



Animal Flight Dynamics I. Stability in Gliding Flight

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Stability is as essential to flying as lift itself, but previous discussions of how flying animals maintain stability have been limited in both number and scope. By developing the pitching moment equations for gliding animals and by discussing potential sources of roll and yaw stability, we consider the various sources of static stability used by gliding animals. We find that gliding animals differ markedly from aircraft in how they maintain stability. In particular, the pendulum stability provided when the centre of gravity lies below the wings is a much more important source of stability in flying animals than in most conventional aircraft. Drag-based stability also appears to be important for many gliding animals, whereas in aircraft, drag is usually kept to a minimum. One unexpected consequence of these differences is that the golden measure of static pitching stability in aircraft—the static margin—can only strictly be applied to flying animals if the equilibrium angle of attack is specified. We also derive several rules of thumb by which stable fliers can be identified. Stable fliers are expected to exhibit one or more of the following features: (1) Wings that are swept forward in slow flight. (2) Wings that are twisted down at the tips when swept back (wash-out) and twisted up at the tips when swept forwards (wash-in). (3) Additional lifting surfaces (canard, hindwings or a tail) inclined nose-up to the main wing if they lie forward of it, and nose-down if they lie behind it (longitudinal dihedral). Each of these predictions is directional—the opposite is expected to apply in unstable animals. In addition, animals with reduced stability are expected to display direct flight patterns in turbulent conditions, in contrast to the erratic flight patterns predicted for stable animals, in which large restoring forces are generated. Using these predictions, we find that flying animals possess a far higher degree of inherent stability than has generally been recognized. This conclusion is reinforced by measurements of the relative positions of the centres of gravity and lift in birds, which suggest that the wings alone may be sufficient to provide longitudinal static stability. Birds may therefore resemble tailless aircraft more closely than conventional aircraft with a tailplane.

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1. Introduction

The ability to maintain a stable attitude and velocity is as essential to flight as lift itself, but biologists have tended to neglect stability, concentrating instead upon mechanisms of lift and power production. Earlier discussions of stability

in animal flight (e.g. Holst & Kuchemann, 1942; Maynard Smith, 1952; Brown, 1963; Herzog, 1968) are limited and generally suppose that more accomplished fliers like birds and insects rely upon active control of stability. This is not a necessary conclusion because, in aircraft, stability may be maintained by passive means (as in a paper dart), by active control (as in the experimental X-29 fighter), or by some combination of the two (as in many modern fighters and some

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commercial aircraft). A similar range of possibilities presumably exists in biological systems. In the case of winged seeds, or samaras (Norberg, 1973), we may be sure that stability is maintained passively, since there is no possibility of active control. On the other hand, since flying animals have widely varying control abilities, we might expect to find the whole gamut of configurations from the inherently stable to the inherently unstable.

Three types of inherent stability can be identified in flying animals—drag-based stability (like that of an arrow or dart), lift-based stability (like that provided by a tailplane) and pendulum stability (like that of a paraglider). In addition, the flight surfaces of animals are rather flexible, which could help in the damping of gusts (Lanchester, 1908; Sneyd *et al.*, 1982) and periodic disturbances due to flapping (Vaughan, 1970a, b). Here we use a rigid-body analysis to examine how gliding animals use each of these mechanisms to maintain stability. This forms an essential prelude to the more complex problem of understanding how stability is maintained in flapping flight (Taylor & Thomas, submitted) and provides a useful vehicle for considering some of the selective pressures shaping animal flight.

2. Evolutionary Considerations

What determines the optimum degree of inherent stability for a given animal? Inherent stability opposes accidental disturbances and voluntary manoeuvres alike, so there is an inevitable trade-off between stability and manoeuvrability in flight. Too much stability leads to a sluggish response to control inputs and may in addition limit the maximum lift-to-drag ratio that can be achieved. Too little stability will make flight difficult or even impossible to control. As in aircraft design, the optimum trade-off will depend upon what kinds of flying qualities are required. For example, the kinds of flying qualities that are desirable in an aerial predator like a swift—speed, agility and manoeuvrability—are similar to the operational requirements of a high-performance fighter, and both will benefit from having a low degree of inherent stability. The flying qualities of a swan, on the other hand, ought more closely to resemble those of an

airliner, since neither needs to be particularly manoeuvrable. Both should benefit from the safer flight that a high degree of inherent stability confers, and perhaps also from a reduction in the mechanical and computational costs associated with maintaining stability actively. Hence, we would predict that aerial predators and other flying animals requiring a high degree of manoeuvrability should inherently be less stable than other flying animals.

Just as computerized stability augmentation systems are a relatively new innovation in aircraft design, the potential for active control was probably limited during the early evolution of animal flight. Early fliers ought, therefore, to require a higher degree of inherent stability to remain airborne than later members of a lineage in which the neuromuscular system has had time to become adapted for flight (Maynard Smith, 1952; de Beer, 1954; Lighthill, 1974). The fossil record does indeed provide several lines of evidence that early fliers were especially stable (Maynard Smith, 1952; Lighthill, 1974). For example, many Palaeozoic insects possessed long abdominal cerci that would have contributed significant drag-based stability during forward flight (Maynard Smith, 1952; Leston, 1963; Wigglesworth, 1976; Ellington, 1991; Wootton & Ellington, 1991; Wootton & Kukalová-Peck, 2000), whilst amongst vertebrates, the early pterosaur *Rhamphorhynchus* possessed a long tail terminating in a diamond-shaped fluke that would have contributed drag-based and perhaps also lift-based stability (Holst & Kuchemann, 1942; Maynard Smith, 1952; Holst, 1957; Pennycuik, 1975). The long frond-like tail of *Archaeopteryx*, the first known bird, would also presumably have been strongly stabilizing (Maynard Smith, 1952; de Beer, 1954; Norberg, 1985; Gatesy & Dial, 1996a, b; Hummel, 1992).

3. Conditions for Stability and Equilibrium

The only external forces capable of doing work upon an animal are its weight (acting through the centre of gravity) and the total aerodynamic force (acting through the centre of pressure). A pair of forces like this will always resolve into a non-zero resultant force unless they are of equal magnitude and opposite direction, in which case a turning

moment called a couple will arise unless the forces are collinear. Hence, the gravitational force and total flight force must be equal, opposite and collinear at equilibrium. For stability, a change in attitude or velocity must induce a change in the forces of appropriate direction and magnitude to restore the animal to equilibrium. Within this definition, two kinds of stability may be distinguished. Dynamic stability refers to the damping of the system over time, whilst static stability refers only to the direction of the system's initial response to a disturbance. Static stability is necessary but insufficient for dynamic stability because a statically stable system could overcompensate for a disturbance, which could in turn lead to divergent oscillations. A full stability analysis would therefore need to consider the dynamics of the system, but since the equations of motion of even a rigid flying body are many and complex and give little intuitive feel of how stability is maintained, we will instead focus here upon static stability.

4. Assumptions and Rationale

We will assume that the animal is a rigid body with six degrees of freedom: three in translation and three in rotation (Fig. 1). Rotations about the x -, y - and z -axis are termed roll, pitch and yaw, respectively. The origin of the axes coincides with the centre of gravity, and we will assume that this is fixed during the development of the equations. The x - and z -axis are directed within the animal's plane of symmetry by aligning the x -axis with some convenient antero-posterior axis. The body axes are termed stability axes if the x -axis is aligned with the oncoming flow at equilibrium, and from time to time we will assume that the body axes are stability axes to simplify the development of the equations. In addition, during straight flight, the animal's plane of symmetry is bound to lie parallel to the flow. Longitudinal motions—that is, translation along the x - and z -axis, and pitching about the y -axis—occur parallel to this plane, and are therefore symmetrical about the equilibrium line of flight. Longitudinal motions are hence unable to induce any lateral force or moment at equilibrium, and in a gliding animal the existence of pure longitudinal motions will depend only upon the existence of a plane of

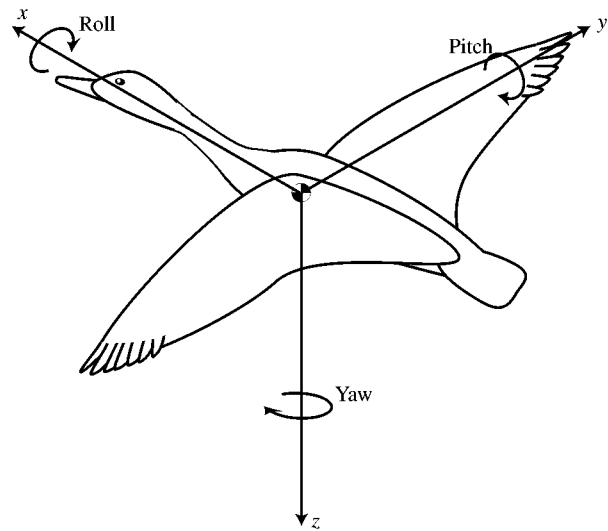


FIG. 1. Six degrees of freedom of an animal approximated as a rigid gliding body. The animal is free to rotate about or move in translation along any of its three axes. The origin of the body axes is fixed at the centre of gravity and the positive senses of the six motions are in the directions shown.

symmetry. We may therefore consider longitudinal motions separately from lateral motions. This reduces the number of degrees of freedom that must be considered simultaneously from six to three, and reduces the number of dimensions that needs to be considered simultaneously from three to two.

Lateral motions (sideslip along the y -axis, roll and yaw about the x - and z -axis) are asymmetric about the line of flight and are coupled in all three dimensions. The existence of pure lateral motions depends additionally upon the more restrictive condition that there is no cross-coupling of the lateral and longitudinal forces and moments (e.g. Etkin & Reid, 1996). This can arise aerodynamically in high performance aircraft as a result of asymmetric vortex formation at high angles of attack or high angular rates of turn (e.g. Nelson, 1989; Etkin & Reid, 1996; Day, 1997). Cross-coupling can also arise inertially in aircraft: principally in supersonic fighter aircraft with slender bodies and low aspect ratio wings, where the concentration of mass in the fuselage leads to coupling of the lateral and longitudinal moments (Nelson, 1989). It is reasonable to assume that neither form of coupling is important in gliding animals, and we may therefore consider lateral and longitudinal stability separately.

5. Longitudinal Stability

5.1. CONDITIONS FOR LONGITUDINAL STABILITY AND BALANCE

Drag damping provides stability with respect to longitudinal velocity in fixed wing aircraft and gliding animals, but cannot provide stability with respect to pitch. The first criterion for static pitch stability is that $\partial M/\partial \alpha < 0$ at equilibrium, where M is the pitching moment about the centre of gravity and α is the overall angle of attack. This in itself is insufficient for stable flight, however, because the angle between the wing zero-lift line and the oncoming flow (α_w) must be positive at equilibrium if useful lift is to be produced. Assuming that $\partial M/\partial \alpha < 0$, the net pitching moment at $\alpha_w = 0^\circ$ (call this M_0) will need to be positive for the animal to balance at a positive angle of attack [Fig. 2(a)]. On the other hand, if the

animal is inherently unstable (i.e. if $\partial M/\partial \alpha > 0$) then M_0 will need to be negative for the appropriate balance to be achieved [Fig. 2(a)]. The two remaining combinations of signs for $\partial M/\partial \alpha$ and M_0 are both unbalanced [Fig. 2(b)].

5.2. CONTRIBUTION OF A SINGLE PAIR OF WINGS: THEORY

The total pitching moment may be synthesized from the contributions of the various parts of the animal, taking account of interference effects by assuming that the various force coefficients and their derivatives are measured *in situ*. We will deal with the contribution of the wings in some detail because the same principles apply to any fixed surface. Thin airfoil theory predicts that the aerodynamic centre, through which the lift due to the incidence of the wing acts, should lie at the quarter chord point (e.g. von Mises, 1959; Jones, 1990; Anderson, 1991; Katz & Plotkin, 1991). Experiments with swept and tapered wings provide empirical confirmation that the aerodynamic centre lies close to the mean quarter chord point for a variety of planforms (Diehl, 1942). For simplicity, we will assume that friction and profile drag also act at the mean quarter chord point, which will give reasonable results at small angles of incidence.

The lift on a wing (call this L_w) is conventionally defined as the component of aerodynamic force normal to the oncoming flow. Drag (call this D_w) is defined as the component of force in the direction of the oncoming flow. In addition to these forces a wing may also produce a net pitching couple (call this M_{ac_w}) that we will assume is independent of α (justification for this is provided later). Taking moments about the centre of gravity, we have

$$M_w = x_w(L_w \cos \alpha_b + D_w \sin \alpha_b) + z_w(L_w \sin \alpha_b - D_w \cos \alpha_b) + M_{ac_w}, \quad (1)$$

using the notation defined above, and where, additionally, α_b is the body angle (measured between the x -axis and the oncoming flow) and (x_w, z_w) are coordinates of the wing aerodynamic centre within the frame defined by the body axes. Equation (1) is made dimensionless by dividing

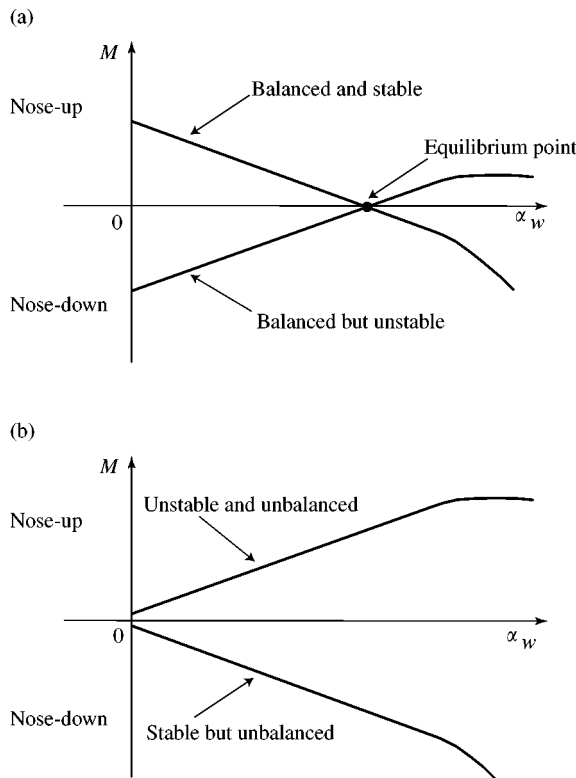


FIG. 2. Four possible graphs of total pitching moment M against wing angle of incidence α_w based upon possible signs of the slope and intercept. (a) Equilibrium is reached with the wings at the same positive angle of attack in both cases, but the animal will only be stable if the slope is negative. (b) Equilibrium cannot be attained with the wings at a positive angle of incidence, so the condition is unbalanced.

through by $\frac{1}{2}\rho U_w^2 S_w c_w$, where ρ is the air density, U_w the speed of the oncoming flow over the wings, S_w the wing area and c_w the wing mean chord (i.e. the mean width of the wing measured parallel to the x -axis):

$$C_{M_w} = \frac{x_w}{c_w} (C_{L_w} \cos \alpha_b + C_{D_w} \sin \alpha_b) + \frac{z_w}{c_w} (C_{L_w} \sin \alpha_b - C_{D_w} \cos \alpha_b) + C_{M_{ac_w}}. \quad (2)$$

The drag terms in eqn (2) are usually dropped in textbook treatments of aircraft stability (Nelson, 1989; Etkin & Reid, 1996; Cook, 1997), because the drag on a well-designed aircraft wing is usually small. This will not be the case in flying animals, however, which operate at low Reynolds numbers (Re) at which viscous drag forces will often be significant. These Reynolds numbers typically lie below a critical transition range ($10^6 > Re > 10^4$) beneath which profile drag increases sharply (see Nachtigall, 1977; Carmichael, 1981 for reviews). Drag coefficients measured on the wings of real or model birds (Nachtigall & Kempf, 1971; Reddig, 1978; Nachtigall, 1979; Withers, 1981a, b; Sugimoto, 1998) and insects (Jensen, 1956; Vogel, 1967b), are indeed higher than those measured for aircraft wings at higher Re (e.g. Jacobs *et al.*, 1937; Pinkerton & Greenberg, 1938). However, since birds' wings also have higher drag coefficients than model aircraft wings operating at similar Re , a combination of wing twist, skin friction, and aeroelastic flutter must also contribute additional drag (Withers, 1981a). In any case, we cannot safely drop the drag terms from the equations for animal flight.

The wing's contribution to $\partial M / \partial \alpha$ is obtained, in coefficient form, by differentiating eqn (2) with respect to α , giving

$$\begin{aligned} C_{M_{x_w}} = & \frac{x_w}{c_w} [(C_{L_{x_w}} + C_{D_w}) \cos \alpha_b \\ & + (C_{D_{x_w}} - C_{L_w}) \sin \alpha_b] \\ & + \frac{z_w}{c_w} [(C_{L_{x_w}} + C_{D_w}) \sin \alpha_b \\ & + (C_{L_w} - C_{D_{x_w}}) \cos \alpha_b], \end{aligned} \quad (3)$$

where the subscript α denotes a derivative with respect to the overall angle of attack, and where, for example, C_{L_w} is the wing lift coefficient, and $C_{L_{x_w}}$ its derivative with respect to α . Equation (3) is cumbersome, but may be simplified by assuming that $C_{D_{x_w}}$ is negligible compared to C_{L_w} and by assuming that the body axes are stability axes, such that $\alpha_b = 0^\circ$ at equilibrium. The slope of the pitching moment coefficient curve is then approximately

$$C_{M_{x_w}} = \frac{x_w}{c_w} (C_{L_{x_w}} + C_{D_w}) + \frac{z_w}{c_w} C_{L_w}, \quad (4)$$

at equilibrium. At small-to-moderate angles of incidence, the lift on a fixed wing is an increasing function of α_w (i.e. $C_{L_{x_w}}$ is positive). The wing's contribution can therefore only be stabilizing if one or both of x_w and z_w is negative (i.e. if the wing aerodynamic centre lies behind or above the centre of gravity). The stability gained if the aerodynamic centre lies behind the centre of gravity is similar to that provided by the tailplane of a conventional aircraft. The common principle is that because lift acts behind the centre of gravity, the increase in lift resulting from a nose-up disturbance will tend to bring the nose back down again. The "pendulum stability" provided by having the centre of gravity beneath the aerodynamic centre is similar to that of a ship (Lighthill, 1974) and is the source of stability in parachutes and paragliders.

The wing's contribution to M_0 is obtained, in coefficient form, by substituting the identity $\alpha_b = \alpha_w - i_w$ into eqn (2) and setting $\alpha_w = 0^\circ$, where i_w is the wing angle between the x -axis and the wing zero-lift chord. Since the lift coefficient at $\alpha_w = 0^\circ$ is zero we have

$$C_{M_{0_w}} = - \frac{C_{D_{0_w}}}{c_w} (x_w \sin i_w + z_w \cos i_w) + C_{M_{ac_w}}, \quad (5)$$

where a zero subscript indicates that the value of the coefficient is to be taken at $\alpha_w = 0^\circ$. Since i_w and x_w are usually small, the drag on the wings will make a positive contribution to M_0 if z_w is negative, but will make a negative contribution to M_0 if z_w is positive. In practice, the wings are most likely to contribute to balance through the

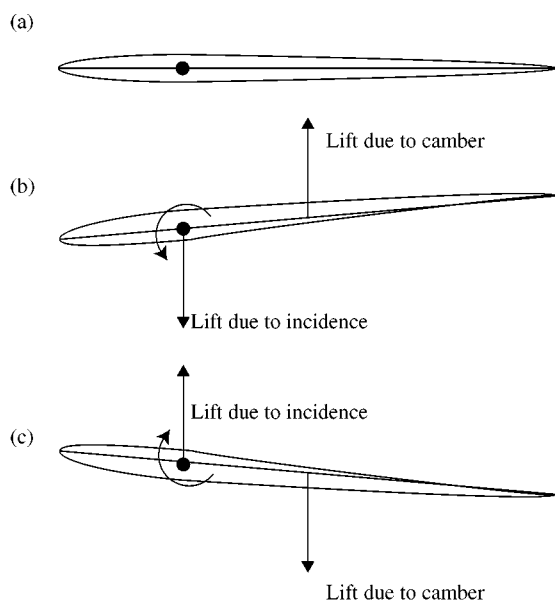


FIG. 3. (a) Symmetric airfoils generate no net pitching moment about the aerodynamic centre. (b) Positively cambered airfoils generate negative (nose-down) pitching moments because the positive lift due to camber forms a negative couple with the negative lift due to incidence when the net lift is zero. (c) Negatively cambered airfoils generate positive (nose-up) pitching moments because the negative lift due to camber forms a positive couple with the positive lift due to incidence when the net lift is zero.

pitching moment coefficient $C_{M_{ac_w}}$ and we must consider how this moment arises in more detail.

Symmetric airfoils [Fig. 3(a)] induce no pitching moment about the aerodynamic centre. This is because all of the lift on a symmetric airfoil derives from its incidence relative to the flow, and acts, by definition, through the aerodynamic centre. The positive camber of a typical airfoil [Fig. 3(b)], however, generates extra lift independent of the incidence of the airfoil. This lift due to camber acts behind the aerodynamic centre, at approximately the midpoint of the airfoil. Hence, when the total lift on the airfoil is zero, the lift due to incidence must be opposite and equal to the lift due to camber. Since the two lift forces act at different points, the resultant of the system will be a negative (nose-down) pitching couple [Fig. 3(b)]. Negative camber [Fig. 3(c)] has the opposite effect, inducing a positive (nose-up) pitching moment. Whereas the nose-up pitching moment generated by negative camber will aid balance in a stable animal, the nose-down moment generated by positive camber will tend to

oppose balance. Reflex-cambered airfoils are positively cambered over most of their surface but deflected upwards close to the trailing edge. They generate near-zero pitching moments about the aerodynamic centre, and are typically designed to provide neutral balance.

Unfortunately, using negative or reflex camber to provide balance reduces the lift that can be generated relative to a wing using positive camber. Hence, to generate the same net lift, a negative or reflex-cambered wing must have a larger surface area than a positively cambered wing, which will increase drag and diminish the lift-to-drag ratio. Selection to improve the lift-to-drag ratio can therefore oppose selection for stable balanced flight. Most flying animals have positively cambered wings that will give a good lift-to-drag ratio but make it harder for a stable animal to balance. For, example, a pair of dragonfly fore- or hindwings glued to a thin supporting rod will only glide in a stable fashion when inverted (Azuma & Watanabe, 1988; Okamoto *et al.*, 1996; G. K. Taylor, pers. obs.), because the negative (nose-down) pitching moment induced by their positive camber upsets their balance.

In addition to the pitching moment due to camber, further pitching moments may be generated by an uneven lift distribution. Suppose that the net lift on the wing is zero (i.e. $\alpha_w = 0^\circ$). In this case, the local lift will only be zero at all spanwise stations across the wing if the wing itself is untwisted. This is probably never the case in flying animals. If the wing is twisted nose-down at the tips (an arrangement termed wash-out) and also swept backward, the negative lift near the tips will generate a positive (nose-up) pitching couple in concert with the positive lift generated on proximal parts of the wings (Fig. 4). The converse would apply if the wing was twisted nose-up at the tips (an arrangement termed wash-in), or swept forwards, rather than backwards. Since any net lift generated at positive angles of incidence can be considered to act through the aerodynamic centre, the wash-out moment and pitching moment due to camber will combine additively to provide a moment about the aerodynamic centre that is independent of the overall angle of attack. A wash-out distribution on a backward-swept wing or a wash-in distribution

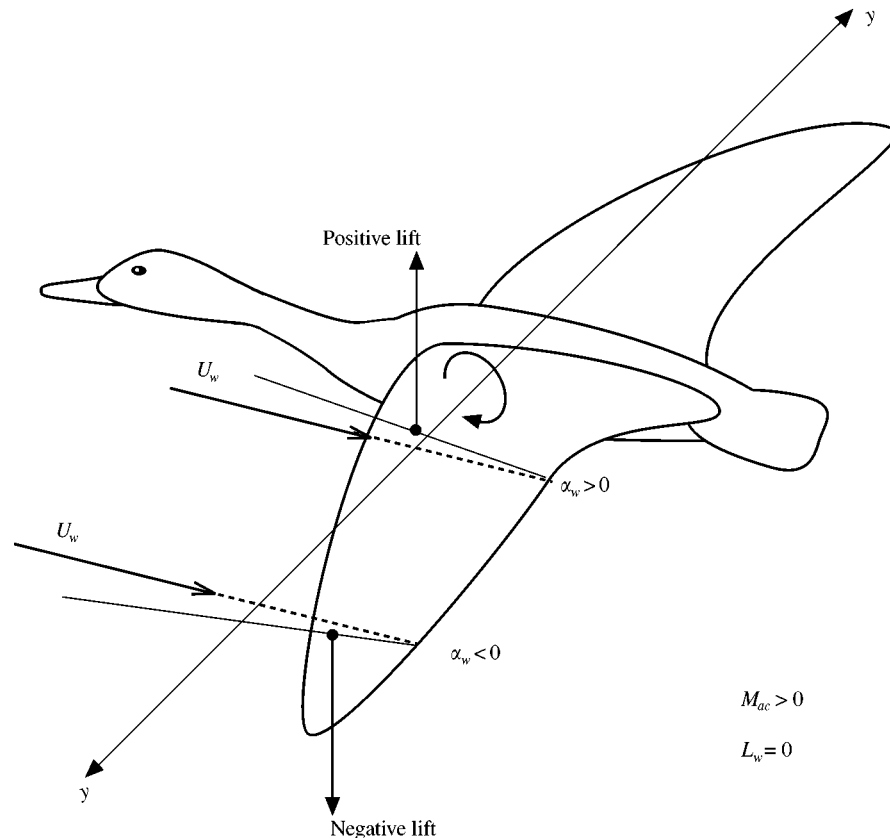


FIG. 4. Effect of wash-out on a backward-swept wing. Nose-down twisting at the tips causes the tips to generate negative lift when net lift is zero. Proximal portions generate positive lift. The resultant of this distribution is a positive (nose-up) pitching couple on a backward-swept wing.

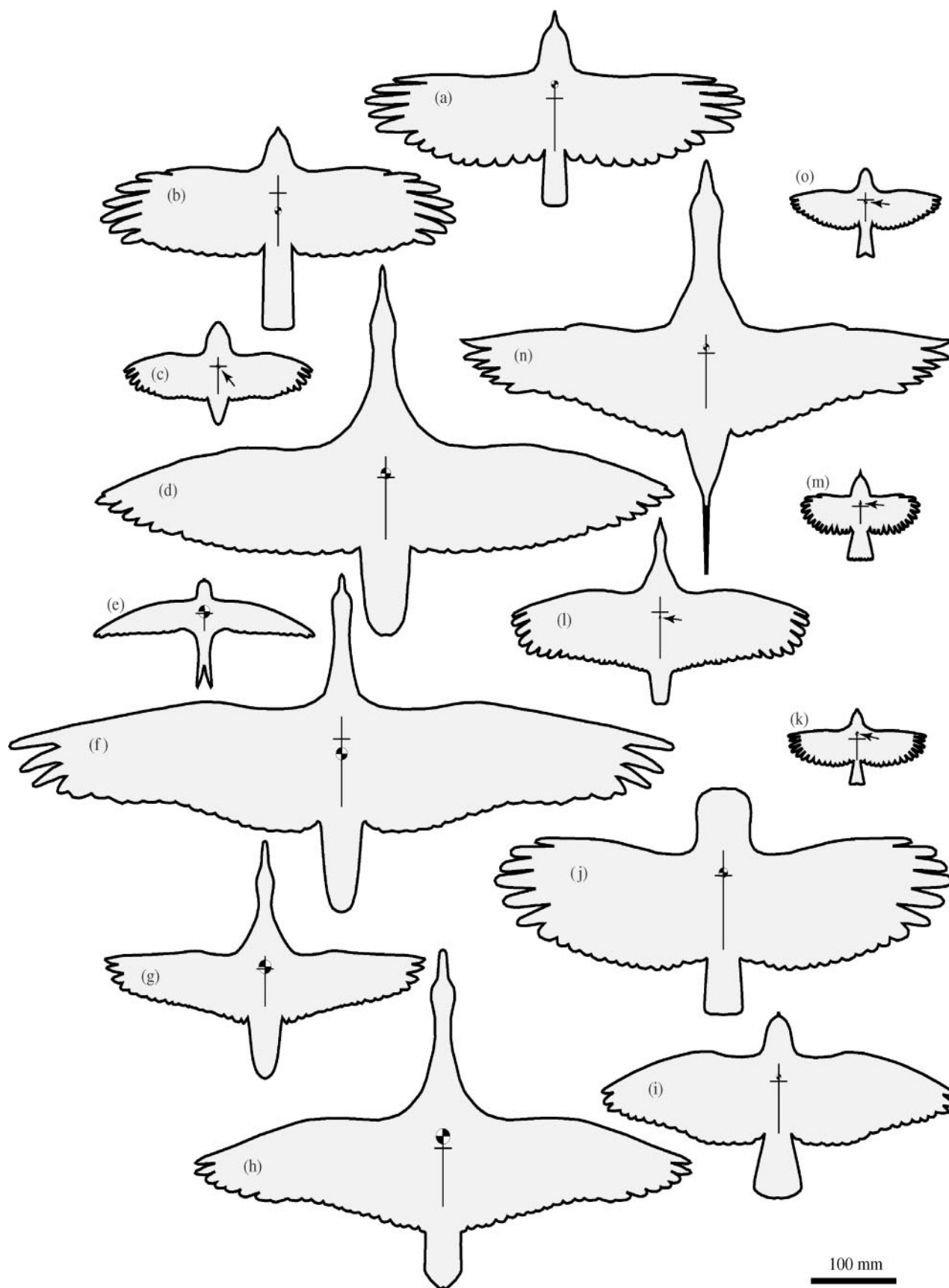
on a forward-swept wing could therefore be used to provide balance in a stable animal, in the same way as a negative or reflex-cambered airfoil. Once again, since twisting and sweeping of the wing both reduce the maximum lift coefficient, selection to improve the lift-to-drag ratio will oppose selection for stable balanced flight.

5.3. CONTRIBUTION OF THE WINGS IN BIRDS

Are the wings sufficient to provide both stability and balance in flying animals? Figure 5 shows the positions of the wing aerodynamic centre and centre of gravity for a variety of birds (see figure legend for methods). Contrary to expectations (Thomas, 1993, 1996b; Thomas & Balmford, 1995), the aerodynamic centre of the wings lies behind the centre of gravity in 11 of the 15 species, suggesting that the antero-posterior placement of their wings is inherently stabilizing [eqn (4)]. Clearly, the validity of this conclusion

depends upon how closely the wing positions correspond to those adopted during gliding. Since the wings are held well forward in Fig. 5, the positions of their aerodynamic centres should represent lower bounds upon stability, reinforcing the conclusion that their antero-posterior placement is inherently stabilizing. Birds will also possess pendulum stability, since their wings are usually held well above the body during glides. This pendulum effect is enhanced by the dorsal location of the air sacs of the respiratory system and by the ventral location of heavier organs such as the intestines (Marey, 1890).

The construction of the flight motor further contributes to the pendulum effect in birds, because the major flight muscles powering the upstroke and downstroke (the supracoracoideus and the pectoralis) both originate beneath the wings. In bats, on the other hand, the upstroke is powered mainly by the dorsal scapular muscles, leading to an inherently weaker pendulum effect



than in birds (Vaughan, 1970c). A special adaptation is required to enable a ventral muscle to power the upstroke in birds—the insertion tendon of the supracoracoideus runs through a foramen in the pectoral girdle and over a process of the coracoid to insert dorsally upon the humerus and reverse the muscle's primitive function. The presence of a pronounced acrocoracoid process and a groove possibly accommodating the supracoracoideus tendon could indicate a similar arrangement in pterosaurs (Padian, 1983, 1985), but others have assumed a bat-like construction (Bramwell & Whitfield, 1974). It is possible that the stability conferred by having a low centre of gravity has been one of the factors contributing to the aerial success of birds, permitting wider variation in flight morphology than might otherwise be possible.

Although the wings of birds may often be stabilizing, their contribution to M_0 would need to be positive for them to be sufficient for balanced flight, which would almost certainly require $C_{M_{ac_w}}$ to be positive. This is consistent with Pennycuick's (1975) observation that birds use backward-sweep with wash-out during fast gliding flight. The total pitching moment about the

aerodynamic centre appears to have been measured only once for the wing of a flying animal: Withers (1981b) measured the forces and moments on the wing of a red-shouldered Hawk *Buteo lineatus* in a wind tunnel. The weight of the wing acted along the pitching axis, so the only forces contributing to the measured pitching moment at $L_w = 0$ were a net drag and the combined moments due to wash-out and camber. Since drag would have operated close to the point about which the forces were measured, it would have contributed little to the total pitching moment. The pitching moment measured by Withers (1981b) at $L_w = 0$ will therefore be approximately equal to $C_{M_{ac_w}}$, which yields a value for $C_{M_{ac_w}}$ of approximately 0.56.

The airfoil sections of birds' wings are positively cambered and therefore generate negative pitching moments about the aerodynamic centre. Hummel & Möllenstädt (1977) calculated the pitching moment due to camber from geometric measurements of the wing of a house sparrow *Passer domesticus* made by Bilo (1971), yielding section pitching moment coefficients between -0.08 and -0.20 . Values for efficient man-made airfoils are also negative but are often smaller—for example, the pitching moment coefficient on a NACA 63-210 airfoil is -0.035 (Anderson, 1991). In any case, since the camber moment on the red-shouldered Hawk's wing should have been negative, the overall positive value of the net pitching moment coefficient must derive from the strong wash-out distribution of the wings. The twist of a red-shouldered Hawk's wing is quantitatively similar to that of other birds in this respect (Withers, 1981a), suggesting that $C_{M_{ac_w}}$ could be comparably large and positive in other species with a similar degree of sweepback.

In conclusion, birds' wings may often be inherently stabilizing and may also be sufficient to provide balance. Despite the presence of a horizontal tail, birds may therefore bear more similarity to tailless aircraft than to conventional tailed types (Thomas, 1993; Nickel & Wohlfahrt, 1994). Certainly, most birds can still fly after losing their tails (Hankin, 1913; Holst & Kuchemann, 1942; Maynard Smith, 1952; Pennycuick & Webbe, 1959; Herzog, 1968; Pennycuick, 1975; Hummel, 1992), though this has usually been interpreted to mean they must be maintaining

FIG. 5. Flight morphology of 15 birds, from tracings around dead specimens with the wings and tail held in gliding position. The stem of each cross marks the length and position of the wing mean chord, determined as wing area over wing span and centred upon the centre of area of the wing. Span, area and centre of area were determined using NIH Image 1.62. The horizontal bar marks the mean quarter chord point, approximately equivalent to the mean aerodynamic centre. The centre of the partially filled circle denotes the position of the centre of gravity, determined as the mean point of intersection of three plumb lines taken by hanging the bird from three different points on its wings and body. The size of the circle marker provides an indication of the absolute measurement error, being the largest circle to scale that would fit within the triangle formed by joining the points of intersection of the three lines. The position of the centre of gravity is indicated with an arrow where the circle marker is very small: (a) jackdaw *Corvus monedula*; (b) sparrowhawk *Accipiter nisus*; (c) quail *Coturnix coturnix*; (d) eider *Somateria mollissima*; (e) swift *Apus apus*; (f) red-breasted Goose *Branta ruficollis*; (g) hooded merganser *Mergus cucullatus*; (h) mallard *Anas platyrhynchos*; (i) stock dove *Columba oenas*; (j) tawny owl *Strix aluco*; (k) chaffinch *Fringilla coelebs*; (l) moorhen *Gallinula chloropus*; (m) robin *Erithacus rubecula*; (n) pintail *Anas acuta*; (o) greenfinch *Carduelis chloris* (data collected by ALRT).

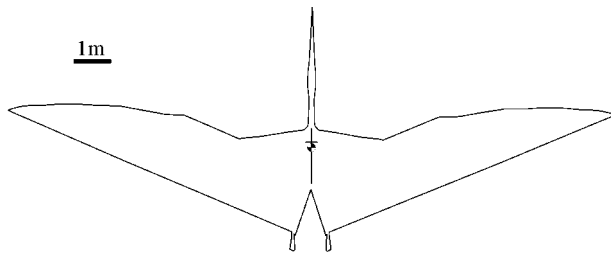


FIG. 6. Reconstruction of the pterosaur *Pteranodon ingens* in gliding flight, redrawn after Bramwell & Whitfield (1974). The stem of each cross marks the length and position of the wing mean chord, determined as in Fig. 5. The horizontal bar marks the mean quarter chord point, approximately equivalent to the mean aerodynamic centre. The centre of the partially filled circle denotes the position of the centre of gravity calculated by Bramwell & Whitfield (1974). The aerodynamic centre appears to have lain ahead of the centre of gravity, so *Pteranodon* would probably have been inherently unstable.

stability actively (e.g. Holst & Kuchemann, 1942; Maynard Smith, 1952; Hummel, 1992). The more parsimonious explanation is that the wings alone are sufficient to provide both stability and balance in birds.

5.4. CONTRIBUTION OF THE WINGS IN OTHER GLIDING ANIMALS

Figure 6 shows the calculated positions of the wing aerodynamic centre and centre of gravity for the pterosaur *Pteranodon ingens* (redrawn after Bramwell and Whitfield, 1974). Unlike in most modern birds (Fig. 5), the pterosaur's aerodynamic centre appears to be ahead of the centre of gravity, lending support to Bramwell and Whitfield's supposition that *Pteranodon* was inherently unstable. If *Pteranodon* were unstable then it would have required a negative pitching moment for balance. Remarkably, the pterosaur literature provides some support for this prediction. The construction of pterosaurs' wrists was such that as the wings were swept forward, the tips were automatically lowered and twisted down at the leading edge (Hankin & Watson, 1914; Short, 1914; Bramwell & Whitfield, 1974). The wings should therefore have developed increasing wash-out as they were swept forward, which would produce a pitching moment in the correct direction to provide balance.

The antero-posterior placement of the wings is also destabilizing in two-winged flying fish *Exocoetus*, irrespective of whether the wings are fully spread [Fig. 7(a)] or swept back through an angle of 30° [Fig. 7(b)]. However, flying fish are stable fliers (Schaller, 1985) with little scope for actively maintaining stability, and they must therefore gain stability through the strong pendulum effect conferred by their high-winged configuration (Hankin, 1926; Breder, 1930; Davenport, 1992). This effect is further enhanced in flying fish by raising the wingtips to provide dihedral (which elevates the aerodynamic centre relative to the centre of gravity) and by inclining the body tail down during flight (which rotates the centre of gravity down with respect to the wings). In general, the pendulum effect seems to be a more important source of stability in flying animals than in aircraft: in animals with no additional stabilizing surfaces it may sometimes be the only source of passive stability.

5.5. CONTRIBUTION OF A SECOND LIFTING SURFACE: THEORY

Although it is possible to make a flying wing that is both balanced and inherently stable, the necessary devices of sweep, twist and camber increase drag and limit total lift production. The resulting conflict in attaining balanced flight with a good lift-to-drag ratio is one of the reasons why tailless aircraft are rare (Nickel & Wolfhart, 1994), and may also explain why many flying animals employ a second lifting surface of some kind. The pitching moment equations for a second lifting surface (e.g. a pair of hindwings) are formed in the same way as for the first pair of wings, substituting

$$C_{L_{w2}} = \frac{2L_{w2}}{\rho U_{w2}^2 S_{w2}}, \quad C_{D_{w2}} = \frac{2D_{w2}}{\rho U_{w2}^2 S_{w2}},$$

$$C_{M_{ac_{w2}}} = \frac{2M_{w2}}{\rho U_{w2}^2 S_{w2} c_{w2}} \quad (6)$$

for the various coefficients, where S_{w2} is the area of the second lifting surface and U_{w2} the speed of flow over it. This is approximately equal to the speed of flow over the wings during

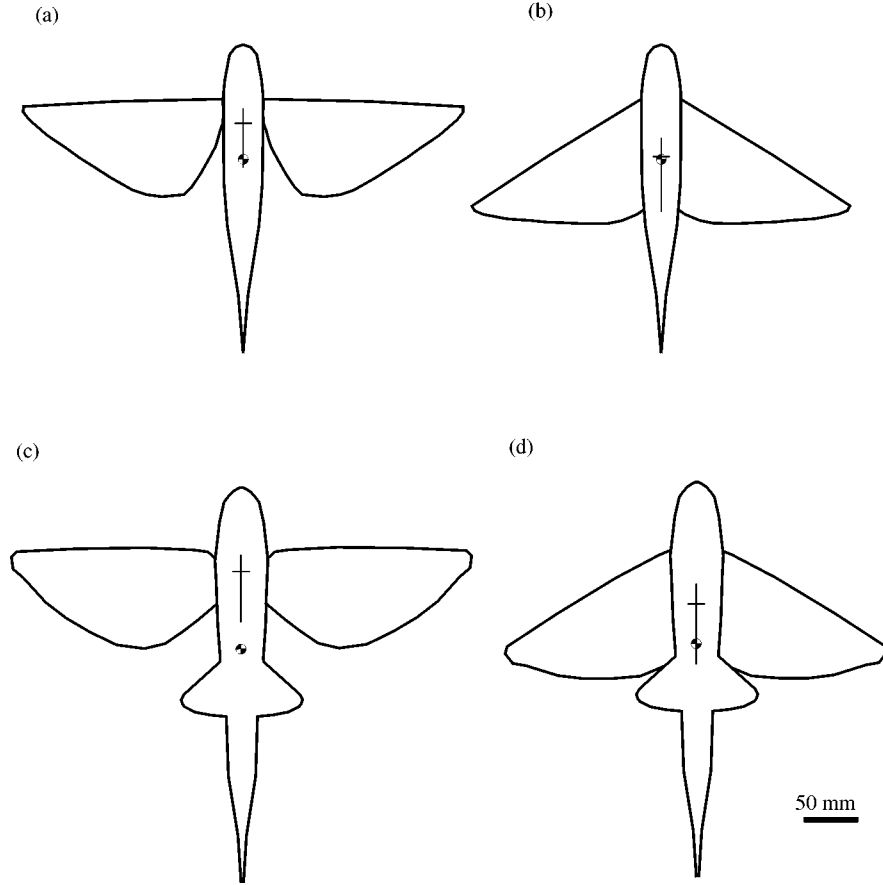


FIG. 7. Flight morphology of the two-winged flying fish *Exocoetis obtusirostris* (a, b) and four-winged flying fish *Cypsilurus cyanopterus* (c, d) redrawn after Davenport (1992). The stem of each cross marks the length and position of the wing mean chord, determined as in Fig. 5. The horizontal bar marks the mean quarter chord point, approximately equivalent to the mean aerodynamic centre. The centre of the partially filled circle denotes the position of the centre of gravity measured by Davenport (1992). (a, c) Wings fully spread. (b, d) Pectoral fins swept back through approximately 30° . The aerodynamic centre lies ahead of the centre of gravity in both cases, so the longitudinal placement of the pectoral fins is inherently destabilizing.

gliding, so we have

$$C_{M_{0_{w_2}}} = \frac{S_{w_2}}{S_w c_w} [C_{L_{0_{w_2}}}(x_{w_2} \cos i_w - z_{w_2} \sin i_w) - C_{D_{0_{w_2}}}(x_{w_2} \sin i_w + z_{w_2} \cos i_w) + C_{M_{ac_{w_2}}} c_{w_2}] \quad (7)$$

for the contribution of a second lifting surface to M_0 . Comparing eqns (7) and (5), we can see that a second lifting surface can provide balance in exactly the same way as a single pair of wings. However, the presence of the lift terms in eqn (7) provides a further mechanism by which this may be achieved. Since i_w is usually small, the effect of

$C_{L_{0_{w_2}}}$ depends primarily upon the sign of x_{w_2} . Since x_{w_2} is bound to be negative for a pair of hindwings, it is clear from eqn (7) that $C_{L_{0_{w_2}}}$ must be negative for a hindwing to make a positive contribution to M_0 .

In a stable animal, the hindwings must generate a negative lift force when the angle of incidence of the forewings is zero if they are to provide a negative (nose-down) pitching moment for balance. This means that the hindwings themselves must be inclined nose-down with respect to the forewings. Notice that this does not imply that the hindwings will generate negative lift at equilibrium, since at equilibrium the incidence of both fore- and hindwings is likely to be positive. Conversely, a canard (for which x_{w_2} is positive) would need to be inclined nose-up with respect to

the wings to provide balance. In both cases, the lifting surfaces form a shallow "V" when viewed from the side—a feature sometimes known as longitudinal dihedral. The opposite arrangement would be required to provide balance in an unstable animal, so the presence of longitudinal dihedral is a good indicator that an animal is inherently stable.

Like other devices to provide balance, longitudinal dihedral lowers the lift-to-drag ratio by reducing the proportion of the animal's weight that the rear lifting surface can support at equilibrium (Maynard Smith, 1952; Thomas, 1996b). This can be alleviated by moving the centre of gravity back, which will lower stability and result in a net positive pitching moment that can be compensated by increasing the incidence of the rear lifting surface, thereby increasing the total lift coefficient at equilibrium (Thomas, 1996b). Making the load on the tail more positive can in turn reduce induced drag (Laitone, 1978a; Butler, 1982; Kroo, 1982; Thomas, 1996b), and modern transport aircraft such as the Boeing 727 could achieve a saving in total drag of about 5% at cruising speeds by taking the appropriate positive load on the tail (Laitone, 1978b). Analogous benefits result from lowering stability on a flying wing, since this reduces the amount of sweep and wash-out required for balance. Lowering stability can therefore improve the glide angle of a flying animal by improving the maximum lift-to-drag ratio attainable during balanced flight. Selection for shallower glide paths and improved energetic efficiency might therefore be expected to lead to the evolution of reduced passive stability in the same way as selection for enhanced manoeuvrability (Maynard Smith, 1952; Thomas, 1993, 1996b; Thomas & Balmford, 1995).

5.6. CONTRIBUTION OF A SECOND LIFTING SURFACE: CANARDS AND HINDWINGS IN NATURE

The primitive condition in pterygote insects is to have two functional pairs of wings. In dragonflies and most other four-winged insects, the hindwings are located in a stabilizing position behind the centre of gravity, and are probably sufficient to make the primitive four-winged configuration of pterygote insects inherently stable (Lighthill, 1974). For example, dead desert

locusts *Schistocerca gregaria* make stable gliders (Wilson, 1968), and the gliding posture of migratory locusts *Locusta migratoria* also appears to favour stability because the hindwings are swept well back against the abdomen (Baker & Cooter, 1979). Longitudinal dihedral may also be used by dragonflies, which rest with their hindwings tilted nose-down with respect to the forewings (G. K. Taylor, pers. obs.).

In cypsilurid flying fish, both sets of paired fins are enlarged to provide lifting surfaces [Fig. 7(c) and (d), cf. Fig. 7(a) and (b)] and longitudinal dihedral is certainly used by four-winged flying fish to provide balance (Breder, 1930). The enlarged pelvic fins of four-winged flying fish also sit well behind the centre of gravity and are probably essential for stability (Breder, 1930; Lighthill, 1974) because the centre of gravity lies even further back in four-winged flying fish than in two-wingers (Fig. 7; Davenport, 1992). The presence of longitudinal dihedral is a good indication that gliding dragonflies and four-winged flying fish are passively stable.

Some flying animals also have a small accessory lifting surface, or canard, ahead of the wings. For example, flying lizards *Draco* and geckoes *Ptychozoon* have independently evolved small winglets on either side of the neck (Schaller, 1985), and the enigmatic *Sharovipteryx*—a lizard-like reptile from the Triassic—is also supposed to have possessed a membranous lifting surface ahead of the main wing (Gans *et al.*, 1987). A canard cannot provide passive stability if it lies ahead of the centre of gravity, so its most likely function is to provide balance or control. Beetles' elytra likewise form a canard-like surface in flight that might be used for balance. Certainly, the prothoracic winglets of certain Palaeozoic insects (see Wootton & Kukalová-Peck, 2000 for review) have usually been considered to have operated as canards to provide balance (Flower, 1964; Wootton, 1976), though it has also been suggested that they acted as mechanical linkages responsible for depressing the wing leading edge to effect a primitive form of flight control (Hankin, 1926).

5.7. CONTRIBUTION OF THE AVIAN TAIL

Horizontal tail surfaces are found in birds, flying geckoes *Ptychozoon* and some gliding

mammals—notably the feathertail glider *Acrobates pygmaeus* (Diprotodontia: Acrobatidae) (Nowak, 1999a). Here we will consider only the tails of birds. Like any other lifting surface, a bird's tail generates lift by imparting additional downward momentum to the mass of air passing over it. However, the aerodynamics differ from those of a conventional wing in several respects, due mainly to the very low aspect ratio of the avian tail. Slender lifting surface theory predicts that the momentum of the flow over the tail will only increase if the tail increases in width along its length such that an increasing mass of air is accelerated into the flow (Thomas, 1993). Positive lift is only expected to be generated by the area of tail ahead of the point of maximum continuous span, and can be considered to act at the centre of area of this part of the tail (Thomas, 1993). The aerodynamic centre of a triangular tail is therefore expected to lie two-thirds back from the apex, rather than a quarter of the way back from the leading edge as for a high aspect ratio tailplane (Thomas, 1996b). This will greatly enhance the lever arm upon which the lift acts, dispensing with the need for a long, drag-inducing tail boom from which conventional aircraft suffer.

Since the distance between the aerodynamic centre of the tail and the centre of gravity along the z -axis is small compared to the distance along the x -axis we may drop the z -terms and write the contribution of a flat triangular tail as

$$M_t = x_t(L_t \cos \alpha_b + D_t \sin \alpha_b), \quad (8)$$

where L_t and D_t are the net lift and drag resolved in the same directions as L_w and D_w , and x_t is the coordinate of the centre of area within the body axes defined earlier. Slender lifting surface theory gives the lift coefficient of a flat triangular tail as

$$C_{L_t} = \frac{\pi}{2} AR_t \alpha_t, \quad (9)$$

where α_t is the effective angle of incidence of the tail, measured between the tail zero-lift line and the oncoming flow after the wings, and where AR_t is its effective aspect ratio, defined as the square of the maximum span over the total area

(Thomas, 1993). The position of the tail in the wake of the body will certainly alter the aerodynamic forces on the tail compared to those on a normal delta wing, but modelling the avian tail as a delta wing nevertheless gives a better feel of its effects upon stability than does modelling it as a conventional tailplane.

Equation (9) describes a force acting normal to the oncoming flow over the tail rather than parallel to L_w as in eqn (8). This difference is the result of downwash from the wings, which can be approximated using lifting line theory if the aspect ratio is sufficiently high (e.g. Jones, 1990; Anderson, 1991; Klatz & Plotkin, 1991). This gives the downwash angle (call this ε), in radians, as

$$\varepsilon \approx \frac{C_{L_w}}{\pi AR_w \phi}, \quad (10)$$

where AR_w is the aspect ratio of the wings, defined as the square of the span over the wing area and ϕ is an efficiency factor that takes a value of one for an ideal elliptic lift distribution, and is in the range 0.6–0.9 in most high performance aircraft (Vinh, 1993). For the common nighthawk *Chordeiles minor*, in which a single wing has been measured to have an aspect ratio of 4.1 and a maximum steady lift coefficient of 1.15 (Withers, 1981a), the maximum induced downwash angle during gliding flight would be around 5° assuming an elliptic lift distribution. This is likely to be an overestimate because the downwash would be smaller if the two wings functioned together as a single wing of high aspect ratio. The downwash from the wings should therefore make a small enough difference to the lift coefficient of the tail that we may reasonably neglect its influence in the equations for stability.

Putting eqn (8) in dimensionless form and substituting eqn (9) yields

$$C_{M_t} = \frac{S_t x_t}{S_w c_w} \left(\frac{\pi}{2} AR_t \alpha_t \cos \alpha_b + C_{D_t} \sin \alpha_b \right), \quad (11)$$

where S_t is the area of the tail. Differentiating with respect to α and assuming that the body axes are stability axes, such that $\alpha_b = 0^\circ$, yields the equilibrium value of the pitching moment

coefficient derivative of the tail:

$$C_{M_{z_t}} = \frac{S_t x_t}{S_w c_w} \left(\frac{\pi}{2} AR_t + C_{D_t} \right). \quad (12)$$

Like any other lifting surface whose aerodynamic centre lies behind the centre of gravity, a triangular tail will be inherently stabilizing. However, it is clear from eqn (12) that the strength of this contribution depends upon just a few simple parameters. For example, since x_t and S_t are increasing linear functions of tail length, whilst AR_t is a decreasing linear function, stability should increase more or less linearly with tail length, provided that C_{D_t} is small. Hummel's (1992) wind tunnel study of the effect of adding a bird-like tail to a rectangular wing provides good empirical confirmation of this prediction.

Although eqn (12) describes the forces on a triangular tail, it is clear that areas of tail behind the point of maximum continuous span, such as streamers, pintails or the tapering part of a graduated tail, will provide stability by increasing C_{D_t} . Such additions usually reduce the lift-to-drag ratio (Evans & Thomas, 1992; Balmford *et al.*, 1993, 1994; Thomas & Balmford, 1995, but see Norberg, 1994; Evans & Thomas, 1997 for a mechanism by which streamers may enhance the lift-to-drag ratio). Selection for drag-based stability offers an adaptive explanation for the possible selection of these kinds of tail prior to—or in the absence of—sexual selection. It is also worth noting in passing that tapering areas of tail, such as on the graduated tail of a magpie *Pica pica*, should theoretically generate negative lift by decreasing the momentum of the flow (Thomas, 1993). Together with the positive lift on the proximal portion of the tail, this could produce a positive pitching couple, analogous to the wash-out moment on a wing. The provision of balance could therefore offer a second adaptive explanation for the evolution of graduated tails. However, since the flow behind the point of maximum continuous span will be dominated by the wake from the area ahead (Thomas, 1993), the biological consequences of this interesting theoretical effect may be small. If birds' tails provide balance at all, then it is more likely that they do so through the conventional mechanism of longitudinal dihedral.

5.8. CONTRIBUTION OF THE BODY AND ITS APPENDAGES

The body itself may sometimes contribute to the total lift in gliding animals. For example, this is probably the case in the zebra finch *Taeniopygia guttata* during the ballistic phase of bounding flight (Csicsácky, 1977). Here we will assume that any body lift may be accounted for by simply augmenting the wing lift coefficient. From the viewpoint of stability, though, the aerodynamic moments generated by the bodies of gliding animals are of greater practical consequence. The aerodynamic moments generated by pressure distributions around streamlined bodies have been the subject of much study, related initially to the design of airships and later to aircraft fuselages. Scale effects mean that viscous effects may also be large, so we will begin by examining the non-viscous forces on a streamlined body and will treat the effects of friction drag separately.

A bilaterally symmetrical body has three directions of equilibrium, corresponding to its three principal axes (Munk, 1924). A turning moment M_b will be generated if the body is orientated in any other direction to the flow. Since a change in the kinetic energy of the flow is required for any work to be done, an equilibrium direction will be stable if the kinetic energy of the flow is a minimum. The kinetic energy of the flow may be expressed as $\frac{1}{2}\rho U_b^2 k$, where U_b is the speed of the oncoming flow over the body and k characterizes the volume of the wake in a given orientation. M_b is equal to the change in the kinetic energy of the flow with a change in the angle of incidence. Hence, since M_b is zero when α_b is 0 or 90°, we may write

$$M_b = \frac{1}{2}\rho U_b^2 (k_1 - k_2) \sin 2\alpha_b, \quad (13)$$

where k_1 and k_2 are coefficients characterizing the volume of the wake when the body is moving parallel to its longitudinal and dorso-ventral axes, respectively (Munk, 1924). Like the moment about the aerodynamic centre of a wing, M_b is an aerodynamic couple and hence does not depend upon the position of the centre of gravity. Equation (13) neglects interference from the wings. Portions of the body in the downwash field behind the wings have a decreased effective angle of incidence, whilst portions of the body in the

upwash field ahead of the wings have an increased angle of incidence. The qualitative result of this interference is a positive pitching moment that increases with the angle of attack (Etkin & Reid, 1996). Approximate methods for estimating the quantitative effects of this induced flow are available in the aircraft literature (e.g. Multhopp, 1942) but we will not consider these here.

The coefficients k_1 and k_2 may be expressed in dimensionless form as fractions of the body's volume (v) denoted by C_{k_1} and C_{k_2} , values of which may be calculated exactly for simple geometrical forms (Lamb, 1918). The difference ($C_{k_1} - C_{k_2}$) is positive for bodies that are longer than they are wide and larger for more elongate forms: other things being equal, the forces on the elongated abdomen of a dragonfly will generate a stronger pitching moment than the forces on the stubby body of a hawkmoth. Putting eqn (13) into dimensionless coefficient yields

$$C_{M_b} = \frac{v}{S_w c_w} (C_{k_1} - C_{k_2}) \sin 2\alpha_b. \quad (14)$$

Since ($C_{k_1} - C_{k_2}$) is always positive, it is clear by inspection that an elongated body will only make a positive contribution to M_0 if the body angle is also positive. This may help provide balance in two-winged flying fish, which fly in a tail-heavy fashion and have no other source of balance besides that afforded by the wings.

Differentiating eqn (14) with respect to α gives

$$C_{M_{\alpha_b}} = \frac{2v}{S_w c_w} (C_{k_1} - C_{k_2}) \cos 2\alpha_b. \quad (15)$$

Since the body angle is likely to be much less than 45° , the non-viscous forces on the body are bound to make a positive, destabilizing contribution to $\partial M/\partial \alpha$, so a streamlined body will always be destabilizing when non-viscous forces dominate (i.e. at high Re). For example, Wootton & Ellington (1991) found that balsa cylinders weighted to be kinematically similar to the bodies of protopterygote insects could only be made to glide stably by adding a tail.

At the low Reynolds numbers at which most flying animals operate, the effects of friction drag will also be significant. Viscous forces are bound

to contribute to the aerodynamic damping, but may also lead to the production of static moments that could be used to provide static stability and balance. The contribution of friction drag is simply

$$C_{M_d} = \frac{S_d}{S_w c_w} C_{D_d} (x_d \sin \alpha_b - z_d \cos \alpha_b), \quad (16)$$

where x_d and z_d are the coordinates of the centre of drag within the body axes defined earlier and S_d is some characteristic area. Like the drag on a wing, friction drag on the body and its appendages should generate a positive pitching moment if the centre of drag lies above the centre of gravity. Legs and other structures that lie beneath the centre of gravity will make it harder for a stable animal to balance unless they are tucked up against the body. For example, many animals hold their wings forwards and widely spread when approaching landing (Tucker, 1992; Thomas, 1993), and this may be associated with the nose-down pitching moment generated by the legs. Spreading of the wings has also been observed to occur together with lowering of the feet and spreading of the toes at low flying speeds in a jackdaw *Corvus monedula*, gliding in a wind tunnel (Rosén & Hedenstöm, 2001).

Assuming that the body axes are stability axes, such that $\alpha_b = 0^\circ$, then differentiating eqn (16) with respect to α yields

$$C_{M_{\alpha_d}} = \frac{S_d}{S_w c_w} (C_{D_d} x_d - C_{D_{z_d}} z_d) \quad (17)$$

at equilibrium. On grounds of energetic efficiency we would expect friction drag on the body to be minimized at equilibrium, so $C_{D_{\alpha_d}}$ should be approximately zero. The dorso-ventral placement of the centre of drag should therefore have little effect upon stability. Hence, since C_{D_d} is always large and positive, friction drag will only make a negative, stabilizing contribution to $\partial M/\partial \alpha$ if the centre of drag lies behind the centre of gravity so that x_d is negative. This is why the flight of an arrow or dart is always found at the rear of the shaft. Similarly, an important role of the long furry tails of gliding mammals must be to confer drag-based stability (Schaller, 1985). In New

World flying squirrels *Glaucomys* the tail is noticeably flattened (Nowak, 1999b) and may also provide some lift-based stability. The abdominal cerci of Ephemeroptera, Plecoptera, Palaeodictyoptera and certain other insects would also be expected to confer a high degree of stability (Maynard Smith, 1952; Leston, 1963; Wigglesworth, 1976; Ellington, 1991; Wootton & Ellington, 1991) as might the long abdomens of odonates and other basal insect groups (Dudley, 2000; Wootton & Kukalová-Peck, 2000). Conversely, the shortened abdomens of certain Diptera may be associated with selection for lowered stability (Dudley, 2000).

The flexibility of insects' cerci will tend to reduce their ability to provide static stability, but even flexible structures can contribute to the dynamic damping of disturbances. This will be especially important if the frequency response of the control system is slow compared to the animal's modes of motion. A neat, if artificial, example of this is provided by flies, which are normally unable to fly following removal of their halteres, which provide reflex stabilization in response to high-frequency perturbations (Nalbach, 1993). Their ability to fly is regained, however, if a small length of thread is tied to their abdomen to provide damping (Fraenkel & Pringle, 1938; Fraenkel, 1939). Although the system may still be inherently unstable, its damping is then sufficient for the slower responses provided by the visual control system to provide stability.

An unexpected outcome of the above considerations is that the viscous and non-viscous forces on a streamlined body generate pitching moments that may be in mutual tension. This is an important result because it indicates that stability characteristics may change with airspeed as the Reynolds number varies with the speed of flow. The pitching moment on a fixed lifting surface is also a function of the Reynolds number, but there the effect is less pronounced because lift always dominates the forces. It is possible to envisage scenarios in which this transition could be beneficial. For example, the elongated body of a dragonfly might be more stabilizing during slow cruising flight (when a high degree of stability is required to spot prey against a moving background), but less so during fast chasing flight (when a high degree of manoeuvrability is required to catch prey).

5.9. THE STATIC MARGIN—A MEASURE OF LONGITUDINAL STABILITY

Since we have accounted for interference by assuming that the force coefficients and their derivatives are measured *in situ*, the expressions for the total pitching moment coefficient C_M and its derivative C_{M_x} are obtained by summing the relevant contributions above. Hence, for a bird, C_{M_x} would be obtained by summing eqns (4), (12), (15) and (17), giving

$$\begin{aligned} C_{M_x} = & \frac{x_w}{c_w} (C_{L_{x_w}} + C_{D_w}) + x_t \frac{S_t}{S_w c_w} \left(\frac{\pi}{2} AR_t + C_{D_t} \right) \\ & + x_d C_{D_d} \frac{S_d}{S_w c_w} + \frac{z_w}{c_w} C_{L_w} \\ & + \frac{2v}{S_w c_w} (C_{k_1} - C_{k_2}) - C_{D_{x_d}} z_d \frac{S_d}{S_w c_w} \end{aligned} \quad (18)$$

at equilibrium, when the body axes are also stability axes. The simplification of this expression is extremely informative and also serves to highlight an important difference in the stability of animals and aircraft. Making use of

$$\begin{aligned} C_D &= C_{D_w} + \frac{S_t}{S_w} C_{D_t} + \frac{S_d}{S_w} C_{D_d} \quad \text{and} \\ C_{L_x} &= C_{L_{x_w}} + \frac{S_t}{S_w} \frac{\pi}{2} AR_t, \end{aligned} \quad (19)$$

where C_D is the total drag coefficient and C_{L_x} the total lift coefficient derivative, and substituting $x_d = x_w - l_d$ and $x_t = x_w - l_t$, where l_t and l_d are the distances along the x -axis from the wing aerodynamic centre to the aerodynamic centre of the tail and centre of drag of the body, respectively, we may rewrite eqn (18) as

$$\begin{aligned} C_{M_x} = & \frac{x_w}{c_w} (C_{L_x} + C_D) - l_t \frac{S_t}{S_w c_w} \left(\frac{\pi}{2} AR_t + C_{D_t} \right) \\ & - l_d C_{D_d} \frac{S_d}{S_w c_w} + \frac{z_w}{c_w} C_{L_w} \\ & + \frac{2v}{S_w c_w} (C_{k_1} - C_{k_2}) - C_{D_{x_d}} z_d \frac{S_d}{S_w c_w}. \end{aligned} \quad (20)$$

Setting the left-hand side of eqn (20) to zero gives the condition for neutral stability. The point at which the centre of gravity would need to be placed to satisfy this condition is called the neutral point, though since both x - and z -coordinates are free to vary the neutral “point” as defined here is really a line of points. Solving the resulting expression for x_w gives the x -coordinate of the neutral point relative to the origin (x_n), which for a fixed morphology at equilibrium depends only upon the dorso-ventral placement of the centre of gravity:

$$x_n = -\frac{1}{(C_{L_x} + C_D)} \times \left[-l_t \frac{S_t}{S_w} \left(\frac{\pi}{2} AR_t + C_{D_t} \right) - l_d C_{D_d} \frac{S_d}{S_w} + z_w C_{L_w} + \frac{2v}{S_w} (C_{k_1} - C_{k_2}) - C_{D_{z_d}} z_d \frac{S_d}{S_w} \right]. \quad (21)$$

Substituting eqn (21) back into eqn (20) yields:

$$C_{M_x} = \frac{1}{c} (x_w - x_n) (C_{L_x} + C_D), \quad (22)$$

implying that the stability of even a complex morphology can be expressed in terms of just a few simple parameters. Equivalent forms of the same expression can be found in any textbook on aircraft stability (e.g. Nelson, 1989; Etkin & Reid, 1996; Cook, 1997).

It is clear from eqn (22) that any morphology can be made stable if the centre of gravity can be placed ahead of the neutral point, such that the difference $x_w - x_n$ is negative. This difference, which is equal in magnitude to the longitudinal distance between the centre of gravity and the neutral point, is conventionally normalized by the wing mean chord and reversed in sign to give a dimensionless parameter called the static margin

$$K_n = \frac{x_n - x_w}{c}. \quad (23)$$

Rewriting eqn (22) in terms of K_n finally yields

$$C_{M_x} = -K_n (C_{L_x} + C_D), \quad (24)$$

which demonstrates that the static margin is a direct measure of static pitching stability. The static margin is an extremely important parameter in flight dynamics, because it completely determines whether a given configuration can be inherently stable in pitch. Moreover, since inherent stability opposes deliberate control actions in the same way as accidental disturbances, the control force required to overcome the restoring torque generated following a deliberate change in the angle of attack is directly proportional to the static margin (e.g. Etkin & Reid, 1996). This is why manoeuvrability declines rapidly with increasing inherent stability and why we would predict the static margin to be smaller in animals requiring a high degree of manoeuvrability.

In subsonic fixed-wing aircraft, the neutral point is essentially fixed with respect to the airframe. In flying animals, however, the position of the neutral point will generally depend upon the angle of attack at which equilibrium is attained. The reason for this difference is that in most conventional aircraft the z -terms and drag terms can be safely dropped from the equations, and the lift coefficients can be linearized with respect to α . Although it is probably also reasonable to linearize the lift coefficients with respect to α in gliding animals, we have already demonstrated that it is usually necessary to retain the z -terms and drag terms in the equations for animal flight. In this case, the neutral point cannot be fixed, even in the sense of being a line of points, because retaining the z -terms causes the wing lift coefficient (C_{L_w}), which is a function of α , to appear on the right-hand side of eqn (21). Similarly, retaining the drag terms means that various drag coefficients also appear in eqn (21) (notably C_D in the denominator) and these are also functions of α . Clearly, the lift and drag coefficient derivatives would also be functions of α if the assumption were not made that the coefficients could be linearized with respect to α . It follows that the static margin must also be a function of the equilibrium angle of attack in flying animals, so stability could vary markedly with adjustments in pitch equilibrium. The neutral point is, however, unique for a given equilibrium angle of attack, so calculating the static margin at equilibrium as we have done still provides a meaningful way of comparing the stability of different animals.

Biologists have often overlooked the importance of the centre of gravity in determining the static margin, and hence stability. For example, the long tail of *Archaeopteryx*, the earliest known bird, would certainly have been stabilizing in the sense of ensuring that the neutral point lay much further back than in modern birds (Maynard Smith, 1952; de Beer, 1954; Norberg, 1985; Gatesy & Dial, 1996a, b; Hummel, 1992). However, since the centre of gravity also lay much further back than in modern birds (Hankin, 1926; Pennycuick, 1986; Gatesy, 1990, 1995; Gatesy & Dial, 1996b; Garner *et al.*, 1999) or even other Mesozoic forms (Serenó & Rao, 1992), the static margin itself may have been no greater than in modern birds. The possession of a large tail is therefore insufficient to prove that *Archaeopteryx* either possessed or required a high degree of inherent stability to compensate for a lack of sophisticated flight control, as is commonly implied (e.g. Maynard Smith, 1952; de Beer, 1954; Gatesy & Dial, 1996b). *Archaeopteryx* may simply have needed a large tail to compensate for the posterior position of its centre of gravity, which was ill-suited to stable balanced flight (Hankin, 1926; Peters & Gutmann, 1985; Garner *et al.*, 1999).

5.10. FACULTATIVE ADJUSTMENT OF STABILITY AND EQUILIBRIUM

So far, we have treated morphological parameters in the equations as though they were fixed for a given animal, but this is clearly not the case. Most flying animals are able to vary their flight morphology to adjust their equilibrium condition and their inherent stability. One of the main ways in which flying animals adjust pitch is by sweeping the wings (Hankin, 1913; Pennycuick & Webbe, 1959; Lighthill, 1974; Pennycuick, 1975; Caple *et al.*, 1983; Tucker, 1992). Sweeping the wings forward always induces a nose-up pitching moment about the centre of gravity, but will alter the animal's equilibrium in different ways according to whether the animal is stable or unstable. If $\partial M/\partial \alpha$ is negative then sweeping the wings forward will simply increase the equilibrium angle of attack, because the negative pitching moment that is produced as the angle of attack is increased opposes the positive pitching

moment caused by sweeping the wings forward. If $\partial M/\partial \alpha$ is positive, then the equilibrium angle of attack will be decreased for the opposite reason, despite the fact that the initial response is still a nose-up pitching moment. This peculiar reversal of the normal method of control (Nickel & Wolfhart, 1994) is one reason why it is extremely difficult for a pilot to control a statically unstable aircraft without the aid of a computer-controlled stability management system.

Increasing the equilibrium angle of attack should permit a flying animal to support its weight at slower speeds. Hence, we would expect an inherently stable animal to sweep its wings forward during slow flight, but would predict an inherently unstable animal to sweep its wings back under the same conditions. Birds usually extend their wings forward during slow flight (Hankin, 1913; Pennycuick & Webbe, 1959; Pennycuick, 1986, 1975; Lighthill, 1974; Tucker & Parrot, 1970; Tucker & Heine, 1990; Tucker, 1992; Rosén & Hedenström, 2001), providing independent support for our earlier conclusion from the morphological data that birds are inherently stable in pitch. Usually, the tail is also spread or lowered during slow flight (*ibid.*, see also Thomas, 1993, 1996a; Thomas & Balmford, 1995) and since the resulting negative pitching moment should decrease the equilibrium angle of attack in a stable animal, this has sometimes been used as evidence that birds are inherently unstable (Maynard Smith, 1952). It seems likely, however, that the main reason for spreading the tail is to increase the total area of the flight surfaces at slow speeds. Clearly, what matters is whether the net result of sweeping the wings forward and spreading the tail is a positive or a negative pitching moment, but this will only be settled by experiment. Under some circumstances it may be desirable to vary wing sweep and tail spread without changing the trim angle, and this could presumably be achieved by spreading the tail and sweeping the wings forwards in a complementary manner (Tucker, 1992; Thomas, 1993, 1996a, b).

Spreading the tail also increases stability. For example, increasing the spread of a tail with feathers of uniform length from 30 to 120° increases its effective aspect ratio by a factor of 2.8 and its area by a factor of 4, which will combine to increase $C_{M_{x_i}}$ by an order of magnitude. This

increase in stability is even more pronounced for birds with forked tails which maximize the increase in the maximum continuous span (Thomas, 1993), so forked tails may be a device for rapidly increasing longitudinal stability (Hummel, 1992; Thomas & Balmford, 1995). Clearly, the animal's balance would also be affected if only the spread of the tail were changed. However, whereas the tail's contribution to the total pitching moment depends upon both its incidence and its spread [eqn (11)], its contribution to $\partial M/\partial \alpha$ is independent of its incidence [eqn (12)]. Stability could therefore be increased without affecting balance by simultaneously spreading and raising the tail. The avian tail therefore provides a very flexible means of independently adjusting stability and balance.

Hang glider pilots are able to control speed and pitch by shifting their centre of gravity, and flying animals are expected to do the same (Lighthill, 1974). Specifically, we predict that the centre of gravity should be shifted in the opposite direction to the wings to produce equivalent or complementary changes in stability and equilibrium. The centre of gravity may also move during load carrying and this will inevitably affect equilibrium. For example, raptors carry prey in their talons, which will tend to shift the centre of gravity down and back. This could be counteracted by spreading the tail or sweeping the wings back, as appears to be the case in a photograph of a Gyrfalcon *Falco rusticolus* carrying prey with its tail partially spread (Dunne *et al.*, 1988). On the other hand, we would predict that passerines and other birds that carry loads in their beaks should furl their tails or sweep their wings forwards to oppose the negative pitching moment caused by the centre of gravity moving forwards.

6. Lateral Stability

6.1. QUALITATIVE DIFFERENCES BETWEEN LATERAL AND LONGITUDINAL STABILITY

There are several important differences between lateral and longitudinal stability. First, there is no fundamental problem of balance, because the animal's symmetry ensures that the lateral forces and moments are zero in the

"normal" symmetric flight condition. Second, the position of the centre of gravity has a far weaker effect upon lateral stability than upon longitudinal stability, because the animal's weight does not normally form a roll or yaw couple with the aerodynamic forces. Third, since roll and yaw motions interact, a full dynamic analysis is required before any definitive conclusions can be drawn about lateral stability. Hence, for example, an animal that is statically stable in a constrained yawing motion like that of a weathercock could still be dynamically unstable in free yawing motion because roll and yaw will interact. We will therefore consider lateral stability only briefly, and in qualitative terms.

6.2. SOURCES OF INHERENT YAW STABILITY

Though the wings strongly influence longitudinal stability, they make little contribution to the total yaw moment if they are symmetrical. In conventional aircraft, static yaw stability—like that of a weathercock—is provided by the large vertical tail fin, which produces a sideways lift force when the aircraft yaws and thereby induces a moment about the centre of gravity tending to restore the aircraft to symmetric flight. Flying animals generally lack any form of a vertical stabilizing surface, though the caudal fin of a flying fish is an obvious exception, providing a high degree of yaw stability (Breder, 1930). Wootton & Ellington (1991) have shown experimentally that the addition of caudal filaments mimicking the abdominal cerci of mayflies can also confer significant yaw stability to otherwise unstable gliding cylinders. Surprisingly, the horizontal tails of birds may also allow provide temporary yaw stabilization. Hummel (1992) has shown that the addition of a twisted triangular or forked tail to a rectangular wing increases yaw stability. This increase in stability is independent of the direction of twist, analogous to the more intuitive result that whether an aircraft's propeller is stabilizing or destabilizing depends upon whether it lies ahead of or behind the centre of gravity and not upon its rotational sense (e.g. Etkin & Reid, 1996). Birds may therefore be able to increase yaw stability transiently by twisting their tail about its longitudinal axis. Unlike conventional aircraft, birds can therefore avoid the

constant drag penalty of using a vertical tail fin to provide yaw stability by twisting their horizontal tails temporarily instead (Thomas, 1993, 1997).

In most flying animals, however, the body itself will be the main determinant of yaw stability. Exactly the same arguments apply to the body's contribution to the total yaw moment as to its contribution to the total pitching moment. Hence, whether the contribution of the body is stabilizing or destabilizing in yaw will depend largely upon the Reynolds numbers at which the body operates. At lower Reynolds numbers, an elongated body might provide yaw stability if the centre of gravity lay far enough forward (Wootton & Ellington, 1991). For example, the lateral component of drag acting on a dragonfly's abdomen as it yaws should provide weathercock stability in yaw (Dudley, 2000). However, in general, it is probably safe to follow Brown's (1963) assumption that most flying animals are at least mildly unstable in yaw.

6.3. SOURCES OF INHERENT ROLL STABILITY

Inherent roll stability presents a more complex problem for analysis. Suppose that the body axes are stability axes such that the x -axis is aligned with the equilibrium line of flight. The aerodynamic forces are then independent of the angle of bank, because a rotation about the x -axis leaves the flow over the animal unchanged. The pendulum effect can provide dynamic roll stability but

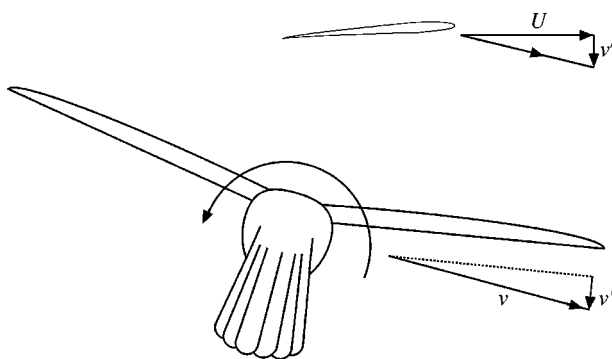


FIG. 8. Positive wing dihedral provides roll stability because the resulting sideslip (v) includes a component normal to the wing (v'). This increases the incidence of the leading wing (see vignette) and decreases the incidence of the trailing wing, thereby generating a roll moment that will tend to restore the animal to level flight.

does not contribute any static roll stability because the line of action of the total aerodynamic force passes through the centre of gravity at equilibrium, and does not change with respect to the body axes following a disturbance from level flight. A weighty body supported beneath the wings could contribute to the inertial damping of roll motions, however, and this probably contributes to dynamic roll stability in locusts and other large insects (Baker, 1979a). In highly manoeuvrable fliers such as swifts (Apodiformes), the wings often lie close to the level of the centre of gravity minimizing roll inertia.

Since rolling itself induces no first-order change in the aerodynamic forces, static roll stability must instead derive from second-order changes in the aerodynamic forces caused by sideslip. Sideslip arises as a geometric consequence of rotation during rolling motions in which the x -axis is not coincident with the line of flight and also occurs because some component of the animal's weight acts along the transverse axis following a disturbance from level flight. Sideslip inevitably leads to asymmetries in the aerodynamic forces. For example, if the wings are held at a positive dihedral angle—that is, if the wings are raised at the tips—then sideslip will increase the incidence of the wing leading the motion and decrease the incidence of the trailing wing (Fig. 8). The resulting rolling moment will tend to restore the animal to its original flight condition, so a wing with positive dihedral will be stable in roll. Negative dihedral—also known as anhedral—has the opposite effect and is therefore destabilizing.

Highly manoeuvrable fliers like swifts *Apus apus* appear to use anhedral during fast glides (G. K. Taylor, pers. obs.), which may enhance roll manoeuvrability, but most other birds use positive dihedral to provide stability during slow glides (Hankin, 1913). Frigate birds (Fregatidae) and gulls (Laridae) have a special form of dihedral in which the proximal part of the wing is raised and the distal part held level or tilted slightly down towards the tips. Flying fish (Breder, 1930) glide with their wings at a dihedral angle, and the muscular winglets of flying lizards *Draco* may also be given positive dihedral to aid roll stability. Locusts (Baker & Cooter, 1979) and dragonflies (Hankin, 1913) use dihedral during glides and many beetles

hold their elytra at a positive dihedral angle. Any form of dihedral reduces the effective span of a wing, however, so once again stability is gained at the cost of a reduced lift-to-drag ratio.

High-winged configurations may contribute to the dihedral effect because deflection of flow by the body increases the incidence of proximal sections of the downward-tipping wing and decreases the incidence of proximal sections of the upward-tipping wing (e.g. Etkin & Reid, 1996). Most birds and insects will gain additional roll stability in this way, though in swifts the placement of the wings midway down the body will tend to minimize any stabilizing moment due the body's effect on the flow. The low-winged configurations of gliding quadrupeds should result in completely the opposite effect, inducing an unfavourable destabilizing roll moment. Roll stability also depends upon the sweep of the wings. On a backward-swept wing, sideslip decreases the effective sweep of the wing leading the motion whilst increasing the effective sweep of the trailing wing. This increases the lift coefficient of the leading wing relative to the trailing wing, which results in a restoring roll couple that will add to any stabilizing roll moment due to dihedral. A forward-swept wing is destabilizing in roll, so whereas roll stability may be reduced if the wings are swept forward for slow flight, the strong degree of sweepback associated with fast flight could increase roll stability (Pennycuick, 1975). However, dihedral is reduced at fast speeds in soaring fulmars *Fulmarus glacialis* (Pennycuick & Webbe, 1959) and wing sweep and dihedral may be reflexively interlocked in birds so as to keep lateral stability within a certain range (Pennycuick, 1975).

Roll handling will also be affected by the shape of the wings. In rigid wings, the area near the wingtips provides inertial and aerodynamic roll damping. This may be one reason why animals that indulge in high-speed aerial chases (e.g. swifts and falcons) have pointed wings. However, if the wings themselves act as roll control devices then the area near the wingtips can provide substantial roll authority because it acts through the longest possible lever arm. Thus, it is expected that animals that require rapid roll responses in low-speed flight, such as animals that hunt by hawking, should have large rounded wingtips.

The only attempt to measure the effect of dihedral in flying animals appears to be a study of beetles in which the role of the elytra as aerodynamic stabilizers was examined (De Souza & Alexander, 1997). Maximum roll angles and oscillation rates were measured for three genera of beetle set on flexible tethers in a flow tank at Reynolds numbers similar to those experienced during flight. As expected, beetles that normally flew with their elytra extended were significantly more stable when the elytra were held out at a dihedral angle than when the elytra were held in the resting position over the body. However, no relationship was found between dihedral angle and either oscillation rate or maximum roll angle, contrary to what the aerodynamic theory would predict. Although De Souza and Alexander were unable to explain this effect satisfactorily, a likely explanation is that because the beetles were slightly positively buoyant, changing the roll angle would not have resulted in sideslip in the same way as it would in a heavier-than-air animal during normal flight. In the absence of sideslip a stabilizing roll moment would not be expected to arise, and the increased stability of beetles whose elytra were extended may instead have resulted from inertial damping in roll.

7. Conclusions

The analysis above suggests several simple ways to tell whether an animal is inherently stable or unstable:

1. Longitudinally stable animals are expected to sweep their wings forwards during slow flight because the wings are required to operate at high angles of attack providing high lift coefficients to support the body weight. These high angles of attack and high lift coefficients will be associated with large nose-down pitching moments, which can be balanced by sweeping the wings forwards or by generating a relative downforce with the tail. By the opposite reasoning, an unstable animal will need to sweep its wings backwards during slow forward flight to counteract the large nose-up pitching moments associated with high angles of attack.

2. In order to balance at a positive angle of attack, longitudinally stable animals with twisted

wings are expected to sweep their wings backwards if the lift distribution is wash-out (i.e. if the wings are twisted down at the tips) and forwards if the lift distribution is wash-in (i.e. if the wings are twisted up at the tips). The opposite combinations of twist and sweep are expected in inherently unstable forms.

3. Longitudinally stable animals with two pairs of wings or a tail are expected to exhibit longitudinal dihedral, such that the forward lifting surface is set at a higher angle of attack than the lifting surface behind it. This is the pattern observed in flying fish, dragonflies and in the elytra of beetles. It is also the typical pattern observed for birds' tails. Longitudinal dihedral is also seen between the small forewings and main wings of flying lizards *Draco* and geckos *Ptychozoon*, and appears also to apply to flying frogs and the multiple-slatted wing posture adopted by flying snakes (A. L. R. Thomas, pers. obs.). The opposite pattern would be expected for unstable four-winged forms. Intriguingly, the aerodynamic literature (Laitone, 1978a, b; Butler, 1982; Kroo, 1982; Thomas, 1996b) suggests that six-winged forms (e.g. certain Palaeozoic insects with prothoracic winglets and two pairs of articulated wings) may be aerodynamically optimal in the sense that adjusting both the positively loaded canard in the upwash ahead of the main wing and the (relatively) negatively loaded hindwing/tailplane in the downwash behind, can provide balance with any combination of centre of gravity and angle of attack. Sadly, no six-winged animals survived beyond the Carboniferous (unless you count the winglets, webbed feet and flattened tail and body of *Ptychozoon*).

4. Although the presence of dihedral in the wings of a flying animal is a good indicator that the wings provide some degree of roll stability, it is not possible to provide any simple rules of thumb for identifying laterally stable flying animals. This is because roll and yaw motions interact, so a full dynamic analysis is required before any general conclusions about lateral stability may be drawn.

5. Finally, the flight of animals with reduced passive stability will be qualitatively different from that of animals with a high degree of inherent stability. Specifically, when an inherently stable animal encounters a gust or other transient

disturbance, the large passive restoring force that results from its inherent stability will tend to knock it off course as the disturbance ends, resulting in an erratic flight path under turbulent conditions. By contrast, little or no passive restoring force will be generated in animals with reduced passive stability, and the flight of such animals is likely to be relatively smooth and direct, provided the animal can adjust rapidly enough in response to the disturbance. Swifts (Apodidae) exemplify the type of flight predicted for animals with reduced passive stability; Turkey vultures *Cathartes aura* display a tipping erratic flight characteristic of that predicted for highly stable gliders, and paper aircraft and soaring butterflies also exhibit the same kind of erratic flight path in gusty conditions. Interestingly, direct flight styles have been observed in unpalatable aposematic butterfly species, in contrast to their palatable mimics, which have a more typical fluttering flight (Srygley, 1994, 1999; Srygley & Kingsolver, 2000). The unpalatable species have lower muscle mass and larger abdomens, presumably associated with lower demand for excess power for escape flights. The resulting rearward position of the centre of gravity would tend to lower their stability, which is in accord with their observed direct flight style.

By considering in detail how gliding animals maintain stability we have found that gliding animals are more stable than has generally been recognized (e.g. Holst & Kuchemann, 1942; Maynard Smith, 1952; Brown, 1963; Herzog, 1968). Although we have established several rules of thumb by which stable fliers can be identified, a more rigorous test of whether gliding animals are stable would require measurement of the forces and moments on real animals. The fact that many gliding animals do appear to be inherently stable in pitch does not diminish the importance of active neuromuscular control in flight stabilization. Although it may be possible to classify flying animals as inherently stable or unstable in pitch during normal flight, we have shown that the variable geometry of animals' wings and tails is such that they may be able to alter their longitudinal stability and equilibrium quite radically (see also Thomas, 1996a). Whereas we can frequently classify aircraft into those that require

active stabilization of the flight path and those that do not, the distinction may not be so simple in flying animals in which the degree of stability may vary markedly during the course of a single flight.

Concerning the extent to which stability may vary in a given animal, it seems reasonable to suggest that an animal that is statically stable during normal flight should not deliberately make itself unstable, except perhaps transiently during unsteady manoeuvres. This is because the control system would need to change its mode of operation completely in order to maintain steady equilibrium (see Section 5.10). Analogous control reversals occur due to control coupling in the space shuttle during the entry phase, and though it is possible for the pilot to fly the aircraft "backwards", control reversal is achieved electronically for safety (Day, 1997). For an animal to make this transition during normal flight would require the use of two different control algorithms. If it is found that flying animals do switch facultatively between stable and unstable flight, then this will surely represent one of the most remarkable capabilities of their locomotor control systems.

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APPENDIX

List of Symbols

Forces and moments

| | |
|----------------|---|
| C_D | drag coefficient |
| C_{D_α} | drag coefficient derivative with respect to α |
| C_L | lift coefficient |
| C_{L_α} | lift coefficient derivative with respect to α |
| C_M | pitching moment coefficient (resolved at centre of gravity) |
| C_{M_α} | pitching moment coefficient derivative with respect to α |
| $C_{M_{ac}}$ | pitching moment coefficient (resolved at aerodynamic centre) |
| D | drag force |

| | |
|----------|--|
| L | lift force |
| M | pitching moment (resolved at the animal's centre of gravity) |
| M_{ac} | pitching moment (resolved at an aerodynamic centre) |
| M_0 | pitching moment when $\alpha_w = 0^\circ$ (resolved at the animal's centre of gravity) |

Further subscripts

Further subscripts are added to specify when the forces and moments above refer to just one part of the body, rather than to the whole animal.

| | |
|-------|--|
| b | body (pressure forces only) |
| d | body (viscous forces only) |
| t | tail |
| w | wings or forewings |
| w_2 | second pair of wings (hindwings or canard) |

General notation

| | |
|---------------|---|
| α | overall angle of attack |
| α_w | angle of incidence of the wing (measured between the wing zero-lift line and the oncoming flow) |
| α_b | body angle (measured between the longitudinal axis and the oncoming flow) |
| α_t | effective angle of incidence of the tail (measured between the tail zero-lift line and the oncoming flow after the wings) |
| ε | wing downwash angle |
| φ | efficiency factor for wing lift distribution |
| ρ | air density |
| AR_t | effective tail aspect ratio (defined as the square of the maximum span over the total area) |
| AR_w | wing aspect ratio (defined as the square of the span over the wing area) |
| c_w | wing mean chord |
| C_{k_1} | dimensionless coefficient characterizing the body's wake when moving parallel to x -axis |
| C_{k_2} | dimensionless coefficient characterizing the body's wake when moving parallel to z -axis |
| i_w | wing angle (measured between the x -axis and the wing zero-lift line) |
| k | volume of the body's wake when moving in a given direction |
| k_1 | volume of the body's wake when moving parallel to x -axis |
| k_2 | volume of the body's wake when moving parallel to z -axis |
| K_n | static margin |
| l_d | distance along x -axis from wing aerodynamic centre to body centre of drag |
| l_t | distance along x -axis from wing aerodynamic centre to tail aerodynamic centre |
| Re | Reynolds number |
| S | characteristic area |
| U | speed of the oncoming flow over the wings |
| v | body volume |
| x_n | x -coordinate of neutral point |
| x, z | Cartesian coordinates within the body frame |