

## A6–WING DESIGN AND AERODYNAMICS

Organised by J. Videler and C. Ellington on behalf of the Biomechanics Group to commemorate Robin Wootton's retirement

### A6.1–Design features of swift wings

J.J. Videler (Leiden and Groningen) and G.D.E. Povel (Leiden)

The common swift (*Apus apus*) spends almost its entire life airborne, sleeping and foraging in the air, mainly coming down to breed. It migrates over thousands of kilometres. We therefore expect wings, body, and tail to show extreme adaptations to enable agile high-speed flight at low energy costs. The swift has a streamlined, 16 cm long body; a short forked tail (closed during fast flight) and long curved scythe-like wings. We present details of the structure of swift wings and relate these to the expected highly specialised function.

The arm skeleton is much shorter than that of songbirds of the same size.

The angle at the elbow joint between the humerus and the radius and ulna is sharp. The extremely short arm wing has a cambered cross sectional profile with a round leading edge as in a conventional airfoil. The hand part of the wing occupies about 85% of the total wing length. Cross sections are rather shallow cambered or flat. In the longitudinal direction, it bends downward towards the wing tip. Numbers and anatomical details of the feathers determine the shape of the wing and its function as an adjustable airfoil. Scanning electron microscopic (SEM) studies show aerodynamically interesting details of the sharp leading edge of the primaries forming the sweptback hand wing. SEM pictures also reveal details of the locking mechanism between the extended primaries. This mechanism is only effective when the wing is under pressure from below. The aerodynamic significance of these structures is discussed.

### A6.2–Aerodynamics of flapping bird wings: insights from direct pressure measurements

J.R. Usherwood and A.A. Biewener (Harvard)

Vertebrates power flight with flapping wings of complex and changing geometries. The aerodynamics of such dynamic aerofoils remains obscure. While a fixed-wing view of aerodynamics is likely to be appropriate for gliding and soaring flight, flapping flight involves accelerations, rotations, wing–wing interactions, and dynamic changes in both planform and sectional wing shape, with potential for strongly 3-dimensional flows. Thus, analogies based on either fixed-wing or propeller aerodynamics are potentially misleading for much of animal flight. Despite aerodynamic inferences drawn from accu-

rate kinematic data and particle image velocimetry of the vortex wake, previous experimental studies of vertebrate flight result in, at best, information on aerodynamics with poor temporal or spatial resolutions. We introduce a technique to provide direct, dynamic pressure measurements along flapping wings, and present results for Canada geese in take-off flight.

Pressure differentials at five sites along goose wings reach over four times the wing loading during downstroke, and reverse at the wingtip during upstroke to a dorsal–ventral pressure close to wing loading. The results show: maintenance of ventral-to-dorsal pressure at the most proximal site throughout the wingstroke cycle; reversal of the pressure sense at the most distal site; and double pressure peaks at the distal sites during the downstroke. Maintenance of pressure differential at wing base, and reversal of pressure sense at wingtip, suggest the view of slow flight as a 'vortex-ring gait' may conceal some interesting details. The double pressure peaks during downstroke may be related to management of the kinetic energy of flapping wings.

### A6.3–Inertial power transfer in avian flapping flight over a range of speeds: muscles, wings and aerodynamics

T.L. Hedrick, OEB, Harvard University; B.W. Tobalske, Biology, University of Portland; A.A. Biewener, OEB, Harvard University.

We investigated the inertial power requirements of flight across a range of speeds in cockatiels (*Nymphicus hollandicus*,  $n=4$ ) and the recovery of wing kinetic energy as whole body potential and kinetic energy increases due to aerodynamic force production. Inertial power requirements were measured by a high-speed 3D kinematic reconstruction of wing motion combined with measurements of wing mass distribution and moments of inertia. Instantaneous aerodynamic forces were measured using a set of four accelerometers mounted on orthogonal axes and attached to the dorsal midline. The accelerometer recordings were oriented to standard XYZ axes by applying roll, pitch and yaw angles calculated from the 3D kinematics. Accelerations due to inertial forces were removed using the 3D kinematics and known mass distribution of the wings. The inertial power requirements were high, ranging from 102 W/kg of flight muscle at a flight speed of 1 m/s to 25 W/kg at a speed of 7 m/s. Recovery of wing kinetic energy, leading to increases in whole body potential and kinetic energy, was maximized at intermediate flight speeds (5 to 9 m/s) where

100% of wing kinetic energy was recovered. Kinetic energy recovery was lower at both slower and faster flight speeds and reached a minimum of approximately 30% at the fastest flight speed the cockatiels achieved: 13 m/s. (Supported by NSF IBN-0090265)

#### **A6.4—Aerodynamic and biomechanical determinants of wing shape in birds**

J.M.V. Rayner and L.B. Coudrick, Biology, University of Leeds

Despite the broad size range of birds, wing proportions vary relatively little owing to the paramount pressures on wing surface area to support the weight in flight. Diversity in relative wing size and aspect ratio have been shown to be correlated with autecology and flight behaviour in response to phylogeny and to selection for aerodynamic factors such as speed and control. New aerodynamic modelling predicts that patterns in wing planform shape in gliding birds are the results of trade-offs between efficient lift generation with low induced drag and the overall weight of the wing (or the strength of the bony elements). The elliptic planform is rarely optimal in birds, and typically gliding wings are slightly pointed. Square, slotted wingtips are optimal for short-winged gliders; such wings would be too heavy in longer-winged species; this is consistent with the distinct vortex wake these wingtips produce and the distribution of slotting and primary feather emargination. Applied to flapping flight, similar modelling arguments allowing for wake geometry and roll-up predict that, independent of aspect ratio, a slightly tapered wing is optimal at low reduced frequencies (a well-known solution when the wake is flat), as for example in terns. More rounded wings are optimal at intermediate reduced frequencies, as in the majority of birds, but sharply tapered wings produce thrust more efficiently at high reduced frequencies, as in ducks and some wading birds.

#### **A6.5—Flying with sails: the aerodynamics of pterosaur wings**

M.T. Wilkinson and C.P. Ellington, Dept. of Zoology, University of Cambridge

Pterosaur wings were, morphologically, the simplest that have yet been developed by a vertebrate flyer, being flexible aerodynamic surfaces supported by a single spar. Such wings resemble modern sails, whose performance is dominated by a mutual interdependence of shape and aerodynamic loading. Despite the superficial similarity, however, pterosaur wings had a number of important morphological differences that have been revealed by analyses of exceptionally well-preserved fossils. Most significantly, the pteroid – a slender bone that articulated at the wrist – appears to have been directed

antero-ventrally in flight, and would have supported a broad forewing in the proximal part of the wing.

The aerodynamic effects of this forewing were ascertained by testing model profiles in a wind tunnel. Very high lift coefficients were obtained, exceeding 2.4 in some instances. The high lift was achieved because the forewing increased the camber of the wing, and enabled the leading edge to be directed into the airflow at high angles of attack, thereby increasing the stalling angle. However, the increased camber also caused extensive flow separation, and the deflected forewing obstructed the airflow over the ventral surface of the wing at low angles of attack. Hence, the profile drag coefficients were very high, and the best lift:drag ratios for the wing were low, ranging between 5.0 and 9.2.

In addition to these features, the forewing also alleviated some of the undesirable characteristics of conventional sails, thanks to the relatively rigid prescription of the leading and trailing edges with respect to each other and the spar.

#### **A6.6—Vortex wakes generated by a thrush nightingale in wind tunnel free flight over a wide speed range**

A. Hedenström and M. Rosén, Animal Ecology, Lund University; G.R. Spedding, Aerospace & Mechanical Engineering, University of Southern California

The aerodynamic properties of bird flight have received much interest, but we still lack crucial information regarding the wake topology and circulation. Previous experiments have shown two wake patterns; at low speeds elliptic rings are shed, while at medium speed there are two undulating wing-tip vortices of constant circulation. At slow speed there is a 50% momentum deficit for weight support, which remains a paradox. Therefore we adapted a DPIV set-up for quantitative wind tunnel observations. A small bird (thrush nightingale) was trained to fly steadily in reduced light conditions allowing DPIV sampling. A total of 4000 images was analysed at speeds 4–11 m/s. At the lowest speeds there were discrete vortex loops, while at the highest speeds the bird shed near constant circulation wing tip vortices. At intermediate speeds there were cross-stream vortices of varying strength, showing a transition type of wake. The transitions between vortex wake patterns were smooth, as measured by vorticity and circulation, and hence there is no support for the notion of distinct ‘gaits’ from our data. A careful accounting of wake circulation gave enough vortex ring impulse for weight support at slow speeds, but only after including positive vorticity near the stopping vortex. This finding is due to the improved resolution of the DPIV visualisation compared to previous methods. We also derive horizontal force and power at low speeds and discuss vortex theory in relation to the new observations.

### A6.7—Can Strouhal number explain wing-beat frequency in birds?

R.L. Nudds, School of Biology, University of Leeds

Small birds have higher wing-beat frequencies than large birds. Previous work has focused on scaling frequency against morphological variables rather than seeking an explanation from aerodynamic principles. Recent theoretical and experimental work has indicated that an oscillating foil attains optimum propulsive efficiency across a narrow range of the dimensionless Strouhal number ( $St$ ):  $St = f \cdot A / U$ , where  $f$  = oscillating frequency (Hz),  $A$  = maximum excursion of the foil and  $U$  = forward velocity. At low values of  $St$  ( $< 0.13$ ) drag is produced, between  $St = 0.13$ – $0.35$  thrust is produced, with optimum propulsive efficiency occurring at  $St = 0.25$ – $0.35$ , and at higher values of  $St$  ( $> 0.35$ ) a piston-like mode dominates and thrust development deteriorates. Analysis of existing data suggests, that in accordance with the findings for oscillating foils, birds converge on the predicted optimum  $St$  range (mean =  $0.26$ ). In this current study flow visualizations of the wake behind flat-plates undergoing a plunging motion with an  $A/c$  ratio of  $0.9$  showed agreement with previous findings where  $A/c$  was typically  $< 0.1$ . At a higher  $A/c$  ratio ( $1.6$ ), however, the values of  $St$  defining the three characteristic wake regions of drag, thrust and piston-like mode were shifted upwards. A shifting of the wake regions implies a shifting of the range of optimum propulsive efficiency. Reasons for why birds with  $A/c$  ratios in excess of  $3$  apparently concur with previous experimental findings using oscillating plates with much lower  $A/c$  ratios are explored.

### A6.8—Insect Flight: lift generating mechanisms and unsteady aerodynamics

A.L.R. Thomas (Oxford)

The superiority of dragonflies in terms of aerodynamic performance is revealed in their success rate in capturing prey in flight—which can be as high as  $97\%$ .

We studied dragonfly flight using free-flight flow visualisation, tethered flight flow visualisation combined with simultaneous instantaneous measurements of the forces and moments they produced. In over  $90\%$  of visualised wingbeats flow over the wings was separated to form a leading edge vortex.

In normal counterstroking flight there was a leading edge vortex present over the forewing and attached flow on the hindwing. The leading edge vortex is formed during rapid increases in angle of attack. In steady flight these rapid increases in angle of attack occur during wing rotation at the start of the downstroke. However, the dragonflies can go from attached flow to leading

edge vortex flow at any stage of the wingbeat by rapidly increasing their angle of attack. The upstroke was almost always unloaded, and there is evidence that the dragonflies can accurately select zero degrees angle of attack.

The detailed features of the leading edge vortex structures generated by dragonflies can be reproduced with a flat plate in pure plunging motion provided the Reynolds number is in the range used by flying animals, and the strouhal number is selected to a value close to  $0.25$  which gives dynamic similarity.

### A6.9—Flow visualisations around insect wings using Digital Particle Image Velocimetry

Richard J. Bomphrey, Graham K. Taylor and Adrian L.R. Thomas, Zoology, Oxford University; Nicholas J. Lawson, Cranfield University

Insects fly using leading edge vortices to generate high lift forces, but the presence of leading edge vortices has only been inferred by using qualitative smoke flow visualisations analysed by eye. Here we present the first objective quantitative analysis using Digital Particle Image Velocimetry (DPIV) to measure the flow field in the wake, around the wings and within the leading edge vortices generated by the hawkmoth (*Manduca sexta*) flying in a wind tunnel. The first simultaneous force–moment measurements with flow visualisation show that the maximum development of the leading edge vortex at the end of the downstroke coincides with the time when the lift force generated by the insect reaches its peak. The structure of the leading edge vortex is different from that recently seen in free-flying butterflies and appears to be similar to that previously described for tethered hawkmoths. The wake is complex, the main structures being a series of elliptical vortex loops but transverse cross-stream vorticity is shed throughout both downstroke and upstroke, indicating that the aerodynamic load on the wings changes continuously throughout the entire stroke.

### A6.10—Evolution of posteromotorist flight in Archaeorthoptera (*Insecta*, *Neoptera*)

O. Béthoux (Paris, Natural History Museum)

Insect posteromotorist flight mode is defined as having a lift production provided mainly by the hindwings during flight. This flight mode can be inferred from fossils based on hindwing shape and the relative sizes of wing pairs. In order to study the evolution of posteromotorist flight, we focused on the Polyneoptera, a clade considered as being 'primitively' posteromotorist.

We performed a cladistic analysis of the Archaeorthoptera, including the Orthoptera (grasshoppers, crickets, locusts), two extinct insect orders (Caloneurodea, Titanoptera), and taxa of uncertain affinity. If the Archaeorthoptera as a whole are posteromotorists, several reversions must have occurred within the clade. The Caloneurodea are obvious bimotorists and the Titanoptera include both bi- and posteromotorists.

Hindwing venation organization of the Archaeorthoptera is compared with that of some posteromotorist Polyneoptera. The primitive 'archaeorthopterid' hindwing organization is similar to that of the Blattodea, but a new organisation was acquired in more derived taxa. The Palaeozoic posteromotorist 'grylloblattids' show another non-homologous organization. As a result of this comparative study, a generalized pattern of 'posteromotorist hindwing organization' can be proposed: an expanded postero-basal area ('vannus') is filled with fan-shaped ramifications originating from a single point; apparently this area is mechanically isolated from the anterior part of the wing ('remigium') by 3–4 simple and straight veins with a developed and opposite relief.

Finally, the posteromotorist flight mode has been subject to much homoplasy within Polyneoptera. Further, several convergent organizations are known among the oldest recorded winged insect faunas (~300MYBP), suggesting an older diversification.

#### **A6.11–Kinematics and aerodynamics of free flight maneuvers in *Drosophila***

S.N. Fry, Institute of Neuroinformatics, University/ETH Zürich, Switzerland; M.H. Dickinson and R. Sayaman, Bioengineering, California Institute of Technology, Pasadena, USA

Although the aerodynamic mechanisms underlying insect flight are increasingly well understood, little is known about how insects control wing motion –and hence flight forces– for flight stabilization and maneuvering.

To explore the aerodynamic basis of flight control, we filmed fast turning maneuvers (saccades) of fruit flies (*Drosophila melanogaster*) in free flight using infra-red 3D high speed (5000 fps) video. We reconstructed the 3D motion of the body and both wings from the image sequences and played the wing motion through a dynamically-scaled flapping robot to obtain the instantaneous aerodynamic forces. The pattern of wing motion was exceedingly consistent. The U-shaped wing trajectory generates force peaks around the middle of each half stroke. The pronounced vertical plunge of the wing at the start of the upstroke results in particularly high forces and an elevated lift-to-drag ratio. Translational forces dominated and the clap-and-fling mechanism was con-

spicuously absent. Furthermore, muscle power calculated from the instantaneous aerodynamic and inertial wing forces lies at least 25% above previous estimates. To initiate a saccade, the outside wing is tilted backward and the stroke plane is increased with respect to the inside wing. The torque thus generated quantitatively explains the time-course of the observed body motion. Remarkably, skin friction on the body is insignificant during saccades, and the fly reverses torque output at the end of the maneuver to actively decelerate. These unexpected results alter our understanding of insect flight biomechanics and provide an important basis for future research on the neural control of insect flight.

#### **A6.12–Aerodynamics and flight mechanics of stability and control in the Desert Locust *Schistocerca gregaria***

G.K. Taylor, Zoology Department, Oxford University, UK

This talk describes the first formal analysis of dynamic stability in a flying animal. By measuring dynamically all six-components of aerodynamic force and moment on tethered Desert Locusts (*Schistocerca gregaria*) I was able to determine how the longitudinal forces and moments varied with imposed changes in pitch attitude and flight speed. I also measured body mass, pitching moment of inertia, and centre of gravity. The measured responses were insufficient to provide complete dynamic stability unless locusts are sensitive to pitch attitude (relative to an inertial or Earth-fixed frame) as well as aerodynamic incidence (relative to the direction of flight). The governing equations of motion identify three natural longitudinal modes of motion: one stable subsidence mode, one unstable divergence mode, and one stable oscillatory mode. The latter corresponds to the short-period mode of aircraft, and consists of rapid pitching oscillations with negligible change in forward speed. The frequency of this mode (10 Hz) is close enough to the wingbeat frequency (22 Hz) that the short-period mode would tend to couple with the flapping cycle if inadequately damped. Pitch rate damping is shown to be highly effective at damping this mode – especially at the small scales associated with insect flight – and may be essential in stabilising locust flight. Having the short-period mode frequency close to the wingbeat frequency is, however, necessary for periodic aerodynamic control inputs at the frequency of the wingbeat to be effective. Birds may avoid this constraint by using the tail to provide control inputs that are unconstrained by wingbeat frequency.

### A6.13—Analysis of maneuvering flight of a dragonfly

S. Sunada, Aerospace, Osaka Prefecture University

Equations of motion for any maneuvering flight of a dragonfly were derived. In the equations, acceleration of the body of a dragonfly is expressed by aerodynamic and inertial forces acting on the wings and by aerodynamic force acting on the body. In this study, the acceleration of the body in the maneuvering flight measured by Wang et al. (2003) was estimated from the aerodynamic and inertial forces acting on the wings and aerodynamic force acting on the body calculated by quasi-steady analysis. This estimated acceleration did not agree well with the measured values, showing that one or both of the following is needed for analyzing a maneuvering flight: (1) The number of data points must be high enough to obtain highly accurate differentiated values of acceleration by using the method of Wang et al. and (2) a method of CFD (Computational Fluid Dynamics), where translational and rotational motions of the body can be taken into account, must be used to calculate the aerodynamic forces acting on the wings and the body with higher accuracy.

### A6.14—Scaling of leading-edge vortices with Reynolds number

G.R. Nolan, U.K. Müller and C.P. Ellington, Department of Zoology, University of Cambridge

Rotary wing motion, like that of a propeller, is similar to flapping flight of hovering insects. During the stroke of an insect wing, a span-wise pressure-gradient is formed because the wing-tip moves faster than the wing base. To understand the fluid dynamics of rotary wings at low Re (comparable to insect flight), we used 3D PIV to analyze fluid motion around three flat, rigid wings. In particular, we wanted to learn how wing shape and Reynolds number affect the leading edge vortex, which was previously identified as an important high-lift mechanism in insect flight.

We tested three different wings, all based on the wing shape of a fruitfly, *Drosophila melanogaster*. Each wing had a different aspect ratio (AR=4, 6, & 8), which is a measurement of the length of the wing relative to its average chord. These wings were steadily rotated at angles of attack from 0 to 50 degrees and Re=100 to Re=10,000. We present lift and drag measurements in addition to 3D PIV visualisations of fluid motion. Through an analysis of fluid velocity, vorticity (and circulation) at 7 distinct span positions along each wing, we describe how the strength and structure of the leading edge vortex depends on Re and wing shape.

### A6.15—Lift and drag forces of hummingbird wings and wing models

D.L. Altshuler (Caltech), R. Dudley (Berkeley) and C.P. Ellington (Cambridge)

A central challenge to the study of animal aerodynamics has been measuring the forces experienced by flapping wings. Estimates are typically made for wings held stationary in a wind tunnel. Under this configuration, the velocity across the mounted wing is constant, whereas the wind velocity of flapping wings varies radially. Not surprisingly, the advent of flapping robots with rotating wings has revealed quite different aerodynamic forces than previous measurements, and estimates of lift and drag are now regularly based on flapping wing models. A problem with this method is that real wings may have lift-enhancing and drag-reducing features that are not present on models. We address this issue using the simple experiment of mounting hummingbird wings and wing models on a rotating motor to measure lift and drag forces. Our results indicate that lift increases substantially as wing models become more sophisticated, i.e., become more like real wings. Furthermore, real wings have much greater lift and much lower drag than our wing models, suggesting that real wings have structural mechanisms for aerodynamic force manipulation. We conclude with a survey of hummingbird wing shapes among taxa and across elevations.

### A6.16—Wing shape, flight styles, and energetic costs of aposematic signaling in butterflies

R.B. Srygley, Seoul National University and Smithsonian Tropical Research Institute

Bates hypothesized that some butterfly species that are palatable gain protection from predation by appearing similar to distasteful butterflies. When undisturbed, distasteful butterflies fly slowly and in a straight line, and Batesian mimics also adopt this non-chalant behavior. When seized by predators, distasteful butterflies are defended by toxic or nauseous chemicals. Lacking chemical defenses, Batesian mimics depend on flight to escape attacks. Here I demonstrate that flight in warning-colored mimetic butterflies and their distasteful models is more costly than closely-related, non-mimetic butterflies. The increased cost is due to differences in both wing shape and kinematics. Batesian mimics and their models slow the angular velocity of their wings to enhance the color signal but at an aerodynamic cost. Moreover, the design for flight in Batesian mimics has an additional energetic cost over that of its models. The additional cost of Batesian mimicry is empirical support

for the theoretically well-founded handicap principle of animal communication. The added cost may cause Batesian mimics to be rare, explaining a general pattern that Bates first observed.

### **A6.17—The engineering of insect wings**

C.W. Smith, R.J. Wootton (Exeter)

Abstract not supplied

### **A6.18—What to do with wings when not on the wing: design problems in wing folding**

F. Haas, Staatliches Museum für Naturkunde, Rosenstein 1, D-70181 Stuttgart

Insect wings are beautiful examples of light-weight structures combining a minimum of material with high performance. This was one reason for the stunning success of pterygotes and is almost proverbial. Very much like sails, wings need to be folded to prevent damage. This is achieved in a variety of—mathematically describable—ways. The circumference of a fan as well as the relation between wing surface area (WSA), number and size of fan sectors, and the promotion angle can be modelled. Also the basic mechanisms found in almost all folding patterns are described mathematically. Apart from the fan-wise folding, other taxa have evolved other folding patterns. The much more compact, and almost tank-like, Coleoptera fit their folded wings into the elytral-abdominal space. This requires a close adaptation of shapes to optimize packing. It is feasible through the plasticity of the hind wing concerning pattern and structure. Thus it was expected to find different folding patterns in differently shaped beetles: long-slender beetles are different to more spherical ones. Flat and cambered abdominal terga yield different adaptations in the folding pattern. The ‘beetle-construction’ yields an unequal distribution of WSA. Very much in contrast to the folding

in Hymenoptera and Dictyoptera with their fan-wise folding, the Coleoptera fold the wing apically. This feature limits the WSA stowable under the elytra and so increases wing loading with possible consequences on flight behaviour, performance and flight muscle physiology.

### **A6.19—Does insect wing structure actually matter?**

R.J. Wootton, Biological Sciences, University of Exeter.

Answer: some of it certainly does—but the rest...? 30 years of research confirm that much insect wing morphology is concerned with semi-automatic control and facilitation of wing deformations in flight: camber, torsion and transverse bending. Yet studies using flat plates still account for most or all of the aerodynamic forces needed for support and propulsion (1), and deformable model wings rotated as propeller blades suggest that camber and spanwise twist (2) and even aspect ratio (3) may have little effect on lift and drag. Our own simple physical models, with little of the structural detail seen in real wings, can replicate many postulated shape-controlling functions. Are many of the variations in venation, relief and microstructure actually non-adaptive? Some certainly are not, though the interpretation of their roles has altered. Camber, for example, appears more concerned with the mechanical control of rigidity, upstroke twist and angle of attack than with direct lift enhancement. The significance and importance of other characters, like distal venation details that may be stable within, but variable between families whose flight capabilities seem indistinguishable, are quite unclear, and present interesting problems for evolutionary theorists. (1) Dickinson, M. H., Lehmann, F.-O. and Sane, S. P. (1999). *Science* 284, 1954–1960 (2) Usherwood, J.R. and Ellington, C.P. (2002a) *J. Exp. Biol.* 205: 1547–1564. (3) Usherwood, J.R. and Ellington, C.P. (2002b) *J. Exp. Biol.* 205: 1565–1576.