Size limits on dragonflies

Stephen W. Hurrell
email: papers@dinox.org

Published: 29th June 2022

Abstract

Dragonflies are obviously limited in size by physical constraints during flight. However, various studies on dragonflies have shown that the exact physical mechanism limiting their size is still unclear. This paper shows that increasing dragonfly size would increase the stress levels in the wing. The increasing wing stress must exceed the maximum allowable stress in the wing tissue at some point and the wing would begin to fail if the dragonfly became any larger. It is proposed that failure of the wing is the true physical size limit for dragonflies.

Key words: Dragonfly, Size limits, Wing failure

1. Introduction to Dragonflies

Present-day dragonflies are relatively large insects noted for their speed and aerial agility. The wings of dragonflies support their weight during flight and have a corrugated arrangement to provide strength and lift. The wings beat and twist independently of each other in a figure-of-eight motion which means they are very aerobatic and can easily fly forwards, backwards and sideways, as well as hover. They often use hovering to spot mates and small insect prey which are caught and devoured in flight.

Dragonflies belong to the order Odonata (toothed jaw) which has three suborders, the Anisoptera (dragonflies), the Zygoptera (damselflies) and the Anisozygoptera. Dragonflies always hold their wings open even at rest and have large eyes which occupy most of the head. They comprise about 5,500 species. Damselflies hold their wings over their body when at rest and have a narrow body. They comprise about 2,500 species. *Anisozygoptera* have wings similar to damselflies but bodies similar to a dragonfly. They are a small suborder that only has two living species although the fossil record is more diverse.

Dragonflies start their lives as aquatic larva which might last for up to a year or more. Most of these live in fresh water although there are a few marine species. Once the larva has matured it will climb up a stem or rock near the water's edge, most likely at night to avoid predators, and transmute into an adult dragonfly.

Male dragonflies hold territories in order to attract a mate. They grasp their mate in flight and some species may continue to fly in tandem for several hours. Eggs are laid in or near water, perhaps on plants. Adult dragonflies usually live for a few months at most.

2. Size limits for dragonflies

Dragonflies are obviously limited in size. Present-day dragonflies seem to be considered large over about 120 mm wingspan but some individuals are larger. Wilson (2009) attempted to give a definitive answer to the question "Which is the world's largest dragonfly living today?" for the Worldwide Dragonfly Association. The article described how there is "a lot of confusing and somewhat conflicting information available in the published literature". The extant dragonfly often credited with the largest wingspan was *Megaloprepus caerulatus*, from South America. This huge but dainty insect was said to have a wingspan of up to 191 mm by various sources. However, 53 specimens examined had a maximum wingspan of 173 mm. It was noted that "there are accounts in the literature and on the worldwide web (notably Wikipedia) indicating *Anax strenuus*, endemic to Hawaii, is one of the World's largest dragonflies with a maximum wingspan reported of up to 190 mm." Several specimens examined measured less than 150 mm wingspan and as such it was considered extremely unlikely that even an exceptionally-sized *Anax strenuus* specimen would attain anywhere near 190 mm. The second largest wingspan appeared to be the gigantic *Tetracanthagyna plagiata* from Malaysia and Borneo. This insect has a wingspan measuring up to 163 mm. The third largest wingspan belongs to *Petalura ingentissima*, which is found in the wet tropics in northern Queensland, Australia. This dragonfly has a wingspan of up to 162 mm (although most specimens measured were significantly smaller). Using these assumptions the largest wingspan measured for the largest three species of extant dragonflies were: 173 mm (*Megaloprepus caerulatus*), 163 mm (*Tetracanthagyna plagiata*) and 162 mm (*Petalura ingentissima*).

In theory, all animals are limited in size by the scale effect in our present gravity. The general principle has been known since Galilei (1638) demonstrated the scale effect on life. Due to the scale effect, as any object increases in size its volume increases quicker than its area and its area increases quicker than its length. Scale effects mean that larger animals have greater stresses imposed upon them because of their larger size. These basic principles should apply to dragonflies. For dragonflies, just as for every form of flying creature, there should be an upper limit to how large they can be.

Before the 1980s it was generally assumed that take-off and hovering were limited by the maximum size of the dragonflies' flight muscles. Pennycuick (1968) had shown that flying animals such as birds struggle to take off as they become larger so it seemed logical that this would be similar for dragonflies. Most limits to size focused on hovering. It seemed that helicopter theory could be used to provide rough estimates of power required for hovering insects. The power per unit mass needed for hovering, by a helicopter of mass m with a rotor of radius r, is $(mg^3/2pr^2)^{0.5}$, where g is the gravitational acceleration and p is the density of air. This would suggest that if all hovering insects of different sizes were geometrically similar they must reach a size limit due to a lack of power as they become larger.

However, when Marden (1987) measured a number of dragonflies to determine the maximum lift produced during take-off he found that all sizes of dragonfly could easily take off and hover. Power production wasn't a problem for dragonflies and Marden showed that all dragonflies can lift about 2.5 times their weight during take-off. Muscle capacity wasn't a size limit. The muscle power lift was found to be approximately 60 N/kg flight muscle mass. Even more confusingly the actual lift capacity tracked the mass of dragonflies in an almost linear manner, so in theory there shouldn't be any limit to a dragonfly size. Marden (1994) later returned to the problem to suggest that the actual limit to size was related to burst and sustainable lift performance, although the exact mechanism wasn't clear.

Noting that most studies consider only hovering or slow flight, May (1991) proposed that high speed and acceleration was especially relevant to dragonfly performance. Perhaps this was the limit to a dragonfly size. However, the power required for repeated acceleration and deceleration seemed to be about the same as the power for steady flight. The maximum power due to horizontal acceleration alone was close to the total available sustained power from the flight muscle mass. It seemed that large fast-flying dragonflies were operating near their maximum power capacity for a significant fraction of the time, even when flying at moderate speed.

Even today, the size limit for a dragonfly is not clearly understood and is still widely debated. Dorrington (2018) rightly stated "It is not known what ecological and/or physiological factors constrain their size" when he discussed the problem. Dorrington used theoretical considerations to propose that the induced power would scale with body mass raised to approximately 7/6 power, seemingly reiterating the theoretical considerations that size is limited by dragonfly flight muscles. This

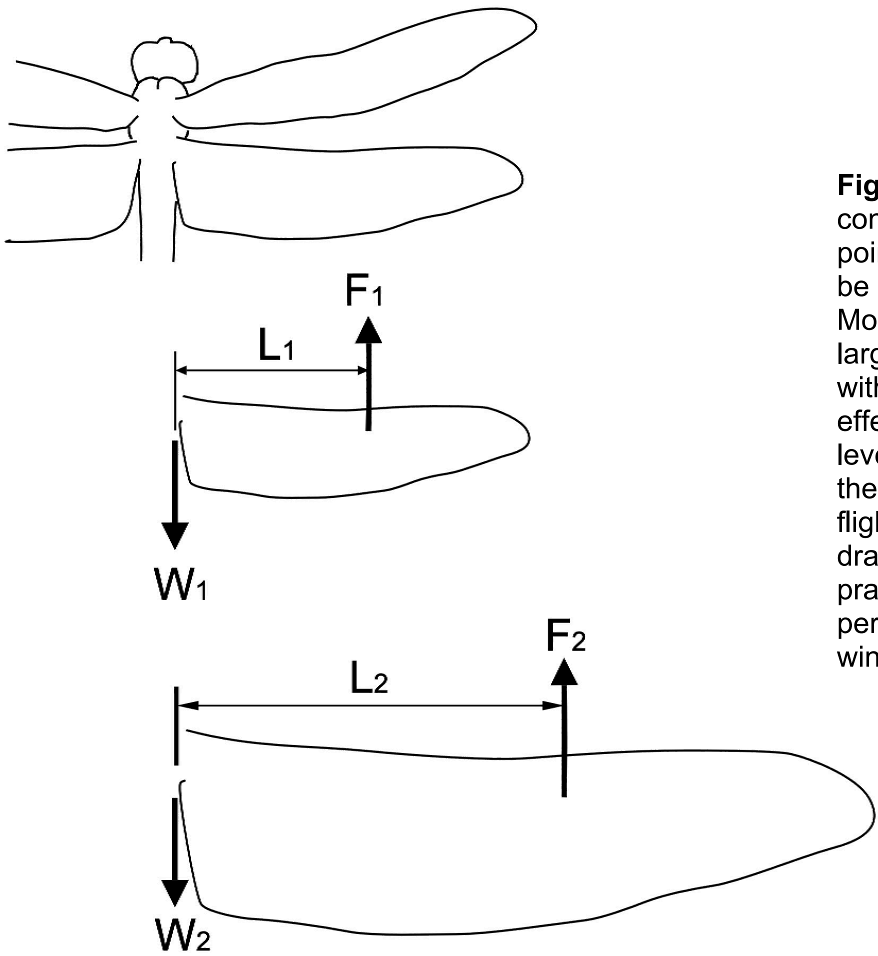

Figure 1. Two simplified dragonfly wings considered as cantilevered beams with point loading. The highest stress would be at the point of maximum Bending Moment at the base of the wing. The larger wing would have a higher stress within the wing fibres due to the scale effects of larger size. This higher stress level due to increasing size would limit the maximum size of a dragonfly while in flight. (N.B. The wings and forces are drawn in plan view for clarity but in practice the forces would be mainly perpendicular to the main surface of the wing).

would clearly indicate the existence of an upper limit to body mass. However, the proposal ignores the actual measured results reported by Marden (1987) that showed lifting force was approximately proportional to body mass.

So if the maximum size of a dragonfly isn't limited by its flight muscle mass then what is the limiting factor? The wings carry all the loads. Dragonfly wings are highly corrugated to increase the stiffness and strength of the wing significantly, resulting in a lightweight structure with good aerodynamic performance. It is proposed that the maximum stress in the wing fibres must increase with size due to the scale effect until an upper size limit is reached. Any further increase in size will result in the failure of the wing.

The exact relationship between size and wing stress can be calculated. Quantifying the stresses within a dragonfly wing is a complex engineering problem but the calculation can be considerably simplified by viewing the wing as a simple beam with point loading.

With reference to figure 1, a proportion of the weight of a small dragonfly, taken as (W_1), acts at the base of one wing while the lifting force (F_1) acts on the mid-pressure point of the wing at some distance (L_1). The effect of these forces is to produce a maximum stress (σ_{max1}) within the wing fibres that will be related to:

$$\sigma_{max1} = y_{max1} . F_1 . L_1 / I_1$$

Where:

σ_{max1} = maximum stress in outer fibre

y_{max1} = distance to outer fibre from neutral axis

F_1 = force acting on wing

L_1 = distance to force

I_1 = Moment of Inertia

For a simple beam the maximum stress will be at the base of the wing and the Moment of Inertia can be considered to be a simple rectangular section.

Thus:

$$I_1 = b_1 . h_1^3 / 12$$

Where:

I_1 = Moment of Inertia

b_1 = width of stressed section

h_1 = height of stressed section

If the size of the dragonfly is doubled, as shown in figure 1, the maximum stress in the simple wing would become:

$$\sigma_{max2} = y_{max2} \, . \, F_2 \, . \, L_2 \, / \, I_2$$

Equating the larger dragonfly to the smaller one, the maximum wing stress in the larger dragonfly could be rewritten:

$$\sigma_{max2} = 2.y_{max1} \, . \, 8.F_1 \, . \, 2.L_1 \, / \, (2.b_1 \, . \, 2.h_1^3 \, / 12)$$

$$\sigma_{max2} = 2 \, . \, \sigma_{max1}$$

Thus the maximum stress (σ_{max2}) in the larger dragonfly wing is found to be twice the maximum stress (σ_{max1}) of the smaller dragonfly wing. The maximum stress (σ_{max}) within a dragonfly wing follows the simple relationship:

$$\sigma_{max} \propto L$$

It therefore follows that increasing stress due to an increase in size must exceed the maximum allowable stress in the wing tissue at some maximum size. It is proposed that failure of the wing is the true physical size limit for dragonflies.

3. Carboniferous and Permian Giants

Many ancestors of the modern dragonfly were much larger than any extant species, particularly during the Carboniferous and Permian Periods. The largest dragonfly ancestor discovered so far is a species of *Meganeuropsis*. This was discovered by Carpenter (1939) and he estimated it had a wingspan of up to 710 millimetres (28 in).

The large size of these giants has produced much confusion. Could present-day dragonflies reach the size of their ancient ancestors? The fact that many different present-day species of dragonfly all reach a similar upper size limit seems to imply that this is the present-day size limit. If this is correct, other conditions must have allowed larger sizes in the past.

The exact nature of these differing conditions has caused debate for over a century. Harle and Harle (1911) suggested that insect large size could be achieved in either a lower gravity or a denser atmosphere. The concept of a denser atmosphere seemed more believable. The denser atmosphere concept has more recently been modified to include an increased oxygen content. This allowed the insects to be more active by allowing oxygen to be more easily distributed along their tracheal system. Dudley (1998) assumed that many animals would be affected by an increased density with a higher oxygen content. However, Berner (2006) outlined more recent models of atmospheric composition in the Carboniferous that seemed to show that increased oxygen content was both later and slower than required to account for gigantic insects. Nel *et al.* (2008) detailed several very large Meganeuridae during the Permian that contradicted the relationship between size and oxygen concentrations at the time.

If dragonflies are limited in size by the strength of their wings, such gigantic dragonflies would be impossible even in a higher oxygen concentration. Such conditions would not strengthen the wing and would not explain why dragonfly ancestors became larger in the past. An increased atmospheric density also presents difficulties since the wings must still be strong enough to support the total weight of the animal in flight.

On the other hand, if gravity was lower in the past then the wing stress would decrease and dragonfly ancestors could have become larger. Hurrell (2012, p310-312) has used a simple dynamic similarity comparison to calculate the reduced gravity that would allow these ancient dragonfly ancestors to fly.

4. Suggested Citing Format

Hurrell, S.W. (2022). Size limits on dragonflies. http://dinox.org/hurrell2022b

5. References

Berner, R. A. (2006). GEOCARBSULF: a combined model for Phanerozoic atmospheric O2 and CO2. Geochimica et Cosmochimica Acta, 70(23), 5653-5664.

Carpenter FM, (1939). The Lower Permian Insects of Kansas. Part 8: Additional Megasecoptera, Protodonata, Odonata, Homoptera, Psocoptera, Protelytroptera, Plectoptera and Protoperlaria. Proceedings of the American Academy of Arts and Sciences 73(3):29-70 [C. Labandeira / C. Labandeira / R. Day]

Dorrington, G. E. (2018). On the scaling of dragonflies. In *10th International Micro-Air Vehicles Conference (IMAVS, 2018)* (p. 53).

Dudley, R. (1998). Atmospheric oxygen, giant Paleozoic insects and the evolution of aerial locomotor performance. The Journal of experimental biology, 201(8), 1043-1050.

Galilei G. (1638). Discourses and Mathematical Demonstrations Relating to Two New Sciences. Holland.

Harle, E., & Harle, A. (1911). Le vol de grands reptiles et insectes disparus semble indiquer une pression atmosphérique élevée. (The flight of extinct giant reptiles and insects seems to indicate an elevated atmospheric pressure). Bull. Soc/ Geol. France (4). XI. 118-121.

Hurrell, S. (2012). Ancient Life's Gravity and its Implications for the Expanding Earth. In *The Earth expansion evidence – A Challenge for Geology, Geophysics and Astronomy* - Selected Contributions to the Interdisciplinary Workshop of the 37th International School of Geophysics. Aracne Editrice, Roma. https://www.earth-prints.org/handle/2122/8838

Marden, J. H. (1987). Maximum lift production during takeoff in flying animals. *Journal of experimental Biology*, *130*(1), 235-258.]

Marden, J. H. (1994). From damselflies to pterosaurs: how burst and sustainable flight performance scale with size. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, *266*(4), R1077-R1084.

May, M. L. (1991). Dragonfly flight: power requirements at high speed and acceleration. *Journal of Experimental biology*, *158*(1), 325-342.

Nel, A., Fleck, G., Garrouste, R., & Gand, G. (2008). The Odonatoptera of the Late Permian Lodève Basin (Insecta). Journal of Iberian Geology, 34(1), 115-122.

Pennycuick, C. J., (1968). Power requirements for the horizontal flight in the pigeon, *Columbia livia*, Journal of Experimental Biology, 49, 527-555.

Wilson, K. (2009). Dragonfly giants. *Agrion*, Newsletter of the Worldwide Dragonfly Association, *13*, 29-31. ISSN 1476-2552.