Approaches to the structural modelling of insect wings

R. J. Wootton^{1*}, R. C. Herbert¹, P. G. Young² and K. E. Evans²

¹*School of Biological Sciences, University of Exeter, Hatherly Laboratories, Prince of Wales Road, Exeter EX4 4PS, UK*

²*School of Engineering and Computer Science, University of Exeter, Harrison Building, North Park Road, Exeter EX4 4QF, UK*

Insect wings lack internal muscles, and the orderly, necessary deformations which they undergo in flight and folding are in part remotely controlled, in part encoded in their structure. This factor is crucial in understanding their complex, extremely varied morphology. Models have proved particularly useful in clarifying the facilitation and control of wing deformation. Their development has followed a logical sequence from conceptual models through physical and simple analytical to numerical models. All have value provided their limitations are realized and constant comparisons made with the properties and mechanical behaviour of real wings. Numerical modelling by the finite element method is by far the most time-consuming approach, but has real potential in analysing the adaptive significance of structural details and interpreting evolutionary trends. Published examples are used to review the strengths and weaknesses of each category of model, and a summary is given of new work using finite element modelling to investigate the vibration properties and response to impact of hawkmoth wings.

Keywords: flight; folding; functional morphology; biomechanics; deformation; finite element

1. INTRODUCTION

Insect wings are remarkable structures, apparently unique among animal propulsive appendages in the degree of automation in their functioning (Wootton 1999).

Flapping flight requires that wings must generate sufficient net upward force during the stroke cycle to support the animal's weight. Unless an animal is hovering with a horizontal stroke plane, this means that the two halves of the stroke cycle must be asymmetrical: the vertical forces must not cancel out. While this force asymmetry is achieved, in part, by altering the angle of attack between upstrokes and downstrokes, and sometimes by the use of unsteady aerodynamic mechanisms around the point of stroke reversal (Ellington 1984a, 1996; Dickinson *et al.* 1999), there is abundant photographic and observational evidence that wings typically enhance force asymmetry by changing shape between upstroke and downstroke. In addition, almost all flying animals fold their wings at rest and this involves still greater deformation. These changes are achieved in birds and bats by the wings' internal musculature, flexing and extending at elbow and wrist, spreading and apposing fingers or feathers.

Insect wings, however, lack internal muscles, and any changes in shape that they undergo in flight and in deployment and folding must necessarily be driven by external forces: by the thoracic musculature, by the inertial and aerodynamic forces which the wings experience, and/or by parts of the body outside the flight system. The extent and form of these deformations are determined by dynamic

interaction between these externally applied forces and the wing's own structure—the internal distribution of rigid and compliant components (Wootton 1981, 1992; Haas & Beutel 2001).

It is evident that the need to facilitate, limit and control deformation in deployment, flight and folding is a major determinant of insect wing structure. Analysing these phenomena, and explaining wing morphology in functional terms, has been a major preoccupation of the Exeter group for more than two decades. The challenge is considerable. Insect wings are extremely diverse—far more so than those of vertebrates. Linear dimensions range over three orders of magnitude. Shapes, and the relative size of fore and hind wings, vary greatly. One or both pairs may be modified for non-aerodynamic functions, reduced, or lost. Venation ranges from the extremely complex to the vanishingly simple. Vein arrangement is hugely varied. Interpreting the functional morphology, even of relatively simple wings, is far from easy, and full-scale structural analysis is dauntingly difficult because of the way in which the components of the wing—overall relief, vein dimensions and cross-sectional geometry, membrane thickness, and the mechanical properties of the cuticle—vary from place to place within the wing (Smith *et al.* 2000).

Modelling has been used since the programme of research began, and has proved to be of the greatest value both in investigating the problems and in communicating the results. All the models have been based on observed information; there is little point in modelling phenomena that are not known to happen. Sources of information have included: high-speed ciné film and videotape of insects in free flight; high-resolution, high-speed still photographs, particularly those by Dalton (1975, 1982) and Brackenbury (1992); and stroboscopic examination of

* Author for correspondence (r.j.wootton@exeter.ac.uk).

One contribution of 20 to a Theme Issue 'Modelling in biomechanics'.

Figure 1. Comparison of a sail with the wing of a tabanid fly. In this conceptual model the sailcloth corresponds to the wing membrane; the mast and boom to the principal supporting areas of the wing, shown in black; the battens to the stiffening veins between.

tethered flying insects; all to investigate how wings actually move and deform in flight. Detailed morphological examination, using light and scanning electronic microscopy, has been conducted on whole wings and on details and sections to investigate how the deformations are facilitated and controlled, and this has been supported and verified by manipulation of anaesthetized or freshly killed insects, and by mechanical testing.

2. APPROACHES TO MODELLING

(a) *The modelling sequence*

The approaches to modelling have developed progressively in a logical sequence, from conceptual models through simple physical models and simple analytical models, to full-scale numerical modelling by the finite element method. Only one example has been taken through the entire sequence: the structure and functioning of the hind wing fan of the desert locust, and by implication of other Orthoptera (Wootton 1995; Herbert *et al.* 2000; Smith *et al.* 2000; Wootton *et al.* 2000). Other examples have been carried through only one or two stages. It is important to stress that each approach has advantages and limitations, and that all can be useful if the limitations are clearly recognized. New models continue to appear at each level.

(b) *Conceptual models*

The principal conceptual analogy for orthodox wings is an oscillating sail (Wootton 1981; figure 1). Sails are the commonest flexible aerofoils in human technology. Like insect wings, they possess: (i) large deformable areas whose contours are moulded by the airflow; (ii) rigid spars, providing anterior and posterior support, and limiting the overall deformation; and (iii) more flexible supports within the deformable areas, influencing the aerofoil section. As in wings, while the angle of attack of the base can be directly determined by muscular action, attitude and shape beyond the base can only be controlled remotely, and are strongly influenced by the shape and detailed structure of the sail: the arrangement of battens, the properties and weave of the cloth. Instantaneous shape is determined by the interaction between the effort of the sailor, the aerodynamic forces and the architecture of the sail. The change in attitude and shape of the wing between

Figure 2. The triangle and supratriangle of anisopterous dragonflies as an automatic mechanism adapted to depress the trailing edge when the wing is generating lift. (a) Physical model in thin card; (b) the hind wing base of *Sympetrum striolatum* (Libellulidae), after Wootton (1991). The broad arrows represent the applied force, the slender arrows the local rotation of the wing components.

Figure 3. The operation of the arcus in Diptera and Odonata to depress the trailing edge when the wing is generating lift. (a) Physical model in thin card. (From Ennos (1989), with permission.) The triangular arrow represents the applied force, the slender arrows the local rotation of the wing components. (b) The wing base of a tabanid fly, illustrating the arcus.

important detail. Since insect wings oscillate at high frequency they are subject to inertial forces, and these are often significantly higher than the aerodynamic forces (Ellington 1984*b*; Herbert 2002). Beside this, the differences in scale are self-evident—and most wings prove to be far more complex in their operation than sails.

Other useful conceptual models have been the consideration of the leading edge spar of dragonfly wings as two plate-girders linked side by side with their short axes mutually at right angles, and the membrane acting as a stressed skin (Newman & Wootton 1986); and of orthopteran hind wings as spiral umbrellas (Wootton 1995; Wootton *et al.* 2000), further discussed below.

(c) Physical models

Insect wings typically consist of expanses of membrane supported by, and continuous with, a framework of—usually—tubular veins. The frameworks may be interrupted by areas or lines of pliant cuticle allowing local bending, torsion or camber change in flight, or folding at rest, or more than one of these. The deformability of the structure may be actively and remotely modifiable by the 'direct' thoracic muscles inserted at the wing's extreme base. This level of complexity is hard to reproduce completely in a physical model. Instead, two approaches have been used

half strokes, which often involves reversal of camber, can be compared with that in a sail 'going about' at the end of a tack. However, the analogy falls down in one

Figure 4. Models showing the generation of camber by wing torsion. OY represents the chord of the wing at rest; h is the height of the wing surface above OY . In (a) the posterodistally directed veins are straight and parallel, and the wing becomes symmetrically cambered about the mid-chord. In (b) the veins are parallel but curved, and the trailing edge is depressed below OY . In (c) the straight veins diverge, and the centre of camber is closer to the leading edge. (From Ennos (1988*a*), with permission, slightly modified.)

Figure 5. The two basic folding patterns. (a) The internal mechanism; (b) the external mechanism; (c) plot of the velocity ratio against the opening angle ε in the internal mechanism shown in (a); (d) plot of the velocity ratio against the opening angle ε in the external mechanism shown in (b). Explanation in the text. (After Haas & Wootton (1996), slightly modified.)

Figure 6. The relation between basal camber and distal flexion and twist in a model wing with median and transverse flexion lines. Explanation in the text. Lettering as in figure 5.

with success: treating the wing as a thin shell; and modelling it as a simplified framework, with or without a membrane.

(i) *Shell models*

Many of the properties of wings can be reproduced in models made of thin card, paper or plastic sheet. Newman (1982) used card to demonstrate the functioning of the 'supratriangle' and 'triangle', two adjacent high-relief vein conformations in the basal area of the wings of anisoptorous Odonata (figure 2). If the model (figure 2a) is held in the centre of the base, at point X on the diagram, and an upward force applied to the point Y at the distal end, representing the proximal end of the vein within whose branches the centre of aerodynamic pressure is located, the anterior and posterior basal angles of the model are levered down. In the actual wing (figure 2b) the anterior area is rigidly supported, but manipulation confirms that the mechanism operates to depress the flexible trailing edge and so to maintain an effective section and angle of attack, as an automatic response to aerodynamic loading. Card models more closely simulating the actual wings show the same effect, and Wootton *et al.* (1998) described an analogous situation, involving different veins, in the wings of some Carboniferous insects of dragonfly type. Card models of these, too, function similarly.

The triangle-supratriangle complex of anisoptorous Odonata is just one of several mechanisms associated with automatic trailing edge depression. Ennos (1989) modelled and described the operation in Diptera of a mechanism associated with a basal transverse vein, the 'arcus'. Here, aerodynamic loading is believed to raise the part of the wing supported by branches of a longitudi-

Figure 7. Camber generation and trailing edge depression in the hind wing fan of a locust-like insect: conceptual model. Promotion of the wing tightens and pulls in the outer margin while the membrane between the radiating veins is still slack. The veins are compressed, and bend like the spokes of an umbrella, curving the wing surface.

nal vein that is hinged to the arculus, again levering down the flexible trailing edge and maintaining an aerodynamically effective wing section and orientation (figure 3). The effect is confirmed by the manipulation of actual wings. Analogous mechanisms are to be found in zygopterous Odonata (Ennos 1989; Wootton 1991), and probably in Neuroptera (Wootton 2002).

The wings of many insects have a cambered transverse section. Models in thin sheet demonstrate that cambered wings show an asymmetric bending behaviour, being far more rigid to forces applied from the concave side than

Figure 8. Top view of finite element mesh of hind wing of *Schistocerca gregaria*.

from the convex. In the former case, forces centred near the centre of the section tend to increase the camber, and hence to increase the rigidity; in the latter, the section tends to flatten and bend readily. Less obviously, the wing also responds asymmetrically to forces applied away from the torsional axis of the section, which twist as well as bend the wing. Wootton (1993) investigated combined bending and torsional rigidity in cantilevered strips of thin plastic sheet, with and without stiffening rods, simulating the cambered wings of some butterflies; and in all cases found marked asymmetry in their response to pronatory and supinatory torques. He also measured the resistance to pronatory and supinatory twisting of real butterfly wings and of similarly sized cambered paper wing models. The tests yielded similar deflection curves, though greater torques were needed to deflect the paper wings. Wootton concluded that camber alone might allow the wing couples of some butterflies to supinate markedly in the upstroke by twisting within their length, while resisting undue pronation in the downstroke.

Physical models of wings in which the camber can be

Figure 9. Deformations under distributed force applied to the anteriormost vein of the model. (a) Dorsal view and (b) latero-dorsal view; the colour represents translation in the z -axis (normal to the undeformed wing plane), either positive (elevation) or negative (depression) in metres. The black lines illustrate the undeformed shape of the wing.

actively altered have also proved informative, and their bending and twisting behaviour is being modelled analytically. They will be discussed below, in § 2d.

(ii) *Deformable framework models*

In this category are models in which individual veins or combinations of veins are simulated by rods or strips. The arculus mechanism described above has been successfully modelled in this way (Wootton & Ennos 1989), and two other examples—the generation of camber by wing torsion in Diptera, and by wing promotion in the hind wing fan of Orthoptera—have been developed as analytical models, and will be described in later sections.

(iii) *Advantages and limitations of physical models*

Physical models of wings can be invaluable for swift investigation and demonstration of simple deformations and the factors influencing them—many of which are not intuitively obvious. Their principal advantages are simplicity and speed of manufacture. Their limitations are inseparable from their role in simplifying complex situations: their functioning can be misleading. They are built to work, and their components are therefore selected to deform appropriately, not necessarily reflecting the properties of the wing components that they are simulating. If the models are to be taken seriously, it is essential to verify them by testing the wings themselves.

(d) *Simple analytical models*

Analytical models of insect wings have usually, though not invariably, been developed from physical models, to generalize these and to investigate the effects of varying the parameters.

(i) *Generation of camber from aeroelastic torsion*

Ennos (1988a) modelled the wings of many Diptera and Odonata as a spar, rigid to bending but compliant in torsion, and representing the leading edge, from which a pennate series of straight, parallel rods, representing veins, diverge posterodistally (figure 4a). He demonstrated that aerodynamic loading centred behind the wing's leading edge would tend to twist it, elevating the pennate veins through angles that increased from the base to the tip of the wing. This would automatically camber the wing, arching the membrane into an inverted parabola, symmetric about the mid-chord, where the displacement of the membrane is maximal. Analysis showed that the camber, defined as the maximum displacement, $h_{\max}$, divided by the chord length, Y , is given by

$$h_{\max}/Y = \Psi Y/4 \tan \Theta,$$

where Ψ is the angle per unit length through which the leading edge spar is twisted, and Θ is the angle between the spar and the parallel veins. The more acute the angle between the veins and the leading edge, the higher would be the camber.

Ennos further demonstrated analytically that as the leading edge spar was twisted, so would be the parallel veins, by the same angle per unit length as the spar but in the opposite direction: they would be supinated rather than pronated. This would not affect the overall shape of the cambered wing if the veins were straight. If they were

curved, however, the maximum upward displacement of the section would be anterior to the mid-chord, and the posterodistal ends of the veins would be deflected down below the level of the uncambered wing—yet another mechanism for trailing edge depression (figure 4b). Vein curvature is common in Odonata, and is particularly marked in species with broad wings, whose trailing edges otherwise lack support (Wootton 1991). Finally, Ennos calculated what would happen if the posterodistally directed veins diverged from each other as well as from the leading edge spar, as for example in aphidoid Homoptera. He found that the apex of the camber would now lie anteriorly to the mid-chord, but with no depression of the trailing edge (figure 4c).

(ii) *Basic wing-folding mechanisms*

Haas & Wootton (1996), investigating folding in the hind wings of Coleoptera, Dermaptera and some blabberid Blattodea, found that most folding patterns were combinations of two basic mechanisms. These are variants of a simple mechanism commonly found in folding-paper structures—pop-up books, three-dimensional greeting cards, etc. Each consists of four sectors separated by four fold-lines meeting at a single point or node, one fold of opposite sense to the other three (one concave, three convex, or vice versa) (figure 5). Some properties of this mechanism had already been described. There is one degree of freedom. If the system is to fold completely, the sums of the angles of non-adjacent sectors at the node must be 180° (Delarue 1992).

Haas & Wootton (1996) distinguished between the 'internal' mechanism, in which folding along one line causes two adjacent sectors to fold together *between* the other two (figure 5a), and the 'external' mechanism, in which the adjacent sectors fold together *outside* the other two (figure 5b). Topologically there is no distinction between the two kinds—the distinction depends solely on their orientation within the wing—but their properties are very different. The authors used vector analysis to find the relationship between the opening angle ε and the position of the line OC in figure 5a,b, and so calculated the change in velocity ratio of the system as it unfolds. Figure 5c,d shows representative plots of the velocity ratio against ε for geometrically similar internal (c) and external (d) mechanisms, differing only in the relative positions of concave and convex folds. In the former, the velocity ratio, and therefore the mechanical advantage, start high and decline nonlinearly as the system unfolds. In the external mechanism, the reverse is true. Internal mechanisms hence exert most leverage as they begin to unfold. In real wings, where the internal and external mechanisms are linked into two-dimensional arrays opening sequentially by leverage from the base, internal mechanisms are found particularly in the proximal part of the wing, where their greater initial leverage is essential to begin the opening process (Haas & Wootton 1996; Haas 1998; Haas & Beutel 2001). Haas (1998) has extended the models to the complex, multi-mechanism arrays occurring in beetle wings, and has compared the results with the wings themselves. The real wings only approximately follow the 'rules'—the wings, for example, do not always need to fold flat—but the models have nonetheless proved to be

extremely useful in understanding the mechanics of the folding process.

(iii) *Control of ventral flexion and wing-tip torsion*

Rather similar principles can be applied to the control of wing bending and torsion in the flight of insects—some Plecoptera, Hemiptera, Megaloptera, Trichoptera, Hymenoptera—whose wings contain a longitudinally oriented median flexion line, allowing active alteration of the basal camber of the wing by the ‘direct’ thoracic muscles inserted at the axilla; and a transverse flexion line facilitating and localizing transverse ventral bending in the upstroke (figure 6). Physical models in card and paper suggest that the height of the camber (which may be actively controllable by the insect) and the shape and orientation of the transverse flexion line (fixed characters of the wing) are intimately related. A cambered wing with a straight transverse flexion line is capable of transverse ventral bending, but is only stable in the unflexed state. If the transverse flexion line is curved, or angular as in figure 6, the wing is bistable: in either the unflexed state, or flexed, with the camber reversed. The degree of flexion is governed by the height of the basal camber and the angularity of the flexion line, and is described by a similar model to the external folding mechanism described above. We are again dealing with four lines of flexibility, three convex and one concave. The height of the camber in the proximal part of the wing is a function of the opening angle ε in the previous model, and the apex of the camber in the part of the wing distal to the transverse flexion line corresponds to the line OC. For a given shape of transverse flexion line, the degree of distal flexion is determined by the height of the basal camber.

If the transverse flexion line is oblique; that is, if a line (not shown) joining B and D in figure 6 is not perpendicular to the median flexion line AO, then ventral flexion in the upstroke causes the distal part of the wing to twist, allowing it to assume a more effective angle of attack than would be possible at the base, which being hinged to the thorax has limited rotational freedom. The degree of distal twist is a function of ε , of the shape of the transverse flexion line BOD, and its angle relative to the wing’s longitudinal axis. An analytical model describing the relationship between these four variables is being developed (R. J. Wootton and F. Haas, in preparation).

(iv) *Advantages and limitations of simple analytical models*

Models of this kind allow phenomena observed in the insects themselves or in physical models to be generalized, so that the effects of altering selected parameters can be explored. They are relatively quick to create, and have considerable predictive value within their limitations. However, they often drastically simplify the wings’ geometry, and they largely ignore both the properties of the materials and the magnitude of the forces that the wings experience in life.

(e) *Numerical models*

Numerical methods, and particularly the finite element approach, are becoming increasingly popular in the study of biological systems. The finite element method is a relatively mature technique for the analysis of traditional engineering structures, but modelling biological systems

often introduces new complications. These may include accurately establishing and defining the geometry, boundary and loading conditions, as well as characterizing the material properties and modelling large nonlinear deformations. Nonetheless, once defined, these complications can, in theory at least, be incorporated into a finite element model, and the system can be modelled to any degree of accuracy. In the biological context, this not only allows one to examine the properties, functioning and adaptive significance of known structures, but also gives scope for investigating the mechanical consequences of observed evolutionary changes.

Finite element analysis was first applied to insect wings by Watanabe (1995) and Kesel *et al.* (1998). In both cases the insects chosen were anisopterous Odonata. Dragonfly wings are perhaps the most complex of all, and the models inevitably included major simplifications. Kesel *et al.* (1998) introduced complexity progressively, achieving increasing realism in computed deformations in response to notional aerodynamic loads. Watanabe used a sophisticated analysis to compare the stresses in wings in which attitude and spanwise torsion were both actively and aero-elastically controlled with those controlled by wing elasticity alone.

We have used finite element analysis to model two examples. These are:

- (i) the desert locust *Schistocerca gregaria* Forskål—camber generation in the hind wing fan;
- (ii) the coupled fore and hind wings of the sphingid moth *Manduca sexta* L.—deformation under aerodynamic loads, the free vibration characteristics of the wing couple, and the response of the fore wing leading edge vein to impact.

(i) *Schistocerca gregaria*

The finite element approach has been used to model the ‘umbrella effect’—the camber induced in the hind wing anal fan by wing promotion during the downstroke. To date, this is the only case for which the complete sequence of modelling approaches has been followed. The described effect was initially recognized during stroboscopic observation of locusts in tethered flight, and confirmed by high-speed filming of free flight and by manipulation (Wootton *et al.* 2000). The mechanism, another adaptation for depression of the wing’s trailing edge, was explained as a consequence of compression buckling of the radiating series of veins that support the fan, due to tension in the wing’s perimeter (figure 7). It was modelled physically using a series of plastic strips of diminishing length radiating from a single point, and joined at their tips by a thread that followed a logarithmic spiral, and represented the wing margin. An analytical model (Wootton 1995) treated the veins as straight slender rods of uniform diameter, capable of buckling only in a vertical plane. The wing perimeter was again modelled as a tensile thread, and the wing’s membrane was otherwise not included. Wootton found that the logarithmic shape caused both tension in the spiral margin and compression in the radiating veins to increase progressively from the tip to the base; and that both marginal tension and radial compression varied inversely with the number

Figure 10. *Schistocerca gregaria* in free flight, illustrating the angle and amount of camber generated in the trailing edge. (a) After Herbert *et al.* (2000), traced from a photograph in Dalton (1975), with permission. (b) The loaded finite element model displaying a similar mode of deformation in the trailing edge (T.E.) with the leading edge (L.E.) at a similar angle.

Figure 11. Deformations under distributed force applied to the anteriormost vein for a simplified numerical model, in which in-plane vein curvature was eliminated. (a) Dorsal view; (b,c) latero-dorsal views. The black lines illustrate the undeformed shape of the wing.

Figure 12. *Manduca sexta* mesh model, shell elements in green and beam elements in red. Note that the two green beam elements extending out from the wing base are used to create restraints beyond the wing model base.

of veins, and the size of the acute angle that they made with the perimeter.

Creating the full numerical model required detailed

measurement both of the geometry and material properties of the hind wing (Herbert *et al.* 2000; Smith *et al.* 2000). This resulted in an accurate description of the wing shape, including a degree of pre-camber ignored in the simpler models, and of the placement and cross-sectional geometry of the six major veins of the anal fan, as well as measured values for the Young's modulus and flexural rigidity of these veins along their length from the tip to the base. Membrane thicknesses and elastic moduli at a discrete number of locations on the hind wing were also measured. A relatively complex finite element model was developed based on these data and is shown in top view in figure 8.

A distributed promotion force was applied to the anteriormost vein of the model, and the response to wing promotion was simulated numerically. The resulting predicted deformation of the hind wing is shown in figure 9. Very good qualitative agreement between the deformations obtained numerically and those observed in

mechanical tests and high-speed photographs was obtained (figure 10). However, quantitative agreement was relatively poor: the numerically computed torque required to induce a 10 mm depression in the hind wing was less than half the value measured experimentally on an excised wing.

A number of less realistic finite element models were also analysed, introducing further assumptions. These included: neglecting the in-plane and out-of-plane curvature of the veins; neglecting the veins' base-to-tip tapering; and approximating the wing planform and vein placement. These simplifications were introduced independently to explore the sensitivity of the predicted deformations to various modelling assumptions. Surprisingly, none of these less sophisticated numerical models reproduced even qualitatively the experimentally observed deformations. Indeed some of the models displayed grossly different deformation patterns completely inconsistent with experimental results, and observations on real wings (figure 11). This highlights the danger of drawing conclusions from a model without in some way testing the simplifying assumptions on which it is based.

(ii) *Manduca sexta*

A finite element model of the wing couple of *M. sexta* was constructed, again based on careful measurements of the wing and vein geometry and material properties (figure 12). This allowed the deformations caused by computed aerodynamic loads to be investigated, and compared with observed data (Herbert 2002). A full account will be published elsewhere.

Innovatively, the model was also used to investigate the resonant properties of the wing couple, and some effects of impact. We summarize the results here, to illustrate some potential uses of finite element modelling.

Free vibration analysis

A modal analysis was performed using a commercial finite element package IDEAS 8.0. The model wing was clamped at the base and was assumed to vibrate *in vacuo*. The first two modes of vibration are shown in figure 13.

The shape of the first mode is consistent with the deformations of the wing couple observed *in vivo*. The wings do not curl significantly, and the combined trailing edge does not oscillate greatly during flight. The numerically computed frequency of the first mode is 31 Hz, which is remarkably close to the normal flapping frequency of *M. sexta*, which is between 20 and 27 Hz during hovering flight (Willmott & Ellington 1997). This raises the intriguing possibility that when actively flapped at this frequency the wings enter a vibration pattern that automatically induces the shapes appropriate to each part of the stroke cycle.

The second mode is a twisting mode with a computed frequency of 88 Hz. The modal shape is very similar to the wing shape observed at the transition between downstroke and upstroke. The axis around which the twisting occurs in the second mode lies directly along a longitudinal line of flexion that interrupts a cross vein in the real wing. Interestingly, the second modal shape is asymmetrical and illustrates well a common inertial property of many insect wings, where the centre of mass is placed behind the torsional axis. When the wing decelerates, this mass

placement enables the wing to rotate about its torsional axis more easily and quickly (Ennos 1988b). The second modal shape reflects this and indicates that the torsional axis cuts across the weakened portion of the cross vein, exactly where one would expect. This suggests very strongly that the flexion line is the preferred axis of twisting in normal flight. This placement of the torsional axis closer to the leading than trailing edge, and in front of the centre of mass of the wing, can explain the changes in wing pitch at stroke reversal without the need for direct muscular action on the wing base.

Impact modelling

To explore the response of the wing to impacts, a simplified finite element model was generated (Herbert 2002). Assuming that when the leading edge vein hits an object the loads carried through the membrane are negligible, the wing was modelled as a central lumped mass element, with two tapered beams representing the leading edge veins (figure 14). The lumped mass node was placed between the two veins at the estimated centre of the thorax and joined to the vein bases by rigid links.

Impacts at 5 m s^{-1} against an effectively rigid cylinder were simulated. The maximum stress computed rarely exceeded 10% of the elastic modulus values of the vein material, good evidence that even at maximal velocities the wing is capable of withstanding single impacts at the margin with rigid objects. In the case of frontal impacts to the tip and mid-vein enough flexion occurred to allow the whole vein to pass the impact object and continue forwards beyond it.

Interestingly, the predicted peak stresses along the central portion during a tip impact were constant along most of the vein length. This would seem to indicate that the distribution of material and rigidity along the vein is optimized for efficiently absorbing impacts along its length. The flexible nature of the veins and membrane within the wing helps both to prevent material damage and to minimize loss of control during impacts. The veins seem very well adapted to provide the appropriate stiffness and flexibility along their length, with economical use of material. Like many biological structures, the wing deforms to dissipate impact energies rather than absorbing them with stiffness, and the key component for successful dissipation is vein design.

(iii) Advantages and limitations of finite element models

As these numerical studies demonstrate, the finite element method can be a very powerful tool in the study of the structural and aerodynamic behaviour of insect wings. However, some of its limitations are evident.

Although in theory models can be of arbitrary complexity, in practice with biological systems an accurate morphological description in a form suitable for meshing can prove very difficult and time consuming. One approach to overcoming this problem is to generate the finite element models automatically from three-dimensional datasets obtained from various medical imaging modalities (e.g. magnetic resonance, computed tomography or micro-computed tomography scans). Resolutions are presently too low to be useful for all but very large wings, but this will improve.

Other problems are defining material properties, and loading and boundary conditions. Biological materials

Figure 13. The first two modes from the modal analysis. The first mode occurs at 31 Hz, the second mode at 88 Hz. The colours represent displacement in the z -axis from red (maximum) to blue (minimum). Two views that best illustrate the mode-shape in each case are given.

Figure 14. A view of the model used for the first transient impact analysis. The vein elements are shown in green, vein contact elements in blue. The lumped mass element representing the body mass is shown as a green square. The red pillar is the impact object, in this case situated near the mid-section of the vein.

have complex properties that are often anisotropic, inhomogeneous and may be dependent on both strain and strain rate. Similarly, loading and boundary conditions are often difficult to ascertain.

Perhaps the most significant limitation is the difficulty in obtaining a qualitative understanding of the mechanisms at work and the relative influence of various parameters, in the same way that an analytical model can provide.

Finally, the work carried out on the umbrella effect in the locust wing serves as a warning. Despite the care and time taken on developing a realistic model, the results for a relatively simple structural problem were quantitatively inaccurate. Furthermore, even minor deviations from this

model caused the system to adopt deformation patterns that were qualitatively different from those observed experimentally. This emphasizes the need to test all the categories of model, each with its own strengths and shortcomings, against each other; and as far as possible against the wings themselves.

REFERENCES

- Brackenbury, J. 1992 *Insects in flight*. London: Blandford.
- Dalton, S. 1975 *Borne on the wind*. London: Chatto and Windus.
- Dalton, S. 1982 *Caught in motion*. London: Weidenfeld & Nicolson.
- Delarue, J.-M. 1992 Minimal folding configurations. *Proc. II Int. Symp. Sonderforschungsbereich* **230**, 31–41.
- Dickinson, M. H., Lehmann, F.-O. & Sane, S. P. 1999 Wing rotation and the aerodynamic basis of insect flight. *Science* **284**, 1954–1960.
- Ellington, C. P. 1984a The aerodynamics of hovering insect flight. IV. Aerodynamic mechanisms. *Phil. Trans. R. Soc. Lond. B* **305**, 79–113.
- Ellington, C. P. 1984b The aerodynamics of hovering insect flight. VI. Lift and power requirements. *Phil. Trans. R. Soc. Lond. B* **305**, 145–181.
- Ellington, C. P. 1996 Unsteady aerodynamics of insect flight. In *Biological fluid dynamics. Proc. 49th Symp. Soc. Exp. Biol.* (ed. C. P. Ellington & T. J. Pedley), pp. 109–129. Cambridge: Company of Biologists Ltd.
- Ennos, A. R. 1988a The importance of torsion in the design of insect wings. *J. Exp. Biol.* **140**, 137–160.
- Ennos, A. R. 1988b The inertial cause of wing rotation in *Diptera*. *J. Exp. Biol.* **140**, 161–169.

- Ennos, A. R. 1989 Comparative functional morphology of the wings of Diptera. *Zool J. Linn. Soc.* **96**, 27–47.
- Haas, F. 1998 Geometrie, Mechanik und Evolution der Flügelfaltung bei den Coleoptera. PhD thesis, University of Jena.
- Haas, F. & Beutel, R. G. 2001 Wing folding and the functional morphology of the wing base in Coleoptera. *Zoology* **104**, 123–141.
- Haas, F. & Wootton, R. J. 1996 Two basic mechanisms in insect wing folding. *Proc. R. Soc. Lond. B* **263**, 1651–1658.
- Herbert, R. C. 2002 Modelling insect wings using the finite element method. PhD thesis, University of Exeter.
- Herbert, R. C., Young, P. G., Smith, C. W., Wootton, R. J. & Evans, K. E. 2000 The hind wing of the desert locust (*Schistocerca gregaria* Forskål). III. A finite element analysis of a deployable structure. *J. Exp. Biol.* **203**, 2945–2955.
- Kesel, A. B., Philippi, U. & Nachtigall, W. 1998 Biomechanical aspects of the insect wing: an analysis using the finite element method. *J. Exp. Biol.* **203**, 3125–3135.
- Newman, D. J. S. 1982 The functional wing morphology of some Odonata. PhD thesis, University of Exeter.
- Newman, D. J. S. & Wootton, R. J. 1986 An approach to the mechanics of pleating in dragonfly wings. *J. Exp. Biol.* **125**, 361–372.
- Smith, C. W., Herbert, R. C., Wootton, R. J. & Evans, K. E. 2000 The hind wing of the desert locust (*Schistocerca gregaria* Forskål). II. Mechanical properties and functioning of the membrane. *J. Exp. Biol.* **203**, 2933–2943.
- Watanabe, H. 1995 Structural analysis of dragonfly wings with FEM at the Kawachi Millibioflight Workshop, Tokyo.
- Willmott, A. P. & Ellington, C. P. 1997 The mechanics of flight in the hawkmoth *Manduca sexta*. I. Kinematics of hovering and forward flight. *J. Exp. Biol.* **200**, 2705–2722.
- Wootton, R. J. 1981 Support and deformability in insect wings. *J. Zool. Lond.* **193**, 447–468.
- Wootton, R. J. 1991 The functional morphology of the wings of dragonflies. *Adv. Odonatol.* **5**, 153–169.
- Wootton, R. J. 1992 Functional morphology of insect wings. *A. Rev. Entomol.* **37**, 113–140.
- Wootton, R. J. 1993 Leading edge section and asymmetric twisting in the wings of flying butterflies (Insecta, Papilionoidea). *J. Exp. Biol.* **180**, 105–119.
- Wootton, R. J. 1995 Geometry and mechanics of insect hind-wing fans: a modelling approach. *Proc. R. Soc. Lond. B* **262**, 181–187.
- Wootton, R. J. 1999 Invertebrate paraxial locomotory appendages: design, deformation and control. *J. Exp. Biol.* **202**, 3333–3345.
- Wootton, R. J. 2002 Design, function and evolution in the wings of holometabolous insects. *Zoologica Scripta* **31**, 31–40.
- Wootton, R. J. & Ennos, A. R. 1989 The implications of function on the origin and homologies of the dipterous wing. *Syst. Entomol.* **14**, 507–520.
- Wootton, R. J., Kukalova-Peck, J., Newman, D. J. S. & Muzon, J. 1998 Smart engineering in the mid-Carboniferous: how well could Palaeozoic dragonflies fly? *Science* **282**, 749–751.
- Wootton, R. J., Evans, K. E., Herbert, R. C. & Smith, C. W. 2000 The hind wing of the desert locust (*Schistocerca gregaria* Forskål). I. Functional morphology and mode of operation. *J. Exp. Biol.* **203**, 2921–2931.