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22 **Abstract**

23 Remarkable flight performance is key to the survival of adult Odonata. They integrate varied  
24 three-dimensional architectures and kinematics of the wings, unsteady aerodynamics, and  
25 sensory feedback control in order to achieve agile flight. Therefore, a diverse range of  
26 approaches are necessary to understand their flight strategy comprehensively. Recently,  
27 Bomphrey *et al.* (2016) have presented new data in several key areas in Odonata such as  
28 measurement of surface topographies, computational fluid dynamic analyses, quantitative  
29 flow visualization using particle image velocimetry, and optical tracking of free flight  
30 trajectories in laboratory environments. In this paper, we briefly review those findings  
31 alongside more recent studies that have advanced our understanding of the flight  
32 mechanics of Odonata still further.

33

34 **Keywords**

35 Odonata; dragonfly; damselfly; biomechanics; flight; aerodynamics; visual control

36

## 37 **Introduction**

38 Flight performance of Odonata greatly affects their survivorship because it directly  
39 influences darting hunts, hawking flights, prey selection, interception and capture, predator  
40 evasion, and fuel economy during short commutes or long migration journeys. The flight of  
41 Odonata, including gliding, hovering, and manoeuvring modes, is achieved by tuning the  
42 aerodynamic forces acting on their wings through the control of wing kinematics on the  
43 basis of input from multiple sensors. Various architectural components in Odonata wings  
44 passively prescribe the posture and shape of the wings. Kinematics of their fore and hind  
45 wings in concert with three-dimensional wing geometries determine aerodynamic  
46 performance through the interaction between the wings and the surrounding air. Sensory  
47 inputs are monitored to coordinate the motor activities for routine flight control and  
48 specialist behavioural modes such as prey capture and conspecific pursuit. Considerable  
49 parts of the overall strategy for efficient and robust flight are still unknown because of the  
50 multiscale complexities of interactions between morphology, aerodynamics, sensory  
51 integration, and motor control.

52 Toward a comprehensive understanding of the strategy of Odonata, Bomphrey, Nakata,  
53 Henningsson, and Lin (2016) have recently presented a wide-ranging description of the  
54 biomechanical and neurophysiological aspects of flight alongside new results acquired using  
55 a broad suite of modern methods. In this paper, we have briefly summarised the results on  
56 the state-of-the-art with some additional updates from more recent studies.

57

## 58 **Structural dynamics of the odonatan wing**

59 The wings of the Odonata are hierarchical structures. Recent research progress, especially  
60 those employing computational approaches, have revealed the function of many structural

61 elements. Wing deformation is controlled passively through interactions of the detailed  
62 structural elements in the wings. Key elements, including the longitudinal veins, cross-veins,  
63 vein-joints (often including flexible resilin sections), the basal complex (defined here as the  
64 three-dimensional structure of proximal part of the wing), nodus, and membrane (Rajabi et  
65 al., 2016), are particularly important, since the dynamically deforming wing shapes directly  
66 affect aerodynamic performance (Young, Walker, Bompfrey, Taylor, & Thomas, 2009).  
67 Computational structural dynamic (CSD) analyses on odonatan wings suggest that specific  
68 geometries of the vein-joints (Rajabi, Ghoroubi, Darvizeh, Appel, & Gorb, 2016) or the nodus  
69 (Rajabi, Ghoroubi, Stamm, Appel, & Gorb, 2017) are responsible for the dorsoventral  
70 asymmetry of the wing deformation. While these elements function to control the wing  
71 deformation under aerodynamic loads passively during flight, collision with obstacles may  
72 lead to excessive loading and structural damage. The rubber-like protein, resilin, present at  
73 some vein-joints can considerably reduce the stress concentration in joints when the wings  
74 are deformed (Rajabi, Shafiei, Darvizeh, & Gorb, 2016), which may help to mitigate effects  
75 of collisions (Mountcastle, Helbling, & Wood, 2019). This is likely to be a secondary function  
76 of resilin, following a principal role in facilitating elastic wing deformation during normal  
77 flight.

78

### 79 **Aerodynamics of gliding and flapping flight**

80 In addition to the wing deformation controlled passively through fluid-structure interactions  
81 and inertial bending, the three-dimensional shape and arrangement of the four wings are  
82 also important for the flight performance of Odonata. Bompfrey *et al.* (2016) have  
83 performed computational fluid dynamic (CFD) analyses of gliding flight using a low Reynolds  
84 number aerodynamic simulator (Liu, 2009) with specific focus on the effect of the

85 corrugated chordwise cross section and the interaction between fore and hind wings in  
86 gliding.

87 The three-dimensional wing geometries required for this analysis were reconstructed by  
88 photographing a series of cross sections illuminated by a laser line projection (figure 1a). By  
89 using the resulting surface topology for CFD analysis, it was found that natural-scale  
90 corrugation does not give rise to a dramatic decrease in the lift-to-drag ratio that was  
91 observed for corrugations amplitudes that were exaggerated, and larger than those found in  
92 nature (figure 1b,c). Therefore, corrugations can substantially increase wing stiffness  
93 without greatly increasing material volume and, moreover, the corrugated structure does  
94 not substantially increase aerodynamic costs.

95 The fore- and hindwing interactions are investigated further by using CFD analyses with the  
96 angle of attack, sweep and dihedral angles of the wings relative to the body measured from  
97 field photography (figure 1d). The fore and hind wings are highly efficient relative to other  
98 insect fliers because of their high aspect ratios. By comparing the aerodynamic performance  
99 of gliding with fore and hind wings in tandem against a baseline of fore and hind wings  
100 acting in isolation – i.e. without aerodynamic interactions – Bomphrey *et al.* (2016)  
101 discovered that the dragonflies keep the performance of each wing high by trimming the  
102 wing angles to glide efficiently (figure 1e-f).

103 In conventional, fixed-wing aircraft, high aspect ratio wings achieve better lift-to-drag ratios  
104 than less-slender alternatives. This typically comes at the cost of manoeuvrability because  
105 the wing's moment of inertia is increased. However, it is worth noting that this relationship  
106 is not always maintained in insects. In genetically modified fruit flies, lines with higher  
107 aspect ratio wings showed enhanced manoeuvrability, albeit at the cost of a higher power  
108 requirement (Ray, Nakata, Henningsson, & Bomphrey, 2016). Odonata overcome this

109 physical trade-off of efficiency versus manoeuvrability by operating their four wings  
110 independently. For example, damselflies achieve yaw turn by the control of the angle of  
111 attack of each wing as well as the flapping velocities of the wings (Zeyghami, Bode-Oke, &  
112 Dong, 2017). Their backward flight is enabled by force vectoring, which is based on tilting  
113 the stroke plane to adjust the direction of the net aerodynamic forces (Bode-Oke, Zyghami,  
114 & Dong, 2018). Abdominal deflection increases the yaw velocity by reducing the moment of  
115 inertia and thus the flight torque required for the manoeuvre (Bode-Oke, Zeyghami, & Dong,  
116 2017b). During take-off, which requires large and finely-tuned aerodynamic forces to  
117 accelerate in a desired direction, damselflies generate aerodynamic forces that reach three-  
118 times body weight, operating each of the four wings at high angles of attack (Bode-Oke,  
119 Zeyghami, & Dong, 2017a). Similarly, dragonflies utilise high angles of attack and the  
120 synchronous flapping of fore and hind wings to generate large vertical forces at the  
121 beginning of take-off, later switching to lower angles of attack and counter-stroking (out-of-  
122 phase) flapping to generate large thrust (Alexander, 1984; Li, Zheng, Pan, & Su, 2018;  
123 Thomas, Taylor, Srygley, Nudds, & Bompfrey, 2004). The orientation of aerodynamic forces  
124 after the take-off are controlled by adjusting the ratio of downstroke to upstroke duration  
125 and the angle of attack of the wings (Shumway, Gabryszuk, & Laurence, 2018).

126 To support their weight when flapping, the Odonata rely heavily on unsteady aerodynamic  
127 mechanisms. In common with many insects, they use a separated flow pattern that delays  
128 aerodynamic stall and allows the wing to operate, momentarily, at angles of attack above  
129 the steady condition stall angle. During this moment of delayed stall, flow separates from  
130 the surface at the leading edge but subsequently re-attaches further back along the chord,  
131 ultimately leaving the trailing edge smoothly and satisfying a requirement for the flow on  
132 upper and lower surfaces to meet at the sharp trailing edge, known as the Kutta condition.

133 Inside the separation bubble (the volume bounded by the point at which flow detaches and  
134 reattaches on the chord), the flow rolls up into a swirling, leading-edge vortex (LEV),  
135 allowing the wing to operate at high angles of attack producing remarkably high lift.  
136 Quantitative flow visualizations using a laser-based technique called particle image  
137 velocimetry (PIV), where the air is seeded with tiny droplets of olive oil, confirmed the  
138 qualitative descriptions of the flow topology shown by Bomphrey *et al.* (2002) and described  
139 in detail by Thomas *et al.* (2004) (figure 2a). The typical, counter-stroking, kinematic pattern  
140 leads to a cylindrical LEV spanning the thorax (figure 2b) from forewing tip to forewing tip  
141 (figure 2c), while the hindwing exhibits conventional attached flow. Using their quantitative  
142 PIV data, from *Sympetrum striolatum* and *Aeshna mixta*, Bomphrey *et al.* (2016) have  
143 further discovered that: 1) the core diameter of the leading-edge vortex is substantially  
144 greater than the mean chord length of the forewings at all spanwise positions from the  
145 centreline to the wing tips; 2) the diameter and circulation increase from root to tip in *A.*  
146 *mixta*; 3) the spanwise contribution to weight support increases from root to tip in both  
147 species; and 4) axial velocities at the core of the leading-edge vortex can be quite strong in  
148 either direction (at least during slow forward flight), and is not, therefore, an essential  
149 prerequisite of vortex stability during the period of a single half stroke as has been  
150 suggested for other insects (Birch & Dickinson, 2001). A recent flow visualization study by  
151 Hefler *et al.* (2018) also confirmed the existence of the LEV on the hind wings during free  
152 flight, suggesting its dynamics are under the effect of the aerodynamic interactions between  
153 fore and hind wings.

154 Bomphrey *et al.* (2016) have also used quantitative flow measurements to estimate the  
155 efficiency with which lift is generated. Span efficiency ( $e_i$ ) is the ratio of the power required  
156 to generate lift under ideal aerodynamic loading conditions on the wing to the power



157 required in reality: the ideal power divided by the induced power. Since the power required  
158 to generate a given lift is derived from the induced flow velocity, span efficiency can be  
159 measured empirically as the deviation of the downwash velocity profile behind the wings  
160 from the theoretical ideal of an even distribution across the span. In the case of a fixed  
161 wing, an elliptical planform gives the highest span efficiency by generating an even  
162 downwash distribution across the span. Because the velocity of flapping wings increases  
163 linearly with distance from the wing hinge, flapping wings will deviate from an elliptical plan  
164 form and maximise their efficiency if the wing is broad at the root and tapers towards the  
165 tip. The tapering should compensate for the wing's velocity distribution. If we ignore wing  
166 twist, or assume that it is comparable across the Odonata, the Anisoptera are, therefore,  
167 predicted to perform better than the Zygoptera, since anisopterans have wing shapes with  
168 chord lengths that taper toward the wing tip, while zygopterans have wing chord lengths  
169 that lengthen towards the wing tip. We tested this prediction by estimating the span  
170 efficiencies for 24 individuals of six Odonata species in free flight in a custom-built wind  
171 tunnel, following the protocol of Henningsson and Bomphrey (2013). Figure 2d shows a time  
172 series of transects through the downwash at 1 millisecond intervals for representative  
173 examples of *Enallagma cyathigerum*. The colour and relief show the magnitude of the  
174 downwash velocity behind the trailing edges of the hind wings, black solid and dashed lines  
175 show the vertical excursion of the undulating left and right hindwing tip vortices throughout  
176 the sequence. Ensemble-averaged temporal variations in span efficiencies are shown in  
177 figure 2e. As predicted from the difference in the wing shape (Bomphrey, et al., 2016), the  
178 Zygoptera with narrower wing base have lower span efficiencies (figure 2e) and span  
179 efficiency is strongly correlated with taper ratio (figure 2f), confirming the relationship  
180 between wing planform and aerodynamic efficiency during flapping flight. At the cost of

181 lowered efficiency, the Zygopteran planform shifts the wing's centre of pressure away from  
182 the insect's centre of mass, which increases the distance swept by the distal area of the  
183 wing. This evolutionary solution might expand the kinematic envelope available and  
184 increase the torque that can be generated at the wing hinge when manoeuvring.

185

## 186 **Flight performance**

187 Bompfrey *et al.* (2016) presented two sets of data on the flight performance of Odonata,  
188 aiming at providing standardized baseline data and showing quantitative differences in flight  
189 performance during cruising, predatory and territorial escort flights. As an example, figure  
190 3a-c shows the total speed, centripetal acceleration and turn rate of nine species of  
191 Odonata in a flight arena, acquired using calibrated stereo-cameras (following the protocol  
192 detailed previously (Henningsson & Bompfrey, 2013; Ray, et al., 2016)). Statistical analyses  
193 suggested that: 1) the Zygoptera tended to fly more slowly than the Anisoptera, but the  
194 majority of species preferred to fly at between 1 and 2 m s<sup>-1</sup>; 2) the centripetal accelerations  
195 were relatively modest, with only *Sympetrum sanguineum* frequently accelerating over 3g  
196 when cornering; 3) turn rates can reach up to 1000 deg s<sup>-1</sup> in several species. Another set of  
197 the probability density function in figure 3d-f shows the speed, turn rate and turn radius of  
198 *Plathemus lydia* during cruising, predatory and territorial flights, recorded using the protocol  
199 described by Mischiati *et al.* (2015). It is clear that the predatory and territorial flights are  
200 more demanding than cruising flight; territorial flight and prey interception flight exhibited  
201 higher speeds more frequently (figure 3d) and also more rapid turns (figure 3e). Territorial  
202 flights in our experimental observations were faster than the predatory flights, but the turn  
203 radius of the predatory flights was slightly tighter than those observed during territorial  
204 flights (figure 3f). We do not expect these behaviours to exhibit the full repertoire of each

205 species, but the standardization within our well-defined and repeatable settings is useful for  
206 benchmarking a conservative flight performance envelope. The metrics provided in this  
207 study highlight coarse interspecies variability for future investigations into comparative  
208 flight performance.

209

### 210 **Neurophysiology of dragonfly vision**

211 The dragonfly's impressive visual abilities have motivated numerous studies on the  
212 neurophysiology of small target detections. The most notable ones can be dated back to the  
213 1980's with the discovery of the target selective descending neurons (TSDNs) that transmit  
214 target movement information from the visual centre in the head to the motor centre in the  
215 thorax (Olberg, 1986). Later, the small target motion detectors (STMDs) were discovered in  
216 the third visual neuropil, lobula (O'Carroll, 1993). Both classes of neurons respond to small  
217 shadows moving in a relatively wide area of the visual field. TSDNs were assumed to be the  
218 downstream neurons of STMDs for a long time, yet a direct evidence has never been  
219 established. On-going work attempts to establish the functional role of TSDNs and the signal  
220 transformation from the visual system.

221 Behavioural studies and physiological studies go hand-in-hand to advance our  
222 understanding of dragonfly vision. Through precise measurement of dragonfly head  
223 movement during repeated prey interception flights, Mischiati *et al.* (2015) established the  
224 predictive nature of dragonfly prey interception behaviour. While the target interception  
225 trajectory can be achieved via a fast reactive control mechanism, the way the dragonfly's  
226 head cancels expected target movement demonstrates the role of predictive control. This  
227 observation was reinforced by the discovery of a strong predictive neural facilitation in  
228 STMDs (Wiederman, Fabian, Dunbier, & O'Carroll, 2017). As the target moves across the

229 receptive field of a STMD neuron, the sensitivity of target detection in front of the current  
230 target position is enhanced by over 50%. This demonstrates that the visual system indeed  
231 has information about the expected future target location. From scrutinizing visual  
232 parameters of the dragonfly's prey selection, we have shown that target selection is highly  
233 tuned to the interception flight dynamics (Lin & Leonardo, 2017). This selection might be  
234 correlated but not purely driven by target detection limits. Dragonflies have incredible  
235 sensitivity to detecting targets that are smaller than single photoreceptor. A recent study  
236 compared the photoreceptor sensitivity to small targets in dragonflies, hoverflies, honey  
237 bee drones, and blowflies (Rigosi, Wiederman, & O'Carroll, 2017). The result confirmed a  
238 similar subpixel target detection level ( $<0.2^\circ$  target) as reported by the target selection  
239 behaviour study (Lin & Leonardo, 2017).

240 Finally, a recent study compared visual motion detection responses in dragonflies and  
241 macaque monkeys (Nitzany et al., 2017). It shows that both systems respond to some  
242 motion cues that cannot be explained by the classic Hassenstein-Reichardt model. With the  
243 discovery of a class of wide-field sensitive neurons in the dragonfly lobula (Evans, O'Carroll,  
244 Fabian, & Wiederman, 2018), we expect dragonflies to serve as an alternative model system  
245 for understanding the fundamental mechanism of motion detection.

246

#### 247 **Concluding remarks**

248 We have briefly reviewed the current state-of-the-art of research on the biomechanics of  
249 odonatan flight. The use of computational structural and fluid dynamic analysis has  
250 separately driven progress toward a more complete understanding of the functional  
251 morphology of the wings of the Odonata and their flight mechanics. Computational analyses  
252 revealed that wing deformation is passively controlled by the hierarchical architecture of

253 odonatan wings, but its effect on flight performance is yet to be resolved. This is because  
254 the coupling of passive wing deformation and unsteady aerodynamics is not yet taken into  
255 account. Nor is it well understood how the steering muscles modify wing shape during  
256 cyclical flapping or manoeuvres. Wing deformations affect the sensory encoding of  
257 mechanosensors mounted on the veins but we do not yet know how wing shape changes  
258 are monitored by the flight controller. It is also not yet clear how body rotations affect wing  
259 deformations and, thus, how those deviations from the encoding expected during straight  
260 and manoeuvring flight could be used in flight control in turbulent atmospheric conditions.  
261 This sensory role of the wings in stabilisation has not been shown in dragonflies although  
262 there is a growing body of work in the context of moth wings acting as gyroscopic sensors  
263 (Pratt, Deora, Mohren, & Daniel, 2017) analogous to the well-studied function of halteres in  
264 Diptera. Therefore, we must work towards a comprehensive wing structural model coupled  
265 with the surrounding fluid dynamics. With this model we can begin to understand the  
266 functional significance of each structural element and also to characterize the role of wing  
267 mechanosensors in flight control. Current advances in computational modelling methods  
268 certainly help towards this comprehensive fluid-structure interaction analysis. Aerodynamic  
269 experiments on real animals, where wing surfaces and flow velocities close to the wings can  
270 be measured simultaneously, are now possible and will be vital for computational model  
271 validation (Nila et al., 2016). The combination of such empirical and computational  
272 approaches would add strength and robustness to the results.

273 Several more key areas that will advance our understanding of the flight strategy of the  
274 Odonata were identified by Bomphrey *et al.* (2016). The behavioural repertoire of the  
275 Odonata is diverse, and we must develop new approaches that allow high throughput, high-  
276 quality wing kinematics measurements (Koehler, Liang, Gaston, Wan, & Dong, 2012; Walker,

277 Thomas, & Taylor, 2009). The use of artificial targets with prescribed perturbation will allow  
278 us to formulate behavioural models by artificially eliciting predictable and repeatable flight  
279 responses (Fabian, Sumner, Wardill, Rossoni, & Gonzalez-Bellido, 2018; Mischiati, et al.,  
280 2015). The wings are, of course, driven by the flight motor and wing hinge; in order to  
281 understand the interplay of these musculoskeletal elements during the various behaviours,  
282 a combination of tethered flight and wireless recording of the flight muscles would be very  
283 useful.

284 Comprehensive analyses are extremely challenging, but flight in Odonata represents a fine  
285 example of a natural aerial system in which complex wing morphology, unsteady  
286 aerodynamics and neural feedback control are integrated to achieve extraordinary flight  
287 behaviour. On-going work focuses on revealing the neural representation of wing  
288 aeroelasticity. Understanding such a system can inspire the development of novel agile  
289 micro aerial vehicles with sophisticated 'fly-by-feel' control systems that use  
290 mechanosensory information about loads on the wing surface in the flight controller.  
291 Finally, while behavioural and neurophysiological studies continue to work synergistically to  
292 advance our understanding of flight control, we believe it is necessary to retain  
293 biomechanics as a fundamental link between the two, to set each in context, and to answer  
294 the proximate questions of flight in the Odonata and other insects.

295

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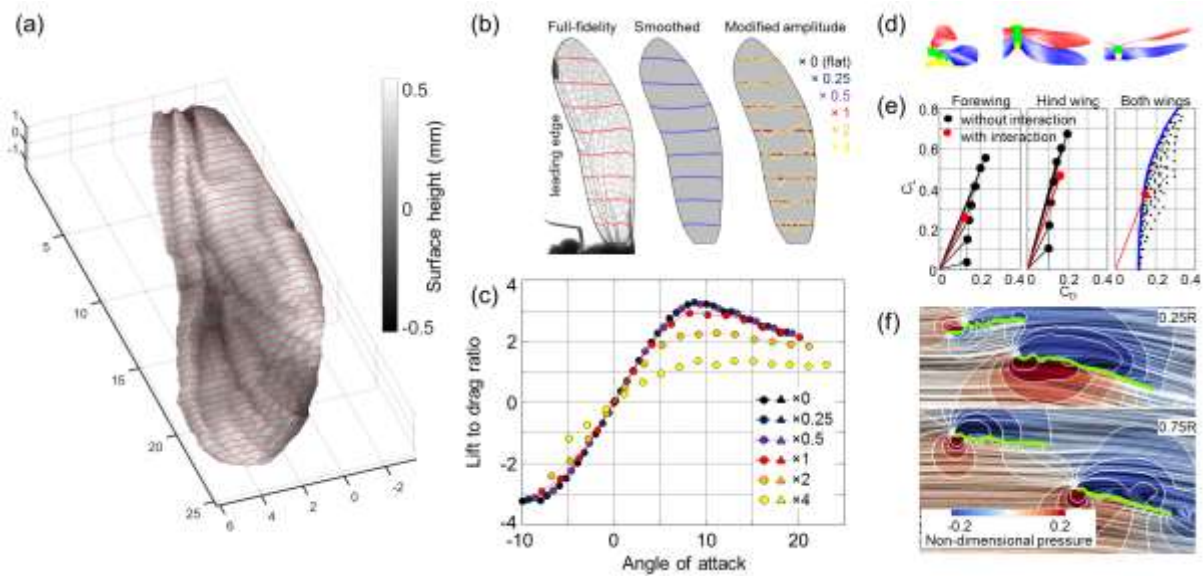
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380 **Figures**

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383 Figure 1. Three-dimensional surface geometry and gliding aerodynamics of dragonfly

384 wings. (a) The complex three-dimensional geometry of the wings for CFD analysis. (b)

385 Selected cross sections of the full-fidelity wing, smoothed wing and the wings with modified

386 amplitude. (c) The lift-to-drag ratio for the exaggerated and reduced corrugation models. (d)

387 Three-dimensional models of the forewing (red), hindwing (blue) and the upper (green) and

388 lower (yellow) surfaces of the thorax. (e) Lift and drag coefficient polars of the fore and hind

389 wings with (red) or without (black) aerodynamic interactions. (e) The two-dimensional flow

390 structure shown by line integral convolution (LIC) streamlines and pressure distribution

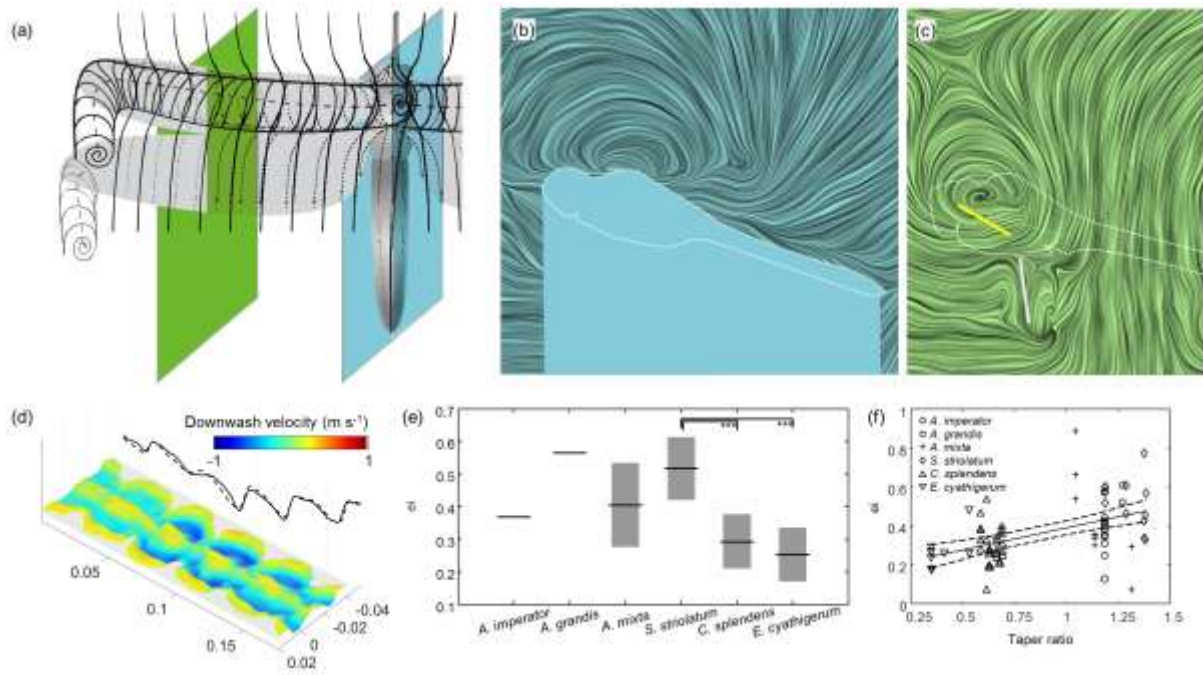
391 contours around the fore and hind wings at 25% and 75% of wing length. The positive and

392 negative pressure regions of each wing connect with each other, revealing an aerodynamic

393 interaction between the ipsilateral wing pairs. This figure is reproduced from Bomphrey *et*

394 *al.* (2016).

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398 Figure 2. Figure 2 Flapping wing aerodynamics of Odonata. (a) Topology of the leading-

399 edge vortex of a dragonfly. Cross section of the flow at (b) the centreline of the body and (c)

400 approximately 45% of the wing's length from hinge to tip measured by PIV, with

401 instantaneous streamlines visualized by LIC. (d) Example sequence of the time-resolved

402 induced downwash of *Enallagma cyathigerum*. Both the relief and colour represent

403 downwash velocity, with shades in blue/cyan representing downward velocities

404 corresponding to positive lift and shades in red/yellow upward velocities corresponding to

405 negative lift. (e) The span efficiency of each species. Boxes show median values with 95%

406 confidence intervals. Post hoc pairwise ANOVA under a/the Tukey criterion shows the

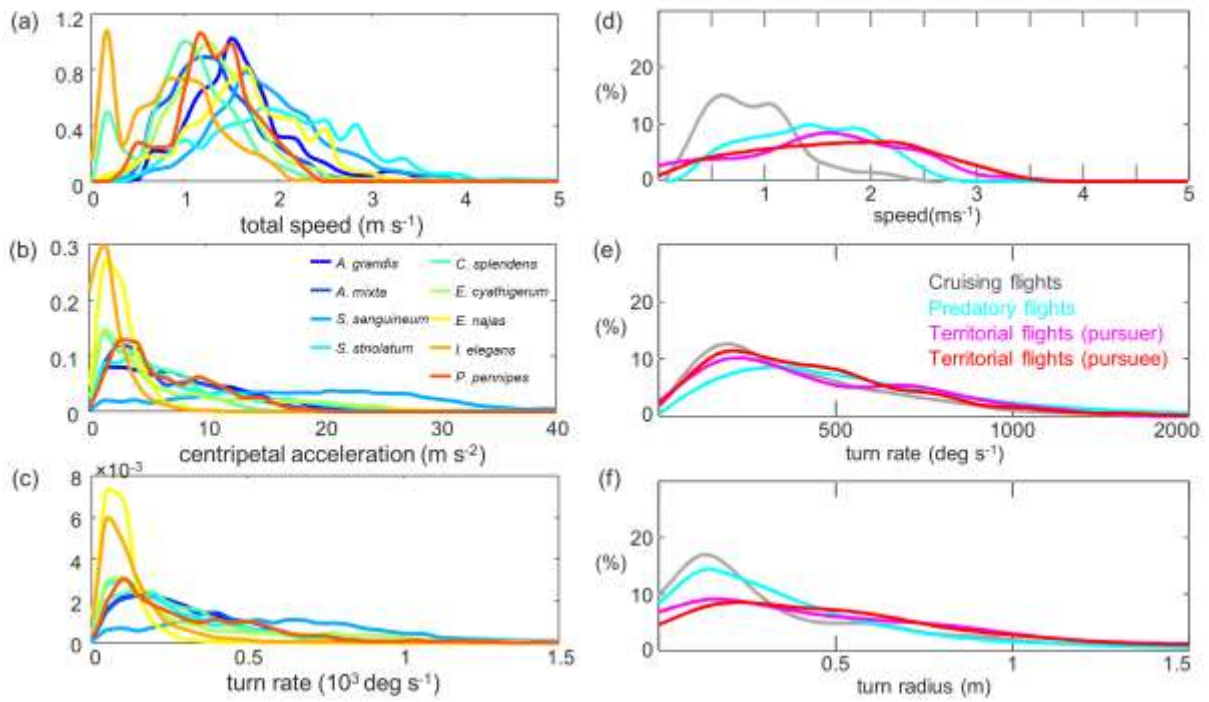
407 differences between *Sympetrum striolatum* and two of the Zygoptera are significant ( $p <$

408 0.001). (f) The taper ratio is positively correlated with span efficiency ( $p < 0.001$ ,  $R^2 = 0.24$ ).

409 Solid and dashed lines show the least-squares regression slope with 95% confidence

410 intervals. This figure is reproduced from Bomphrey *et al.* (2016).

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414 Figure 3. Flight performance of Odonata. (a) Total speed, (b) centripetal acceleration, and

415 (c) turn rate of nine species of Odonata. (d) Speed, (e) turn rate and (f) turn radius of

416 *Plathemus Lydia* during cruising, hunting and territorial flights. This figure is reproduced

417 from Bomphrey *et al.* (2016).