



Why do Birds have Tails? The Tail as a Drag Reducing Flap, and Trim Control

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Birds have tails, bats do not. Does this fundamental difference in flight morphology reveal a difference in flight capability, and if so are birds or bats better fliers? I use Munk's stagger theorem, and Prandtl's relation for the induced drag of a biplane to show that for a given lift, and given wingspan, the induced drag of the wing-tail combination is lower than the induced drag of a wing alone. However the same reduction in induced drag could be achieved by slightly increasing the wingspan. While increasing the wingspan reduces induced drag, it can also increase profile drag and wing inertia. Induced drag is dominant at low speeds and during turns. Profile drag dominates at high speeds. The tail allows birds to have the wings needed for efficient cruising and high speed flight (when the tail can be furled giving little drag), at the same time the tail can be spread at low speeds or during turns to reduce induced drag. The tail can play a role in maintaining stability and balance, and it appears that the stability of birds is tailored so that the tail is required to generate lift at low speeds, when the interaction between the wings and the tail can also most effectively reduce induced drag.

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Introduction

Why do birds have a tail? Conventional aerodynamic theory suggests that the highest efficiency (in terms of lift for a given drag) is given by a single high aspect ratio wing. Bats have this morphology, but birds do not. Even birds like swifts (Apodidae) and swallows (Hirundinidae) that are aerial insectivores and must therefore be under selection pressures for flight performance that are similar to those acting on bats, the tail can be a substantial part of the birds total lifting surface area (with the interesting exception of spinetail swifts).

Recent work provides a theoretical picture of how the tail would work in isolation (Thomas, 1993) and these theoretical results has been confirmed both by wind tunnel experiments (Hummel, 1992) and by comparative analyses (Thomas & Balmford, 1995; Balmford *et al.* 1993, 1994). These results have revealed a number of aerodynamic functions of the

tail—for example to provide lift in addition to that of the wings, and to control pitch and yaw. These results have also revealed a number of non-aerodynamic functions of the tail—for example as a sexual selected ornament or as a mechanical prop to aid climbing. However the interaction between the flows over wings and tail and the tails role in maintaining stability have not been analysed.

Pennycuick (1975) speculated that birds' tails could act as "split flaps", where the flow over the tail modifies the flow over the wing increasing the maximum lift coefficient the birds wings could generate. This would increase performance in slow flight and during turning or acceleration. Tucker (1992) has suggested that the tail acts as a stabiliser, balancing the pitching moments generated in slow flight when the wings are extended and brought forwards.

Here I use Prandtl's biplane theory and Munk's stagger theorem to investigate the interactions between the flow over the wings, and the flow over the tail, and to investigate the effect of a second lifting surface on flight efficiency. I then derive the optimum

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position for the centre of gravity for peak performance in steady stable flight for both birds and bats and discuss the improved off peak performance that can be achieved by birds using the tail to generate lift when induced drag is high. I use the theory to predict the variation in wing and tail morphology that birds should use to minimise induced drag over a range of flight speeds.

Theoretical Analysis

In the following analysis I calculate the effect of the interaction between the wings and tail from first principles, but follow the methods and notation of Laitone (1978a,b). The analysis is robust—the same result can be obtained by using the entirely different technique of Trefftz plane flow field analysis (Butler, 1982; Kroo, 1982). Munk's stagger theorem states that the total interference drag of any system of wings (or wings and tail) is unchanged if the lifting surfaces are displaced relative to each other along the line of flight, provided the total lift remains the same.

Munk's stagger theorem assumes that the wings can be treated as lifting lines. While lifting line theory can be used to calculate the flow over a bird's wings—by assuming that the wings are thin, planar and of high aspect ratio, the same is not true of the tail—which is a low aspect ratio lifting surface. However, using lifting surface theory it is possible to calculate the aerodynamic properties of the tail (Thomas, 1993), and once these aerodynamic properties are known, they can be used to deduce an equivalent lifting line that would have the same properties. This deduced lifting line is assumed in the following analysis. The position of the centre of the equivalent lifting line for a tail would be at the aerodynamic centre of the tail, which is at a position on the tail centreline two-thirds of the distance from the apex of the tail to the point at which the tail has maximum continuous width. The horizontal stagger and vertical gap are defined as the vertical and horizontal separations between the aerodynamic centre of the tail and the aerodynamic centre of the wings. The aerodynamic centre of the wings lies at the centreline on the quarter chord point for a straight wing, and displaced forwards or backwards if the wing is swept.

Prandtl's biplane theory is based on the assumption of an elliptic spanwise loading on both wings. For high aspect ratio wings this may not be the case, but for the low aspect ratio tail the spanwise loading is inevitably elliptical at the point of maximum span (Katz & Plotkin, 1991, p. 221; Thomas, 1993). The influence on induced drag of any tail area behind

that point can be safely neglected (Thomas, 1993). Prandtl's biplane relation can therefore be applied to the general case of a birds tail and tail shape need only be considered in so far as it determines the horizontal separation (h) and vertical gap (g) and the position and strength of the equivalent lifting line.

The interference drag and total induced drag of the wings and tail can be derived by assuming that the wings and tail form a biplane with large horizontal stagger (h) and small vertical gap (g) between the aerodynamic centres of the wings and the tail. Prandtl's biplane theory gives the total induced drag (D_i) as:

$$\pi q D_i = \frac{L_1^2}{b_1^2} + 2\sigma \frac{L_1 L_2}{b_1 b_2} + \frac{L_2^2}{b_2^2}, \quad (1)$$

where q is the dynamic pressure ($1/2\rho V^2$, ρ = air density, V = velocity), $L_{1,2}$ are the lifts generated by the wings and tail respectively, $b_{1,2}$ are the spans of the wing and tail respectively. σ is the Prandtl coefficient which represents the mutual downwash effects of the wing and tail on each other, and is limited by $\sigma \leq b_2/b_1 \leq 1$. σ depends on the span ratio $b_2/b_1 \leq 1$ and also the vertical gap between wings and tail (see Fig. 1).

With no vertical gap ($g = 0$) between the wing and tail (or more specifically between the positions of their equivalent lifting lines) we have $\sigma = b_2/b_1$ and;

$$\pi q D_i = \frac{L_1^2}{b_1^2} + 2 \frac{L_1 L_2}{b_1^2} + \frac{L_2^2}{b_2^2} = \frac{W^2}{b_1^2} + \frac{L_2^2}{b_2^2} \left(1 - \frac{b_2^2}{b_1^2}\right), \quad (2)$$

where $W (=L_1 + L_2)$ is the birds weight. This is the case considered by Naylor (1946) and clearly here minimum induced drag occurs with zero tail load.

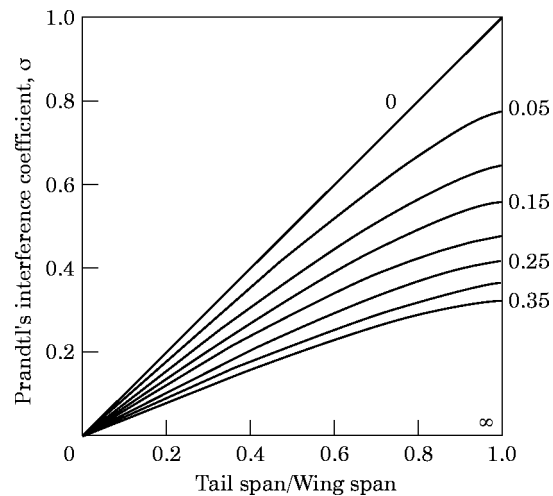


FIG. 1. Variation in Prandtl's biplane coefficient, σ , with span ratio (after Laitone, 1978b).

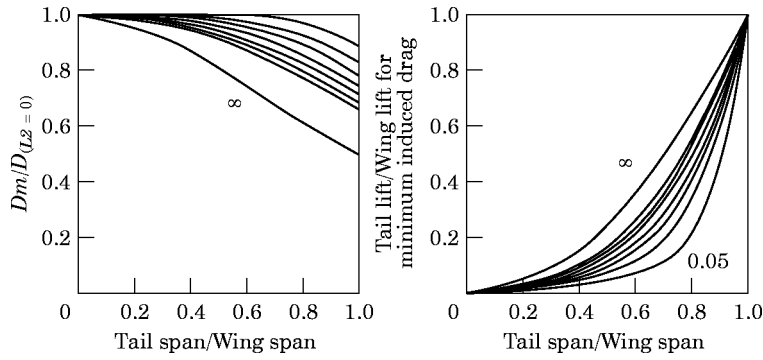


FIG. 2. (a) Ratio of the minimum induced drag that can be achieved with a loaded tail to the induced drag without the tail. (b) The ratio of the lift on the tail to that on the wings that achieves minimum total induced drag. In both graphs the multiple lines have been drawn for values of the gap ratio (vertical gap to wingspan) of 0.05, 0.1, 0.15, 0.2, 0.25, 0.3, 0.35 and infinity.

With a finite vertical gap ($g > 0$), $\sigma < b_2/b_1 \leq 1$ and;

$$\pi q D_i = \frac{W^2}{b_1^2} - 2 \left(1 - \sigma \frac{b_1}{b_2} \right) \left(\frac{W L_2}{b_1^2} \right) + \left(1 - 2\sigma \frac{b_1}{b_2} + \frac{b_1^2}{b_2^2} \right) \left(\frac{L_2}{b_1} \right)^2. \quad (3)$$

The middle term here proves that a tail load $L_2 > 0$ gives lower induced drag than either $L_2 < 0$, or $L_2 = 0$ as would be the case for a wing alone.

Minimum induced drag occurs at the tail load:

$$\frac{L_2^2}{W} = \left(1 - \sigma \frac{b_1}{b_2} \right) \left(1 - 2\sigma \frac{b_1}{b_2} + \frac{b_1^2}{b_2^2} \right)^{-1} > 0, \quad (4)$$

[Fig. 2(a)] and the minimum induced drag [Fig 2(b)] is:

$$\pi q D_i \min = \frac{W^2}{b_1^2} \left(1 - \left(\frac{\sigma b_1}{b_2} \right)^2 \left(1 - 2\sigma \frac{b_1}{b_2} + \frac{b_1^2}{b_2^2} \right)^{-1} \right), \quad (5)$$

$$= W^2 (1 - \sigma^2) (b_1^2 - 2\sigma b_1 b_2 + b_2^2)^{-1}. \quad (6)$$

This analysis holds for inviscid potential flow. Birds fly in real viscous air. However, the results of viscous flow effects, such as wake roll-up behind the wings, will be to increase the savings that can be achieved by a lifting tail. We can at least partly account for viscous effects by non-dimensionalising and introducing appropriate efficiency factors.

With $D_i = C_{d_i} q S$ (where C_{d_i} is the induced drag coefficient), $L_1 = C_{l_1} q S_1$ (C_{l_1} = wing lift coefficient, S_1 = wing area), $L_2 = C_{l_2} q_2 S_2 = E C_{l_2} q S_1$ (C_{l_2} = tail lift coefficient, q_2 = dynamic pressure at the tail, $E = (S_2/S_1)(q_2/q_1)$ and $A_{1,2}$ = aspect ratio (b^2/S) of the wing and tail respectively. The non-dimensionalised

form of eqn (1) can be written, after some manipulation:

$$C_{d_i} = \frac{C_{l_1}^2}{\pi A_1 e_1} + \frac{\sigma b_1}{b_2 e_3} \frac{2 C_{l_1}}{\pi A_1} E C_{l_2} + \frac{S_1}{S_2} \frac{(E C_{l_2})^2}{\pi A_2 e_2}, \quad (7)$$

where the e_n are efficiency factors for tail, wing and for the combination and $e_2 \leq e_1 < 1 < e_3$ (Laitone, 1978b). The induced drag without a tail is:

$$D_0 = \frac{1}{\pi q} \frac{W^2}{b_1^2} = \frac{C_{l_0}^2}{\pi A_1 e_1} q S_1. \quad (8)$$

Using eqn (8) and the relation $C_{l_1} = C_{l_0} + E C_{l_2}$ eqn (7) can be rewritten:

$$C_{d_i} = \frac{C_{l_0}^2}{\pi A_1 e_1} - \left(1 - \frac{\sigma b_1 e_1}{b_2 e_3} \right) \frac{2 C_{l_0}}{\pi A_1 e_1} E C_{l_2} + \left(1 + \frac{b_2^2 e_2}{b_1^2 e_1} \left(1 - \frac{2\sigma b_1 e_1}{b_2 e_3} \right) \right) \left(\frac{q_2}{q} \right)^2 \frac{S_2}{S_1} \frac{(C_{l_2})^2}{\pi A_2 e_2}. \quad (9)$$

Since $\sigma b_1/b_2 \leq 1$ and $e_1 < 1 < e_3$, the middle term (representing the component of induced drag due to the interaction between wings and tail) proves that induced drag is always greater with negative tail lift or with zero tail load than with the tail generating positive lift. The minimum induced drag is now given with the positive tail load at:

$$\frac{E C_{l_2}}{C_{l_0}} = \frac{L_2}{W} = \left(1 - \frac{\sigma b_1 e_1}{b_2 e_3} \right) \left(1 - \frac{2\sigma b_1 e_1}{b_2 e_3} + \frac{b_1^2 e_1}{b_2^2 e_2} \right)^{-1}, \quad (10)$$

which gives a minimum drag from eqn (9) of:

$$C_{d_m} = \frac{C_{l_0}^2}{\pi A_1 e_1} \left(1 - \frac{\sigma^2 e_1 e_2}{e_3^2} \right) \left(1 + \frac{b_2^2 e_2}{b_1^2 e_1} \left(1 - \frac{2\sigma b_1 e_1}{b_2 e_3} \right) \right)^{-1}. \quad (11)$$

By comparison with eqn (8) (where $Cd_0 = C_l^2 / (\pi A_1 e_1)$) this proves that **the induced drag is lower when the tail generates a positive lift than with either zero tail lift or a tail download**. With the efficiency factors set all equal to one (i.e. inviscid flow) eqn (11) reduces to eqn (6). However as $e_2 \leq e_1 < 1 < e_3$ it is clear that in a real viscous flow the tail load for minimum induced drag is even higher than that in inviscid flow, and the saving in induced drag is also higher.

Equation (9) suggests a physical interpretation of the reduction in induced drag (Fig. 3). The circulation on the tail will tilt the local freestream velocity vector at the wing so that the wing operates in an airstream with a slight rising component and with any vertical gap between the wing and tail the flow over the wing will also be slightly accelerated—this will tilt the wing lift vector to give a component of thrust. The wing will have an equal and opposite effect on the tail, but because the tail has a smaller span and is less efficient than the wing, and because with any vertical gap the flow velocity will be slightly reduced at the tail, the drag or thrust produced by the tail is less than that acting on the wing. Butler (1982) and Kroo (1982) derive a similar relation and provide a similar physical interpretation by using a Trefftz plane flowfield analysis of the influence of the wing on the tail with

the tail at downstream infinity. The result of increased force acting on the forwards wing will be familiar to anyone who sails as it is exactly the same relationship between two lifting surfaces that produces a greater force from the jib or foresail in combination with the mainsail than could be produced by the two sails acting separately.

For aircraft the area of the tail is fixed, and it has been shown that current 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—with obvious economic implications (Laitone, 1978a). Birds, however have the option of reducing the tail area by closing the tail. The tail generates profile drag:

$$D_{pro} = qS_2 C_{d_{pro}} \quad (12)$$

which increases as V^2 . In steady level flight birds should cease to use the tail at the speed where the profile drag of the tail is equal to the difference between the minimum induced drag $D_{i, \min}$ and D_i , the induced drag without the tail.

Induced drag is the main component of drag at low speeds, and is high during turning or accelerating flight, so birds should use their tails in these situations.

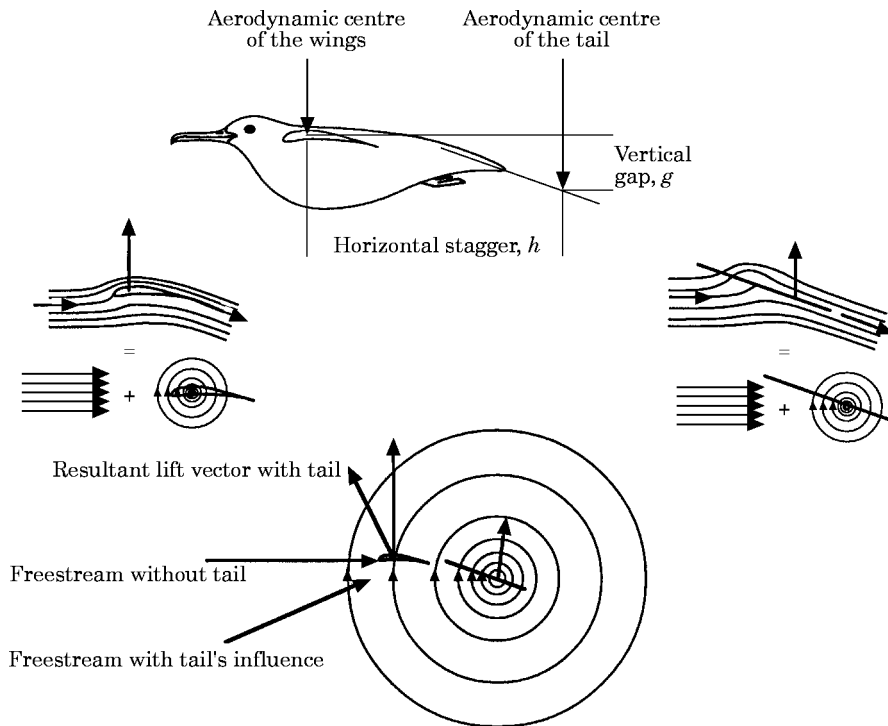


FIG. 3. Physical interpretation, and definition of the main terms used in the analysis. The flow around both the wings and tail can be considered as the sum of the freestream velocity—a uniform flow—and a vortex bound on the lifting surface. The upwards component of the bound vortex flow rotates the freestream velocity at the wing so that the wing lift vector is inclined slightly forwards (very much exaggerated here). This gives a small component of thrust, which acts to reduce the induced drag on the wing.

While the induced drag of the tail is independent of tail shape and tail area, the profile drag of the tail is proportional to tail area and therefore depends on tail shape (Thomas, 1993). Therefore, the speed in steady flight at which birds should switch from closed to open tails will depend on tail morphology. Forked tailed birds will get a reduction in total drag from using their tails at a higher speed than birds with other types of tail.

Balance and Stability in Pitch—the Position of The Centre of Gravity

A conventional wing produces a nose down pitching moment when generating lift (this is the reaction to the bound circulation on the wing). The pitching moment (M_w) generated by the wing about its aerodynamic centre is given by;

$$M_1 = qC_m c \quad (13)$$

where C_m is the wing pitching moment coefficient, and c is the wing mean chord. In gliding flight C_m is a function of the aerofoil section, and wing twist. In flapping flight a time averaged value for C_m can be derived which is dependent on the sum of the moments produced by the wings throughout the wingbeat (a detailed analysis of the stability of flying animals will appear elsewhere).

For steady flight this moment must be balanced. Balance requires (neglecting the relatively small destabilising moment produced by the body);

$$M = M_1 - L_1(x_1 - x_{c.g.}) + L_2(x_2 - x_{c.g.}) = 0, \quad (14)$$

where M is the total pitching moment, and the $x_{1,2}$, $c.g.$ are the positions of the centres of lift of the wing and tail and the centre of gravity of the animal respectively. With tail lift equal to zero and $L_1 = W$ (as is the case for bats) balance can be achieved in two ways. Either the centre of gravity be positioned so that;

$$x_{c.g.} - x_1 = \frac{-M_1}{W}, \quad (15)$$

in which case the couple generated by the aerodynamic lift and the weight then balances the nose down pitching moment generated by the wing. Which gives a balance at one flight speed only [because of the influence of Q , the dynamic pressure—equal to $1/2\rho V^2$ —in eqn (12)]. As the position of the centre of gravity is fixed during flight, to maintain balance a bird or bat would have to sweep its wings backwards to reduce $x_1 - x_{c.g.}$ at low speeds and forwards to increase $x_1 - x_{c.g.}$ at high speeds. The opposite movement of the wings relative to the centre of

gravity has been observed in several species (e.g. Tucker, 1992).

Alternatively balance could be achieved by setting $M_1 = 0$, either by using an aerofoil with reflex camber, or a wing with washout (nose down twist in the wing outboard towards the wingtips). Both washout and reflex camber reduce the efficiency of the wing.

The condition for static longitudinal (pitch) stability is obtained by differentiating eqn (14) with respect to angle of attack (α);

$$\frac{\partial M_1}{\partial \alpha} = \frac{\partial L_1}{\partial \alpha} (x_1 - x_{c.g.}) - \frac{\partial L_2}{\partial \alpha} (x_2 - x_{c.g.}) < 0. \quad (16)$$

The result must be less than zero for static stability so that a change in angle of attack produces an opposing moment. One possible means of ensuring stability is to position the centre of gravity well below the aerodynamic centre or centre of lift (Lighthill, 1975). Hot air balloons and paragliders use this technique to achieve stability, and it provides a contribution to the stability of many high-winged aircraft. However, in most birds, the centre of gravity is not far below the aerodynamic centre of the wings, so that pendulum stability can only make a small contribution (a detailed analysis will appear elsewhere). Therefore, stabilising moments must be produced by an aerodynamic means—by using a lifting surface to control trim. The trim surface stabilizing moment must be such that;

$$\frac{\partial L_2}{\partial \alpha} (x_2 - x_{c.g.}) > \frac{\partial L_1}{\partial \alpha} (x_1 - x_{c.g.}). \quad (17)$$

Substituting from eqn (15) gives;

$$\frac{\partial L_2}{\partial \alpha} (x_2 - x_{c.g.}) > \frac{\partial L_1}{\partial \alpha} \left(\frac{-M_1}{W} \right). \quad (18)$$

For a numerical example consider a bird or bat with mean cord = 0.1 m, wing moment coefficient -0.05 , mean wing chord of 0.1 m, wing area 0.1 m^2 and mass 1 Kg. At 10 ms^{-1} flight speed the animal would be balanced with the centre of lift at the quarter cord position and the centre of gravity further back at 5.25 cm from the leading edge. A tail of aspect ratio 1 with centre of lift 15 cm back from the leading edge would be adequate to give static stability in pitch to this animal. For this hypothetical animal to maintain balance at lower speeds the centre of lift of the entire animal would have to move back. At higher speeds this centre of lift would have to move forwards, or the tail would have to generate a down force. These changes in the position of the centre of lift of the entire animal could be achieved by shifting the wings backwards and forwards relative to the centre of

gravity—sweepback at low speeds and sweep forwards at high speeds, by changes in washout and reflex camber in the wing, or by using the tail to generate lift at low speeds and to generate a downforce at high speeds. At intermediate speeds (the value depends on the position of the centre of gravity) the tail need generate no lift.

Discussion

The theoretical analysis presented here demonstrates that the minimum induced drag for a system with wings and tail (e.g. a bird) is achieved with the tail generating a positive lift. The conditions required for balance and for static stability in pitch have been described, and it has been shown that birds and bats could achieve balance at a particular speed with zero tail load. Above this balanced speed both birds and bats will suffer some reduction in efficiency. Below this balanced speed bats could use active control to maintain stability and achieve balance by sweeping the wings backwards at low speeds and forwards at high speeds. This is not the pattern of changes in morphology with flight speed that is observed. Therefore, bats must use some part of their wings to generate balancing and stabilising forces instead of to generate lift. This will inevitably result in a reduction in performance and an increase in the power required for flight. In particular performance in turning and accelerating flight are strongly affected by the wing loading. Bats generally have lower wing loading than birds (Norberg, 1990) this may be an adaptation to cope with the requirements for balance and stability.

The curve of speed against power is U shaped with induced drag dominant at low speeds and profile and parasite drag dominant at high speeds. By using the tail to generate lift birds can have the small wings required for efficient high speed flight, but still achieve efficient slow flight and high turning performance.

Fruitbats forage by climbing in fruit trees. They roost at communal sites. Efficient flight while commuting between foraging and roost sites may therefore have particular significance for fruitbats. For most efficient commuting flight, fruitbat morphology should be optimised to give aerodynamic balance at their maximum range speed. With this morphology slow flight performance would be rather poor. This may explain the rather unsophisticated landing technique used by fruitbats (they crash).

Insectivorous bats may be under strict selection pressure for efficient foraging flight, and insectivorous bats would achieve peak performance by being aerodynamically balanced under foraging flight

conditions—they may be balanced at low speeds or even when making tight turns. Morphology optimised for foraging flight would lead to low wing loading, centre of gravity set well back from the leading edge of the wing, high manoeuvrability and efficient slow flight. It may also impose high costs during commuting flight.

Maximum span, maximum chord and maximum wing area are all fixed for both birds and bats—but in contrast to most aircraft they can reduce each of these components of morphology from its maximum value and they can also alter the curvature of the wing section and can twist the wings (Pennycuik, 1975; Norberg, 1989; Tucker, 1992). The ability to change the morphology of the wings will allow birds and bats a more versatile performance than can be achieved by fixed-wing aircraft—in particular by reducing the wing area birds and bats could reduce the cost of fast flight. However, the maximum values of these morphological parameters cannot be exceeded, and for bats this morphological limit must define an upper bound to aerodynamic performance (particularly the maximum turning and accelerating flight performance and the minimum cost of flight). Birds can exceed this performance limit defined by wing morphology because they can use the tail.

Birds can have the small wings needed for fast flight (with the tail closed) and still have good performance in slow flight, during turns, or when accelerating. Comparing a bird and bat adapted to the same set of flight performance criteria, the performance of the bat can be as good as or even slightly better than that of the bird at the prescribed peak performance (even a closed tail must cause some drag). However the bird's off-peak performance will be very much better than that of the bat because it can use the tail. One good reason why birds have tails is that the tail offers increased versatility in flight performance.

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REFERENCES

- ANDERSON, J. D. (1991). *Fundamentals of aerodynamics*. New York: McGraw-Hill.
- BALMFORD, A., THOMAS, A. L. R., & JONES, I. L. (1993). Aerodynamics and the evolution of long tails in birds. *Nature* **361**, 628–630.

- BALMFORD, A., JONES, I. L., & THOMAS, A. L. R. (1994). How to compensate for sexually-selected tails: the evolution of sexual dimorphism in wing length in long-tailed birds. *Evolution* **48**, 1062–1070.
- BUTLER, G. F. (1982). Effect of downwash on the induced drag of canard-wing combinations *J. Aircraft* **19**(6), 410–411.
- HUMMEL, D. (1992). Aerodynamic investigations on tail effects in birds. *Zeitschrift für Flugwissenschaften Weltraumforsch* **16**, 159–168.
- KATZ, J., & PLOTKIN, A. (1991). *Low-speed Aerodynamics From Wing Theory to Panel Methods*. New York: McGraw Hill.
- KENDALL, E. R. (1985). The theoretical minimum induced drag of three-surface airplanes in trim. *J. Aircraft*, **22**(10), 847–854.
- KROO, I. M. (1982). Minimum induced drag of canard aircraft. *J. Aircraft*, **19**(9), 792–794.
- LIGHTHILL, J. (1975). Aerodynamic aspects of animal flight. In: *Swimming and Flying in Nature* (T. Y. Wu, C. J. Brokaw & C. Brennen, eds) New York: Plenum press.
- LAITONE, E. V. (1978a). Ideal tail load for minimum aircraft drag. *J. Aircraft*, **15**(3), 190–192.
- LAITONE, E. V. (1978b). Positive tail loads for minimum induced drag of subsonic aircraft. *J. Aircraft*, **15**(12), 837–842.
- NAYLOR, C. H. (1946). Notes on the induced drag of wing-tail combinations. *British R & M* **2528** July 1946.
- NORBERG, U. M. (1989). *Vertebrate Flight: Mechanics, Physiology, Morphology, Ecology and Evolution*. Heidelberg: Springer Verlag.
- PENNYCUICK, C. J. (1975). Mechanics of flight. In: *Avian Biology* Vol 5, (Farner D. S & King J. R. eds) pp 1–75. London: Academic Press.
- THOMAS, A. L. R. (1993). On the aerodynamics of bird's tails. *Phil. Trans. Roy. Soc. Lond. B.* **340**, 361–380.
- THOMAS, A. L. R., & BALMFORD, A. (1995). How natural selection shapes bird's tails. *Am. Nat.* **46**, 848–868.
- TUCKER, V. A. (1992). Pitching equilibrium, wing span and tail span in a gliding Harris' Hawk, *Parabuteo unicinctus*. *J. Exp Biol.* **165**, 21–43.