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ENERGY METABOLISM OF DRAGONFLIES (ODONATA: ANISOPTERA) AT REST AND DURING ENDOTHERMIC WARM-UP

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SUMMARY

1. Energy metabolism at rest and during pre-flight warm-up was measured in a variety of anisopterous dragonflies.

2. Resting oxygen consumption was similar in its relation to body temperature (T_b) and body mass to that of other insects. At 30 °C, $\log M = 0{\cdot}91 \log m + 0{\cdot}44$, where M is metabolism (W) and m is body mass (kg).

3. Metabolism during warm-up was calculated both from measurements of T_b and from oxygen consumption. By the former method, $\log M = 1{\cdot}01 \log m + 2{\cdot}22$ at the maximum T_b attained during warm-up, and $\log M = 0{\cdot}90 \log m + 1{\cdot}87$ at $T_b = 30$ °C. Oxygen consumption measurements mostly gave values of M about 15% higher.

4. Total energy cost of warm-up is directly related to mass, thermal conductance and T_b at takeoff, and inversely related to warm-up rate.

INTRODUCTION

In most animals, both resting and active metabolism (M) can be related to whole body mass (m) by empirical equations of the form $M = am^b$. Considerable interest has centred on whether the exponent, b, reflects either proximate or ultimate forces controlling rates of metabolism. As yet, efforts to elucidate this relationship have met with very limited success. Nevertheless, such equations are of considerable value for at least two reasons. First, body mass has such a large effect on whole-body metabolism in most taxa that knowledge of this parameter can permit reasonable estimates of metabolism in untested species once the general relationship is known. Second, by showing how much variation in metabolism is accounted for by size, the residual variation becomes evident and its causes become more accessible to investigation.

The relation of energy utilization to body size is known only for a few groups of insects (Keister & Buck, 1974). Respiratory metabolism of adult Odonata, in particular, is little studied, although the larvae have received some attention (Sayle, 1928;

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Petitpren & Knight, 1970). The data that do exist refer primarily to insects at rest although many species warm up by synchronous contractions of the thoracic muscles before flight (e.g. Krogh & Zeuthen, 1941; Dorsett, 1962; Kammer & Heinrich, 1974). This phenomenon is well known in moths and bees and also occurs in numerous other groups, but little is known of its relation to body size (Heinrich & Casey, 1973; May, 1976*b*).

In this paper I attempt to fill in some of these gaps in our knowledge of insect energetics. I have measured the energy requirements of various species of dragonflies covering a wide range of body weights, both at rest and during warm-up. In some cases I have also determined the effect of temperature on metabolism. These data may eventually contribute to determination of complete energy budgets for these insects.

METHODS

Adult dragonflies were collected near Gainesville, Florida, U.S.A. (30 °N, 82 °W), in the Panama Canal Zone (9 °N, 80 °W), and near Urbana, Illinois, U.S.A. (40° N, 88° W). Animals were used on the day of capture in measurement of resting O_2 consumption, or one to three days later in other experiments. The masses reported are those of live or freshly killed specimens. Ten male *Anax junius* and five male *Tramea lacerata* dried at 90 °C to constant mass had dry mass = 34% 'wet' mass (32–36%).

Statistical differences between sample means have been determined using Student's t test; the criterion for significance is $P < 0{\cdot}05$. Other statistical procedures are discussed as appropriate. Grouped data are expressed as mean ± S.D. unless otherwise noted.

Resting O_2 consumption

Rate of O_2 consumption in dragonflies at rest was determined by standard manometric techniques using a Gilson differential respirometer. Single individuals were introduced into flasks of 20–150 ml, depending on the species, and allowed at least one hour in dim light (an opaque cloth was placed over the respirometer) to acclimate to the flask and to come to thermal equilibrium. Thereafter, measurements were taken at 5–15 minute intervals for at least two hours. I did not observe activity directly. Intervals in which vigorous activity occurred were obvious because of greatly elevated O_2 consumption, and these measurements were discarded. Carbon dioxide was absorbed by soda lime in each flask. An energy equivalent of $2{\cdot}01 \times 10^4$ J.l^{-1} of O_2 ($4{\cdot}8$ cal.ml^{-1}) was assumed. Experiments were run between 10.00 and 21.00 hours Eastern Daylight Savings Time.

Metabolism during warm-up

Energy utilization during endothermic warm-up was estimated from data on T_b and heat loss and from O_2 consumption rates. Warm-up rate is nearly constant throughout most of the warming period, so

$$M_a = [R + K(T_b - T_a)]s\,(m_t/60),$$

where M_a is rate of heat production during activity (W), R is warm-up rate (°C.min^{-1}), K is a cooling constant (min^{-1}), T_b and T_a are body and ambient temperatures respectively (°C), s is the specific heat of tissue (J.kg^{-1}.°C^{-1}), and m_t is mass of the thorax (kg). Use of this equation required continuous recording of T_b during warm-up at constant T_a, then determination of K from records of T_b vs time during passive cooling (Heath & Adams, 1969). Cooling constants ordinarily were measured in dead specimens in which K was minimal (May, 1976*a*), except in experiments where oxygen consumption was also measured (Table 2).

Body temperatures were monitored during warming and cooling with copper–constantan thermocouples (0·003 in or 0·002 in lead diameter) implanted into the thoracic muscles through a pinhole in the metepisternum. Thermocouple output was monitored continuously on a strip chart recorder fitted with an appropriate reference junction. Ambient temperature was controlled to ± 1 °C in a Lab-Line constant temperature room or, in Panama, at 25 ± 1 °C with room air conditioning. Variation in T_a during any one experiment was ordinarily less than 1·0 °C. Warm-up commenced spontaneously or after I pinched the abdomen of the specimen.

Oxygen consumption during warm-up in three species of dragonflies from Illinois, *Anax junius*, *Boyeria vinosa* and *Tramea lacerata*, was measured in an open flow system. Compressed air was driven successively through a column of Drierite desiccant, a metabolism chamber (a Plexiglass tube 2·54 cm diameter × 13 cm long, volume reduced as appropriate with Styrofoam plugs), a second column of Drierite, and an RGI flowmeter, and into a Beckman F3 O_2 analyser, then vented to the atmosphere. Flow rate was about 70 ml.min^{-1} and was read to the nearest ml.min^{-1}. The flushing time constant (τ) for the system was 24–27 s (mean 25·2). This parameter was determined by quickly switching a three-way valve to change the inflow from air to a mixture of 20·31% O_2–79·69% N_2, thus imposing essentially a step change in O_2 concentration. The time required for the change in concentration to reach 63% of its final value is equal to τ. There was also an absolute lag of about 30 s between chamber and analyser. Output of the analyser was monitored on a Honeywell Electronik 16 Multipoint chart recorder. Ambient temperature was controlled to ± 1 °C with room air conditioning.

Animals were prepared for measurement by cutting their wings off within 0·5 cm of the base and implanting a thermocouple into their thorax as described above. Air temperature within the chamber was also monitored with a copper–constantan thermocouple. Thermocouple leads were brought through a side arm in the chamber and connected to the chart recorder.

I calculated $\dot{V}_{O_2}$ according to Depocas & Hart (1957), assuming an RQ of 1·0 and an energy equivalent of 2·13 × 10^4 J.l^{-1} of O_2 (Bartholomew, 1968). Carbon dioxide was not removed from the gas outflow, so, if RQ was actually less than 1·0, $\dot{V}_{O_2}$ was underestimated (about about 10% if RQ = 0·7). The energetic equivalent of a litre of O_2 decreases with decreasing RQ, however, so that at the flow rates and approximate levels of $\dot{V}_{O_2}$ involved here the calculated heat production would vary only 2% for any RQ from 0·7 to 1·0. The RQ probably is less than 1·0 (Kallapur & George, 1973), as implicitly assumed in calculating M_r.

Since oxygen concentration changed rapidly and recording was discontinuous

(recorder cycle time, 28·5 s), I determined peak $\dot{V}_{O_2}$ by drawing straight lines through the two points immediately before and the two immediately after the interval containing the peak. Minimum oxygen concentration was taken as a point midway between the intersection of these lines and the lowest recorded points. In three cases, simultaneous records on another recorder with a continuous trace gave results within 1% of the value of $\dot{V}_{O_2}$ calculated as above.

When $\dot{V}_{O_2}$ is changing rapidly as during warm-up, apparent values underestimate actual instantaneous $\dot{V}_{O_2}$ because of mixing within the metabolism chamber. Bartholomew, Vleck & Vleck (1979) calculated instantaneous $\dot{V}_{O_2}$ by assuming that the change within each recorded time interval is a step function. Then

$$t = \tau \ln \frac{1}{1-z} \tag{2}$$

where t is the interval between measurements (s) and $z = (O_t - O_i)/(O_{eq} - O_i)$, where O_t, O_i and O_{eq} are, respectively, chamber oxygen concentrations at the end of the interval, at the beginning of the interval, and at equilibrium (Christensen, 1947; Lasiewski, Acosta & Bernstein, 1966). If mixing within the chamber is complete, $z = 1 - e^{-t/\tau}$ (Tyner & May, 1968). Therefore

$$O_{eq} = \frac{O_t - O_i}{1 - e^{-t/\tau}} + O_i \tag{3}$$

and an estimate of $\dot{V}_{O_2}$ can be calculated from O_{eq}. Equation 3 is from Bartholomew *et al.* (1979).

Total oxygen consumption was calculated by graphically integrating oxygen concentration over time, from the time warm-up began until oxygen concentration rose again to resting levels. This quantity was converted to total heat production (E_o) as above. A corresponding value of total heat production, E_a, was determined from the record of T_b by measuring R and the median value of $T_b - T_a$ within each interval from the time warm-up commenced until T_b began to drop exponentially. The average rate of heat production was calculated for each interval and summed over all intervals.

Specific heat

I determined s (equation 1) for whole dragonflies by modifying the method of Hart (1951). A calorimeter, consisting of a 450 ml Dewar flask with a Styrofoam lid, contained about 200 ml of water. A thermometer graduated in 0·1 °C and readable with a lens to 0·01 °C extended through a hole in the lid. A plastic screen attached by wooden supports to the lid held the dragonflies beneath the water. The thermal equivalent mass of the assembled calorimeter, including a small, magnetic stirring bar, was determined by rapidly introducing a known quantity of water at a known temperature above that of the flask and determining the equilibrium temperature. Four replications gave an average value equivalent to 18 g of water, and this was added to the actual mass of water in determinations of s.

The contents of the calorimeter were mixed continuously with a magnetic stirrer and were near room temperature, 21–22 °C. I killed and removed the wings from 30–35 dragonflies (*Libellula luctuosa*, with a few *L. pulchella*) weighing 10–12 g

Table 1. *Rate of metabolism of dragonflies at rest; all were collected at Gainesville, Florida*

(N is sample size, other symbols are defined in the text; M_r and M_r/m are expressed as mean ± S.D., range in parentheses.)

Species number	Species	N and sex	T_b (°C)	Mean m (g)	Mean* $\dot{V}_{O_2}$ (ml.h^{-1})	$M_r \times 10^3$ (W)	M_r/m (W.kg^{-1})	Q_{10}
1	*Anax junius*	3♂ 4♀	30	1·019	1·04	5·8 ±0·38 (5·2–6·4)	5·8 ±0·91 (4·2–6·9)	
2	*Brachymesia gravida*	1♂ 7♀	30	0·344	0·39	2·2 ±0·37 (1·8–2·9)	6·4 ±0·68 (5·2–7·3)	
3	*Erythemis simplicicollis*	4♂ 4♀	30	0·263	0·22	1·2 ±0·18 (1·0–1·5)	4·7 ±0·56 (4·1–5·5)	
4	*Erythrodiplax berenice*	4♂ 4♀	30	0·125	0·11	0·61 ±0·076 (0·46–0·69)	4·9 ±0·70 (4·3–6·0)	
5*a*	*Erythrodiplax connata*	7♂	20	0·052	0·024	0·13 ±0·030 (0·088–0·18)	2·6 ±0·44 (1·9–3·4)	2·7
5*b*	*Erythrodiplax connata*	11♂ 3♀	30	0·054	0·069	0·37 ±0·073 (0·24–0·50)	7·0 ±1·3 (5·1–10·3)	2·4
5*c*	*Erythrodiplax connata*	7♂	40	0·049	0·14	0·80 ±0·088 (0·66–0·90)	16·5 ±2·0 (14·3–19·1)	
6	*Libellula auripennis*	3♂ 5♀	30	0·464	0·35	2·0 ±0·43 (1·3–2·5)	4·2 ±0·54 (3·4–4·9)	
6′	*Libellula needhami*	3♂ 5♀	30	0·518	0·42	2·4 ±0·64 (1·7–3·4)	4·5 ±0·68 (3·7–5·6)	
6*a*	*Libellula* spp. (combined)	4♂ 4♀	20	0·419	0·16	0·90 ±0·25 (0·62–1·4)	1·8 ±0·21 (1·5–2·1)	2·4
6*b*	*Libellula* spp. (combined)	6♂ 10♀	30	0·491	0·39	2·2 ±0·57 (1·3–3·4)	4·4 ±0·61 (3·4–5·6)	2·1
6*c*	*Libellula* spp. (combined)	2♂ 5♀	40	0·443	0·80	4·6 ±0·68 (3·1–5·1)	10·3 ±0·85 (8·7–11·5)	
7*a*	*Miathyria marcella*	2♂ 6♀	20	0·171	0·096	0·53 ±0·047 (0·47–0·63)	3·1 ±0·30 (2·7–3·6)	2·7
7*b*	*Miathyria marcella*	4♂ 8♀	30	0·184	0·28	1·6 ±0·27 (1·0–1·9)	8·5 ±0·78 (7·3–9·4)	2·0
7*c*	*Miathyria marcella*	2♂ 6♀	40	0·172	0·52	2·9 ±0·53 (2·1–4·0)	17·2 ±3·0 (13·4–21·2)	
8*a*	*Pachydiplax longipennis*	8♂	15	0·200	0·048	0·27 ±0·84 (0·13–0·39)	1·3 ±0·36 (0·84–2·0)	3·4
8*b*	*Pachydiplax longipennis*	4♂ 4♀	20	0·186	0·079	0·44 ±0·11 (0·26–0·59)	2·4 ±0·51 (1·8–3·5)	2·5
8*c*	*Pachydiplax longipennis*	6♂ 2♀	25	0·200	0·14	0·77 ±0·29 (0·18–1·09)	3·8 ±0·84 (2·1–4·7)	1·9
8*d*	*Pachydiplax longipennis*	8♂ 8♀	30	0·190	0·18	1·0 ±0·21 (0·69–1·4)	4·7 ±0·45 (4·3–6·4)	2·8
8*e*	*Pachydiplax longipennis*	6♂ 2♀	35	0·187	0·27	1·5 ±0·42 (0·90–2·1)	8·1 ±2·1 (6·1–12·8)	2·2
8*f*	*Pachydiplax longipennis*	5♂ 3♀	40	0·192	0·43	2·4 ±0·75 (1·4–3·7)	12·1 ±2·3 (9·7–15·7)	
9	*Pantala flavescens*	2♂ 4♀	30	0·339	0·42	2·4 ±0·26 (2·2–2·9)	7·1 ±0·69 (6·4–8·4)	
10	*Perithemis tenera*	9♂	30	0·061	0·083	0·49 ±0·13 (2·2–3·2)	6·7 ±0·64 (5·8–7·9)	
11	*Tramea carolina*	1♂ 9♀	30	0·383	0·45	2·5 ±0·30 (2·2–3·2)	6·7 ±0·64 (5·8–7·9)	

* STPD.

altogether, and heated them to 37–40 °C in a closed container with moist paper towelling. One specimen had a thermocouple implanted, and its temperature was taken as the average temperature of the entire mass of dragonflies. After the temperature of the dragonflies and of the calorimeter stabilized (the latter within 0·01 °C), the implanted dragonfly was removed and the remainder quickly transferred to the calorimeter. The temperature change was noted to the nearest 0·01 °C at intervals for 30–50 min. The value of s was calculated according to Weber (1941).

RESULTS

Resting metabolism

Table 1 summarizes data on resting metabolism of dragonflies taken during June–August. The table emphasizes the effects of taxonomic differences, size and temperature. Two species of *Libellula* are treated as one taxon. They occur together and are similar in behaviour and thermoregulatory ability (May, 1976*a*), and mass-specific rates of metabolism do not differ significantly at 30 °C (Table 1).

Diel changes were not systematically investigated. All individuals were tested during their normal activity periods except four *Libellula*, four *Pantala* and two *Tramea* that were run after 1900 h. For each combination of species and temperature in which some species were tested relatively early and some relatively late in the day, data on mass-specific metabolism obtained before and after 1500 h were compared. Only in the case of *Miathryria marcella* at 40 °C was there a significant difference (14·7 ± 1·6 W.kg^{-1} before 1500 h, 19·2 ± 2·6 W.kg^{-1} after 1500 h, four individuals in each group). Thus all data are lumped without regard for the time of day.

Sex made a significant difference in only one case, *Pachydiplax longipennis* at 30 °C. Mass-specific metabolism of females was 5·8 ± 0·67 W.kg^{-1} (n = 8) and of males was 4·7 ± 0·45 W.kg^{-1} (n = 8). At 20, 35 and 40 °C also, female *Pacyhdiplax* had higher rates of metabolism than males, but the differences were not significant. Data are lumped without regard to sex except for intraspecific comparisons within *Pachydiplax*.

The effect of T_b on mass-specific resting metabolism of four taxa of Libellulidae appears in Table 1. Values of Q_{10} mostly vary from 2 to 3 in the range 20–40 °C. All species are similar in temperature sensitivity. Fig. 1 shows in more detail the variation with temperature in male *Pachydiplax*. Male *Pachydiplax* were also tested in April and these results likewise appear in Fig. 1. In all cases metabolic rates were higher in April than at the corresponding temperature in June–August, although the difference was significant only at 30 °C. On the other hand, seven male *Erythrodiplax connata* at 30 °C expended 6·1 ± 0·71 W.kg^{-1} in April, less than in June–August although not significantly so. In April at Gainesville, mean high temperature is 27·4 °C, mean low is 14·3 °C. In July the corresponding range is 32·5–21·7 °C (T. Walker, personal communication).

Fig. 2. shows the effect of body size on mean resting metabolic rate (M_r) at 30 °C. This temperature is near the low end of the normal range of daytime body temperature of many dragonflies in the field (May, 1976*a*). Least-squares linear regression of the log transformed variables yields $\log M_r = 0{\cdot}91 \log m + 0{\cdot}44$, $r = 0{\cdot}97$. Similar regressions at 20 °C and 40 °C give $\log M_r = 0{\cdot}92 \log m + 0{\cdot}079$ and $\log M_r = 0{\cdot}79$

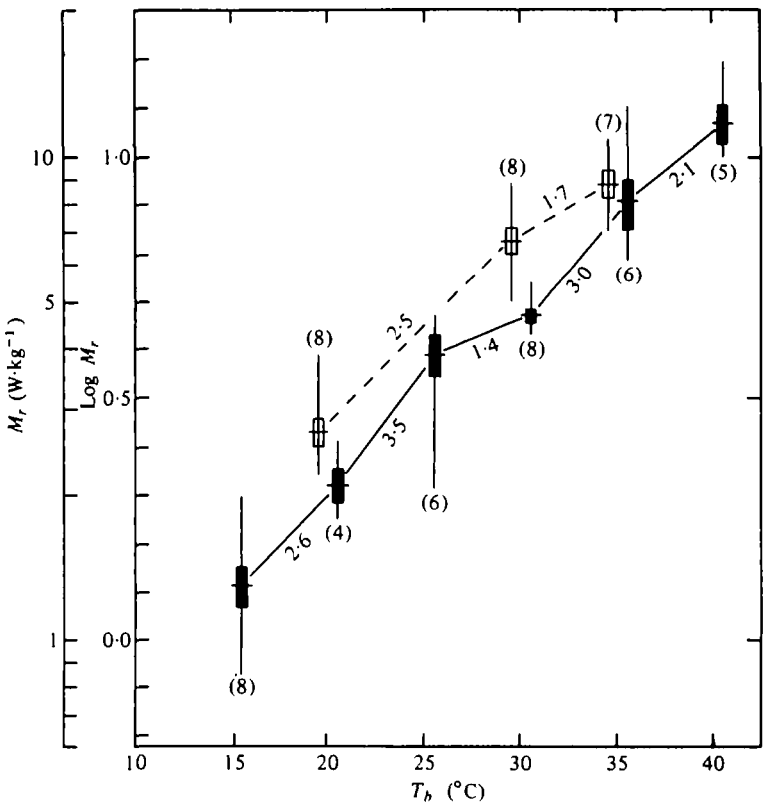

Fig. 1. Resting metabolism as a function of temperature in ♂ *Pachydiplax longipennis*. The horizontal line represents the mean, the vertical line the range, and the bars ± 1 S.E. The small numerals in parentheses are the number in each sample, the larger numerals indicate the Q_{10} over each temperature range. The upper set of data is from individuals collected in April, the lower set from individuals collected in June–August.

log m + 0·32 respectively, but these are based only on *Libellula* spp., *P. longipennis*, *M. marcella* and *E. connata*.

Corbet (1963) recognized two broad behavioural categories among dragonflies – perchers and fliers. Perchers spend much of their time on stationary perches and make sallies from time to time to feed, defend their territory, etc. Fliers remain almost continuously on the wing during periods of activity. Four of the species shown in Fig. 2 are fliers, the remainder perchers. If these groups are analysed separately the relations of metabolism to mass are: fliers – log M_r = 0·77 log m + 0·062, r = 0·99; perchers – log M_r = 0·81 log m + 0·025, r = 0·97. Analysis of covariance using a randomized groups design (Edwards, 1966) indicates that fliers have significantly higher resting metabolism at a given body mass than perchers (P < 0·005).

For four taxa in which oxygen consumption was measured in 12 or more individuals at 30 °C, the relation of individual metabolism to mass was: *E. connata* – log M_r = 0·99 log m + 0·77, r = 0·78, n = 14, 95% confidence limits of the slope = 0·60 – 1·39; *Libellula* – log M_r = 1·73 log m + 3·05, r = 0·92, n = 16, confidence limits = 1·51 – 1·95; *M. marcella* – log M_r = 1·60 log m + 3·17, r = 0·94, n = 12, confidence limits

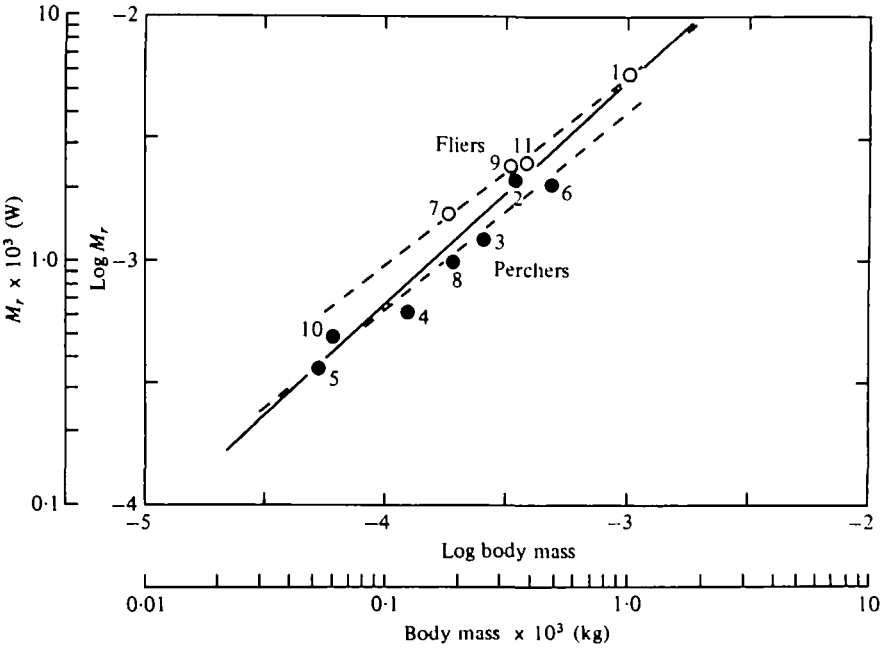

Fig. 2. Mean resting metabolism at 30 °C as a function of body size in dragonflies. The solid line is the least-squares regression for all points, the dashed lines are the regressions for fliers and perchers separately. The points represent mean values of M_r and m for each species. Numbers beside each point correspond to the species numbers in Table 1; sample sizes also appear in that table.

= 1·36 − 1·84; *P. longipennis* − log M_r = 1·02 log m + 0·80, r = 0·78, n = 16, confidence limits = 0·66–1·38.

Metabolism during warm-up

The relationship to mass of mean M_a calculated from equation 1 is shown for 15 species of dragonflies in Fig. 3. Data on cooling constants, warm-up rates, and maximum T_b in these species have been presented elsewhere (May, 1976*a*, *b*) except for *Tetragoneuria cynosura* collected in Illinois. In this species at T_a = 25 °C and T_b = 30 °C, mean warm-up rate of six individuals = 6·6 °C.min^{-1} (5·6–8·6 °C.min^{-1}). Mean T_b at takeoff was 35·3 °C (31·2–39·7 °C). In three individuals that warmed to very high T_b, warm-up rate decreased before takeoff so that mean warm-up rate at takeoff was only 5·7 °C.min^{-1}. Mean K = 0·47 min^{-1}, body mass = 0·191 g, and thoracic mass = 0·095 g.

Since warm-up rate was nearly constant except in *Tetragoneuria*, calculated M_a at takeoff approximates the maximum rate of heat production during warm-up. Its relation to mass (Fig. 3) is log M_a = 1·01 log m + 2·22, r = 0·91. Large species tend to initiate flight at higher T_b than small species, so Fig. 3 also includes values of M_a calculated at T_b = 29–30 °C. Then log M_a = 0·90 log m + 1·87, r = 0·94. *Miathyria marcella* took off at an average T_b of 27·3 °C and so is excluded from the latter regression.

Most workers have assumed that the specific heat of insect tissue is about 3·3 × 10 J(kg.°C)$^{-1}$ as stated by Krogh & Zeuthen (1941), although these authors did not actually measure it. Three replicate determinations of specific heat of whole dragon-

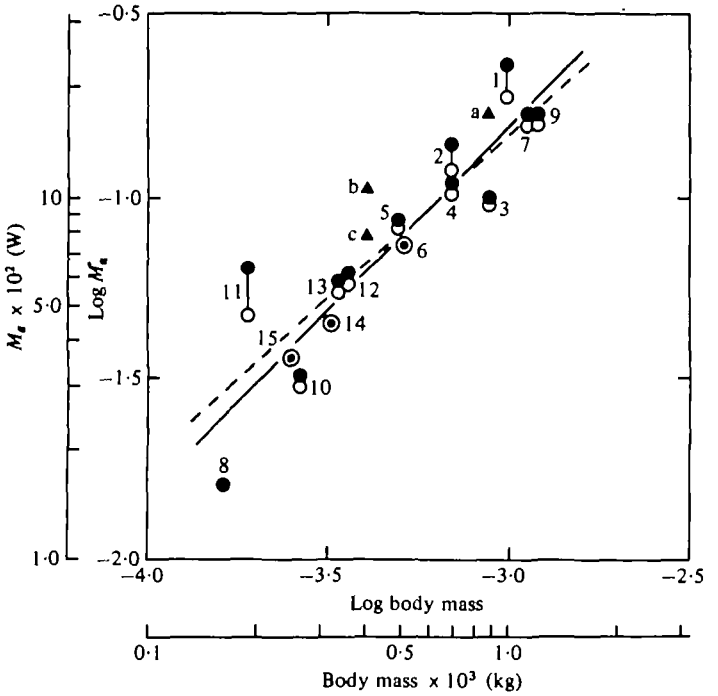

Fig. 3. Metabolism during warm-up at T_a = 25 °C as a function of body size in dragonflies. The solid and open circles represent mean M_a for each species as calculated by equation (1), at takeoff and T_b = 29–30 °C respectively. Vertical lines connect the two means for each species. Circled dots indicate species that took off at T_b between 29 and 39 °C; the value of M_a at takeoff was used in both regressions. The solid line is the least-squares regression of M_a at takeoff on m, the dashed line is the regression of M_a at 30 °C on m. Species are as follows: 1, *Anax junius* (n = 10); 2, *Coryphaeschna perrensi* (n = 11); 3, *Gynacantha gracilis* (n = 5); 4, *G. membranalis* (n = 3); 5, *G. nervosa* (n = 8); 6, *G. tibiata* (n = 7); 7, *Macromia taeniolata* (n = 5); 8, *Miathyria marcella* (n = 12); 9, *Staurophlebia reticulata* (n = 6); 10, *Tauriphila argo* (n = 7); 11, *Tetragoneuria cynosura* (n = 6); 12, *Tramea carolina* (n = 6); 13, *T. cophysa* (n = 5); 14, *T. walkeri* (n = 5); 15, *Triacanthagyna septima* (n = 6). Triangles represent maximum M_a for the following species: a, *Anax junius* (n = 5); b, *Boyeria vinosa* (n = 9); c, *Tramea lacerata* (n = 5).

flies gave values of 3·47, 3·37 and 3·26 × 10^3 J.kg^{-1}.°C^{-1}, in excellent agreement with the accepted value, which was therefore used in calculating M_a above. Shinozaki (1957) determined values ranging from 2·8 to 3·5 J.kg^{-1}.°C^{-1} for four insect species.

Maximal heat production (M_o) and cumulative energy expenditure (E_o) during warm-up were also estimated independently from O_2 consumption. In these experiments, only animals that warmed uninterruptedly, or at most with one or two brief pauses, were used.

Most dragonflies warming in the chamber wing-whirred continuously for a period of several minutes, then apparently tried to fly. Thereafter they usually struggled violently or alternately struggled, wing-whirred and cooled at brief intervals. During these periods $\dot{V}_{O_2}$ might decrease or remain approximately constant. Body temperature rose slowly or fluctuated about a nearly constant level. When struggling ceased, calculated $\dot{V}_{O_2}$ usually dropped to resting levels within 60 s, although in some cases it remained elevated for several minutes. Table 2 summarizes data on M_o, M_a, E_o and E from these experiments.

Table 2. *Maximum rate of metabolism and total energy utilization of dragonflies during warm-up*

(M_a, M_o, E_a and E_o are expressed as mean ± S.D.)

Species	N	T_a (°C)	m (g)	m_t (g)	T_b at takeoff* (°C)	R (°C.min^{-1})	K (min^{-1})	M_a (W)	M_o (W)	% diff.	E_a (J)	E_o (J)	% diff.
Anax junius	5	21·5	0·826	0·399	33·1	4·4	0·21†	0·150 ± 0·016	0·167 ± 0·016	12	23·3 ± 5·02	25·8 ± 4·89	11
Anax junius	6	25	0·783	0·385	32·5	3·9	0·22†	0·119 ± 0·016	0·133 ± 0·025	11	17·2 ± 1·51	19·3 ± 3·73	12
Boyeria vinosa	3	20	0·383	0·180	31·5	4·2	0·30	0·075 ± 0·0049	0·086 ± 0·0038	15	12·8 ± 2·59	14·7 ± 0·84	17
Boyeria vinosa	9	25	0·398	0·172	33·0	5·4	0·30	0·075 ± 0·016	0·107 ± 0·024	42	6·77 ± 2·84	8·65 ± 3·47	28
Tramea lacerata	5	25	0·399	0·215	31·9	3·8	0·29	0·070 ± 0·012	0·078 ± 0·015	10	10·2 ± 2·88	11·7 ± 3·39	15

* T_b at which the dragonfly switched from warm-up to struggling or attempts to fly.

† Corrected to account for augmented heat loss during cooling (May, 1976*a*); in the other species K was not measurably elevated at these levels of T_a.

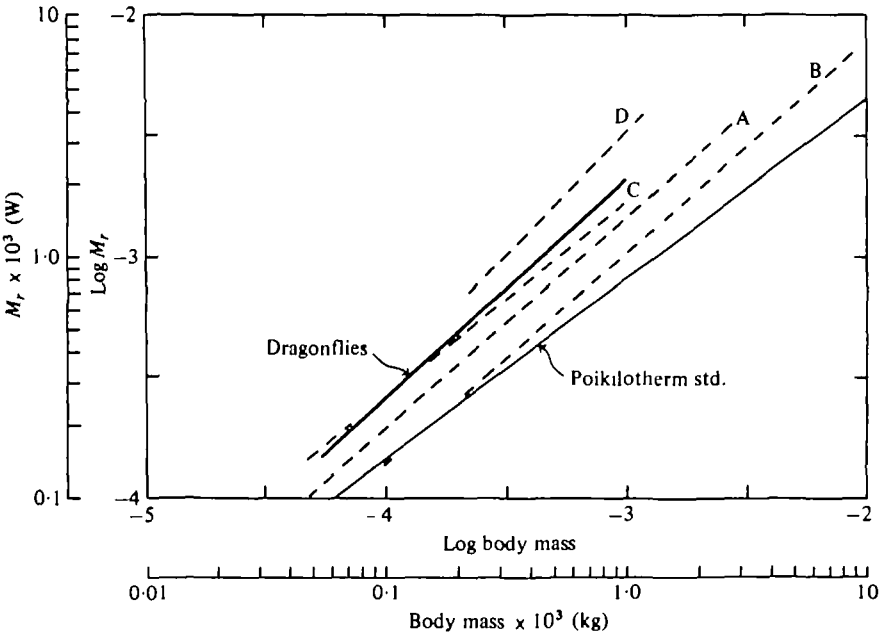

Fig. 4. Comparison of the relation of resting metabolism to mass in various groups of insects and in poikilotherms generally; all corrected to T_b = 20 °C. The heavy solid line is the regression of log M_r on log m for dragonflies, from this study. The thin solid line is Hemmingsen's (1960) standard curve for poikilotherms. The dashed lines are regressions calculated by me from data on other insects: (A) beetles (Kittel, 1941), (B) beetles (Bartholomew & Casey, 1977), (C) cockroaches (Gunn, 1935), (D) moths (Zebe, 1954).

DISCUSSION

Resting metabolism

Resting metabolism of dragonflies is unremarkable in either its magnitude or its relation to size. My results for adult *A. junius* at 30 °C agree closely with those of Petitpren & Knight (1970). They found a heat production of $6{\cdot}3 \times 10^{-3}$ W in this species. Fig. 4 compares heat production at rest in Odonata with Hemmingsen's (1960) equation for poikilotherms in general as well as that of other adult insects of comparable size. All the data were adjusted to a temperature of 20 °C by assuming a Q_{10} of 2·5, the average for dragonflies from Table 1. The results for insects are mostly above the 'standard' line probably in part because the insects were not starved nor was the possibility of low levels of activity eliminated. The slope of the regression for each of the insect groups is higher than the standard slope of 0·75, although the difference is statistically significant only for Kittel's data. Nevertheless, the consistency of the differences in slopes suggests that within many insect orders resting metabolism may increase more rapidly with mass than is the case in animals generally.

Fliers have slightly but uniformly higher M_r than perchers of the same size. The fliers represented in Fig. 2 also tend to have smaller thoraxes than the perchers, so the difference in M_r is not due to greater mass of flight muscle in fliers. It is possible, however, that fliers were more active during experiments than were perchers. When fliers and perchers are considered separately the slopes of log M_r vs. log m are lower

than that of all species taken as a whole, and nearer 0·75. Nevertheless, if individual species are examined (1 flier, 3 perchers), these slopes are higher than the slope based on the means of all species. The difference is highly significant in the cases of *Libellula* and *Miathyria*. The small intraspecific size range greatly increases the possibility for error in the latter cases and makes it unwise to attach much weight to individual slopes. Nonetheless, the occurrence of relatively high slopes in all four species strengthens the suggestion that the relation of metabolism to mass varies between different subgroups within the Odonata.

The response of M_r to temperature also is well within the range of variation shown by other insects (Keister & Buck, 1974). All species show a slight tendency towards lower temperature sensitivity as T_b increases. This may result in some energy saving, since daytime body temperatures in the field are relatively high (May, 1976*a*), although in summer males of *P. longipennis* the region of lowest sensitivity corresponds to a temperature range just below that maintained most often in the field.

Fig. 1 suggests seasonal compensation of M_r in male *Pachydiplax*, although the difference is significant only at 30 °C. A similar compensatory change occurs in the upper limits of temperature tolerance in this species (May, 1976*a*). Results from *E. connata* show, however, that if seasonal adjustments occur they are not uniform throughout the order.

Metabolism during warm-up, and metabolic scope

Inaccuracies exist in determining true rates of heat production from either M_o or M_a. The principal of these in the former case results from the lag in the response of the apparatus to changes in O_2 uptake. The method of Bartholomew *et al.* (1979) should largely correct for such errors. Nevertheless, $\dot{V}_{O_2}$ still may be underestimated slightly in most cases, since this parameter changes continuously rather than in a series of steps.

The data on total O_2 consumption provide an independent estimate of the error of maximum $\dot{V}_{O_2}$ measurement since total O_2 is not subject to underestimation due to system lags. Total heat production as calculated from total O_2 consumption should exceed total heat production calculated from T_b by approximately the same amount that true M_o exceeds M_a (see below), provided that true $\dot{V}_{O_2}$ and total O_2 consumption are well correlated. A close linear correlation exists between apparent $\dot{V}_{O_2}$ and total O_2 consumption ($r = 0{\cdot}84$), suggesting that the latter condition is met. Since E_o consistently exceeded E_a by about the same percentage that M_o exceeded M_a (Table 2), M_o is probably a good estimate of true heat production.

Both E_o and M_o exceed E_a and M_a, respectively, by 10–40% (Table 2). The differences apparently result from the fact that equation 1 does not account for evaporative heat loss, heat loss consequent to increased convection during wing movements, or variation in heat loss due to variable circulation from thorax to abdomen during warm-up.

The latter was not monitored during oxygen consumption measurements, but in separate experiments concurrent measurements during warm-up of thoracic temperature and the temperature of the basal abdominal segments indicated very little heat loss via circulation. At takeoff, the average change in thoracic temperature/change in abdominal temperature was: *A. junius* – 13·6 °C/0·57 °C ($N = 17$, $T_a = 15$–30 °C);

Table 3. *Calculated evaporative heat loss of dragonflies during warm-up*

(% refers to the percentage of the difference between M_a and M_o or between E_a and E_o that can be accounted for by evaporative cooling; heat loss is expressed as mean ± S.D., range in parentheses.)

Species	T_a (°C)	Max. evaporative heat loss × 10^3 (W)	%	Total evaporative heat loss (J)	%
Anax junius	21·5	1·26 ± 0·17 (1·08–1·45)	83	1·66 ± 0·46 (1·12–2·15)	66
Anax junius	25	0·95 ± 0·17 (0·67–1·15)	80	1·40 ± 0·36 (0·98–1·77)	58
Boyeria vinosa	20	0·61 ± 0·039 (0·57–0·65)	58	0·87 ± 0·096 (0·80–0·98)	46
Boyeria vinosa	25	0·76 ± 0·22 (0·39–1·02)	29	0·65 ± 0·30 (0·25–1·20)	35
Tramea lacerata	25	0·56 ± 0·13 (0·40–0·72)	80	0·84 ± 0·31 (0·59–1·27)	56

B. vinosa – 7·1 °C/0·03 °C ($N = 6$, $T_a = 25$ °C). Also, in several other insects (Heinrich & Bartholomew, 1971; Heinrich, 1976), as well as dragonflies (Heinrich & Casey, 1978), heat loss through this channel has proved to be negligible during warm-up.

Wind velocity in the vicinity of the thorax of intact *A. junius* during wing-whirring was assessed with a hot-bead anemometer (Vogel, 1969). Velocity was less than 0·1 $m.s^{-1}$ at all points, corresponding to an increase in heat loss of less than 10–12%. Also, warm-up rates of eight *A. junius* with the wings excised near the base averaged 5·02 ± 0·80 °C.min^{-1} vs. 4·77 ± 0·96 °C.min^{-1} for the same specimens with intact wings. It is not known whether wing removal affects parameters other than convective cooling, however. I estimated evaporative heat loss (H_e) by assuming that the ventilation rate was 1200 l $(kg.h)^{-1}$ (Weis-Fogh, 1967), and that dry air entering the tracheae at T_a was saturated at T_b and expired without cooling. Body temperature was taken to be the average T_b during warm-up and struggling. The results appear in Table 3. Estimates of convective and evaporative losses depend on assumptions, noted above, that undoubtedly introduce errors into the calculations. To the extent that they are reliable, however, such estimates suggest that the sum of these two avenues of heat loss is very close to the observed differences between M_a and M_o and between E_a and E_o.

On the whole, therefore, data on oxygen consumption are consistent with calculated values of M_a and E_a. The small differences between M_o and M_a are readily explained in four out of five cases on the basis of evaporative cooling and a small increase in convective heat loss due to the vibrating wing stumps. Experiments with *B. vinosa* at $T_a = 25$ °C showed greater than usual discrepancies between the two methods of calculating metabolic rate. The reason is not clear, as the difference apparently cannot be attributed to greater rates of evaporation or circulation by *B. vinosa*. The fact that in this case M_o exceeded M_a by considerably more than E_o exceeded E_a suggests that M_o actually might have been overestimated, since for other species and conditions the respective differences were about the same. Such discrepancies necessitate some caution in accepting heat production values determined by either method, but the

overall agreement of the techniques supports their reliability and that of the data in Fig. 3.

Based on the data of Table 2, the regression shown in Fig. 3 probably underestimates actual metabolism by roughly 15% irrespective of m. At $T_b = 30$ °C and $M = 10^{-3}$ kg, expected $M_a + 15\%$ is about 32·5 times expected M_r, while at $m = 10^{-4}$ kg, $M_a + 15\%$ is 29·5 times M_r. All the species used in determining M_a were fliers, however, and when M_a is compared to M_r for fliers only, the relative values of $M_a + 15\%$ are 29·5 M_r at 10^{-3} kg and 19·5 M_r at 10^{-4} kg, suggesting that metabolic scope may decrease with decreasing mass. Bartholomew & Casey (1977) found a similar relationship of metabolic scope to mass in beetles during maximal terrestrial activity.

The relation of M_a to m is also dependent on T_b. In large species with relatively low cooling constants, the contribution to M_a of the $K(T_b - T_a)$ term (equation 1) is small relative to the contribution due to warming rate (R). In small species, however, $K(T_b - T_a)$ may greatly exceed R at high $T_b - T_a$. In other words, in the latter case the cost of overcoming heat loss is greater than that required for heat storage. Thus, in order to maintain constant R, small species must increase M_a more rapidly with T_b. For example, at the very beginning of warm-up at $T_b = T_a = 25$ °C, $M_a = \mathrm{R}s(m/60)$ and the regression of M_a on m is $\log M_a = 1{\cdot}07 \log m + 2{\cdot}26$. This implies that metabolic scope and the absolute level of M_a are more temperature sensitive in small than in large species. If the same is true of flight metabolism the consequences for small dragonflies in flight may be profound, since in the field T_b is generally more variable in small than in large species. Heat production probably depends strongly on the rate of muscle firing, however (Heinrich & Bartholomew, 1971; Kammer & Heinrich, 1974) and there is evidence to suggest that in moths wingbeat frequency is less dependent on temperature in flight than during warm-up (Heinrich & Bartholomew, 1971; unpublished observations). Wingbeat frequency has not been examined as a function of T_b in dragonflies.

Data on *A. junius* (Table 2) imply that T_a may influence M_a independently of T_b, since maximum M_a is higher at $T_a = 21$ °C than at $T_a = 25$ °C, although T_b at takeoff is not significantly different. This result is surprising in view of contrary data for moths (e.g. Heinrich & Casey, 1973) and of *a priori* arguments that warm-up should proceed at the maximum possible rate. Blest (1957) showed that wing-whirring in moths can induce bird attacks, so any decrease in R may increase the risk of predation. Also, total energy expenditure during warm-up is minimal when R is greatest. A preliminary model for total energy expenditure can be derived from equation 1. Total energy expenditure should be equal to the average value of M_a during warm-up multiplied by the duration of warm-up. If R is constant from $T_b = T_a$ until takeoff ($T_b = T_{to}$), then the duration of warm-up $= (T_{to} - T_a)/R$ and the average value of $(T_b - T_a) = \frac{1}{2}(T_{to} - T_a)$. Then, substituting $\frac{1}{2}(T_b - T_{to})$ for $(T_b - T_a)$ and multiplying equation 1 by duration,

$$\begin{aligned} E &= [R(T_{to} - T_a)/R + K\tfrac{1}{2}(T_{to} - T_a)(T_{to} - T_a)/R]sm_t \\ &= [(T_{to} - T_a) + (K/2R)(T_{to} - T_a)^2]sm_t. \end{aligned} \tag{4}$$

I emphasize that equation 4 needs additional experimental verification. The relationships of E to R, K, T_{to} and m_t are probably qualitatively about as indicated but may

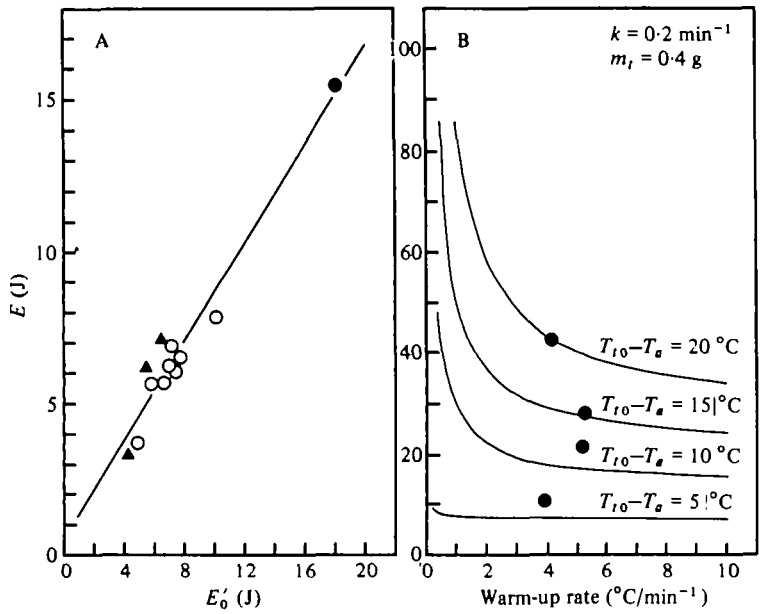

Fig. 5. (A) The relationship of E (calculated from equation 4) to E_0', the total energy consumed during warm-up, excluding that consumed during subsequent struggling. E_0' was calculated by graphically integrating O_{2t} (equation 3) from the beginning of warm-up to attempted takeoff. The solid circle indicates *A. junius*, open circles *B. vinosa*, and triangles *T. lacerata*; criteria for selecting data to be included are discussed in the text. The regression equation is $E = 0{\cdot}81\ E_0' + 0{\cdot}51$, $r = 0{\cdot}97$. (B) The predicted relation of E to R and $T_b - T_a$ at values of K and m_t near those of *A. junius*. The solid circles are predicted values of E for *A. junius* warming at different levels of T_a; data from May (1976*a*).

differ in detail if, for example, R is not constant throughout warm-up. Nevertheless, the model has predictive value in cases where warm-up begins with $T_b - T_a < 1$ °C and is continuous, and where subsequent struggling does not obscure the peak of O_2 consumption at takeoff. Fig. 5(A) shows that when such conditions occur E_0 is very closely correlated with E calculated by equation 4. Fig. 5(B) suggests that in *A. junius*, when R is sufficiently high E is comparatively insensitive to R.

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REFERENCES

BARTHOLOMEW, G. A. (1968). Energy metabolism. In *Animal Function: Principles and Adaptations* (ed. M. S. Gordon), pp. 48–65. London: Macmillan.

BARTHOLOMEW, G. A. & CASEY, T. M. (1977). Body temperature and oxygen consumption during rest and activity in relation to body size in some tropical beetles. *J. thermal Biol.* **2**, 173–176.

BARTHOLOMEW, G. A., VLECK, D. & VLECK, C. M. (1979). Instantaneous rates of oxygen consumption and temperature control in heterothermic moths. *J. exp. Biol.* (In the Press.)

BLEST, A. D. (1957). The function of eyespot patterns in the Lepidoptera. *Behaviour* **11**, 209–255.

CHRISTENSEN, B. G. (1947). A simple apparatus for simultaneous measurement of the standard metabolism and respiratory quotient in small laboratory animals, supplemented with investigations on normal and hypophysectomized rats. *Acta physiol. Scand.* **12**, 11–26.

CORBET, P. S. (1963). *A Biology of Dragonflies*. Chicago: Quadrangle Books.

DEPOCAS, F. & HART, J. S. (1957). Use of the Pauling oxygen analyzer for measurement of oxygen consumption of animals in open circuit and short-lag closed circuit apparatus. *J. appl. Physiol.* **10**, 388–392.

DORSETT, D. A. (1962). Preparation for flight by hawk-moths. *J. exp. Biol.* **39**, 579–588.

EDWARDS, A. L. (1966). *Experimental Design in Psychological Research*. New York: Holt, Rinehart and Winston.

GUNN, D. L. (1935). The temperature and humidity relations of the cockroach. III. A comparison of temperature preference, and rates of desiccation and respiration of *Periplaneta americana*, *Blatta orientalis*, and *Blatella germanica*. *J. exp. Biol.* **12**, 185–190.

HART, J. S. (1951). Calorimeter determination of average body temperature of small mammals and its variation with environmental conditions. *Canad. J. Zool.* **29**, 224–233.

HEATH, J. E. & ADAMS, P. A. (1969). Temperature regulation and heat production in insects. In *Experiments in Physiology and Biochemistry*, vol. 2 (ed. G. A. Kerkut), pp. 275–293. New York: Academic Press.

HEINRICH, B. (1976). Heat exchange in relation to blood flow between thorax and abdomen in bumblebees. *J. exp. Biol.* **64**, 561–585.

HEINRICH, B. & BARTHOLOMEW, G. A. (1971). An analysis of pre-flight warm-up in the sphinx moth *Manduca sexta*. *J. exp. Biol.* **55**, 223–239.

HEINRICH, B. & CASEY, T. M. (1973). Metabolic rate and endothermy in sphinx moths. *J. comp. Physiol.* **82**, 195–206.

HEINRICH, B. & CASEY, T. M. (1978). Heat transfer in dragonflies: 'fliers' and 'perchers'. *J. exp. Biol.* **74**, 17–36.

HEMMINGSEN, A. M. (1960). Energy metabolism as related to body size and respiratory surfaces, and its evolution. *Rep. Steno. Mem. Hosp.* **9**, 1–100.

KALLAPUR, V. L. & GEORGE, C. J. (1973). Fatty acid oxidation by the flight muscles of the dragonfly, *Pantala flavescens*. *J. Ins. Physiol.* **19**, 1035–1040.

KAMMER, A. E. & HEINRICH, B. (1974). Metabolic rates related to muscle activity in bumblebees. *J. exp. Biol.* **61**, 219–227.

KEISTER, M. & BUCK, J. (1974). Respiration: some exogenous and endogenous effects on rate of respiration. In *The Physiology of Insecta* (ed. M. Rockstein), pp. 469–509. New York: Academic Press.

KITTEL, A. (1941). Körpergrösse, Körperzeiten und Energiebilanz. II. Der Sauerstoffverbrauch der Insekten in Abhängigkeit von Körpergrösse. *Z. vergl. Physiol.* **28**, 533–562.

KROGH, A. & ZEUTHEN, E. (1941). The mechanism of flight preparation in some insects. *J. exp. Biol.* **18**, 1–10.

LASIEWSKI, R. C., ACOSTA, A. L. & BERNSTEIN, M. H. (1966). Evaporative water loss in birds. I. Characteristics of the open flow method of determination, and their relation to estimates of thermoregulatory ability. *Comp. Biochem. Physiol.* **19**, 445–457.

MAY, M. L. (1976*a*). Thermoregulation and adaptation to temperature in dragonflies (Odonata: Anisoptera). *Ecol. Monogr.* **46**, 1–32.

MAY, M. L. (1976*b*). Warming rates as a function of body size in periodic endotherms. *J. comp. Physiol.* **111**, 55–70.

PETITPREN, M. F. & KNIGHT, A. W. (1970). Oxygen consumption in the dragonfly *Anax junius*. *J. Ins. Physiol.* **16**, 449–459.

SAYLE, M. H. (1928). Factors influencing the rate of metabolism of *Aeschna umbrosa* nymphs. *Biol. Bull.* **54**, 212–230.

SHINOZAKI, J. (1957). The specific heat of insects. *J. Fac. Sci. Hokkaido Univ. Ser. VI Zool.* **13**, 470–474.

TYNER, M. & MAY, F. P. (1968). *Process Engineering Control*. New York: Ronald Press.

VOGEL, S. (1969). Low speed wind tunnels for biological investigations. In *Experiments in Physiology and Biochemistry*, vol. 2 (ed. G. A. Kerkut), pp. 295–325. New York: Academic Press.

WEBER R. L. (1941). *Temperature Measurement and Control*. Philadelphia: Blakiston.

WEIS-FOGH, T. (1967). Respiration and tracheal ventilation in locusts and other flying insects. *J. exp. Biol.* **47**, 561–587.

ZEBE E. (1954). Über den Stoffwechsel der Lepidopteran. *Z. vergl. Physiol.* **36**, 290–317.