted level of significance = 0.05 (two tailed test applied).

Percentage of Ash Material

The relationship between ash free dry weight and dry weight is presented in a double logarithmic plot (Figure 5). Initial growth is associated with a low percentage of ash material which decreases subsequently as size increases (Figure 6). Hence, naiads weighing 4 mg (dry weight) contain approximately 97 per cent ash free dry material in contrast to 87 per cent in individuals weighing 300 mg.

There is no significant difference between oxygen consumption expressed either as QO_2 (Figure 9) or as ash QO_2 (Figure 7); (the statistical comparison between QO_2 and ash QO_2 is given in Table 4).

TABLE 4.--Statistical comparison between mean log oxygen consumption ($\pm$ 95 per cent confidence intervals) expressed as log ash free dry weight and as log dry weight for Anax junius naiads. Comparison based on 100 mg body weight.

Expt Temp (C)	Mean Log Respiration (l/g/hr)		
	Log Ash Free Dry Wt	n	Log Dry Wt
13	2.6677 $\pm$ 0.3160*	(73)	2.6349 $\pm$ 0.3162
20	2.9286 $\pm$ 0.3104	(119)	2.8989 $\pm$ 0.3108
27	3.2498 $\pm$ 0.3114	(104)	3.1791 $\pm$ 0.3146
34	3.3627 $\pm$ 0.3147	(100)	3.3131 $\pm$ 0.3146

*Overlapping of confidence limits at any comparable temperature is taken to indicate no significant difference.

Figure 5. Relationship between log ash free dry weight and log dry weight for Anax junius naiads.

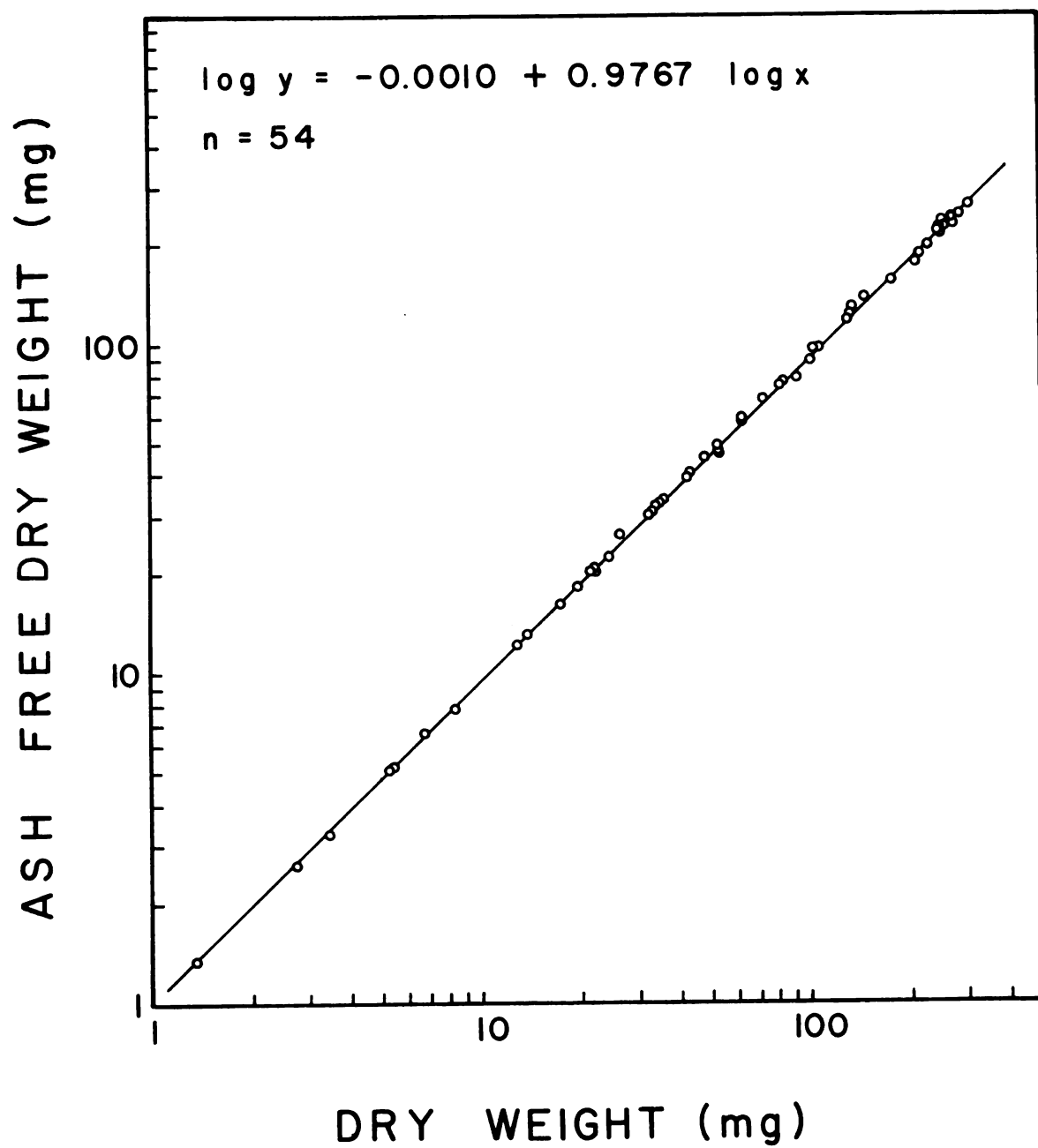


Figure 6. Change in the per cent ash free dry weight relative to increasing dry weight for Anax junius naiads. Regression determined from equation given in Figure 5.

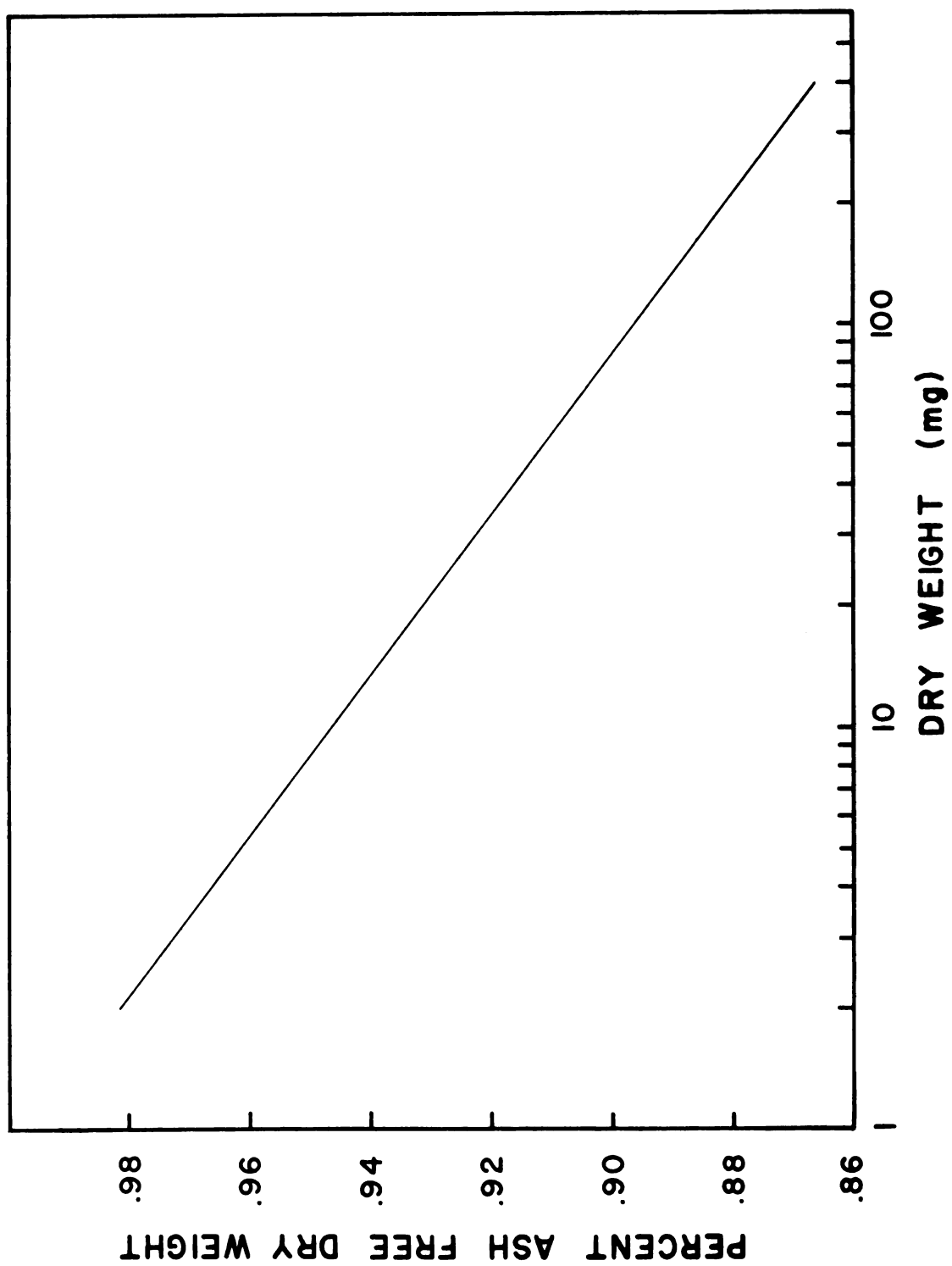
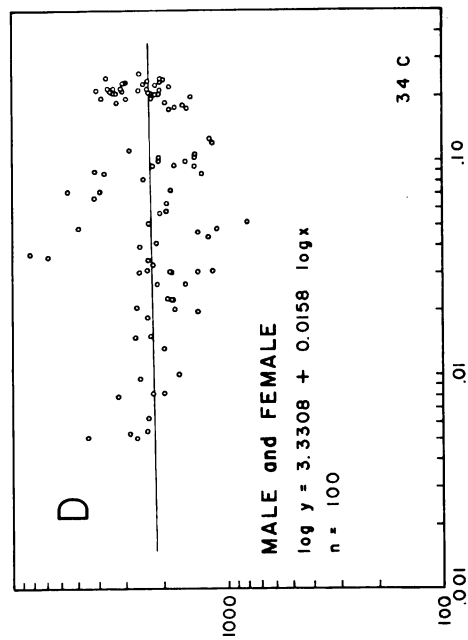
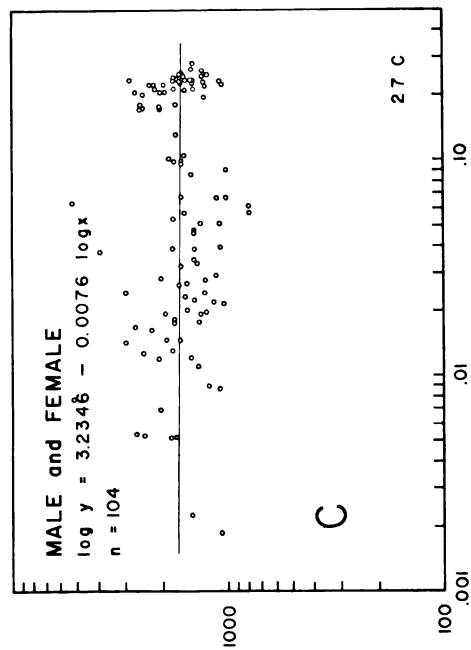
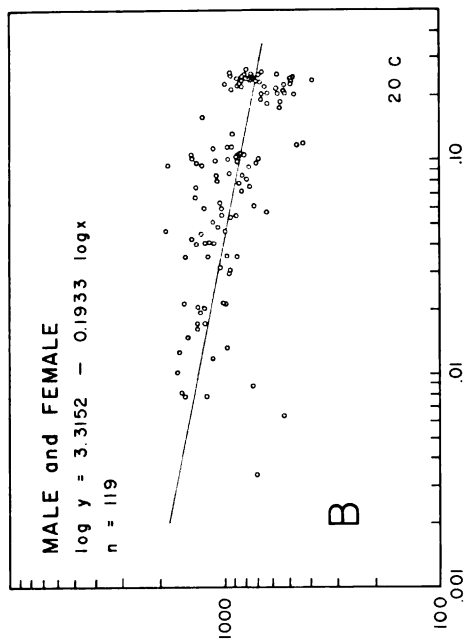
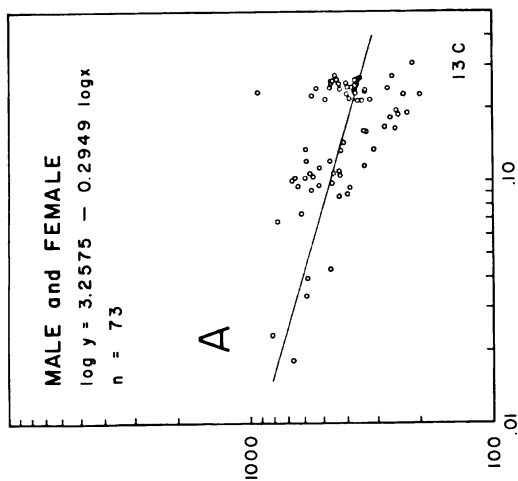


Figure 7. Relationship between log oxygen consumption and log ash free dry weight for Anax junius naiads compared at different temperatures.



ASH FREE DRY WEIGHT (g)

OXYGEN CONSUMPTION (μl/g ash free dry wt/hr)

The decreased QO_2 with increasing dry weight may be explained, in part, by the progressive increase in the percentage of ash material directly related to growth.

Influence of Body Weight

To ascertain the influence of body weight (dry wt), $\log O_2$ consumption was regressed against $\log$ dry weight at different temperatures (Figure 8) and tested by the hypotheses:

$$H_0: b = 1$$

$$H_1: b \neq 1$$

$\log$ oxygen consumption was related to $\log$ dry weight by coefficients of regression of 0.69, 0.79, 0.95, and 0.96 at 13, 20, 27, and 34 C, respectively (Figure 8). The null hypothesis ($H_0: b=1$) was rejected at 13 and 20 C but accepted at 27 and 34 C (Table 5) indicating that $\log$ oxygen consumption significantly decreased with increasing $\log$ dry weight at 13 and 20 C but not at 27 and 34 C.

Figure 9 shows $\log$ oxygen consumption calculated on a per unit weight basis. These data indicate that oxygen consumption is significantly influenced by body weight at 13 and 20 C but not at 27 and 34 C.

Figure 8. Relationship between log oxygen consumption and log dry weight for Anax junius naiads compared at different temperatures.

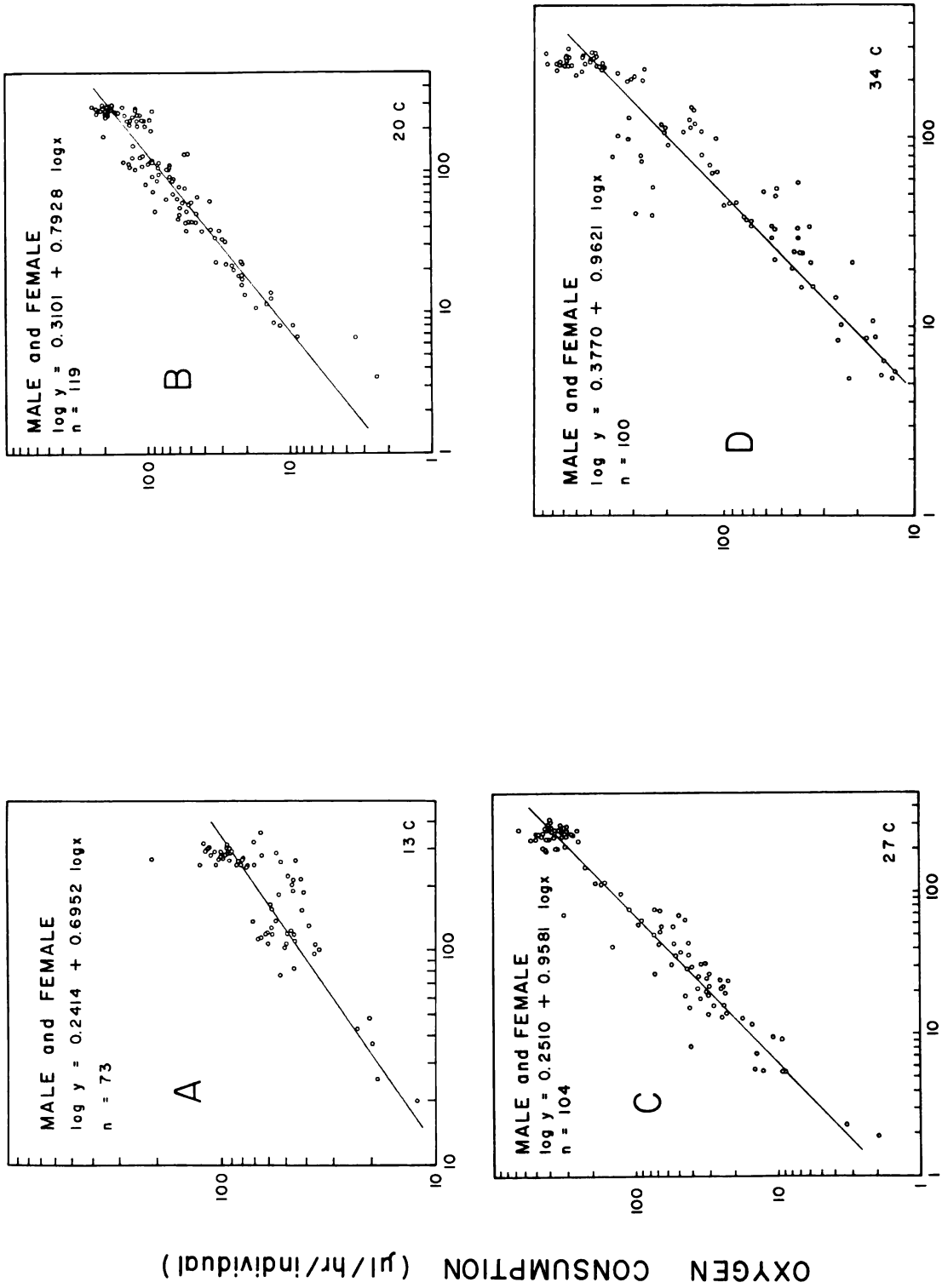


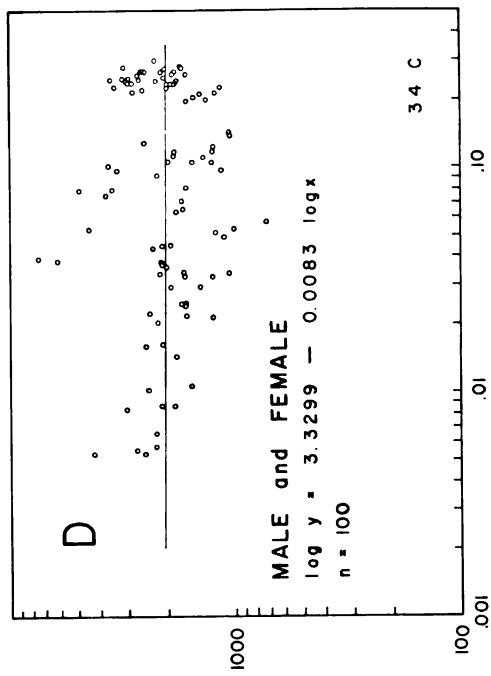
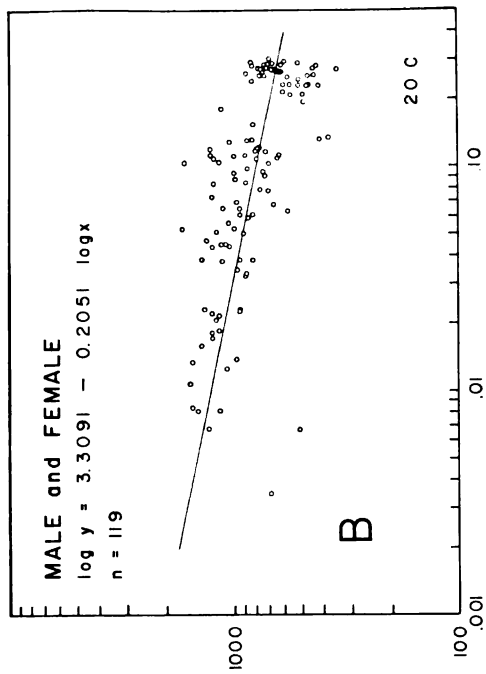
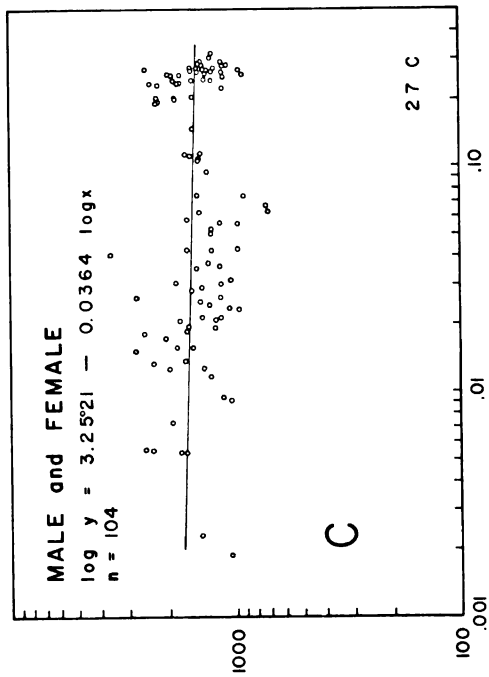
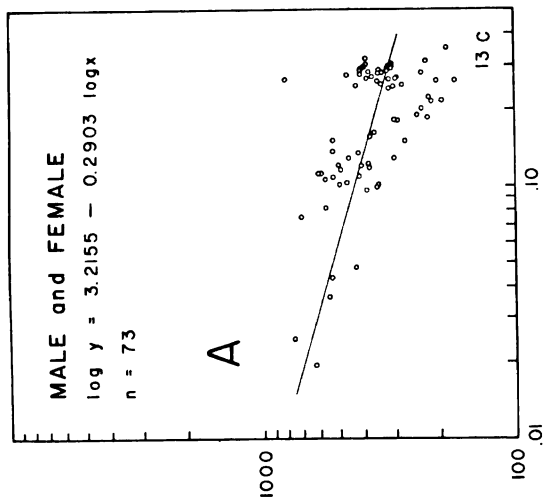
TABLE 5.--Statistical analysis comparing the influence of log dry weight on log oxygen consumption in Anax junius naiads compared at different temperatures.¹

Expt. Temp. (C)	b	d.f.	s ² _p	t	r	H ₀ : b = 1
13	0.695	72	0.727	-7.140	0.844	rejected
20	0.792	118	0.351	-6.459	0.954	rejected
27	0.958	103	0.291	-0.791	0.968	accepted
34	0.962	99	0.294	-0.708	0.924	accepted

¹Accepted level of significance = 0.05 (two tailed test applied).

Figure 9. Relationship between log dry weight and log oxygen consumption per unit weight for Anax junius naiads compared at different temperatures.

OXYGEN CONSUMPTION ($\mu\text{l/g dry wt/hr}$)



DRY WEIGHT (g)

Influence of Temperature

The effect of temperature on QO_2 is demonstrated in a temperature-respiration curve (T-R curve), (Figure 10), and expressed quantitatively, relative to dry body weight, utilizing van't Hoff's (1884) Q_{10} approximation (Figure 11).

Q_{10} is the increase in reaction velocity caused by a 10 C rise in temperature. The value is calculated with data obtained over any temperature range from the general formula:

$$\log Q_{10} = \frac{10(\log k_1 - \log k_2)}{t_1 - t_2}$$

where k_1 and k_2 are the velocities at t_1 and t_2 , respectively (Hoar, 1966).

The Q_{10} approximation in thermobiological reactions is about two (Prosser and Brown, 1961). Yet, for meaningful comparisons of the effects of temperature on the rates of various biological processes, the rates of reaction must be compared for the same temperature interval (Giese, 1961).

At all comparable temperature intervals the Q_{10} of A. junius increased directly with body weight (Figure 11). However, Q_{10} variance, in relation to increasing dry weight, was less at the higher temperature intervals (Figure 11; D and E). Between 27-34 C the Q_{10} change

Figure 10. Semi-log T-R curve for male (broken line) and female (solid line) Anax junius naiads. Each point represents the mean $\dot{Q}O_2$ based on Figure 4 regressions. All values were corrected to 100 mg dry wt.

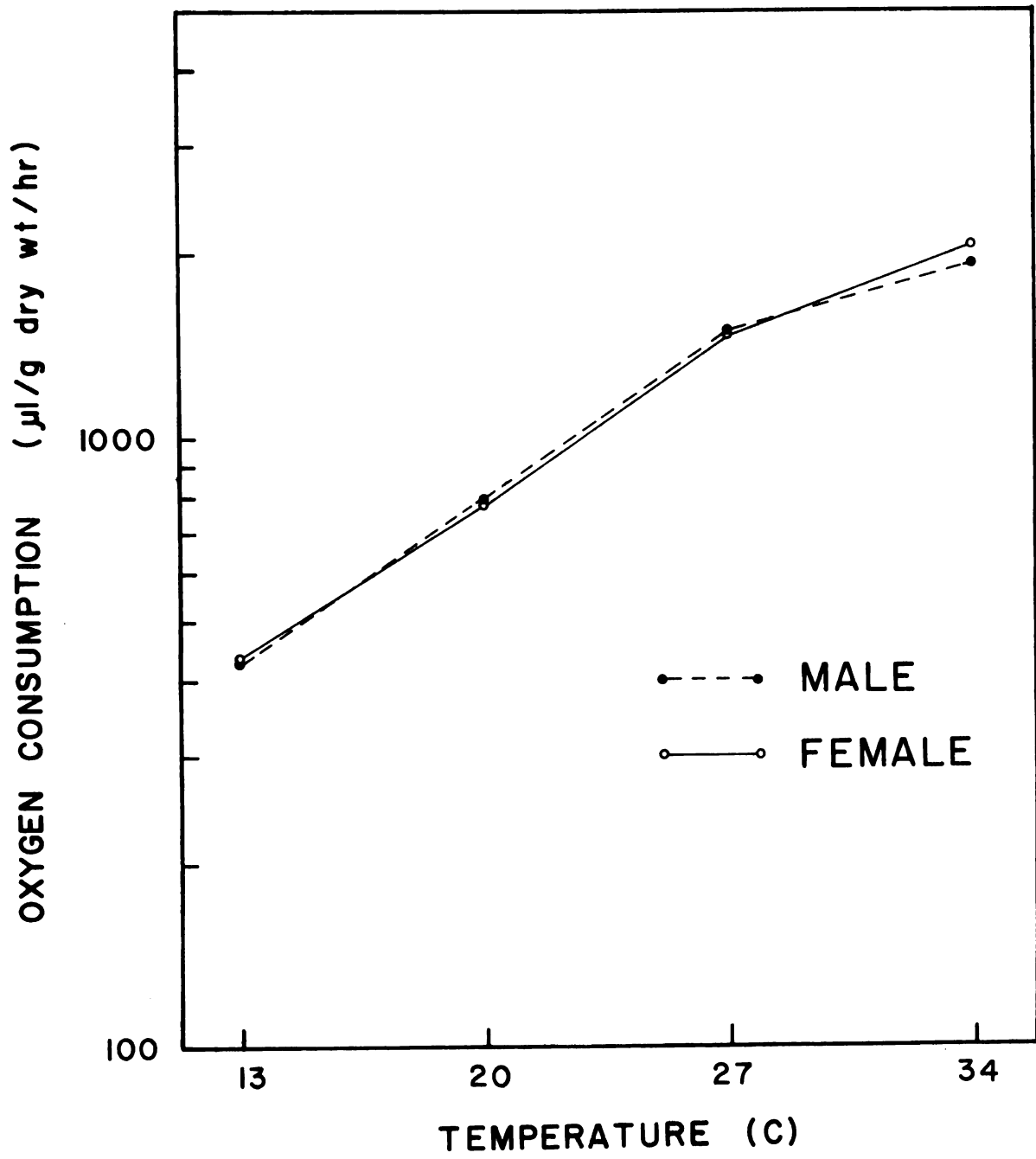
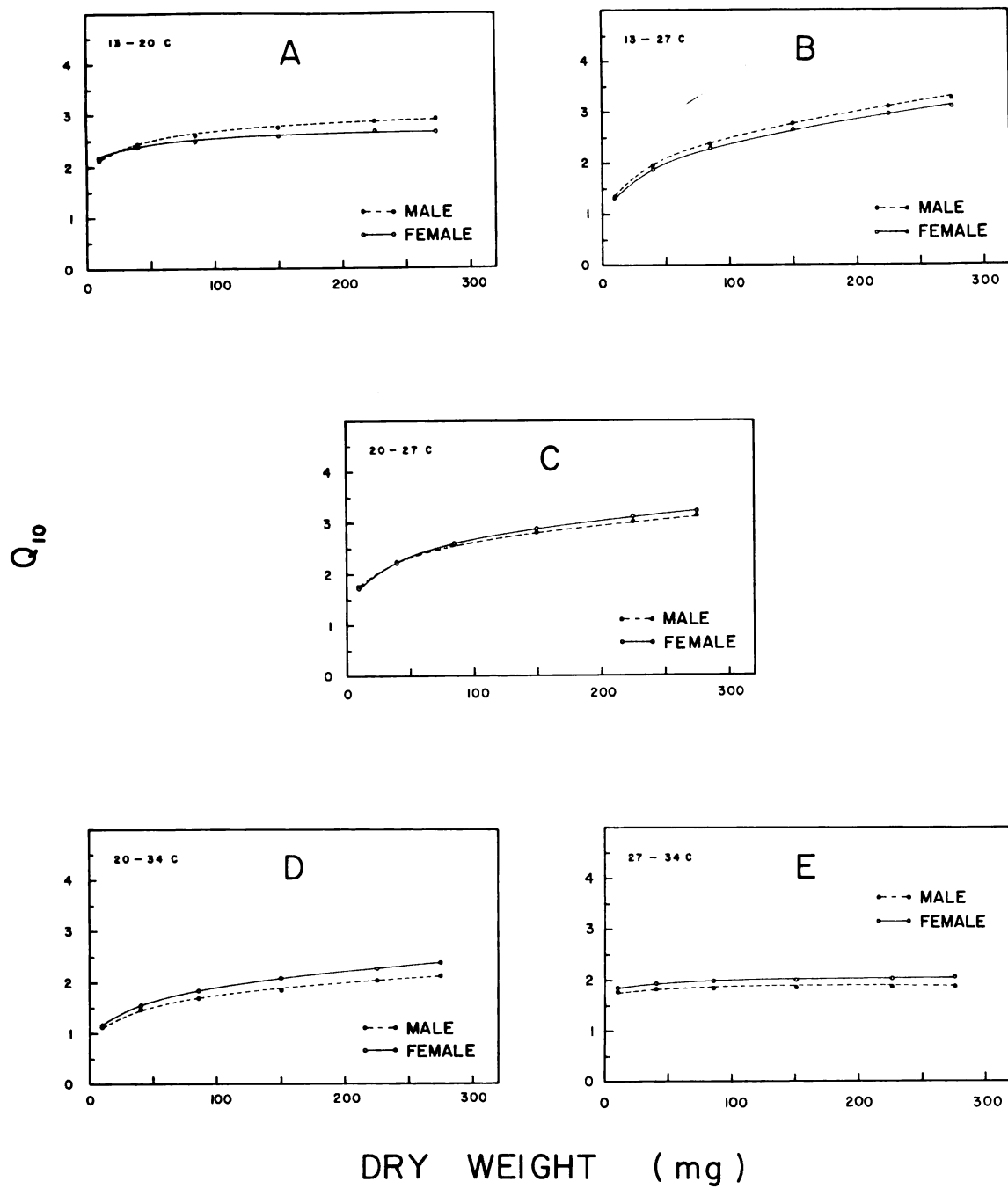


Figure 11. Relationship between Q_{10} and size (wt)
for Anax junius naiads.



was nearly independent of weight. In general, Q_{10} values decreased inversely with temperature.

Although male and female A. junius naiads responded to temperature change by showing generally parallel increases in Q_{10} values, a certain difference was noted. Based on Figure 11, males showed less increase in metabolic rate at low temperature intervals (13-20 and 13-27 C) than females, but a significant increase at the higher temperature intervals.

Influence of Life Stage

An attempt was made to delimit individual instars by regressing head capsule width, total body length, meso-wing sheath length, labium length, labium width, and oven dry body weight in different combinations. The meso-wing sheath length regressed against oven dry body weight appeared to give the best possible instar separation, but was still too variable to be of definitive value. Consequently instars were not deemed definable. However, based on the studies of Calvert (1934) and Macklin (1964) it was apparent that the dragonfly naiads utilized as test organisms in the present study were in their sixth through fourteenth (terminal) instars. It seems that instars are definable, with certainty, only if reared from egg to adult.

Naiads nearing the terminal instar showed a decrease in oxygen consumption at 13 and 20 C, but

appeared to maintain a relatively constant rate at 27 and 34 C (Table 6). Adult respiration (Table 7) at 30 C was about three times greater when compared to naiads of similar weight and at comparable temperatures (27 and 34 C).

TABLE 6.--Influence of life stage on the log oxygen consumption of Anax junius naiads ($\mu\text{l/g dry wt/hr}$).

Temperature (C)	Log Dry Weight (mg)									
	1.000		1.602		1.929		2.176		2.352	
	M*	F	M	F	M	F	M	F	M	F
13	2.950	2.937	2.757	2.758	2.519	2.661	2.573	2.588	2.516	2.536
									2.488	2.510
20	3.125	3.116	2.989	2.980	2.915	2.906	2.860	2.850	2.820	2.810
									2.801	2.790
27	3.229	3.206	3.196	3.184	3.179	3.172	3.165	3.163	3.157	3.156
									3.151	3.163
34	3.320	3.330	3.300	3.333	3.288	3.335	3.279	3.337	3.273	3.338
									3.270	3.338

*M = male; F = female.

TABLE 7.--The log oxygen consumption ($\mu\text{l/g dry wt/hr}$) of four Anax junius adults.¹

Temperature (C)	Log Dry Wt (mg)	Sex	Oxygen Consumption
30	2.225	male	3.845
30	2.242	female	3.861
30	2.272	male	3.713
30	2.327	male	3.684

¹Oxygen consumption equals the mean of five independent measurements per individual.

DISCUSSION AND CONCLUSIONS

Field Methods

Crum and Marrow ponds were physically and chemically similar while Long Woods Pond showed somewhat lower concentrations of dissolved oxygen and alkalinity. Double logarithmic plots of log oxygen consumption with log dry weight were compared between organisms from Crum Park Pond and Long Woods Pond. Since log oxygen consumption of organisms from the two ponds was apparently not significantly different the collection site was not considered as a factor influencing respiration.

Respirometry

Influence of Light and Shaking Rate

The effect that light exerts on the respiration of A. junius is unknown, but because light has been shown to modify the respiratory rate of certain dragonfly naiads (Sayle, 1928; and Lutz, 1960) light reaching the reaction vessels was maintained at a constant level. In the future it would be interesting to evaluate the influence of light upon the respiratory rate of A. junius

Although the effect of shaking rate on the respiration of A. junius was not evaluated, Edwards (1957 and 1960) found no significant difference in respiration either between groups of midge larvae, Chironomus riparius Meigen, shaken at twice the normal rate or among several groups of Asellus aquaticus L. evaluated at four times the normal shaking rate. No reference was found in the literature comparing the effect of shaking or non-shaking on an organism's respiratory rate.

Oxygen bubbled through test water prior to oxygen consumption evaluation assured that the test water was saturated with dissolved oxygen. Maloeuf (1936) found that respiration in A. junius is more or less dependent upon the oxygen tension in the water. Although the oxygen tension in the reaction vessels was not evaluated after oxygen consumption measurements, Small (1967), using a Gilson Respirometer on organisms up to 40 mg over a six-hour period under similar experimental conditions, found that the oxygen tension in the flasks never fell below 153 mm Hg (approximately 95 per cent saturation).

Diel and Seasonal Effects on Respiration

Time of day and season can modify the metabolic rate in diverse groups of animals (for reviews, see Scholander et al., 1953; Zeuthen, 1954; Bullock, 1955; and Harker, 1958). Yet, these mediators of metabolic

rate have apparently received little attention in regards to the truly aquatic insects.

Under conditions of controlled temperature, illumination, humidity, and chemical content of the medium, metabolic rate may fluctuate substantially as a function of time (Prosser and Brown, 1961). Lang (1951), later supported by Edwards (1960), disclosed a diel rhythm in Asellus aquaticus L. exhibiting maximum oxygen consumption between 1700-1800 and minimum between 1100-1300. Likewise, Edwards (1950) showed that the metabolic rate of the fiddler crab, Uca pugelator (Bosc) is one-third greater in the night than in the daytime. On the contrary, McFarland (1965) found no diel or seasonal change in the metabolic rate of the grass shrimp, Palaeomonetes vulgaris (Say).

The "apparent" lack of a diel metabolic rhythm in A. junius is certainly not unique. Perhaps the ability to maintain a relatively constant metabolic rate, in spite of 5-7 C diel temperature fluctuations common in the natural environment, might explain the wide distribution of this species (Walker, 1958) in the temperate and tropical zones. However, such a suggestion can be refuted by Pattee's (1965) excellent study on metabolic differences between stenothermous and eurythermous invertebrates. In comparing the sensitiveness to variations of temperature among nine species of freshwater

poikilotherms, he concluded that, "the daily temperature variations do not seem to play an important part in the distribution of the aquatic fauna."

Knowledge of the seasonal effect on respiration is at a comparatively more advanced stage than is the diel influence. Hence, various authors have attested to intraspecific seasonal changes in respiration among a wide variety of aquatic poikilotherms. Numerous examples of seasonal change in metabolic rate are available: Edwards (1958), in a midge, Chironomus riparius Meigen; Berg and Ockelmann (1959), in Danish fresh water snails; Lutz (1960), in a dragonfly, Tetragoneuria cynosura Say; Beamish (1963), in brook and brown trout; Istenic (1963), in a stonefly Perla marginata Pz.; Eriksen (1964), in a mayfly, Ephemera simulans Walker; and Davies (1967), in the limpets, Patella vulgata and P. aspera. In contrast, Edwards and Gonzalez (1954) indicate no seasonal change in respiration among six species of dragonflies (Aeschnidae), an aquatic hemipteran (Belostoma sp.), and six species of aquatic Coleoptera (three Dytiscidae and three Hydrophilidae). Likewise McFarland and Pickens (1965) find no seasonal change in the respiration of the grass shrimp, Palaemonetes vulgaris; nor do Small and Hebard (1967) for a marine crustacean, Euphausia pacifica Hansen.

Many different theories have been postulated to explain seasonal changes in metabolic rates, but photoperiod and temperature seem to be cited most frequently. Lutz (1960) has shown that the metabolic rate in Tetragoneura cynosura is increased dramatically if nymphs are maintained on a 14-hour photoperiod as opposed to an 11-hour photoperiod. He concludes that a high respiratory rate is apparently required before emergence can take place. Since T. cynosura has a winter dormancy, oxygen consumption was related to photoperiodic induction of the termination of diapause. Because A. junius apparently lacks a diapause (Macklin, 1964), photoperiod probably does not influence its respiration as it does in T. cynosura. However, Sayle (1928) has shown that the metabolic rate of Aeshna umbrosa Walker nymphs is decreased progressively with weeks in darkness and that the physiological condition is so affected that the nymphs die. Therefore, light is apparently important and will be the object of anticipated future studies.

Istenič (1963) indicates that temperature and body size are important factors acting on seasonal metabolic rate in the stonefly, Perla marginata. Oxygen consumption increased only in the heaviest larvae; summer respiration being related to the body weight and winter respiration to the body surface.

In A. junius, as in P. marginata, it is the larger individuals which appear to be more sensitive to temperature change. If respiration were to vary seasonally in A. junius, the change would most likely be reflected by comparatively lower winter respiratory rates in the larger naiads. However, since respiration was compared only in spring and summer, the presence or absence of a seasonal change in the rate of respiration in A. junius remains somewhat uncertain.

Influence of Sex

In most animals the male has a higher rate of metabolism than the female, but among the insects this relationship has not been as clearly demonstrated as it has among the vertebrates (Edwards, 1953). Nevertheless, when the rate of respiration is found to be influenced by the sex of an insect, differences in body weight, temperature sensitivity, or physiological age are the factors which are most often suggested as possible explanations.

Thus, Knight and Gaufin (1966) feel that the higher oxygen consumption frequently observed in certain stoneflies, on the unit weight basis, can be explained, in part, by the fact that the males (larvae and adults) are smaller than the females. They further speculate that the difference could be due to the gravid condition of the female. Similarly, the oxygen uptake in Artemia males increases more rapidly than in the females

(Gilchrist, 1958). The increase was correlated with the comparatively larger area of the male's second antennae in sea water. However, in concentrated brine the oxygen consumption of males and females was of the same magnitude. Furthermore, Crescitelli (1936) finds that male Galleria mellonella (L.) pupae are smaller and lighter than the females and have a higher metabolic rate (on the average) through most of the pupal period, but lower than females near the termination of the pupal stage. Burkett (1962) supports Crescitelli with the stipulation that the difference in respiration between male and female is statistically significant only at temperatures between 30 and 45 C.

Edwards (1958) has reported that male Tribolium, studied at 18 C, show an increased oxygen consumption as weight increases, while the female shows decreased consumption with increasing weight. He found that lighter females were more sensitive to temperature than were the lighter males. Although Edwards found no significant difference in respiration between males and females, the females nevertheless showed a "trend" towards a higher metabolic rate than did the males. The relative amount of respiring tissue in the sexes was advanced by Edwards as one possible factor contributing to the higher respiration in males.

The significantly higher rate of respiration at 13 and 20 C in A. junius females as compared to males is disconcerting. Possible explanations for the differences might be found by comparing temperature sensitivity, relative surface area, or enzymatic reactions between males and females.

Light weight females show less oxygen consumption at 13 and 20 C than do light weight males. This may possibly result in counter-clockwise rotation of the regression line (Figure 3) thereby increasing the slope in a positive direction in favor of the females. Such an explanation is highly speculative since it is based on a very small number of light weight male and female naiads.

In conclusion, if the difference between male and female respiration at 13 and 20 C were real, no definite explanation can be given until further respiratory studies are conducted on light weight individuals. Should the difference be found to persist after extensive evaluation utilizing light weight forms, then the variation might be explained by differences in relative amounts of active tissues, different muscle tone, or hormonal effects (Prosser and Brown, 1961).

Percentage of Ash Material

Metabolic rate is commonly expressed as a function of wet weight, dry weight, ash free dry weight, or percentage of organic nitrogen. Much controversy appears

to exist as to which criterion is best for expressing the rate of metabolism.

Keister and Buck (1963) advocate wet body weight over dry body weight since the latter is based on two common misconceptions: (1) that water is metabolically inert, and (2) that tissue hydration necessarily changes with changing body water content. However, it is suggested that dry body weight is the best basis for expressing metabolic rate in A. junius because the relative concentration of water remaining in the abdominal respiratory chamber in organisms of different size may be variable.

It has been shown in A. junius that the per cent ash material increases with growth. The increase was determined by combusting naiads at 520 C so as to remove oxidizable substances such as proteins, carbohydrates, fats, and lipids. The nonoxidizable material remaining after combustion was regarded as mineral material. However, no significant difference was found when respiration was expressed as per unit ash free dry weight or per unit dry weight. Nevertheless respiration of larger naiads was not depressed as much when oxygen consumption was expressed as ash QO_2 than it was when expressed in terms of dry weight. Since mineral material is often quite variable in a species and may change with growth, it is important to consider the relative percentage of mineral material when conducting metabolic studies.

Organic nitrogen is seldom used to express metabolic rate. Davies (1967), however, did determine organic nitrogen in limpets (Patella vulgata and P. aspera) by the Kjeldahl procedure. He found no significant difference in metabolic rate when expressed as either dry weight or total nitrogen content. It would be interesting to determine organic nitrogen in the case of A. junius and compare this with the present oxygen consumption rates.

Influence of Weight

Much information has been compiled relating body weight to metabolic rate in a wide variety of animals (cf. Kleiber, 1947 and Zeuthen, 1955). Rubner (1883) was the first to observe that metabolism was not simply proportional to the weight, but very nearly to the two-thirds power of the weight, which was considered to be more or less equal to the external surface of the animal. This discovery led to the formulation of the "surface law" relating respiration to the two-thirds power of the body weight.

A priori there is no logical explanation why an animal's external surface should dictate its metabolic rate. To be certain, surface area, both internal and external, is not constant, but may vary intraspecifically with growth, sex, season, and reproductive development. Nevertheless, when a weight-respiration regression is found to have a coefficient of regression near 0.73,

attention is often focused upon the "surface law." As regards to insects, worms, and spiders, Edwards (1963) points out that their respiration may vary from coefficients of regression of 0.177 to 0.981 mg O₂/g/hr on a unit weight basis. Consequently, respiration in poikilotherms is highly variable, in relation to the body surface, and for this reason there will be no attempt to correlate respiration in A. junius with the "surface law."

Generally, metabolic rate in animals decreases progressively with increasing size (Zeuthen, 1955). Exceptions, however, are noted in certain poikilotherms where the metabolic rate increases in nearly direct proportion with increasing weight. Such exceptions have been observed in certain fresh water snails (Berg and Ockelmann, 1959); in the stonefly Perla marginata at 15 C and size range 100-300 mg (Istenič, 1963); in the terrestrial isopod Oniscus asellus L. at 20-140 mg during all months of the year except during May, June, and July when seasonal aberrance associated with reproductive activities occurred (Phillipson and Watson, 1965); and in a vertically migrating crustacean Euphausia pacifica Hansen (Small and Herbard, 1967).

A. junius appears to have a weight-independent metabolism, but only at 27 and 34 C. The fact that respiration was not influenced by weight at high temperatures might well be explained by considering the previous

temperature history and the relative sensitivity to temperature among different sized animals.

Bullock (1955) indicates an erroneous assumption frequently advanced in regard to temperature change and metabolic rate. If evaluated at a higher or lower temperature than previously experienced in nature, it is ordinarily assumed that the metabolic rate is not seriously affected by the speed of the temperature change or the length of time spent at the new temperature. The importance of considering the previous temperature history and the time spent at a new temperature has been shown for Aeschna umbrosa nymphs which were initially found to have a higher respiratory rate in warm and slower in cold water, but to return to approximately the same level with time (Sayle, 1928).

The progressive decrease in metabolic rate at 13 and 20 C that occurs as weight increases in A. junius is regarded as a response to the initial acute cold depression due to the previously higher temperature experienced in nature. It seems apparent that growth in A. junius is associated with increased sensitivity to temperature. Hence, when naiads are subjected to colder temperatures than experienced in nature, an apparent loss of equilibrium is experienced by the larger naiads. Since the smaller naiads are apparently more tolerant to temperature change than are the larger forms, they seem to be able to

maintain a rather constant metabolic rate over relatively large temperature ranges.

In the future it would be interesting to evaluate respiration of A. junius as a function of starvation and the time spent at temperatures above and below that experienced in nature.

Influence of Temperature

The influence of temperature on aquatic poikilotherms has been well documented in the literature. However, few studies equal the contributions of Scholander et al. (1953), Rao and Bullock (1954), and Bullock (1955).

The extent to which temperature may influence an organism is well presented by the statement made by Rao and Bullock (1954),

. . . temperature response is a complex function and in many respects varies among animals (e.g., Q_{10} as a function of temperature measured acutely over a wide range) so that we are recognizing common trends rather than rules at this stage of refinement.

When Dehnel and Segal (1956) measured the oxygen consumption of equal-weight nymphs of Periplaneta americana at 20 C, animals maintained at a lower temperature had a higher metabolic rate. The midge Chironomus riparius was found by Edwards (1958) to increase its metabolic rate 2.6 times when measured at 20 C as opposed to 10 C; whereas the aquatic sow bug Asellus aquaticus was shown, by Edwards and Learner (1960), to increase its rate by

a factor of 1.5 over the same temperature range. Collardeau-Roux (1966) presents information indicating that the caddisfly, Micropterna testacea (Gmel.), increases its oxygen consumption slowly between 3 and 7 C, more rapidly but still regularly from 10 C to 20-25 C. Collardeau (1961) finds three other tricopteran larvae to maintain a constant metabolic rate between 4 and 10 C, increase slightly within the 10 to 20 C range, and finally to increase metabolic rate quite steeply and often two fold above 22 C. Knight and Gaufin (1966) found that the Q_{10} for certain stoneflies varied from one temperature interval to another, but generally increased at lower temperatures. Similarly, Chaudhry and Kapoor (1967) reported that the Q_{10} approximation is higher in the red flower beetle at lower temperatures and decreases at higher temperatures.

Two points are made apparent from the examples given above: (1) temperature influences different species in different ways; and (2) that certain "common trends" in response to temperature are reflected both among and within species.

It is generally accepted that within the physiological range, i.e., the conditions under which poikilotherms generally exists in nature, increasing the temperature results in acceleration of the metabolic rate. Sweeney and Hastings (1961) relate temperature influence to increases in the rates of chemical reactions involved.

They reason that since temperature is a measure of the kinetic energy of molecules, it follows that molecules, upon possessing a greater energy, collide more frequently resulting in an increased rate of reaction. However, it is not the intention of Sweeney and Hastings to explain temperature influence merely by increases in the rates of chemical reactions involved. To be certain temperature acts on biological systems in a far more complex manner and does not lend itself to such a simple explanation.

A trend which is frequently observed is the ability of certain poikilotherms to maintain a rather constant metabolic rate despite temperature changes. This ability seems to indicate a degree of homeostasis somewhat similar to that found in homeotherms. Such compensation for temperature has been comprehensively reviewed by Bullock (1954).

It might appear, at first glance, that respiration in A. junius is somewhat independent of temperature at 27 to 34 C. However, this may not be a case of temperature independence, but rather heat inactivation response at 34 C. At high temperatures enzymes and other proteins are denatured. Hoar (1966) points out that the denaturation process, in which molecular bonds are broken causing disordered arrangement of molecules, results in the destruction of the metabolic or structural

potentialities of the denatured protein. Since an upper lethal temperature limit has not been established for A. junius, it is not possible to evaluate the effect that a temperature of 34 C might be imposing on metabolic rate or survival.

Quite often Q_{10} values are found to increase inversely with temperature and directly with body weight (size), the trend having been well documented by Scholander et al. (1953) and Rao and Bullock (1954). However, Q_{10} data serve to compare different organisms or temperatures but do not give any qualitative information about the underlying metabolism (Keister and Buck, 1964).

A. junius was found to follow the "trend" of decreasing Q_{10} with increasing temperature and decreasing body weight. The fact that Q_{10} increased directly with increasing weight seemed to indicate that temperature influenced respiration progressively as growth increased. It might be surmised that changes in respiratory physiology occur with growth and might contribute to the increased temperature sensitivity associated with growth.

Influence of Life Stage

Very little information is apparently available on respiration of egg, naiad, and adult stages of the Hemimetabolous insects. Comparatively, much more, however, is known about the metabolism of the Holometabola and Paurometabola.

It is apparent that the metabolic rate of different sized individuals varies with temperature. Further, it was observed that size did not affect respiration at 27 and 34 C and that at 13 and 20 C respiration decreased progressively with growth. Generally, within the physiological range of an animal, respiration per unit weight decreases with growth. For example, Knight and Gaufin (1966) found the metabolic rate in the stonefly larva, Acroneuria pacifica Banks, to decrease 35 per cent from year class 1 to year class 2. They pointed out that the difference was probably attributable to differences in relative amounts of active tissue. In A. junius respiration decreased from 10 mg to 300 mg by 46 per cent and 50 per cent at 13 and 20 C, respectively. As previously mentioned in discussing temperature, this decrease may be due to cold depression in larger naiads.

Oxygen consumption of adult dragonflies was about three times as high as it was for naiads of about the same weight. This can probably be attributed to the greater activity of the adult. Also, more active tissues such as well developed testes and ovaries might contribute to a higher metabolic rate in adults.

The influence of life stage on respiration, as well as sex, body weight, temperature, season, and time of day, certainly can not be isolated and evaluated without considering the other modifiers of respiration.

This is to say, respiration is highly complex and no individual modifying factor can be completely isolated and understood as a separate entity. Also, the basic consideration is at the species level and for this reason it is often vain to attempt correlaries on an interspecific level.

LITERATURE CITED

LITERATURE CITED

- American Public Health Association. 1965. Standard methods for the examination of water and wastewater. 12th ed. New York. 769 p.
- Beamish, F. W. H. 1964. Seasonal changes in the standard rate of oxygen consumption of fishes. Can. J. Zool. 42:189-194.
- Berg, K. and K. W. Ockelmann. 1959. The respiration of freshwater snails. J. Exp. Biol. 36:690-708.
- Bullock, T. H. 1955. Compensation for temperature in the metabolism and activity of poikilotherms. Biol. Rev. 30:311-342.
- Burkett, B. N. 1962. Respiration of Galleria mellonella in relation to temperature and oxygen. Ent. Exp. & Appl. 5:305-312.
- Calvert, P. P. 1934. The rates of growth, larval development and seasonal distribution of dragonflies of the genus Anax (Odonata:Aeshnidae). Proc. Amer. Phil. Soc. 73:1-70.
- Chaudhry, H. S. and R. P. D. Kapoor. 1967. Studies on the respiratory metabolism of the red flour beetle. J. Econ. Ent. 60:1334-1336.
- Collardeau, C. 1961. Influence de la température sur la consommation d'oxygène de quelques larves de Trichoptères. Hydrobiol. 18:252-264.
- Collardeau-Roux, C. 1966. Influence de la température sur la consommation d'oxygène de Micropterna testacea (Gmel.) (Trichoptera Limnophilidae). Hydrobiol. 27:385-394.
- Crescitelli, F. 1935. The respiratory metabolism of Galleria mellonella (bee moth) during pupal development at different constant temperatures. J. Cell. Comp. Physiol. 6:351-368.

- Davies, P. Spencer. 1967. Physiological ecology of Patella. II. Effect of environmental acclimation on the metabolic rate. J. Mar. Biol. Ass. U. K. 47:61-74.
- Dehnel, P. A. and E. Segal. 1957. Acclimation of oxygen consumption to temperature in the American cockroach (Periplaneta americana). Biol. Bull. 111:53-61.
- Edwards, D. K. 1958. Effects of acclimatization and sex on respiration and thermal resistance in Tribolium (Coleoptera: Tenebrionidae). Can. J. Zool. 36:363-382.
- Edwards, G. A. 1953. Respiratory metabolism. In: Insect Physiology, edited by K. D. Roeder. John Wiley and Sons, New York. pp. 96-146.
- Edwards, G. A. and M. D. P. Gonzales. 1954. The influence of temperature upon the respiratory metabolism of certain tropical aquatic insects. Acta. Physiol. Latinoam. 4:121-132.
- Edwards, R. W. 1957. The relation of oxygen consumption to body size and to temperature in the larvae of Chironomus riparius Meigen. Exp. Biol. 35:383-395.
- Edwards, R. W. and M. A. Learner. 1960. Some factors affecting the oxygen consumption of Asellus. J. Exp. Biol. 37:706-718.
- Eriksen, C. H. 1964. Evidence of a spring rise in metabolic rate in the burrowing mayfly Ephemera simulans Walker. Hydrobiol. 23:506-510.
- Giese, A. C. 1963. Cell Physiology. 2nd ed. W. B. Saunders Co., Philadelphia. 592 p.
- Gilchrist, B. M. 1958. The oxygen consumption of Artemia salina (L.). Hydrobiol. 12:27-37.
- Gilson, W. E. 1963. Differential respirometer of simplified and improved design. Science. 141: 531-532.
- Harker, J. E. 1958. Metabolic rhythms. Biol. Rev. 33:1-52.
- Hoar, W. S. 1966. General and Comparative Physiology. Prentice-Hall, Inc., New Jersey. 815 p.

- Istenič, L. 1963. Poraba kisika pri licinkah Perla marginata Pz. V odvisnosti od velikosti telesa in temperature. Spreieto na seji IV. Raspr. Odj. mat. fiz. tech. Nauke jugosl. Akad. Znan. 7:201-236.
- Keister, M. and J. Buck. 1964. Respiration: Some exogenous and endogenous effect of rate of respiration. 618-658 p. In: The Physiology of Insecta, edited by M. Rockstein. Academic Press, New York. 692 p.
- Kleiber, M. 1947. Body size and metabolic rate. Physiol. Rev. 27:511-541.
- Knight, A. W. and A. R. Gaufin. 1965. Oxygen consumption of several species of stoneflies (Plecoptera). J. Insect Physiol. 12:347-355.
- Lang, J. and M. Ruzickova-Langova. 1951. Periodicity in oxygen consumption of Asellus aquaticus. Mem. Soc. Zool. Tcheosl. 15:89-98.
- Li, J. C. R. 1964. Statistical Inference I. Edwards Brothers, Inc., Ann Arbor, Michigan. 658 p.
- Lutz, P. E. and C. E. Jenner. 1960. Relationship between oxygen consumption and photoperiodic induction of the termination of diapause in nymphs of the dragonfly Tetragoneuria cynosura. J. Elish. Mitch. Sci. Soc. 76:192-193.
- Macklin, J. M. 1964. Notes on the life history of Anax junius (Drury) (Odonata:Aeshnidae). Proc. Ind. Acad. Sci. 72:154-163.
- Maloeuf, N. S. R. 1936. Quantitative studies on the respiration of aquatic arthropods and on the permeability of their outer integument to gases. J. Exp. Zool. 74:323-351.
- McFarland, W. N. and P. E. Pickens. 1965. The effects of season, temperature, and salinity on standard and active oxygen consumption of the grass shrimp, Palaemonetes vulgaris (Say). Cand. J. Zool. 43:571-585.
- Pattee, E. 1965. Sténothermie et eurythermie les invertébrés d'eau douce et la variation journalière de température. Annales de Limnologie, t. 1, fasc. 3, pp. 281-434.

- Patton, R. L. 1963. Introductory Insect Physiology. Saunders, Philadelphia. 245 p.
- Phillipson, J. and J. Watson. 1965. Respiratory metabolism of the terrestrial isopod Oniscus asellus L. Oikos. 16:78-87.
- Prosser, C. L. and A. F. Brown, Jr. 1961. Comparative Animal Physiology. 2nd ed. W. B. Saunders, Philadelphia. 688 p.
- Rao, K. P. and T. H. Bullock. 1954. Q_{10} as a function of size and habitat temperature in poikilotherms. Amer. Nat. 88:33-44.
- Rubner, M. 1883. Ueber den Einfluss der Korpergrosse auf Stoff-und Kraftwechsel. Z. Biol. 19:536-562. (Not seen in original form).
- Sayle, M. H. 1928. Factors influencing the rate of metabolism of Aeschna umbrosa nymphs. Biol. Bull., Woods Hole. 54:212-230.
- Scholander, P. F., W. Flagg, V. Walters, and L. Irving. 1953. Climatic adaptation in arctic and tropical poikilotherms. Physiol. Zool. 26:67-92.
- Small, L. F. and J. F. Hebard. 1967. Respiration of a vertically migrating marine crustacean Euphausia pacifica Hansen. Limnol. Oceanog. 12:272-280.
- Snedecor, G. W. 1957. Statistical Methods. 5th ed. Iowa State College Press, Ames. 534 p.
- Steel, R. G. D. and J. H. Torrie. 1960. Principles of Procedures of Statistics. McGraw-Hill Book Co., Inc., 481 p.
- Sweeney, B. M. and J. W. Hastings. 1961. Effects of temperature upon diurnal rhythms. Cold Spr. Harb. Symp. Quant. Biol. 1960. 25:87-104.
- Umbreit, W. W., Burris, R. H., and Stauffer, J. F. 1964. Manometric Techniques. 4th ed. Burgess, Minneapolis. 305 p.
- Van't Hoff, T. H. 1884. Etudes de Dynamic Chimique. Muller, Amsterdam. (Not seen in original form).
- Walker, E. M. 1958. The Odonata of Canada and Alaska. Vol. II. Univ. of Toronto Press. 318 p.

- Whedon, A. D. 1927. The structure and transformation of the labium of Anax junius. Biol. Bull. Wood's Hole, Mass. 286-300.
- Zeuthen, E. C. R. 1955. Comparative physiology (Respiration). Ann. Rev. Physiol. 17:459-482.

APPENDIX

TABLE I.--Measurements (mm) of Anax junius oven-dry naiads collected from Crum Park Pond, Long Woods Pond, and Marrow Pond.

Labium		Head	Body		Meso-wing	Sex*
Length	Width	Width	Length	Width	Length	
Crum Park Pond						
4.1	2.1	3.8	16.9	13.5	1.0	M
4.0	2.0	3.4	14.5	10.9	0.9	F
4.9	2.4	4.2	18.9	23.0	1.2	M
4.4	2.2	4.0	16.3	8.2	1.0	F
4.9	2.4	4.3	18.8	17.3	1.3	F
4.9	2.4	4.3	18.8	12.6	1.4	F
-	-	-	-	13.9	-	-
-	-	-	-	6.8	-	-
-	-	-	-	22.2	-	-
4.4	2.4	3.9	17.8	18.3	1.1	F
3.8	1.8	3.7	13.7	8.5	0.7	F
3.8	1.8	3.3	10.4	3.5	0.9	U
4.3	2.1	3.6	13.6	6.7	-	U
5.1	2.6	4.2	18.7	23.2	1.6	M
6.9	4.8	5.8	26.4	38.8	2.2	F
6.7	3.1	5.7	22.1	21.8	2.1	M
6.3	3.2	5.1	23.6	44.7	2.5	M
6.8	3.2	5.5	25.1	38.5	2.8	F
7.7	3.6	5.8	25.0	60.8	3.6	F
4.7	2.2	3.9	15.5	8.2	1.3	F
7.8	4.0	6.6	30.2	70.0	4.4	F
8.3	3.9	6.9	32.3	78.7	5.1	F
8.9	4.6	6.8	27.0	46.7	4.3	M
8.0	3.9	6.6	28.9	79.1	4.3	M
6.8	3.3	5.8	27.2	33.6	2.5	M
8.2	4.7	7.1	31.8	44.9	4.5	F
7.0	3.4	5.7	23.9	50.6	2.8	M
8.5	3.6	6.6	30.4	65.5	4.6	F
8.6	4.0	6.6	31.6	56.1	4.6	M
8.1	4.4	6.8	28.6	59.7	4.3	F
8.7	4.5	7.0	31.8	56.9	4.3	F
6.0	3.0	4.9	21.8	20.7	2.0	M
6.4	3.1	5.1	23.0	44.0	2.3	F
6.0	3.4	5.4	23.9	18.6	2.4	M
10.6	5.0	8.6	43.0	121.3	10.0	F
5.3	2.6	4.5	20.0	22.9	1.5	F
8.6	3.8	6.8	33.0	94.7	4.5	M
9.0	4.2	6.6	35.5	117.1	4.4	M
10.8	5.0	8.4	44.2	257.1	10.5	F
10.0	4.7	7.0	42.5	113.8	9.6	M
4.5	2.5	4.0	10.8	15.9	1.0	F

TABLE I.--continued.

Labium		Head	Body		Meso-wing	Sex*
Length	Width	Width	Length	Width	Length	
Crum Park Pond						
10.0	5.0	8.6	43.4	252.6	10.0	M
10.8	5.0	8.5	43.8	232.3	10.0	F
9.9	4.9	8.4	42.0	120.2	10.8	M
10.6	5.0	8.7	43.5	129.9	10.2	M
8.9	4.4	6.8	34.0	112.9	5.2	F
10.5	5.0	8.4	45.0	289.0	10.0	M
10.4	4.9	8.5	43.2	249.6	10.0	M
8.4	3.6	6.9	33.8	62.9	4.4	M
6.4	3.0	5.1	23.2	38.0	2.3	M
7.0	3.4	5.8	26.4	32.2	2.4	F
8.5	3.8	6.9	33.5	141.0	5.0	F
6.9	3.3	5.7	27.0	74.7	2.9	M
6.9	3.4	5.9	28.8	73.0	3.0	F
7.0	3.3	5.6	30.8	78.3	3.0	M
5.3	2.6	4.5	22.9	34.3	1.7	F
6.7	3.0	5.3	26.0	50.4	2.8	M
10.0	5.1	7.9	42.5	199.7	10.0	M
10.0	4.7	8.4	43.2	202.1	9.7	F
6.0	3.0	5.0	23.9	25.2	2.0	F
6.7	3.2	5.9	27.2	30.8	2.9	F
10.0	4.7	8.3	43.3	202.3	9.7	M
9.9	4.9	8.1	42.3	194.7	9.4	F
5.7	2.4	4.5	20.9	20.8	1.8	F
-	-	-	-	41.0	-	F
11.0	5.7	8.0	43.6	206.3	10.4	M
9.9	4.7	8.2	40.8	209.2	9.3	M
7.2	3.7	6.1	30.2	43.7	3.2	M
2.3	1.1	2.0	7.9	1.9	-	U
3.0	1.6	2.6	9.8	2.3	0.5	F
3.8	1.8	3.2	12.9	5.5	0.7	F
3.3	1.9	3.0	11.0	5.4	0.6	F
5.8	3.1	5.0	23.2	37.5	2.0	F
5.9	3.1	5.0	23.4	23.8	2.0	M
4.1	2.2	3.9	16.1	17.4	1.0	M
5.8	3.0	5.1	22.6	18.2	1.8	M
6.0	3.2	5.0	23.9	23.2	1.9	F
6.9	3.4	5.8	29.3	68.0	2.4	M
5.8	3.0	5.0	22.8	20.8	1.9	F
5.6	2.9	4.9	22.0	18.8	1.9	F
7.5	3.8	6.2	31.6	42.6	2.7	F
5.9	3.0	5.0	23.0	21.4	1.9	M
5.8	3.2	5.0	22.3	21.7	1.8	M

TABLE I.--continued.

Labium		Head Width	Body		Meso-wing Length	Sex*
Length	Width		Length	Width		
Crum Park Pond						
5.8	3.2	5.0	22.5	31.6	1.6	F
5.8	3.0	4.9	21.2	30.4	1.7	M
4.6	2.2	3.7	14.9	7.3	1.0	F
4.6	2.6	4.0	17.3	8.2	1.0	F
3.2	1.6	2.8	11.7	5.6	0.5	U
8.6	4.0	6.7	33.2	100.3	4.4	F
8.2	3.8	6.7	32.8	53.7	3.9	F
10.5	4.9	8.6	44.1	234.4	9.9	M
10.5	4.8	8.3	42.9	203.2	9.9	M
8.5	3.7	6.6	32.0	80.1	4.5	M
8.2	3.7	6.8	35.5	80.8	4.4	F
8.1	3.3	6.7	31.9	53.2	3.6	F
7.9	3.9	6.8	31.3	51.4	4.0	M
5.5	2.7	4.8	20.4	16.3	1.8	M
9.8	4.9	8.3	38.4	79.3	9.6	F
7.9	4.0	6.8	29.6	38.5	4.5	M
6.4	3.2	5.5	24.2	24.6	2.9	F
6.8	3.4	5.5	26.8	43.3	2.6	F
10.0	5.0	8.5	40.1	97.2	10.0	F
8.0	3.9	5.9	31.0	39.5	4.6	F
8.1	4.0	6.8	32.7	57.2	4.8	F
8.3	3.8	6.9	33.9	74.3	4.4	F
10.2	4.9	8.4	41.6	126.0	10.6	F
10.3	5.2	8.6	39.1	116.7	8.7	M
8.3	3.9	7.0	34.9	90.7	4.6	F
9.9	4.8	8.5	41.0	105.4	10.4	F
4.5	2.4	3.0	15.3	5.3	1.1	F
8.2	4.0	6.9	31.9	65.1	4.6	M
6.2	3.4	5.4	21.8	16.0	1.9	M
10.1	5.3	8.2	43.8	236.8	10.3	F
6.7	3.4	5.8	23.0	22.3	2.4	M
10.5	5.3	8.3	43.5	235.5	10.9	F
3.0	1.5	2.9	10.0	2.8	0.6	U
8.5	4.0	6.8	30.5	70.5	4.3	F
6.6	3.0	5.3	23.2	24.3	2.4	F
10.8	5.0	8.5	44.4	227.6	10.0	M
6.3	3.0	5.4	24.4	21.5	2.0	F
10.3	5.0	8.7	41.8	106.4	9.6	M
4.0	2.0	3.9	15.0	6.5	0.9	F
8.2	4.1	6.7	28.5	33.5	4.1	M
10.3	4.9	8.7	41.8	111.3	9.8	M
6.1	3.3	5.5	23.3	17.4	2.0	F

TABLE I.--continued.

Labium		Head	Body		Meso-wing	Sex*
Length	Width	Width	Length	Width	Length	
Long Woods Pond						
10.9	5.5	7.9	44.4	291.4	10.2	F
10.0	5.0	8.4	41.7	249.0	10.0	F
10.2	4.8	8.0	42.2	265.2	10.2	M
10.3	4.6	8.6	41.0	184.6	9.9	F
10.0	5.0	8.4	43.0	251.6	10.8	M
9.8	4.5	8.0	41.0	222.9	9.6	F
10.9	5.4	8.8	45.8	298.5	10.8	M
10.6	5.0	8.3	43.4	261.2	10.0	M
10.6	4.9	8.7	41.6	136.0	9.9	F
10.8	5.2	8.9	48.0	315.8	10.3	M
10.9	5.2	8.3	44.0	276.6	10.5	M
10.2	4.8	8.5	44.5	254.8	10.4	F
10.6	4.8	8.3	44.0	287.9	11.0	F
10.7	6.0	8.7	45.7	266.9	10.8	M
10.3	4.8	8.3	45.1	282.6	10.7	F
10.6	5.0	8.6	43.2	273.2	10.8	M
10.8	5.0	8.0	43.9	302.2	10.9	F
10.0	5.0	8.4	42.0	272.0	10.2	F
10.7	5.5	8.5	45.2	294.2	10.7	F
10.8	5.4	8.5	43.9	267.8	10.9	M
10.5	4.7	8.2	41.5	281.0	10.5	M
10.3	4.9	8.4	43.2	272.7	9.9	F
10.5	5.1	7.9	44.8	250.0	9.9	F
8.2	4.4	7.0	32.9	76.3	4.4	F
10.8	5.4	8.8	45.9	290.5	10.6	M
10.6	5.6	8.5	44.4	278.5	10.5	M
10.5	4.9	8.4	44.7	269.5	10.2	M
10.8	4.9	8.7	43.5	280.5	10.7	M
10.6	5.2	8.6	43.9	245.9	10.6	M
10.0	5.4	8.2	42.7	251.2	10.5	M
10.7	5.5	8.8	39.0	155.1	10.8	M
8.7	4.0	7.0	34.0	104.7	4.6	M
9.4	4.3	7.2	34.5	104.7	4.5	M
8.7	4.2	7.0	32.2	67.3	5.0	F
8.4	4.0	7.2	32.0	88.5	5.2	M
8.6	4.0	7.0	34.4	109.1	5.2	M
8.0	3.8	6.8	29.4	60.7	4.4	F
8.6	4.0	6.8	33.0	111.1	5.0	F
8.7	4.4	7.3	31.7	90.8	4.7	F
-	-	-	-	211.7	-	-
-	-	-	-	219.7	-	-
-	-	-	-	52.6	-	-

TABLE I.--continued.

Labium		Head	Body		Meso-wing	Sex*
Length	Width	Width	Length	Width	Length	
Long Woods Pond						
-	-	-	-	34.4	-	-
-	-	-	-	43.9	-	-
-	-	-	-	32.9	-	-
8.5	4.0	6.9	33.5	73.6	4.3	F
6.2	3.0	5.2	23.0	38.4	2.0	M
8.7	4.3	7.0	31.8	108.7	4.6	F
11.2	5.4	9.0	41.6	233.5	11.2	M
10.0	5.0	8.4	42.4	296.8	10.0	F
-	-	-	-	131.2	-	-
-	-	-	-	232.4	-	-
-	-	-	-	63.0	-	-
-	-	-	-	109.3	-	-
-	-	-	-	93.9	-	-
8.4	3.9	7.0	31.8	84.7	4.6	F
7.9	3.9	6.9	29.2	65.5	4.6	M
6.3	3.4	6.0	26.0	52.9	2.8	M
6.7	3.4	5.7	23.4	50.4	2.6	M
8.6	3.9	7.0	34.0	101.9	4.7	M
8.4	4.0	7.0	32.0	97.9	4.7	M
9.9	5.0	8.5	45.5	270.7	10.2	F
10.7	5.5	8.9	42.3	203.6	10.8	F
8.2	3.9	6.5	33.0	104.2	4.0	M
9.9	4.7	8.2	42.6	261.8	8.6	F
10.5	5.0	8.6	44.4	278.2	9.8	M
10.4	5.2	8.8	43.6	298.5	10.0	M
10.5	5.3	8.6	40.0	198.7	9.8	F
8.6	4.2	6.7	33.0	135.6	4.3	M
-	-	-	-	276.7	-	-
-	-	-	-	180.4	-	-
-	-	-	-	255.2	-	-
-	-	-	-	290.3	-	-
10.0	4.9	8.7	42.1	257.4	10.4	F
9.9	4.6	8.4	42.9	277.4	10.6	M
8.6	4.1	6.8	33.7	113.5	4.6	M
9.8	4.9	8.4	43.9	268.7	9.4	M
10.0	4.9	8.8	43.3	276.1	10.0	F
10.2	4.8	8.7	45.5	284.1	10.0	F
10.4	5.0	8.9	43.6	285.0	9.8	M
10.8	5.3	8.8	39.4	117.4	10.0	M
10.3	5.2	8.9	38.8	127.1	10.0	F
10.0	5.0	8.7	42.4	191.2	9.9	F
9.9	4.6	8.1	40.8	236.7	9.6	M
10.9	5.0	8.9	42.0	236.8	11.0	F

TABLE I.--continued

Labium		Head	Body		Meso-wing	Sex*
Length	Width	Width	Length	Width	Length	
Long Woods Pond						
10.8	5.1	8.8	44.5	292.1	10.0	M
10.8	5.1	8.8	44.0	277.3	10.0	M
10.5	5.0	9.0	45.6	283.0	10.5	M
10.8	5.1	8.8	44.5	233.3	10.0	F
10.4	5.1	8.6	42.8	263.2	10.4	F
10.8	5.1	8.8	44.6	272.4	10.7	M
10.3	5.0	8.2	44.3	243.0	10.0	M
10.9	5.0	8.9	45.0	271.9	10.4	M
8.7	4.0	6.9	32.9	97.7	4.6	M
10.0	4.9	8.4	41.7	264.6	10.8	F
10.8	4.8	8.8	43.1	212.8	10.0	F
10.8	5.6	8.4	45.2	276.5	11.4	M
10.7	5.3	8.2	45.0	279.8	11.0	F
10.3	5.1	8.4	43.5	276.2	10.0	F
10.5	5.0	8.8	43.1	257.6	9.4	M
11.0	5.1	8.6	45.9	302.3	10.4	M
9.9	4.8	8.6	40.9	133.4	9.4	M
10.0	4.9	8.6	43.0	264.6	10.2	M
8.3	3.7	6.8	32.3	87.0	4.6	M
9.9	5.2	8.3	40.8	237.0	9.5	F
10.5	4.8	8.4	43.7	324.2	9.8	M
10.2	5.0	8.1	43.9	269.5	10.3	M
10.4	5.2	7.8	45.2	278.7	10.2	M
10.0	4.9	8.3	43.4	264.7	9.4	M
10.4	5.1	8.3	42.1	264.4	9.6	F
10.3	4.5	8.3	44.9	299.4	9.0	M
10.0	5.6	7.7	42.8	232.5	10.0	F
9.9	5.1	8.4	43.0	287.5	8.8	M
7.7	3.7	6.5	30.2	74.8	3.2	M
10.0	4.9	8.4	40.7	294.9	9.4	F
7.4	4.0	6.3	31.3	52.6	3.0	F
7.3	3.7	6.3	30.4	56.5	3.0	M
8.5	4.2	7.0	34.9	75.1	4.8	F
10.0	5.1	7.8	41.4	238.3	10.2	F
8.5	4.0	6.7	33.0	74.5	5.2	F
7.3	3.7	6.2	30.7	50.5	3.0	M
11.0	4.0	8.6	45.0	283.9	10.0	F
6.3	2.6	5.0	23.4	36.3	1.8	M
7.6	3.5	6.0	29.5	58.8	2.8	F
9.9	4.9	7.8	41.6	245.1	9.6	F
10.6	5.0	8.0	44.2	271.3	9.6	M
7.0	3.6	6.1	31.0	69.8	2.9	M
4.8	2.2	3.9	17.8	13.5	1.0	M

TABLE I.--continued.

Labium		Head Width	Body		Meso-wing Length	Sex*
Length	Width		Length	Width		
Long Woods Pond						
4.0	2.4	3.9	17.4	13.9	1.2	F
5.3	2.5	4.0	17.6	12.9	1.1	M
4.5	2.4	4.0	18.3	19.2	1.2	F
4.0	2.0	3.5	13.5	10.3	-	U
5.5	3.0	4.8	22.0	35.4	1.8	M
6.9	3.5	6.1	27.4	63.8	2.6	F
3.6	1.9	3.0	13.2	9.2	0.7	U
6.8	3.1	4.5	22.5	26.4	2.2	M
4.8	2.4	4.0	17.7	15.8	1.1	F
9.5	5.1	8.0	42.0	258.3	10.3	F
10.4	5.2	8.0	43.6	270.3	10.0	F
10.7	5.8	8.5	42.0	256.7	9.7	M
10.0	5.3	8.0	42.7	257.5	9.8	F
10.8	5.6	7.8	44.4	245.8	9.7	M
10.4	5.5	8.0	43.2	275.4	10.0	F
-	-	-	-	272.0	-	-
10.2	4.9	7.9	43.8	260.6	9.5	F
10.5	4.9	8.4	45.3	309.7	10.0	F
5.9	2.9	4.9	23.8	42.7	1.8	F
-	-	-	-	237.3	-	-
6.0	2.9	5.0	23.9	24.5	1.8	M
6.4	3.1	5.5	26.4	29.2	2.0	F
7.4	3.6	6.0	31.4	96.0	3.3	M
9.4	4.5	6.8	35.5	89.5	5.0	M
4.2	2.3	3.9	17.8	12.8	1.1	M
4.8	2.4	3.9	17.8	15.8	1.3	F
7.9	3.8	6.3	31.7	56.4	2.9	M
-	-	-	-	15.2	-	-
5.6	2.8	4.4	22.0	26.3	1.6	F
4.3	2.6	4.0	17.4	11.7	1.0	F
5.5	2.5	4.6	20.2	19.7	1.9	M
10.4	5.6	8.6	44.7	243.9	10.9	F
10.6	5.7	8.6	42.2	251.1	11.0	F
10.4	4.7	8.2	44.9	262.2	10.0	M
10.6	5.0	8.0	44.8	250.1	11.0	F
10.0	4.5	8.4	41.5	233.8	9.9	M
10.6	5.0	8.6	45.5	264.9	11.0	F
10.9	5.0	8.8	44.8	280.7	11.0	M
10.0	5.0	7.6	41.4	240.8	10.4	F
10.0	4.5	7.9	40.8	213.3	10.9	F
10.0	4.9	8.2	41.7	266.6	9.0	M
9.8	4.3	8.0	40.0	249.7	9.0	F

TABLE I.--continued.

Labium		Head Width	Body		Meso-wing Length	Sex*
Length	Width		Length	Width		
Long Woods Pond						
10.8	5.5	8.3	40.1	241.9	9.7	M
10.4	4.8	8.2	41.0	234.7	9.4	F
10.1	5.0	8.1	38.3	235.4	9.9	F
10.0	5.2	8.2	41.2	225.7	9.9	F
10.8	5.3	8.4	43.6	297.3	10.5	F
7.0	3.2	5.5	26.0	44.6	3.0	M
Marrow Pond						
10.4	5.2	8.6	41.5	153.5	10.4	F
8.7	4.2	7.2	32.8	82.1	4.4	F
8.2	4.2	6.7	32.9	117.6	4.4	F
10.3	5.4	8.7	41.8	262.9	10.1	F
7.9	3.9	6.3	33.0	119.5	4.6	M
8.0	3.8	6.9	32.0	107.7	4.6	M
6.0	3.2	5.0	20.4	25.0	2.2	F
10.9	5.7	9.0	41.0	157.4	10.0	M
5.8	3.1	5.0	19.6	19.6	2.2	F
10.4	4.6	8.8	37.6	137.0	9.8	F
6.2	3.2	5.5	22.8	43.5	2.4	M
10.6	5.2	8.0	39.9	154.3	9.5	F
10.5	4.9	8.0	36.8	121.4	8.9	M
10.0	4.9	8.5	41.6	224.2	10.0	M
10.2	4.9	8.5	40.0	182.8	10.5	F
10.2	4.8	8.0	44.7	307.0	10.3	F
10.8	5.2	8.6	43.8	201.3	11.0	F
10.9	5.2	8.6	45.9	296.3	10.9	M
10.7	5.5	8.8	41.8	129.0	9.8	M
10.8	5.1	7.9	43.6	300.5	11.0	M
10.5	5.0	7.8	42.8	291.2	10.0	M
10.2	5.0	8.6	42.5	190.8	9.8	M
10.7	4.8	8.7	45.4	355.3	11.2	F
10.0	4.9	8.4	43.3	217.6	9.9	M
10.0	4.4	8.4	41.9	188.5	10.0	M
10.9	5.4	8.2	46.0	302.0	10.5	M
10.9	4.9	8.0	45.9	317.0	11.0	M
10.5	5.0	8.4	38.8	130.3	9.0	F
10.6	4.9	8.7	45.0	216.2	10.0	M
10.9	4.9	8.8	42.8	164.7	10.0	F
10.6	5.5	7.6	45.9	287.4	10.5	F

TABLE I.--continued.

Labium		Head Width	Body		Meso-wing Length	Sex*
Length	Width		Length	Width		
Marrow Pond						
10.0	4.5	6.9	39.3	119.8	10.0	F
10.5	4.6	8.4	43.0	262.2	10.0	M
8.7	3.7	6.6	33.0	107.3	4.4	M
8.3	3.9	6.9	32.3	105.7	4.2	F
7.9	3.7	6.8	33.6	102.5	4.6	M
8.0	3.6	6.9	33.4	100.0	4.6	F
6.5	3.0	5.4	23.3	48.0	2.6	F
9.4	4.5	7.5	38.3	112.4	8.0	F
7.9	3.9	6.8	32.0	110.1	4.4	F
8.0	3.6	6.3	31.4	122.0	4.0	M
9.8	4.6	6.9	34.4	112.8	8.5	F
8.0	3.6	6.9	33.0	124.2	4.8	F
6.4	2.8	5.3	22.9	37.0	2.5	M
8.5	3.8	6.6	31.0	97.0	4.8	M
10.5	5.0	8.2	45.0	294.0	9.8	M
9.9	5.0	8.4	40.5	174.6	9.9	F
9.9	4.5	8.0	42.9	275.4	10.0	F
10.4	5.0	8.6	39.6	152.1	10.0	F
10.7	5.2	8.6	41.8	212.9	10.0	F
8.1	4.0	7.0	34.2	117.9	4.9	M
3.4	1.9	4.2	14.0	9.6	1.0	U
2.8	1.4	3.6	10.8	5.4	0.8	U
10.0	5.1	8.4	36.9	109.7	9.0	F
8.0	3.5	6.7	31.0	83.4	4.2	M
6.2	3.0	4.6	21.5	28.4	2.0	F
10.0	4.6	8.5	39.0	108.3	10.0	M
10.2	5.0	8.2	40.2	227.5	10.6	M
10.6	5.0	8.0	44.9	284.1	11.0	M
7.8	3.4	6.0	28.0	63.2	4.2	M
10.0	4.4	8.2	38.9	116.6	10.0	M
9.5	5.0	8.4	43.0	259.3	10.2	U
10.0	5.0	8.6	37.9	115.4	10.0	M
9.6	5.0	8.2	37.0	112.0	9.7	F
10.3	5.4	8.5	39.4	149.2	9.9	F
10.0	4.0	7.8	43.6	246.1	9.8	F
10.5	5.0	8.0	42.7	246.8	10.2	F
9.8	4.8	8.0	41.2	289.0	9.6	F
9.9	5.2	8.5	40.9	272.6	10.0	M
10.7	4.7	8.2	42.0	274.5	8.9	M
9.6	4.5	7.9	40.1	252.5	9.3	F
9.8	4.6	8.0	43.8	267.8	9.6	M
10.0	5.0	8.6	35.5	111.2	10.0	F

TABLE I.--continued.

Labium Length	Labium Width	Head Width	Body Length	Body Width	Meso-wing Length	Sex*
Marrow Pond						
10.4	5.0	8.0	43.0	260.6	10.8	M
10.0	5.0	8.0	40.8	229.9	10.0	F
9.9	4.6	7.8	41.6	254.5	9.18	F
10.3	4.9	8.4	39.3	199.2	10.8	F
10.0	4.7	7.8	41.2	244.6	10.8	F
10.4	5.0	7.9	43.0	275.7	10.8	M
10.5	4.8	8.3	37.6	214.6	10.0	M
10.3	5.2	7.6	42.0	272.5	11.1	M
5.9	2.7	5.0	22.8	29.1	1.8	M
6.0	3.0	5.2	23.0	24.8	2.0	M
7.2	3.8	6.0	25.5	35.8	2.8	M
6.9	3.5	5.8	25.9	48.4	2.9	F
6.0	3.0	5.1	23.8	36.1	2.0	M
7.0	3.5	5.8	23.8	29.1	2.6	M
8.7	4.2	6.8	28.9	63.4	4.0	M
5.5	2.5	4.4	19.0	14.3	1.2	M
6.0	3.0	5.0	21.0	32.8	2.0	F
10.4	5.1	8.8	38.6	122.2	10.0	M
9.6	4.8	8.0	36.9	138.3	8.9	F
10.0	5.0	8.5	36.9	96.5	9.2	M
10.0	4.6	8.2	41.5	197.7	10.0	M
10.7	4.9	7.7	41.8	210.2	10.5	F
9.7	4.9	8.0	37.3	105.7	9.8	F
10.3	5.0	8.5	38.3	117.8	10.0	F
10.2	4.6	8.5	40.9	142.2	9.9	M
10.2	4.8	8.0	40.4	225.1	10.4	F

*M = male; F = female; U = unknown.

TABLE II.--Statistical parameters of Figure 3.

Statistic	Figure			
	A	B	C	D
ΣX	87.1888	76.2922	110.9210	84.1111
ΣY	69.5547	61.7225	105.9564	80.1372
ΣX^2	202.0245	169.2823	230.6216	171.1038
ΣY^2	128.8535	110.7514	207.2989	152.4710
ΣXY	160.9376	136.6660	217.3744	161.1554
n	38.0000	35.0000	56.0000	44.0000
Y intercept	0.2637	0.2105	0.5307	0.3455
slope	0.6827	0.7124	0.6872	0.7720
$\bar{X}$	2.2944	2.1798	1.9807	1.9116
Quadric $\bar{X}$	2.3057	2.1992	2.0293	1.9720
S^2_x	0.0520	0.0820	0.1949	0.2345
S_x	0.2280	0.2919	0.4415	0.4842
Cov.	0.0994	0.1339	0.2229	0.2533
$S_{\bar{x}}$	0.0370	0.0493	0.0590	0.0730
$\bar{Y}$	1.8304	1.7635	1.8921	1.8213
Quadric $\bar{Y}$	1.8414	1.7789	1.9240	1.8615
S^2_y	0.0406	0.0544	0.1218	0.1481
S_y	0.2014	0.2332	0.3490	0.3849
Cov.	0.1100	0.1323	0.1845	0.2113
$S_{\bar{y}}$	0.0327	0.0394	0.0466	0.0580
Corr. Coef.	0.7728	0.8917	0.8695	0.9713

TABLE II.--continued.

Statistic	Figure			
	E	F	G	H
ΣX	85.3653	89.2480	79.9010	103.8278
ΣY	91.9803	98.2030	91.6397	122.1760
ΣX^2	172.7983	176.1795	161.1001	209.3194
ΣY^2	198.6997	209.3484	208.9938	285.6545
ΣXY	184.7823	191.5972	182.9221	242.8545
n	45.0000	50.0000	42.0000	56.0000
Y intercept	0.2456	0.2390	0.3860	0.3809
slope	0.9479	0.9664	0.9439	0.9712
$\bar{X}$	1.8970	1.7850	1.9024	1.8541
Quadric $\bar{X}$	1.9596	1.8771	1.9585	1.9334
S^2_x	0.2413	0.3375	0.2116	0.3003
S_x	0.4913	0.5810	0.4654	0.5480
Cov.	0.2590	0.3255	0.2446	0.2956
$S_{\bar{x}}$	0.0732	0.0822	0.0718	0.0732
$\bar{Y}$	2.0440	1.9641	2.1819	2.1817
Quadric $\bar{Y}$	2.1013	2.0462	2.2307	2.2585
S^2_y	0.2376	0.3294	0.2154	0.3411
S_y	0.4874	0.5740	0.4641	0.5840
Cov.	0.2385	0.2922	0.2127	0.2677
$S_{\bar{y}}$	0.0727	0.0812	0.0716	0.0780
Corr. coef.	0.9554	0.9782	0.9466	0.9113

TABLE III.--Statistical parameters of Figure 4.

Statistic	Figure			
	A	B	C	D
ΣX	87.1891	76.2922	111.9156	84.1111
ΣY	96.3155	90.2164	162.3913	128.0265
ΣX^2	202.0258	169.2821	233.6715	171.1036
ΣY^2	244.9601	233.0887	472.3664	373.4140
ΣXY	220.3567	195.8746	322.2825	242.3962
n	38.0000	35.0000	56.0000	44.0000
Y intercept	3.2715	3.1456	3.3501	3.3435
slope	-0.3211	-0.2604	-0.2253	-0.2269
$\bar{X}$	2.2944	2.1797	1.9985	1.9116
Quadric $\bar{X}$	2.3057	2.1992	2.0427	1.9720
S^2_x	0.0520	0.0852	0.1787	0.2345
S_x	0.2280	0.2919	0.4228	0.4842
Cov.	0.0994	0.1339	0.2115	0.2533
$S_{\bar{x}}$	0.0370	0.0493	0.0565	0.0730
$\bar{Y}$	2.5346	2.5776	2.8998	2.9097
Quadric $\bar{Y}$	2.5390	2.5806	2.9043	2.9132
S^2_y	0.0220	0.0156	0.0260	0.0204
S_y	0.1484	0.1248	0.1614	0.1428
Cov.	0.0586	0.0484	0.0556	0.0491
$S_{\bar{y}}$	0.0241	0.0211	0.0216	0.0215
Corr. coef.	-0.4932	-0.6092	-0.5906	-0.7699

TABLE III.--continued.

Statistic	Figure			
	E	F	G	H
ΣX	85.2283	89.3444	79.9010	103.0954
ΣY	143.1231	158.8522	138.1198	183.4271
ΣX^2	172.1132	176.6300	161.0999	208.7828
ΣY^2	456.7956	505.4153	455.1395	613.6385
ΣXY	270.4872	283.2280	262.4471	343.9165
n	45.0000	50.0000	42.0000	55.0000
Y intercept	3.2836	3.2426	3.3539	3.3242
slope	-0.0544	-0.0366	-0.0343	0.0057
$\bar{X}$	1.8940	1.7869	1.9024	1.8745
Quadric $\bar{X}$	1.9557	1.8795	1.9585	1.9483
S^2	0.2377	0.3397	0.2166	0.2825
S_x^x	0.4875	0.5828	0.4654	0.5315
Cov.	0.2574	0.3263	0.2446	0.2835
$S_{\bar{x}}$	0.0727	0.0824	0.0718	0.0717
$\bar{Y}$	3.1805	3.1770	3.2886	3.3350
Quadric $\bar{Y}$	3.1861	3.1794	3.2919	3.3402
S_y^2	0.0354	0.0147	0.0220	0.0346
S_y	0.1881	0.1213	0.1484	0.1861
Cov.	0.0591	0.0382	0.0451	0.0558
$S_{\bar{y}}$	0.0280	0.0172	0.0229	0.0251
Corr. coef.	-0.1412	-0.1764	-0.1078	0.0164

TABLE IV.--Statistical parameters of Figure 5.

Statistic	Value
ΣX	93.1879
ΣY	90.9676
ΣX^2	179.2494
ΣY^2	170.8367
ΣXY	174.8993
n	54.0000
Y intercept	-0.0010
slope	0.9767
$\bar{X}$	1.7257
Quadric $\bar{X}$	1.8219
S^2_x	0.3414
S_x	0.5843
Cov.	0.3386
$S_{\bar{x}}$	0.0795
$\bar{Y}$	1.6846
Quadric $\bar{Y}$	1.7787
S^2_y	0.3258
S_y	0.5708
Cov.	0.3388
S_y	0.0777
Corr. coef.	0.9998

TABLE V.--Statistical parameters of Figure 7.

Statistic	Figure			
	A	B	C	D
ΣX	159.5144	225.7946	182.7812	181.0867
ΣY	190.7664	350.8508	335.0154	332.6271
ΣX^2	353.5072	453.4537	354.4196	355.5970
ΣY^2	499.9017	1037.0910	1081.2841	1120.4830
ΣXY	415.3902	660.8778	588.5418	608.8296
n	73.0000	119.0000	104.0000	100.0000
Y intercept	3.2575	3.3152	3.2346	3.3308
slope	-0.2949	-0.1933	-0.0076	0.0158
$\bar{X}$	2.1851	1.8974	1.7575	1.8292
Quadric $\bar{X}$	2.2006	1.9521	1.8460	1.8952
S^2_x	0.0678	0.2103	0.3190	0.2461
S_x	0.2604	0.4586	0.5648	0.4961
Cov.	0.1192	0.2417	0.3214	0.2712
$S_{\bar{x}}$	0.0305	0.0420	0.0554	0.0499
$\bar{Y}$	2.6132	2.9483	3.2213	3.3599
Quadric $\bar{Y}$	2.6169	2.9521	3.2244	3.3642
S^2_y	0.0190	0.0225	0.0202	0.0294
S_y	0.1378	0.1499	0.1421	0.1713
Cov.	0.0527	0.0508	0.0441	0.0510
$S_{\bar{y}}$	0.0161	0.0137	0.0139	0.0172
Corr. coef.	-0.5575	-0.5921	-0.0301	0.0478

TABLE VI.--Statistical parameters of Figure 8.

Statistic	Figure			
	A	B	C	D
ΣX	163.4810	231.3144	187.4687	186.3202
ΣY	131.2771	220.2879	205.7264	216.9696
ΣX^2	371.3067	476.0333	372.8041	374.0304
ΣY^2	239.6047	426.0032	441.1476	499.8896
ΣXY	297.6035	449.1296	404.2562	430.1193
n	73.0000	119.0000	104.0000	100.0000
Y intercept	0.2414	0.3101	0.2510	0.3770
slope	0.6952	0.7928	0.9581	0.9621
$\bar{X}$	2.2395	1.9438	1.8026	1.8632
Quadric $\bar{X}$	2.2553	2.0001	1.8933	1.9340
S_x^2	0.0712	0.2219	0.3353	0.2688
S_x	0.2668	0.4710	0.5791	0.5184
Cov.	0.1191	0.2423	0.3213	0.2783
$S_{\bar{X}}$	0.0312	0.0432	0.0568	0.0518
$\bar{Y}$	1.7983	1.8512	1.9781	2.1697
Quadric $\bar{Y}$	1.8117	1.8920	2.0596	2.2358
S_y^2	0.0483	0.1531	0.3288	0.2913
S_y	0.2198	0.3913	0.5734	0.3597
Cov.	0.1222	0.2114	0.2899	0.2488
$S_{\bar{Y}}$	0.0257	0.0359	0.0562	0.0540
Corr. coef.	0.8439	0.9544	0.9677	0.9242

TABLE VII.--Statistical parameters of Figure 9.

Statistic	Figure			
	A	B	C	D
ΣX	163.4813	231.3141	187.0279	185.5882
ΣY	187.2788	346.3286	331.4031	328.1132
ΣX^2	371.3077	476.0315	370.8737	373.4954
ΣY^2	481.8692	1010.7509	1058.7914	1090.3358
ΣXY	417.8967	667.7837	594.7182	614.8764
n	73.0000	119.0000	104.0000	100.0000
Y intercept	3.2155	3.3091	3.2521	3.3299
slope	-0.2903	-0.2051	-0.0364	-0.0083
$\bar{X}$	2.2395	1.9438	1.7983	1.8746
Quadric $\bar{X}$	2.2553	2.001	1.8884	1.9423
S^2_x	0.0712	0.2219	0.3321	0.2585
S_x	0.2669	0.4710	0.5763	0.5084
Cov.	0.1192	0.2423	0.3204	0.2712
$S_{\bar{x}}$	0.0312	0.0432	0.0565	0.0511
$\bar{Y}$	2.5655	2.9103	3.1866	3.3143
Quadric $\bar{Y}$	2.5692	2.9144	3.1907	3.3187
S^2_y	0.0194	0.0237	0.0265	0.0291
S_y	0.1391	0.1541	0.1628	0.1706
Cov.	0.0542	0.0529	0.0511	0.0515
$S_{\bar{y}}$	0.0163	0.0141	0.0160	0.0171
Corr. coef.	-0.5568	-0.6274	-0.1291	-0.0249

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