

REVIEW

Aerodynamic interference depends on stroke plane spacing and wing aspect ratio in damselfly model wings

Fritz-Olaf Lehmann* and Henja-Niniane Wehmann

Department of Animal Physiology, Institute for Biosciences, University of Rostock, Rostock, Germany

The fluid dynamics of aerodynamic force control in insects depends on how oscillating wings interact with the surrounding air. The resulting flow structures are shaped by the flow induced by the wing's instantaneous motion but also on flow components resulting from force production in previous wing strokes and the motion of other wings flapping in close proximity. In four-winged insects such as damsel- and dragonflies, the flow over the hindwings is affected by the forewing downwash. In these animals, a phase-shift between the stroke cycles of forewing and hindwing modulates aerodynamic performance of the hindwing via leading edge vortex destruction, changes in local flow condition and the wake capture effect. This review is engaged in the significance of wing-wake interference for force control, showing that in damselfly model wings the strength of phase-dependent force modulation critically depends on the vertical spacing between forewing and hindwing stroke planes and the aspect ratio of both wings. We conclude that damsel- and dragonflies reach maximum steering capacity for body posture control when forewings and hindwings flap in close proximity and have similar length. The latter findings are of significance for the evolution and diversification of insect wings because they might explain why forewings and hindwings are little different in the order Odonatoptera.

Keywords: unsteady aerodynamics; flight control; wing–wing interaction; wing–wake interaction; phase-shifted stroking; mechanical wing model; Odonata; dragonfly

Flight with tandem wings

Damselflies and dragonflies are dramatic, successful aerial predators, notable for their flight agility and endurance. They are capable of a diversity of flight techniques including tandem flight during copulation, low-speed manoeuvring, and hovering. This extraordinary performance is due to direct flight musculature acting on each wing base that enables these animals to control each wing independently. Thus, dragonflies differ from other four-winged insect species such as locusts, caddisflies, mayflies, butterflies, bees, wasps and ants, in which forewing and hindwing beat always in phase. In several of the latter lineages, moreover, fore- and hindwings are mechanically coupled throughout the entire stroke cycle (Gorb, 2001; Stocks, 2008).

For decades, research has been devoted to flight capabilities of dragonflies, including a vast variety of experimental and computational work on the aerodynamic characteristics of turning flight (Hino & Inamura, 2018; Li & Dong, 2017), the significance of tandem wings for forward flight (Broering & Lian, 2015; Shumway, Gabryszuk, & Laurence, 2018) and gliding flight (Bode-Oke, Zeyghami, & Dong, 2018; Shi, Huang, Zheng, & Zhao, 2016), the kinematics and aerodynamics of backward flight (Bode-Oke et al., 2018), and take-off capabilities and behaviour

*Corresponding author. Email: fritz.lehmann@uni-rostock.de

(Bode-Oke, Zeyghami, & Dong, 2017). Other research has focused on the significance of dorsal wing clapping (“clap and fling kinematics”) in dragonflies for force enhancement (Takizawa et al., 2015), force production with eight flapping wings during mating flights, in which males and females bodies are mechanically coupled (Davidovich & Ribak, 2016), and dragonfly-inspired man-made micro-air-vehicles (Jang & Yang, 2018; Kok, Fatiaki, Rosser, Chahl, & Ogunwa, 2017; Sivasankaran et al., 2017; Takahashi, Concordel, Paik, & Shimoyama, 2016). Recent comprehensive reviews were published on the aerodynamics of the different types of flight manoeuvres (Sun, Gong, & Huang, 2017), the two-dimensional flows around flapping tandem wings (Lua, Lu, Zhang, Lim, & Yeo, 2016) and on the link between flight muscle system, flight mechanics and aerodynamics in damselflies and dragonflies (Bomphrey, Nakata, Henningsson, & Lin, 2016).

Wing corrugation and phasing

Besides this variety of research topics, two features of wing flapping and design in the order Odonoptera attracted researchers in particular: the function of the corrugated wing surface (wing profile) and the aerodynamic consequences of phase-shifted stroking, in which forewings and hindwings flap with different timing. Both aspects have been studied in great detail, also with respect to the development of micro-air-vehicles. While wing camber and corrugation change lift and drag characteristics of wings (Anwer, Ashraf, Mehdi, Ahmad, & Grafi, 2013; Blanke, 2018; Chen & Skote, 2016; Hou, Zhong, Yin, Pan, & Zhao, 2017; Rajabi et al., 2016; Shi et al., 2016; Shumway & Laurence, 2019; Vargas, Mittal, & Dong, 2008; Wang, Zhang, Ren, Chen, & Wu, 2017), phase-shifted stroking results in a complex dynamic of flow patterns, in which flow over the forewing determines and alters the flow over the hindwing. Since vortex shedding at the stroke reversals is predominant in flapping flight, many studies previously focused on wing–wake and wing–vortex interactions using numerical 2- and 3-dimensional models (Isogai et al., 2004; Li & Dong, 2017; Sun & Huang, 2007; Sun & Lan, 2004; Wang & Sun, 2005; Xie & Huang, 2015; Young, Lai, & Germain, 2008; Zheng, Wu, & Tang, 2016), physical models such as robotic wings (Dileo & Deng, 2009; Gravish, Peters, Combes, & Wood, 2015; Lai, Yan, Motamed, & Green, 2005; Lu, Shen, & Su, 2007; Usherwood & Lehmann, 2008), or by quantifying vortical structures in the wake of tethered and freely flying dragonflies (Fu, Hefler, Qiu, & Shyy, 2014; Hefler, Qiu, & Shyy, 2016; Thomas, Taylor, Srygley, Nudds, & Bomphrey, 2004).

Damselflies and dragonflies actively vary their phase relationship between ipsilateral forewings and hindwings with different flight behaviours (Norberg, 1975; Wakeling, 1993). In this respect, damselflies and dragonflies differ from other, more primitive orders of functionally four-winged insects, such as locusts, in which phase relationship is highly consistent during flight with only little variation during steering manoeuvres (Wortmann & Zarnack, 1993). Behavioural studies have reported three major categories of phase relationships: parallel stroking, counterstroking and phase-shifted stroking of forewings and hindwings. During straight forward flight, upward flight, escape behaviour – during which the animal produces peak lift of approximately 20 times its body weight – and manoeuvring flight, dragonflies typically use a conventional flight mode (Reavis & Luttges, 1988; Soms & Luttges, 1985; Wang, Zeng, Liu, & Chunyong, 2003). A highly consistent characteristic for this flight mode is a 15–28% cycle phase-shift during which the hindwing leads forewing motion (Fu et al., 2014; Sun & Huang, 2007; Wakeling & Ellington, 1997). Larger phase differences of up to 50% (counterstroking) have been found in hovering dragonflies and manoeuvring animals flying freely in a wind tunnel (Alexander, 1986).

Previous studies with mechanical wings emphasise that in vertically stacked forewing–hindwing stroke planes, force production by the hindwing is maximum when the hindwing leads

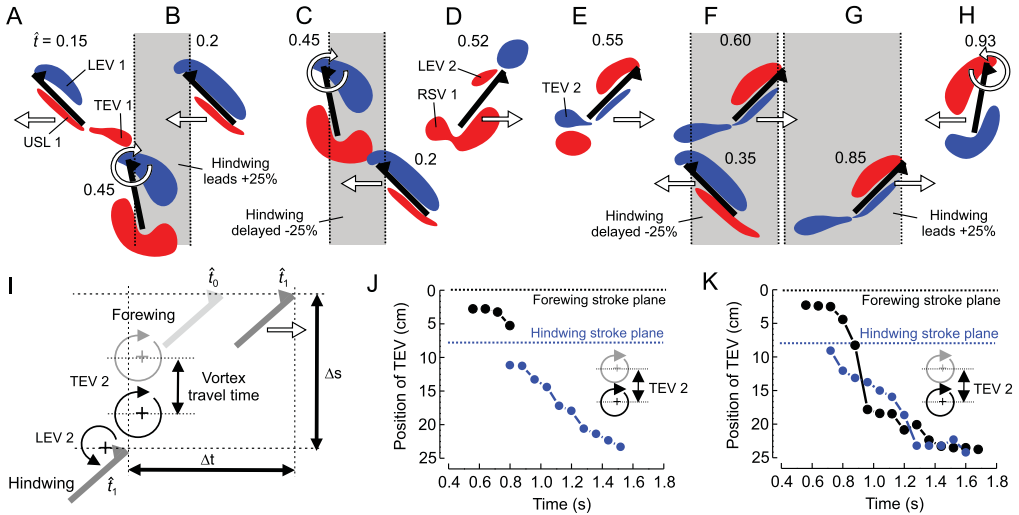


Figure 1. Schematics of vorticity in a tandem, mechanical wing model of a damselfly (Usherwood & Lehmann, 2008). (A–H) Upper row shows positions of the forewing blade throughout the stroke cycle at seven selected times (\hat{t}) of the stroke cycle ($\hat{t} = 0 \dots 1$). Triangle on the dorsal surface indicates leading wing edge and wing motion starts to the left. See also Figure 2A for kinematic pattern. Lower row shows the wing blade position of the hindwing at four selected times ($\hat{t} = 0.2, 0.35, 0.45$ and 0.85) that stem from two phase lags. When the hindwing leads wings motion by $\sim 25\%$ stroke cycle (forewing motion delayed), the forewing phase is $\hat{t} = \sim 0.2$ and ~ 0.6 , while the hindwing phase is $\hat{t} = \sim 0.45$ and ~ 0.85 as shown in *B* and *G*, respectively. When the forewing leads wings motion by $\sim 25\%$ stroke cycle (hindwing motion delayed), the forewing phase is $\hat{t} = \sim 0.45$ and ~ 0.6 , while the hindwing phase is $\hat{t} = \sim 0.2$ and ~ 0.35 as shown in *C* and *F*, respectively. Coloured structures show vorticity at the blades with clockwise rotation in blue and counterclockwise rotation in red. LEV, leading edge vortex; TEV, trailing edge vortex (start vortex); USL, underwing shear layer; RSV, rotational start vortex. The proximity between the forewing and hindwing blades at the above timing pairs is indicated by the grey areas. Grey in *C* and *F* indicates times in which the forewing start vortex interferes with the hindwing wake. Grey in *B* and *G* shows times in which hindwing vortices are less affected by forewing vorticity. (I) Schematics of trailing edge vortex (start vortex) travel in tandem wings. Δs , distance between forewing and hindwing stroke plane. (J, K) Vertical position of forewing (black) and hindwing (blue) start vortices (TEV) after shedding at the beginning of the downstroke when the forewing in *J* (hindwing in *K*) was leading by a quarter stroke cycle. Data are derived from the experimental apparatus shown in Figure 2.

by a quarter stroke cycle and minimum when the hindwing is temporally delayed by a quarter cycle (Figure 1A–H; Lehmann, 2008; Maybury & Lehmann, 2004; Usherwood & Lehmann, 2008). The approximately twofold change in aerodynamic performance of the hindwing follows a sinusoidal curve when phase relationship linearly changes from -50% (forewing leads wing motion) to $+50\%$ stroke cycle (hindwing leads wing motion, counterstroking). This relationship implies that small changes in phase lag of around -25% to $+25\%$ stroke cycle only produce moderate changes in hindwing lift production, whereas in parallel stroking the same phase alterations produce considerable larger modulations in hindwing lift.

The reconstruction of vorticity in the vortical structures and velocity measurements of the oncoming fluid suggest two distinct fluid dynamic phenomena for hindwing lift modulation: first, the destruction of the leading edge vortex due to the proximity of the forewing's starting vortex; and second, the changes in strength and orientation of the local flow vector (Maybury & Lehmann, 2004). Vortex interaction between the two wings is minimum at maximum force production, i.e. when the hindwing leads phase by a quarter stroke cycle (Figure 1B, G). The hindwing even gains instantaneous lift in excess of the instantaneous lift produced by a single flapping wing during the second half of each half stroke. This effect occurs because the hindwing's leading edge vortex development is not hindered by the proximity of the forewing's start vortex but gains lift by the wake capture mechanisms (Usherwood & Lehmann, 2008). The enhanced wake capture effect is caused by the favourable orientation of the forewing downwash

that lowers the kinetic energy in the wake and improves both hindwing lift and aerodynamic efficiency (Usherwood & Lehmann, 2008). By contrast, when the hindwing is delayed by a quarter stroke cycle, the forewing's start vortex and induced flow negatively affects the hindwing's leading edge vortex and effective angle of attack throughout the stroke cycle (Figure 1C, F).

In general, forewing–hindwing interaction arises from the low viscous dissipation rate of shed vortical structures from the forewing, and their travel velocity (Figure 1I). Travel velocity of the hindwing's start vortices appears to be broadly independent of the phase lag between forewing and hindwing stroke cycle. By contrast, when the hindwing leads wing motion by a quarter stroke cycle, the forewing's start vortices are accelerated near the hindwing stroke plane (Figure 1K). This effect likely results from an elevated pressure gradient in the space between the two stroke planes, sucking vortices from the forewing towards the hindwing stroke plane. Thus, a vortex passing through this space might experience a higher acceleration compared to a vortex shed by a single flapping wing. This phenomenon is not observed when hindwing motion is delayed with respect to the forewing stroke cycle because in this case the forewing start vortex dissipates due to the proximity of the hindwing leading edge vortex (Figure 1C, J). Altogether, these findings suggest that vortex interaction should be highly sensitive to vertical separation between the forewing and hindwing stroke planes and to forward flight speed, as both parameters strongly determine vortex travel time from the forewing to the hindwing stroke plane.

Wing size and wing shape

Two often neglected factors for wing–wake interaction are wing size (area) and wing shape (aspect ratio). Wing loading, for example, i.e. the ratio between body mass and wing area, is very variable across dragonfly species. Relatively large wings favour high turning moments because of a long moment arm between the centre of force and the body's centre of mass. Shorter wings may reduce muscle mechanical power requirements due to smaller inertial power requirements during wing flapping. Wootton and Newman (2008) were some of the first researchers to review the various forms of wings in Odonatoptera and linked wing shape and thoracic attachment to flight style and flight performance. For example, narrow-based wings are often linked to species with relatively slow flight. As, at slow forward speed, wing areas near the hinge face little air velocity, proximal wing areas are reduced (Wootton & Newman, 2008). Species that are able to fly fast in the forward direction should in turn exhibit broad wings near the hinge in order to benefit from the translational velocity component. Thus, for example, damselflies (Zygoptera) with slender wings often are slow flyers, while dragonflies (Anisoptera) with broad wings typically operate at elevated forward speeds. Wings with a high aspect ratio have also been found in fossil Archizyoptera (Wootton & Newman, 2008).

Besides flight energetics and behaviour, wing shape and thus aspect ratio also determines the distance between the stroke planes of forewing and hindwings. With decreasing aspect ratio, the distance between the stroke planes is thought to increase. The greatest range of wing planforms, and thus presumably the largest variation in stroke plane distance, is found in the family Libellulidae, in which broad wings are largely associated with gliding and soaring flight (Ennos, 1989; Wakeling, 1997; Wootton, 1991). Due to the considerable variation and the link between wing shape and the energetic costs of flight, it has also been suggested that interspecific differences in wing shape are in part due to selection (Johansson, Söderquist, & Bokma, 2009). Comparative studies in dragonflies suggest that long-distance migration, high manoeuvrability, and predation have shaped the forewing and hindwing planforms (Johansson et al., 2009; Kuchta & Svensson, 2014). Other work has explored 37 taxa of the damselfly family Calopterygidae and found that with decreasing second moment of wing area, which depends on aspect ratio, flight costs

decrease while the range of flight speeds increases (Outomuro, Adams, & Johansson, 2013). Although wing shape is expected to evolve to optimise wing kinematics and thus flight performance, Outomuro and Johansson (2011) emphasised that other selective factors such as wing sexual ornaments might be important factors determining wing shape. Moreover, a study with dragonfly-inspired mechanical wings found Kelvin–Helmholtz instabilities at the leading edge vortex at wings with elevated aspect ratios, and also vortex bursting at the outer spanwise locations. It has been suggested that the latter phenomenon might be the reason that insects normally have low aspect ratio wings (Fu et al., 2014).

Altogether, despite the finding that wing shape is linked to flight behaviour and performance, there is no satisfying, mechanistic explanation for how stroke plane spacing and wing aspect ratio determines flight aerodynamics and steering capacity in damselflies and dragonflies. This review highlights this aspect with respect to recent publications and revisits experimental data that have previously been published on mechanical wing aerodynamics (e.g. Lehmann, 2008; Maybury & Lehmann, 2004; Usherwood & Lehmann, 2008). A mechanical model mimics the flapping kinematics of the damselfly *Sympetrum sanguineum* that flaps its forewings and hindwings in a horizontal stroke plane and typically uses phase-shifting kinematics with the hindwing leading by a quarter stroke cycle (Figure 2A, B; Wakeling & Ellington, 1997). We simplified the complex wing planform of this insect and used rectangular wings with rounded edges (Figure 2C). From sensors at the wing hinge, we recorded aerodynamic forces and moments while varying the spacing between the two stroke planes, the wing's aspect ratios, and kinematic phase lag. The results contribute to two major questions of flight in Odonatoptera: (1) why are forewings and hindwings rather similar in length despite large interspecific variations in wing shape; and (2) how does phase shift-modulated force production change with changing spacing between forewing and hindwing stroke planes?

Force modulation and spacing of stroke planes

Figure 3 shows that force modulation of the mechanical hindwing is smallest when fore- and hindwing hinges are separated by at least five mean chord widths. At this spacing there is negligible ground effect on the forewing by the hindwing surface and the forewing produces mean lift similar to the performance of a single wing (data not shown; red, Figure 3B). Despite the dissipation of forewing vorticity at elevated distance, however, the hindwing is still affected by the uniform forewing downwash, and generates $\sim 15\%$ less lift than a single wing flapping free of forewing downwash (red, Figure 3C). The direction of forewing downwash determines the spatial overlap with the hindwing stroke plane. This overlap is thought to change with changes in inclination of both stroke planes with respect to the horizontal and also with forward flight velocity. The latter parameter likely deflects the wake in the horizontal plane and thus away from the hindwing stroke plane, resulting in a reduced overlapping area.

The phase lag at which the hindwing achieves maximum mean lift, at 1.25 wing chord spacing, is thought to decrease with increasing spacing because of an increase in the travel time of shed forewing vortices (Figure 1I–K). This prediction was validated by the data shown in Figure 3C. As expected from wing–vortex interaction between the forewing start vortex and the hindwing, Figure 3E (red) shows that kinematic phase lag for maximum hindwing lift decreases linearly with increasing wing separation. By contrast, phase lag for maximum forewing lift tends to increase with increasing spacing (black, Figure 3E). In-phase, or parallel stroking, produces maximum hindwing lift *only* when the two stroke planes are separated by approximately 2 mean wing chords (Δ_{FW-HW} , Figure 2C) – a value that is close to the measured estimate in *Sympetrum sanguineum* (Wakeling & Ellington, 1997). Notably, stroke plane spacing of 2.5 wing

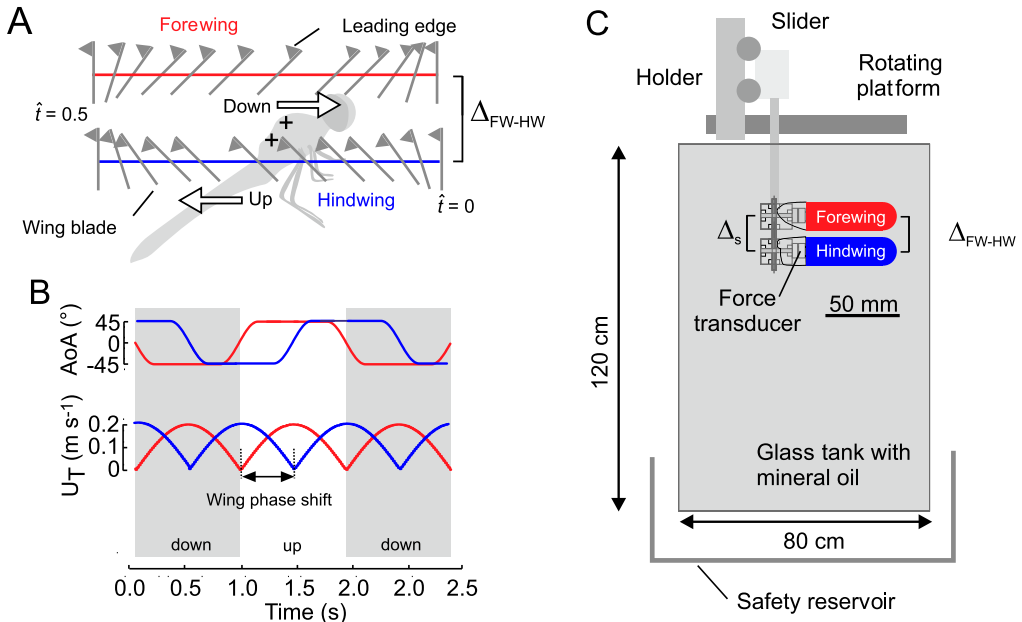


Figure 2. Mechanical damselfly and flapping kinematics. (A) Wing kinematics during forewing and hindwing flapping motion of the mechanical wing. The wingtip paths reported for a hovering damselfly (Wakeling & Ellington, 1997) describe approximately horizontal stroke planes, with vertically stacked wings. The mechanical model of a damselfly’s right wings was flapped at controlled fore-hind phases. Wing blade element is indicated by the black lines and the black triangle on the dorsal wing surface represents the wing’s leading edge. (B) Angle of attack (AoA) and wing tip velocity (U_T) of the stroke cycle. In this graph, the hindwing (blue) leads wing motion by a quarter (25%) stroke cycle. Mean Reynolds number for wing flapping is ~ 120 . (C) Experimental set-up showing gear boxes and wings of the mechanical model. The rigid, non-cambered, translucent plastic wings are immersed in a tank filled with mineral oil. Sizes of gears and wings are not to scale. Scale bar applies to the mechanical wings only. The terms Δ_s and Δ_{FW-HW} indicate the distance between the wing hinges and wing tips, respectively. For more detail see Maybury and Lehmann (2004).

chords produces maximum forces at parallel stroking due to beneficial wing–wake interactions (purple, Figure 3D). As larger spacing induces longer vortex travel time in tandem wing systems, this requires phase adjustments in the neuromuscular activation pattern for wing motion when the insect actively changes forewing and hindwing tip paths. Maximum force modulation and thus maximum steering capacity is measured when forewing and hindwing stroke plane are closest (Figure 3F, G). This finding might explain why stroke plane spacing is often minimal in damselflies and dragonflies although lift production is maximum at a spacing of 2.5 wing chords (Figure 3D). Despite the advantage of small spacing for force modulation, flight efficiency (lift–drag ratio) is more prone to changes in kinematic phase lag when stroke planes are closest (Figure 3H).

Force modulation and wing aspect ratio

Besides stroke plane spacing, force modulation in tandem wings depends on wing shape and thus aspect ratio. For example, it is likely that a short forewing (low aspect ratio, Figure 4) leads to a decrease in lift modulation of the hindwing because of a reduced forewing downwash. A long hindwing (high aspect ratio), in turn, likely picks up more of the forewing’s downwash that should lead to an increase in phase-dependent hindwing lift modulation. These dependencies are mapped in experiments in which we systematically altered forewing (Figure 4C, D) and hindwing (Figure 4G, H) length, while wing chord and wing tip geometry remained unchanged.

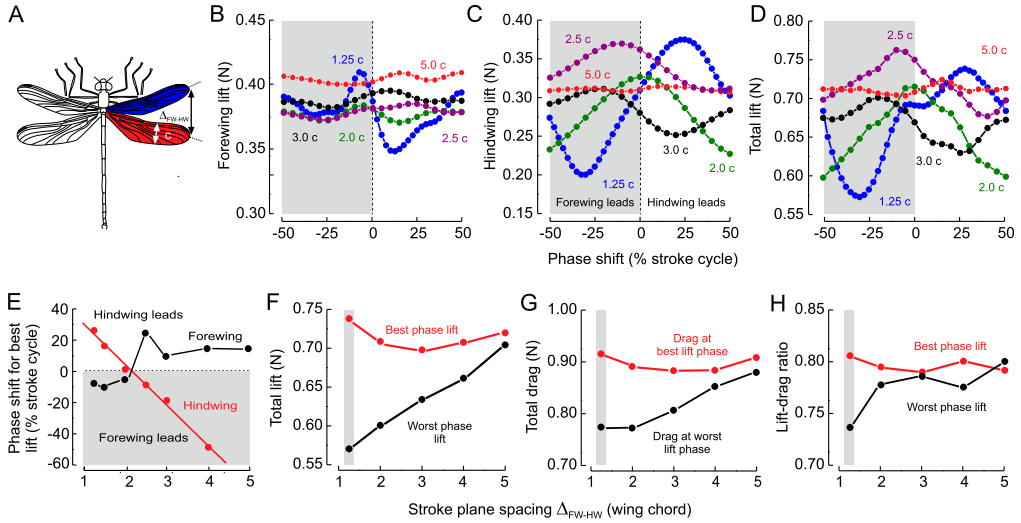


Figure 3. Modulation of cycle-averaged vertical lift during phase shifting kinematics as a function of stroke plane separation and kinematic phase shift. (A) Wing tip separation Δ_{FW-HW} in dragonflies is modelled by wing hinge separation Δ_s in the mechanical model (see Figure 1C). Phase-shift dependency of (B) mean forewing lift, (C) mean hindwing lift, and (D) mean total lift across the entire flapping cycle. Negative (positive) phase shift indicates that the forewing (hindwing) leads wing motion, thus hindwing (forewing) motion is delayed with respect to the forewing (hindwing) cycle. Data show lift modulation for a wing separation of 1.25, 2.0, 2.5, 3.0, and 5.0 wing chord (c). Data are smoothed by a mathematical 5-point Gavitzky–Golay filter. (E) Phase shift at maximum total lift production (shown in D) plotted against wing hinge spacing for hindwing (red) and forewing (black) lift. Red, linear regression fit, $R^2 = 0.99$, $P < 0.0001$. ((F–H) Maximum (best phase) and minimum (worst phase) total lift in F, drag in G, and lift-drag ratio in H plotted as a function of wing hinge spacing. Grey areas indicate times at which the forewing leads wing motion in B–E and maximum difference between best and worst measures in F–H.

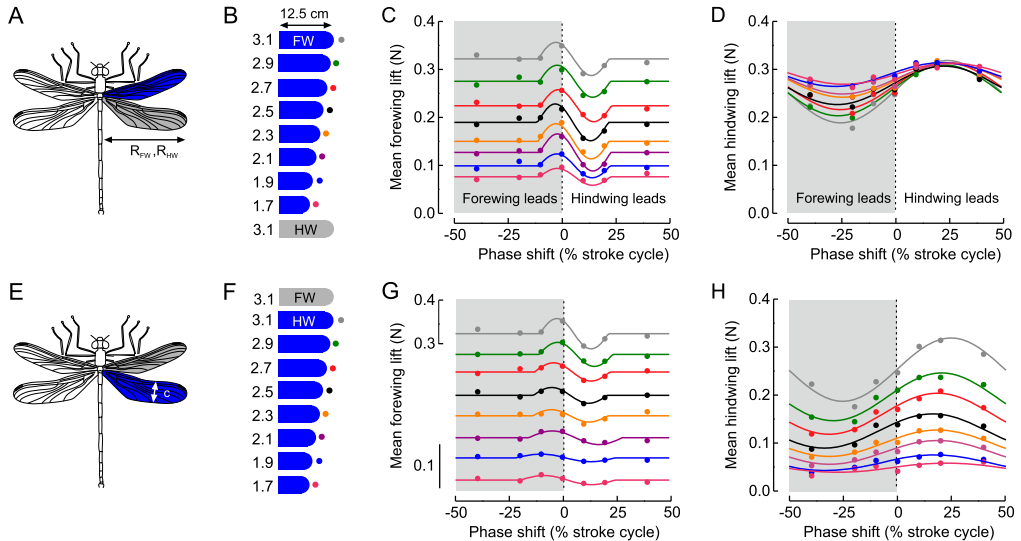


Figure 4. Modulation of vertical lift and horizontal drag during phase shifting kinematics in dragonfly model wings owing to changes in wing aspect ratio. Data show changes in cycle-averaged mean forewing and hindwing lift with changing shape of (A–D) the forewing and (E–H) the hindwing. Colours and numbers indicate the wing’s aspect ratio (AR). Hindwing length in A–D and forewing length in E–H is constant in all tested cases and amounts to 12.5 cm at an $AR = 3.1$. Lines are sine fit functions to data between $\pm 15\%$ stroke cycle in C and G and to $\pm 50\%$ stroke cycle in D and H. Note that in G the phase lag-averaged forewing lift is similar in all tested hindwings. The kinematic pattern used in the experiments is shown in Figure 2B and stroke plane spacing is 1.25 wing chord.

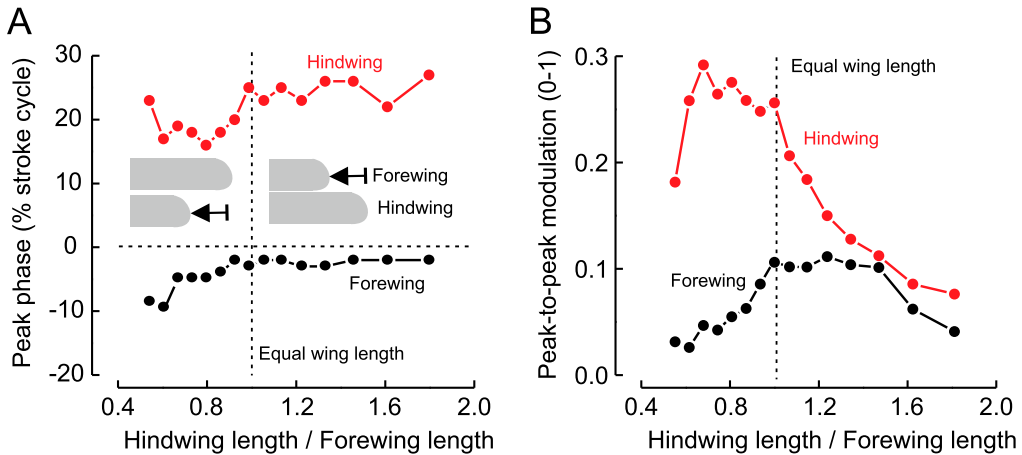


Figure 5. Phase-shift-induced, relative modulation of mean lift production depends on wing length in tandem model wings. (A) Peak phase at which forewing (black) and hindwing (red) produce maximum cycle-averaged lift. Data are plotted against the ratio between hindwing and forewing length. A value of 1.0 means that the two wings are of equal length. (B) Strength of peak-to-peak modulation of forewing (black) and hindwing (red) lift production. Modulations were derived from sinusoidal fits to the dataset (forewing lift: fit on data between $\pm 15\%$ phase-shift, hindwing lift: fit on all data) as shown in Figure 4. Insets in A show the shape of the model wings used in the experiments. The rounded wing tip was similar in all wings. Aspect ratio varied between approximately 1.7 (6.9 cm wing length) and 3.1 (12.5 cm wing length), respectively. Wing chord is 4.0 cm. Vertical distance between the wings was 1.25 wing chord and the kinematic pattern is as shown in Figure 2.

The measurements show that both forewing and hindwing lift production change with changing wing aspect ratio. In cases in which the aspect ratio of the forewing decreases, mean lift production and phase-shift-induced lift modulation of the forewing decreases (Figure 4C). This is as expected because conventional aerodynamic theory predicts that lift production is linearly dependent on wing surface area. The changes in peak-to-peak amplitude of modulation in forewing lift are limited to a small window of approximately $\pm 15\%$ phase lag, as already shown in Figure 3. With increasing forewing downwash, phase shift-induced hindwing lift modulation increases. Figure 4D shows that the forewing downwash does not significantly alter hindwing lift when the hindwing leads by a quarter stroke cycle ($+25\%$) but primarily impairs hindwing lift at the worst kinematic phase (-25%). Thus, the combined lift of both wings shows two characteristic positive peaks: a smaller peak during parallel stroking (0% phase lag) owing to the ground effect on the forewing, and a larger lift peak during phase-shifted stroking ($+25\%$ phase lag) due to beneficial wake capture of the hindwing (data not shown). In cases in which the aspect ratio of the hindwing is lower, lift modulation of the forewing decreases while mean forewing lift is little affected (Figure 4G). As expected from aerodynamic theory, mean hindwing lift and lift modulation decreases with decreasing hindwing aspect ratio (Figure 4H).

Wing aspect ratio does not change vortex shedding frequency during wing flapping in insects. Thus, the relationship between wing-phasing and force production should change only a little with changing wing shape. This prediction might have implications for the evolution and diversity of damselfly- and dragonfly species because in this case wing shape and neural phase control would be two independent traits. Figure 5A suggests that the phase lag for maximum hindwing lift production is scattered around a quarter stroke cycle ($+25\%$) and largely independent of forewing wing length. Small phase adjustments for maximum lift in both wings, however, are required when the hindwing length decreases. In this case, the required phase lag for peak lift slightly decreases by up to $\sim 8\%$ stroke cycle for forewing and hindwing lift (Figure 5A). The latter finding might mean that the evolution of phasing control is more tightly coupled to the evolution of hindwing shape than forewing shape.

Conclusions – the significance of stroke plane spacing and wing aspect ratio

The data revisited by this review suggest that the distance between the stroke planes of forewing and hindwing, and wing aspect ratio are two traits that determine force production in damselflies and dragonflies. As damselflies and dragonflies are successful predators, force control and thus the ability to *modulate* forces are thought to be predominant evolutionary factors besides the animal's capacity to *produce* elevated mean lift (Bomphrey et al., 2016). If phase-shift-induced lift modulation is key for control, we should also expect an elevated selective pressure on morphological traits that reinforce the animal's ability to modulate lift. This prediction is evident from Figure 3F for stroke plane spacing and Figure 5B for wing aspect ratio. The latter figure suggests that combined, peak-to-peak lift modulation of forewing and hindwing is at a maximum when both wings are of the same length and thus aspect ratio. If the hindwing is shorter than the forewing, the animal loses steering capacity during forewing motion. If the forewing is shorter than the hindwing, steering capacity decreases due to a strong decrease in force modulation capacity of the hindwing. In other words: when insects change the phase lag between forewing and hindwing to modulate the total amount of generated lift, the degree of modulation is affected by the ratio of forewing to hindwing length. Consequently, in an animal with long forewings and short hindwings, changes in phase lag mainly modulate how much lift is generated by the hindwings, while in animals with short forewings and long hindwings *both* wings might experience significant modulations in mean lift. Notably, the above conclusions are limited to the tested experimental case that mimics the flow conditions in a damselfly with horizontal stroking. In hovering dragonflies with vertical stroke planes, wing–wake interactions should be minimal, but potentially increase with increasing forward speed (Lua et al., 2016; Sun et al., 2017). Thus, the investigated particular case cannot be the only solution to a general understanding of how body morphology and wing motion determine posture stability and course control in the order Odonatoptera.

References

- Alexander, D. E. (1986). Wind tunnel studies of turns by flying dragonflies. *Journal of Experimental Biology*, 122, 81–98.
- Anwer, S. F., Ashraf, I., Mehdi, H., Ahmad, A., & Grafi, H. (2013). On the aerodynamic performance of dragonfly wing section in gliding mode. *Advances in Aerospace Science and Applications*, 3, 227–234.
- Blanke, A. (2018). Analysis of modularity and integration suggests evolution of dragonfly wing venation mainly in response to functional demands. *Journal of the Royal Society Interface*, 15, 20180277. doi:10.1098/rsif.2018.0277
- Bode-Oke, A. T., Zeyghami, S., & Dong, H. (2017). Aerodynamics and flow features of a damselfly in takeoff flight. *Bioinspiration & Biomimetics*, 12, 056006. doi:10.1088/1748-3190/aa7f52
- Bode-Oke, A. T., Zeyghami, S., & Dong, H. (2018). Flying in reverse: kinematics and aerodynamics of a dragonfly in backward free flight. *Journal of the Royal Society Interface*, 15, 20180102. doi:10.1098/rsif.2018.0102
- Bomphrey, R. J., Nakata, T., Henningsson, P., & Lin, H.-T. (2016). Flight of the dragonflies and damselflies. *Philosophical Transactions of the Royal Society London B*, 371, 20150389. doi:10.1098/rstb.2015.0389
- Broering, T. M., & Lian, Y. (2015). Numerical study of tandem flapping wing aerodynamics in both two and three dimensions. *Computers & Fluids*, 115, 124–139. doi:10.1016/j.compfluid.2015.04.003
- Chen, Y., & Skote, M. (2016). Gliding performance of 3-D corrugated dragonfly wing with spanwise variation. *Journal of Fluids and Structures*, 62, 1–13. doi:10.1016/j.jfluidstructs.2015.12.012
- Davidovich, H., & Ribak, G. (2016). Flying with eight wings: inter-sex differences in wingbeat kinematics and aerodynamics during the copulatory flight of damselflies (*Ischnura elegans*). *The Science of Nature*, 103, 65. doi:10.1007/s00114-016-1390-z
- Dileo, C., & Deng, X. (2009). Design of and experiments on a dragonfly-inspired robot. *Advanced Robotics*, 23, 1003–1021. doi:10.1163/156855309X443160
- Ennos, A. R. (1989). Comparative functional morphology of the wings of Diptera. *Zoological Journal of the Linnean Society*, 96, 27–47. doi:10.1111/j.1096-3642.1989.tb01820.x
- Fu, J.-J., Heffer, C., Qiu, H.-H., & Shyy, W. (2014). Effects of aspect ratio on flapping wing aerodynamics in animal flight. *Acta Mechanica Sinica*, 30, 776–786. doi:10.1007/s10409-014-0120-z
- Gorb, S. (2001). *Attachment devices of insect cuticle*. Dordrecht: Kluwer Academic Publishers.

- Gravish, N., Peters, J. M., Combes, S. A., & Wood, R. J. (2015). Collective flow enhancement by tandem flapping wings. *Physical Review Letters*, *115*, 188101. doi:10.1103/PhysRevLett.115.188101
- Hefler, C., Qiu, H., & Shyy, W. (2016). Dragonflies utilize flapping wings phasing and spanwise characteristics to achieve aerodynamic performance. *arXiv preprint arXiv:1612.05353*.
- Hino, H., & Inamura, T. (2018). Turning flight simulations of a dragonfly-like flapping wing-body model by the immersed boundary-lattice Boltzmann method. *Fluid Dynamics Research*, *50*, 065501. doi:10.1088/1873-7005/aaad78c
- Hou, D., Zhong, Z., Yin, Y., Pan, Y., & Zhao, H. (2017). The role of soft vein joints in dragonfly flight. *Journal of Bionic Engineering*, *14*, 738–745.
- Isogai, K., Fujishiro, S., Saitoh, T., Yamamoto, M., Yamasaki, M., & Matsubara, M. (2004). Unsteady three-dimensional viscous flow simulation of a dragonfly hovering. *AIAA Journal*, *42*, 2053–2059. doi:10.1016/S1672-6529(16)60439-0
- Jang, J., & Yang, G.-H. (2018). Design of wing root rotation mechanism for dragonfly-inspired micro air vehicle. *Applied Sciences*, *8*, 1868. doi.org/10.3390/app8101868
- Johansson, F., Söderquist, M., & Bokma, F. (2009). Insect wing shape evolution: independent effects of migratory and mate guarding flight on dragonfly wings. *Biological Journal of the Linnean Society*, *97*, 362–372. doi.org/10.1111/j.1095-8312.2009.01211.x
- Kok, J., Fatiaki, A., Rosser, K., Chahl, J., & Ogunwa, T. (2017). *Dragonfly inspired MAVs-adaptive and evolutionary approaches*. Paper presented at the 17th Australian International Aerospace Congress: AIAC 2017, Barton, Australian Capital Territory, Australia, pp. 129–138. ISBN: 9781922107855
- Kuchta, S. R., & Svensson, E. I. (2014). Predator-mediated natural selection on the wings of the damselfly *Calopteryx splendens*: differences in selection among trait types. *The American Naturalist*, *184*, 91–109. doi.org/10.1086/676043
- Lai, W., Yan, J., Motamed, M., & Green, S. (2005). *Force measurements on a scaled mechanical model of dragonfly in forward flight*. Paper presented at the 12th International Conference on Advanced Robotics, IEEE, Seattle, Washington, pp. 595–600. 10.1109/ICAR.2005.1507469
- Lehmann, F.-O. (2008). Wing-wake interaction reduces power consumption in insect tandem wings. *Experiments in Fluids*, *46*, 765–775. doi.org/10.1007/978-3-642-11633-9_17
- Li, C., & Dong, H. (2017). Wing kinematics measurement and aerodynamics of a dragonfly in turning flight. *Bioinspiration & Biomimetics*, *12*, 026001. doi.org/10.1088/1748-3190/aa5761
- Lu, Y., Shen, G. X., & Su, W. H. (2007). Flow visualization of dragonfly hovering via an electromechanical model. *AIAA Journal*, *45*, 615–623. doi.org/10.2514/1.22088
- Lua, K., Lu, H., Zhang, X., Lim, T., & Yeo, K. (2016). Aerodynamics of two-dimensional flapping wings in tandem configuration. *Physics of Fluids*, *28*, 121901. doi.org/10.1063/1.4971859
- Maybury, W. J., & Lehmann, F.-O. (2004). The fluid dynamics of flight control by kinematic phase lag variation between two robotic insect wings. *Journal of Experimental Biology*, *207*, 4707–4726. 10.1242/jeb.01319
- Norberg, R. A. (1975). Hovering flight of the dragonfly *Aeshna juncea* L., kinematics and aerodynamics. In T. Y.-T. Wu, C. J. Brokaw & C. Brennen (Eds.), *Swimming and Flying in Nature*, vol. 2 (pp. 763–781). New York: Plenum Press. doi.org/10.1007/978-1-4757-1326-8_19
- Otomuro, D., Adams, D. C., & Johansson, F. (2013). Wing shape allometry and aerodynamics in calopterygid damselflies: a comparative approach. *BMC Evolutionary Biology*, *13*, 118. doi.org/10.1186/1471-2148-13-118
- Otomuro, D., & Johansson, F. (2011). The effects of latitude, body size, and sexual selection on wing shape in a damselfly. *Biological Journal of the Linnean Society*, *102*, 263–274. doi.org/10.1111/j.1095-8312.2010.01591.x
- Rajabi, H., Rezaeefat, M., Darvizeh, A., Dirks, J.-H., Eshghi, S., Shafiei, A., Mostofi, T. M., & Gorb, S. N. (2016). A comparative study of the effects of constructional elements on the mechanical behaviour of dragonfly wings. *Applied Physics A*, *122*, 19. doi.org/10.1007/s00339-015-9557-6
- Reavis, M. A., & Luttges, M. W. (1988). Aerodynamic forces produced by a dragonfly. *AIAA Journal*, *88*–0330, 1–13. doi.org/10.2514/6.1988-330
- Shi, X., Huang, X., Zheng, Y., & Zhao, S. (2016). Effects of cambers on gliding and hovering performance of corrugated dragonfly airfoils. *International Journal of Numerical Methods for Heat & Fluid Flow*, *26*, 1092–1120. doi.org/10.1108/HFF-10-2015-0414
- Shumway, N., Gabryszyk, M., & Laurence, S. J. (2018). Flapping tandem-wing aerodynamics: dragonflies in steady forward flight. In *2018 AIAA Aerospace Sciences Meeting*, Kissimmee, FL, pp. 1290. doi.org/10.2514/6.2018-1290
- Shumway, N., & Laurence, S. J. (2019). The impact of deformation on the aerodynamics of flapping dragonfly wings. In *AIAA Scitech 2019 Forum*, San Diego, CA, pp. 1378. doi.org/10.2514/6.2019-1378
- Sivasankaran, P. N., Ward, T. A., Salami, E., Viyapuri, R., Fearday, C. J., & Johan, M. R. (2017). An experimental study of elastic properties of dragonfly-like flapping wings for use in biomimetic micro air vehicles (BMAVs). *Chinese Journal of Aeronautics*, *30*, 726–737. doi.org/10.1016/j.cja.2017.02.011
- Stocks, I. (2008). Wing coupling. In John L. Capinera (Ed.), *Encyclopedia of entomology*. (pp. 258–262). Dordrecht: Springer. doi.org/10.1007/978-1-4020-6359-6_2680
- Somps, C., & Luttges, M. (1985). Dragonfly flight: novel uses of unsteady separated flows. *Science*, *228*, 1326–1329. 10.1126/science.228.4705.1326
- Sun, M., & Huang, H. (2007). Dragonfly forewing-hindwing interaction at various flight speeds and wing phasing. *AIAA Journal*, *45*, 508–511. doi.org/10.2514/1.24666
- Sun, M., & Lan, S. L. (2004). A computational study of the aerodynamic forces and power requirements of dragonfly (*Aeshna juncea*) hovering. *Journal of Experimental Biology*, *207*, 1887–1901. 10.1242/jeb.00969

- Sun, X., Gong, X., & Huang, D. (2017). A review on studies of the aerodynamics of different types of maneuvers in dragonflies. *Archive of Applied Mechanics*, 87, 521–554. doi.org/10.1007/s00419-016-1208-7
- Takahashi, H., Concordel, A., Paik, J., & Shimoyama, I. (2016). The effect of the phase angle between the forewing and hindwing on the aerodynamic performance of a dragonfly-type ornithopter. *Aerospace*, 3, 4. doi.org/10.3390/aerospace3010004
- Takizawa, K., Tezduyar, T. E., & Buscher, A. (2015). Space–time computational analysis of MAV flapping-wing aerodynamics with wing clapping. *Computational Mechanics*, 55, 1131–1141. doi.org/10.1007/s00466-014-1095-0
- Thomas, A. L. R., Taylor, G. K., Srygley, R. B., Nudds, R. L., & Bomphrey, R. J. (2004). Dragonfly flight: free-flight and tethered flow visualizations reveal a diverse array of unsteady lift-generating mechanisms, controlled primarily via angle of attack. *Journal of Experimental Biology*, 207, 4299–4323. 10.1242/jeb.01262
- Usherwood, J. R., & Lehmann, F.-O. (2008). Phasing of dragonfly wings can improve aerodynamic efficiency by removing swirl. *Journal of the Royal Society Interface*, 5(28), 1303–1307. doi:10.1098/rsif.2008.0124.
- Vargas, A., Mittal, R., & Dong, H. (2008). A computational study of the aerodynamic performance of a dragonfly wing section in gliding flight. *Bioinspiration & Biomimetics*, 3, 026004. doi.org/10.1088/1748-3182/3/2/026004
- Wakeling, J. M. (1993). Dragonfly aerodynamics and unsteady mechanisms: a review. *Odonatologica*, 22, 319–334.
- Wakeling, J. M. (1997). Odonata wing and body morphologies. *Odonatologica*, 26, 35–52.
- Wakeling, J. M., & Ellington, C. P. (1997). Dragonfly flight II. Velocities, accelerations, and kinematics of flapping flight. *Journal of Experimental Biology*, 200, 557–582.
- Wang, H., Zeng, L., Liu, H., & Chunyong, Y. (2003). Measuring wing kinematics, flight trajectory and body attitude during forward flight and turning maneuvers in dragonflies. *Journal of Experimental Biology*, 206, 745–757. 10.1242/jeb.00183
- Wang, J. K., & Sun, M. (2005). A computational study of the aerodynamics and forewing–hindwing interaction of a model dragonfly in forward flight. *Journal of Experimental Biology*, 208, 3785–3804. 10.1242/jeb.01852
- Wang, X., Zhang, Z., Ren, H., Chen, Y., & Wu, B. (2017). Role of soft matter in the sandwich vein of dragonfly wing in its configuration and aero dynamic behaviors. *Journal of Bionic Engineering*, 14, 557–566. doi.org/10.1016/S1672-6529(16)60421-3
- Wootton, R. J. (1991). The functional morphology of the wings of Odonata. *Advances in Odonatology*, 5, 153–169.
- Wootton, R. J., & Newman, D. J. (2008). Evolution, diversification, and mechanics of dragonfly wings. In Alex Córdoba-Aguilar (Ed.), *Dragonflies and damselflies: Model organisms for ecological and evolutionary research* (Chap. 20, pp. 261–274). New York: Oxford University Press.
- Wortmann, M., & Zarnack, W. (1993). Wing movements and lift regulation in the flight of desert locusts. *Journal of Experimental Biology*, 182, 57–69.
- Xie, C.-M., & Huang, W.-X. (2015). Vortex interactions between forewing and hindwing of dragonfly in hovering flight. *Theoretical and Applied Mechanics Letters*, 5, 24–29. doi.org/10.1016/j.taml.2015.01.007
- Young, J., S. Lai, J., & Germain, C. (2008). Simulation and parameter variation of flapping-wing motion based on dragonfly hovering. *AIAA Journal*, 46, 918–924. doi.org/10.2514/1.31610
- Zheng, Y., Wu, Y., & Tang, H. (2016). An experimental study on the forewing–hindwing interactions in hovering and forward flights. *International Journal of Heat and Fluid Flow*, 59, 62–73. doi.org/10.1016/j.ijheatfluidflow.2015.12.006