



# Dragonfly flight: morphology, performance and behaviour

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Odonata flight performance capabilities and behaviour and their body and wing form diversity are explored, and their interrelationships discussed theoretically and from observational evidence. Overall size and particularly wing loading appear predictably to be related to speed range. In Anisoptera at least, relatively short bodies and long wings should favour high speed manoeuvrability, though further information is needed. Medium and low aspect ratio wings are associated with gliding and soaring, but the significance of aspect ratio in flapping flight is less straightforward, and much depends on kinematics. Narrow wing bases, petiolation, basal vein fusion, distal concentration of area and a proximally positioned nodus – described by a newly defined variable, the “nodal index” – all allow high torsion between half-strokes and favour habitually slow flight, while broad wing bases are useful at higher speeds. The “basal complex” in all families seems to be a mechanism for automatic lowering of the trailing edge and maintenance of an effective angle of attack, but the relative merits of different configurations are not yet clear. There is serious need for more quantitative information on a wider range of species and families.

**Keywords:** Odonata diversity; flight behaviour; flight performance capabilities; kinematics; size; body proportions; wing shape; aspect ratio; first moment of area; venation

## Introduction

Adult Odonata are highly adapted for a wide range of flight capabilities and behaviours. They also vary greatly in size and design. As their flight has been particularly extensively studied (e.g. Bomphrey, Nakata, Henningson, & Lin, 2016; Newman, 1982; Ruppell, 1989; Thomas, Taylor, Srygley, Nudds, & Bomphrey, 2004; Wakeling, 1997; Wakeling & Ellington, 1997a, 1997b, 1997c) they are perhaps the most appropriate of any insect group in which to explore the relationships between morphological diversity and the various techniques, performance capabilities and strategies of flight.

Odonatan flight is unique. In other high-performance insects – Diptera, Hymenoptera, Lepidoptera – meso- and metathorax are effectively combined into a springy, flexible box, with the main power concentrated in the mesothorax. The wings, muscles and thoracic cuticle cyclically store and restore elastic energy, forming a resonant system that imposes narrow limits on stroke frequency. In Odonata, meso- and metathorax are morphologically similar and to a great extent operate independently, being capable of changing their mutual phasing and varying stroke amplitude and instantaneous wing shape and angle of attack both between the segments and on the two sides of the body. Frequency too can be varied – by a factor of 4 in displaying male *Chlorocypha cancellata* (Günther, 2015); and this unique kinematic flexibility allows remarkable levels of

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skill and versatility, reaching extremes in the diverse, complex behaviour patterns of calopterygoid damselflies (Günther, 2006, 2015; Hilfert-Rüppell & Rüppell, 2007; Orr, 2009; Rüppell, 1989).

## **Diversity: behaviour, performance, morphology**

### ***Behavioural categories***

Odonata use flight in gaining food, in territorial defence, reproductive behaviour, escaping predators and dispersal.

Three feeding strategies can conveniently be distinguished, all involving flight. *Hawking* is typical of Aeshnidae, Neopetaliidae, Cordulegastridae, Chorogomphidae, Macromiidae, Synthemistidae, Corduliidae and a few Libellulidae. *Perch-darting* is used by most Libellulidae, Gomphidae, Petaluridae, Calopterygidae and Lestidae. *Hover-gleaning* – taking prey from a surface – is usual in most Coenagrionidae, and can occur in some Aeshnidae and Corduliidae. Hawking and perch-darting are also typical methods of territory defence.

Reproductive flight behaviours include agonistic interactions between males, courtship display, mate-guarding, tandem flight, and oviposition.

Dispersal may take the form of relatively short journeys to find available territories, but can involve major migrations, sometimes involving riding winds and/or thermals over considerable distances.

### ***Performance capabilities***

Most important are:

- (1) Speed range. Relevant speeds are: minimum speed without stalling; maximum speed for escape and pursuit; minimum power speed for prolonged flight in a small area; maximum range speed for long distance migration.
- (2) Stamina, more or less equivalent to power economy.
- (3) Acceleration. This includes linear acceleration, again for escape and pursuit, either in the air or from a perch; and manoeuvrability/agility, ranging from turns “on the spot” to banked turns at high speed. Most Odonata seem to be capable of turning in their own length when hovering or flying slowly, but high speed agility certainly varies considerably.

### ***Morphological variables: size, proportions and wing-venation***

#### ***1. Size***

In the study of flight the most generally useful measurement of size is the wing-loading – the weight carried per unit area of wing, given by weight/total wing area. If all dragonflies were the same shape – isometric – their masses would vary as lengths<sup>3</sup>, and areas as lengths<sup>2</sup>, so that wing loadings would vary in proportion to length. As Odonata are not isometric, wing loadings will vary according to the insects’ proportions as well as their overall size: lower or higher if the wings are disproportionately large or small.

This is important because, according to aerodynamic theory, characteristic flight speeds increase as wing loading<sup>0.5</sup>. All Odonata are probably capable of hovering – zero ground speed – but the other characteristic speeds would be predicted to increase with size, and even hovering should be more expensive in larger dragonflies. For high speed flight, therefore, large size seems

desirable. In smaller species one would expect disproportionately smaller wings. And the contrary is true: small size and/or disproportionately large wings would favour a slower lifestyle, appropriate for hover-gleaning in vegetation or for aerial predation on slow-flying prey.

How far is this actually the case? We have limited data for Odonata on the costs of hovering or intermediate speeds, and very few reliable values for maximum speeds, but common experience generally confirms that larger, heavier species can fly faster than small ones. Ruppell (1989) recorded speeds of  $7.5 \text{ m s}^{-1}$  for *Anax imperator* and  $10 \text{ m s}^{-1}$  for *Aeshna cyanea*, both with wing-loadings around  $4 \text{ N m}^{-2}$ , while the Zygoptera he measured, with wing-loadings below  $2 \text{ N m}^{-2}$ , had maximum speeds of  $2.5 \text{ m s}^{-1}$  or below, and three libellulids with intermediate wing-loadings flew at intermediate speeds. It is dangerous to generalise. Grabow and Ruppell (1995), measuring 1300 individuals of 30 species, showed that wing loadings vary widely between individuals, between seasons, and particularly between the sexes, with female wing loadings significantly higher than for males, in Zygoptera and aeshnoids at least. Can females fly faster?

## 2. Body proportions

While body shape variables like relative length and bulk probably relate to other aspects of lifestyle, some do have aerodynamic consequences. Disproportionately long abdomens will have higher drag and a higher moment of inertia, and in Anisoptera at least these should tend to reduce manoeuvrability, which will be improved if the body is shorter and the centre of mass near that of aerodynamic force. In Zygoptera, which can move the centre of force by varying their stroke plane, turning speed will be less limited by body inertia (Wakeling & Ellington, 1997b), and abdomens are often absurdly long. In some, hovering Pseudostigmatidae for example, they may well be useful in providing passive physical stability.

Relative muscle size is also likely to be important. Odonata have the highest proportion of flight muscle to body mass of any insect. High instantaneous power would be particularly valuable in fast linear acceleration, and May (1981) and Marden (1987) found significantly greater values in perch-darting Anisoptera, for which this would be particularly useful, than in “fliers” – hawking species.

## 3. Wing proportions

Figure 1 illustrates the wing planforms, at widely different scales, of a selection of Odonata, colour-coded to indicate systematic position. Wing shapes are hard to characterise numerically. The most convenient descriptors are the aspect ratio AR, measuring the relative breadth of a wing pair; and the relative distance of the wing's centroid from its base, as a fraction of its length. AR is given by  $4R^2/S$ , where R is the wing length and S is the area of both wings in a pair on the same segment. The relative centroid-to-base distance,  $\check{r}_1 S$ , is the dimensionless radius of the first moment of area – a convenient measure of the distribution of area along the wing (Ellington, 1984). Both AR and the centroid position, and hence  $\check{r}_1 S$ , are easily found using shape analysis applications such as ImageJ (Wayne Rasband, National Institutes of Health, USA).

In orthodox aerodynamics, AR is a guide to the efficiency of a wing: a high AR delivers a high ratio of lift to drag, and less power is needed to stay aloft. If this applies to Odonata one would particularly expect to find narrow wings in species that fly continually for long periods. Unfortunately, things are not that simple. In the range of sizes and speeds that Odonata occupy, although the cost of overcoming the induced drag, consequent on lift generation, falls with increasing AR, the profile drag of the wings is predicted to rise; and for gliding at least a medium to low aspect ratio is theoretically optimal (Ennos, 1989; Wakeling & Ellington, 1997a). Broader wings are indeed typical of many species that habitually glide, such as trameine libellulids (Figure 1t),

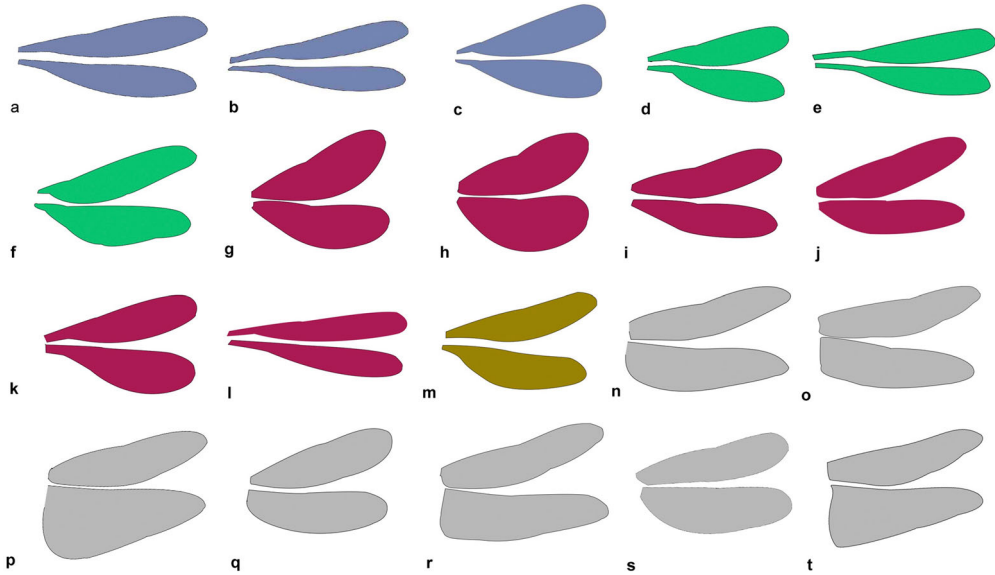


Figure 1. A selection of wing outlines, traced from photographs, to illustrate planform diversity. To different scales. Blue: Coenagrionoidea. Green: Lestoidea. Red: Calopterygoidea. Olive: Epiophlebioidea. Grey: Anisoptera. (a) *Enallagma cyathigerum* (Coenagrionidae); (b) *Austrosticta fieldi* (Isostictidae); (c) *Megaloprepus caeruleus* (Pseudostigmatidae); (d) *Lestes sponsa* (Lestidae); (e) *Perissolestes paprzyckii* (Perilestidae); (f) *Thaumatoneura inopinata* (Megapodagrionidae); (g) *Calopteryx splendens* (Calopterygidae); (h) *Sapho gloriosa* (Calopterygidae); (i) *Hetaerina americana* (Calopterygidae); (j) *Dysphaea ethela* (Euphaeidae); (k) *Aristocypha fenestrella* (Chlorocyphidae); (l) *Watuwila vervorti* (Chlorocyphidae); (m) *Epiophlebia superstes* (Epiophlebiidae); (n) *Petalura ingentissima* (Petaluridae); (o) *Macromia illinoisensis* (Macromiidae); (p) *Chlorogomphus papilio* (Chlorogomphidae); (q) *Cordulephya pygmaea* (Corduliidae); (r) *Libellula pulchella* (Libellulidae); (s) *Tetrathemis polleni* (Libellulidae); (t) *Tramea lacerata* (Libellulidae).

which include the extreme migrant *Pantala flavescens*, and they are also found in the montane Chlorogomphidae (Figure 1p), which soar extensively in rising air. For flapping flight, dominated by unsteady aerodynamic mechanisms (Bomphrey et al., 2016; Thomas et al., 2004) the situation is far less clear theoretically, and experimental evidence is sparse. Phillips et al. (2015), using a mechanical flapper to investigate the effect of AR on the extremely complex, vortex-dominated airflow around insect-sized rectangular model wings, found that lift generation was optimal around an aspect ratio of 6 for a single wing – i.e. AR = 12 for a wing pair – and suggested that this may be why few insect wings have values above 5. Many zygopteran wings are far above this: *Enallagma* (Figure 1a) at *c.*8.5, *Perissolestes* (Figure 1e) and *Watuwila* (Figure 1l) at *c.*10, and *Austrosticta* (Figure 1b) at *c.*11, are examples measured here. The kinematics and wing-phasing in particular flight behaviours and the consequent degree of interaction of the wing pairs will in any case be hugely important. Information on the kinematics of more Odonata is badly needed, and field observations, too, are extremely valuable.

Generalisations are risky. Most hawking Anisoptera have higher aspect ratio wings than most perchers, but there are plenty of exceptions. The greatest contrasts are found among the calopterygoid families. Broad-winged calopterygids (Figure 1g, h) and narrow-winged chlorocyphids (Figure 1l) both indulge in male–male confrontations, but with totally different kinematics. Males of some species of the latter may face each other in the air for up to an hour at a time, so that stamina will be crucial to reproductive success. This suggests that their high aspect ratio wings are extremely efficient, particularly as one pair may be held stationary for significant periods (Günther, 2015; Orr, 2009). Interestingly, broader winged chlorocyphids (Figure 1k) apparently do not perform these extreme prolonged confrontations, and appear to fly

more like Calopterygidae (A.G. Orr, personal communication). Calopterygids, which have some of the broadest wings of all, make extensive use of “clap and fling”, one of many mechanisms for generating high lift that involve the creation of large transient vortices above the leading edge. The wings may need to be broad enough for the mass airflow to reattach to the upper surface, or they will stall.

Relatively long wings may also contribute to high speed manoeuvrability. Short wings aid tighter turning in aircraft; but in flapping flight, where the wings are driving the turn, the greater moments that come from long wings may assist fast banked turns. A long-winged, short bodied dragonfly like *Libellula pulchella* (Figure 1r) would seem ideally designed for high-speed agility.

Aerodynamics may not be the only factor involved. Broad wings make excellent banners. Calopterygidae use theirs in agonistic and courtship display, and this may be a factor in many broad-winged, brightly patterned libellulids.

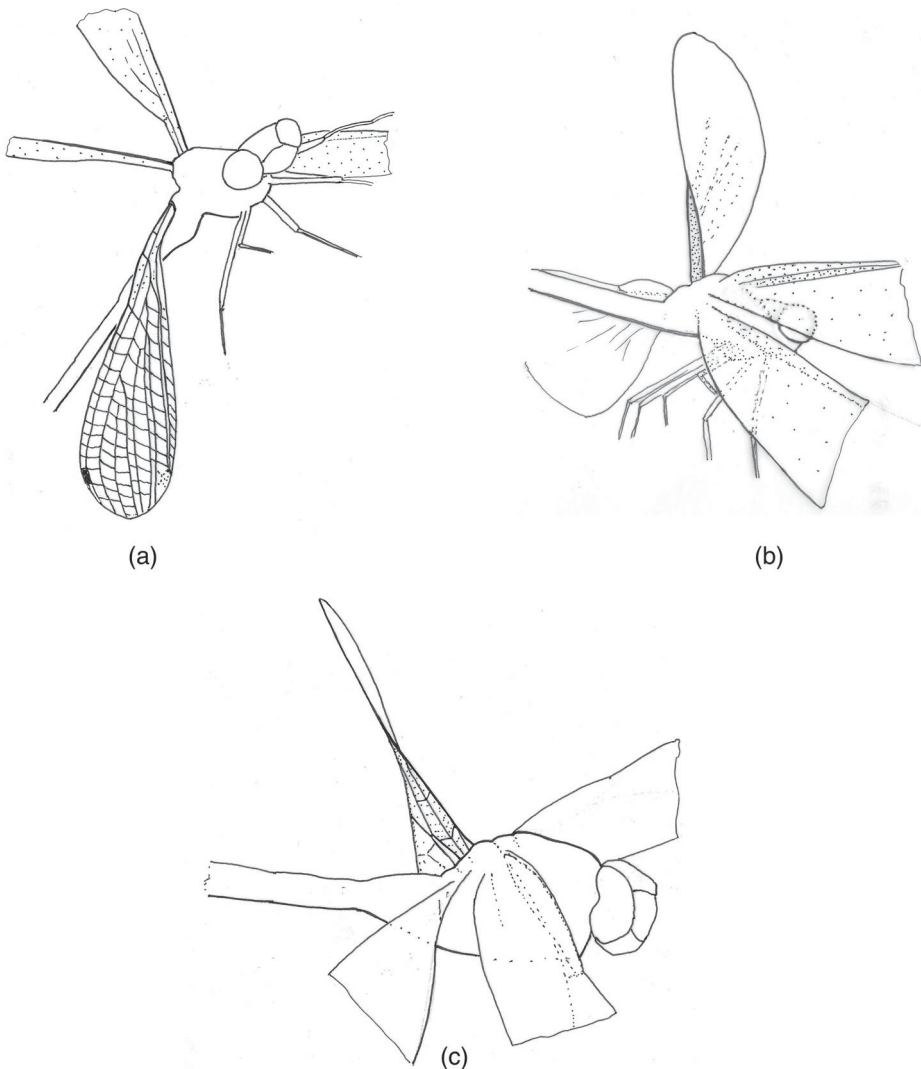


Figure 2. Supinatory twisting in mid-upstroke, traced from published photographs. (a) *Coenagrion puella*, from Dalton (1982); (b) *Calopteryx haemorrhoidalis*; (c) *Aeshna cyanea*. Both from Hilfert-Rüppell & Rüppell (2007).

The distribution of area along the wing, described by  $\check{r}_1S$ , appears in several insect orders to be related to speed range. This makes sense: in slow flight the extreme base of a flapping wing is moving at the same speed as the body and generates little lift. The speed of the airflow past the wing increases linearly along the span, and in habitually slow fliers like coenagrionoid and lestoid damselflies it is advantageous to have the area concentrated towards the distal part of the wing where it has most effect. In fast flight, however, the basal part of the wing *is* effective, and concentration of area toward the base, as in anisopteran hindwings, evens out the distribution of lift along the span and incidentally reduces the wing's moment of inertia, helping to reduce the cost of flapping. The pattern of airflow over the wings is more complex than this implies (Bomphrey et al., 2016; Thomas et al., 2004), but the principle seems to hold.

Narrow-based wings have another important advantage: the closer together are the vein stems, the more easily they undergo passive twisting and the greater is the proportion of the wing area generating lift in the morphological upstroke. Along with a proximal position of the nodus – see the next section – this allows a high degree of wing torsion, clearly seen in photographs and movies of coenagrionoid and lestid damselfs. The two halves of the stroke cycle appear nearly symmetrical, and in combination with a stroke-plane close to the horizontal this would seem ideal for slow, near-hovering flight.

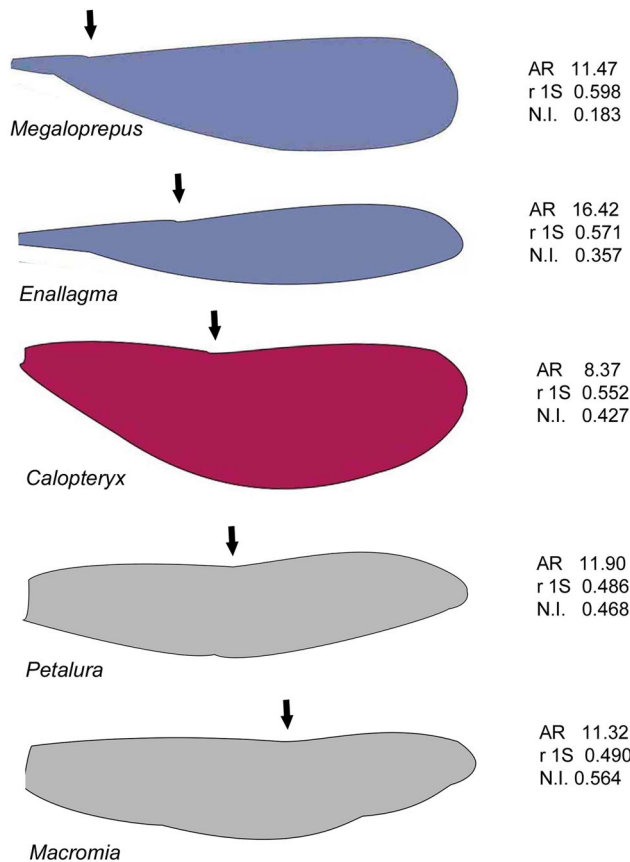


Figure 3. The position of the nodus, the aspect ratio,  $\check{r}_1S$  and nodal index in five forewings. Colours as in Figure 1.

#### 4. Venation

The venational differences amongst Odonata are too many and complex to be discussed here at length (Wootton, 1991; Wootton & Newman, 2008), and the relative importance of many may only become clear through careful computational modelling of particular wing components. Two aspects will be considered: the basal complex, including the arculus and the discoidal cell; and the position of the nodus.

The basal complex is a lever system that responds automatically to more distal loading by depressing the wing's trailing edge and maintaining an aerodynamically effective section and angle of attack (Wootton, 1991). In Zygoptera, upward pressure in the radial area of the wing raises the radial veins around the arculus, forcing down the quadrilateral discoidal cell and creating a cambered section. In Anisoptera it is the median vein that raises the apex of the triangle and hypertriangle, rotating the triangle and the trailing edge downwards. The basal complex takes many forms. Physical models (Wootton & Newman, 2008) indicate that all serve the same basic roles, and the sophisticated computational modelling by Rajabi, Ghoroubi, Darvizeh, and Gorb (2016) has confirmed this; an important contribution to our understanding of the relative merits of particular designs.

The nodus is not a hinge, as in some other insects whose wings undergo transverse bending in the upstroke, but is a shock-absorber, coping with stress concentration at a point where the torsional rigidity of the leading edge spar undergoes a sharp change. The dorsally concave antenodal area is stiffened to both bending and torsion by the three-dimensional primary antenodal cross veins – or by a series of high antenodals in calopterygoids and libellulids. However, distally to the nodus, where there is no free subcosta, the spar is dorsally convex, and is far less resistant to supinatory torsion than the antenodal region, so that the distal area of the wing twists extensively for the morphological upstroke, giving lift on both half-strokes like the sail of a tacking yacht.

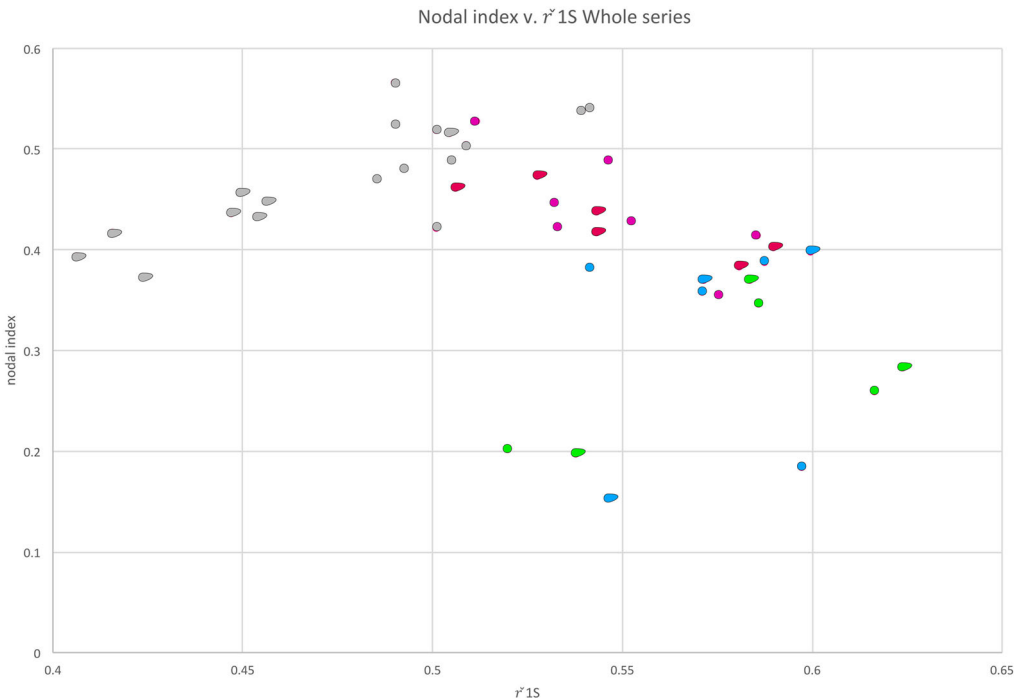


Figure 4. A plot of the nodal index against  $\check{r}_1S$  for forewings (circles) and hindwings (tear-drops) of a selection of Zygoptera and Anisoptera, colour-coded as in Figure 1.

High speed photographs and movies clearly show that the degree of twist and the proportion of the wing that twists vary with the position of the nodus along the span (Wootton & Newman, 2008) (Figure 2). The most extreme torsion is seen in the habitually slow-flying coenagrionoid and lestoid Zygoptera, which tend to operate with a nearly horizontal stroke plane, driving air downwards on both half-strokes, in contrast to Anisoptera which use a more oblique stroke plane and in which much less of the wing undergoes twisting.

In comparing species one can express the nodus position as a *nodal index*: its distance from the base as a fraction of the wing length. Figure 3 compares a range of forewings, from the pseudostigmatid *Megaloprepus*, whose wings can twist through particularly large angles as it hovers, to *Macromia*, which hovers relatively infrequently.

In Figure 4, nodal index is plotted against  $\check{r}_1S$  for a selection of odonate wings. The grey outliers to the left are anisopterous hindwings, and those at the bottom are giant Zygoptera: *Megaloprepus* and the waterfall-haunting lestoid *Thaumatoneura*. The remainder suggest a broad negative relationship between the two variables; understandable since low values of the former and high values of the latter can both contribute to habitual slow, near-hovering flight.

## Conclusions

High speed cinematography, kinematic analysis, modelling, field observation and aerodynamic theory together allow us to make some sense of the relationships between morphology, performance capability and behavioural diversity in Odonata.

High wing loadings, resulting from large size and/or disproportionately small wings, should make for a wide speed range; i.e. for faster flight, as all Odonata can probably hover. The influences of aspect ratio are not straightforward. Medium and low aspect ratio wings may assist gliding and soaring, but the effects of AR in flapping are complicated, and are likely to depend greatly on the kinematics involved. In calopterygids, at least, broad wings are associated both with the clap and fling mechanism for generating high lift and with display. Short bodies and long wings should assist agility, especially at high speed. Narrow and stalked wing bases with distal concentration of the wing area are adaptations for habitually slow flight, and the high torsional compliance provided by the closely apposed vein stems and a proximally situated nodus also assist slow flight, close to hovering. And the converse applies.

Our existing knowledge of the range of dragonfly flight performance and behaviours is probably greater than that for any other insect order, but we still have detailed quantitative data for only a handful of species in a limited range of families, and theoretical predictions need testing with reference to a far greater variety of Odonata. There is plenty still to be done.

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