

DRAGONFLY FLIGHT: POWER REQUIREMENTS AT HIGH SPEED AND ACCELERATION

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Summary

Most studies of insect flight deal primarily with hovering or with forward flight at constant, moderate speed. This paper reports investigations of flight characteristics that are especially relevant to the performance of dragonflies at high and/or changing velocity. Dragonflies were filmed in free flight in the field to determine velocity and acceleration. The power required for repeated acceleration is shown to be large, in some circumstances, relative to the estimated maximum available power and probable top power requirements for steady flight. Distributions of velocity and acceleration, and concomitant power requirements, differ markedly among species, however. In addition, parasite drag was measured in winds of $2\text{--}7\text{ m s}^{-1}$ and drag coefficients determined to be about 0.40 at Reynolds number greater than 10^4 . This result implies substantially lower power requirements at high speeds, compared to previous estimates. Other aspects of power output, including the probable magnitude of inertial power, are considered in relation to published data.

Introduction

Recent analyses of insect flight, including both metabolism (Kammer and Heinrich, 1978; Casey, 1988; Ellington *et al.* 1990) and aerodynamic and mechanical requirements (Ellington, 1984, 1985; Dudley and Ellington, 1990*a,b*; Casey and Ellington, 1989), have substantially advanced our understanding of the phenomenon. Most studies, however, consider only hovering flight, although a few have investigated forward flight at moderate, nearly constant speed. Relatively little is known about the performance of insects near their upper limits of velocity and power or during rapid acceleration, or about behavioral contexts in which high performance is employed.

Dragonflies (Odonata: Anisoptera) have long excited aesthetic admiration and scientific interest because of their unusual aerial agility. Their remarkable flight is, nevertheless, based on morphologically primitive thoracic and wing structure (Matsuda, 1970) and probably on unusual aerodynamic mechanisms, at least during hovering (Weis-Fogh, 1973; Norberg, 1975; Savage *et al.* 1979; Soms and

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Luttges, 1985). Recently Azuma *et al.* (1985) and Azuma and Watanabe (1988) analyzed free forward flight of dragonflies in a wind tunnel, presenting a power curve and preliminary estimates of maximum power output and flight velocity for *Anax parthenope*. Marden (1987) experimentally estimated maximum lift in several species, while Polcyn (1988) measured oxygen consumption of dragonflies during hovering and/or attempted escape flights from metabolism chambers. Finally, Ruppell (1989) used cinematography to determine flight velocities and accelerations of dragonflies in the field, with descriptions of associated wing movements. Thus, a picture is beginning to emerge of the flight performance and power output and input of which dragonflies are capable.

My aim in this paper is to augment this picture with further information on velocity and acceleration during unhindered flight in the field and with data on parasite drag from several species of Odonata. The power required to overcome parasite drag on the body may become an important component of aerodynamic power at high flight speed. Similarly, the power required for acceleration may be significant during the rapid maneuvers so characteristic of Anisoptera. I have also tried to bring together, from a variety of sources, other information pertinent to the relationship between power requirements and power availability in dragonflies. Thus, the results reported here are steps towards a more complete description of high-performance flight in Odonata.

Materials and methods

Flight characteristics

Flight speed in the field was determined for four species: *Micrathyria atra* (Libellulidae), *Epiptera* (*Tetragoneuria*) *cynosura* (Corduliidae), *Macromia taeniolata* (Macromiidae) and *Anax junius* (Aeshnidae). The insects were not individually marked, but data for *E. cynosura* probably all pertain to a single territorial male; in other species, at least five individuals were filmed on 2–3 different days. All species were filmed at mating rendezvous sites (Corbet, 1980), where nearly all individuals were males. *Anax junius* were also filmed while swarm feeding over beach dunes; roughly two-thirds of these insects were probably females.

Except for feeding *A. junius*, flying individuals were filmed from above using a Canon Auto Zoom 814 Super 8mm ciné camera aimed vertically downwards, about 3–4m above their usual plane of flight. Patrolling dragonflies remained within a horizontal plane about 0.3–1.0m above water level (brief upward excursions occurred but were not filmed), so errors in measuring frame-to-frame displacement due to parallax or to vertical components of movement are small. Distance measurements were calibrated by suspending an object of known dimensions in the flight plane at the beginning of each film. Interframe interval (nominally 1/24 or 1/40s) was calibrated by filming a stopwatch. Feeding *A. junius* did not all fly in the same horizontal plane. The average body length of the insects was assumed to be 7.5 cm (Needham and Westfall, 1955) and was used as

the distance standard for each flight; no correction for vertical movement components was attempted. All filming was carried out under nearly still wind conditions and, except for feeding *A. junius*, at sheltered sites. Also, the heading and course of the insects usually coincided quite closely, except in *E. cynosura* during very slow flight. Wind speed and direction were not determined, however, so magnitudes of flight velocity are actually ground speeds. I assume that these approximate to air speed under the conditions described.

Films were viewed frame by frame either using an 8 mm film editor and plotting position on overlaid acetate sheets or using a binocular microscope fitted with a *camera lucida* and plotting each position on paper. Small shifts in the field of view were corrected by superimposing images of stationary objects within succeeding frames. Final images were 0.07–0.1 times life size (0.03–0.1 times for feeding *A. junius*).

Position records (cumulative distances along the flight path from the first sighting, ignoring direction) were smoothed, as described by Lanczos (1957) and Rayner and Aldridge (1985). Smoothed velocity and acceleration were then calculated, also as described by those authors except that, owing to the slow filming speed, I assumed piecewise time-constant acceleration, or change in acceleration, over only three adjacent points and adjusted the smoothing formulae accordingly, following the derivation in Lanczos (1957). This procedure is equivalent to calculating a two-point running average of the frame-by-frame value of each quantity. The filming speeds I used cannot resolve very rapid changes in acceleration, such as those reported by Ruppell (1989), and the smoothing procedure may result in considerable oversmoothing (high sampling frequency error in the terminology of Harper and Blake, 1989). Thus, these results should not be taken as instantaneous values but as two-frame averages, i.e. averages over about 2–4 wingbeats depending on species and filming speed (see Table 1). Force was estimated by multiplying smoothed values of acceleration for each interval by the average mass of the species sampled at the filming location. Power requirements were calculated as force times smoothed velocity for each interval.

Parasite drag

I removed the wings from dead male dragonflies, fixed the legs and other parts in a natural flight posture using small drops of glue, and dried the bodies until rigid. They were suspended upside down, parallel to an airstream, by gluing the thoracic venter to a force transducer (see below). Wind was generated by an open-circuit, open-section wind tunnel with an aperture of 20 cm × 20 cm (Wilkin, 1990); velocity was controlled by altering fan speed with a variable transformer. Swirl and turbulence were slight at the center of the working section, as judged by the appearance of parallel smoke streams. Wind velocity was measured near the test object using an Alnor thermo-anemometer (hot wire).

Drag was measured using an apparatus consisting of a tubular metal arm about 40 cm long and 0.6 cm o.d., connected *via* a 15 cm length of fine cotton thread, under slight tension, to a rigidly mounted aluminum strain-gauge transducer

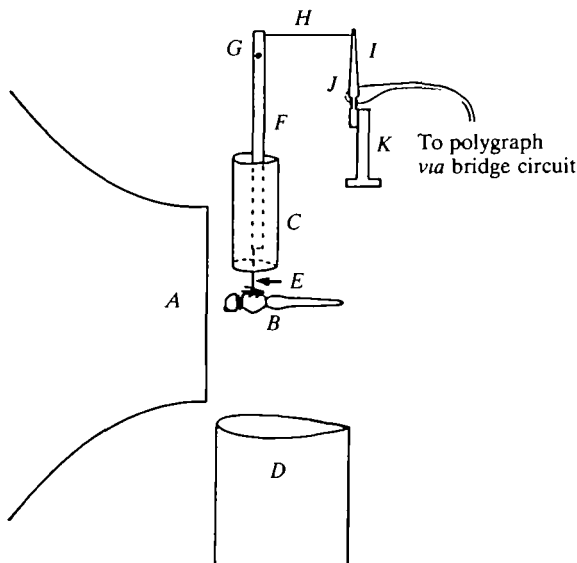


Fig. 1. Schematic diagram of apparatus used for parasite drag measurements; not to scale. *A*, aperture of wind tunnel; *B*, body of dragonfly; *C*, upper shielding; *D*, lower shielding, moved down to expose test object; *E*, mounting rod; *F*, freely swinging arm; *G*, pivot; *H*, thread, under tension; *I*, strain gauge transducer; *J*, strain gauges; *K*, fixed support of transducer.

(Fig. 1). The arm pivoted freely on a thin brass rod 3 cm from its upper end. At the other end, a 7.5 cm length of brass rod (1.3 mm diameter) was glued parallel to the tube; a small (2 mm × 3 mm) brass plate soldered to the end of the rod allowed the test body to be glued on firmly. The tube and rod were shielded from wind to within about 3 cm of the end by a sheet of brass shim stock bent to form a streamlined section. The end of the rod and the test object were similarly shielded prior to each measurement; this lower shielding could be moved down out of the airstream to expose the object to wind. The transducer was a tapered aluminum rod with four semiconductor strain gauges (BLH Electronics) glued along a section at the base that had been machined flat. Output was recorded with a Grass Polygraph.

The apparatus was calibrated by orienting it horizontally, using a lead counterweight to balance the arm, and suspending small weights (25–391 mg) from the end of the rod. Bridge output (mV) was a linear function of force ($r^2=0.999$). Drag on the exposed end of the supporting rod was measured as described below and subtracted from the measured drag of each test object; support drag was about 40% of the drag of the smallest dragonflies and about 15% that of the largest. Drag on three smooth plastic spheres was also determined, to check the accuracy of the method.

Wind velocity took about 1 min to stabilize after the fan had been started, and the transducer output tended to drift slowly and almost linearly, so the following procedure was adopted. The test object was positioned on the arm at the center of

the tunnel aperture with the upper shield in place. Wind velocity was adjusted to the desired level (nominally $2\text{--}7\text{ m s}^{-1}$). The lower shield was moved up and bridge output was recorded with the object shielded until the trace stabilized, after which the lower shield was removed. A transient oscillation persisted for several seconds after initial exposure to wind, but then the record again stabilized or continued to drift slowly. The response (in mV) was determined by linear extrapolation of the trace to the instant of first wind exposure. Each drag value represents the mean of at least five (spheres) or seven (dragonflies) responses at each velocity.

The area of maximum transverse section (S) of the dragonflies was estimated by measuring maximum head width and maximum height from the mesothoracic wing base to the ventral surface of the folded legs and assuming an elliptical cross section. Equivalent flat plate areas (A) and drag coefficients (C_D) were calculated from drag measurements after Pennycuick (1969).

Results

Flight characteristics in the field

Fig. 2 indicates the distribution of flight speeds for each species. All hover at least occasionally during flight at mating rendezvous sites and all show infrequent bursts of relatively rapid flight, mostly while chasing or evading rivals. Thus, all the distributions are at least slightly positively skewed. A strong dichotomy exists, however, between *A. junius*, in which the velocity distribution approached normality, and *E. cynosura* and *M. atra*, in which a very great preponderance of low-speed flight occurred; *M. taeniolata* had an intermediate distribution, but was more like *A. junius*.

Table 1 gives average morphometric and wingbeat frequency data for each species, along with data on maximum acceleration. For *E. cynosura* and *M. atra*, values may be somewhat underestimated compared to those for *A. junius* and *M. taeniolata*, since acceleration was averaged over more wingbeats in the former. Table 1 also includes maximal values of power required for acceleration, i.e. in addition to the power required to maintain level flight. Note that maximal power requirements need not correspond to flight sequences during which maximum acceleration occurred, since more power is required to accelerate at high than at low velocity.

Parasite drag

Drag coefficients for the spheres are shown in Fig. 3. These are about 5–20% higher than other experimentally determined values, especially at low Reynolds numbers (Re). This could be the result of small systematic underestimates of wind velocity (the anemometer was not independently recalibrated) and/or an effect of interference drag due to interaction of the mounting rod and test body (Tucker, 1990). These results suggest that drag on dragonfly bodies might be similarly overestimated, but the data are sufficiently accurate to permit a reasonable first approximation of parasite drag and power.

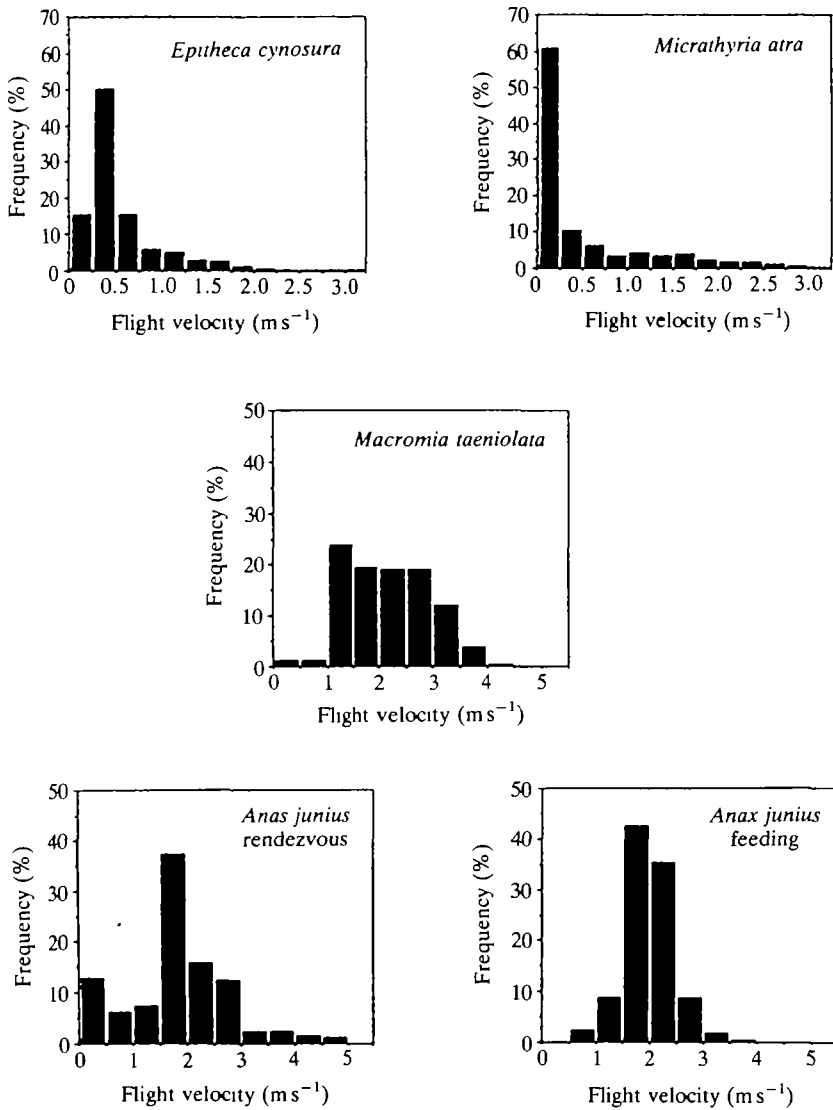


Fig. 2. Flight velocity distributions for four species of dragonflies filmed in the field. Note that axes for *Epitheca cynosura* and *Micrathyria atra* are different from those for *Anax junius* and *Macromia taeniolata*. The means (\pm s.d.), medians and skewness of the distributions and number of frames sampled for each species are as follows: *E. cynosura*, 0.43 ± 0.43 m s⁻¹, 0.29 m s⁻¹, 2.31 , 566 ; *M. atra*, 0.38 ± 0.66 m s⁻¹, 0 m s⁻¹, 1.79 , 634 ; *M. taeniolata*, 1.89 ± 0.78 m s⁻¹, 1.82 m s⁻¹, 0.14 , 242 ; *A. junius* at rendezvous site, 1.60 ± 0.93 m s⁻¹, 1.60 m s⁻¹, 0.44 , 241 ; *A. junius* feeding, 1.73 ± 0.45 , 1.73 , 0.24 , 560 .

Data for morphometrics, drag, A , C_D (based on cross-sectional area) and Re (based on body length) of dragonflies appear in Table 2. Fig. 4 shows the relationship of C_D to Re in these and several other insects. As noted by Dudley

Table 1. Morphological and flight characteristics of species filmed in the field

Species	Mass (\pm s.d.) ($\text{kg} \times 10^4$)	Muscle mass ($\text{kg} \times 10^4$)	Maximum available power ^a ($\text{W} \times 10^2$)	Wingbeat frequency (Hz)	Acceleration (m s^{-2})		Power ^b ($\text{W} \times 10^2$)		
					Maximum ^c	90% ^d	Maximum ^c	90% ^d	
					Mean ^e	Mean ^e	Mean ^e	Mean ^e	
<i>Epietha cynosura</i>	1.75 \pm 0.22 N=69	0.77	0.77	43	11.4 (10.9–11.8)	3.6	0.41 (0.35–0.51)	0.034	0.016
<i>Micrathya atra</i> ^f	2.14 \pm 0.23 N=14	1.09	1.09	39	15.0 (14.0–15.9)	6.9	0.67 (0.55–0.82)	0.17	0.040
<i>Anax junius</i> ^{g,h}	8.04 \pm 0.70 N=11	3.37	3.37	29	12.9 (11.4–13.7)	6.7	3.61 (3.34–3.96)	1.23	0.39
<i>Anax junius</i> ^{f,i}	10.38 \pm 2.29 N=43	3.92	3.92	29	13.5 (11.8–15.1)	6.3	3.08 (2.51–4.59)	1.14	0.38
<i>Macromia taeniolata</i> ^g	11.80 \pm 0.67 N=35	5.65	5.65	31	19.0 (14.9–27.8)	6.9	3.94 (3.62–4.45)	1.53	0.51

Data on mass were obtained for specimens from the same population as those filmed, but not the same individuals.

Wingbeat frequencies are expected mean values for the same (or in the case of *M. atra*, similar) species from May (1981b), assuming thoracic temperatures of about 37°C.

^a Assuming a maximum specific power of 100 W kg⁻¹ (Ellington, 1985).

^b Calculated as estimated mass (from column 1) \times acceleration \times velocity, using smoothed values of velocity and acceleration as described in the text.

^c Mean (range) of five highest measurements.

^d 90th percentile value.

^e Average of all values, assuming no power cost for deceleration.

^f Filmed at 24 frames s⁻¹.

^g Filmed at 40 frames s⁻¹.

^h At mating rendezvous site.

ⁱ Feeding.

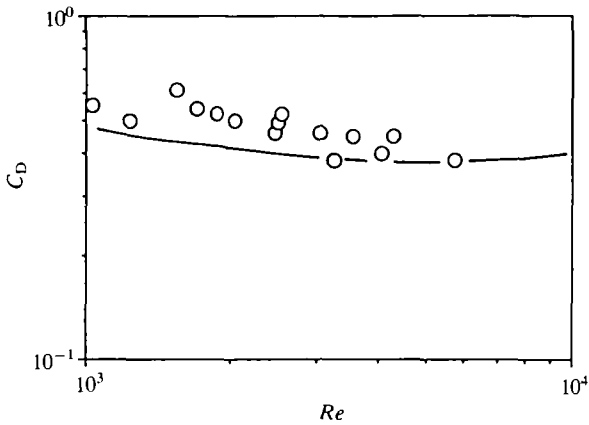


Fig. 3. Drag coefficient (C_D) of plastic spheres as a function of Reynolds number (Re). Spheres were 7.8, 9.5 or 12.5 mm in diameter and each was run at nominal wind velocities of 2.0, 3.0, 4.0, 5.0 and 7.0 m s^{-1} ($\pm 2\%$ maximum deviation from mean). The solid line is based on a large body of published data, from Goldstein (1965; his Fig. 2).

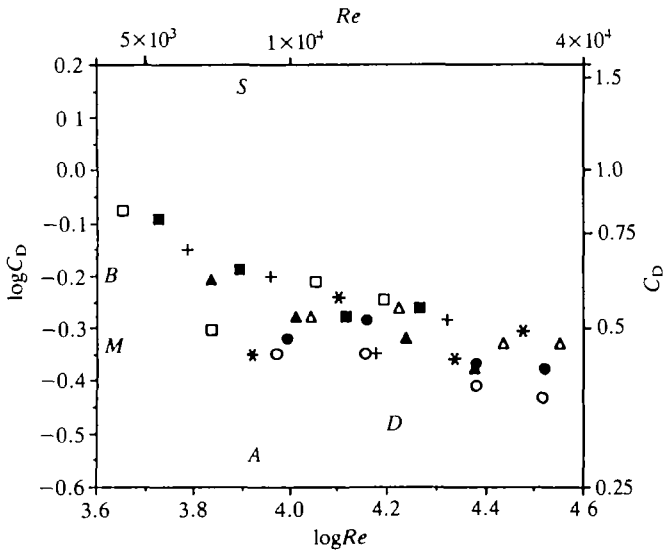


Fig. 4. Drag coefficient (C_D) as a function of Reynolds number (Re) of dragonfly bodies. Each specimen is represented by a different symbol (see Table 2). Wind velocities were as in Fig. 3. Letters indicate drag coefficients of other insects: *S*, *Schistocerca gregaria* (desert locust; Weis-Fogh, 1956); *B*, *Bombus terrestris* (bumblebee; Dudley and Ellington, 1990b); *M*, *Melolontha vulgaris* (cockchafer beetle; Nachtigall, 1964); *A*, *Acilus sulcaus*; and *D*, *Dytiscus marginalis* (dytiscid beetles; Nachtigall, 1977).

Table 2. Morphology and drag characteristics of dried dragonfly bodies determined as described in the text

Species	Mass ^a (kg×10 ³)	S ^b (m ² ×10 ⁵)	A ^c (m ² ×10 ⁵)	Re×10 ⁻³	Drag (N×10 ⁴)	C _D ^d
<i>Pachydiplax longipennis</i> (□)	0.135	2.46	2.07	4.49	0.48	0.84
			1.23	6.84	0.66	0.50
			1.52	11.3	2.22	0.62
			1.41	15.6	3.95	0.57
<i>Pachydiplax longipennis</i> (■)	0.221	3.52	2.84	5.32	0.69	0.81
			2.30	7.79	1.24	0.65
			1.87	13.0	2.69	0.53
			1.95	18.4	5.58	0.55
<i>Tramea carolina</i> (+)	0.364	4.96	3.07	6.79	0.72	0.62
			2.67	10.3	1.45	0.53
			2.38	17.3	3.65	0.48
			2.10	23.9	6.15	0.42
<i>Boyeria vinosa</i> (*)	0.391	6.28	2.82	8.32	0.64	0.45
			3.60	12.7	1.90	0.57
			2.71	21.6	4.14	0.43
			3.13	29.9	9.17	0.50
<i>Libellula luctuosa</i> (▲)	0.398	4.64	3.30	6.07	0.79	0.71
			2.91	9.16	1.60	0.63
			2.11	15.0	3.12	0.45
			2.43	20.9	6.93	0.52
<i>Anax junius</i> (○)	0.870	8.96	4.06	9.43	0.95	0.45
			4.04	14.3	2.19	0.45
			3.49	24.1	5.34	0.39
			3.31	32.9	9.44	0.37
<i>Anax junius</i> (●)	1.004	9.45	4.56	9.86	1.14	0.48
			4.95	14.4	2.65	0.52
			4.11	24.1	6.17	0.43
			4.00	33.2	11.4	0.42
<i>Macromia taeniolata</i> (△)	1.197	11.4	6.12	11.0	1.50	0.53
			6.33	16.7	3.55	0.55
			5.43	27.3	8.17	0.47
			5.42	35.6	15.5	0.47

Wind velocities were nominally 2.0, 3.0, 5.0 and 7.0 m s⁻¹ (±2% maximum deviation from mean). The symbol beside a name is the key to symbols in Figs 4 and 5.

^aFresh mass of whole insect.

^bArea of maximum transverse section, calculated as described in the text.

^cEquivalent flat plate area (Pennycuick, 1969).

^dParasite drag coefficient based on cross-sectional (frontal) area.

Re, Reynolds number.

and Ellington (1990*b*), C_D consistently declines as Re increases. To facilitate extrapolation to other dragonflies, drag and A are plotted in Fig. 5 as a function of body mass and wind velocity.

Discussion

Velocity and acceleration in the field

Anax junius and *M. taeniolata* patrol widely at rendezvous sites, interacting aggressively with conspecific males wherever they are encountered. The other two species, however, are strongly localized and apparently territorial. *Epietheca cynosura*, like *A. junius* and *M. taeniolata*, is a 'flier' as defined by Corbet (1963), but individuals hover or fly slowly for extended periods in a small area, chasing other dragonflies when they approach closely. *Micrathyria atra* is a 'percher' (except at low air temperature) and flies for only about 40% of its time on territory (May, 1977); clearly, from Fig. 2, most of this flight time is spent hovering.

In both territorial species, the films only recorded the beginning of chases and, once, a close approach of two individuals of *M. atra*. The single *E. cynosura* was in an area of relatively low population density, so chases may have been less frequent than usual. Even in the patrolling species, intense chases were recorded rarely and physical clashes not at all. Thus, it is very likely that the films did not record maximum velocity or acceleration. The two larger species rarely exceeded 4 m s^{-1} , while maximum velocity for the smaller species was less than 3 m s^{-1} . Ruppell (1989) reported maximum speeds of 7.5 m s^{-1} in *A. junius* and 10 m s^{-1} in *Aeshna cyanea*, although average flight velocities were much lower. Most large species are probably capable of speeds close to or exceeding 10 m s^{-1} , but they apparently fly at high velocity only rarely.

Azuma and Watanabe (1988) estimated aerodynamic plus inertial power requirements over a range of speeds for *Anax parthenope*, a species very similar in size and morphology to *A. junius*. Their analysis contrasts with the conclusions of some others about aerodynamic mechanisms in dragonflies (Norberg, 1975; Soms and Luttges, 1985) and about the form of the power curve in other insects [in particular, no strong minimum in power requirements at intermediate velocity was found by Dudley and Ellington (1990*b*) and Ellington *et al.* (1990)]. Nevertheless, their curve provides a useful point of departure for assessing relative effects of velocity and acceleration.

The average velocity of *A. junius*, during both patrolling and feeding, and of *M. taeniolata* is close to the velocity predicted to minimize the rate of energy expenditure in *Anax parthenope* (cf. Fig. 6; Azuma and Watanabe, 1988). In part, this is an accidental effect of periods of hovering being averaged with rapid flight, but in *A. junius* the modal and median speeds are also close to this value, and both species should benefit from maximizing time aloft. If dragonflies exhibit a power curve with a strong minimum, as Azuma and Watanabe (1988) suggest, then 'cruising speed' in these situations may, in fact, be adjusted to minimize flight costs, with periods of more expensive hovering and chasing being interspersed

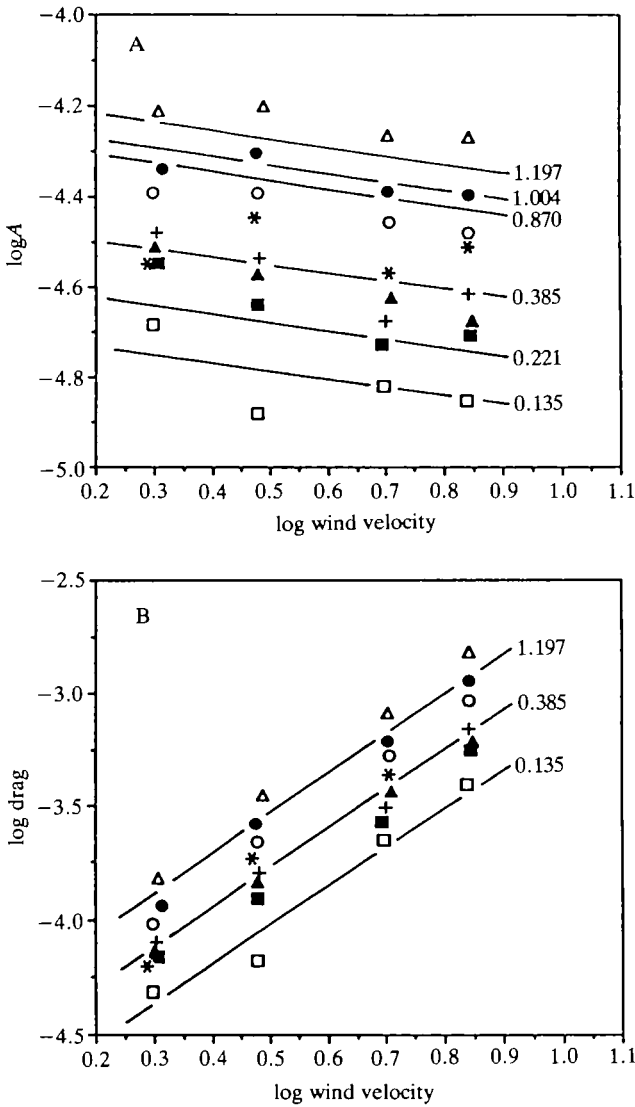


Fig. 5. (A) Equivalent flat plate area (A) of dragonflies as a function of body mass and wind velocity. Each specimen is represented by a different symbol (see Table 2). Lines are the multiple regression lines for each body mass ($\text{kg} \times 10^3$) shown on the right; masses correspond to fresh masses of the specimens tested, except that the average value, 0.385, for three species, *Tramea carolina*, *Boyeria vinosa* and *Libellula luctuosa* was used for clarity. The multiple regression equation is $\log A = 0.53 \log \text{mass} - 0.20 \log \text{velocity} - 2.64$, $r^2 = 0.90$. (B) Drag as a function of body mass and wind velocity. Symbols as in A. For clarity, multiple regression lines are shown only for one intermediate and the extreme masses. The multiple regression equation is $\log \text{drag} = 0.53 \log \text{mass} + 1.80 \log \text{velocity} - 2.85$, $r^2 = 0.98$.

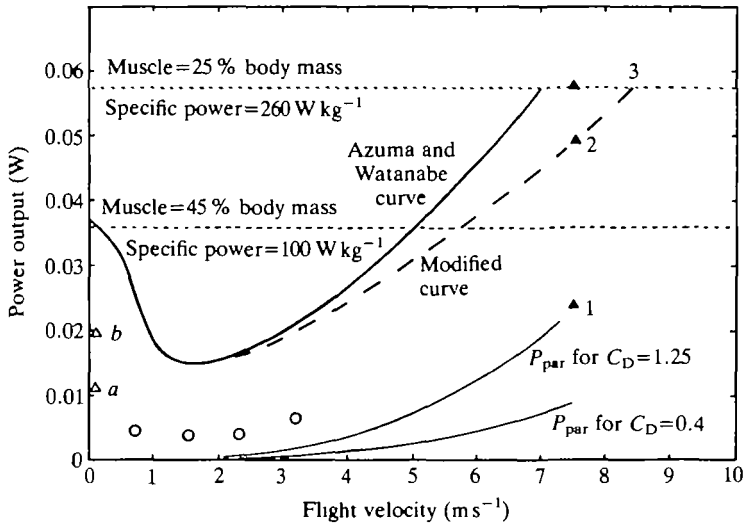


Fig. 6. Analysis and proposed modifications to the power curve of Azuma and Watanabe (1988) for *Anax parthenope* (heavy solid line). The lower curves show parasite power requirements (P_{par}), calculated according to Pennycuik (1969) for $C_D=1.25$, as assumed by Azuma and Watanabe, and for C_D values for *A. junius* from the present study (Table 2). The dashed curve is a power curve recalculated by simply subtracting the difference between the two parasite power curves from Azuma and Watanabe's original curve. The horizontal dotted lines represent estimates of maximum available power from the flight muscles, based on assumptions that flight muscle is 25% of body mass and specific power is 260 W kg^{-1} muscle vs 45% of body mass and 100 W kg^{-1} . Circles indicate values of inertial power required, assuming no elastic storage, for the four flights filmed by Azuma and Watanabe; the calculations followed Ellington (1984) and were based on wing moments of inertia from May (1981a). The open triangles on the left axis represent estimates of inertial power for wing mass (a) plus wing virtual mass (b) in an *Anax* hovering with stroke angle and frequency equal to those observed in *Aeshna juncea* by Norberg (1975). The closed triangles on the right represent inertial power required to move the wing mass (1) plus wing virtual mass, (2) plus parasite power requirements (3) for an *Anax* flying at 7.5 m s^{-1} with stroke characteristics observed for *A. junius* flying at that speed (Rüppell, 1989).

In the two small, territorial species, modal velocities are near zero, presumably indicating that selection for strong localization and territorial defense is more important than potential energy savings. Of course, if the power curve at low speed is nearly flat, as found by Dudley and Ellington (1990b) for bees, little additional cost is associated with hovering, but if the curve is qualitatively similar to that proposed by Azuma and Watanabe (1988), the energy costs of territorial vigilance, aside from actual fighting, are substantial, possibly double the theoretical minimum.

In general, the magnitude of the higher accelerations observed here were comparable to, and often slightly greater than, those recorded by Rüppell (1989) for acceleration averaged over several wingbeats. All species are capable of ver

abrupt deceleration. It is not known whether this was always energetically passive, resulting, for example, from twisting the wings to maximize air resistance, or in some cases required active production of negative thrust.

In the films of feeding *A. junius*, measurement errors obviously occurred as a result individual size variation, especially since both males and females were filmed and because the insects were moving (causing slight blurring) and may not always have been oriented exactly normal to the camera. The last problem was largely obviated by the fact that they flew horizontally most of the time, although different individuals flew at quite different altitudes. During actual pursuit of prey, however, abrupt maneuvers away from a horizontal plane occurred. Dragonflies often climbed suddenly, briefly maintained position, then dived back to the original plane of flight. Thus, some apparent decelerations actually represent changes of direction, some accelerations may have been assisted by gravity, and power expended to attain upward velocity is not accounted for. I think that the velocities recorded are generally representative of the true velocity of the insects, but clearly their translation into acceleration and power demand is less accurate than for the other situations filmed.

A. junius did not hover during feeding, and the velocity distribution is nearly normal, with a standard deviation much lower than that of *A. junius* at a rendezvous site. The mean is again close to the predicted velocity for minimum energy expenditure (Fig. 6), and, since prey were probably not being seriously depleted and were apparently not highly clumped (both conclusions based on observation of the dragonflies' behavior), maximizing time aloft for a given energy cost might be more advantageous than, for example, minimizing cost of transport. I emphasize that this is not, in itself, a strong argument for a power curve with a distinct minimum, however, since other physical or ecological factors might also select for a well-defined modal velocity.

Parasite power

Dragonflies are fairly well streamlined compared to other insects (Fig. 4), especially since wetted surface area is probably high and Re based on length is inflated compared to that of some other groups (Vogel, 1983), owing to the long, narrow bodies of Odonata. Although clearly far from those of an ideally streamlined body (Dudley and Ellington, 1990b), values of C_D are less than half that of a locust at comparable Re (Weis-Fogh, 1956); the lowest values, at Re values greater than 10^4 , are lower than those previously measured for any insect except dytiscid beetles (Nachtigall, 1977). Streamlining may, in part, be the accidental consequence of a body form that evolved for reasons unrelated to drag (e.g. large rounded eyes for visual acuity, elongate abdomen for passive flight stability), but it probably also reflects selection by requirements for rapid flight.

The power required to overcome parasite drag (Pennycuick, 1969) can probably be regarded as nearly negligible for large insects operating at or below their normal cruising speed (e.g. Dudley and Ellington, 1990b). At high speeds, however, parasite power may become a substantial fraction of total power. The C_D

estimated by Azuma and Watanabe (1988) was 1.25, 2–3 times my values, based on the assumption that drag on the body of a dragonfly is about twice that on a smooth cylinder of similar dimensions (A. Azuma, personal communication, 1990). Fig. 6 shows the effect on their power curve of substituting the lower values of C_D . The power reduction at their estimated top speed is about 20%, resulting in an increase in maximal speed of about 1.5 m s^{-1} . Drag and parasite power will, of course, be higher if the body is not parallel to the relative wind, but during high-speed level flight, the body angle of dragonflies is usually very close to horizontal (Azuma and Watanabe, 1988; M. L. May, personal observation).

Available power and its allocation

Substantial uncertainties affect estimates of maximum power and velocity, as Azuma and Watanabe (1988) noted. For example, they assumed that muscle mass is about 25% of body mass, but 40–45% is a much more realistic figure (Marden, 1987; M. L. May, unpublished data). This could increase available power estimates to about 0.095 W and estimated maximum speed to well above 10 m s^{-1} . In contrast, Ellington (1985) argued that, for locust muscle, and, by inference, for other insects with synchronous flight muscle, maximum specific power output should be about 80 W kg^{-1} , rather than 260 W kg^{-1} as assumed by Azuma and Watanabe (1988), following Weis-Fogh and Alexander (1977). Ellington's figure seems to be borne out by recent direct measurements (Stevenson and Josephson, 1990). Allowing for the fact that only about 7% of dragonfly muscle volume is sarcoplasmic reticulum (Smith, 1966), rather than 20% as in locust, but assuming that shortening speed and strain rate are similar to those of locust muscle, specific power may be roughly 100 W kg^{-1} . If so, the power available to *A. parthenope* would be less than 0.04 W.

A further complication is that inertial power may be spared to an unknown degree by elastic recovery of kinetic energy of the wings (Weis-Fogh, 1972; Ellington, 1985). Maximum power savings for the flights measured by Azuma and Watanabe (1988) could be about 30% (Fig. 6; these estimates do not include the effects of wing virtual mass, since they were not considered in calculating the original power curve). Inertial costs are lower compared to aerodynamic costs in dragonflies than in bumblebees (Dudley and Ellington, 1990*b*), probably because wingbeat amplitude is unusually low in dragonflies (Azuma and Watanabe, 1988; Norberg, 1975), and because moments of inertia per wing (and thus, roughly, per unit of aerodynamic surface) tend to be low relative to wing length (estimated from May, 1981*a*, and compared to data for Diptera, Hymenoptera and Lepidoptera from Ellington, 1984).

Inertial power requirements might continue to increase at high velocity and/or acceleration, since Rüppell (1989) found marked increases in both wingbeat frequency and stroke amplitude under such conditions. Based on his data for *A. junius* flying at 7.5 m s^{-1} , I calculated approximate inertial power requirements, assuming no elastic energy storage; these results also appear in Fig. 6. The total markedly exceeds the predicted maximum available power, particularly when

requirements to overcome parasite drag are added. This calculation takes no account of profile power costs, which are likely to be substantial at high velocity (Dudley and Ellington, 1990b).

Moreover, although power required for hovering, as estimated by Azuma and Watanabe (1988), is about equal to the maximum available power (Fig. 6), Marden (1987) showed that dragonflies can lift about 2.5 times their weight during take-off. They may use this capability naturally when capturing very large prey (a rare event for *Anax* but fairly frequent for some species; M. L. May, personal observation) or when males support females during tandem mating flights (females may stop beating their wings for considerable periods during such flights; M. L. May, personal observation). If induced power during hovering is accurately predicted by the actuator-disk equation (Pennycuick, 1969), this result implies the capability for a 3.9-fold induced power increase, i.e. from about 0.006 W to 0.022 W in *A. parthenope* or *A. junius*. This represents a minimum estimate of induced power, since actuator-disk analysis assumes uniform wing disk loading and does not account for power losses due to wake vortices (Ellington, 1984). The extra power for load lifting, i.e. at least 0.016 W, is apparently in excess of maximum specific power, even without accounting for the effects of wing virtual mass or possible increases in profile power.

The discrepancy might be accounted for in two ways. First, power for hovering may actually be little higher than that required for forward flight at $2\text{--}3\text{ m s}^{-1}$. This is obviously at variance with the calculations of Azuma and Watanabe (1988) but is in accordance with the results of Dudley and Ellington (1990b) for bees. In that case, the addition of 0.016 W would bring the total very close to the estimated maximum. Alternatively (or in addition), if (1) wingstroke angle and frequency were similar to those in hovering *Aeshna juncea* (i.e. 60° and 36 Hz, respectively; Norberg, 1975), another dragonfly similar to *A. parthenope* in size and morphology, and (2) a substantial fraction of inertial power could be recovered by elasticity of the thorax, then the results of Marden (1987) and of Azuma and Watanabe (1988) could be approximately reconciled with estimated maximum power. The assumption that gross kinematics during load lifting is similar to that of hovering *A. juncea* is obviously speculative. Nevertheless, if the estimate for maximum specific power is correct, some reduction of inertial losses seems essential at very high speeds, and probably also at low speeds during load lifting or acceleration. Weis-Fogh (1972) demonstrated the feasibility of very sizable elastic recovery in dragonflies.

Power requirements for hovering and steady level flight have been measured or calculated for a number of flying animals, but costs of natural variation in flight acceleration have rarely been studied. Table 1 indicates that these may be quite large over short periods. In both *A. junius* and *M. taeniolata*, the maximum power due to horizontal acceleration alone is close to the total available sustained power estimated from average flight muscle mass, again on the assumption of 100 W kg^{-1} muscle. Naturally these individual, extreme figures need to be interpreted cautiously, since the possibility of wind- or gravity-assisted acceleration or simple

measurement error cannot be ruled out. Nevertheless, in 10% of measurements, calculated power expenditures for acceleration were at least 27% of available power and, for *Anax*, about equal to Azuma and Watanabe's (1988) estimate of the minimum cost of steady flight. Thus, large fast-flying species may operate near their maximum power capacity for a significant fraction of the time, even when flying at moderate speed.

The average power expended on acceleration, assuming that deceleration was entirely passive, was 9.8–11.5% of estimated available power for *A. junius* and *M. taeniolata*. The significance of this power requirement to the energy budget of large patrollers is uncertain, but these average expenditures would be 25–30% of the minimum power requirements of *Anax* estimated by Azuma and Watanabe (1988) during level flight.

Power associated with acceleration was substantially lower in proportion to estimated available power for *E. cynosura* and *M. atra* (2.0 and 3.7%, respectively), not because these species accelerated less rapidly but because their average velocity during acceleration was much lower. As noted above, the films probably missed the periods when extra power demands were greatest, but it seems reasonable that these were less frequently very high and had less overall effect on energy budget than in the large patrollers.

In summary, flight at speeds sometimes recorded in the field probably pushes power output close to its upper limit, despite relatively well-streamlined bodies that reduce parasite drag below previous estimates; hovering or rising with a load may also require near-maximal power. Horizontal acceleration at moderate speeds can greatly increase power demand for brief periods and, in some species, might contribute appreciably to total energy expenditures. Rapid climbs and maneuvers, not studied here, must add still more to power requirements. It appears likely that dragonflies routinely, albeit for short intervals, operate near their maximum sustainable power output during flight.

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