VORTEX FORMATION IN THE TETHERED FLIGHT OF THE PEACOCK BUTTERFLY *INACHIS IO* L. (LEPIDOPTERA, NYMPHALIDAE) AND SOME ASPECTS OF INSECT FLIGHT EVOLUTION

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Summary

High-speed filming has been used to investigate the performance of the peacock butterfly *Inachis io* while flying in a wind-tunnel. The wake of the butterfly in 'feeding' flight is a system of discrete pairs of vortex rings: in each pair the vortex rings are coupled at right angles. The flow distribution around the butterfly and the dynamics of the vortex rings suggest that useful force is produced continuously throughout the wingbeat. The butterfly's flapping flight can be divided into three successive stages: during the downstroke, force generation can be explained by quasi-steady aerofoil action; during the upstroke and supination, by unsteady aerofoil action; and during pronation, by a jet mechanism.

The study of airflow around the peacock butterfly throws light on the evolutionary changes in the pattern of interaction between insect wings and the air. At the first stage of the evolution of insect flight, documented in a subimago of the mayfly *Heptagenia sulphurea* and some other primitive insects, flapping wings generate a system of coupled vortex rings; the aerodynamic force, being perpendicular to the stroke plane, coincides with the direction of the longitudinal body axis. At the second stage, this force is directed forwards and upwards relative to the body axis; the vortex wake is the same as that at the first stage. From this point, two paths of evolution are possible. The first leads to the vortex pattern recorded in the peacock butterfly. The second is typically found in higher orders, where the narrow and relatively short wings flap with lower amplitude and higher frequency, leaving in their wake two chains of uncoupled small vortex rings.

Introduction

The present paper is the first attempt to study the structure of the vortex wake for insects flying in a wind-tunnel. It is tempting for a researcher studying insect flight to seek visualizations of the airflow around free-flying animals. This has been achieved in recent years for birds and bats, which show wake patterns of limited diversity: vortex rings correlated to downstroke in slow forward flight (Kok-

shaysky, 1979; Spedding *et al.* 1984; Spedding, 1986; Rayner *et al.* 1986), and trailing undulating pairs of vortices in the fast flight of long-winged species (Rayner *et al.* 1986; Spedding, 1987). In these experiments, a bird (or bat) was trained to fly through a cloud of visualizing material. However, insects are too small to be filmed while flying in a broad corridor, and they cannot be trained to fly along a path on which a camera can be focused with sufficient precision. These difficulties led us to seek other ways to make high-speed films of the vortex wake of insects.

There are many technical difficulties in visualizing the flow around a free-flying insect. Initially, scientists restricted themselves to the study of moving wing models (e.g. Maxworthy, 1979; Savage *et al.* 1979). Then they analysed the airflow around tethered insects (Chance, 1975; Ellington, 1978). Considerable progress was later achieved by using a flat sheet of illumination to visualize patterns of flow (Brodsky, 1984; Brodsky and Ivanov, 1983, 1984). Flat sections of the flow made it possible to reconstruct the wake of a flying insect in three dimensions. However, the flow visualization technique used in that experiment was restrictive because it was carried out in still air. *Lycopodium* spores were either blown onto the flying insect or released from above using a special device (Brodsky and Grodnitsky, 1985). Although this did not prevent us from determining the shape of the wake, the analysis was limited in that the experimental conditions did not conform to free flight, where an insect 'encounters' a constant airflow. The next step in approaching free-flight conditions is therefore to study vortex wakes in a wind-tunnel.

In this paper, results are presented from high-speed films of tethered peacock butterflies flying at an air speed equal to that encountered in free flight. Wind flowing over the head stimulates the antennae. In the absence of tarsal contact, this stimulus initiates and maintains flight (Weis-Fogh, 1949). The importance of airflow on the head in maintaining the natural work of the wings has been shown by many authors (e.g. Camhi, 1970; Gewecke, 1967) and for many species. In free flight, the nymphalid butterfly *Aglais urticae*, which is closely related to the peacock butterfly, holds its antennae forward in the flight position using muscles at the base (Niehaus and Gewecke, 1978). Thus, the position of the antennae may be an indicator of free-flight conditions.

The flight behaviour of peacock butterflies has a number of peculiarities. Like most other members of the family Nymphalidae, the peacock butterfly is characterized by a high flight velocity. With each wingbeat the insect covers a relatively long distance, and periodic changes in altitude and direction of flight give it the appearance of fluttering. Such a mode of flight results from rare flaps of broad wings through a large amplitude. For broad-winged butterflies there are also indications that wing supination during the upstroke is small and partly compensated by body pitching (Kozlov *et al.* 1986); during the downstroke the thorax is directed horizontally, but during the upstroke it is nearly vertical. Another characteristic of butterflies is the frequent use of intermittent gliding. The peacock butterfly, like members of other families of diurnal butterflies, is also capable of sharp jerks forward, performed at high speed with the wings lifted above the body.

Materials and methods

A suction-type wind-tunnel (Brodsky and Ivanov, 1974) was used in the experiments (Fig. 1). In a side wall of the glass working section (250 mm× 150 mm×150 mm) there was a small hole for the tethering device; the rest of the working chamber was completely closed. A lattice constructed of thick paper with a 5 mm×5 mm mesh was mounted at the entrance to the working section. Small paper tubes with a square cross section (3 mm×3 mm at their downstream end) were inserted into the meshes at intervals, which prevented smoke at different velocities from mixing. The tubes could be arranged in a single line either horizontally or vertically. A smoke comb of 12 tubes arranged in a vertical plane was used in this study. This enabled visualization of a planar section of the wake, for comparison with earlier studies. All of the lattice holes were closed except for those into which tubes were inserted. The smoke used for visualization was generated in a closed chamber upstream of the working section and consisted of a mixture of potassium chlorite, colophony (rosin) and ammonium chloride.

A thin steel guitar string was used to tether the insect. It was glued to the butterfly at the anterior, dorsal end of the abdomen. The wire was bent so that it could not hinder the wings, and it was taken through the hole in the side wall. This flexible method of tethering allowed the butterfly to assume a natural flight
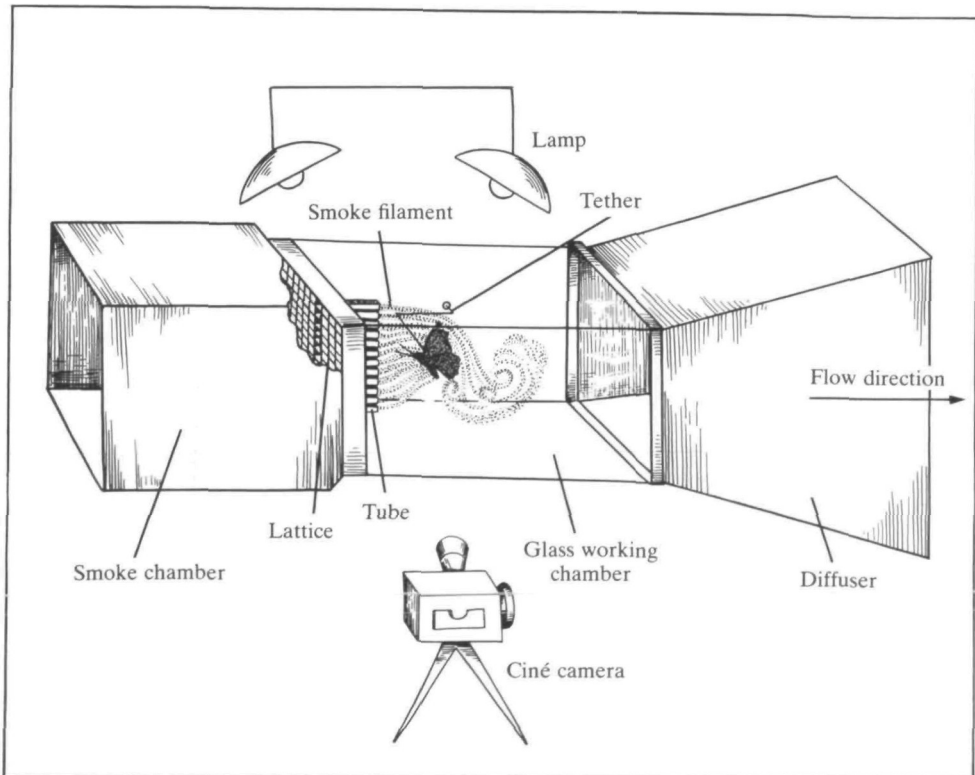

Fig. 1. Equipment used for flow visualization (not to scale).

posture and pitching movements of the body were not restricted. The tethering wire was connected to the side wall of the working chamber, and the tunnel fan and the smoke generator were started.

A Pentazet 35 high-speed 35 mm ciné camera was used for filming at speeds of $1000-2000$ frames s^{-1}. The exposure time of 2000 frames s^{-1} is equal to $1/2100$ s. Colour negative film FUJI-8514 (400 ASA) was used.

Nine specimens, caught in the wild, were studied. Filming began after the butterfly had assumed the flight posture with the wings making regular flaps, the legs folded and pressed against the body, and the antennae held in the flight position (see above). The maximum duration of flight was about 1 h, and the air speeds were $0.6-1.0$ m s^{-1}. All specimens tested showed similar flight perform-ance, and the parameters of wing movements were similar except for the amplitude of the wingbeat. In the experiments, the amplitude of the wingbeat varied from 120 to 180°. In the latter case, the wings clapped together at the top and bottom of the stroke. A single individual could perform wingbeats of different amplitude. The most frequent flights recorded had stroke amplitudes of 120–130° and 160–180°, which are characteristic of feeding and migration flights, respect-ively (Brodsky, 1988). All flights observed in experiments were therefore divided into two groups on the basis of the wingbeat amplitude. The most comprehensive data on the vortex formation pattern were obtained for 'feeding' flights (amplitude 120–130°), but we also discuss data from 'migration' flights (amplitude 160–180°).

Results

A feeding flight

Kinematics

The ciné film selected for analysis is a sequence of tethered flight that can be regarded as a typical feeding flight. One complete stroke cycle lasts about 0.06 s, and can be divided into four phases of wing motion: pronation (Fig. 2A–E), the downstroke (Fig. 2E–H), supination (Fig. 2I,J) and the upstroke (Fig. 2J–L). At the beginning of the cycle, when the wings are raised to their maximum height (Fig. 2A), the dorsal surfaces clap together and the wings begin to pronate. The pronation phase of the wing motion takes about 40 % of the cycle period, and is indicated by a rapid backward movement of the vortex ring (Fig. 2A–E). During the subsequent downstroke, which lasts 27 % of the cycle period, a starting vortex forms downstream of the wings (Fig. 2E–H). This phase of the stroke is characterised by a rapid lowering of the wings, the wing position being changed abruptly from one frame to another. At the bottom of the stroke the wings supinate quickly to move upwards. As soon as supination takes place, a stopping vortex forms below the trailing edges of the hindwings (Fig. 2I,J). The supination phase lasts for 10 % of the cycle period. The stopping vortex gradually increases in strength during the upstroke (Fig. 2J–L), which lasts for 23 % of the cycle period and is somewhat quicker than the downstroke. The phases of the stroke do not
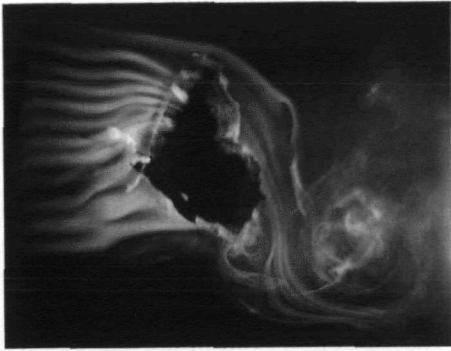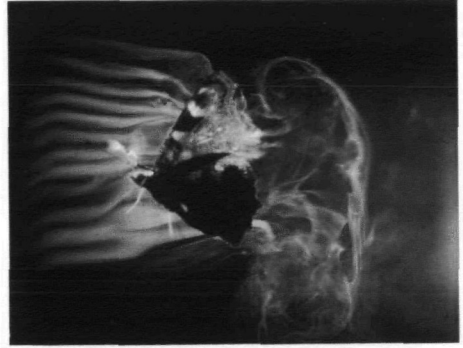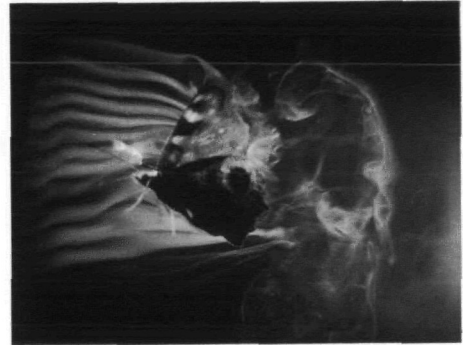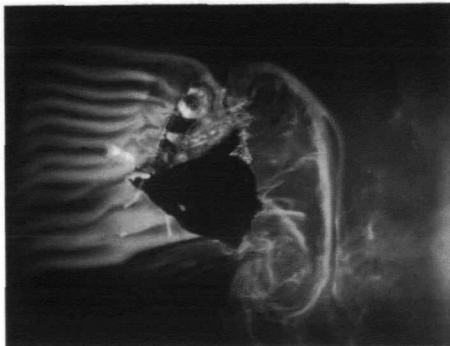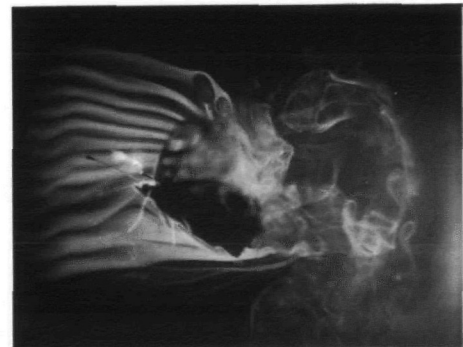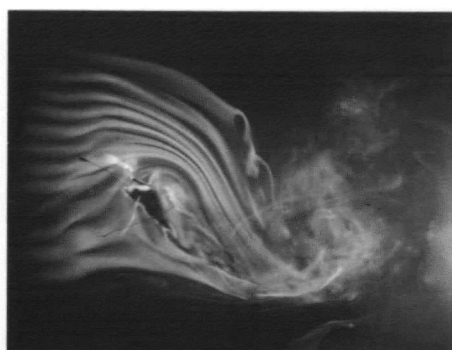
Fig. 2. The tethered flight of the peacock butterfly *Inachis io* flying in a wind-tunnel. Consecutive film tracings from a single wingbeat. (A–E) Pronation; (E–H) the downstroke; (I,J) supination; (J–L) the upstroke. The time between frames is 5 ms.
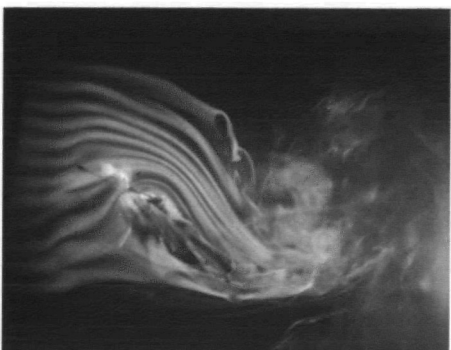
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coincide exactly with the frames, since one frame can include the end of one phase and the beginning of the next one.

The terms 'pronation' and 'supination' are used here in two senses: to describe the position of the wing in the stroke cycle and the inclination of the wing surface. As the supinated wings approach their upper extreme, the leading edges are brought closer together but they do not always collide. The wing surfaces are then pronated: first, the anterior edges of the wings are bent outwards, and the bend then passes posteriorly over the wings. As this proceeds, the leading edges diverge and the trailing edges are brought closer together. This type of wing surface deformation during pronation is characteristic of broad-winged butterflies and resembles Ellington's 'flat peel model' (Ellington, 1984): it differs mainly in that the wing bending is sharper. The butterfly's forewing bends along the medial flexion line (Fig. 2B), but some additional lines (Fig. 2A), as well as the rear border of the forewing (Fig. 2C), are also involved. The gap between the right and left wings closes at the moment of collision of the leading edges of the wings. Wing supination resembles pronation, but the whole motion takes place in the opposite direction. The bending upwards of the leading edge passes from the anterior to the posterior border of the wing.

The stroke amplitude was 120–130° which, as mentioned above, is similar to that observed in feeding flights. The angle between the wing-stroke plane and the body axis was about 90°, the same as that in free flight. Wingbeat frequency was 15–20 Hz. The body angle relative to the horizontal changes considerably during the cycle, and reaches a maximum towards the end of the upstroke. Supination of the wings during the upstroke is distinct. Therefore, one must assume that considerable body-angle fluctuations (pitching movements) in the stroke cycle are brought about by some cause other than by a necessity to compensate for the insufficient degree of wing supination.

Aerodynamics

In Fig. 2, a complete stroke cycle is represented by 12 frames. This series begins with pronation of the wings (Fig. 2A), as described above. The pronated part of the forewing is illuminated. With the beginning of pronation, a stable vortex motion is formed along the leading edge: the leading-edge vortex (Fig. 2A). The airflow that passes into the gap between the pronating wings moves sharply downwards and enters the centre of a vortex ring; in the vertical section of the flow visualization, this ring appears as a pair of contra-rotating vortices, with a stopping vortex on the left and a starting vortex on the right. The axis of the vortex ring is nearly vertical and the ring itself is horizontal: the *horizontal vortex ring*. The airflow rises only slightly in front of the butterfly's body.

Pronation continues in the second frame (Fig. 2B), with the anterior edge of the wing moving backwards. The leading-edge vortex motion becomes more intensive. A new vortex forms in the cavity of the outer edge of the forewings. It rotates anticlockwise towards the stopping vortex, and both vortices become part of a new vortex ring connected with the horizontal one by the old stopping vortex. The axis

of this ring is horizontal and the ring is vertical: the *vertical vortex ring*. The flow passing through the gap between the wings moves along the axis of the vertical vortex ring. As soon as it appears, the vertical vortex ring begins to move backwards.

In the third frame (Fig. 2C) the forewings are pronated completely. The outer edges of the hindwings approach each other and form a tunnel. Air streams through it, moving the vertical ring backwards. The starting vortex begins to dissipate. In the next frame (Fig. 2D), the forewings are shifted backwards. The flow through the tunnel intensifies, and the vertical ring continues to move backwards while gradually dissipating. The old starting vortex breaks down completely, and a new starting vortex is formed in the cavity of the forewing's outer edge. It is important to note that the new starting vortex is not related to the vertical vortex ring, which continues to move backwards.

The fifth frame (Fig. 2E) coincides with the beginning of the rapid lowering of the wings. When the wings are completely pronated they stop for a while and only then does the downstroke begin. During this period, the air between the closed outer edges of the hindwings continues its motion, and rotation of the new starting vortex increases. The anterior edges of the forewings leave the sagittal plane, and the leading edge vortex therefore becomes invisible. The vertical vortex ring moves still further backwards and continues to dissipate.

In the next two frames (Fig. 2F,G) the wings move down, and the flow velocity above the insect body increases. The starting vortex becomes larger in diameter and shifts downwards and backwards. The vertical vortex ring dissipates completely. By the end of the downstroke (Fig. 2H), the starting vortex has shifted downwards and slightly backwards. The flow velocity above the body continues to increase. At this phase of the stroke, one can see the lines of flow streaming over the body and wings, as in the classical case of flow around an aerofoil.

When the wings reach the bottom of the downstroke (Fig. 2I), a stopping vortex begins to form near the edges of the hindwings. The turning of the wings in preparation for the upstroke is accompanied by strong wing supination (Fig. 2J). The stopping vortex continues to increase and, together with the starting vortex, it forms a horizontal vortex ring. At this time, the flow velocity above the body is still high (Fig. 2J,K). When the strongly supinated wings move upwards (Fig. 2K), the body acquires a more vertical position and the airflow is directed nearly downwards. The formation of the horizontal vortex ring is completed. The last frame (Fig. 2L) shows the final phase of the upstroke; the leading edges of the right and left wings are about to meet. Passing through the narrowing gap between the wings, the flow turns down abruptly into the hole of the vortex ring.

Each wingstroke therefore produces two vortex rings: one during the downstroke, the other during the upstroke. They are coupled by the stopping vortex and form an L-shaped vortex structure that is thrown back at the top of the stroke.

A migration flight

One complete stroke cycle lasts about 0.1 s, and it includes the same phases as

the feeding flight. The main difference is that the wings produce a strong clap both at the top and at the bottom of the stroke. The stroke angle amplitude reaches 180°, and the wingbeat frequency is 10–13 Hz. It is interesting to note that in both cases (in feeding and migration flights) the mean speed of the forewing tip in the stroke cycle is the same, approximately $2 \, \text{m s}^{-1}$. However, the vortex formation pattern is different. At the top of the stroke, a butterfly in migration flight claps its wings, their dorsal surfaces being pressed firmly against each other. With the beginning of pronation, the vertical vortex ring moves quickly backwards. At the bottom of the stroke the wings shed the horizontal vortex ring downwards and backwards. Unlike in feeding flight, where the horizontal ring is coupled with the vertical one and is therefore retained near the edges of the hindwings (Fig. 2I–L), in migration flight the clap at the bottom of the stroke is accompanied by vortex ring shedding. Leaving the wings, the horizontal vortex ring moves downwards and backwards. The ring would move in the same direction in feeding flight if it were released at the bottom of the stroke (Fig. 2I). On the ciné film one can clearly see how the stopping vortex is formed. At the beginning of the upstroke, after the vortex ring has left the wings, a new starting vortex is created. A similar vortex ring was recorded by Ellington (1980) in the large cabbage white butterfly during take-off. At the end of the first downstroke, the wings almost clap together, throwing downwards a large-cored vortex ring.

Discussion

Flight of the peacock butterfly

The data obtained allow us to estimate the dynamics of force impulses acting on the butterfly during the stroke cycle. During the upstroke and the downstroke the air is accelerated and is thrown downwards and backwards. The force impulse received by the insect is therefore directed forwards and upwards. The rate of change of the trailing and/or shed vortices is related to force generation, and this can be deduced from the ciné film analysis. From classical mechanics for an incompressible fluid, conservation of flow demands that:

$$v_1 S_1 = v_2 S_2 \, ,$$

$$v_2 = v_1 \frac{S_1}{S_2} \, ,$$

where v_1 is the speed, normal to the cross section, of a flow tube just in front of the butterfly's wing, and S_1 is the cross-sectional area of this flow tube; v_2 and S_2 are equivalent variables for the same flow tube immediately behind the butterfly's wing. The phasing of force generation can thus be estimated with some degree of confidence from relative velocities of the airflow just in front of and just behind the butterfly's wings and from their directions (Fig. 3). Additional information can be obtained by identifying small changes in the pitch of the insect during the stroke cycle.

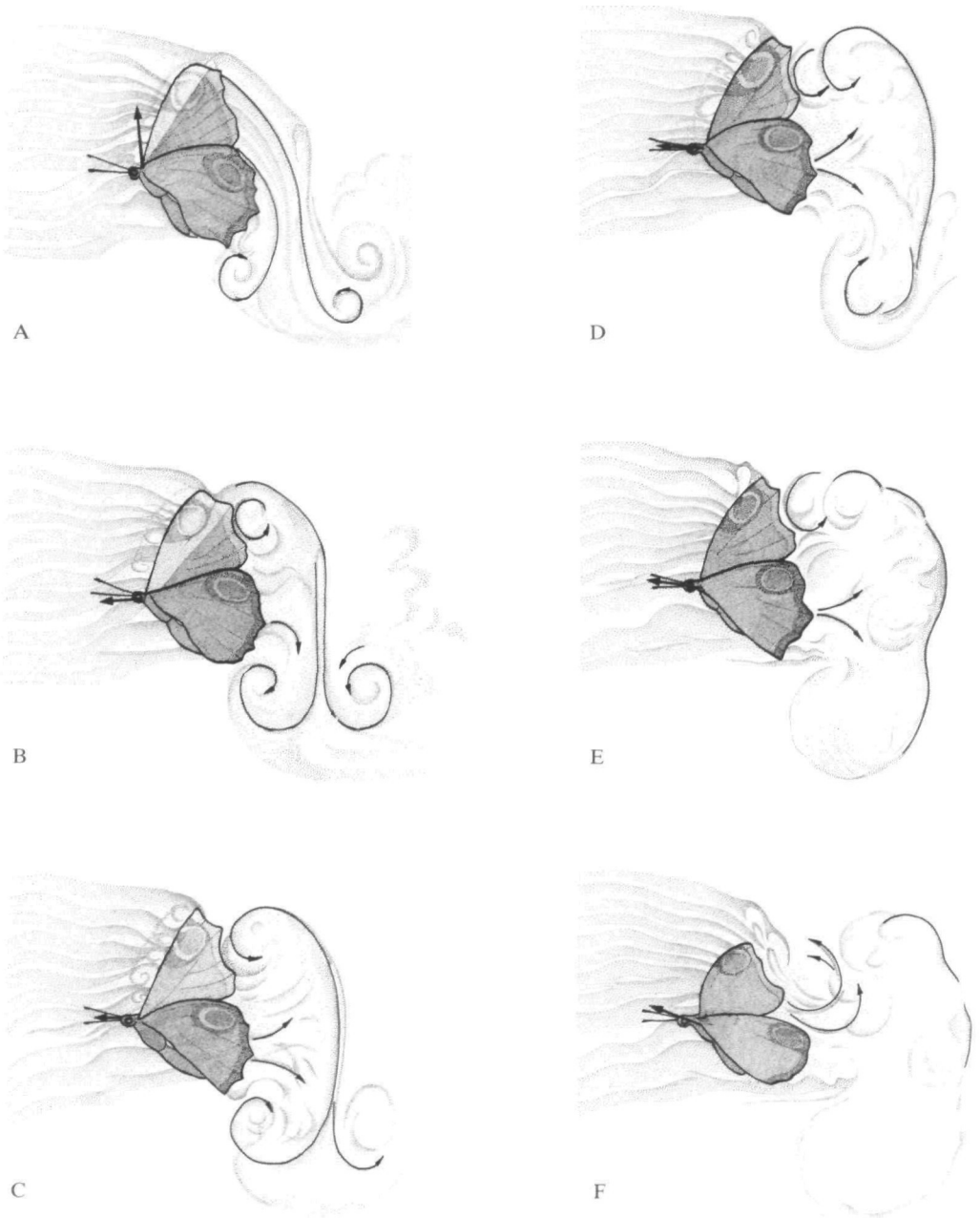The analysis shows that the velocity of air accelerated by the butterfly's wings
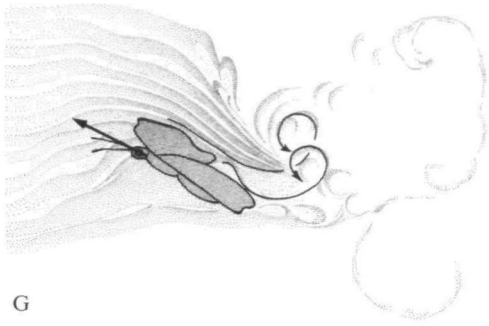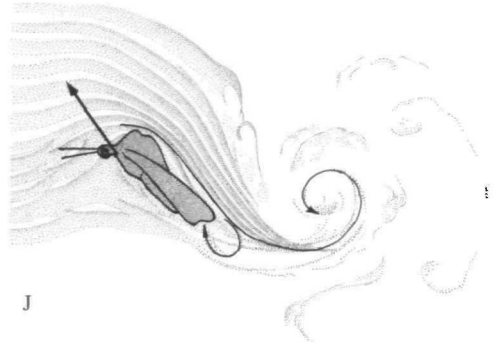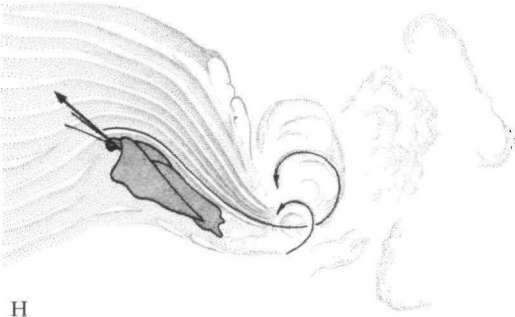
Fig. 3. Dynamics of the resultant aerodynamic force vector (bold arrow) presumed to be acting on the butterfly, in 12 successive moments of wingbeat in 'feeding' flight. The thin arrows indicate the airflow. (A–E) Pronation; (E–H) the downstroke; (I,J) supination; (J–L) the upstroke.

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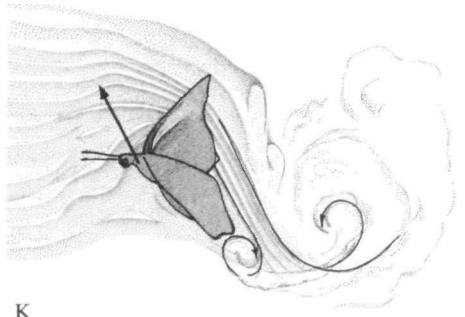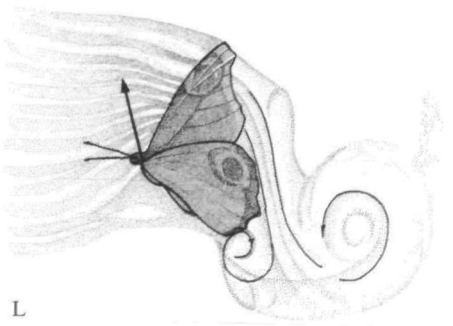reaches its maximum by the middle of the downstroke (Fig. 3G). At that point, the velocity of the airflow immediately behind the wings is three times greater than that of the undisturbed flow. During the downstroke (Fig. 3E–H), a vortex ring ■losing on the wings is formed. Its hind part can be seen from the smoke streams to ƀe a starting vortex. Its fore part forms a circulation around the wings and this is

responsible for the difference in flow velocities above and below the wings. The force impulse received by the butterfly is directed forwards and upwards. Therefore, the nature of force generation during the downstroke may be explained by quasi-steady aerofoil action.

At the lower end of the stroke, the wings, through the stopping vortex, shed the horizontal vortex ring (Fig. 3I). Even after it has been shed, this ring continues to play an important role in accelerating flow above the butterfly's body (Fig. 3J–L). This is why the butterfly creates useful forces even when the wings, having reached the bottom of the stroke, stop momentarily (Fig. 3I).

During the upstroke a negative circulation is created around the wings; this is shown by the formation of a stopping vortex behind the elevating wings; it is also a starting vortex for the upstroke (Fig. 3J–L). However, this circulation makes a negligible contribution to force production compared with the powerful current above the body created by the downstroke ring. Owing to the influence of this ring on the airflow, the force acting on the insect during the upstroke is directed forwards and upwards (Fig. 3J–L). Therefore, the nature of force generation during the upstroke (and also during supination) can be explained not by quasi-steady aerofoil action but by unsteady aerofoil action.

The pitch angle reaches its maximal value during the upstroke (Fig. 3J–L). At this point, the airflow, after interacting with the wings, turns sharply downwards. Therefore, one can deduce that considerable body angle fluctuations in the stroke cycle are caused by periodic changes in the direction of aerodynamic forces acting on the butterfly's body.

With the beginning of the clap (the near-clap for feeding flight) the vertical vortex ring formed during the upstroke is shed (Fig. 3A). As it moves away from the wings (Fig. 3B–E), the horizontal vortex ring no longer accelerates the airflow above the insect. The velocity of the vertical vortex ring moving backwards is 1.5 times greater than that of the undisturbed flow. As the vortex ring moves away from the butterfly, the hindwings form a tunnel through which a small amount of air is pushed backwards (Fig. 3B–E). A similar tunnel has been observed in the flight of butterflies of another family (Bocharova-Messner and Aksyuk, 1981), and it was postulated that this tunnel played an important role in jet motion of the butterfly. It is not clear, however, if the backwards movement of the vertical vortex ring is caused by the airflow pushed from the tunnel or by some other force. The vertical vortex ring begins moving backwards (Fig. 3A) before the tunnel is formed (Fig. 3B), so it seems likely that during wing pronation the butterfly merely throws the vertical vortex ring backwards. If true, the near-clap would create the jet motion, as was predicted on theoretical grounds by Ellington (1984). In his work of 1984 he writes: 'If we neglect any circulation remaining around the wings from the upstroke for a moment, then the clap would create the jet motion...' The flow visualization experiments show that the near-clap produces the jet motion, the exact mechanism of which is slightly different from that predicted by Ellington. The circulation remaining around the wings from the upstroke is important for creating the jet motion. Indeed, the vorticity shed from

the leading edges of the clapping wings rolls up onto the inner wall of the vertical vortex ring, which directs the airflow backwards (Fig. 3B–D). Thus, the near-clap sheds the vertical vortex ring from the wings and the subsequent pronation throws it backwards. This motion corresponds to a brief backward jet of air, and the wings must experience a forward reaction to this jet (Fig. 3B–E). The jet force acts on the butterfly's body until the starting vortex of the downstroke is formed (Fig. 3D), and the cycle is repeated.

Thus, the process of useful force generation is continuous, and it allows the butterfly to make fast jerks forwards without losing altitude. Particularly efficient is the jerk forwards with the wings lifted above the body; at that moment the butterfly continues moving upwards by inertia (Fig. 3A) and, when the ring is thrown backwards, it receives an additional forward thrust (Fig. 3B–E). The loss of altitude that is observed periodically in free feeding flight is accomplished by a temporary halt in the stroke cycle in this position. The adaptive importance of such behaviour is apparently related to avoiding potential enemies (e.g. insectivorous birds). However, this characteristic is absent in the case of fast, steady migration and searching flights.

Evolutionary changes in the structure of the wake behind flying insects

The experimental results for the structure of the vortex wake of the peacock butterfly can be compared with those from other well-studied insects, such as the hesperiid butterfly *Thymelicus lineola* (the Essex skipper) (Brodsky and Ivanov, 1974; Brodsky and Grodnitsky, 1985) and the crane fly *Tipula paludosa* (Brodsky, 1986). We need to be sure that our experimental data on the vortex wake shape are consistent with conditions in the wake behind free-flying insects. As discussed at the beginning of this paper, the data obtained in wind-tunnel experiments give realistic information about the shape of the vortex wake. The experiments in still air and in a wind-tunnel sometimes give the same results (e.g. for the Essex skipper). Therefore, one can assume that the principles of vortex wake formation obey physical laws that are the same for any object moving in a fluid. The most common, but not the simplest, shape of a vortex wake is a system of coupled vortex rings inclined alternately to the left and to the right. A section of such a wake through the sagittal plane gives Golubev's famous vortex wake, which differs from Karman's one by virtue of the direction of vortex rotation. Golubev's wake was recorded behind swimming fish (Hertel, 1967), vibrating wing models (Polonsky, 1950; Savchenko, 1971) and in many other cases when a flapping object generated a propulsive force. In other words, we can usefully compare the vortex wake parameters obtained by different methods: the wake caused by any flapping movement, if it dominates the propulsive movement (which is the case for insects), must consist of vortex rings. Thus, the shape of the vortex wake depends on the way in which the vortex rings are arranged, which is primarily a question of wing shape and wingbeat kinematics.

There are only a few comparable observations on the flight of primitive insects. A study of the tethered flight of mayflies (Brodsky, 1985, 1988) showed that their

wings created a chain of coupled vortex rings, as described above. The wing-stroke amplitude of the subimago mayfly *Heptagenia sulphurea* was smaller than that of the imago: 87° compared with 122° (Brodsky, 1988). The vortex wake recorded in the subimago is considered to be the most primitive among insects, and is essentially the same as that behind the vibrating wing model when it operates at the same angle of attack. Being equal in magnitude, the angle of attack is positive during the downstroke and negative during the upstroke.

The wake behind the imago mayfly *Heptagenia sulphurea* is similar to that of the subimago, differing mainly in force variation during the stroke cycle. Let us consider the process of aerodynamic force generation based on the detailed data for the tethered flight of the Essex skipper; this process is the same for the imago mayfly. During the downstroke, the wings of the Essex skipper generate lift and thrust (Fig. 4A). The vortex ring formed will have an impulse directed downwards and backwards. The corresponding airstream during the downstroke is oriented in the same way (*a* in Fig. 4A). During the upstroke, a negative circulation around the wings is responsible for the generation of thrust and negative lift, and the ring will have an impulse directed upwards and backwards, as will the airstream formed during that period (*b* in Fig. 4B). If the forces created during the downstroke and the upstroke were equal (Fig. 4A,B), the net aerodynamic force acting on the insect would be directed forwards; i.e. the insect would be creating thrust only. This is exactly what is observed in the flight of the subimago mayfly (Brodsky, 1988), and it explains why the *subimagos* always fly with a large pitch angle, directing the net aerodynamic force vector forwards and upwards. However, in the case of the imago mayfly (unlike the subimago) and of the Essex skipper, the angle of attack of the wings during the downstroke is larger than that during the upstroke. This produces an aerodynamic asymmetry, with larger forces during the downstroke. The ring shed at the end of the downstroke expands during the upstroke and accelerates the air at 45° to the horizontal (*c* in Fig. 4C). As a result, a force impulse directed forwards and upwards is produced (Fig. 4C).

These three streams (*a*, *b* and *c*) can be found in the wake of many insects (Brodsky, 1988). Because of the aerodynamic asymmetry between the downstroke and the upstroke, the insect can fly even if the pitch angle is zero. The net aerodynamic force for a complete stroke cycle is directed forwards and upwards; during the downstroke the wings produce lift and thrust, during the upstroke they generate thrust only. Thus, in the evolution of the flight of winged insects the angle between the resultant aerodynamic force vector and the axis of the wake is important (Fig. 5). It is small in such primitive insects as the mayfly (Fig. 5A) and scorpion fly (Fig. 5B), but larger in the more advanced Essex skipper (Fig. 5C) (see Brodsky, 1988). In the subimago mayfly this angle is zero, and its wake flow was found to lack the stream *c*. As a result of periodic changes in circulation around the wings with each half of the stroke cycle, a chain of coupled vortex rings is formed behind the Essex skipper in flight (Fig. 4D). The main wake flow passes through the centres of the coupled rings, acquiring a wave-shaped form.

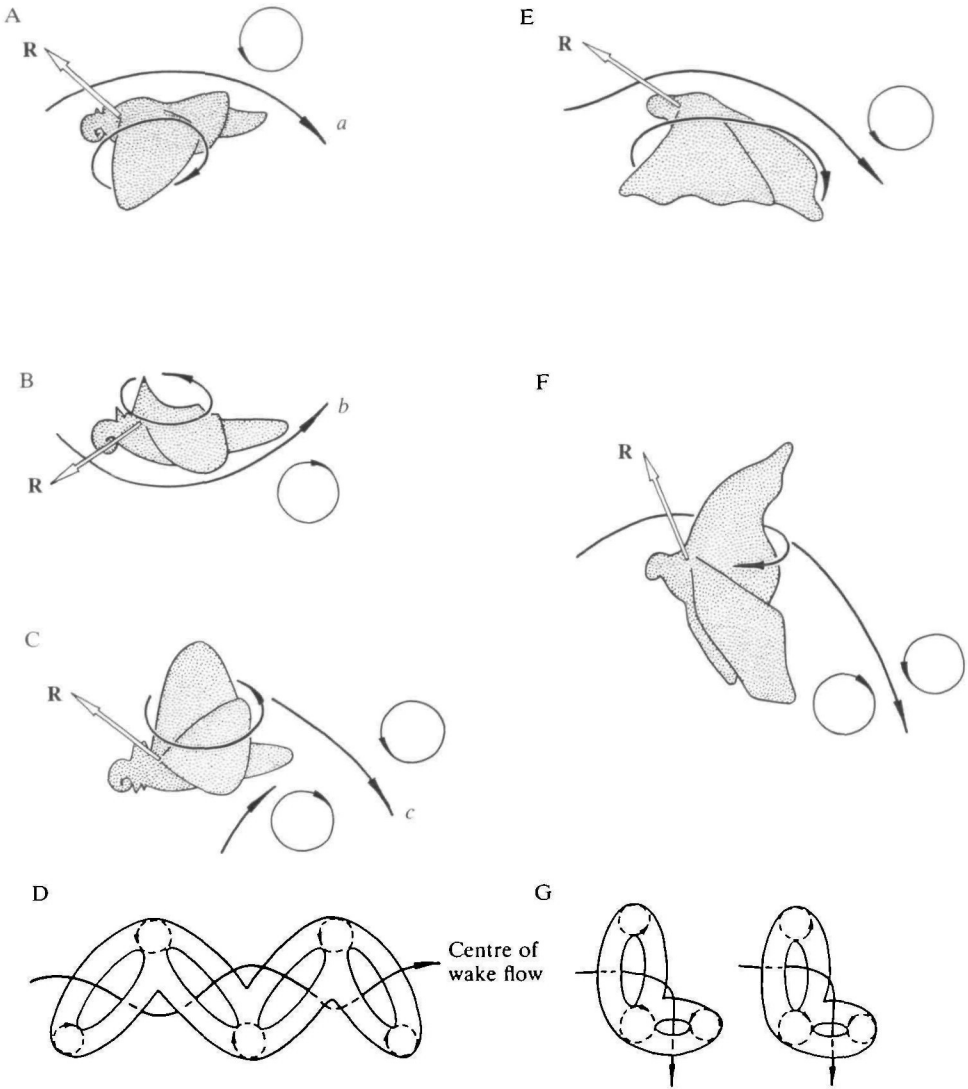It is thought that the flight of the first winged insects was characterized by

Fig. 4. Orientation of vortex rings and airflow in different phases of the wingbeat for the Essex skipper (*Thymelicus lineola*) (A–C) and the peacock butterfly (*Inachis io*) (E,F). Phases of the stroke: the downstroke (A,E), the upstroke (B,F) and the end of the upstroke (C). Open arrows indicate the resultant aerodynamic force vector (**R**) in corresponding phases of the stroke, and filled arrows show the airstreams. The airstreams *a*, *b* and *c* are explained in the text. (D) Wake shape of *Thymelicus lineola* in tethered flight. (G) Wake shape of *Inachis io* in 'feeding' flight.

aerodynamic symmetry between the downstroke and the upstroke, as in the flight of the subimago mayfly *Heptagenia sulphurea*. The variation of forces in the stroke cycle observed in the Essex skipper was the first step in the disturbance of this initial aerodynamic symmetry. In the peacock butterfly one can observe a further
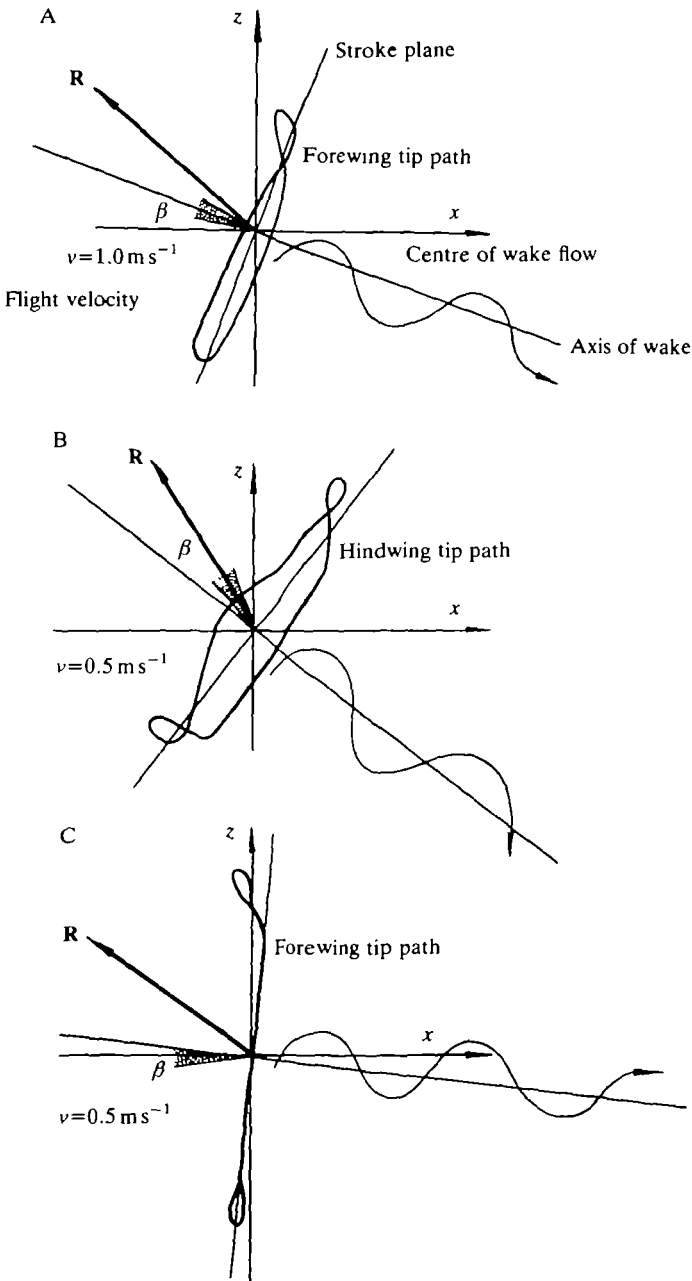
Fig. 5. Wing-tip path and resultant aerodynamic force **R** generated by several flaps in different insects. (A) Mayfly (the imago) *Ephemera vulgata*; (B) scorpion fly *Panorpa communis* (Mecoptera); (C) Essex skipper *Thymelicus lineola*. The mean body angle is β, and the longitudinal body axis fluctuates in the stippled sector. Note that vector **R** does not coincide with the axis of the wake, which is perpendicular to the stroke plane. All measurements were carried out in a wind-tunnel; the flow velocities (v) are indicated.

development of this trend. In this species, the downstroke forces are generated in essentially the same way as in the Essex skipper (Fig. 4E), but considerable differences are found during the upstroke: a powerful flow is observed over the dorsal surface of the wings (Fig. 4F), owing to the vortex ring formed by the wings during the downstroke. This flow decreases the negative circulation around the wings, and the force impulse is directed forwards and upwards. The vortex ring formed during the downstroke does not expand during the upstroke, as it does in the Essex skipper, and it is therefore smaller in diameter than is the upstroke ring. Furthermore, the two rings are coupled, and they are coupled at a right angles. At the top of the stroke the coupled rings are blown backwards by the jet forced out of the tunnel between the lifted, pronating wings. As the cycle repeats, a new pair of coupled rings is formed in their place (Fig. 4G). Thus, broad wings operating at low frequency and large amplitude shed discrete pairs of differently sized vortex rings (e.g. in feeding flight). When the frequency decreases and the amplitude increases (e.g. in migration flight) the flapping wings shed discrete vortex rings.

The other trend in insect flight evolution is an increase in wingbeat frequency accompanied by a decrease in stroke amplitude and by narrowing of the wings. This trend is most evident in such higher orders as Diptera and Hymenoptera. The data on the vortex wake structure in Diptera and Hymenoptera are rather limited. When the tethered crane fly *Tipula paludosa* tries to turn, the wing on each side produces its own system of vortex rings (Fig. 6A). Viewed from above, one can see that separate flows pass through the centres of the right and left wings (Fig. 6B). Each wing, therefore, sheds a separate chain of uncoupled small vortex rings. To see the centre wake flow for the Essex skipper, the vertical light plane has to be directed along the sagittal plane (Fig. 7A), but for the crane fly it has to be positioned in the middle of each wing (Fig. 7B).

By directing the chain of right or left vortices sideways, the crane fly can turn sharply, thus performing fast yaw movements. It is not surprising that insects with a high wingbeat frequency possess great manoeuvrability, because each of their wings serves as a separate vortex generator. The sharp turns of these flies are brought about with the wing on one side folded over the back (Nachtigall, 1979). The wingbeat frequency of the crane fly *Tipula paludosa* is 58 Hz (Brodsky, 1986). It is thought that the other members of the order Diptera, with even higher wingbeat frequencies, can also produce two chains of uncoupled small vortex rings, especially during searching and courtship flights.

In summary, experimental studies of insect flight aerodynamics show that evolutionary changes in flight mechanics are accompanied by changes in the wake structure. The structure of the vortex wake behind the peacock butterfly flying in a wind-tunnel shows considerable differences from the wakes previously described for insect flight. A vortex wake consisting of discrete vortex rings was recorded for broad-winged butterflies (Ellington, 1980; the present study, a migration flight). Vortex rings have also been described in the wake of small passerines (Kok-shaysky, 1979) and for a pigeon and a jackdaw (Spedding *et al.* 1984; Spedding, 1986) in slow flight. These animals have much in common: a low aspect ratio of the
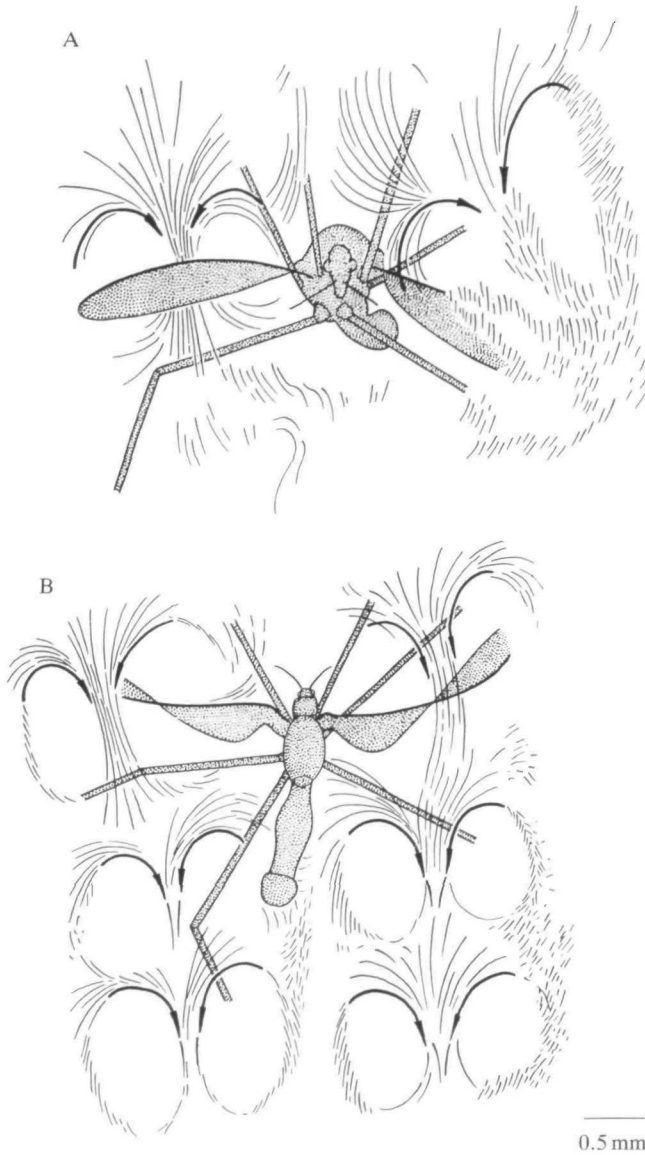
Fig. 6. Flow around the crane fly *Tipula paludosa* in tethered flight, using light planes passing through the wing base and exposure times of 2 ms. (A) Front view at the bottom of the stroke, using a vertical light plane. (B) View from above, using a horizontal light plane. The tethered crane fly is trying to turn to the left. Note the two chains of uncoupled small vortex rings.

wing, a low wingbeat frequency and a large wingbeat amplitude. The advance ratio is small or equal to zero in all these cases. Such a structure of the vortex wake can be reasonably explained by the wing shape and the stroke parameters, although the flying passerine produces vortex rings only on the downstroke, while
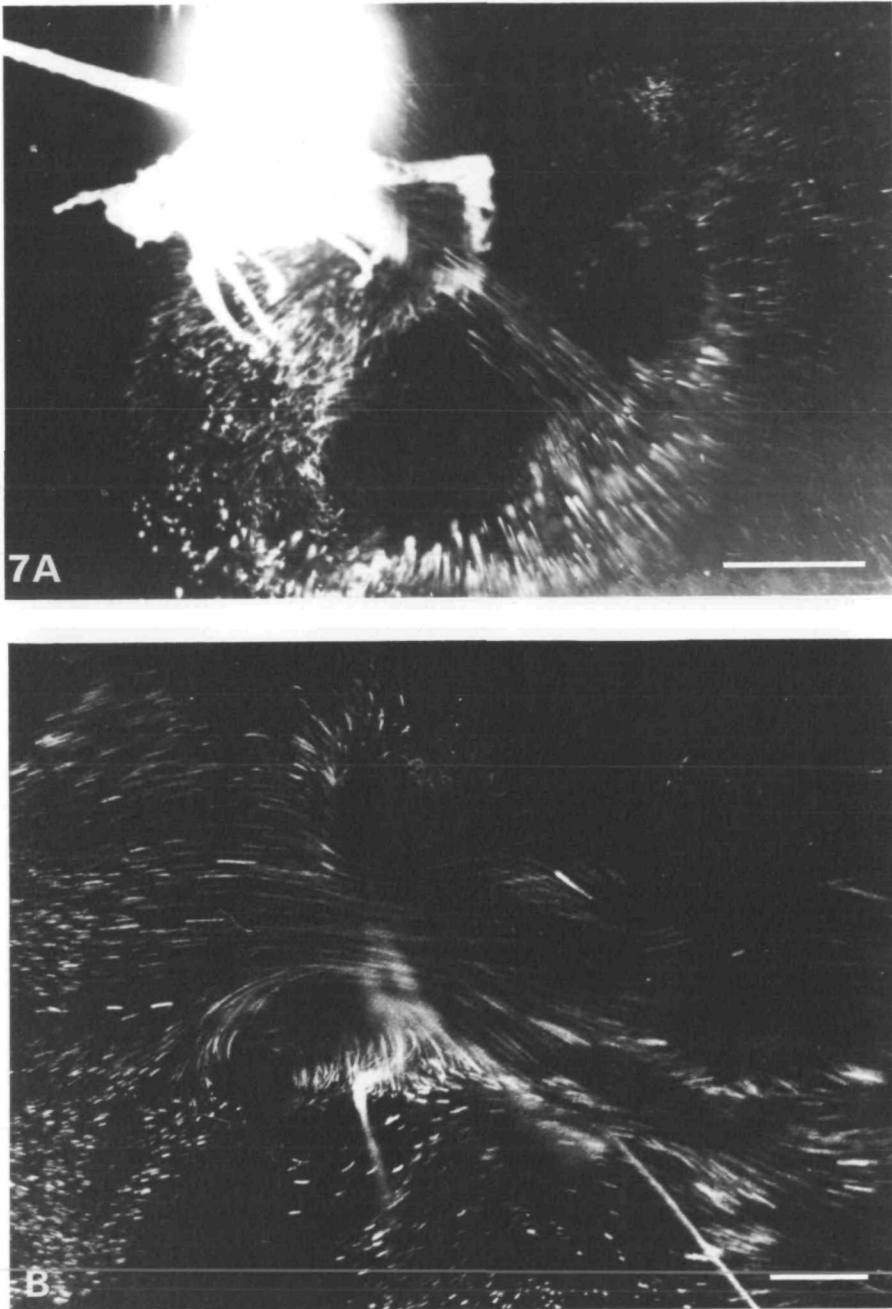
Fig. 7. Side view (the head to the left) of the flow around tethered insects, using a vertical light plane and 2 ms exposures. (A) Essex skipper *Thymelicus lineola*, with the light plane passing through the sagittal plane. (B) Crane fly *Tipula paludosa*, with the light plane passing through the middle of the left wing. In both cases one can see the airflow passing through the centres of the vortex rings. Scale bars, 0.5 mm.

the butterfly creates them both on the downstroke and on the upstroke. An increase in wingbeat frequency leads to changes in the structure of the wake. In the first stage, only two vortex rings are coupled, as in the feeding flight of the peacock butterfly; then the flapping wings shed a chain of coupled vortex rings, as in the tethered flight of the Essex skipper; and finally, as in the crane fly, the wings produce a pair of chains consisting of uncoupled small vortex rings. The evolutionary development of the flight of winged insects commenced with the stage when the wake behind the flying insect was represented by a chain of coupled vortex rings.

I have discussed only the shape of the vortex wake and have not considered such important questions as the influence of wing-pair interactions and the functions of different parts of the wing in vortex formation. Attention should first be focused on the role of pronation and supination, two critical moments in the vortex cycle; vortices are formed during pronation and they are shed during supination.

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