UNUSUAL PHASE RELATIONSHIPS BETWEEN THE FOREWINGS AND HINDWINGS IN FLYING DRAGONFLIES

By DAVID E. ALEXANDER*

Department of Zoology, Duke University, Durham, NC 27706, U.S.A.

Flying insects can generally be divided into two groups: 'primitive' orders with forewings and hindwings that move independently (for example, Odonata, Orthoptera, Isoptera) and more 'advanced' orders with wings that are functionally one pair, with the fore- and hindwings in contact so as to function as one wing (for example, Hymenoptera, Lepidoptera, Homoptera), or with only one pair of wings that functions primarily as a lifting surface (for example, Diptera, Strepsiptera).

Some insects in more primitive orders, such as locusts, maintain a fixed phase relationship between their forewings and hindwings with the hindwings leading slightly (Chadwick, 1953; Weis-Fogh, 1956; Wilson, 1968). Dragonflies normally beat their forewings and hindwings out of phase, with the hindwings about a half stroke ahead of the forewings, i.e. in antiphase (Chadwick, 1940; Neville, 1960; Alexander, 1982). Many textbooks state that the antiphase relationship is more efficient (Chadwick, 1953, p. 582; Wigglesworth, 1972, p. 161; Romoser, 1973, p. 162). Wilson (1968), however, suggested that individual dragonflies may exhibit large variations in this phase relationship.

In this study, I have made high-speed ciné films of dragonflies flying in a wind tunnel; the dragonflies were free to turn about their vertical and longitudinal axes. From these films, I assessed the forewing–hindwing phase relationship in straight flight, turning flight, and flight requiring larger than normal aerodynamic forces.

The techniques were as previously described (Alexander, 1982, and in preparation) and may be summarized as follows. Field-caught dragonflies were flown in an open-section wind tunnel. Most were flown on a tethering system that allowed them to yaw (turn about their dorsal-ventral axis) or roll (turn about their anterior-posterior axis), but a few were flown without a tether. The tether was attached to the posterio-ventral surface of the thorax so as to minimize interference with the wing articulations. Several dragonfly species were used, primarily *Libellula luctuosa* and *Celithemis elisa*. The animals were filmed in flight with a LOCAM II (Redlake Corporation) 16 mm, high-speed ciné camera at film speeds of 400 to 550 frames s^{-1}. Each film sequence consisted of the dragonfly performing a turn or a continuous series of turns, and a sequence ended with the dragonfly leaving the field of view of the camera or stopping its flapping. The films were analysed by projecting them at a low frame rate with an L-W International Mark V film analyser. For each sequence, I recorded the

speed and type of turn (Alexander, 1982) and the forewing–hindwing relation ship during turns and straight flight. Usually, the forewings and hindwings were either obviously out of phase or obviously in phase, with very quick (one or two wingbeat) transitions, so the phase relationship was normally very easy to distinguish. In one case, the phase relationship was quite complex and appeared to change constantly throughout the stroke. This was an isolated occurrence however, and the unusual appearance of the turn it produced is described in detail elsewhere (Alexander, 1982, and in preparation).

During 48 of the 91 high-speed film sequences, dragonflies flapped their forewings and hindwings in phase for short periods interspersed among much longer periods of flapping out of phase. Also, dragonflies flapped in phase during 25 of the 30 yaw turn sequences filmed; yaw turns are extremely fast turns (90° in two or three wingbeats) where the dragonfly pivots about a vertical axis without rolling about a longitudinal axis (Alexander, 1982, and in preparation). Fig. 1 shows a sequential series of sketches from the film of one stroke, taken during typical episodes of flapping out of phase (Fig. 1A), and in phase (Fig. 1B). The wing stroke pattern is not unusual in any other way in the latter sequence.

The untethered sequences clearly show that flapping in phase is not an artifact of the tethering system. Dragonflies in six of the eight untethered sequences used in-phase flapping; Fig. 1C illustrates part of one such sequence. These sequences suggest
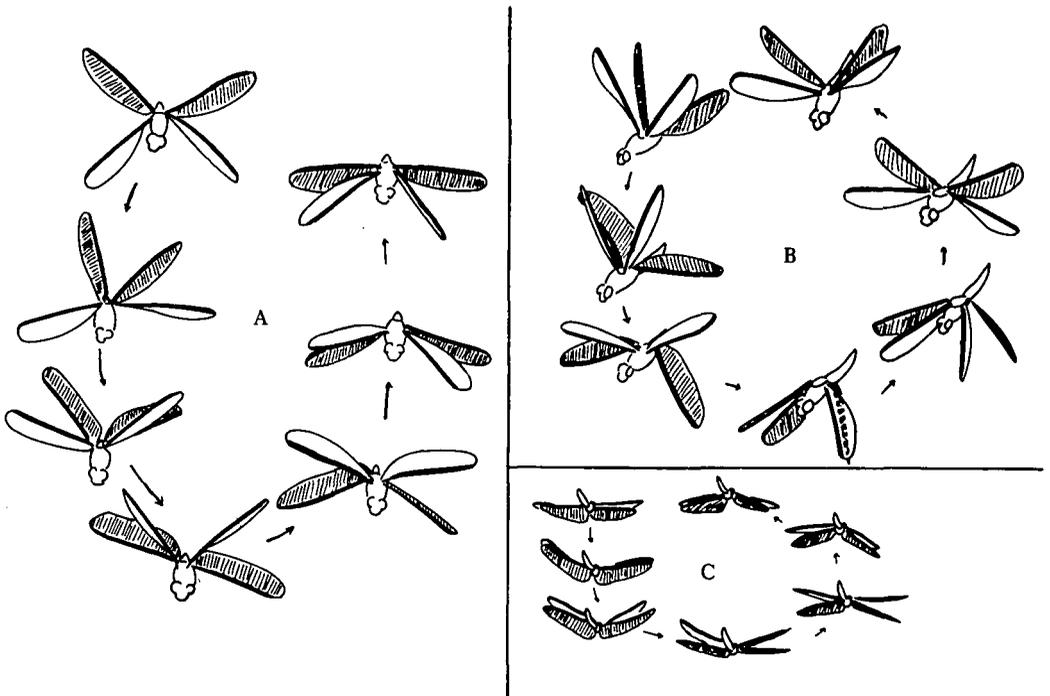

Fig. 1. Tracings of dragonflies in every other frame from three different film sequences. Hindwings shaded and wing leading edges darkened in all tracings. (A) Tethered, head-on view, out-of-phase wingbeat; (B) tethered, oblique view, in-phase wingbeat; (C) untethered, back view, in-phase wingbeat. Dragonflies in (A) and (B) are turning, and dragonfly in (C) is hovering.

t dragonflies use in-phase flapping quite often, particularly upon take-off and uring hovering.

The free-flight films show that dragonflies often take off with in-phase flapping, and then the forewings slow and the hindwings speed up their beat so that the animal assumes the normal antiphase pattern in one or two beats. Similarly, when shifting from normal to in-phase flapping during flight, the forewings shorten and speed up their stroke (and the hindwings may also extend their stroke) so that the transition is made in one beat. This quick transition from one pattern to the other is not surprising, as the dragonflies rarely flapped in phase for more than five or six beats at a time, in either free or tethered flight.

Flapping in phase appears to be employed in situations that call for greater than normal force production. A few sequences show spontaneous (rather than forced) take-offs, and dragonflies usually flapped in phase during such manoeuvres; take-off obviously requires more force than straight and level flight. Also, in-phase flapping often occurs during yaw turns, which are extraordinarily fast. Finally, animals trying to reverse direction and overcome the inertia of the tether almost always flapped in phase until they were moving in the new direction. (This could be analogous to attempting to escape from a predator.)

It is unfortunate that the most important aspect of this behaviour made it nearly impossible to analyse in detail as was done previously for turning (Alexander, 1982, and in preparation): by virtue of being in phase, the wings appear to overlap in the films, so that many of the measurements needed to determine positions and angles could not be made.

For a functionally four-winged insect, the advantages and disadvantages of different fore–hind phase relationships are not at all clear-cut. Two long, narrow wings working independently should have a higher lift:drag ratio than the same two wings hooked together and acting as a single wing, due to the differences in aspect ratio (Mises, 1959; Bertin & Smith, 1979). However, two wings in tandem, and flapping in phase, would interfere with each other's lift production: according to biplane theory, as two wings in tandem are brought closer together, the lift produced by each wing is reduced (Milne-Thomson, 1966). In simple terms, this reduction is because the air deflected down by the forewing ('downwash') reduces the hindwing's angle of attack, and hence its lift, while the hindwing partially deflects the forewing's downwash, and so reduces the forewing's lift production. Forewings and hindwings flapping in phase should produce less lift because they would always be closer together than wings flapping out of phase. Also, if the forewing produces a turbulent wake, the lift production of the hindwing would be reduced, so the net lift would be lower for the wings in tandem than for separated wings. Large insects such as dragonflies probably produce turbulent wakes, but this has not been clearly demonstrated. Also, there is another potential problem with flapping out of phase: the wing articulations and musculature of the fore- and hindwings must be able to operate completely independently, in spite of being in close physical proximity.

If the dragonfly has evolved a structure that allows it to fly with the presumably advantageous out-of-phase pattern, why should it abandon this mode and flap in phase? One possibility is that some situations require a large increase in force over a short riod of time (a high impulse), in which case the dragonfly may have evolved a

mechanism that trades off a reduction in the lift per wing for a greater total lift during the period of the downstroke. The initial beat during take-off might be such a situation. But since the dragonfly consistently used in-phase flapping for more than one or two beats, there must be another reason. Such episodes, when they tried to reverse direction and had to overcome the inertia of the tether (lasting five or six beats) were much more common than the shorter ones. If flapping in phase merely provides a larger pulse of force on the downstroke, the average force over several strokes should be lower due to the adverse aerodynamic interactions. All other things being equal, this lower average force does not seem advantageous in a situation that calls for high force production.

Although steady-state aerodynamics may suggest otherwise, in-phase flapping could have some aerodynamic function. It is possible that dragonflies may be taking advantage of some unsteady effect with this behaviour; Ellington (1980) has described a vertical vortex-shedding mechanism for lift production in butterflies that depends on the unsteady nature of flapping flight, and dragonflies may use some similar effect.

A more plausible explanation for the in-phase pattern is that there are mechanical constraints on the wing articulation that limit the total force that can be applied to the wings during out-of-phase flapping. The fore and hind articulations are physically attached to each other and thus cannot be completely mechanically isolated; when the hindwings are being lowered, there should be a slight, adverse force on the forewing articulation, which is being raised, and raising the forewing should cause a slight adverse force on the hindwing articulation. Thus, flapping out of phase makes the forewing and hindwing articulations somewhat antagonistic. By manipulating the wings of freshly-killed dragonflies, one can show a small amount of mechanical linkage between the fore- and hindwings at extreme stroke angles, but no apparent linkage at angles similar to stroke angles used in straight, level flight. This suggests that the forewing and hindwing articulations are not antagonistic in normal flight, in spite of their close proximity. However, this mechanical isolation seems to break down at high stroke angles: when dragonflies use very high stroke angles to increase lift or thrust, the antagonistic action may interfere with lift production, at which point the animal would switch to flapping in phase.

Flapping in phase usually occurred during strokes with stroke angles higher than normal by 10 or 20°. Such strokes were rarely as large as the 140° or greater stroke angles needed to demonstrate mechanical linkage on dead specimens. I believe, however, that it is reasonable to suppose that the linking effect is more pronounced when produced by the insect's flight muscles acting in close proximity on the articulations themselves, rather than when the wingtip is moved on a dead specimen.

Whatever the mechanism, in-phase flapping appears to serve as the dragonfly's primary means of greatly increasing lift and thrust. In only one sequence did a dragonfly appear to use the well-known 'clap-fling' (Weis-Fogh, 1973) unsteady lift-enhancement mechanism; this occurred during flapping out of phase. ('Clap-fling' is a modification of the wingstroke where the wings 'clap' together at the top of the upstroke and then open like a book, or 'fling', at the beginning of the downstroke; apparently, this motion increases the duration of lift production by establishing the lift-producing flow pattern earlier in the downstroke; Weis-Fogh, 1973; Ellington, 1980.) The rare occurrence of this phenomenon in dragonflies, and their common use

in-phase flapping suggests that dragonflies have evolved a method of lift enhancement different from 'clap-fling', probably made possible in part by their two independent pairs of wings.

REFERENCES

ALEXANDER, D. E. (1982). Studies on flight control and aerodynamics in dragonflies. Ph.D. dissertation. Duke University, Durham, NC.

BERTIN, J. L. & SMITH, M. L. (1979). *Aerodynamics for Engineers*. Englewood Cliffs, NJ: Prentiss-Hall, Inc.

CHADWICK, L. E. (1940). The wing motion of the dragonfly. *Brooklyn Entomological Soc. Bull.* 35, 109–112.

CHADWICK, L. E. (1953). The motion of the wings. In *Insect Physiology*, (ed. Kenneth D. Roeder), pp. 577–614. New York: John Wiley & Sons, Inc.

ELLINGTON, C. P. (1980). Vortices and hovering flight. In *Instationäre Effekte an Schwingenden Tierflügeln*, (ed. Werner Nachtigall), pp. 64–101. Mainz: Akademie der Wissenschaften und der Literatur; Wiesbaden: Franz Steiner Verlag.

MILNE-THOMSON, L. M. (1966). *Theoretical Aerodynamics*, 4th ed. New York: Dover Publications, Inc.

MISES, R. VON (1959). *Theory of Flight*. New York: Dover Publications, Inc.

NEVILLE, A. C. (1960). Aspects of flight mechanics on anisopterous dragonflies. *J. exp. Biol.* 37, 631–656.

ROMOSER, W. S. (1973). *The Science of Entomology*. New York: Macmillan Publishing Co., Inc.

WEIS-FOGH, T. (1956). Biology and physics of locust flight. II. Flight performance of the desert locust (*Schistocerca gregaria*). *Phil Trans. R. Soc. Ser. B.* 239, 459–510.

WEIS-FOGH, T. (1973). Quick estimates of flight fitness in hovering animals, including novel mechanisms for lift production. *J. exp. Biol.* 59, 169–230.

WIGGLESWORTH, V. B. (1972). *The Principles of Insect Physiology*, 7th ed. London: Chapman & Hall.

WILSON, D. M. (1968). The nervous control of insect flight and related behaviors. *Adv. Insect Physiol.* 5, 289–338.
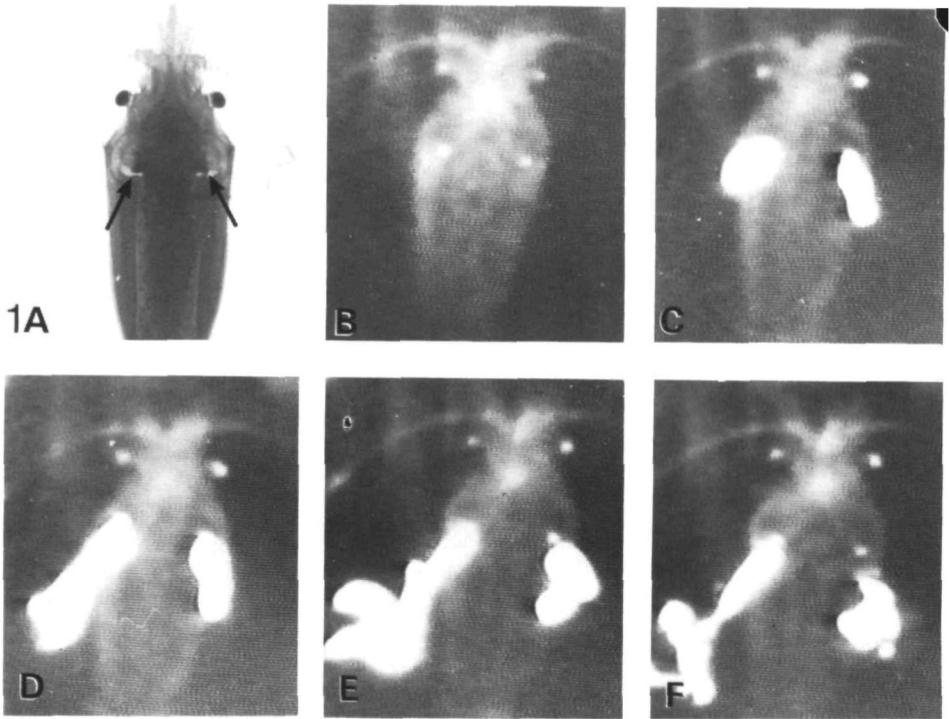
Fig. 1. Ventral aspect of *Gnathophausia ingens* showing (A) the position the gland openings on the 2nd maxillae (arrows) and (B–F) the sequence of *G. ingens* secreting luminescent fluid. B–F are image intensified-video photographs; time between frames, 0·5 s; photographs are actual size.