

On the Scaling of Dragonflies

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ABSTRACT

Anisopteran dragonfly allometry is discussed. Induced power during hover is found to scale with body mass raised to the $\sim 7/6$ power. The possible existence of an upper body mass limit is suggested and a scenario where the maximum load factor for flight manoeuvres decreases with size. Some brief comments are also made about Meganisoptera, bats and birds.

1 INTRODUCTION

Any correlation in the scaling of micro-air vehicle parameters would merely reflect the design tools employed. In contrast, correlations found in the scaling of flying insect (Pterygota) parameters could offer insight into the principles that govern the evolution of their morphology. Dragonflies (Odonata, Anisoptera) are of interest in this regard since their physiology may have evolved over the past ~ 180 million years. In the present epoch their adult forms have wing lengths, L , varying between ~ 15 mm and ~ 85 mm, but it is not known what ecological and/or physiological factors constrain their size. One possibility is that adult upper size limit is constrained by flight power demands.

Suppose that the scaling of any flying creature is exactly isometric. In this idealised case the total wing area, S , scales with L^2 and total body mass, m , with L^3 . In stationary hover (outside ground effect), according to simple Rankine-Froude theory, the time-averaged, ideal, induced power is given by $P_{\text{ind}} = W^{3/2} / (2 \rho A)^{1/2}$, where $W = mg$ is the total body weight, ρ is the atmospheric density and A is the actuator area which varies with L^2 . Consequently, P_{ind} scales with $L^{7/2}$, or with $m^{7/6}$. Since the 'engine' (flight muscle apparatus) may be expected to be less than some maximum feasible fraction of the total body mass and the mass-specific power output must also be constrained, the maximum feasible

power output may reasonably be expected to scale with m . At first sight, this divergence in scaling indicates a possible fundamental limit: at some upper size the power required to hover would exceed the engine power available or, alternatively expressed, some upper feasible body mass would be reached. This Flight Power Size Limit (FPSL) hypothesis was similarly proposed by Pennycuik [1] for birds and by Lindhe Norberg & Norberg [2] for bats. Unfortunately, whilst the FPSL is compelling, it is difficult to confirm or disprove.

As introduced above, the FPSL hypothesis is over-simplistic. For dragonflies (and for other flying creatures) a number of complicating factors need to be considered. First, the scaling of parameters is not isometric. Second, the total flight power in hover is also determined by the wing profile and inertial power of the flapping quad-wing configuration. Third, the muscle power output of dragonflies may not be a simple linear function of muscle mass and could be affected by the efficiency of the power production process - which is influenced by heat transfer. Fourth, the maximum power output required by any dragonfly species is unlikely to be determined by the need to perform stationary hover. All species must necessarily perform more power demanding flight manoeuvres during conspecific combat/mating as well as during predator-prey interactions. Male dragonflies also carry females during copula and females carry significant egg loads. In other words, the behavioural repertoire (which strongly influences fitness for natural selection) is dependent on the ability of any species to generate excess power and thrust, i.e. each species must be capable of achieving a maximum thrust NW , where N greater than unity.

All these complicating factors will be partially addressed in the following presentation. Despite many unresolved issues and concerns, it is confirmed that for anisopteran dragonflies P_{ind} does scale with $\sim m^{7/6}$ and the FPSL hypothesis remains plausible and warrants further investigation.

2. ALLOMETRY

In biology, a convenient description of scaling is referred to as “allometry” - the premise that some physiological parameter, y , varies as a simple power of another parameter, x , i.e., $y=x^n$. Although biological systems may have fractal characteristics, there is no proven fundamental rationale for any allometric relation among species in any genus, family, or order. It is therefore important to bear in mind that allometry is just a convenient empirical description of parameter scaling.

Anisopteran dragonfly families include: Aeshnidae, Petaluridae, Gomphidae, Libellulidae and Corduliidae. The allometry of each of these families is different and dependent on the sample chosen [3]. For example, for Aeshnidae, May [3] found that m scales with $L^{2.750}$ and wing area, S , scales with $L^{2.076}$. For a larger sample of Anisoptera from four of the aforementioned families, m scales with $L^{2.586}$ and S with $L^{1.749}$ [3, 4]. It should be noted that across these four families wing aspect ratio increases as size increases, since L^2/S scales approximately with $L^{0.25}$, but within the Aeshnidae aspect ratio remains roughly invariant. This illustrates that caution is needed when comparing samples from different families.

Before determining the scaling of induced flight power, it is worthwhile considering the non-isometric scaling of mass. In order to maintain constant mass-specific induced power, among species of varying size, total body mass would have to scale with L^2 , but this is evidently not feasible. Wing mass, m_w , is not a dominant mass, but illustrates the difficulty of such scaling. If m_w scaled with L^2 , then large wings would become too flexible (see section 4.4). In a sample of 32 Anisoptera, unpublished data (see acknowledgements) reveals m_w actually scales with $L^{2.826}$. Similar structural arguments apply to the thoracic cage that must withstand muscle contraction forces and to the abdomen that acts as pitch counter-balance to the head and thorax. Some body items, e.g., the compound eyes, might vary in a manner closer to L^2 , but the mass of major structural items are expected to vary with $\sim L^3$ in order to maintain a constant structural safety factor. The only possibility to (partially) circumvent this structural scaling demand would be for the load factor, N , to decrease with size.

To date, no evidence has been presented in the literature to show that the dragonfly wing flapping sweep angle, ϕ , varies with scale (in any family) and it will assumed this parameter is invariant hereafter, such that the effective actuator area, A , scales exactly with L^2 . Hence for the Aeshnidae, combining the aforementioned allometric relations predicts that ideal induced power P_{ind} scales with $L^{3.125}$, or with $m^{1.136}$. In this case, the scaling constant can be found noting that when $L=62.2$ mm, $m=1.09$ g [4].

3. INDUCED POWER SCALING

3.1 METHOD

In this study, instead of simply combining allometric relations in order to obtain the scaling for P_{ind} (like the previous section), the induced power of individuals of known body mass and forewing length, L , was first calculated assuming the actuator area is directly proportional to L^2 . Forewing length was used except in a minority of cases when hind-wings were larger, and then the latter was used to define L .

A sample of 328 individuals with masses ranging from 52 mg and 2710 mg from five families was used: 295 Libellulidae, 26 Aeshnidae, 5 Petaluridae, 1 Gomphidae, 1 Corduliidae. Of these, 314 individuals were measured in the USA (see acknowledgements), 12 were measured by the author in Australia [4] and 2 were measured in New Zealand (see acknowledgements).

3.2 RESULTS

A log-log plot of the calculated P_{ind} values is shown in Fig. 1. It can be seen that P_{ind} scales remarkably closely to with 7/6 power index as expected from isometric relations, i.e. $P_{ind} \propto m^{1.168}$ when the best fit for body mass is $m \propto L^{2.618}$.

Removing all the Libellulidae, reducing the sample to 33 individuals, alters the mass range to 513-2710 mg and the scaling becomes $P_{ind} \propto m^{1.154}$ and $m \propto L^{2.99}$.

Isolating the Libellulidae alone alters the mass range to 52-642 mg and the scaling shifts to: $P_{ind} \propto m^{1.154}$ when $m \propto L^{2.353}$. When 25 *Plathemis lydia* and 12 *Perithemis tenera* are removed from this Libellulidae sample, the scaling shifts to $P_{ind} \propto m^{1.159}$ and $m \propto L^{2.489}$.

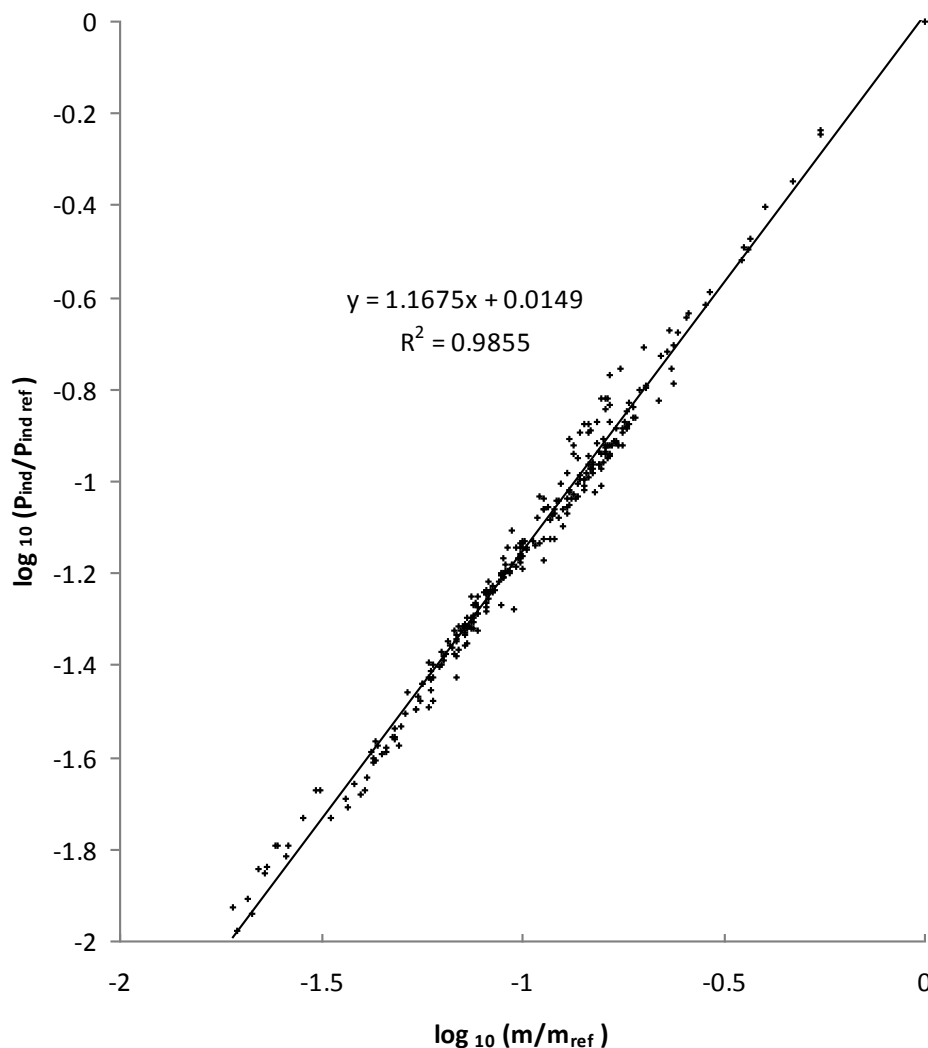


Figure 1 - Ideal induced power of 328 individuals with $m_{ref} = 2710$ mg

4. DISCUSSION

4. 1 FLIGHT POWER SCALING

The flight power of any animal is the dependent on distinct separable terms that could all scale differently. The total flight power is the sum of: the ideal induced power, P_{ind} ; the aerodynamic profile power required to flap the wings $P_{profile}$; the inertial power associated with oscillatory flapping motion, $P_{inertia}$; the sensory and control system power, $P_{sensory}$; finally, the basal metabolic power, P_{basal} , which is the minimum power level during rest. Unfortunately it is not yet possible to arrive at such a confident scaling for all these flight power terms.

Although the kinematics of (insect) flapping has been extensively described in the literature, the scaling of profile power is less often specified. At simplest, for rigid wings, $P_{profile}$ varies in proportion to $\rho S \phi^3 L^3 f^3 C_{Dp}$ where f is the flapping frequency and C_{Dp} is the time-averaged profile drag coefficient which could be a weak function of Reynolds number.

For anisopteran dragonflies May [5] found that flapping frequency scales as $L^{-0.473}$. The unsteady flow over corrugated flapping dragonfly wings is likely to involve leading edge separation, not steady laminar attached flow for which Reynolds scaling would be significant. If Reynolds scaling is ignored, then using May's findings $P_{profile}$ scales $L^{3.33}$ or with $m^{1.297}$. This is similar to the

$\sim m^{7/6}$ scaling of induced power, but the correlation is somewhat poorer and the power index for P_{profile} is strongly influenced by the sample chosen. For a sample with mass proportional to $L^{2.887}$, P_{profile} should scale directly in proportion to P_{ind} at $N=1$ when May's frequency scaling is used. In order to arrive at a more confident scaling the flapping frequencies and sweep angles of individuals would have to be measured and then used to calculate individual P_{profile} values. It would also be necessary to predict how C_{DP} varies with Reynolds number and other flow conditions in the domain of interest.

The magnitude and variation of the flapping inertia power term, P_{inertia} , is also poorly constrained. For a perfect elastic oscillating system the inertial energy invested into each stroke is fully recovered. For a system with zero recovery P_{inertia} will scale with $m_w \phi^2 L^2 f^3$. If m_w scales with m , then P_{inertia} will vary in proportion to P_{ind} provided that $L^2 f^3$ scales with $m^{1/6}$. Using May's flapping frequency correlation that occurs when m scales with $L^{3.486}$. Given the uncertainty with regard to the recovery factor, it is not unreasonable to assume P_{inertia} also scales in proportion to P_{ind} .

The other power terms listed above will vary with size, but are assumed to be relatively small compared to the sum of P_{ind} , P_{profile} and P_{inertia} . Hence the total flight power may simply be reduced to being some constant factor, k_1 , greater than P_{ind} at $N=1$, i.e. $k_1 P_{\text{ind}N=1}$. If the load factor N increases, then the induced power increases to $N^{3/2} P_{\text{ind}N=1}$ and the total lift force must also increase, i.e., Nm is proportional to $\rho S \phi^2 L^2 f^2 C_L$ where C_L is the time averaged lift coefficient. For fixed m , ϕ and C_L , the flapping frequency must increase as N increases, such that $f = f_{N=1} N^{1/2}$, and for fixed C_{DP} , the profile power increases to $N^{3/2} P_{\text{profile}N=1}$. Alternatively for fixed m , C_L and f , the sweep angle may increase such that $\phi = \phi_{N=1} N^{1/2}$ which also leads to the same result. It is therefore tempting to speculate that the total flight power scales with $N^{3/2} P_{\text{ind}N=1}$.

4.2. MUSCLE POWER SCALING

Pennycuik & Rezende [6] suggest the maximum direct muscle-mass-specific power output is $P_m/m_m = f(\sigma_m/\rho_m)\Delta L_m/L_m$ where: m_m is the total flight muscle mass; σ_m is the mean

dynamic stress in the muscle which is independent of scale; ρ_m is muscle density, also independent of scale; L_m is the muscle length; and ΔL_m is its contraction length. It is reasonable to assume L_m scales approximately with L . To determine the variation ΔL_m of it is necessary to consider the lever mechanism of dragonfly wings. Schilder & Marden [7] show that the main basalar muscle contributing to forewing depression is attached to the wing by an apodeme at a distance, L_{lever} , from the wing hinge point. By measuring this distance in a sample of Aeshnidae and Libellulidae, L_{lever} was found to scale with $L^{1.466}$ or with $m^{0.474}$ [4]. Ignoring wing flexing, the basalar muscle contraction distance must be proportional to θL_{lever} where the stroke angle θ associated with basalar muscle is assumed to be invariant with scale (like the sweep angle ϕ). Hence the specific muscle power scales with $f L^{0.466}$. Marden [8] reports that the anisopteran mean muscle mass fraction, m_m/m is ~ 0.46 and there is some confidence that this fraction is independent of scale. Based on these assumptions the body-mass-specific power output of Anisoptera scales according to, $L^{-0.007}$, i.e. it is found to be approximately invariant with scale [4]. However, it should be noted that this result is at variance with Schilder & Marden [7] who use another commendable approach and conclude that muscle power output varies with $\sim m^{7/6}$. If they are correct, then it indicates that muscle power output could match required flight power requirements with N invariant with scale.

4.3. MAXIMUM LOAD FACTOR SCALING

Dragonflies are not only capable of prolonged near-stationary hover, but also rapid darting manoeuvres including short bursts of high speed horizontal flight or vertical climb, in order to fulfil a variety of behaviour functions. To perform such manoeuvres, the lifting load factor N must be significantly larger than unity. Marden [9] performed artificial load carrying experiments on a variety of insects and found that load factors of $N=2-3$ are typical. Males and female dragonflies also fly in copula, and there is some evidence that the males (of relatively large species) are capable of lifting females alone without female assistance, which also suggests that load factors of $N \sim 2.2$ can be sustained [4].

If the required total flight power is given by $P_{\text{tot}} = k_1 N^{3/2} P_{\text{ind}N=1} = k_1 N^{3/2} m^{7/6}$, but maximum muscle power output is $k_2 m$, then the maximum feasible size is given by $m_{\text{max}} = (k_1/k_2)^6 N^9$ when N is assumed to be scale invariant. This relation appears to implausibly sensitive to both the constants $k_{1,2}$ and N . Another possibility is that N is a function of scale: if N scales as $m^{-1/9}$ (i.e. it is just a weak function of size), then the maximum flight power varies linearly with body and muscle mass. In this case there is no body mass limit, but a point is reached when N declines to 1. For example, if existing species have $N=2$ at $m=1$ g, then $N=1$ is reached when $m=500$ g. Such an extreme limit could only possibly apply to the Palaeozoic Meganisoptera, see section 4.5.

Evidence is clearly needed to substantiate the speculation above. Perhaps the best way forwards is to perform more artificial lift load experiments on a wide mass range of Anisoptera, where wing beat frequency is also recorded. Such experiments would have to be well designed, since some species may have unnatural responses to artificial loading. Use of flight dynamic data might also be revealing, although agility it is not only related to excess thrust-to-weight. Flight agility may improve with reduced wing loading. As size increases, there is a trend for W/S to increase, but the correlation is not strong possibly because some species opt for longer endurance gliding-type flight. As W/S increases, flight speeds in level flight increase assuming the mean cruise lift coefficient is invariant. However, lifting turn radii are likely to decrease as W/S decreases. If larger species are less agile than smaller ones, then it may not be a result of reduced N , but increases in W/S .

At some future date, it may be possible to attach strain gauges to dragonfly wing spars (costa and radius veins) to deduce the forces during flight and thereby find the total flight power output.

4.4. SCALING OF WINGS

Dragonfly wing geometry provides evidence of maximum feasible flight loading. For fixed dynamic pressure, as size increases the aerodynamic forces on the wing would vary with NS and the wing bending moment scales with NL^3 . Using simple beam bending theory, in order for

the wing bending radius of curvature to vary in proportion to L , for fixed elasticity, the sectional second moment of area of the main wing spars, I_{xx} , would have to vary as NL^4 . The main spars are arranged in a corrugated layout at a distance, λ , from the neutral plane, such that $I_{xx} = \sum s_i \lambda_i^2$ where s_i is the cross sectional area of each spar (or vein), Fig. 2. By comparing the values of s_i and λ_i for different species at the same relative wing position, it would be possible to find the actual scaling of I_{xx} . The wing mass could also be verified using $m_w = \sum s_i l_i \tau_i$, where l_i is the effective length of each spar and τ_i allows for spar tapering. Without reliable detailed spar data, however, a simplifying assumption is required to make progress: if the wing profile has some optimum thickness-to-chord ratio, then λ would be proportional to wing chord. For Anisoptera, chord scales with $\sim L^{0.75}$. Assuming the aforementioned result that m_w scales with $L^{2.826}$ and also with the average value of $s_i L$, it follows that s_i values scale with $\sim L^{1.826}$, i.e. I_{xx} scales with $L^{3.326}$. This indicates that N would have to scale with $\sim L^{-0.6}$ which across a range of 15 to 85 mm is too severe to be plausible. On the other hand, for Aeshnidae chord scales with $\sim L$ and I_{xx} scales with $L^{3.826}$ indicating N scales with $\sim L^{0.17}$. This illustrates the necessity to establish an accurate scaling of I_{xx} .

Note also: as size increases, W/S increases, hence dynamic pressure should strictly not be held fixed.



Figure 2 - Cross section through wing of *Petalura ingentissima* set in wax with corrugation depth ~ 1.1 mm, see acknowledgements

4.5. COMPARISONS

Of course, extant dragonflies are not the heaviest known flying insects. The largest recorded dragonfly body mass is 2.71 g for one female *Petalura ingentissima* [4], whereas, for example, the author measured three individuals of the Empress Cicada, *Pomponia imperatoria*, with masses of 6.84-7.83 g. The past existence of

Meganisoptera with wing spans up to ~710 mm also demonstrates that much larger dragonfly-like insects were feasible in the atmospheric conditions of the Palaeozoic. Although the fossil record of megalisopteran bodies is sparse and estimation of their mass is speculative, one of the largest species may have had a body mass of ~34 g [4], see Table 1.

	<i>Petalura ingentissima</i>	<i>Pomponia imperator</i>	<i>Meganeuropsis permiana</i>
Mass/g	2.71	7.83	34? [4]
Forewing /mm	83	83	330
Thorax width /mm	12	24	28? [4]
Body length/mm	122	64	?
Forewing area/mm ²	1273	2282	~11,000

Table 1 – Comparison of large insects

Disregarding atmospheric changes, it seems unlikely that any extant dragonflies are close to any FPSL. Nevertheless, it is still possible that selective pressures presently limit extant dragonfly size. If predation of dragonflies by birds is a strong selective pressure, then the ability to evade predation during flight becomes important, i.e. decreased N would reduce fitness. Without this pressure, during the Palaeozoic (before the emergence of birds and pterosaurs), large megalisopterans may have been relatively sedate fliers with limited load lifting capability [4]. If this speculative viewpoint is correct, then collaborative evidence might be sought in wing geometry parameters: compared to extant dragonflies, megalisopteran wings would have had relatively thinner spars and/or the relative wing corrugation depth would be reduced.

Some comparisons with the possible FPSLs for extant birds and bats are also worth mentioning. Bird species that are capable of low specific power soaring are much larger than species that depend on prolonged hovering. Altshuler *et al.* [10] studied the load lifting capability of 677 individual hummingbirds representing 75 taxa with masses ranging from ~2.2 to ~12 g, at four different altitude settings. They found that wing beat frequency varies with muscle mass according to m^{-a} where the index $a = 0.43-0.591$, and total lifted mass varies according

to m^b , where $b = 0.8558-0.6474$. As they point-out, the latter result is in contrast to Marden's proposal for universal isometric relation between total lifting load and muscle mass [11].

Lindhe Norberg & Norberg [2] propose a FPSL limit of ~1.6 kg for bats. For bat body masses between 35 and 700 g, they found flight power varies as $m^{1.18}$ (close to the isometric expectation), but wing beat frequency varies with $m^{-0.27}$ and muscle power output varies with $m^{0.73}$. This decline in specific muscle power with size may result from energy limits influenced by heat transfer, i.e. maximum permissible body temperature.

5. CONCLUSIONS AND RECOMMENDATIONS

The scaling of dragonfly ideal induced power shown Fig. 1 agrees remarkably well with the $m^{7/6}$ allometric relation predicted for birds [1] and bats [2]. If profile power and inertia power also scale in this manner (and preliminary findings indicate this is possible), whilst muscle power output scales linearly [4, 6], then it's possible that the upper mass of dragonflies is constrained. However, such a limit must be established at the maximum loaded flight power condition, and it may be a 'soft' selective limit that is dependent on the possible decline of the load factor N with size. It is therefore recommended that artificial lift load experiments, like those performed by Marden [9] on insects and Altshuler *et al.* [10] on hummingbirds, need to be performed on a wide mass range of Anisoptera species to determine the scaling of N with size. In such experiments wing beat frequency needs to be recorded to arrive at an allometry for total flight power at the maximum loaded condition. Another promising method to determine the scaling of N is to examine the variation of wing structural geometry parameters, and/or by possibly strain gauging wing spars to obtain in-flight load measurements. With advances in micro-air-vehicle technology, in-flight data logging should be feasible.

Wood [12] states "biology is a useful tool" for the development of flapping wing micro-air vehicles (as small as 60 mg), but equally such engineering efforts could be useful in our attempts to better understand the evolution and physiology of flying insects.

ACKNOWLEDGEMENTS

Much of the data used in section 3 was kindly supplied by Wade Worthen and Ruud Schilder (whose data also included wing masses). Two Uropetala (Petaluridae) specimens were kindly measured by Mark Galatowitsch in New Zealand. Geoff Monteith measured the mass of the heaviest Petalura (section 4.5). The image shown in Fig. 2 was obtained by Suk Yeo and Pengtu Zhang during 4th year undergraduate projects with the support from the RMIT Microscopy and Microanalysis Facility.

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