



## **Animal Flight Dynamics II. Longitudinal Stability in Flapping Flight**

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Stability is essential to flying and is usually assumed to be especially problematic in flapping flight. If so, problems of stability may have presented a particular hurdle to the evolution of flapping flight. In spite of this, the stability of flapping flight has never been properly analysed. Here we use quasi-static and blade element approaches to analyse the stability provided by a flapping wing. By using reduced order approximations to the natural modes of motion, we show that wingbeat frequencies are generally high enough compared to the natural frequencies of motion for a quasi-static approach to be valid as a first approximation. Contrary to expectations, we find that there is nothing inherently destabilizing about flapping: beating the wings faster simply amplifies any existing stability or instability, and flapping can even enhance stability compared to gliding at the same airspeed. This suggests that aerodynamic stability may not have been a particular hurdle in the evolution of flapping flight. Hovering animals, like hovering helicopters, are predicted to possess neutral static stability. Flapping animals, like fixed wing aircraft, are predicted to be stable in forward flight if the mean flight force acts above and/or behind the centre of gravity. In this case, the downstroke will always be stabilizing. The stabilizing contribution may be diminished by an active upstroke with a low advance ratio and more horizontal stroke plane; other forms of the upstroke may make a small positive contribution to stability. An active upstroke could, therefore, be used to lower stability and enhance manoeuvrability. Translatory mechanisms of unsteady lift production are predicted to amplify the stability predicted by a quasi-static analysis. Non-translatory mechanisms will make little or no contribution to stability. This may be one reason why flies, and other animals which rely upon non-translatory aerodynamic mechanisms, often appear inherently unstable.

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### **1. Introduction**

In order to fly straight or to turn steadily, flying animals need to maintain functional stability about all axes (Fig. 1). This could derive solely from inherent structural or morphological features (as in a paper aeroplane), solely from active control (as in the experimental X-29 aircraft), or from a combination of the two (as in many modern fighters and some commercial aircraft). Since

inherent stability opposes accidental disturbances and deliberate turning manoeuvres alike, there is an inevitable trade-off between stability and manoeuvrability, which has a number of interesting evolutionary consequences (Maynard Smith, 1952; Thomas & Taylor, in press). For example, there is some evidence (see Thomas & Taylor, in press for review) that early fliers such as *Archaeopteryx*, the first known bird, possessed a high degree of inherent stability to compensate for their primitive flight control systems' putative inability to maintain stability actively. We would therefore predict that inherent

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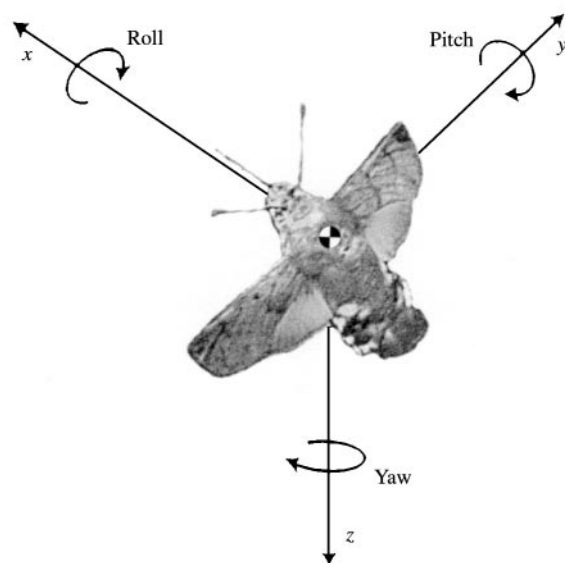


FIG. 1. Under the quasi-static approximation, we may treat a flying animal as a rigid body with six degrees of freedom: the animal is free to rotate about, or translate along, each of three orthogonal axes originating at the centre of gravity (part-filled circle). Translations and rotations are all positive in the direction shown.

stability should decrease through evolutionary time under selection for enhanced manoeuvrability (Maynard Smith, 1952; Lighthill, 1974), at a pace presumably limited by the rate of evolution of the flight control system.

Whereas the inherent stability of gliding animals is likely to resemble that of fixed wing aircraft (Thomas & Taylor, *in press*), this is not so for the inherent stability of flapping animals. The stability of flapping flight has never been rigorously analysed and cannot be assumed similar to that of helicopters, which, although closer to flapping animals than fixed wing aircraft in some respects, have many peculiar instabilities associated with the lateral asymmetry of the advancing and retreating rotor blades. Such asymmetries are absent in the reciprocating motion of flapping animal wings during straight, forward flight. Any difference in inherent stability between flapping and gliding flight is clearly of biological significance, not least because many scenarios for the evolution of flapping flight in insects (Hinton, 1963; Wigglesworth, 1963, 1973, 1976; Flower, 1964; Wootton, 1976) and vertebrates (see Norberg, 1990 for review) involve an intermediate gliding stage.

A flapping animal may be said to be inherently stable if the forces acting on it tend to restore it to equilibrium without any modification of the flapping cycle (Maynard Smith, 1952). For example, for an animal to be inherently stable in pitch (Fig. 1), a disturbance from equilibrium must passively induce an opposing pitching moment, so the inequality

$$\frac{\partial M}{\partial \alpha_b} < 0 \quad (1)$$

must be true at equilibrium, where  $M$  is the total pitching moment about the centre of gravity and  $\alpha_b$  is the overall angle of attack, defined as the angle between the longitudinal body axis and the oncoming flow vector.

The kind of stability expressed by eqn (1), referring only to the direction of the initial response, is termed static stability. Static stability is necessary for dynamic stability, which refers to the damping of a disturbance over time. However, a statically stable system could overcompensate for a disturbance, leading to oscillations that could be either damped or divergent (Fig. 2), so static stability alone is insufficient to guarantee dynamic stability. This kind of dynamic instability can only arise in more complex systems governed by second-order (or higher) differential equations, such as that governing the motion of a flying body. If the uncoupled (first order) motions are all statically stable then any dynamic instability must result from coupling (second order or higher) between the various degrees of freedom.

## 2. The Quasi-static Approximation

Strictly speaking, a static analysis of stability cannot be applied where flapping or deformation of the flight surfaces occurs, because dynamic changes in the forces could couple with the animal's natural modes of motion. Such coupling is unlikely to occur if the frequency of flapping or aeroelastic flutter is sufficiently high compared to the animal's natural frequencies of motion. The dynamically changing forces will then exhibit no resonance with the animal's gross motion and we may consider them to be replaced by a quasi-static force like that on a rigid gliding body. This is the basis of the quasi-static approximation,

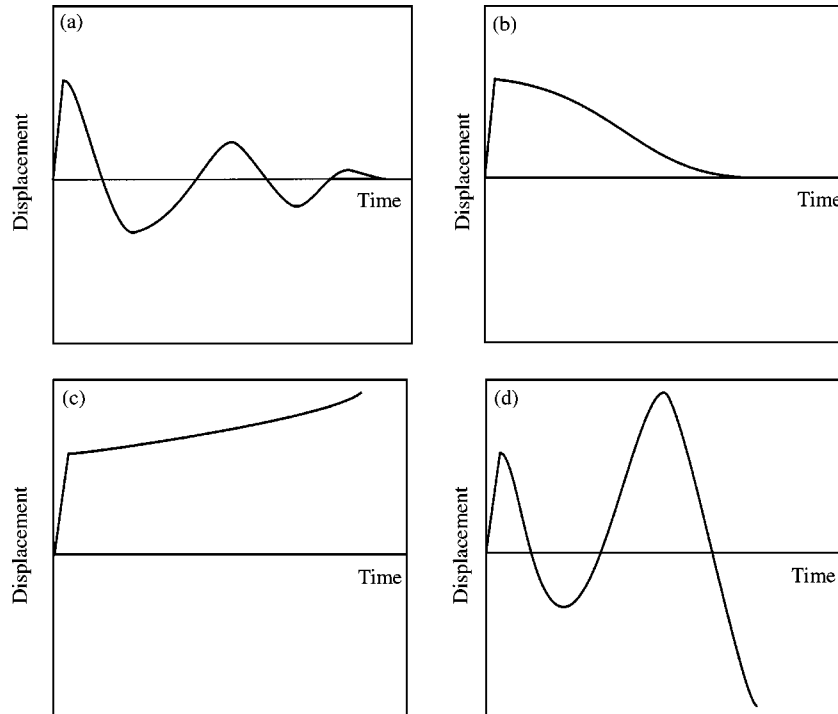


FIG. 2. Possible responses in a single degree of freedom of an arbitrary system following a disturbance: (a) damped oscillations (statically and dynamically stable); (b) monotonic damping (statically and dynamically stable); (c) monotonic divergence (statically and dynamically unstable); (d) divergent oscillations (statically stable but dynamically unstable).

first introduced by Hohenemser (1939) to simplify helicopter rotor dynamics, and now commonly used to make problems of stability and control analytically tractable in helicopters (Johnson, 1980; Padfield, 1996) and fixed wing aircraft with high aeroelasticity (Bryson, 1994).

In helicopters, quasi-static analyses yield essentially identical results to analyses incorporating the complete rotor dynamics when the rotor frequency is an order of magnitude higher than the frequency response being considered (Miller, 1948; Kaufman & Peress, 1956; Hohenemser & Yin, 1974). In general, the approximation works well if the lowest frequency of flapping or flutter is at least ten times the highest undamped frequency of interest (Bryson, 1994). Provided that this is the case, we may approximate the animal as a rigid flying body with six degrees of freedom: three in translation and three in rotation (Fig. 1). Bilateral symmetry ensures that motions parallel to the plane of symmetry are independent of any lateral motions (e.g. Etkin & Reid, 1996), which means that longitudinal motions may be con-

sidered separately from the lateral motions. This is an extremely useful simplification because it reduces the number of degrees of freedom that must be considered simultaneously from six to three (pitching about the  $y$ -axis and translation along the  $x$ - and  $z$ -axis) and reduces the number of dimensions from three to two.

### 3. Longitudinal Modes of Motion

#### 3.1. NATURAL FREQUENCIES OF MOTION

The aerodynamic literature provides good empirical confirmation of the general validity of the quasi-static approximation, but is a quasi-static analysis likely to be valid in the specific case of animal flight? Unsteady aerodynamic mechanisms are important in many flying animals (Weis-Fogh, 1973; Norberg, 1975; Cloupeau *et al.*, 1979; Ellington, 1984b,c; Ennos, 1989; Dudley & Ellington, 1990; Wilkin, 1990; Zanker & Götz, 1990; Wilkin & Williams, 1993) but present no special problems for analysis because

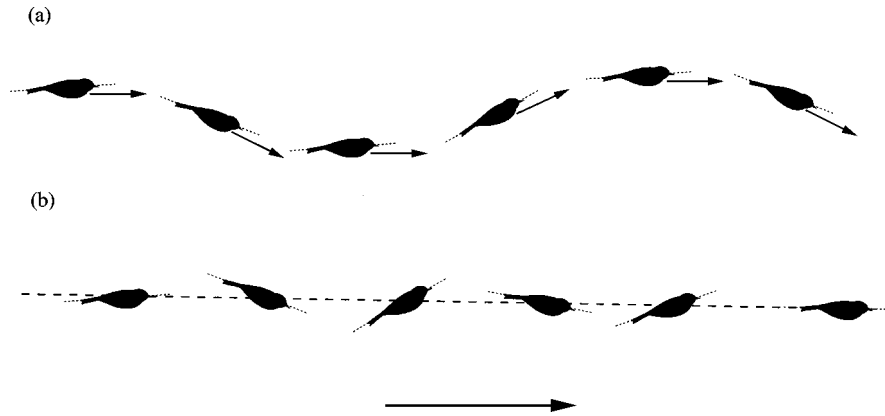


FIG. 3. Reduced order approximations for the two longitudinal modes of motion: (a) long period phugoid motion in which the total energy and the angle between the velocity vector (arrow) and the x-axis (dotted line) are assumed to remain constant; (b) short period pitching motion in which the velocity is assumed to remain constant.

their frequency is either the same or higher than that of the wingbeat. The validity of the approach therefore depends critically upon how an animal's natural frequencies of motion compare to its wingbeat frequency.

Most aircraft display two basic longitudinal modes that are excited whenever the aircraft is disturbed from longitudinal equilibrium (e.g. Cook, 1997). One mode—the phugoid—is lightly damped in conventional aircraft and consists of a slow rise and fall representing an interchange between kinetic and potential energy, during which the angle of incidence remains approximately constant. The other mode is heavily damped in conventional aircraft and of much shorter period, consisting mainly of fast pitch oscillations. Reduced order approximations are available for both modes (e.g. Nelson, 1989; Etkin & Reid, 1996; Cook, 1997). Since we are interested only in gaining general insight into the motions and in getting some idea of their frequency response in animals, we will apply the approximations here in their most reduced forms.

The phugoid is classically assumed to be a motion of constant total energy (Lanchester, 1908) in which the angle between the velocity vector and the x-axis remains constant [Fig. 3(a)]. Lanchester's approximation yields the expression

$$T_p = \pi\sqrt{2} \frac{U_0}{g} \quad (2)$$

for the period of the phugoid, where  $g$  is the acceleration due to gravity and  $U_0$  the speed of forward motion at the top and bottom of the oscillation (Etkin & Reid, 1996). For a typical light aircraft (the NA-154 Navion) for which  $U_0 = 54 \text{ m s}^{-1}$ , this gives an approximate period of 24 s, which is reasonably close to the exact period of 29 s (Nelson, 1989).

The short period mode is usually approximated by assuming that the forward velocity is constant (Nelson, 1989), but the expression this yields is still too involved for our purposes. If we further assume that vertical motion is zero then the mode becomes equivalent to a constrained pitching motion [Fig. 3(b)], as if the animal were tethered in a wind tunnel and free to pivot about only its transverse axis. The period of such a motion is given by

$$T_{sp} = \frac{2\pi}{\sqrt{-M_\alpha}}, \quad (3)$$

(see Nelson, 1989), where

$$M_\alpha = \frac{\partial M}{\partial \alpha_b} \bigg/ I_y, \quad (4)$$

in which  $I_y$  is the moment of inertia about the y-axis. For the NA-154 Navion, this gives an approximate period of 2.1 s, which is reasonably close to the exact period of 2.5 s (Nelson, 1989). In

this example, both the long and short period approximations underestimate the true period by less than 20%.

It is clear from eqn (2) that the phugoid period is roughly proportional to flight speed and is therefore strongly scale-dependent. Its natural frequency (in Hz) is simply  $1/T_p$ , which for a Desert Locust *Schistocerca gregaria* flying at its preferred speed of  $3.5 \text{ m s}^{-1}$  (Weis-Fogh, 1956a) is approximately 0.63 Hz. This is  $< 1/30$ th its 20 Hz wingbeat frequency (Jensen, 1956; Cloupeau *et al.*, 1979; Wilkin, 1990), so we would expect a locust to flap its wings 30 times during a single phugoid oscillation. It is reasonably clear-cut that the phugoid should be independent of the flapping cycle under these conditions. For a fast-flying bird like the Common Guillemot *Uria aalge*, flying at  $19.1 \text{ m s}^{-1}$  (Pennycuik, 1990), the phugoid frequency is 0.12 Hz, which is  $< 1/70$ th its flapping frequency of 8.7 Hz. For a slow-flying bird like the Little Blue Heron *Egretta caerulea*, flying at  $8.8 \text{ m s}^{-1}$  (Pennycuik, 1990), the phugoid frequency is approximately 0.25 Hz, which is still an order of magnitude lower than its flapping frequency of 3.6 Hz. The phugoid should therefore be independent of the flapping cycle in most flying animals.

The period of the short period mode is inversely related to  $M_z$ , which is normalized by dividing through by the moment of inertia. The frequency of the short period mode is therefore a direct function of the static pitching stability of the system, and typically falls within the range 0.15–1.5 Hz in conventional aircraft (Cook, 1997). Since flapping animals are expected to be less stable than conventional aircraft (Maynard Smith, 1952; Weis-Fogh, 1956b; Brown, 1963; Wilson, 1968), the frequency of their short period mode is likely to lie within or below this range. Flapping should therefore occur at a high enough frequency not to excite the short period mode, except perhaps in butterflies and slow-flying birds such as herons (Ardeidae), which show periodic pitching oscillations when flapping. The phugoid frequency may also be rather similar to the frequency of the short period mode in flying animals, so the two modes may be coupled. Coupling of the modes is considered undesirable in aircraft since it confers unusual handling qualities (Cook, 1997), although it is possible that bounding or

undulating flight patterns might arise as dynamic instabilities resulting from coupling of the short period and phugoid modes. However, this does not affect the validity of the quasi-static approach, which should still offer a good first approximation to longitudinal stability in flapping flight.

### 3.2. CRITERIA FOR LONGITUDINAL DYNAMIC STABILITY

For an animal to be dynamically stable, it is essential that it be statically stable with respect to changes in both attitude and velocity. Since the static speed stability of flapping flight is reasonably well known, we will begin by briefly considering the effects of speed perturbations. Viscous drag forces and pressure drag forces increase monotonically with increasing flight speed. The increase in flapping power required to overcome these increasing drag contributions would therefore tend to oppose speed perturbations across the whole range of flight speeds, were it not for the accompanying decrease in the induced power required to accelerate air into the wake during flapping flight. The resulting U- or J-shaped curves of total required power against flight speed are well known for aircraft (e.g. Vinh, 1993) and have also been found for flying vertebrates (see Norberg, 1990; Ellington 1991 for reviews).

A generalized vertebrate power curve is shown in Fig. 4, from which it can be seen that across a certain range of power outputs, there exist two equilibrium flight speeds for any given power. Disturbances from equilibrium will only be opposed if the slope of the curve is positive (i.e. if the required power increases with increasing flight speed), so whereas the higher of each pair of equilibrium speeds is stable, the lower of the pair is unstable. Essentially the same relation applies during gliding flight, where decreasing induced drag (representing the cost of generating the trailing wingtip vortices) substitutes for decreasing induced power (Lighthill, 1974).

Empirical demonstrations of the classical U- or J-shaped power curve are lacking in insects (Wakeling & Ellington, 1997; Dickinson *et al.*, 1998), and there is some evidence to suggest that the classical form of the power curve may not

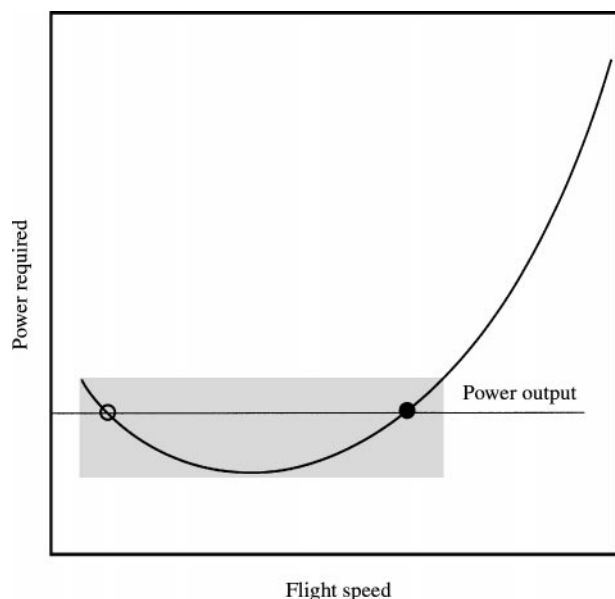


FIG. 4. Generalized curve of power required against flight speed for a flying vertebrate. Note that there are two equilibrium speeds for a given power output across the shaded range of power outputs. The lower equilibrium speed (open circle) is unstable. The higher equilibrium speed (filled circle) is stable.

apply even in birds (Thomas, 1996b; Thomas & Hedenstöm, 1998). For example, in insects, overall power requirements calculated for *Bombus terrestris* exhibit very shallow minima, with overall power requirements nearly independent of flight speed (Dudley & Ellington, 1990). If this situation is representative of insects in general, then flying insects may possess approximately neutral speed stability.

The question of whether flapping animals are statically stable in pitch appears never to have been analysed properly. We will defer answering this question until the next section, and ask instead whether even an animal that is statically stable with respect to both speed and pitch would necessarily possess full dynamic longitudinal stability in flapping flight. We noted in Section 1 that if a system is statically stable with respect to each of its degrees of freedom then dynamic instability can only arise as a result of coupling between its different degrees of freedom. In fixed wing aircraft, all of the aerodynamic forces and moments are proportional to the dynamic pressure. In this case, speed has an effect upon pitch

that is proportional to the equilibrium value of the pitching moment—i.e. zero (Padfield, 1996). Hence, static stability with respect to speed and pitch is usually sufficient to ensure longitudinal dynamic stability in fixed wing aircraft. This is not the case in helicopters, in which an increase in forward velocity increases lift on the advancing blade and decreases lift on the retreating blade, causing the rotor tip path to “flap” backwards and generate a positive pitching moment. The result of this flapping mode is a coupling of longitudinal velocity and pitch, leading to mildly unstable longitudinal dynamics.

An analogous aeroelastic effect could operate in flapping animals with wings susceptible to bending about a chordwise axis, either at the basal articulation or across the span. In this case, the increased forward velocity would increase lift on the wings during the downstroke but decrease lift during the upstroke. This will tend to lift the wingtip through the course of the downstroke and push it down through the downstroke, with the result that the wingtip path should tilt backwards with an increase in forward velocity. Static pitch stability may therefore be insufficient to ensure full dynamic stability in flapping animals with wings having a high degree of aeroelasticity. This kind of instability is less likely to arise in flapping animals like birds with wings that are relatively more rigid. With these caveats in mind we will now consider the static pitch stability provided by a flapping wing.

#### 4. A Blade Element Model of Static Pitching Stability

##### 4.1. ASSUMPTIONS

Although a quasi-static analysis is appropriate when considering the animal's gross motion, we must consider how the instantaneous forces vary with disturbances before averaging across the flapping cycle. The blade element theory of propellers was developed to cope with some of the analytical problems posed by a moving wing whose speed, incidence and airfoil section may vary along its length (e.g. Glauert, 1947; Von Mises, 1959; Stepniewski & Keys, 1984). Blade element theory has frequently been applied to

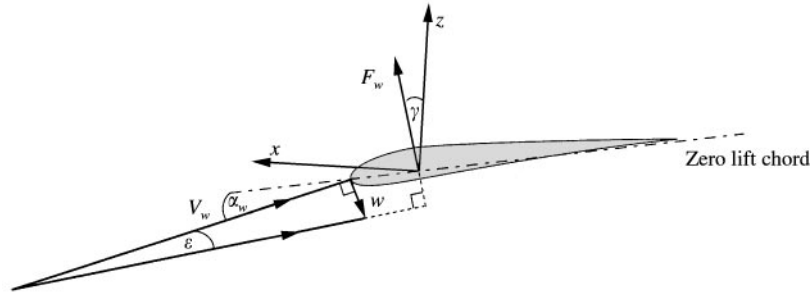


FIG. 5. Wing section showing the angles and other variables used in the blade element model ( $r$  and  $t$  subscripts omitted for clarity). Note that the section angle of attack,  $\alpha_w$ , is deemed positive when the flight force has a positive  $z$ -component.

animal flight to model quasi-steady force production (Norberg, 1990).

Consider a chordwise wing element of infinitesimal width  $R dr$  and chord  $c$  at spanwise station  $r$  from the root, where  $r$  is expressed as a proportion of the wing length  $R$ . The instantaneous aerodynamic forces on such an element may be represented as a force, (call this  $F_{w(r,t)}$ ), operating at a fixed point called the aerodynamic centre, together with a pitching moment (call this  $M_{ac(r,t)}$ ) about this point. Most flying animals have efficient positively cambered airfoil sections that would be expected to generate negative pitching moments about the aerodynamic centre under quasi-steady flow conditions (Hummel & Möllenstädt, 1977; Thomas & Taylor, in press). The bracketed subscripts denote that the force and moment are functions of time ( $t$ ) and spanwise station ( $r$ ). The element's contribution to the total pitching moment about the centre of gravity may be written as

$$M_{w(r,t)} = \cos \sigma_{(t)} [x_{w(r,t)}(F_{w(r,t)} \cos \gamma_{(r,t)}) + z_{w(r,t)}(F_{w(r,t)} \sin \gamma_{(r,t)}) + M_{ac(r,t)}], \quad (5)$$

where  $\sigma_{(t)}$  is the sweep angle between the wing's long axis and the  $y$ -axis in the plane containing the oncoming flow vector, where  $x_{w(r,t)}$  and  $z_{w(r,t)}$  are the distances of the local aerodynamic centre from the centre of gravity along the  $x$ - and  $z$ -axis in a coordinate system fixed with respect to the body, and where  $\gamma_{(r,t)}$  is the forward inclination of  $F_{w(r,t)}$  from the  $z$ -axis (Fig. 5). Differentiating eqn (5) with respect to

$\alpha_b$  gives

$$\frac{\partial M_{w(r,t)}}{\partial \alpha_b} = \cos \sigma_{(t)} \times \left[ x_{w(r,t)} \left( \cos \gamma_{(r,t)} \frac{\partial F_{w(r,t)}}{\partial \alpha_b} - F_{w(r,t)} \sin \gamma_{(r,t)} \frac{\partial \gamma_{(r,t)}}{\partial \alpha_b} \right) + z_{w(r,t)} \left( \sin \gamma_{(r,t)} \frac{\partial F_{w(r,t)}}{\partial \alpha_b} + F_{w(r,t)} \cos \gamma_{(r,t)} \frac{\partial \gamma_{(r,t)}}{\partial \alpha_b} \right) + \frac{\partial M_{ac(r,t)}}{\partial \alpha_b} \right]. \quad (6)$$

Readers who are familiar with the theory of static stability in aircraft will note that the derivative  $\partial M_{ac(r,t)} / \partial \alpha_b$  is usually dropped at this stage—the moment about the aerodynamic centre being normally independent of the wing's angle of attack (e.g. Nelson, 1989; Etkin & Reid, 1996; Cook, 1997). The reasons for retaining this derivative in eqn (6) will become clear in due course.

Our goal is to derive analytical expressions for

$$F_{w(r,t)}, \quad \frac{\partial F_{w(r,t)}}{\partial \alpha_b}, \quad \frac{\partial M_{ac(r,t)}}{\partial \alpha_b} \quad \text{and} \quad \frac{\partial \gamma_{(r,t)}}{\partial \alpha_b}$$

to allow us to rewrite eqn (6) in more useful terms, and thereby to compare the pitch stability provided by a flapping wing with that of a fixed wing. We will assume that every point on the wing sweeps a fixed path with respect to the body axes. This implies that the stroke path, airfoil

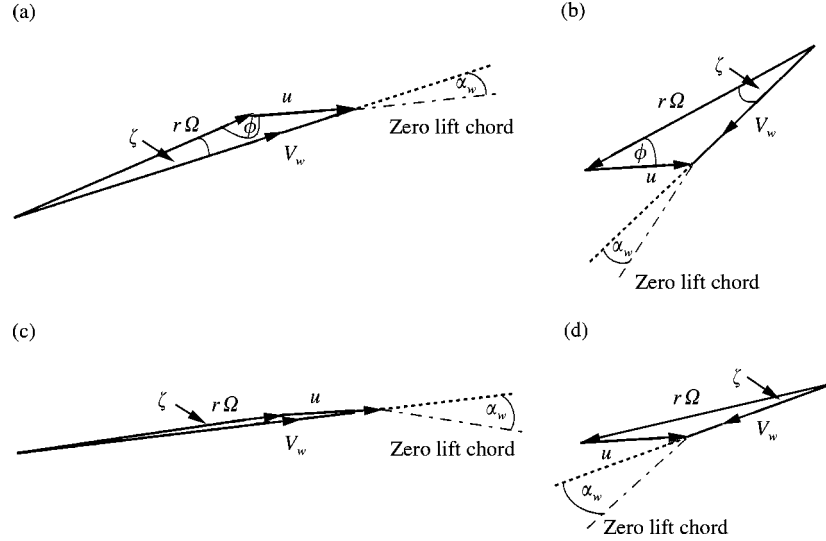


FIG. 6. Vector diagrams illustrating how the angular relations of the flow components change in response to pitching disturbances ( $r$  and  $t$  subscripts omitted for clarity). Note that the section angle of attack,  $\alpha_w$ , is deemed positive when the flight force has a positive  $z$ -component, as would be the case in all of these diagrams: (a) downstroke reference case; (b) upstroke reference case; (c) downstroke case following a nose-up disturbance; (d) upstroke case following a nose-up disturbance.

section and inclination of each blade element are always fixed with respect to the body axes. This assumption is more restrictive than merely assuming that active modification of the flapping cycle does not occur, because it additionally implies that the wings do not deform passively in response to disturbances. This is unlikely to be the case, and one possible consequence of wing deformation has already been discussed in Section 3.2 above. However, the resulting simplifications justify the use of this assumption in the absence of detailed knowledge of how the wings deform.

#### 4.2. EXPRESSIONS FOR THE LOCAL FLIGHT FORCE $F_{w(r,t)}$

The quasi-steady lift on an element is equal to the product of its area,  $c_{(r)} R dr$ , times the section lift coefficient,  $C_{l(r,t)}$ , times the local dynamic pressure, defined as  $Q_{(r,t)} = \frac{1}{2} \rho V_{w(r,t)}^2$ , where  $\rho$  is the air density and  $V_{w(r,t)}$  is the speed of relative flow over the element:

$$F_{w(r,t)} = Q_{(r,t)} C_{l(r,t)} c_{(r)} R dr. \quad (7)$$

Note that the section lift coefficient of a given blade element may vary through the course of the

stroke as the wing deforms, as indicated by the subscript  $t$ . The relative flow over an element results from a combination of the animal's forward motion and the wing's own translational velocity. The latter varies linearly with distance from the wing root, and may be written as  $rR\Omega_{(t)}$  if we neglect spanwise bending, where  $\Omega_{(t)}$  is the angular tip velocity in radian measure. The chordwise component of the flow due to the animal's forward velocity will also vary through the stroke as the sweep,  $\sigma_{(t)}$ , of the wing varies, and will be denoted  $u_{(t)}$ . We will neglect any spanwise component of flow, because the blade element approach is intrinsically two dimensional in the limit. By inspection of Fig. 5, the cosine rule gives the relative flow over an element as

$$V_{w(r,t)} = \sqrt{r^2 R^2 \Omega_{(t)}^2 + u_{(t)}^2 - 2rR\Omega_{(t)}u_{(t)} \cos \phi}, \quad (8)$$

that is, the scalar value of the vector sum of the two flow components, where  $\phi$  is the included angle. Note that the same relation applies on both the upstroke and the downstroke, since  $\phi$  always denotes the included angle between  $rR\Omega_{(t)}$  and  $u_{(t)}$ , as indicated in Fig. 6.



## 4.3. EXPRESSIONS FOR THE LOCAL FORCE DERIVATIVE

$$\partial F_{w(r,t)}/\partial \alpha_b$$

Differentiating eqn (7) with respect to  $\alpha_b$  yields

$$\frac{\partial F_{w(r,t)}}{\partial \alpha_b} = c_{(r)} R dr \left( Q_{(r,t)} \frac{\partial C_{l(r,t)}}{\partial \alpha_b} + C_{l(r,t)} \frac{\partial Q_{(r,t)}}{\partial \alpha_b} \right). \quad (9)$$

The inclusion of the dynamic pressure derivative,  $\partial Q_{(r,t)}/\partial \alpha_b$ , may seem surprising, since the dynamic pressure of a fixed wing depends only upon the speed of forward motion and is independent of the overall angle of attack. This is not the case for a flapping wing, because the velocity of the relative flow is a function of  $\phi$  [eqn (8)] which in turn is a function of  $\alpha_b$  (Fig. 5). The fact that  $\partial Q_{(r,t)}/\partial \alpha_b$  is non-zero on a flapping wing is also the reason that the derivative  $\partial M_{ac(r,t)}/\partial \alpha_b$  does not drop immediately from eqn (6).

Since the direction of the wing's flapping velocity is fixed with respect to the body axes,  $\phi$  increases directly with  $\alpha_b$  during pitch disturbances, so we may write  $\partial \phi / \partial \alpha_b = 1$ . Making use of eqn (8) to differentiate  $Q_{(r,t)} = \frac{1}{2} \rho V_{w(r,t)}^2$  by substitution, we then have

$$\frac{\partial Q_{(r,t)}}{\partial \alpha_b} = \rho r R \Omega_{(t)} u_{(t)} \sin \phi \quad (10)$$

from which it is clear that changes in the dynamic pressure due to pitching are largest when  $\sin \phi$  is a maximum. This occurs when the stroke plane is at right angles to the direction of flight, which is most nearly the case in fast-flying animals. Changes in the local dynamic pressure will also affect the pitching moment about the aerodynamic centre of the blade element.

Since the section lift curve slope is defined by the airfoil section and surface characteristics (both of which are assumed to be unaffected by pitch disturbances) changes in the section lift coefficient can result only from changes in the section angle of attack. For small to moderate angles of attack, the section lift coefficient will increase approximately linearly with the section angle of attack, measured between the relative flow and the zero lift chord, and denoted by  $\alpha_{w(r,t)}$ . If we define  $\alpha_{w(r,t)}$  as being positive when

the flight force has a positive z-component, we may write  $C_{l(r,t)} = a_{(r,t)} \alpha_{w(r,t)}$  where  $a_{(r,t)}$  is the section lift curve slope. During hovering, the section angle of attack would be unaffected by pitch disturbances, assuming that the wing kinematics remained fixed with respect to the body axes, in which case the lift coefficient derivative,  $\partial C_{l(r,t)}/\partial \alpha_b$ , would be zero. During forward flight, however, the section angle of attack changes with pitching disturbances, so the lift coefficient derivative will not in general be zero.

Since the zero lift chord and stroke plane are mutually fixed relative at a given instant, any perturbation to the angle between the zero lift chord and the relative flow vector (i.e.  $\alpha_{w(r,t)}$ ) will be matched by an equal change in the angle between the stroke plane and the relative flow vector (i.e. the angle denoted as  $\zeta_{(r,t)}$  in Fig. 6). It is clear by inspection of the angular relations in Fig. 6 that these changes in  $\alpha_{w(r,t)}$  and  $\zeta_{(r,t)}$  occur in opposite directions, and that this applies on both the upstroke and the downstroke. Hence, we may write

$$\frac{\partial C_{l(r,t)}}{\partial \alpha_b} = -a_{(r,t)} \frac{\partial \zeta_{(r,t)}}{\partial \alpha_b}. \quad (11)$$

By inspection of Fig. 6,  $\zeta_{(r,t)}$  is given by the sine and cosine rules as

$$\begin{aligned} \zeta_{(r,t)} &= \arcsin \left( \frac{u_{(t)} \sin \phi}{V_{(r,t)}} \right) \quad \text{and} \\ \zeta_{(r,t)} &= \arccos \left( \frac{(rR\Omega_{(t)})^2 + V_{(r,t)}^2 - u_{(t)}^2}{2rR\Omega_{(t)}V_{(r,t)}} \right), \end{aligned} \quad (12)$$

respectively. Although either of eqns (12) may be differentiated to obtain  $\partial \zeta_{(r,t)}/\partial \alpha_b$ , the differentiation and subsequent simplification become more straightforward if eqns (12) are first combined to yield

$$\zeta_{(r,t)} = \arctan \left( \frac{u_{(t)} \sin \phi}{rR\Omega_{(t)} - u_{(t)} \cos \phi} \right), \quad (13)$$

whence  $V_{(r,t)}$  drops from the equation.

Bearing in mind that  $\partial \phi / \partial \alpha_b = 1$ , differentiating with respect to  $\phi$  is equivalent to differentiating with respect to  $\alpha_b$ . Hence, eqn (13) may be

readily differentiated with respect to  $\alpha_b$  by making use of a substitution for the bracketed terms and differentiating the substitution with respect to  $\phi$  using the quotient rule:

$$\begin{aligned} \frac{\partial \zeta_{(r,t)}}{\partial \alpha_b} &= \frac{\partial \zeta_{(r,t)}}{\partial \phi} \frac{\partial \phi}{\partial \alpha_b} = \frac{\partial \zeta_{(r,t)}}{\partial \phi} \\ &= \frac{\frac{u_{(t)} \cos \phi}{(rR\Omega_{(t)} - u_{(t)} \cos \phi)} - \frac{u_{(t)}^2 \sin^2 \phi}{(rR\Omega_{(t)} - u_{(t)} \cos \phi)^2}}{1 + \frac{u_{(t)}^2 \sin^2 \phi}{(rR\Omega_{(t)} - u_{(t)} \cos \phi)^2}}. \end{aligned} \quad (14)$$

Equation (14) then simplifies to

$$\frac{\partial \zeta_{(r,t)}}{\partial \alpha_b} = \frac{rR\Omega_{(t)} \cos \phi - u_{(t)}^2}{r^2 R^2 \Omega_{(t)}^2 - 2rR\Omega_{(t)} u_{(t)} \cos \phi + u_{(t)}^2}. \quad (15)$$

Making use of  $Q_{(r,t)} = \frac{1}{2} \rho V_{w(r,t)}^2$  and  $C_{l(r,t)} = a_{(r,t)} \alpha_{w(r,t)}$  and substituting eqns (8), (10), (11) and (15) into eqn (9) finally yields

$$\begin{aligned} \frac{\partial F_{w(r,t)}}{\partial \alpha_b} &= \frac{1}{2} \rho u_{(t)}^2 a_{(r,t)} c_{(r)} R dr \\ &\times \left( \frac{rR\Omega_{(t)}}{u_{(t)}} (2\alpha_{w(r,t)} \sin \phi - \cos \phi) + 1 \right), \end{aligned} \quad (16)$$

where all angles are in radians. The product outside of the square brackets is simply the elemental lift curve slope for a chordwise element on a fixed gliding wing. Equation (14) therefore indicates that, for a given flight speed, characterized by  $u_{(t)}$  in eqn (14), the local force derivative  $\partial F_{w(r,t)}/\partial \alpha_b$  should increase with increasing angular flapping velocity  $\Omega_{(t)}$ . This is hardly surprising, given that the basic reason for flapping is to increase the aerodynamic force produced by the wings.

#### 4.4. EXPRESSION FOR THE DERIVATIVE OF THE PITCHING MOMENT ABOUT THE AERODYNAMIC CENTRE $\partial M_{ac(r,t)}/\partial \alpha_b$

The equation for the instantaneous pitching moment about the local aerodynamic centre may

be written by analogy to the expression for the instantaneous local force [eqn (7)]:

$$M_{ac(r,t)} = Q_{(r,t)} C_{Mac(r,t)} c_{(r)}^2 R dr, \quad (17)$$

where  $C_{Mac(r,t)}$  is a dimensionless coefficient, which unlike the section lift coefficient is independent of the angle of attack. Note that unlike in eqn (7), chord ( $c_{(r)}$ ) appears squared, which is necessary for the non-dimensionality of  $C_{Mac(r,t)}$  because the units of a turning moment are force times distance. As in a fixed wing aircraft (see Nelson, 1989; Etkin & Reid, 1996; Cook, 1997), the pitching moment coefficient  $C_{Mac(r,t)}$  will be independent of the section angle of attack. Making use of eqn (10), we may therefore write

$$\begin{aligned} \frac{\partial M_{ac(r,t)}}{\partial \alpha_b} &= \frac{\partial Q_{(r,t)}}{\partial \alpha} C_{Mac(r,t)} c_{(r)}^2 R dr \\ &= \rho u_{(t)} C_{Mac(r,t)} c_{(r)}^2 r R^2 \Omega_{(t)} dr \sin \phi. \end{aligned} \quad (18)$$

#### 4.5. EXPRESSION FOR THE DERIVATIVE OF THE LOCAL FORCE INCLINATION $\partial \gamma_{(r,t)}/\partial \alpha_b$

The non-viscous forces on an infinitely long wing resolve into a resultant force operating normal to the oncoming relative flow. In reality, however, the vortices shed at the tips of a finite wing drag the surrounding air down with them, which induces a downwash that lowers the effective angle of attack and rotates the local lift vector back through the local downwash angle, denoted by  $\varepsilon_{(r,t)}$  in Fig. 5. The induced drag resulting from this rotation of the lift vector is an inevitable cost of lift production in flying animals and aircraft alike. The preceding section's analysis neglects modification of the effective angle of attack due to changes in the downwash during pitch disturbances, but this is reasonable if we can assume that changes in the downwash angle are small. On the same assumption, the effect of changes in the downwash angle upon changes in the inclination of the local flight force may also be neglected. Is the assumption that the downwash angle is small justified?

Thomas & Taylor (in press) show that changes in the downwash angle during pitch disturbances will indeed be small in gliding animals, with

typical maxima for the downwash angle itself being less than  $5^\circ$ . During flapping flight, however, the induced downwash velocity may be very much larger. After all, acceleration of air into the downwash is the very basis of lift production in flapping flight, so the downwash can hardly be insignificant! However, application of the Biot–Savart law to a semi-infinite vortex filament gives the result that the induced velocity is directly proportional to the value of the circulation, which is in turn proportional to the oncoming flow velocity under quasi-steady conditions (e.g. Anderson, 1991). Hence, since the downwash velocity varies directly with the speed of the oncoming flow, the downwash angle is independent of the relative flow speed and will remain small irrespective of how large the downwash velocity becomes. Although these relations will not necessarily apply in unsteady flows, we may therefore assume that changes in the downwash angle have a negligible effect upon the effective angle of

attack and the inclination of the local flight force vector under the quasi-steady flow conditions assumed in the present model. This both validates the preceding analysis and allows us to write the expression for the change in the inclination of the local flight force vector with respect to the body axis as simply

$$\frac{\partial \gamma_{(r,t)}}{\partial \alpha_b} = -\frac{\partial \zeta_{(r,t)}}{\partial \alpha_b}, \quad (19)$$

an expression for which was derived in eqns (14) and (15).

#### 4.6. RESULTS: THE QUASI-STATIC PITCH STABILITY PROVIDED BY A FLAPPING WING

We are now in a position to rewrite eqn (6), which formed the starting point of this analysis. Substituting in eqn (7) and rearranging, we have

$$\frac{\partial M_{w(r,t)}}{\partial \alpha_b} = \cos \sigma_{(t)} \left\{ \begin{aligned} & (x_{w(r,t)} \cos \gamma_{(r,t)} + z_{w(r,t)} \sin \gamma_{(r,t)}) \frac{\partial F_{w(r,t)}}{\partial \alpha_b} \\ & + (z_{w(r,t)} \cos \gamma_{(r,t)} - x_{w(r,t)} \sin \gamma_{(r,t)}) Q_{(r,t)} C_{l(r,t)} c_{(r)} R dr \frac{\partial \gamma_{(r,t)}}{\partial \alpha_b} \\ & + \frac{\partial M_{ac(r,t)}}{\partial \alpha_b} \end{aligned} \right\}. \quad (20)$$

Substituting in eqns (16) and (18) together with the expressions for the local dynamic pressure and section lift coefficient defined in Sections 4.2 and 4.3 gives:

$$\frac{\partial M_{w(r,t)}}{\partial \alpha_b} = \frac{1}{2} \rho a_{(r,t)} c_{(r)} R dr \cos \sigma_{(t)} \left\{ \begin{aligned} & (x_{w(r,t)} \cos \gamma_{(r,t)} + z_{w(r,t)} \sin \gamma_{(r,t)}) [r R \Omega u_{(t)} (2\alpha_{w(r,t)} \sin \phi - \cos \phi) + u_{(t)}^2] \\ & + (z_{w(r,t)} \cos \gamma_{(r,t)} - x_{w(r,t)} \sin \gamma_{(r,t)}) \left( V_{w(r,t)}^2 \alpha_{w(r,t)} \frac{\partial \gamma_{(r,t)}}{\partial \alpha_b} \right) \\ & + \frac{2u_{(t)}}{a_{(r,t)}} C_{Mac(r,t)} c_{(r)} r R \Omega_{(t)} \sin \phi \end{aligned} \right\}. \quad (21)$$

Equations (8), (15) and (19) are then substituted in to give:

$$\frac{\partial M_{w(r,t)}}{\partial \alpha_b} = \frac{1}{2} \rho u_{(t)}^2 a_{(r,t)} c_{(r)} R dr \cos \sigma_{(t)} \left\{ \begin{aligned} & (x_{w(r,t)} \cos \gamma_{(r,t)} + z_{w(r,t)} \sin \gamma_{(r,t)}) \left[ \frac{r R \Omega}{u_{(t)}} (2\alpha_{w(r,t)} \sin \phi - \cos \phi) + 1 \right] \\ & + (z_{w(r,t)} \cos \gamma_{(r,t)} - x_{w(r,t)} \sin \gamma_{(r,t)}) \left[ \alpha_{w(r,t)} \left( \frac{r R \Omega}{u_{(t)}} \cos \phi - 1 \right) \right] \\ & + \frac{r R \Omega_{(t)}}{u_{(t)}} \left( \frac{2c_{(r)} C_{Mac(r,t)} \sin \phi}{a_{(r,t)}} \right) \end{aligned} \right\}. \quad (22)$$

Finally, following the terminology of classical propeller theory, we may rewrite eqn (22) in terms of the instantaneous advance ratio, defined here as  $u_{(t)}/R\Omega_{(t)}$ , and denoted by  $J_{(t)}$ :

$$\frac{\partial M_{w(r,t)}}{\partial \alpha_b} = \frac{1}{2} \rho u_{(t)}^2 a_{(r,t)} c_{(r)} R dr \cos \sigma_{(t)} \left\{ \begin{aligned} & (x_{w(r,t)} \cos \gamma_{(r,t)} + z_{w(r,t)} \sin \gamma_{(r,t)}) \left[ \frac{r}{J_{(t)}} (2\alpha_{w(r,t)} \sin \phi - \cos \phi) + 1 \right] \\ & + (z_{w(r,t)} \cos \gamma_{(r,t)} - x_{w(r,t)} \sin \gamma_{(r,t)}) \left[ \alpha_{w(r,t)} \left( 1 - \frac{r}{J_{(t)}} \cos \phi \right) \right] \\ & + C_{Mac(r,t)} \left[ \frac{2rc_{(r)} \sin \phi}{J_{(t)} a_{(r,t)}} \right] \end{aligned} \right\}. \quad (23)$$

What can this expression tell us about stability in flapping flight? The term  $\frac{1}{2} \rho u_{(t)}^2 a_{(r,t)} c_{(r)} R dr$  outside of the curly brackets is equivalent to the slope of the curve of lift vs. angle of attack for a fixed blade element. Hence, if the oncoming flow is zero (i.e. if the animal is hovering),  $\partial M_{w(r,t)}/\partial \alpha_b$  will also be zero and there will be neutral first-order stability. This result is striking, but not unexpected, because it is well known that helicopters possess no first-order stability in hover (e.g. Gessow & Amer, 1949; Johnson, 1980). The explanation of this phenomenon is quite straightforward (Taylor, in press): an instantaneous change in altitude does not directly

that the mean upward-canted coning angle of the wings of a hovering insect could provide both pitch and roll stability in a similar way (Dudley, 2000; Taylor, in press).

Since first-order stability in flapping flight can only arise through a combination of flapping and forward motion, it makes sense to consider how flapping modifies the stability of flight at a given forward speed. The conventional way of doing this is to express the equation in non-dimensional terms, which here means dividing through by  $\frac{1}{2} \rho u_{(t)}^2 c_{(t)}^2 R dr$ , giving the dimensionless total pitching moment coefficient derivative as

$$\frac{\partial C_{Mw(r,t)}}{\partial \alpha_b} = a_{(r,t)} \cos \sigma_{(t)} \left\{ \begin{aligned} & \left( \frac{(x_{w(r,t)} \cos \gamma_{(r,t)} + z_{w(r,t)} \sin \gamma_{(r,t)})}{c_{(r)}} \right) \left[ \frac{r}{J_{(t)}} (2\alpha_{w(r,t)} \sin \phi - \cos \phi) + 1 \right] \\ & + \left( \frac{(z_{w(r,t)} \cos \gamma_{(r,t)} - x_{w(r,t)} \sin \gamma_{(r,t)})}{c_{(r)}} \right) \left[ \alpha_{w(r,t)} \left( 1 - \frac{r}{J_{(t)}} \cos \phi \right) \right] \\ & + C_{Mac(r,t)} \left[ \frac{2r \sin \phi}{J_{(t)} a_{(r,t)}} \right] \end{aligned} \right\}. \quad (24)$$

affect the relative flow of air over the wings in hovering, so there is no change in the static aerodynamic forces, and hence no change in the net moment about the centre of gravity if the kinematics remains the same with respect to the body. Any passive stability or instability in hovering flight must therefore arise as a result of second-order changes in the aerodynamic forces caused by translation of the insect as the flight force is redirected with respect to gravity. This is the means by which the dihedral of a fixed wing aircraft provides roll stability, and it is possible

This equation encapsulates the stability of a flapping wing, so the next task is to consider how the terms it contains may vary. Since the sweep angle,  $\sigma_{(t)}$ , is always between  $-\pi/2$  and  $\pi/2$ , the term  $\cos \sigma_{(t)}$ , which multiplies the whole expression, always takes positive values less than one. The effect of sweeping the wings is therefore equivalent to reducing the static lift curve slope, which is intuitively satisfying because static sweep produces a similar lift reduction on a fixed wing. Other things being equal, a vertical stroke (i.e. one in which the sweep is zero throughout)

with maximize  $\partial C_{Mw(r,t)}/\partial \alpha$  for the set of possible stroke paths in which the mean position of the blade element is constant.

Equation (24) is very general, applying on both the upstroke and the downstroke. It is clear from Fig. 5 that  $\phi$ , the included angle between the flow due to flapping and the oncoming flow vector, is obtuse on the downstroke (i.e.  $\pi/2 \leq \phi \leq \pi$ ), and acute on the upstroke (i.e.  $0 \leq \phi \leq \pi/2$ ). Hence, whereas  $\sin \phi$  is positive on both the upstroke and the downstroke,  $\cos \phi$  will be positive on the upstroke but negative on the downstroke. Since the section angle of attack,  $\alpha_{w(r,t)}$ , is expected to be positive throughout the downstroke, it follows that all three of the expressions contained within square brackets in eqn (23) will take positive values during the downstroke. Whether a wing element makes a stabilizing or destabilizing contribution to the animal's stability during the downstroke therefore depends only upon the coordinates of its aerodynamic centre ( $x_{(r,t)}$ ,  $z_{(r,t)}$ ), the forward inclination of the flight force vector ( $\gamma_{(r,t)}$ ), and the sign of the pitching moment coefficient about the aerodynamic centre ( $C_{Mac(r,t)}$ ).

Since  $\gamma_{(r,t)}$  is always small and positive on the downstroke, it will always be possible to ensure that the mean quasi-static force produced by a given element is stabilizing by ensuring that its point of action lies far enough behind and/or above the centre of gravity. The terms  $(x_{w(r,t)} \cos \gamma_{(r,t)} + z_{w(r,t)} \sin \gamma_{(r,t)})$  and  $(z_{w(r,t)} \cos \gamma_{(r,t)} - x_{w(r,t)} \sin \gamma_{(r,t)})$  will then be negative for the majority of the stroke, ensuring that  $\partial C_{Mw(r,t)}/\partial \alpha_b$  is negative and hence stabilizing. This condition is qualitatively identical to the condition for stability in gliding flight (Thomas & Taylor, in press). Unlike in gliding flight, however, the negative pitching moments associated with positively cambered airfoil sections like those of flying animals and aircraft could also help make  $\partial C_{Mw(r,t)}/\partial \alpha_b$  negative. This effect arises solely through the changes in the dynamic pressure that can result from changes in the geometry of the flow vectors during pitching disturbances, so we do not expect its consequences to be especially significant.

Things are more complicated on the upstroke, because the first two expressions contained within square brackets in eqn (24) could take either positive or negative values on the upstroke, de-

pending upon the values of  $\phi$  and  $J_{(t)}$ . Specifically, if  $\phi$  and  $J_{(t)}$  are small, then one or both of these expressions could be negative. In fact,  $\phi$  and  $J_{(t)}$  are bound to be small in slow forward flight with an active upstroke, which uses a low advance ratio by definition, and an almost horizontal stroke plane by necessity. Under the same conditions,  $\gamma_{(r,t)}$  will also be small and positive. Because the sign of  $\alpha_{w(r,t)}$  is implicitly determined by the direction of the flight force in the equations above (here,  $\alpha_{w(r,t)}$  is deemed positive when the flight force has a positive  $z$ -component),  $\alpha_{w(r,t)}$  will always be positive on an active upstroke generating useful aerodynamic force. Following this convention,  $\alpha_{w(r,t)}$  remains positive on the upstrokes of hummingbirds and insects, even if the wing itself is flipped over such that its morphological angle of attack is negative. It follows that if the first two expressions contained within square brackets in eqn (24) are negative, then the stability criterion for the placement of the aerodynamic centre will be the reverse of that applying on the downstroke. An active upstroke could therefore diminish the stability provided by a stabilizing downstroke in slow forward flight. This accords with experience of free-flying insects, which appear to have some stability when they are flying slowly, but less than in fast forward flight.

During fast forward flight with an active upstroke, the upstroke is usually responsible for the majority of thrust production. The forward inclination of the flight force,  $\gamma_{(r,t)}$ , may then be quite large, which could change the balance of terms in eqn (24) in ways that are hard to predict without further parametrization of the variables. However, in many flying vertebrates (which flex their wings on the upstroke), and in birds in particular (which also separate their flight feathers to avoid large retarding forces), the aerodynamic forces may be rather small on the upstroke (Norberg, 1990). It is also possible that the upstroke might generate a downforce, which would alter the relations in eqn (24) by reversing the sign of  $\alpha_{w(r,t)}$ , providing a further reason (beyond the obvious inefficiency in lifting the body weight) why generating a downforce is undesirable. However, whatever the nature of the upstroke, the magnitude of the expressions contained within the first two square brackets will inevitably be larger on

the downstroke (reflecting the faster relative flow and higher dynamic pressure) so the influence of the downstroke will always be stronger. Hence, whilst an active upstroke could sometimes diminish the stability provided by a stabilizing downstroke, the net contribution of an element will still be stabilizing provided the mean quasi-static force it produces acts far enough behind and/or above the centre of gravity.

Finally, we must consider the effect of varying the advance ratio  $J_{(t)}$ . Neglecting the potentially destabilizing effects of an active upstroke, it is clear that flapping the wings faster will amplify  $\partial C_{Mw(r,t)}/\partial \alpha_b$  by reducing the advance ratio. The consequent amplification of  $\partial M_{w(r,t)}/\partial \alpha_b$  will be compounded by the increase in forward speed that is likely to accompany any increase in flapping velocity [eqn (23)]. Comparing gliding (i.e.  $1/J_{(t)} = 0$ ) with horizontal flapping flight at the same airspeed, it is clear that a blade element with the same position and angle of attack will provide more stability in the course of flapping than in the course of gliding, because the magnitude of  $\partial C_{Mw(r,t)}/\partial \alpha_b$  will be smaller during glides. This difference in the magnitude of  $\partial C_{Mw(r,t)}/\partial \alpha_b$  is essentially a reflection of the lower dynamic pressure and flight forces associated with gliding flight. The overriding conclusion must therefore be that there is nothing intrinsically destabilizing about flapping: beating the wings faster merely amplifies any existing stability or instability by increasing the magnitude of  $\partial M_{w(r,t)}/\partial \alpha_b$  whilst leaving its sign unchanged. This runs counter to the expectations of most biologists (e.g. Maynard Smith, 1952; Weis-Fogh, 1956b; Brown, 1963; Wilson, 1968), who have assumed that flapping flight is inherently unstable.

#### 4.7. RESULTS: QUASI-STATIC PITCH EQUILIBRIUM IN FLAPPING FLIGHT

The logical implication from the preceding analysis of single blade elements is that, just as in gliding flight, the wings will only be stabilizing if the total mean quasi-static force acts behind and preferably above the centre of gravity. This is not the whole story, however, because the point of action of the total mean quasi-static force is constrained by the requirement for the net moment on the animal to be zero at pitch equilibrium.

Denoting the total mean quasi-static force by  $F_w$ , and defining the coordinates of its point of action ( $x_w, z_w$ ) as the mean position of the aerodynamic centres of all of the blade elements, weighted by the component of the instantaneous local aerodynamic force normal to the respective axis, we may write the equilibrium condition

$$F_w(x_w \cos \gamma + z_w \sin \gamma) + M_{ac} = 0, \quad (25)$$

where  $\gamma$  is the inclination of  $F_w$  to the  $z$ -axis and where  $M_{ac}$  is the total mean quasi-static pitching moment about ( $x_w, z_w$ ). Note that a true mean aerodynamic centre may not exist in the classical sense of being a fixed point about which the pitching moment is independent of the angle of attack. However, it is immediately clear that  $M_{ac}$  will need to be positive at equilibrium, if  $x_w$  and  $z_w$  are made negative to provide stability.

What sign is  $M_{ac}$  likely to take? The negative pitching moments about the local aerodynamic centres will sum to give a net negative pitching moment about ( $x_w, z_w$ ). Some other mechanism is therefore needed for balance. In fixed wing aircraft, balance is sometimes provided by sweeping the wings back and twisting the tips nose-down to provide wash-out. Alternatively, the wings may be swept forward and the tips twisted up to provide wash-in. In either case, a net positive pitching moment is produced by the resulting distribution of elevated lift ahead of the aerodynamic centre and diminished lift behind. Wash-out seems to be used by many gliding birds (Thomas & Taylor, in press), and it is likely that an analogous mechanism could provide balance in flapping flight.

The situation is more complicated on a flapping wing, because variation in the relative flow direction with spanwise variation in the advance ratio is such that an untwisted flapping wing has an effective wash-in lift distribution on the downstroke. This is because the angle of attack is highest near the tips where the component of flow due to flapping is strongest. Most animals' wings are in fact twisted to provide morphological wash-out on the downstroke (insects: Jensen, 1956; Nachtigall, 1966, 1979, 1980; Weis-Fogh, 1973; Wootton, 1981; Ellington, 1984a, Ennos, 1989; but see Vogel, 1967; bats: Vaughan, 1970a; Norberg, 1976; birds: Brown 1948; Greenewalt,

1960; Hertel, 1966; Herzog, 1968; Bilo, 1971). Hence, whether the lift distribution is wash-out or wash-in will depend upon the balance between the morphological wash-out and the effective wash-in due to flapping.

Flying animals could therefore generate positive pitching moments during flapping flight by appropriately twisting their wings. If this were the case, we would predict morphological wash-out to decrease as the wings sweep forwards on the downstroke and to increase as the wings sweep back on the upstroke. This may be less important in insects that reverse their wings on the upstroke but still keep camber positive with respect to wing movement throughout the stroke, because the camber moments will be of opposite sense on the upstroke and downstroke and will partially cancel.

#### 4.8. OTHER CONTRIBUTIONS TO THE TOTAL PITCHING MOMENT

In principle, the body could generate positive pitching moments for balance during forward flight. For example, the stable orientation for an elongated body moving through a non-viscous fluid is with its long axis normal to the flow (Munk, 1924), so the body will have a natural tendency to pitch nose-up at positive body angles. This may be counteracted by the viscous forces, however, because viscous drag will produce negative pitching moments at positive body angles if it acts behind the centre of gravity (Thomas & Taylor, in press). This appears to be the case in bumblebees, for example, in which the abdomen generates a nose-down pitching moment (Dudley & Ellington, 1990) that will make it harder to balance if the total mean quasi-static force acts in a stabilizing position above or behind the centre of gravity.

Like conventional aircraft, birds may use their tails to generate steady positive moments for balance during fast forward flight (Maynard Smith, 1952; Thomas, 1993a, 1996a, b; Thomas & Balmford, 1995). This will not be possible during hovering, when there is no steady stream of air past the tail. However, hovering Pied Flycatchers *Ficedula hypoleuca* apparently damp out pitch oscillations caused by antero-posterior movement of the wings through the flapping

cycle (and perhaps also by large unsteady forces produced at the end of the downstroke) by pitching their tails up and down in antiphase with the wings (Norberg, 1975). The opposite has been found in bats (Vaughan, 1970a, b; Norberg, 1976) and other birds (Brown, 1948; Gatesy & Dial, 1993; A. L. R. Thomas, pers. obs.) in slow forward flight, during which the tail or uropatagium is generally pitched in phase with the wings.

This difference in wing-tail phase presumably arises because the tail must exert its own push against the air during hovering (i.e. its pitching velocity determines the moment it produces: Thomas, 1997; Balmford *et al.*, 2000), whereas in forward flight there is already a flow of air past the tail (i.e. its pitch attitude is what primarily determines the moment it produces). We would therefore expect the phase of the wings and tail to change at the transition from hovering to slow forward flight, although this may not occur in bats, in which movements of the wings and uropatagium are mechanically coupled. Similar considerations may also explain why insects generally lack fixed lifting surfaces, because the free-stream velocity is so slight at the slow speeds and low advance ratios at which most insects operate that the flapping wings will completely dominate force production. This will be especially so where unsteady aerodynamic mechanisms are important.

#### 4.9. CONTRIBUTION OF UNSTEADY AERODYNAMIC MECHANISMS TO PITCH STABILITY AND EQUILIBRIUM

The blade element model derived above describes the stability provided by the quasi-steady aerodynamic forces on the wings. However, unsteady aerodynamics are important in force production in most insects (Weis-Fogh, 1973; Cloupeau *et al.*, 1979; Ellington, 1984b, c; Ennos, 1989; Dudley & Ellington, 1990; Wilkin, 1990; Zanker & Götz, 1990; Wilkin & Williams, 1993) and some birds (Norberg, 1975), and we must therefore consider their effect upon stability. This will vary according to whether the mechanism in question is translatory (like delayed stall) or non-translatory (like rotational circulation or clap-and-fling).

Delayed stall (Ellington *et al.*, 1996; Willmott *et al.*, 1997) effectively extends the lift curve at

high angles of attack and may therefore be incorporated directly into the blade element model above. Its effects may be modelled by assuming that the wings operate at a higher angle of incidence, such that the main effect is to increase  $\alpha_{w(r,t)}$ . The lift curve slope  $a_{w(r,t)}$  might also be greater at such high angles of attack. In either case, delayed stall will enhance any existing stability in essentially the same way as flapping *per se*.

The effects of non-translatory mechanisms such as clap-and-fling and rotational circulation (e.g. Weis-Fogh, 1973; Ellington, 1984b; Dickinson *et al.*, 1999) will be quite different. Assuming that the lift they generate combines additively with the translatory lift, then any stability they provide will combine additively with the stability expressed in eqn (16). Non-translatory mechanisms are essentially independent of the oncoming flow because they rely upon rapid wing rotation or relative movement of the two wings to enhance the circulation. Non-translatory mechanisms are therefore unlikely to be affected by changes in the overall angle of attack, and will therefore confer no additional stability.

Non-translatory mechanisms will have potentially more significant consequences for balance and control. Whereas translatory mechanisms effectively amplify quasi-steady force production, non-translatory mechanisms can produce forces in directions different from the instantaneous quasi-steady force. Dickinson *et al.* (1999) find that non-translatory mechanisms produce large horizontal thrust and drag forces that largely cancel when taken across the whole stroke. Using a model wing mimicking the kinematics of *Drosophila melanogaster*, Dickinson *et al.* (1999) were able to show that large thrust forces tended to appear at the bottom of the downstroke, with large drag forces tending to appear at the top of the upstroke. Depending upon the orientation of the stroke with respect to the body axes, the resulting force couple could be used to generate the positive pitching moment required for balance if the total mean quasi-static force acted in a stabilizing position behind the centre of gravity. Actively varying the magnitudes of the horizontal unsteady aerodynamic forces produced at the top and bottom of the stroke, or changing the orientation of the stroke plane to vary the strength

of the resulting force couple could also provide a potent means of pitch control. This is likely to be especially important in functionally two-winged insects, such as flies, wasps, bees and hawkmoths, which, unlike functionally four-winged insects, cannot adjust the balance of lift between the forewings and hindwings for pitch control (Taylor, in press).

## 5. Discussion

The main conclusion of this paper—that flapping is not inherently destabilizing, and can in fact increase stability if the mean quasi-static flight force acts in an appropriate place—runs counter to the received wisdom amongst biologists (Maynard Smith, 1952; Weis-Fogh, 1956b; Brown, 1963; Wilson, 1968). Indeed, gliding birds often begin flapping in turbulence (Hankin, 1913; A.L.R. Thomas, pers. obs.) and this may be a mechanism to increase static pitch stability. The problem of maintaining stability when flapping has often been considered to be one of the major hurdles that needed to be overcome for powered flight to evolve (e.g. Caple *et al.*, 1983), particularly in scenarios involving an intermediate gliding stage. Norberg (1985a, b; 1990) opposed this notion, arguing that good stability and control were probably achieved before the evolution of powered flight, but provided no clear evidence that an animal that could glide in a stable, controlled fashion would necessarily be stable when flapping. The present analysis indicates that this should, in fact, be the case, provided that the mean quasi-static flight force in flapping acts at the same point as the resultant aerodynamic force in gliding. This implies that the development of sophisticated active control to replace passive stability may not have been as important to the evolution of flapping flight as has previously been thought.

Whilst the assumption of this analysis has been that it is generally a good thing if some degree of passive pitch stability can be attained during flapping flight, there are some cases in which it may be beneficial to lower stability in order to enhance manoeuvrability. One obvious case is during landing, which requires a particularly high degree of manoeuvrability, especially during point landings requiring the animal to alight on



a branch or other such objects (Caple *et al.*, 1983). In birds, sweeping the wings and/or spreading the tail provides a potent means of varying stability and balance (Thomas, 1993a, 1996a, b; Thomas & Taylor, in press), with forward sweep usually being observed during slow flight and landing (Hankin, 1913; Pennycuick & Webbe, 1959; Pennycuick, 1968, 1975; Lighthill, 1974; Tucker & Parrot, 1970; Tucker & Heine, 1990; Tucker, 1992; Rosén & Hedenstöm, 2001). The blade element analysis above indicates that this will tend to reduce stability and enhance manoeuvrability, just as in gliding flight (Thomas & Taylor, in press). However, the observation that an active upstroke might also reduce stability suggests an alternative, aerodynamic mechanism by which flying animals could lower their stability. Birds often switch to an active upstroke during slow forward flight and landing (Norberg, 1990), which presumably serves to enhance lift production, but will also tend to reduce pitch stability and enhance manoeuvrability just when this is required.

Some of the perceived differences in the stability of different flying animals may be explained by differences in the position of the centre of gravity and in kinematic parameters such as the inclination of the stroke plane. In addition, which unsteady aerodynamic mechanisms an animal uses (if any) may also determine differences in stability. Specifically, since non-translatory unsteady mechanisms are not expected to confer any stability, animals in which such mechanisms are the main source of lift are likely to possess a very low degree of static pitch stability. This may be the case in flies, for example, which appear to rely heavily upon unsteady rotational mechanisms (Weis-Fogh, 1973; Ennos, 1989; Dickinson *et al.*, 1993, 1999; Dickinson & Götz, 1996) and become dynamically unstable after removal of the halteres controlling flight (Derham, 1713; Pringle, 1957). The biological intuition that sophisticated active control is often required to replace passive stability in flapping flight may therefore be correct in animals in which non-translatory unsteady mechanisms are the main source of lift. The flip side of this is that such animals should be highly manoeuvrable, and this may go some way towards explaining the remarkable aerobatic abilities of flies.

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## APPENDIX A

### Nomenclature

$a_{(r,t)}$	local instantaneous section lift curve slope
$c_{(r)}$	local wing chord
$C_{l(r,t)}$	local instantaneous section lift coefficient
$C_{Mac(r,t)}$	local instantaneous pitching moment coefficient about the aerodynamic centre of a blade element
$C_{Mw(r,t)}$	pitching moment coefficient for a blade element's contribution to the moment about the centre of gravity
$F_w$	mean total quasi-static force on the wing
$F_{w(r,t)}$	local instantaneous force on a blade element
$g$	acceleration due to gravity
$I_y$	moment of inertia about the y-axis
$J$	instantaneous advance ratio at the wing tip
$M$	total pitching moment about the centre of gravity
$M_\alpha$	pitching moment derivative normalized by the moment of inertia about the y-axis
$M_{ac}$	mean total quasi-static pitching moment about the mean point of action of the total quasi-static flight force
$M_{ac(r,t)}$	local instantaneous pitching moment about the aerodynamic centre of a blade element
$Q$	dynamic pressure
$Rdr$	width of blade element of wing
$R$	wing length
$r$	spanwise station of blade element, expressed as a proportion of wing length

$T_p$	period of phugoid mode of motion (see text for details)
$T_{sp}$	period of short period mode of motion (see text for details)
$U_0$	flight speed at top and bottom of phugoid oscillation
$u_{(t)}$	instantaneous chordwise component of flow due to the animal's forward velocity
$V_{w(r,t)}$	local instantaneous speed of the relative flow over a blade element
$w_{(r,t)}$	local instantaneous downwash velocity
$x_w$	x-coordinate of the point of action of the mean total quasi-static force
$x_{w(r,t)}$	instantaneous x-coordinate of the aerodynamic centre of a single blade element
$z_w$	z-coordinate of the point of action of the mean total quasi-static force
$z_{w(r,t)}$	instantaneous z-coordinate of the aerodynamic centre of a single blade element
$\alpha_b$	overall angle of attack (measured between the longitudinal body axis and the oncoming flow)
$\alpha_{w(r,t)}$	angle between the local instantaneous relative flow and the local zero-life chord of a blade element (deemed positive when the flight force points above the stroke plane)
$\varepsilon_{(r,t)}$	local instantaneous downwash angle
$\gamma$	forward inclination from the z-axis of the mean total quasi-static force
$\gamma_{(r,t)}$	forward inclination from the z-axis of the local instantaneous force
$\rho$	air density
$\phi$	included angle between the chordwise components of flow due to flapping and forward motion
$\sigma_{(t)}$	sweep angle, measured between the wing's long axis and the y-axis in the plane containing the oncoming flow vector
$\zeta_{(r,t)}$	angle between the local instantaneous relative flow and the stroke plane
$\Omega_{(t)}$	instantaneous angular velocity at the wingtip

NB: The bracketed subscripts ( $r$ ) and ( $t$ ) denote that a variable is a function of spanwise station and time through the wingbeat, respectively.