

Flexible Wings and Fins: Bending by Inertial or Fluid-Dynamic Forces?¹

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SYNOPSIS. Flapping flight and swimming in many organisms is accompanied by significant bending of flexible wings and fins. The instantaneous shape of wings and fins has, in turn, a profound effect on the fluid dynamic forces they can generate, with non-monotonic relationships between the pattern of deformation waves passing along the wing and the thrust developed. Many of these deformations arise, in part, from the passive mechanics of oscillating a flexible air- or hydrofoil. At the same time, however, their instantaneous shape may well emerge from details of the fluid loading. This issue—the extent to which there is feedback between the instantaneous wing shape and the fluid dynamic loading—is core to understanding flight control. We ask to what extent surface shape of wings and fins is controlled by structural mechanics versus fluid dynamic loading. To address this issue, we use a combination of computational and analytic methods to explore how bending stresses arising from inertial-elastic mechanisms compare to those stresses that arise from fluid pressure forces. Our analyses suggest that for certain combinations of wing stiffness, wing motions, and fluid density, fluid pressure stresses play a relatively minor role in determining wing shape. Nearly all of these combinations correspond to wings moving in air. The exciting feature provided by this analysis is that, for high Reynolds number motions where linear potential flow equations provide reasonable estimates of lift and thrust, we can finally examine how wing structure affects flight performance. Armed with this approach, we then show how modest levels of passive elasticity can affect thrust for a given level of energy input in the form of an inertial oscillation of a compliant foil.

INTRODUCTION

Wings and fins deform, often dramatically, as they propel animals through air or water (see for example Wootton, 1992 for insects; Biewener and Dial, 1995 for birds; Swartz *et al.*, 1992 for bats, and Fish, 1999 for fish bodies). The functional consequences of such complex, three-dimensional patterns of deformation is a central issue underlying our understanding of wing and fin design for locomotion. Recent work has shown that the kinematics of wings and fins (*e.g.*, rotations and supinations, fin-body interactions) can have dramatic consequences to the fluid forces for flight and swimming (Sane and Dickinson, 2002; Ellington, 1995; Lauder, 2000). Associated with all of these dynamical processes are a host of enigmatic issues surrounding the inertial mechanisms that determine the instantaneous shape of wings and fins. The challenge we have faced over the years is how to approach this potential coupling between fluid dynamic loading and wing shape.

In engineering circles, this coupled problem gave rise to an entire field of “Aeroelasticity” in which practitioners of this rarefied discipline examine how wing bending and flutter arise from an interaction between aerodynamic loads and elastic-inertial events (*e.g.*, Bisplinghoff and Ashley, 1975). The crux of the issue is that we logically presume wing shape to be determined by a combination of the fluid dynamic pressure forces associated with flapping and the inertial-elastic processes that yield bending, even in the

absence of surrounding fluid. Unfortunately, the instantaneous curvature itself is likely to play a critical role in determining the spatial distribution of pressure stresses and, therefore, bending moments derived from fluid forces. Thus coupling between fluid and solid loads is a pervasive and often unresolved issue (Fig. 1).

For flapping wings, there is, however, a possible inroad to this dilemma that has not been formally considered. If, for example, the inertial-elastic moments derived from the forces of flapping motions are far greater than those derived from fluid forces, the phenomenon is no longer coupled in a practical sense. Thus one could, in theory, predict the instantaneous shape of a wing or fin from a combination of its mechanical properties as well as the dynamics of the end motions to which it is subject. From this predicted shape one could then compute the fluid dynamic pressure forces and, in turn, the thrust or lift generated by the wing. This then provides a significant inroad to how we can examine the functional consequences of the shape and mechanical properties of wings and fins.

A SIMPLE SCALE ARGUMENT FOR FLAPPING WINGS AND FINS

Just how large is the inertial force required to oscillate a wing relative to the total lift that the wing must support? Interestingly, the few studies that have explored this issue seem to point to an overwhelmingly large contribution of wing inertia to the total forces that must be generated (Lehmann and Dickinson, 1997; Zanker and Gotz, 1990; Ennos, 1988; Ellington, 1984; Weis-Fogh, 1975). To understand this issue we develop a simple scale argument to see how the moments needed to oscillate a wing or fin compare to

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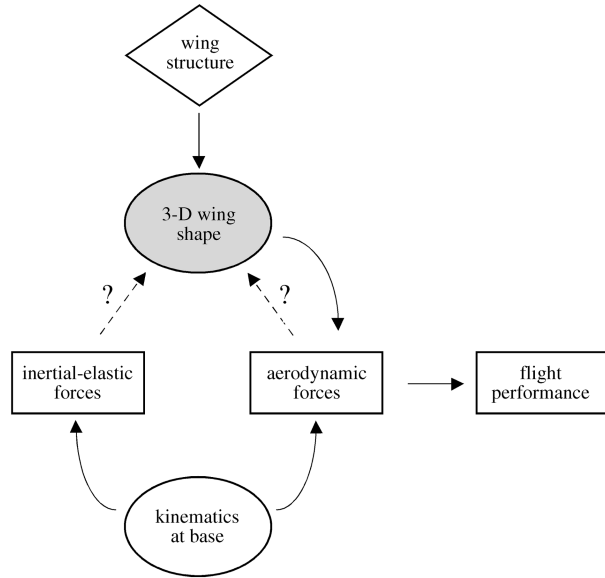


FIG. 1. The factors that affect wing shape are outlined here. Wing structure (material properties and geometry), combined with aerodynamic and inertial-elastic forces conspire to determine the three dimensional shape of a wing. How the wing is controlled at its base (the boundary conditions) is also a critical determinant of shape. The solid arrows indicate effects in which we can compute the influence of each factor. The broken arrows represent our uncertainty about the relative contributions of two key underlying factors.

those needed to sustain the weight of an animal or produce thrust. With wings and fins modeled as simple rectangular plates we can compute these moments rather easily.

Wings and aerodynamic forces

For a flying animal, the moment produced by a uniformly distributed pressure load that sustains the weight of an animal ($m_b g$) is:

$$M_{fluid} = m_b g L/4 \quad (1)$$

where m_b is the mass of the body; g , the earth's gravitational acceleration; and L , the length of the wing. The factor of 4 follows from the fact that two wings sustain the weight at their midpoint.

To oscillate a wing of density ρ_w requires a moment applied to the base of the wing. That moment drives the wing through a stroke amplitude Θ at a frequency ω . We assume the motion to be sinusoidal. We calculate that moment by integrating the tangential accelerational moment over the length (L) of the wing. Thus the elemental oscillatory moment at any station along the wing is:

$$\begin{aligned} dM_{oscil}(l, t) &= lA(l)dl\rho_w a(t) \\ &= l^2 A(l)dl\rho_w \Theta \omega^2 \sin(\omega t) \end{aligned} \quad (2)$$

where l is the position along the wing; $A(l)$, the local cross-sectional area; and $a(t)$, the local tangential acceleration. Taking the maximum position in the cycle ($\sin(\omega t) = 1$) and a constant cross-sectional area, we integrate this moment over the length of the wing to

find the total oscillatory moment applied to the wing base:

$$\begin{aligned} M_{oscil} &= \int l^2 A dl \rho_w \Theta \omega^2 = \rho_w \Theta \omega^2 A L^3 / 3 \\ &= m_w \Theta \omega^2 L^2 / 3 \end{aligned} \quad (3)$$

where m_w is the total mass of the wing. The ratio of the oscillatory moment to that sustaining the weight of the animal is therefore:

$$R_w = (m_w / m_b) 4 \Theta \omega^2 L / 3g. \quad (4)$$

When this ratio is greater than 1, oscillations of the mass of the wing dominate the total moments required for flight; far less than 1, aerodynamic pressure forces dominate the total moments. As an example, in the hawkmoth *Manduca sexta*, with a wing length of 5 cm, wings beating at a frequency of 25 hz ($\omega = 2\pi 25$) through a stroke amplitude of $\pi/2$ radians, and a wing to body mass ratio of 0.02, we predict a moment ratio of about 5, suggesting that inertial moments for wing oscillations are indeed quite large. *Drosophila*, despite a considerably smaller wing length, has a similar ratio owing to a vastly higher wing beat frequency. The square term for wing beat frequency becomes increasingly important as body (and wing) size declines.

One could derive a general scale argument that follows from the correlations among wing mass, wing length, wing beat frequency and body mass for a wide range of flying animals (insects, birds and bats, assuming size independent stroke amplitude; Greenewalt, 1962). This ratio, however, follows from a wide swath of scale arguments and cannot be applied with any confidence to a single taxonomic group. Within such groups the correlations reported by Greenewalt (1962) do not apply.

Fins and hydrodynamic forces

For neutrally buoyant, steadily swimming animals, propulsive surfaces such as caudal fins produce thrust to overcome average drag forces. Thus, rather than having the weight uniformly distributed over wings as in equation 1, we take the average drag distributed over a fin to compute the fluid dynamic moment:

$$M_{fluid} = \rho S_b C_{db} U_b^2 L/4 \quad (5)$$

where ρ is the density of the fluid; S_b , the projected area of the body; C_{db} its drag coefficient; U_b its forward speed, and L is the fin span.

As with the wings above, oscillating a fin with mass m_f requires a moment (M_f) that depends on its length, frequency and amplitude of motion:

$$M_f = m_f \Theta \omega^2 L^2 / 3 \quad (6)$$

Thus the ratio of the oscillatory moment to the fluid dynamic moment is:

$$R_f = 4 m_f \Theta \omega^2 L / (3 \rho S_b C_{db} U_b^2) \quad (7)$$

With a density of 1,000 kg/m³ for water, it would require extraordinarily large fins operating at very high

frequencies for that ratio to ever exceed 1. Thus, it appears that for swimmers, in contrast to flying animals, the moments required to overcome fluid forces are indeed the dominant factor underlying the mechanical determinants of instantaneous fin shape.

THE IMPORTANCE OF WING SHAPE AND KINEMATICS

Over the past several years, considerable attention has focused on how wing and fin kinematics and shape affect flight and swimming performance. In insects, for example, such kinematic parameters as wing rotations, instantaneous angles of attack, accelerations, and velocities are all key determinants of lift and thrust (Sane and Dickinson, 2002; Ellington, 1995).

Wing and fin shape also strongly affect the total forces that these appendages generate. In addition to morphological characters such as aspect ratio or the spanwise variation in chord length, the thickness and the cross-sectional geometry of a wing or fin are important in determining lift and thrust (Batchelor, 1967).

Instantaneous camber (chordwise bending) is yet another variable in fluid dynamic force production. In a sense, this is something of an amalgam of shape and kinematics in that temporal patterns of bending interact with intrinsic wing structure to determine instantaneous shape. Such bending induced by the motion of the appendage may significantly affect the amount of lift and thrust an animal may generate. For example, a very slight (2%) change in camber nearly doubles the lift and thrust that can be generated by a wing at low angles of attack (Batchelor, 1967).

Such bending is, importantly, not merely a static phenomenon. As wings and fins heave and pitch, their inertia and the pressure forces of the fluid around them conspire to produce waves of bending that propagate along the wing. These bending waves can greatly alter the fluid dynamic forces generated by wings and fins. The classic papers by Wu (1971) showed that such chordwise bending waves propagating along a wing (at high Reynolds numbers) are exceedingly effective ways to produce thrust and lift. These waves interact with wing planform shape to yield a host of possible thrust and lift behaviors (Combes and Daniel, 2001; Daniel, 1987) that keenly depend on both the overall shape of the wing as well as on its motions.

Given that wing and fin bending is an important determinant of locomotor forces, it seems reasonable to examine the morphological, mechanical and kinematic factors that determine the dynamics of these deformations. The scaling argument developed above doesn't really address these dynamic issues. In that case, we merely ask how large total wing inertia may be relative to the average upward force. To address dynamic issues of wing bending, we expand on the simple argument developed above. As with that scaling argument, our goal here is to compare the relative contributions of the fluid dynamic pressure stresses with the bending stresses derived from the geometry and structure of wings and the kinematics of wing motions. Since our intuition, in this regard, is not partic-

ularly useful, we resort to a combination of analytic and computational approaches.

MOTIONS OF AN ELASTIC WING

To explore the relative contributions of inertial-elastic processes and fluid pressure stresses to wing bending, we adopt a two-pronged approach. First, we imbue a simple rectangular wing with a material stiffness (Young's modulus) E , thickness t , width w , and length L . This wing moves up and down at its leading edge with a frequency ω and an amplitude a . This combination of motion, geometry, and mechanical properties gives rise to waves of bending that propagate in the length direction (chordwise) of the wing. If no appreciable fluid forces act upon this wing then its motion is described by the classic fourth order beam equation:

$$\frac{\partial^4 y}{\partial x^4} = -\frac{\rho_w A}{EI} \frac{\partial^2 y}{\partial t^2} \quad (8)$$

where y is the vertical position of the wing; x , the position along the wing; E , the Young's modulus of the wing; I , the wing's second moment of area; ρ_w , the wing's density; A , the wing's cross-sectional area; and t , time. With the boundary conditions that the trailing edge is free and the leading edge is controlled by a pure heaving motion, and initial conditions that the wing starts at rest, a solution to this equation can be found by the method of displacement influence functions (Timoshenko *et al.*, 1974). For our particular problem, the boundary conditions are (1) the wing is heaved in an oscillatory manner at the leading edge, (2) there is no bending moment at the trailing edge, and (3) there is no shear at the trailing edge. At the start of the problem, the wing is not moving. With these initial and boundary conditions, the solution to $y(x, t)$ is

$$y(x, t) = g(t) - \sum_{i=1}^{\infty} \frac{X_i}{p_i} \int_0^L X_i dx \times \int_0^t \frac{d^2 g(t')}{dt'^2} \sin p_i(t - t') dt' \quad (9)$$

$$p_i = \left(\frac{k_i}{L}\right)^2 \sqrt{\frac{EI}{\rho A}} \quad (10)$$

$$g(t) = a \sin(\omega t) \quad (11)$$

$$X_i = \cosh(k_i x) \cos(k_i x) - A_i [\sinh(B_i x L) - \sin(B_i x L)] \quad (12)$$

$$B_i = \frac{1}{(1 - (\omega/p_i)^2)} \quad (13)$$

$$A_i = \frac{\cosh(k_i) + \cos(k_i)}{\sinh(k_i) + \sin(k_i)} \quad (14)$$

and the values of k_i are calculated from the transcendental frequency equations for our boundary conditions (Timoshenko *et al.*, 1974). In practice, the first

5 terms of the series yield sufficient convergence for the results below.

BENDING MOMENTS IMPOSED BY ELASTIC WAVES OR FLUID PRESSURE: WHICH ARE GREATER?

The elastic bending waves described above generate fluid dynamic pressures that yield lift and thrust. For the high Reynolds numbers commonly associated with insects, birds, and fish, these propulsive forces are generally well described by inviscid flow theory (e.g., Wu, 1971; Lighthill, 1975).

The key issue here is that, with prescribed motions $y(x,t)$, and known geometry and material properties, we can compute not only the bending waves but also the moments required to produce those waves. Moreover, these motions can be inserted into a fairly simple fluid dynamic model of propulsion to assess the potential contributions of fluid dynamic processes. Thus we can compute the moments due to fluid dynamic pressure stresses and ask how large they are relative to the bending moments that arise from the elastic wave propagation. In doing so we compute two key terms: an average elastic bending moment and an average fluid dynamic moment. The former follows directly from the solution to $y(x,t)$. Since the motions are periodic and we are interested in a measure of the bending energy, we take average root-mean-square moment over the length of the wing and the period of the flap (T):

$$\bar{M}_{elastic} = \frac{EI}{TL} \int_0^T \int_0^L \frac{\partial^2 y(x,t)}{\partial x^2} dx dt \quad (15)$$

For wing motions that follow some periodic wave function, Wu (1971) provides a straightforward way to calculate the moment generated by the pressure distribution over the wing:

$$\begin{aligned} M_{fluid} &= \int_{-1}^1 \Delta p x dx \\ &= \frac{\pi}{2} \rho \left\{ U[\alpha(\tau) + b_2(t)] + \frac{1}{4} \frac{d}{dt} [b_1(t) - b_3(t)] \right\} \end{aligned} \quad (16)$$

$$\alpha(t) = b_1 - (b_o + b_1)\Theta(\sigma) \quad (17)$$

$$b_n(t) = \frac{2}{\pi} \int_0^\pi V(x,t) \cos n\theta d\theta \quad (18)$$

$$V(x,t) = \frac{\partial y}{\partial t} + U \frac{\partial y}{\partial x} \quad (19)$$

$$\Theta(\sigma) = \frac{K_1(i\sigma)}{K_0(i\sigma) - K_1(i\sigma)} \quad (20)$$

$$\sigma = \frac{\omega L}{U} \quad (21)$$

where the coefficients b_1 , b_2 , b_3 and a follow from the elastic bending motions we derived for the oscillating wing. The average fluid dynamic moment is:

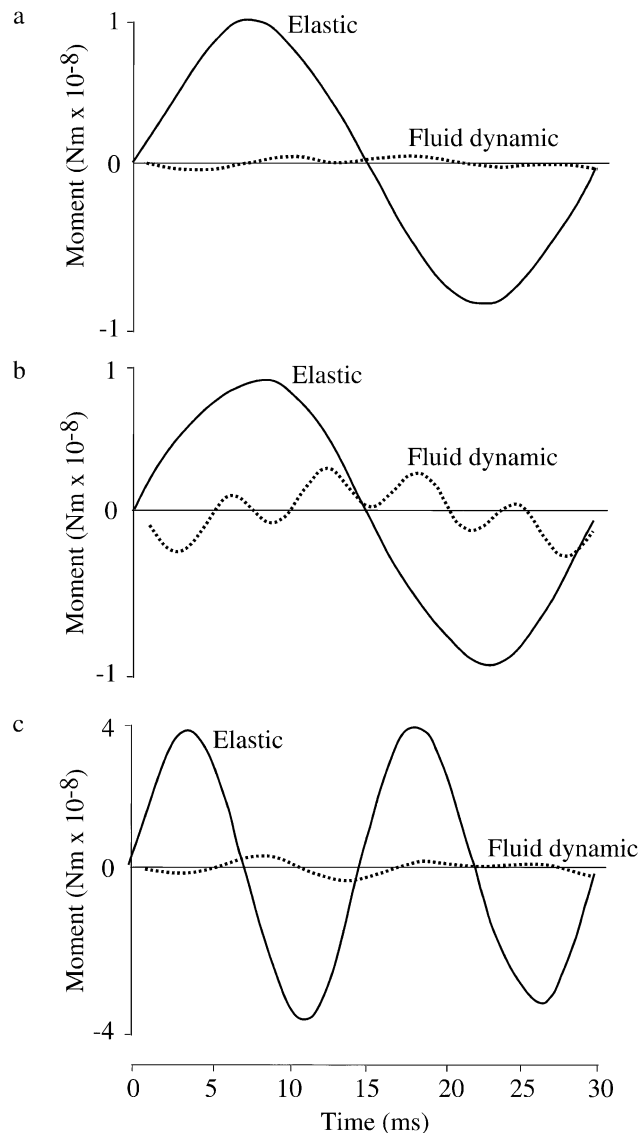


FIG. 2. The moments contributed by inertial-elastic forces and fluid dynamic stresses are plotted against time for a beating *Manduca sexta* wing (2 cm chord length, $EI = 6 \times 10^{-6}$ Pa m⁴). (a) At a wing beat frequency of 30 Hz, inertial-elastic effects dominate. (b) Increasing the chord length to 3 cm reduces the relative importance of inertial-elastic forces, though they still dominate. (c) Increasing the frequency to 60 Hz also slightly reduces the relative importance of inertial-elastic forces though, again, they still dominate.

$$\bar{M}_{fluid} = \frac{1}{TL} \int_0^T \int_0^L M_{fluid} dx dt \quad (22)$$

Armed with these moment estimates, we can determine the extent to which local bending is determined by the inertial-elastic stresses or by fluid stresses. Simple inspection of the above equations does not provide much insight, so we used Mathematica to compute and compare fluid dynamic and inertial-elastic moments.

SIMULATION RESULTS

The flexural stiffness of insect wings varies quite strongly with wing size and even within an individual

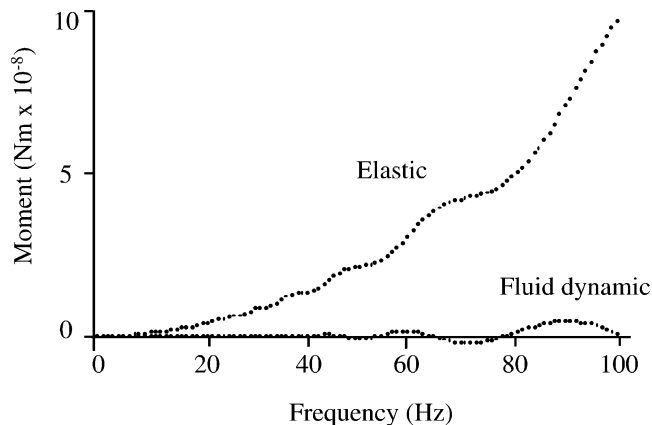


FIG. 3. The moments contributed by inertial-elastic forces and fluid dynamic stresses are plotted against frequency for beating *Manduca sexta* wings (2 cm chord length, $EI = 6 \times 10^{-6} \text{ Pa m}^4$). At frequencies above 10 Hz, the contribution of fluid dynamic forces is negligible.

wing itself (Combes, 2002). For the purposes of simulation, we focused initially on wings of the hawkmoth *Manduca sexta*. Their wings have a chord length of about 2 cm at the midspan and an average chordwise flexural stiffness (EI) at this position of about $6 \times 10^{-6} \text{ Pa m}^4$ (Combes, 2002). Oscillating these wings at 25 Hz yields inertial-elastic moments that are far greater (about 10 fold) than the fluid dynamic moments (Fig. 2a). Increasing either the chord length or the flapping frequency reduces the relative importance of inertial-elastic moments, but these moments are still far greater than those generated by fluid dynamic pressure stresses (Fig. 2b, c).

The average bending moments for either fluid or inertial-elastic processes increases nonlinearly and non-monotonically with oscillation frequency (Fig. 3). In the range of frequencies that correspond to those of *Manduca* (20–30 Hz) the ratio of moments is always greater than 5, indicating that wing bending is, for all practical purposes, independent of the fluid dynamic loads.

THE INITIAL PROOF

The simulations above suggest that aerodynamic loads are relatively unimportant in determining bending patterns in oscillating wings. Thus a wing oscillated in a vacuum would bend, to a large extent, as one oscillated in air. Indeed, Combes (2002) tested this idea by oscillating *Manduca* wings at 25 Hz in a chamber that could be filled with either normal air (density 1 kg/m^3) or helium (density 0.15 kg/m^3). If aerodynamic bending motions are important, oscillating wings in helium, a fluid whose density is 85% that of air would lead to dramatically different patterns of bending. Using high-speed videography, Combes (2002) found that the overall wing motions and bending patterns are quite similar, despite this 85% reduction in fluid density, suggesting that the contribution of aerodynamic forces are relatively small compared

to the contribution of inertial-elastic processes. Since a figure of such motions is rather difficult to reproduce, we have posted the movies of wings oscillating in the two different fluid media at <http://faculty.washington.edu/danielt/movies>.

CONCLUSIONS

This study provides something of a “good news/bad news” message. For studies of animal flight, we suggest that the somewhat intractable problem of fluid-solid coupling in wing design does not need to be addressed. Rather, one can use either simplified linear beam theory (as above) or more accurate computational models (e.g., finite element models of Combes, 2002) of wing mechanical design to compute the instantaneous spatial patterns of wing bending. These predicted motions can, in turn, be inserted into analytic models of the fluid dynamic forces (as above) or more complex computational models (such as those of Liu in this volume). Our “bad news” is that the very high density of water requires a solution to a full set of equations coupling fluid and solid dynamics to understand the functional consequences of fin mechanical design. However, as we learn more about exceedingly stiff passive fins (flukes) or the role of active musculature in fins this may prove to be less problematic.

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REFERENCES

- Batchelor, G. K. 1967. *An introduction to fluid dynamics*. Cambridge University Press, Cambridge.
- Biewener, A. A. and K. P. Dial. 1995. In vivo strain in the humerus of pigeons (Columbia livia). *J. Morphology* 225:61–75.
- Bisplinghoff, R. L. and H. Ashley. 1975. *Principles of aeroelasticity*. Dover Press, New York.
- Combes, S. A. 2002. Wing flexibility and design for animal flight. Ph.D. Diss., University of Washington.
- Combes, S. A. and T. L. Daniel. 2001. Shape, flapping and flexion: Wing and fin design for forward flight. *J. Exp. Biol.* 204:2073–2085.
- Daniel, T. L. 1987. Forward flapping flight from flexible fins. *Can. J. Zool.* 66:630–638.
- Dickinson, M. H., F. O. Lehmann, and S. P. Sane. 1999. Wing rotation and the aerodynamic basis of insect flight. *Science* 184: 1954–1960.
- Ellington, 1984. The aerodynamics of hovering insect flight. Part VI: Lift and power requirements. *Phil. Trans. R. Soc. London B* 305:145–181.
- Ellington, C. P. 1995. Unsteady aerodynamics of insect flight. In C. P. Ellington and T. J. Pedley (eds.), *Biological fluid dynamics* pp. 109–129. The Company of Biologists, Cambridge, U.K.
- Ennos, A. R. 1988. The importance of torsion in the design of insect wings. *J. Exp. Biol.* 140:137–160.
- Fish, F. E. 1999. Performance constraints on the maneuverability of flexible and rigid biological systems. In *Eleventh International Symposium on unmanned untethered submersible technology*, pp. 394–406. Autonomous Undersea Systems Institute, Durham, N. H.

- Greenewalt, 1962. Dimensional relationships for flying animals. *Smithsonian Misc. Coll.* 144(2):1–46.
- Lauder, G. V. 2000. The function of the caudal fin during locomotion of fishes: Kinematics, flow visualization, and evolutionary patterns. *Amer. Zool.* 40:101–122.
- Lehmann, F. O. and M. H. Dickinson. 1997. The changes in power requirements and muscle efficiency during elevated force production in the fruit fly *Drosophila melanogaster*. *J. Exp. Biol.* 200:1133–1143.
- Lighthill, M. J. 1975. *Mathematical biofluidynamics*. Society for Industrial and Applied Mathematics, Philadelphia.
- Sane, S. P. and M. H. Dickinson. 2002. The aerodynamic effects of wing rotation and a revised quasi-steady model of flapping flight. *J. Exp. Biol.* 205:1087–1096.
- Swartz, S. M., M. B. Bennett, and D. R. Carrier. 1992. Wing bone stresses in free flying bats and the evolution of skeletal design for flight. *Nature* 359:726–729.
- Timoshenko, S., D. H. Young, and W. J. Weaver. 1974. *Vibration problems in engineering*. John Wiley & Sons, New York.
- Weis-Fogh, 1975. Flapping flight and power in birds and insects, conventional and novel mechanisms. In T. Y. Wu, C. J. Brokaw, and C. J. Brennan (eds.), *Swimming and flying in nature* pp. 729–762. Plenum Press, New York.
- Wootton, R. J. 1992. Functional morphology of insect wings. *Ann. Rev. Entomology.* 37:113–140.
- Wu, T. Y. 1971. Hydrodynamics of swimming propulsion. Part 1: Swimming of a two dimensional flexible plate at variable forward speeds in an inviscid fluid. *J. Fluid Mech.* 46:337–355.
- Zanker, J. M. and K. G. Gotz. 1990. The wing beat of *Drosophila melanogaster* II: Dynamics. *Phil. Trans. Roy. Soc. London B* 327:19–44.