

ALLOMETRIC ANALYSIS OF BODY AND WING DIMENSIONS OF MALE ANISOPTERA

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Several body dimensions were measured in 29 spp. The relationship between pairs of dimensions was determined by allometric analysis. In general, the wings of dragonflies become relatively longer and narrower as body mass increases; fliers have longer but thinner wings than perchers of comparable size. These trends are probably the result of differences in energetic and structural requirements in flight. Thoracic diameter and volume increase more rapidly than expected as thoracic mass increases and are relatively greater in fliers than in perchers. Thoracic dimensions are partly determined by increased selection for insulating, sub-cuticular air sacs in large fliers.

INTRODUCTION

Since its introduction by HUXLEY (1932), allometric analysis has been used widely in studies of the dimensional relationships of animals (GOULD, 1966). Among other uses, this approach may allow prediction of quantities that are comparatively difficult to measure, e.g. area of an irregular surface, from others that are quite easy, like body mass or a convenient linear dimension. Additionally, departures from geometric similarity with changing size became readily apparent and quantifiable; such information can in turn suggest functional reasons for or consequences of trends in body shape (e.g. GREENEWALT, 1960, 1962, 1975).

This paper presents dimensional data for males of 29 species of Anisoptera from the eastern United States. These are believed to be representative of Nearctic dragonflies and probably of male Anisoptera generally, inas-

much as all families are represented. The dimensions selected for comparison reflect my interests in heat exchange and flight energetics, but include those I considered most generally useful in describing dragonfly size and shape.

MATERIAL AND METHODS

All specimens were collected as adults and measured within one day of capture except for *Tachopteryx thoreyi* and *Cordulegaster sayi*, which were mailed alive from the site of capture and measured about three days after collection. All individuals were obtained at sites in central or southern New Jersey, USA, except the following: *T. thoreyi*, *C. sayi*, *Macromia georgina*, 4 of 5 *M. taeniolata*, *Nasiaeschna pentacantha*, and 2 of 4 *Tramea carolina*, all from Alachua Co., FL; 1 of 5 *M. taeniolata* and 1 of 3 *Epicordulia princeps*, Roane Co., TN. I made no attempt to analyze geographic variation.

Mass (M), thoracic mass (M_t) and wing mass (M_w) were measured with an Ainsworth 24N analytical balance (max. sensitivity 0.01 mg), thoracic diameter in the frontal plane (D_t) to the nearest 0.01 cm with a vernier caliper, and wing length (L_w) to the nearest 0.05 cm with a millimeter ruler. I painted excised wings with opaque paint and measured their area (A_w) to 0.1 cm² with a LiCor Area Meter (mean of three readings). Wing loading (WL) was calculated as $M \div A_w$, disc loading (DL) was calculated as $M \div \pi r^2$, where r = the mean of forewing (L_{fw}) and hind wing (L_{hw}) lengths. Moment of inertia of the wings (I_w) was determined for selected specimens by strip analysis (NORBERG, 1972), using five strips of approximately equal width for each wing.

Data on aspect ratio ($L_w^2 \div A_w$) of individual wings and on approximate area, length and chord (measured at the nodus) of most North American genera were obtained by photocopying wing photographs from NEEDHAM & WESTFALL (1955), measuring length, chord and area with ruler and LiCor Area Meter, respectively, then reducing to approximate true dimensions by assuming that the actual hind wing length was equal to the mid-point of the range given by Needham & Westfall.

Finally, surface area (A_t), total volume (V_t) and muscle volume (V_m) were determined for isolated thoraxes of single individuals of four species. Thoraxes were dissected from live specimens and fixed for one week in Kahle's solution (50 parts 95% ETOH: 10 formalin: 5 acetic acid: 35 distilled water). Preliminary tests revealed no perceptible shrinkage or swelling of muscle tissue in this fixative. The thoraxes were stored in 70% ETOH for up to four months, then dehydrated and embedded in cellogen. Thick sections (0.25 - 0.5 mm) were cut, then photographed or drawn using a camera lucida. The perimeter of each slice was measured with a cartographers wheel and the total area and area occupied by muscle with a planimeter; dimensions were reduced by an appropriate magnification factor determined with a stage micrometer. The corresponding surface areas and volumes of each section

or muscle within a section were calculated by assuming that each was a frustum of a cone with the measured anterior and posterior perimeters and end areas and height equal to section thickness. The anterior end section, however, was treated as a segment of a sphere. Areas and volumes for each section were summed to give total areas and volumes for the whole thorax.

Regression analyses used an SAS General Linear Models Procedure. Statistical differences are considered significant at the $p = 0.05$ level unless otherwise stated.

RESULTS

The main results are summarized in Tables I-III. These give regression statistics for several body and wing dimensions as a function of M and Lhw ($Lfw = Lhw + 3-5\%$ for all dragonflies, $r^2 = 0.998$). The independent variables were chosen because they are measured easily and unambiguously and in most cases they were the best predictors of other variables (M_t and D_t were also tried as independent variables). In addition, the full data for selected regressions are shown in Figures 1-4.

In Table I the regression coefficients are compared to those expected in geometrically similar organisms. Several significant departures from predicted values occur. The relationships of D_t to M and M_t to D_t both suggest

Table I
Coefficients of the allometric equations showing the relationships among various dimensions of dragonflies

Independent variable	Dependent variable	Slope	Intercept	r^2	N	Expected slope
M	M_t	1.015	-0.278	0.987	107	1.000
	D_t	0.405*	-0.020	0.973	109	0.333
	Lhw	0.355	0.719	0.918	111	0.333
	Aw	0.615	1.357	0.882	107	0.667
	Mw	1.026	1.661	0.972	107	1.000
	WL	0.384	-1.358	0.747	107	0.333
	DL	0.296	-1.944	0.664	105	0.333
Lhw	M	2.586*	-1.904	0.918	111	3.000
	M_t	2.614*	-2.208	0.904	107	3.000
	D_t	1.063	-0.799	0.917	109	1.000
	Aw	1.749*	0.104	0.980	107	2.000
	Mw	2.755*	-0.345	0.962	107	3.000
	WL	0.833	-2.006	0.483	107	1.000
	DL	0.605	-2.424	0.380	105	1.000
D_t	M_t	2.442*	-0.245	0.967	105	3.000

* Slopes differ significantly from expected values.

Table II
Coefficients of allometric equations showing relationships among dimensions of dragonflies,
by family

Independent variable	Dependent variable	Family*	Slope	Intercept	r ²	N
M	Mt	Aeshnidae ^a	1.010	-0.325	0.983	20
		Corduliidae ^b	1.034	-0.282	0.999	14
		Gomphidae ^b	1.048	-0.258	0.981	12
		Libellulidae ^c	1.076	-0.199	0.993	45
	Dt**	Aeshnidae ^a	0.333	-0.0246	0.982	20
		Corduliidae ^{ab}	0.246	-0.120	0.934	15
		Gomphidae ^c	0.327	-0.0893	0.879	13
		Libellulidae ^{bc}	0.424	-0.0062	0.982	44
	Lhw	Aeshnidae ^a	0.302	0.715	0.830	21
		Corduliidae ^a	0.387	0.749	0.972	15
		Gomphidae ^b	0.320	0.638	0.755	13
		Libellulidae ^a	0.351	0.724	0.917	45
	Aw	Aeshnidae ^a	0.623	1.381	0.777	20
		Corduliidae ^a	0.671	1.416	0.951	14
		Gomphidae ^b	0.684	1.282	0.759	13
		Libellulidae ^a	0.626	1.396	0.919	44
	Mw	Aeshnidae ^a	1.022	1.672	0.968	20
		Corduliidae ^b	1.159	1.719	0.970	14
		Gomphidae ^b	0.886	1.496	0.869	13
		Libellulidae ^a	1.024	1.687	0.982	44
	WL	Aeshnidae ^a	0.369	-1.386	0.551	20
		Corduliidae ^a	0.325	-1.418	0.814	14
		Gomphidae ^b	0.320	-1.280	0.406	13
		Libellulidae ^a	0.374	-1.396	0.808	44
	DL	Aeshnidae ^a	0.394	-1.937	0.695	20
		Corduliidae ^a	0.221	-2.013	0.764	13
		Gomphidae ^b	0.351	-1.801	0.460	13
		Libellulidae ^a	0.309	-1.949	0.676	43
Lhw	M	Aeshnidae ^a	2.750	-2.015	0.830	21
		Corduliidae ^a	2.511	-1.900	0.972	15
		Gomphidae ^b	2.358	-1.672	0.755	13
		Libellulidae ^a	2.614	-1.954	0.917	45
	Mt	Aeshnidae ^a	2.728	-2.332	0.803	20
		Corduliidae ^a	2.555	-2.228	0.968	14
		Gomphidae ^b	2.243	-1.928	0.785	12
		Libellulidae ^a	2.797	-2.295	0.901	45

Table II (continued)

Dt**	Aeshnidae ^{ab}	0.916	-0.696	0.821	20
	Corduliidae ^{ac}	0.616	-0.587	0.907	15
	Gomphidae ^b	0.806	-0.651	0.725	13
	Libellulidae ^c	1.128	-0.844	0.926	44
Aw**	Aeshnidae ^{ab}	2.076	-0.102	0.951	20
	Corduliidae ^{bc}	1.697	0.134	0.967	14
	Gomphidae ^a	2.105	-0.067	0.976	13
	Libellulidae ^c	1.781	0.107	0.993	44
Mw	Aeshnidae ^a	2.984	-0.497	0.910	20
	Corduliidae ^b	2.903	-0.482	0.967	14
	Gomphidae ^c	2.489	-0.152	0.932	13
	Libellulidae ^a	2.774	-0.357	0.962	44
WL	Aeshnidae ^a	0.636	-1.892	0.180	20
	Corduliidae ^a	0.760	-2.009	0.708	14
	Gomphidae ^b	0.259	-1.607	0.036	13
	Libellulidae ^a	0.841	-2.064	0.546	44
DL	Aeshnidae ^a	0.745	-2.519	0.274	20
	Corduliidae ^a	0.489	-2.400	0.624	13
	Gomphidae ^b	0.317	-2.175	0.051	13
	Libellulidae ^a	0.648	-2.479	0.391	43

* For each dependent variable, categories sharing the same superscript do not differ significantly in adjusted mean square of the dependent variable.

** Slopes differ significantly among families.

that thoracic diameter (and presumably thoracic volume) increases more rapidly than expected with mass. Also, M, M_t, Aw and Mw all increase less rapidly than L_{hw}, i.e. larger dragonflies have relatively longer, narrower wings.

Table II indicates dimensional differences among the major families investigated. Data for Cordulegastridae, Macromiidae, and Petaluridae are not included in this table because insufficient material was available for statistical analysis. However, some data on these families appear in Figures 1-4. The most consistent interfamilial difference is that Gomphidae tend to have small L_{hw} and Aw for a given M, thus high WL and DL. The sample of gomphids was small and did not cover the full range of size of the family, however, and included mainly *Gomphus*. Generalizations about the family therefore must remain tentative. Wing mass is small in relation to total mass in Gomphidae and Corduliidae, but for different reasons; corduliids have wings of normal size but low Mw for their length, while gomphids have short wings that are rather massive for their length. M_t makes up a varying

fraction of M in different families, with aeshnids having a relatively low M_t , corduliids and gomphids somewhat larger M_t , and libellulids relatively the largest. The variation with size (slope) of the various dimensions is mostly similar from family to family (except for D_t) and also similar to variation within the suborder as a whole (Tab. I).

Several species or species groups are noteworthy. The libellulid, *Plathemis lydia*, resembles gomphids in that it has small wings for its mass ($A_w = 77\%$ of expected value from Tab. I) and high M_w relative to L_{hw} (149% of expected value). The ratio of M_t/M is also unusually high. *Cordulegaster sayi* likewise has unusually small wings ($A_w = 67\%$ of expected value), although in this case M_w is unexceptional. At the other end of the scale, trameine libellulids (*Tramea* and *Pantala*) have longer and broader wings ($L_{hw} = 116\%$ expected, $A_w = 145\%$ expected) than most dragonflies of similar mass, as do the aeshnids *Boyeria* ($L_{hw} = 120\%$ expected, $A_w = 138\%$ expected) and, to a somewhat lesser extent, *Nasiaeschna* ($L_{hw} = 116\%$ expected, $A_w = 124\%$ expected).

Table III compares dragonflies that differ in habit of flight, i.e. that are either "perchers" or "fliers" (CORBET, 1963; MAY, 1976); fliers remain on the wing during most of their active period and often glide, while perchers alternately perch and engage in relatively short flights. Of the species considered here, all gomphids and libellulids except the Trameinae are perchers; *C. sayi* is considered a percher on the basis of its behavior away from breeding sites, but many male *Cordulegaster* act as fliers when patrolling a territory. Aeshnids, corduliids, macromiids, and trameine libellulids are all fliers. Fliers and perchers differ in the magnitude of most dimensions relative to M or L_{hw} . Generally fliers of a given M have longer wings with greater A_w than comparable perchers. M_w for a given L_{hw} is smaller in fliers, however. Fliers also have smaller M_t/M than perchers (largely because of the high M_t of libellulid perchers). Moreover, fliers tend to have a distinctly larger D_t over the entire range of M_t .

Data based on wing photographs from NEEDHAM & WESTFALL (1955) are consistent with those on real wings. From the former source, $\log A_w = 1.823 \log L_{hw} + 0.0748$, $r^2 = 0.960$, $n = 64$ (cf. Tab. I). Also, aspect ratio (AR) increases with wing length in both forewings and hindwings: $\log AR_{fw} = 0.190 \log L_{hw} + 0.596$, $r^2 = 0.517$, $n = 64$; $\log AR_{hw} = 0.220 \log L_{hw} + 0.455$, $r^2 = 0.478$, $n = 64$.

Both correlations are significant, although in geometrically similar organisms no significant correlation would be expected. Aspect ratio can also be conveniently calculated as the ratio of wing length to wing chord (C_w) at nodus: $AR_{fw} = (1.183 \pm 0.0305 \text{ S.D.}) L_{fw}/C_{fw}$; $AR_{hw} = (1.150 \pm 0.0607) L_{hw}/C_{hw}$.

Figure 5 shows the relation of total wing moment of inertia (I_w) to L_{hw} .

Table III
Coefficients of allometric equations showing relationships among dimensions of dragonflies,
by activity type (flier vs. percher - see text)

Independent variable	Dependent variable	Habit*	Slope	Intercept	r ²	N
M	Mt**	Flier ^a	0.999	-0.307	0.985	50
		Percher ^b	1.049	-0.234	0.991	57
	Dt**	Flier ^a	0.358	-0.034	0.946	51
		Percher ^b	0.413	-0.020	0.980	58
	Lhw	Flier ^a	0.333	0.729	0.889	53
		Percher ^b	0.337	0.689	0.926	58
	Aw	Flier ^a	0.582	1.385	0.802	49
		Percher ^b	0.575	1.294	0.906	58
	Mw	Flier ^a	1.050	1.680	0.952	49
		Percher ^a	1.008	1.641	0.974	58
	WL	Flier ^a	0.414	-1.387	0.677	49
		Percher ^b	0.423	-1.295	0.839	58
	DL	Flier ^a	0.335	-1.968	0.670	47
		Percher ^b	0.331	-1.889	0.748	58
Lhw	M	Flier ^a	2.670	-1.991	0.889	53
		Percher ^b	2.750	-1.945	0.926	58
	Mt	Flier ^a	2.673	-2.305	0.897	50
		Percher ^b	2.890	-2.280	0.929	57
	Dt**	Flier ^a	0.939	-0.737	0.819	51
		Percher ^b	1.154	-0.832	0.938	58
	Aw	Flier ^a	1.787	0.087	0.955	49
		Percher ^a	1.711	0.116	0.982	58
	M	Flier ^a	2.971	-0.513	0.962	49
		Percher ^b	2.873	-0.365	0.970	58
	WL	Flier ^a	0.858	-2.065	0.368	49
		Percher ^b	1.035	-2.059	0.615	58
	DL	Flier ^a	0.666	-2.499	0.336	47
		Percher ^b	0.761	-2.464	0.485	58
Dt	Mt	Flier ^a	2.622	-0.246	0.921	48
		Percher ^b	2.501	-0.197	0.986	57

* For each dependent variable, categories sharing the same superscript do not differ significantly in adjusted mean square of the dependent variable.

** Slopes differ significantly between activity habits.

This plot includes data from one female *Epiaeschna heros*; all other specimens were males. The correlation is quite high, but the slope is significantly less than that expected for geometrically similar insects (i.e., 5.00). This is in accord with the results given above showing that M_w increases only as $L_{hw}^{2.76}$. The most marked deviations from the regression occur in *Tetragoneuria cynosura*, which, like many corduliids, has very light wings, and *Tramea carolina*, in which mass is concentrated basally because of the expanded anal region of the hind wings. WEIS-FOGH (1973) proposed that for insects in general the moment of inertia of a wing could be predicted from the formula $I_w = 1/6 M_w L_w^2$. For dragonflies a regression of I_w on $M_w L_w^2$ gives $I_w = 0.218 M_w L_w^2 - 0.0091$, $r^2 = 0.998$. Thus Weis-Fogh's equation holds if the coefficient is changed to about 1/5, but the relationship only slightly increases accuracy of predicting I_w , at least in this limited sample of fairly similar insects.

The values of M , M_t , D_t , A_t , V_t and V_m for males of four species appear in Table IV. The sample is too small to attach much significance to any supposed allometry but preliminary equations are: $\log A_t = 1.75 \log D_t + 0.69$, $r^2 = 0.978$; $\log V_t = 2.89 \log D_t - 0.060$, $r^2 = 0.986$. Alternative expressions, of equal predictive value and possibly more convenient as rules of thumb are: $A_t = 5.10 D_t^2 + 0.132$, $r^2 = 0.985$; $V_t = 0.978 D_t^3 - 0.020$, $r^2 = 0.989$; i.e. to a first approximation $S_t = 5 D_t^2$ and $V_t = D_t^3$.

Density of the thorax (M_t/V_t) is lower in the aeshnid fliers (*Boyeria* and *Anax*) than in the libellulid perchers and within each of those groups appears to decrease with increasing size. Likewise, the proportion of the thorax that is filled with muscle (V_m/V_t) is lower in the aeshnids and also decreases with increasing size. As expected, A_t/V_t decreases markedly with increasing size.

Table IV
Relationships among mass and thoracic dimensions in four individual dragonflies

Species	M (g)	M_t (g)	D_t^* (cm)	S_t (cm ²)	V_t (cm ³)	V_m (cm ³)	M_t/V_t	V_m/V_t	S_t/V_t (cm ³)
<i>Pachydiplax longipennis</i>	0.156	0.087	0.45	1.26	0.092	0.058	0.948	0.627	13.7
<i>Libellula incesta</i>	0.377	0.241	0.69	2.60	0.285	0.172	0.846	0.603	9.1
<i>Boyeria vinosa</i>	0.395	0.177	0.64	2.03	0.216	0.102	0.819	0.472	9.4
<i>Anax junius</i>	1.090	0.415	0.84	3.79	0.575	0.232	0.722	0.403	6.6

* Measured from drawings of sections.

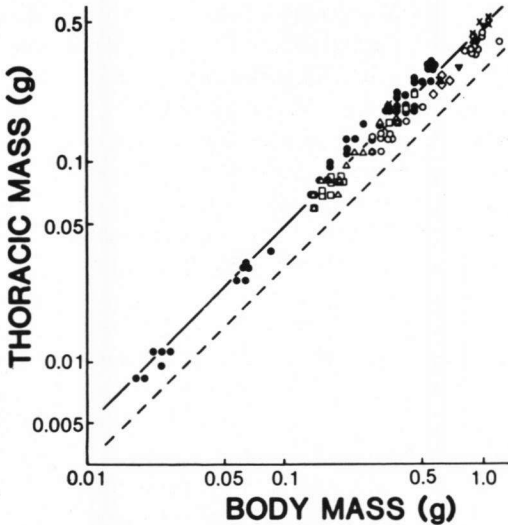


Fig. 1. Thoracic mass (M_t) as a function of total mass (M) in male Anisoptera. Solid line is least squares regression of $\log M_t$ on $\log M$. Dashed line indicates slope expected for geo-metrically similar organisms (intercept of this line is arbitrary). Symbols: ● - Libellulidae, ○ - Aeshnidae, □ - Corduliidae, △ - Gomphidae, × - Macromiidae, ◇ - Cordulegasteridae, ▼ - Petaluridae.

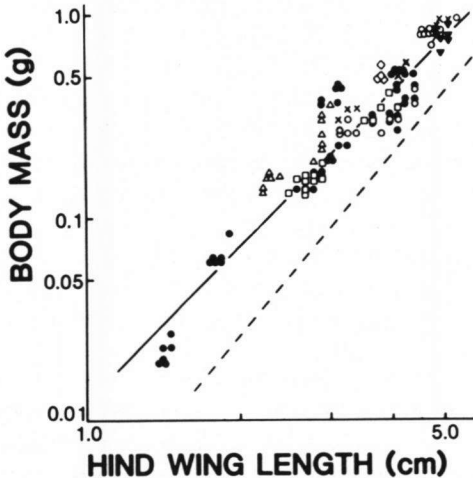


Fig. 2. Total mass (M) as a function of hindwing length (L_{hw}) in male Anisoptera. Symbols as in Fig. 1.

DISCUSSION

An important reason for presenting the equations of Tables I-III is to make possible estimation of several dimensions from others more easily measured. For example, approximate body mass of the living insect can be calculated from wing length of a dried specimen. Another potential utility of such regressions lies in the light they may shed on the nature of adaptive changes in shape with variation in size and of departures from predicted dimensions (GOULD, 1966, 1975; SMITH, 1980). The following discussion represents an attempt to elucidate some of these adaptations.

WING PROPORTIONS

One of the most consistent allometric trends revealed by these data is that toward relatively longer (Fig. 2) and narrower, hence lighter, wings with increasing body size. Relationships of M , A_w , AR , and I_w to L_{hw} all reinforce this conclusion. Sphingid and saturniid moths exhibit somewhat similar allometry (BARTHOLOMEW & CASEY, 1978). GREENEWALT's (1962) extensive data for the

entire spectrum of flying animals shows a slight trend toward relatively longer wings at high body mass, but little apparent departure from geometric similarity in the relation of A_w to L_w . In insects as a group there is, if anything, a trend toward disproportionately high area as wings lengthen, mainly because butterflies and large moths have long and very broad wings.

The functional significance of long, narrow wings in large dragonflies is not certain, but several benefits to flight performance can be suggested. In general the energy required for flight, relative to energy available (i.e. maximum metabolism), is greater in larger flying animals (PENNYCUICK, 1969). Thus large dragonflies may be, to a greater extent than small species, under selective pressure to minimize energy expenditure in flight. This could be especially true since the flight muscle mass of large species may be relatively less than in small species (see below). Long, narrow wings increase the area swept by the moving wing (wing disc area; PENNYCUICK, 1969) and probably increase lift coefficient and lift-to-drag ratio (see, e.g. OLSON, 1961) while at the same time minimizing wing mass. The latter results in decreased I_w , and therefore reduced inertial power losses (WEIS-FOGH, 1973), and possibly increased wingbeat frequency (GREENEWALT, 1960). GREENEWALT (1975) showed that for birds minimum mass-specific power requirements for flight increase with mass and wing area but decrease with increasing wing length, at least in part for the reasons cited above. Cost of transport also decreases with wing length but increases with area. Thus lengthening L_{hw} while minimizing A_w should be increasingly advantageous as power requirements increase. The fact that fliers have relatively longer wings than perchers is consistent with this suggestion since fliers must, of course, sustain flight for longer periods.

GREENEWALT (1975) also demonstrated that the speed at which power output is minimal increases with mass but decreases with both wing area and length. Since the necessity to maintain high speed must limit maneuverability, large dragonflies that fly for long periods in situations where space is limited should ideally have long, broad wings. *Boyeria* patrols among roots and overhangs along small streams, often in dim light, and it is characterized by unusually long, broad wings; so, to a lesser extent, is *Nasiaeschna*, another flier of wooded streams and swamps. Another notable example are members of the tropical, forest-dwelling genus *Gynacantha* (May, unpublished data).

Another important wing characteristic is strength. A structure subject to buckling stress should increase in thickness relative to its length as the latter increases (McMAHON, 1973), in order to maintain comparable strength. This generally means that mass should increase proportionally faster than L^3 . Just such a relationship is found in weight-bearing bones (PRANGE, et al., 1979) and in the wings of flying animals generally

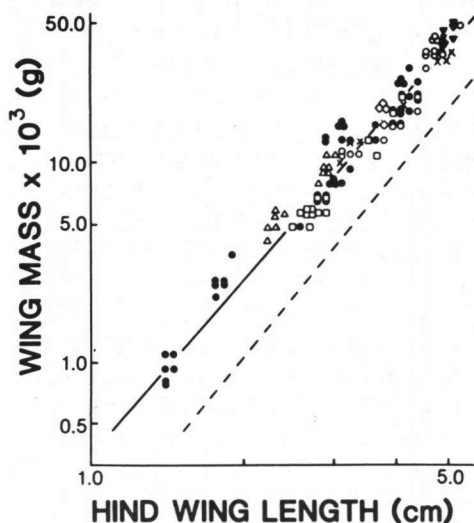


Fig. 3. Wing mass (M_w) as a function of hindwing length (L_{hw}) in male Anisoptera. Symbols as in Fig. 1.

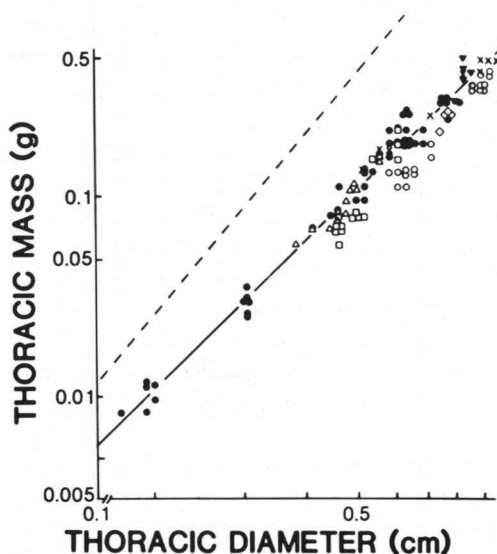


Fig. 4. Thoracic mass (M_t) as a function of thoracic diameter (D_t) in male Anisoptera. Symbols as in Fig. 1.

(GREENEWALT, 1962). It is not seen in Anisoptera (Tab. II), but the picture here is confounded by the proportionate decrease in wing area. In fact, $M_w/A_w \propto L_{hw}^{1.6}$ in perchers and $L_{hw}^{1.8}$ in fliers, suggesting that thickness does increase disproportionately relative to length; the ratio should increase as $L_{hw}^{1.0}$ in dimensionally similar animals.

Perchers have higher wing mass for a given L_{hw} than do fliers (Fig. 3), and some perchers that habitually rest on the ground (Gomphidae and *Platthemis*) have the greatest relative wing mass. This suggests that frequent, sudden take-offs, especially when wing movement may be restricted or wings may strike the substrate on the first stroke, may require greater wing rigidity than does sustained flight. It should be noted, however, that ground-perching *Erythemis* do not have especially massive wings and that *Corulegaster sayi*, which has massive wings (for their length), does not perch on the ground.

THORACIC PROPORTIONS

Although V_t probably increases approximately with D_t^3 , M_t increases only with

D_t^{24} (Fig. 4). In addition, fliers tend to have relatively less massive thoraxes (Fig. 1) and lower V_m/V_t than perchers. These characteristics are all probably related to parallel differences in heat exchange and possible also power requirements for flight.

In all Anisoptera the thoracic musculature is largely surrounded by subcuticular air sacs that provide substantial insulation to the flight muscles; the degree of insulation is greatest in large species, especially large fliers (CHURCH, 1960; MAY, 1976, 1978). In very small species, the ratio of thoracic surface to volume (Tab. IV) may be so high that no amount of

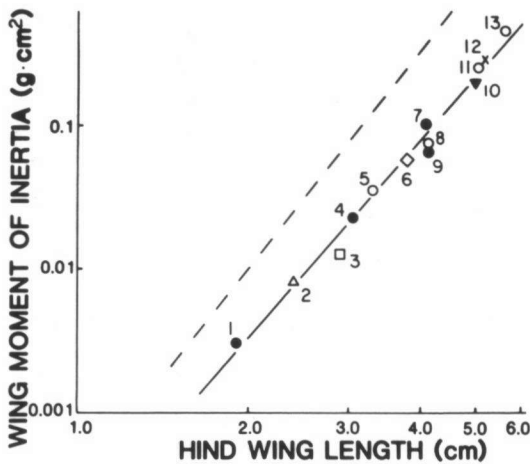


Fig. 5. Moment of inertia of all four wings (I_w) as a function of hindwing length (L_{hw}) in Anisoptera: (1) *Perithemis tenera*, — (2) *Gomphus exilis*, — (3) *Tetragoneuria cynosura*, — (4) *Pachydiplax longipennis*, — (5) *Basiaeschna janata*, — (6) *Cordulegaster sayi*, — (7) *Libellula pulchella*, — (8) *Boyeria vinosa*, — (9) *Tramea carolina*, — (10) *Tachopteryx thoreyi*, — (11) *Anax junius*, — (12) *Macromia taeniolata*, — (13) *Epiaeschna heros*. Symbols as in Fig. 1.

insulation can greatly retard heat exchange, while in larger dragonflies a significant insulating effect, and thus selection for increased insulation, is possible. In addition, since fliers generally are endotherms (MAY, 1976), good insulation to prevent excessive heat loss during flight probably is of greater selective advantage than in largely ectothermic perchers. The characteristics listed at the beginning of this section are all due to the relative increase in the peripheral air space in large dragonflies, especially large fliers. In the sections used to determine V_t and V_m it was impossible to distinguish air spaces from haemocoel, but the reduction in thoracic density in parallel with reduced V_m/V_t tends to confirm that the latter was due mainly to an increase in air sac volume.

I did not measure directly the relative mass of dragonfly flight muscle, but if its density is about 1.06 g.cm^{-3} (data for frog muscle; SPECTOR, 1956), then from Table IV the tissue should be about 25% of M in fliers and about 45% in perchers. These percentages are about the same as found by MAGNAN & PERRILLIAT-BOTONET (1932) for fliers but much higher

than their figures for perchers. The reduced relative muscle mass of fliers, especially aeshnids, could indicate that maximum short-term power requirements are usually less for species characterized by sustained flight than for those that typically make repeated sudden takeoffs.

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