

**SOME ASPECTS OF WING KINEMATICS IN  
*CALOPTERYX SPLENDENS* (HARRIS)  
(ZYGOPTERA: CALOPTERYGIDAE)**

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Wing beat frequency, wing tip curves during first stroke cycle, and ipsilateral wing coordination in *C. splendens* are described. Characteristics of wing kinematics in this species are: constant beat frequency, irregular wing tip curves, and the specific type of wing coordination. Ipsilateral wings do not alternate. They are prevented from colliding by beating in phase, with the forewing leading in the upstroke.

**INTRODUCTION**

The characteristic aerial locomotion of insects is that of flapping flight, the kinematics and dynamics of which have been worked out to a wide extent in certain four-winged and dipterous insects by various authors. In those four-winged insects examined so far of the orders Heteroptera, Orthoptera, and Coleoptera, both pairs of wings are dissimilar in shape. In a considerable number of Coleoptera, aerodynamic effect is restricted to one pair of wings (SCHNEIDER, 1975) and in Lepidoptera and Hymenoptera the ipsilateral wings are coupled together. There are only a few insects which fly using four morphologically similar but functionally separate wings; e.g. the Odonata and some *Ephemeridae* and Neuroptera. In the most versatile flying anisopterous Odonata the ipsilateral wings are moved independently with varying phase shift, while many zygopterous dragonflies seem to keep a constant phase shift of 180° between fore- and hind-wing as has been shown by BULL (1909) and VOSS (1914) in *Coenagrion* species. However, this is not true for the European *Calopterygidae*, the agile flight performance of which is outstanding in Zygop-

tera. None of the groups mentioned has been examined more deeply so far, except for the aerodynamics of *Ephemera vulgata* (BRODSKY, 1971). In this paper the first results of a detailed study on the kinematics of the wings of *Calopteryx splendens* are presented.

### MATERIAL AND METHODS

The kinematics of the wings were calculated from high speed films and multiple or single exposure photographs taken from tethered animals suspended from a balance and flying in front of a wind tunnel with an approximately smooth jet, the speed of which equalled that of the flight speed. Air speed was measured by a Wallac anemometer. The wind tunnel technique and the balance device were fundamentally in accordance with those described by WEIS-FOGH (1956) and NACHTIGALL (1966), but there was no servo-mechanism controlling wind speed in relation to the insect's thrust. In addition, films and photographs were taken from unrestrained animals. Other details concerning flight performance and photographic technique have been reported elsewhere (RUDOLPH, 1976).

The hinges of the forewings are taken as the origin of a rectangular coordinate system  $x, y, z$ , defining three planes  $xy, xz,$  and  $yz$  (Fig. 1). Angles in this coordinate system are named  $\beta, \gamma, \delta,$  and  $b$ , with an H or F added, indicating hindwing or forewing. The inclination of the stroke planes to the  $z$ -axis is the stroke plane angle  $b$ . The stroke plane angles differ significantly in fore- and hindwings when projected upon the  $xz$ -plane (Fig. 1).

The wing tips move on a sphere with its centre in the fulcrum. Three meridians of the sphere are given in Fig. 1, representing the intersections between the sphere and the coordinate planes. At the end of every upstroke the wings clap together in the  $xz$ -plane, and the wing tips meet at  $P_F$  and  $R_H$ , respectively (Fig. 1). The angle  $\gamma$  is the projection upon the  $yz$ -plane of the instantaneous position of the wing long axis, so it is not the true stroke amplitude  $\phi$ , which was calculated using  $b$  and  $\gamma$ :

$$\phi = 90 + \epsilon$$

$$\tan \epsilon = \cot (180 - \gamma) \cos b.$$

In the flying animal  $b$  was measured with a protractor.

The wing tip path, as projected upon one of the three coordinate planes, was constructed on graph paper after direct measurement of the corresponding coordinates of the wing tip in successive frames of high speed films or in multiple exposure photographs, using a "Three-Panel-Projection"-technique (NACHTIGALL, 1970), so that the instantaneous wing positions were projected simultaneously upon the three coordinate planes in one frame. Perspective deformation was neglected with regard to the long focal distance of the optical system ( $f = 250$  mm). The angle  $\delta$  is made up by the projection of the wing long

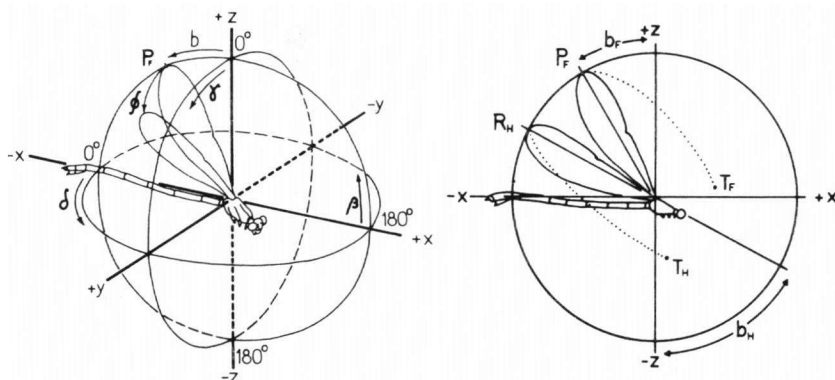


Fig. 1. Left: The coordinate system of a flying *Calopteryx splendens*. One forewing is indicated at the end of an upstroke ( $P_F$ ) and during a downstroke, forming the angle  $\phi$ . Right: Projection of the extreme wing tip positions ( $P_F - T_F$ ;  $R_H - T_H$ ) upon the xz-plane during flight. Approximative wing tip path is marked by dotted line.

axis upon the xy-plane. It represents the geographic longitude of the wing tip. The true latitude was calculated from  $\gamma$  and the apparent length of the long wing axis.

In straight horizontal flight there is no pitch, so that the abdomen coincides with the negative x-axis, while the positive x-axis indicates the direction of flight. The wing long axis is given by a line connecting the distal end of Radius 1 with the proximal end of Radius-Media (wing venation terms after CORBET, LONGFIELD & MOORE, 1960).

### WING BEAT FREQUENCY

Wing beat frequency was controlled by recording electrical activity of the wing depressor muscles or by counting from high speed films. In tethered flight beat frequency (16 H<sub>z</sub>) is surprisingly constant and by no means affected by air speed or the frequency of stroboscopic illumination, as it has been observed in other insects and even in a dragonfly, *Sympetrum darwinianum*, where at the moment of shift in a stroboscopic frequency the wing beat frequency was less stable (HISADA, TAMASIGE & SUZUKI, 1965). In *C. splendens* there is no increase in beat frequency during an initial phase of flight and no decrease in frequency preceding spontaneous cessation of flight. In free flight the wing beat frequency is slightly variable, e.g. during the landing reaction, or shows a more significant increase during a certain phase of courtship flight in the male, when stroke amplitude is remarkably diminished. In "artificial" landing reactions during tethered flight no change of wing beat frequency could be observed. The *Calopterygidae* in fact seem to have the lowest wing beat frequency in the whole

order Odonata. There are many observations from early authors (VOSS, 1914; MAGNAN, 1934) concerning wing beat frequency of European Odonata, which agree well with my own measurements.

### WING MOVEMENT AT THE START OF FLIGHT

In *C. splendens* the wings are brought to a resting position in the  $xz$ -plane, with their morphological upper sides clapped together, and the forewings completely enclosed by the hindwings. During rest the wing tips touch the  $xz$ -meridian at one point only. A typical feature of the wings of most Calopterygoidea is their low aspect ratio (3,2 in both wings of *C. splendens* and 2.6 in the hindwings of *Calopteryx* species) with the longest chord in the more distant wing regions. The aspect ratio of forewings in other Zygoptera is 4,8 (*Enallagma cyathigerum*), and in Anisoptera 4,9 (*Anax tristis*).

Moreover, the ipsilateral fulcra are located very close together, at a distance of less than 1 mm, so that in the resting position the wing long axes approximately coincide. From this it follows that, if in *C. splendens* at the start of flight the forewings were to begin the down stroke earlier than the hindwings, they would have to be moved forward in the  $xz$ -plane for at least  $35^\circ$  to get clear of the hindwings. However, the wing fulcra are to be considered as hinges opening like books, not allowing the forewings any extensive deviation in the  $xz$ -plane. As previously described (RUDOLPH, 1976) in *C. splendens* fresh flight can be started from only one point in the wing beat cycle, that is with a downstroke of the hindwings.

### MOVEMENT OF THE HINDWING

In slow start as well as in fast start the hindwing is moved straight down from its dorsal position. On the sphere the tip of one hindwing approximately follows a great circle, intersecting the  $xy$ -plane with an angle  $\delta$  averaging  $70^\circ$ . The intersection of the great circle with the  $xz$ -plane is considered as the stroke plane angle,  $b_H$ , which is about  $55^\circ$  (Fig. 1). There is another intersection of this circle with the  $yz$ -plane at a certain  $\gamma$  below the  $xy$ -plane (Fig. 2). Stroke amplitude  $\phi$  as calculated from  $\gamma_H$  averaged  $140^\circ$  at  $1 \text{ m}\cdot\text{sec}^{-1}$  airspeed. The wing circle is inclined to the  $z$ -axis in the  $xz$ -plane as well as to the negative  $x$ -axis in the  $xy$ -plane, forming the angle  $\delta$ . Since  $\delta$  does not equal  $90^\circ$ , tips of opposite wings of course move on different great circles penetrating each other at  $R_H$  with an angle of about  $145^\circ$ , opening to the  $-x$  direction. At the end of the first upstroke the wing tip returns to its resting position  $R_H$ . The horizontal distance between the wing tip curves in downstroke and upstroke varies, but at an airspeed of  $1 \text{ m}\cdot\text{sec}^{-1}$  both curves quite often coincide, at least partially (Fig. 2).

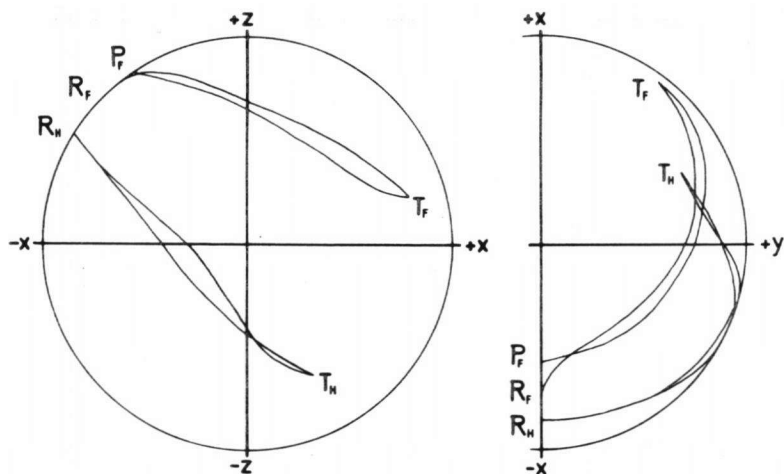


Fig. 2. Wing tip curves of right wings during the first wing beat cycle in spontaneous slow start, projected upon the  $xz$ -plane (left) and upon the  $xy$ -plane (right).

### MOVEMENT OF THE FOREWING

In slow start the forewings are opened from  $R_F$  forming an acute angle to the direction of flight (Fig. 2). They are moved forward and downward, the forward movement predominating at first, but diminishing continuously. Maximum forward movement is about  $20^\circ$  of arc.

On the sphere a great circle can be inserted connecting the extreme up and down positions of the wing tip during full flight. The intersection of this circle with the  $xz$ -plane is the stroke angle,  $b_F$  (Fig. 1). There is another intersection with the  $yz$ -meridian above the  $xy$ -plane at a certain  $\gamma$ . The wing long axis at maximum stroke amplitude projected upon the  $xy$ -plane gives an angle  $\delta$ , which always exceeds  $90^\circ$ .

The great circle does not represent the true wing tip path on the sphere. Since the wing tip curve during the downstroke as well as during the upstroke intersects with the  $yz$ -plane at a  $\gamma$  greater than that of the great circle, the wing tip curve is part of the perimeter of a cone's base, the tip of which is located in the fulcrum.

With no exception at any position in the wing beat cycle and under all experimental conditions,  $\gamma_F$  is smaller than  $\gamma_H$  when projected upon the  $yz$ -plane. At the end of the first upstroke the forewing tip returns to  $P_F$ , which is ahead of the resting position. Shortly after cessation of flight the fore wings are tilted caudad in the  $xz$ -plane until their tips meet with the hindwing tips at  $R_H$ . After repeated stimulation in tethered animals the forewing tips often

remain at  $R_F$  (Fig. 2), from where the next flight is started. During flight the forewing tips never meet at  $R_F$  or  $R_H$ .

During full flight there is little or no horizontal distance between the downstroke and upstroke curves. Generally the wing tip path of a complete stroke cycle resembles a line at an airspeed of  $1 \text{ m}\cdot\text{sec}^{-1}$ . As described elsewhere (RUDOLPH, 1976) in quick start the wings are opened with the "fling" mentioned by WEIS-FOGH (1973) for minute insects. The forewings are moved straight downward, at first overlapping the hindwings' costae, but overlapping is continuously reduced within the upper quarter of the trajectory due to different stroke plane inclinations. Since at the end of an upstroke the forewing does not return to  $R_F$  but to  $P_F$  (Fig. 2), the upper third of the wing tip path in quick downstroke lies behind that of the upstroke.

#### COORDINATION OF IPSILATERAL WINGS DURING FULL FLIGHT

At the beginning of the downstroke the forewings follow the hindwings with a certain delay with regard to the downward movement. This delay may vary within every wing beat cycle in one individual (Fig. 3), but it is not correlated with external flight conditions. Stroke amplitude is approximately identical in both wings on one side, and generally both wings arrive synchronously at their lower turning points,  $T_F$  and  $T_H$ . Despite its delay at the very beginning of the downstroke, the forewing may overtake the hindwing (Fig. 3). In every case, during the upstroke the forewing is accelerated and reaches the dorsal position first. This lead may vary with each wing beat cycle. The maximum value of forewing lead was about  $60^\circ$ .

Having reached their dorsal position,  $P_F$ , the forewings remain clapped together until the hindwings arrive at the  $xz$ -meridian and enter the next downstroke. Due to different stroke plane angles the forewings are only partially enclosed by the hindwings at the end of an upstroke, but with no exception in free and tethered flight the forewings will not enter the next downstroke prior to the hindwings. Thus there is a pause in forewing movement, which is rather conspicuous in normal free flight.

Hence the type of ipsilateral wing coordination in *C. splendens* is characterized by a delay of the forewing during downstroke, by a lead of the forewing during upstroke, and by a pause in forewing movement at the end of an upstroke. This is shown in Figure 3, in which the instantaneous wing positions (measured as stroke amplitude  $\phi$  during three successive wing beat cycles) are compared. The wing coordination in *C. splendens* thus contrasts with all other known types of coordination.

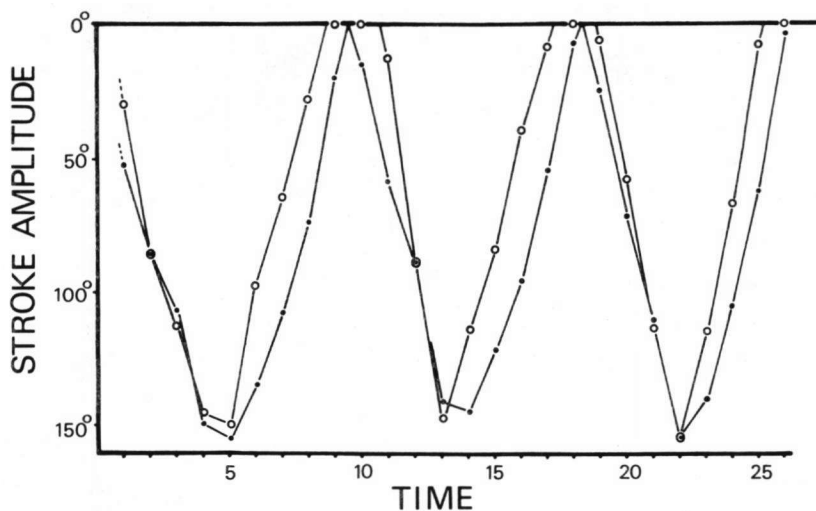


Fig. 3. Coordination of ipsilateral wings during tethered flight, measured as variation of stroke amplitude  $\phi$  per unit time. (One time interval =  $1/140$  s, —●—● hindwing; -○-○ forewing; — flight velocity:  $1 \text{ m. sec}^{-1}$ ).

## DISCUSSION

The wing kinematics are not uniform throughout the order Odonata. In all zygopterans the wing beat frequency is identical in ipsilateral and contralateral wings, as it is in beetles (SCHNEIDER, 1975), locusts (WEIS-FOGH, 1956), and cockroaches (POND, 1972). In the last three groups frequency differences are prevented by the mechanical design of the pterothorax, whereas in Odonata there is no fixed coupling between mesonotum and metanotum. In anisopteran Odonata varying frequency shift between the two pairs of wings can be observed (VON HOLST, 1950).

There are some details of wing kinematics in *C. splendens* which contrast with those of other insects. In *C. splendens* the wing beat frequency is remarkably constant under all experimental conditions, while in other insects, and indeed in libellulid species, it may vary considerably (HISADA et al., 1965).

A characteristic feature of dipteran flight is the uniformity of kinematic parameters during long sequences of successive wing beat cycles. This uniformity is not met in insects with low wing beat frequency such as in *C. splendens*. In locusts, too, irregularities are to be seen in successive wing beat cycles (WEIS-FOGH, 1956; JENSEN, 1956). In *C. splendens* especially the wing tip curve varies in each stroke, being a line or an extremely flattened zero figure, but never that significant figure of eight described in *Coenagrion* (BULL, 1909) and in

other insects, where a rather great horizontal distance between parts of the downstroke and upstroke curves has been reported. In tethered and unrestrained *C. splendens* instantaneous stroke angles are rather often asymmetrical in opposite wings without any noticeable consequence to flight performance. Probably the effect of asymmetrical movement on aerodynamics is compensated by the other wings.

The most striking character of wing kinematics in *C. splendens* is the unique type of coordination in ipsilateral wings. In *Schistocerca gregaria* the wing tip curves can be considered as slightly depressed sinusoidal curves, crossed with a constant phase shift of about  $50^\circ$  (WEIS-FOGH, 1956), the hindwing being always ahead of the forewing (JENSEN, 1956). Hindwing leads in the downstroke in *C. splendens* as well, but due to increased acceleration the forewing may overtake it and without exception leads in the upstroke. Thus the calopterygoid wing coordination takes the advantage of avoiding collision of ipsilateral wings in the more dorsal part of their path. At first this coordination, which is also found in *Calopteryx virgo* with an even lower aspect ratio, seems to be based upon anatomical reasons, especially on the low wing aspect ratio, since all European coenagrionid species tested having a higher aspect ratio utilize a different coordination. So it remains to prove the assumption that other genera of the family *Calopterygidae* with low aspect ratio, such as *Phaon* and *Neurobasis* and members of some related families with similar shaped wings such as *Chalcopteryx* and *Polythore* perform the type of coordination found in *C. splendens*. In accordance with this, other species of the *Calopterygidae* with a higher aspect ratio, such as *Caliphaea*, might perform another type of coordination, e.g. that of *Coenagrionidae*.

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