
On the Aerodynamics of Birds' Tails

Adrian L. R. Thomas

Phil. Trans. R. Soc. Lond. B 1993 **340**, 361-380

doi: 10.1098/rstb.1993.0079

References

Article cited in:

<http://rstb.royalsocietypublishing.org/content/340/1294/361#related-urls>

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

On the aerodynamics of birds' tails

ADRIAN L. R. THOMAS

Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K.

CONTENTS

	PAGE
1. Introduction	362
2. Theoretical analysis: the forces on the tail	363
(a) Formulation of the model	363
(b) Slender lifting surface theory	363
3. Conclusions from the model	365
(a) The effect of tail morphology on aerodynamic performance	365
(b) Lift and the lift slope: limitations of the model	365
(c) Profile drag, induced drag and control by leading edge suction	367
(d) Leading edge vortices: roll and pitch control of high angles of attack and the effect of tail asymmetry	367
(e) Stability of the flow system: vortex asymmetry and vortex bursting at extreme α	367
4. Discussion	368
(a) Aerodynamic function of the tail	368
(b) Sexual selection and elongated tails: four specific examples	371
(c) Peak and off-peak performance: optimization of a bird's tail	375
References	379

SUMMARY

The aerodynamic properties of a bird's tail, and the forces produced by it, can be predicted by using slender lifting surface theory. The results of the model show that unlike conventional wings, which generate lift proportional to their area, the lift generated by the tail is proportional to the square of its maximum continuous span. Lift is unaffected by substantial variations in tail shape provided that the tail initially expands in width along the direction of flow. Behind the point of maximum width of the tail the flow is dominated by the wake of the forward section. Any area behind this point therefore causes only drag, not lift. The centre of lift is at the centre of area of the part of the tail in front of the point of maximum width. The moment arm of the tail, about its apex, is therefore more than twice the moment arm of a conventional wing about its leading edge. The drag of the tail is a combination of induced drag proportional to lift, and profile drag proportional to surface area. Induced drag can be halved by drooping the outer tail feathers to generate leading edge suction. This may be used for control, particularly in slow flight when both wings and tail are generating maximum lift.

The slender lifting surface model is very accurate at angles of attack below about 15° . At higher angles of attack vortex formation at the leading edge can stabilize the flow over the tail and thereby generate increased lift by a detached vortex mechanism. Asymmetry in the orientation of the leading edges with relation to the freestream (either in roll, yaw or caused by asymmetry in the planform) is amplified in the flow field and leads to large rolling and yawing forces that could be used for control in turning manoeuvres.

The slender lifting surface model can be used to examine the effect of variations in tail shape and tail spread on the aerodynamic performance of the tail. A forked tail that has a triangular planform when spread to just over 120° gives the best aerodynamic performance and this may be close to a universal optimum, in terms of aerodynamic efficiency, for a means to control pitch and yaw. However, natural selection may act to optimise the performance of the tail when it is not widely spread. The tail is normally only widely spread during manoeuvres, or at low speeds, selection may act to improve the efficiency of the tail when it is spread to only a relatively narrow angle – for example to maximize the bird's overall lift to drag ratio – the optimum shape at any angle of spread is that which gives a straight

trailing edge to the tail. This will always give a slightly forked planform, but fork depth will depend on how widely the tail is spread when selection acts, and this depends on the criteria for optimization under natural selection. A forked tail is more sensitive to changes in angle of attack and angle of spread, than other tail types. Forked tails are more susceptible to damage than other tail morphologies, and suffer a greater loss of performance following damage. Forked tails also confer less inherent stability than any other type of tail. Aerodynamic performance may not be an important optimization criterion for birds that fly in a cluttered environment, or do not fly very much. Natural selection, under these conditions, may favour tails of other shapes.

The aerodynamic costs of sexually selected elongated tails can be predicted from the model. These predictions can be used to distinguish between the various models for the evolution of elongated tails. Elongated graduated tails and pintails could have evolved either through a Fisherian or Handicap mechanism. The evolution of long forked tails can be initially favoured by natural selection, the pattern of feather elongation seen in sexually selected forked tails is predicted by the Fisher hypothesis (Fisher 1930) but not by any of the other theories of sexual selection.

1. INTRODUCTION

The tails of birds have two main functions. During flight the tail is constantly moving, changing in spread, in angle of attack, and in roll relative to the body. Evidently, the tail has an aerodynamic function. Tails may also be used as signals, in particular an elongated tail may increase its owner's attractiveness to mates and so become modified through sexual selection. This paper provides a basic theoretical model of the aerodynamics of the avian tail. By using this model the aerodynamic forces acting on the tail, and the costs of modifications of the tail (such as elaboration through sexual selection) can be predicted from simple morphological parameters of the tail. The model follows standard aerodynamic practice, as applied to the design of delta-winged aircraft, but with modifications to account for the different scale and morphology of birds' tails.

The aerodynamic function of the tail has been the subject of much speculation (Borodulina 1951; Maynard Smith 1952; Cone 1962*a*; Pennycuik 1975; Norberg 1989). In slow flight the tail is widely spread and may act to enhance the flow over the wings acting in the same way as the slots and flaps on the wing of an aircraft (Pennycuik 1968*a*, 1975; Tucker 1987; Tucker and Heine 1990). The interaction between the flow on the wings and the flow over the tail is intense and the bird is best considered as a single complex lifting surface. Forces generated by such a complex three-dimensional lifting surface could be calculated by using a surface panel method (Klatz & Plotkin 1991), but the model could hardly be general. Under normal flight conditions the tail acts independently of the wings and probably functions aerodynamically as a control surface (Tucker & Heine 1990; Tucker 1992). In a 'conventional' tailless aircraft, stability in pitch and roll can be achieved by means of washout (reduced angle of attack at the wingtips), dihedral (where the wingtips are raised above the wing root) and by having the centre of gravity well below the wing. Stability in yaw, particularly during turning flight, can be achieved by a combination of washout and aft swept wings, or by adding a vertical tail surface. These alterations to the shape of the wing,

which confer stability, also reduce the efficiency of the wing. Birds are able to avoid this reduction in efficiency by using the tail as a horizontal control surface (Maynard Smith 1952; Thomas 1993). The modifications that are necessary to achieve yaw stability are essentially the same as those that achieve pitch stability. The presence of a horizontal tail, but not a vertical tail, is thus something of a puzzle, especially as bats seem to fly perfectly well without it, and as pterosaurs seem to have experienced a directional selection towards reduction in any tail area during their long evolutionary history (Padian 1988). Surprisingly there has been no attempt to calculate the forces generated by the tail. This has been due, in part, to uncertainty about the flow conditions around the tail.

By using quantitative flow visualization, Spedding (1987*a*) has shown that the wake of a gliding kestrel is indistinguishable from that of a simple high aspect ratio, straight, planar wing, with an elliptic planform. Furthermore, in normal cruising flight the circulation on the wings is constant, and while there is variation in wing span (to provide thrust) the flow over the central section of the wings is essentially the same as in gliding flight (Spedding 1987*b*). This result has been confirmed for a variety of birds and bats (Thomas 1993), but in some cases the lift distribution may be closer to Jones loading (Jones 1980) than elliptic loading (figure 1).

Both forms of wing loading distribution give a smooth variation in circulation across the wing span. For an elliptic loading the downwards velocity of the flow generated by the wings, the downwash, is constant across the span. For Jones loading downwash increases slightly towards the wing tips. The small variation in downwash across the centre of the wingspan suggests that the air velocity at the tail in forward flight will be simply a steady flow made up of the vector sum of the flow due to the flight velocity and the flow velocity induced by the wings. The tail can therefore be considered as if it were acting as a separate aerofoil in a slightly altered velocity field. Given this simplifying assumption the forces on the tail can be calculated analytically by following the classical aerodynamic theory of the flow over a slender lifting surface.

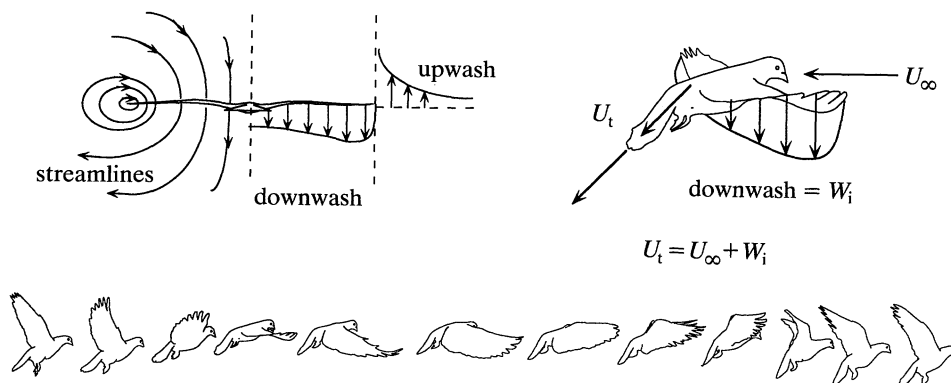


Figure 1. Top: the flow field around a bird in gliding or cruising flight. Loading distribution across the wing is intermediate between elliptic and Jones loading. At the centre of the wingspan the loading distribution is constant spanwise. The flow over the tail is the vector sum of the freestream velocity and the induced downwash. Bottom: the wingbeat of a pigeon in slow forwards flight at approximately 4 m s^{-1} (after Brown 1953) successive images separated by 0.01 s . Even in slow flight the tail is independent of the wings, and moves steadily with only slight adjustments in angle of attack at the ends of the wing strokes.

2. THEORETICAL ANALYSIS: THE FORCES ON THE TAIL

(a) Formulation of the model

Much of the performance of a wing is determined by its aspect ratio which is defined, in dimensionless form, as the square of the wingspan divided by the wing area. The tail is a low aspect ratio lifting surface that expands from an apex where it meets the body of the bird. In many birds the tail has a roughly triangular planform. The familiar conventional aerodynamic theory, lifting line theory, is applicable only to high aspect ratio wings. In a high aspect ratio wing the influence of the three-dimensional flow in the region of the wingtips is relatively small, and the flow can be considered to be essentially two-dimensional in the freestream direction (see Anderson (1991) or Klatz & Plotkin (1991) for a general discussion). For a low aspect ratio lifting surface, like the tail, the flow over the surface is dominated by the wing tip vortices and is more nearly two-dimensional across the span. The lifting line model cannot be used to calculate the forces acting on such a wing. Lifting surface theory must be used instead. Here a particular slender lifting surface theory is formulated in a way that is suitable to estimate the forces generated by a bird's tail. The model can be used to predict the effects of alterations of the tail morphology, and changes in the flow over the tail. The analysis follows the method of R. T. Jones (Jones 1946; see Jones 1990; Klatz & Plotkin 1991), with typographical errors in the equations for lift corrected.

(b) Slender lifting surface theory

The notation used here follows that of Jones (1990) (table 1).

Consider the tail as a thin flat delta-shaped wing of low aspect ratio at an angle of attack α that is small enough to avoid leading edge separation. The frame of reference is at rest with respect to the undisturbed fluid (figure 2).

Now consider the flow in a two-dimensional plane normal to the direction of movement of the tail, cutting the tail at a distance x back from its apex. As the tail moves through this plane, the movement of the slice of the tail cut by the plane will be downwards, within the plane. The velocity of the slice of the tail within the plane is determined by an angle of attack and velocity of the tail and given by $U\alpha$. The flow around the slice of the tail within the plane will be the same as the two-dimensional flow around a flat plate moving at a velocity $U\alpha$ perpendicular to its long axis. This two-dimensional flow does not generate lift, but if we consider the flow in a similar two-dimensional slice slightly further downstream along the tail, the flow will be identical except that as the span of the tail has increased, the scale of the flow will have increased. The increase in scale means that mass has been accelerated into the flow. As the movement of the tail within the slice is downwards the acceleration of this mass of air must be downwards. The result is a lift force (L) that is equal to $U\alpha$ times the local rate of increase of added mass m' :

$$L = U\alpha(dm'/dt) = U^2\alpha(dm'/dx) \text{ (as } U = dx/dt). \quad (1)$$

Table 1. Notation used in model

AR = aspect ratio	b_{\max} = maximum span
b = span	x = freestream direction
c = chordwise distance	co-ordinate
C_l = lift coefficient	C_{d_i} = induced drag coefficient
C_f = skin friction coefficient	C_{d_p} = pressure drag coefficient
L = total lift force	l = local lift force
D_i = induced drag	D_f = skin friction drag
D_p = pressure (form) drag	m' = local added mass
ΔP = Pressure distribution	ρ = air density
U = flow velocity	μ = coefficient of viscosity
Re = Reynolds number ($= \rho U c / \mu$)	S = reference area
α = angle of attack	

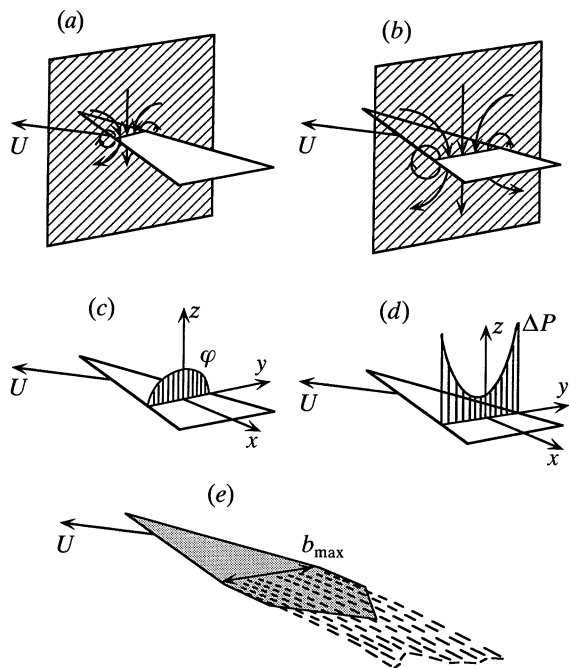


Figure 2. The aerodynamics of a low aspect ratio slender thin triangular wing such as a bird's tail. (a) The flow velocity field induced in a stationary two-dimensional plane as the tail cuts through it, the flow is the same as that around a two-dimensional plate moving perpendicular to its long axis. (b) The flow around the plate a few seconds later is identical except that the scale is increased because the span of the tail has increased. (c) Surface potential distribution, and thus loading distribution across the tail (at any $x = \text{constant}$ plane) have an elliptic distribution, identical to that on a two-dimensional flat plate. (d) The spanwise pressure difference distribution shows a sharp peak at the leading edges of the tail, and these are therefore disproportionately important in determining the performance of the tail. (e) Areas behind the point of maximum continuous span are in the influence of the wake of the forward section and generate drag but not lift.

Two-dimensional flow theory gives:

$$dm' = (\pi/4)\rho b^2 dx, \quad (2)$$

where b is the local width of the plate and

$$dm'/dx = \pi(b/2)\rho(db/dx). \quad (3)$$

Lift per unit length is

$$l = \pi \alpha (\rho/2) U^2 (db/dx) dx. \quad (4)$$

Divide by $(\rho/2)U^2$ and area $b dx$ to get the local lift coefficient

$$C_l = \pi \alpha (db/dx). \quad (5)$$

Two-dimensional flow theory suggests that the lift and pressure distributions can be calculated by considering the surface potential distribution. Returning to the concept of a two-dimensional flat plate moving through the fluid in a direction perpendicular to its long axis at a speed $U\alpha$, the surface potential (ϕ) is distributed spanwise across the plate according to the ordinates of an ellipse;

$$\phi = \pm U\alpha \sqrt{((b/2)^2 - y^2)}. \quad (6)$$

An instant later the ordinates will be those of a slightly larger ellipse. The pressure distribution in this unsteady co-ordinate system will be given by the local rate of increase of ϕ ;

$$\Delta p = 2\rho U (\partial\phi/\partial b) (db/dx), \quad (7)$$

where $(\partial\phi/\partial b)$ is a function of y . Differentiating equation (7) gives, after some algebra;

$$\Delta p = \rho/2 U^2 \frac{b}{\sqrt{((b/2)^2 - y^2)}}. \quad (8)$$

At the leading edge an infinite pressure drop and infinite velocity is indicated by equation (8), but detailed analysis of the flow in the immediate region around the leading edge shows that this singularity reduces to a leading edge suction force which cuts the drag by 1/2. For this drag reduction to be maintained the flow must be attached at the leading edge. Whereas the model assumes a thin flat plate, in practice for the tail to operate at reasonable angles of attack without flow separation, the leading edge has to be either rounded or drooped.

Equations (7) and (8) show that the lift depends on the increase in span along the tail. A straight sided section of the tail would generate no lift. Theoretically a tapering part would generate a negative lift, but the flow over any section of the tail downstream of the point of maximum continuous span would be dominated by the wake of the section upstream of that point. Effectively the Kutta condition is enforced at the point of maximum span, and the flow leaves this area smoothly with equal pressures above and below the tail (Jones 1990). By introducing a free surface of discontinuity composed of parallel vorticity extending downstream from the vortices over the tail at the point of maximum span, a potential flow satisfying both the boundary conditions in front of, and behind the point of maximum width can be generated. Although the vortex sheet is wider than the rearwards portion of the tail the vortices are parallel in this region, the scale of the flow does not increase along the tail, and no lift is developed behind the point of maximum continuous width.

The spanwise load distribution and induced drag can be obtained from the potential flow at the widest point. The potential distribution is elliptic so the loading distribution is also elliptic. Integrating for local forces gives:

$$L = (\pi/4)\rho \alpha U^2 b_{\text{max}}^2. \quad (9)$$

For lift, and for induced drag:

$$D_i = (1/2)L \alpha. \quad (10)$$

Note that, at a given angle of attack and freestream velocity, lift and induced drag depend on the maximum continuous span of the tail, and not on either the tail shape or area.

The lift and induced drag coefficients are:

$$C_l = (\pi/2)AR \alpha \text{ and } C_{d_i} = \frac{C_l^2}{\pi AR} = C_l(\alpha/2). \quad (11)$$

The total drag on the tail will be the sum of the induced drag, which is the drag associated with

accelerating air to generate lift, and the profile drag which results from the viscous interactions between the tail and the air. There are two components to profile drag; skin friction drag (D_f) and pressure drag (D_p). These are given by the familiar formulae:

$$D_f = (1/2)\rho U^2 S C_{d_f}, \quad (12)$$

for skin friction, where the reference area S is the wetted surface area (= twice the plan area) of the tail and:

$$D_p = (1/2)\rho U^2 S C_{d_p}, \quad (13)$$

for pressure drag but now the reference area S is the frontal projected area of the tail.

For a laminar flow ($Re < 10^5$) C_{d_f} can be calculated by the Blasius solution for the drag of a flat plate;

$$C_{d_f} = \frac{1.328}{\sqrt{Re}} \quad (14)$$

At $Re > 10^6$ the boundary layer is turbulent and the skin friction coefficient is approximately:

$$C_{d_f} = \frac{0.074}{\sqrt[5]{Re}} \quad (15)$$

The pressure drag coefficient is more difficult to estimate. For a flat plate at zero angle of attack drag consists solely of skin friction. Indeed, given that the flow is not separated, inviscid flow theory (Anderson 1991) predicts that there will be no net pressure drag at any angle of attack. In a real fluid this is not the case and there will be a small but finite contribution from pressure drag to the total drag of the tail. The variation of C_{d_p} with angle of attack for a flat plate follows a quadratic curve with $C_{d_p} = 0$ at 0° and a maximum $C_{d_p} = 2$ at 90° . Over a realistic range of steady angles of attack for bird tails of -10 to 25° (Tucker 1992), the pressure drag coefficient will be at least an order of magnitude lower than the skin friction drag coefficient and the reference area S (frontal projected area) will never be more than one-quarter of the reference area for skin friction drag. For the precise conditions of the model – when the flow is attached – the pressure drag is effectively identical with the induced drag, and it is only once the flow has separated that the two need be distinguished. Therefore neglecting pressure drag produces no error within the conditions required by the model.

The pitching moment about the apex of the tail can be calculated from the integral (from Klatz & Plotkin 1991):

$$M_0 = \int_0^c \frac{dL}{dx} x dx = \frac{\pi}{4} \rho U^2 \int_0^c x \frac{d}{dx} (\alpha(x) b(x)^2) dx. \quad (16)$$

For a simple flat triangular tail with constant α :

$$b(x) = b_{\max}(x/c). \quad (17)$$

Substituting this into equation (16) gives:

$$M_0 = \frac{\pi}{4} \rho U^2 \int_0^c x \frac{d}{dx} \left(\alpha \frac{x^2}{c^2} b_{\max}^2 \right) dx. \quad (18)$$

Therefore:

$$M_0 = (\pi/4)\rho U^2 \alpha b_{\max}^2 (2c/3) = L(2c/3), \quad (19)$$

and the position of the centre of pressure in x is at the centre of area of the forwards triangular area of the tail:

$$x_{cp}/c = M_0/Lc = 2/3. \quad (20)$$

So that the lift generated by the tail can be considered as acting through the centre of area of the forwards triangular section that is generating lift. This centre of area is two thirds of the distance from the apex of the tail to its point of maximum continuous width.

3. CONCLUSIONS FROM THE MODEL

(a) *The effect of tail morphology on aerodynamic performance*

The slender lifting surface model shows that at a given angle of attack the forces generated by the tail depend on only two features of morphology: tail width, and tail area. The maximum continuous span of the tail determines lift, tail moment, and induced drag. The area of the tail determined profile drag. Both area and width depend on the tail shape and how widely the tail is spread. The effect of these two parameters on the aerodynamic properties of the tail can be seen by using the model to estimate the aerodynamic forces generated by a representative range of tail shapes over a range of spreading angles (figure 3). Calculations follow the slender lifting surface theory exactly, and were done on an Apple Macintosh IIci using the MathSoft application MathCad. Copies of the programs can be provided on receipt of a 3.5'' disc.

(b) *Lift and the lift slope: limitations of the model*

The slope of lift coefficient against angle of attack for a bird's tail ($\pi/2AR$) is small compared to that for a high aspect ratio wing ($\approx 2\pi$). High aspect ratio wings suffer flow separation and therefore stall at angles of attack over about 15° . However, low aspect ratio delta wings, like the tail, show an increase in the lift slope immediately following flow separation. As the flow separates from the leading edges large vortices form above the wing. These vortices stabilize the flow up to large angles of attack and high lift coefficients can be obtained. Flat triangular plate with an apical angle of 60° can generate a lift coefficient of about 1.3 at 20° angle of attack, and will not stall below at an angle of attack below 35° .

Slender lifting surface theory accurately predicts aerodynamic performance at angles of attack below about 15° . Above 15° lift is generated by a detached vortex mechanism provided the flow remains stable and the lifting theory slightly underestimates the aerodynamic efficiency and performance of the tail.

The low value of the lift slope means that the lift produced by the tail is insensitive to small changes in angle of attack. The bird therefore has a considerable margin of safety when adjusting the tail to the incident flow. In normal flight the flow at the tail is

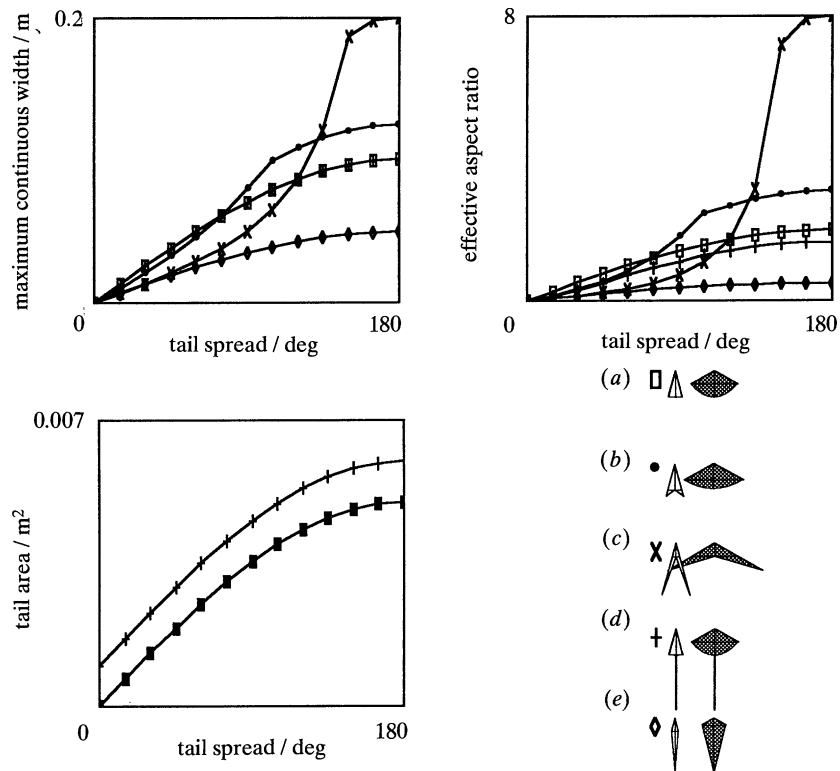


Figure 3. Morphological parameters of the various tail types against tail spreading angle. The tails are shown spread to 30° in outline, and 120° in stipple. (a) Normal tail all feathers the same length (5 cm). (b) Shallow fork, outer tail feathers increased in length by one-quarter. (c) Deep fork, outer tail feather length doubled. (d) Pintail, tail (a) plus a 5 mm by 10 cm extension to the central feathers. (e) Outer feathers one-quarter the length of the central feather. Tails are modelled as smooth continuous thin flat plates. 'Effective aspect ratio' is the maximum continuous span divided by the area of the tail.

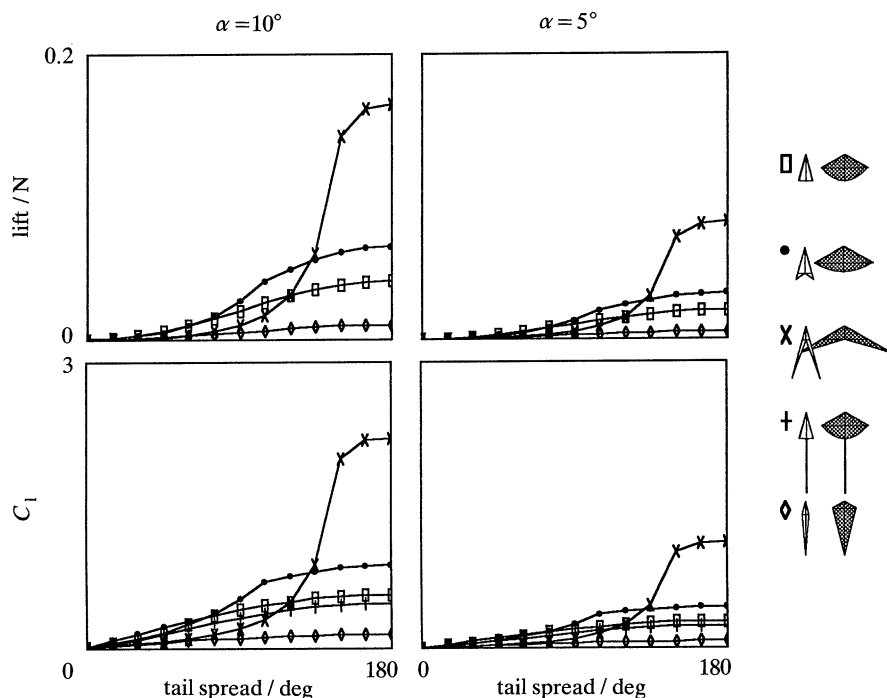


Figure 4. Lift, and lift coefficients of the different tails plotted against spread of the tail at 5° and at 10° angle of attack. Incident flow velocity = 5 m s^{-1} . The curves of lift and lift coefficient against tail spread shown in figure 4 are similar to the curve for span for each tail type because the lift produced by the tail depends on the maximum continuous span. The forked tails achieve greater span than the other morphologies when spread, and so generate more lift. The extreme lift coefficient of tail (c) at wide spreading angles indicates that it lies outside the range covered by the model. A curved lifting line approach would be more appropriate for this tail type and would suggest a maximum lift coefficient just over 1. The lift coefficients achieved by the other tail types are relatively modest even at 10° angle of attack.

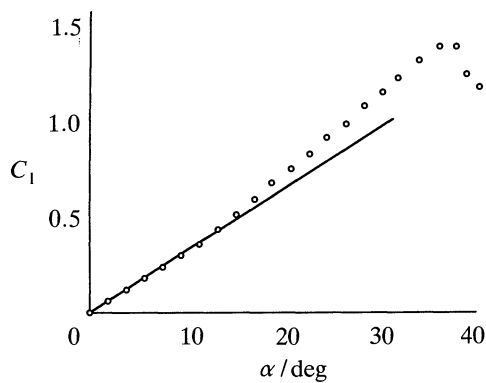


Figure 5. Comparison of the lift coefficient predicted by the slender lifting surface theory presented here (dotted line) and measured in wind tunnel experiments (circles). Reynolds number is $\approx 10^6$, the lifting surface is triangular and has an aspect ratio of 1 and a 90° apical spreading angle (experimental data from Klatz & Plotkin (1991)).

relatively steady but in slow flight the induced velocity generated by the wings is very much higher than the flight velocity, so there may be substantial variations in the flow conditions over the tail. The low slope of lift coefficient against angle of attack means that the tail is particularly suited to providing a steady lift force under these varying flow conditions.

The contribution of induced drag to total drag becomes higher at high lift coefficients. The aerodynamic efficiency of the tail therefore increases as the lift coefficient increases. To operate at a high lift coefficient the angle of attack of the tail must be high. Together with the inclination of the incident flow at the tail induced by the wings, this may account for the relatively high angles of attack of the tail observed in slow flight. For example Tucker (1992) reports tail angles up to 20° in the Harris hawk gliding in a wind tunnel.

(c) Profile drag, induced drag and control by leading edge suction

The equation for the induced drag coefficient (11) shows the effect of the leading edge suction. The vector lift force will be oriented half way between the normal to the surface of the tail and the normal to the freestream direction, whereas a conventional wing generates a vector lift force roughly normal to its surface. This inclination of the force vector results in a significant reduction in drag. The drag coefficient with leading edge suction is given by $C_l \alpha / 2$. Once flow has separated the drag coefficient is better approximated by $C_l \tan(\alpha)$. Leading edge suction can only be maintained when the flow is attached at the leading edge. For a flat plate this will only be at relatively low angles of attack. By introducing a drooped flap to the leading edge the advantages of leading edge suction can be maintained at higher angles of attack.

The ability to deform the transverse cross section of the tail would allow the leading edge suction to be turned on and off at will. Birds may be able to alter the induced drag of their tails by as much as a factor of 2 simply by drooping the outer tail feathers. When

the tail is operating at high angles of attack and at high lift and drag coefficients (for example when landing) this change in induced drag could give a very powerful means of establishing control authority without needing to alter either the area or angle of attack of the tail. A bird could therefore adjust its flight attitude so that both the wings, and the tail, are operating at their maximum lift generating performance and maximum C_l ; that is on the point of stall. In this flight condition any other flying animal, or machine, would be unable to manoeuvre except by reducing lift. A bird with all its aerodynamic surfaces operating at maximum C_l , would still have control in pitch because raising or drooping the outer tail feathers generates leading edge suction and can substantially change the induced drag of the tail.

(d) Leading edge vortices: roll and pitch control at high angles of attack and the effect of tail asymmetry

The greatest pressure drop and majority of lift on the tail is generated by the outer tail feathers. At high angles of attack leading edge vortices are responsible for the lift of the tail and these vortices interact intensely with each other. A tail set at an angle of roll relative to the direction of incident flow, or an asymmetric tail, develops an asymmetric vortex pattern over its top surface. This vortex asymmetry can result in large rolling moments and considerable sideways force (Hummel 1978; Katz 1984; Shanks 1963).

When these turning forces result from asymmetry in the outer tail feathers they must represent a constant cost to the bird. By deliberately tilting the tail to some angle of roll, vortex asymmetry could be actively induced to provide the bird with suitable forces to control turning.

(e) Stability of the flow system: vortex asymmetry and vortex bursting at extreme α

The stability of the flow over the tail depends on the angle of attack, and shape of the tail. As the angle of attack of the tail increases, although flow separation can be delayed by drooped leading edges, and following separation the flow can be stabilized by the leading edge vortices, eventually at an angle of attack that may be as much as 40° the flow over the tail will become unstable.

The form of the instability depends on the shape of the tail. A low aspect ratio tail ($AR < 1$) will develop asymmetric leading edge vortices at high angles of attack even with the tail set symmetrically to the flow. The asymmetry will generate large rolling and sideways forces, and may suddenly switch from side to side (this phenomenon is similar to the flow that sets up oscillations in the rope on a flagpole, the tapes around roadworks or the halyards on a mast). A tail of aspect ratio greater than 1 will experience vortex bursting at extreme angles of attack. In this condition, which is similar to the stall of a conventional wing, the tail suffers a considerable reduction in lift, and a substantial increase in drag. As the aspect ratio increases the

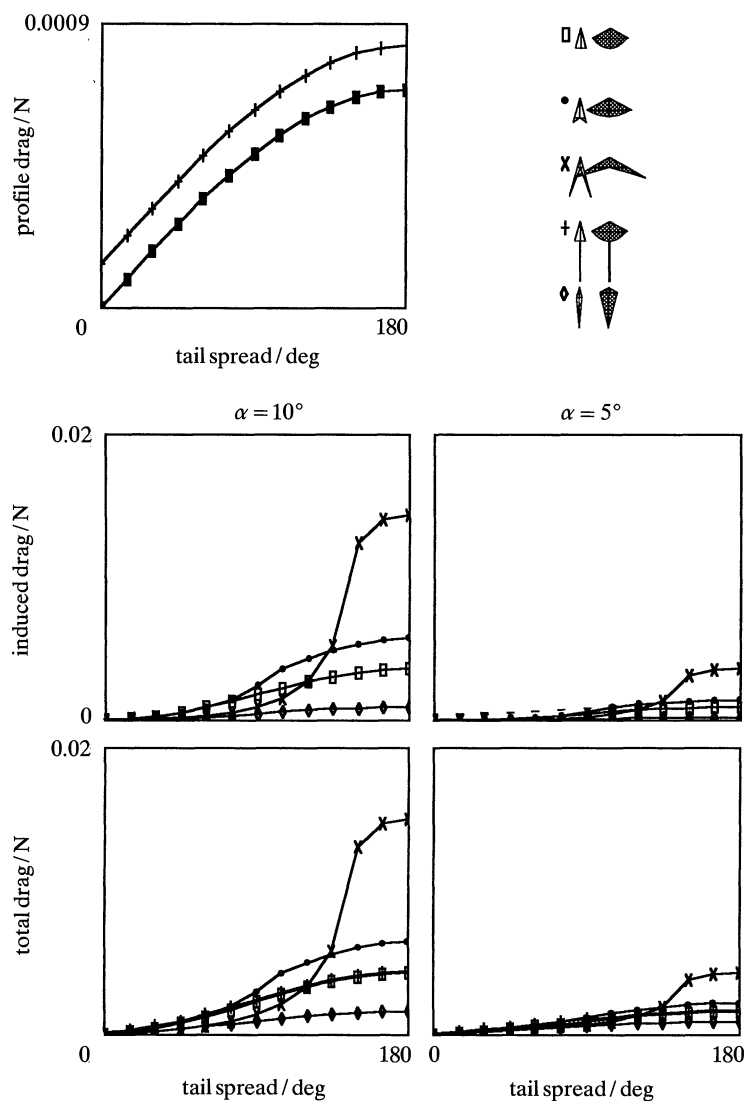


Figure 6. Drag against tail angles for typical tails. Incident flow velocity = 5 m s^{-1} . The profile drag of the tail is proportional to the area. As the tail morphologies modelled here have, with the exception of the pintail, the same area at all angles of spread they all have the same profile drag. The pintail has a slightly higher area and therefore a higher drag than the other types. At the two angles of attack shown here induced drag dominates over profile drag.

flow over the tail is stable over a narrower range of angles of attack and the properties of the tail become more like those of a conventional high aspect ratio wing.

4. DISCUSSION

(a) Aerodynamic function of the tail

The slender lifting surface theory gives a description of the aerodynamics of the avian tail. A number of features of the aerodynamics of the tail are different from those of conventional wings, and these differences may help to explain the way that birds use their tails. One feature that is shared between conventional wings and the tail is that they can both develop a high lift to drag ratio. At normal angles of attack the tail can generate an order of magnitude more lift than drag. The absolute maximum lift the tail could produce is typically twice the absolute maximum drag it could produce (if it was acting as a parachute), and

lift can be directed. So it is very unlikely that a bird will ever use its tail to generate drag as a brake. When a bird needs to generate substantial forces with its tail it will use the tail to generate lift.

There are two situations when birds will need to generate substantial forces from the tail: in slow flight, and during manoeuvres. In slow flight the wings must generate very high lift coefficients, and are spread as widely as possible. As the angle of attack is increased, to increase the lift coefficient, the centre of pressure of the wings moves forward relative to the aerodynamic centre. As the wings spread they move forwards because of the nature of the shoulder joint, and the centre of lift also moves forwards relative to the centre of gravity. The movement of the centre of pressure, and of the centre of lift will cause a destabilizing (nose up) pitching moment. To counteract this pitching moment, and to aid the wings in supporting the body, the tail will be spread widely, at a high angle of attack, during slow flight. In this situation the tail has a dual function: it can act both as a control surface,

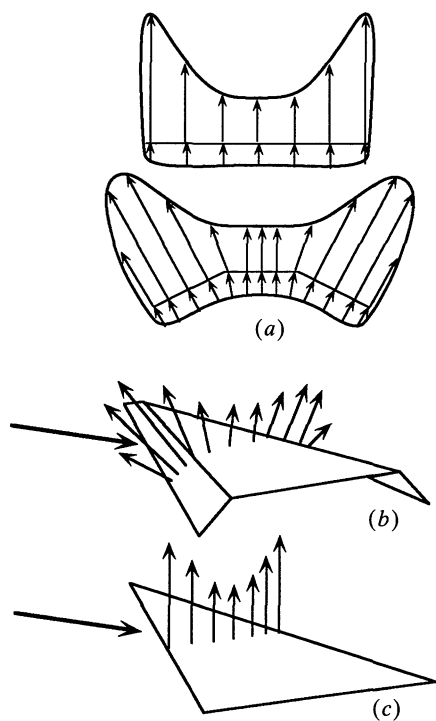


Figure 7. Distribution of the change in pressure induced by triangular tails moving through the air at a steady velocity and at an angle of attack of around 10° . Arrow length is proportional to the change in pressure at the surface. (a) The pressure distributions in transverse sections across triangular shaped tails moving through the air at an angle of attack. The pressure difference acts very nearly perpendicularly to the tail surface in both cases (after Andersson 1991). (b) The drooped leading edges of the tail gives a vector force that is inclined forwards, reducing drag. (c) The vector force on a flat tail is inclined slightly backwards across the whole of the tail.

and possibly as a form of aerodynamic flap to redirect the flow off the wings and delay stall (Pennycuik 1975; Tucker 1992). Birds that are adapted for slow flight will tend to have large wings, and large tails (Maynard Smith 1952).

The second situation in which birds will need to generate large forces from the tail is for control during manoeuvres. In very slow or hovering flight, the induced flow generated by the wings becomes significant, and the velocity at the tail may change substantially. A low aspect ratio tail is particularly insensitive to variations in flow velocity and direction, and so may be the best solution for a control device that has to function both in the steady flow conditions of normal flight and under the unsteady conditions that occur in slow flight.

In birds that use a vortex ring gait in slow flight (Spedding *et al.* 1986; Thomas 1993) the tail may be shaped to fit in with the wings at the end of the downstroke when the ring is shed, to allow the bound vorticity on each wing to link across the body efficiently. The tail would therefore have a somewhat rounded trailing edge. At the end of the downstroke the whole of the bird would form a semi-lunate lifting

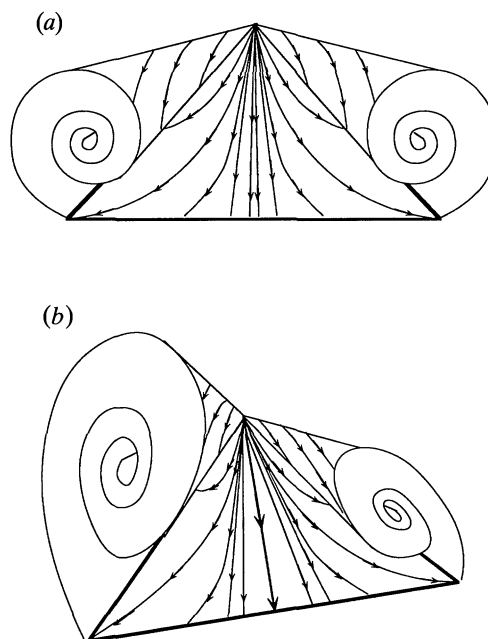


Figure 8. Flow velocities and vortex distributions over a delta wing at 20° angle of attack. The freestream direction is out of the paper. Arrows indicate the direction of flow along streamlines. (a) Flow measured over a symmetric delta wing (after Hummel 1978). (b) Vortex asymmetry induced by a constant roll angle (after Klatz & Plotkin 1991). The flow over a tail with an asymmetric planform would be similar to that in (b) even if the tail were held at no angle of roll.

surface, which may be the most efficient shape to shed vortex rings (Lighthill 1986).

In hovering flight in hummingbirds the wing turns over at the end of each stroke. In this case and in many other birds, which use a tip-reversal upstroke, the circulation on the wing is reversed at the end of each wingstroke (Brown 1953; Thomas 1993). Longitudinal vortices follow the path of the wingtips.

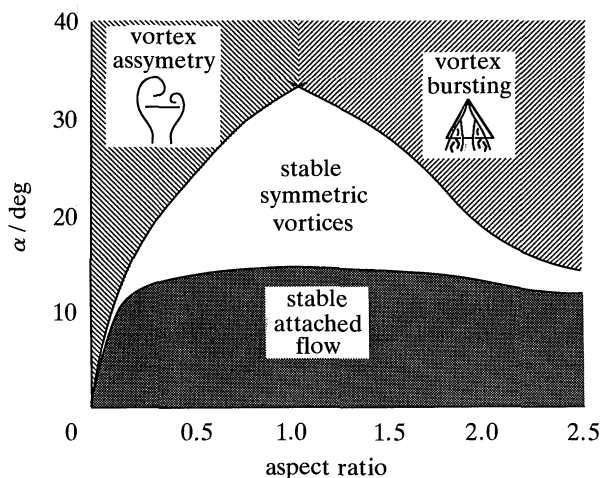


Figure 9. Stability boundaries for the flow over a tail in relation to angle of attack and aspect ratio (after Polhamous 1971). The slender lifting surface model is strictly applicable in the dark region but slightly underestimates lift and overestimates drag in the clear region. In the upper striped area the flow is unstable and the tail is effectively stalled.

Transverse vortices are shed at the end of each stroke. The transverse and longitudinal vortices form a ladder like wake linking the wingtips but the vortex cores well away from the body. This type of wake gives a downwash over the tail that varies in direction but has a fairly constant velocity. If the tail is used to generate steady force then the lifting surface model is certainly applicable but control in hovering flight, particularly in hummingbirds, is often achieved by moving the tail

very rapidly, relative to the body, in a sculling motion. It is very difficult to predict the aerodynamic properties of the tail, the nature of the flow, or the force being generated during this type of control movement, but this could be a situation where the tail is used to generate drag rather than lift.

In normal flight the flow over the tail is steady. Control forces are produced by changing the attitude of the tail relative to the flow, and the force produced by the tail is likely to be reasonably steady. Manoeuvres can be conveniently separated into longitudinal pitching manoeuvres, and lateral rolling and yawing manoeuvres; the aerodynamics are quite distinct.

During pitching manoeuvres, the tail is used as a control surface and, by controlling the overall angle of attack of the animal, directs the much larger forces generated by the wings. So, for example, during the approach to a landing platform a bird will initially tip the tail upwards so that the tail has a negative angle of attack and generates a downwards force. The resulting turning moment will cause the bird to rotate in a nose up direction. The angle of attack of the wings is therefore increased, and the wings generate greater lift. The lift on the wings is then directed upwards and partly backwards (for braking). As the bird slows the lift coefficient of the wings must increase, if the bird is to support its weight. As the lift coefficient increases the pitching moment of the wings will also increase. To stop itself somersaulting backwards the bird has to generate an upwards force with the tail. The tail is therefore lowered to give a positive angle of attack and lift directed upwards. The bird can then maintain this tail down posture with the wings and tail both widely spread and both generating close to maximum lift, right through to the point of landing. Consider the white backed vulture (*Gyps africanus*) shown in figure 10 (span = 2.2 m; wing area = 0.8 m²; $C_l \approx 1$; bodymass 60 N, $U \approx 15 \text{ m s}^{-1}$. Data from Pennycuik (1971a)). The lift generated by the wings at least matches the body mass during the entire descent; the descent is steady. Given the wingspan, the width of the tail can be estimated directly from the film images and reaches

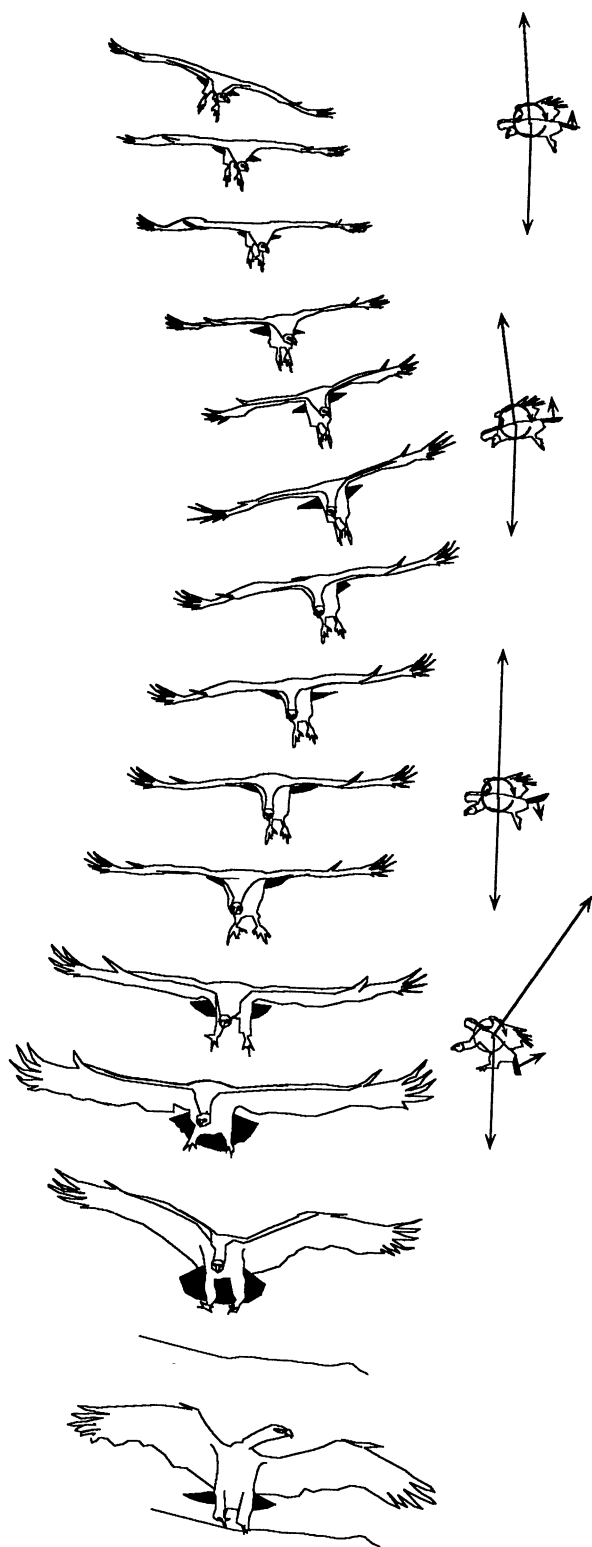


Figure 10. Use of the tail during the approach to a landing by a white backed vulture (*Gyps africanus*). The tail is shown stippled. Time between successive images is one fifth of a second. Arrow length is proportional to the force acting on the tail and wings. In the first four images the bird is gliding steadily at around 15 m s^{-1} , turning is initiated by twisting the wings to induce roll and tilting the tail to induce yaw. The tail remains tilted during the turn to counteract sideslip. The wing twist and tail roll are reversed to roll and straighten out of the turn. To slow down during the approach to landing the tail is raised, causing the whole bird to tilt nose up, the angle of attack and lift of the wing increases, and is directed partly backwards to help show the bird's descent. Once the bird is at maximum pitch angle the tail is brought down to provide lift to counteract the nose up pitching moments generated by the wings, and the bird remains in a nose up position with both wings and tail generating maximum lift, directed upwards and backwards, until touchdown.

a maximum of 0.41 m. The outer tail feathers on specimens in the Cambridge University Museum of Zoology measure 0.32 m on average ($n=4$) which would give a width of 0.41 m when spread to an angle of just over 80° and an aspect ratio just over 2. Peak lift of the tail can be estimated by assuming a maximum angle of attack of 20° (figure 9), and can be no more than 12.5 N at 15 m s^{-1} . During landing the lift coefficient on the wings could easily reach 1.5 which would give a total lift of over 140 N, almost three times the body mass and an order of magnitude larger than the tail lift. If the whole tail acted as a parachute or brake during landing the peak force it could produce would be no more than 17 N, assuming 90° angle of attack, and the maximum possible C_d of 2. Acting as a brake, the vulture's tail produces slightly more force than when it generates lift, but the force acts directly in line with the freestream direction at the tail – backwards and downwards – and could not be used to hold the wings at a high angle of attack. It seems likely that even during extreme manoeuvres such as landing the tail is used to generate lift to control the angle of attack, and attitude, of the wings rather than as any kind of a braking device itself.

In lateral turning manoeuvres the role of the tail is more complex; it is not just involved in generating vertical forces. A wing can be made to be stable in steady level flight without any kind of tail, but once banked in roll there is a tendency to develop an unsteady sideslip. Yet in forward flight it is necessary to produce a sideways force to turn, and this can best be achieved by rolling to a constant angle so that the lift of the wings acts in the direction of the turn. Stability when banked, could be achieved (as it is in hanggliders) by a combination of washout, sweep and dihedral (Pennycuik 1975) but each of these features reduces the efficiency of the wing. One major function of the vertical tailfin on an aircraft is to counteract sideslip by acting like a weathercock. Birds could actively achieve the same effect by tilting the tail to induce vortex asymmetry. The consequent yawing and rolling moments could be used to counteract the adverse yaw and sideslip that are induced when banked over to turn. Birds that are banked in a turn often hold the tail at an angle of roll relative to the body. Unlike conventional aircraft they can avoid the constant drag penalty of a vertical tail fin. Note that bats and insects (and possibly pterosaurs) cannot benefit from this effect because they lack a separate tail. In wind tunnel experiments on a model wing with a flat plate added to the trailing edge to mimic the bird's tail, Hummel (1992) provides an empirical confirmation of this feature of the bird's tail by showing that, if the tail is set at any angle of roll relative to the body, it contributes to both lateral stability and control.

(b) Sexual selection and elongated tails: four specific examples

The slender lifting surface theory shows that only the part of the tail in front of the point of maximum continuous width is aerodynamically functional. Any

area of the tail behind this point does not affect the lift producing capabilities of the tail. Although the aft section of the tail does not contribute to lift, it does cause drag through skin friction, but this component of drag is typically an order of magnitude smaller than either lift or induced drag. The tail behind the point of maximum continuous width is therefore relatively free from aerodynamic selection pressures. The relative lack of constraint on the aft section of the tail may be the reason it is bizarrely elaborated in some species.

Figures 11 and 12 show how the predicted aerodynamic costs of the tail are affected by elongation. In each of the four illustrated species the elaboration of the tail imposes a substantial cost. For example in Jackson's widowbird (*Euplectes jacksonii*), if the tail generates lift then the cost of the tail in nuptial plumage (mean tail length = 21 cm) is more than the total cost of flight in non-breeding plumage (mean tail length ≈ 7 cm). The bird probably could not fly in this state and actually shows adaptations in the tail to prevent it from forming a continuous lifting surface at an angle of attack. Elaboration of this degree cannot be explained through the usual processes of natural selection. Darwin proposed selection by female preference in relation to sex to account for elaborate male ornaments of this kind (Darwin 1871).

A relationship between female mate choice and male tail length has been demonstrated in several species (e.g. swallow (*Hirundo rustica*), Møller 1988; Jackson's widowbird (*Euplectes jacksonii*), S. Andersson 1992; long-tailed widowbird (*Euplectes progne*), M. Andersson 1982; and, at least by implication, the scarlet-tufted malachite sunbird (*Nectarinia johnstoni*), Evans & Hatchwell 1992a). Several experimental studies have also shown that the possession of an elongated tail places a cost on the male (Møller 1989; Evans & Hatchwell 1991b). In scarlet-tufted malachite sunbirds, the direct nature of the cost has been shown, both theoretically and by experiment, to be a combination of the aerodynamic drag (up to 5% of total power for flight) and the mechanical inertia of the tail elongation (Evans & Thomas 1992). However, other consequences of tail elongation (such as increased predation risk) could also be important.

Two theoretical models dominate the literature of sexual selection (Maynard Smith 1991). Viability indicator models suggest that the male trait is a signal that indicates heritable viability. Only the fittest males can afford the cost of full development of the elaborate trait. By choosing males with exaggerated ornaments a female might be able to select good genes for her offspring. For the trait to act as a signal it must be costly or it would be open to cheating (Zahavi 1975; Hamilton & Zuk 1982; Grafen 1990a,b). Fisherian models show that if there is variation in female preference for a male trait, and variation in the male trait, the most discriminating females will tend to mate with the most extreme males. Assortative mating will tend to result in a positive correlation in an individual between the presence of the genes for the trait and the genes for the preference. Once started, the preference for a trait can be self-reinforcing because females are selecting both for the trait and,

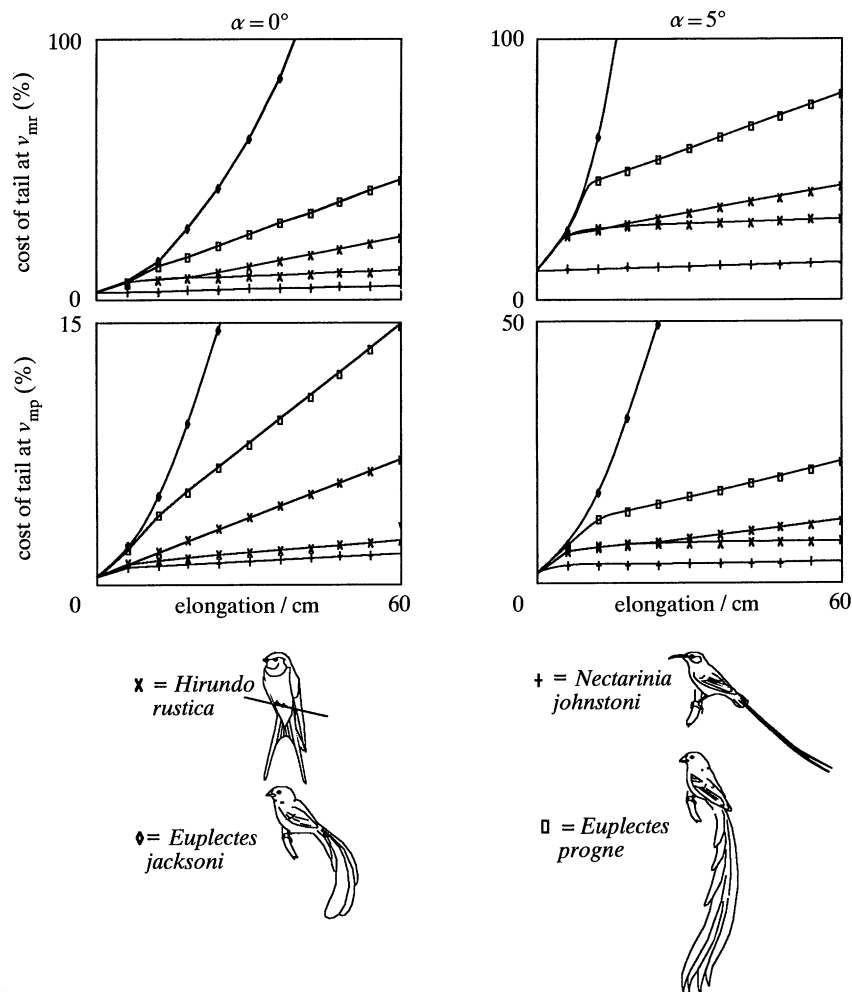


Figure 11. The costs of sexually selected tail elongation. The cost of the tail is calculated at maximum range speed (v_{mr}), and minimum power speed (v_{mp}). Cost is presented as the percentage of the total power for flight, with a normal tail, that is represented by the mechanical power required by the tail alone. The tail is modelled as a smooth flat plate. The power requirement at 0° angle of attack represents the absolute minimum power required for flight with the tail at a particular airspeed. At 5° angle of attack the tail generates useful lift and induced drag is the major component of total drag. Power requirements have been calculated by using Pennycuick's standard model of animal flight (Pennycuick 1989). The swallow is modelled with two forms of tail extension, the lower curve in each case represents elongation by the addition of narrow extensions to the outer feathers, the higher curve assumes that the central tail feathers are constant in length, all other feathers elongate so as to form a smooth straight trailing edge to the tail.

indirectly, for the preference. Trait and preference can then be exaggerated in a runaway fashion by this positive feedback (Fisher 1930; Lande 1980, 1981). In his original exposition of the model Fisher suggested that if a trait is to be elaborated through sexual selection it must be initially beneficial under natural selection. Female preference can then develop for the beneficial trait. The female preference itself could then drive the trait to elaboration beyond the naturally selected optimum form. This special case of the Fisherian mechanism not only gives a reason for the origin of the female preference but, because we can predict the type of trait that would be aerodynamically beneficial under natural selection, can also be used to make a revealing specific critical prediction about the evolution of elongated tails in birds that is not provided by modern Fisherian models.

The theoretical models of sexual selection can be tested by considering the trajectories of cost against elongation through evolutionary time (Balmford *et al.* 1993). Viability indicator models require that the tail is costly, and that the slope of cost against elaboration is positive at all stages in the evolution of an elongated tail. Modern Fisherian models are indifferent to the cost of the tail, and can accommodate any trajectory. Fisher's original model required that the initial elongation had some benefit, however slight, under natural selection.

The graphs of cost against elongation in figures 11 and 12 are intended to illustrate the actual trajectories of cost for the species shown, but the species have been selected to represent the range of common tail types. The trajectories for any forked-tailed bird would be qualitatively similar to those for the swallow, for

Table 2. Morphology and flight performance of four species with sexually selected tail elongation (Power requirements have been calculated by using Pennycuik's momentum jet model (Pennycuik 1975, 1989).)

species	mass/g	span/m	shortest tail		longest tail feather/mm	$v_{mp}/(m\ s^{-1})$		power without tail at v_{mp}		power without tail at v_{mr}		minimum power for tail at v_{mp}		minimum power for tail at v_{mr}	
			feather/mm	feather/mm		$v_{mp}/(m\ s^{-1})$	$v_{mr}/(m\ s^{-1})$	W	W	W	W	W	W		
<i>Nectarinia johnstoni</i>	16	20	54	170	5.7	9.8	0.27	0.34	0.0030	0.0117	0.0030	0.0117	0.0030	0.0117	
<i>Euplectes jacksonii</i>	43	28.5	210	210	6.6	11.2	0.77	0.98	0.0900	0.3355	0.0900	0.3355	0.0900	0.3355	
<i>Euplectes progne</i>	45	43	15	51	5.5	9.5	0.49	0.63	0.0632	0.2486	0.0632	0.2486	0.0632	0.2486	
<i>Hirundo rustica</i>	20	33	45	103	4.8	8.5	0.21	0.27	0.0023	0.0098	0.0023	0.0098	0.0023	0.0098	

example. In each case as the tail is elongated the cost of the tail increases, but in the case of the swallow this cost is more than compensated by an initial increase in the lift to drag ratio, and the moment to drag ratio. Good genes models could account for the evolution of long pintails and graduated tails, but can only be reconciled with the evolution of a long forked tail if female preference for a long tail occurred in a population that was already at the aerodynamic optimum for tail shape. Modern Fisherian models could account for the evolution of any of these tail types. Pintails are aerodynamically costly at any stage of elongation. Fisher's model could only account for the evolution of pintails if there is a non-aerodynamic advantage to the initial elongation of a pintail. The trajectories for costs during the evolution of long forked tails fit Fisher's requirements precisely. The evolution of graduated tails is consistent with Fisher's model if selection initially favoured a large tail, for example because a large tail moment was required to increase agility.

Fisher's model can be used to make another kind of prediction. In the initial evolution of a forked tail natural selection acts to increase the length of the outer tail feathers relative to the central tail feather. Fisher's theory would therefore predict that in the elongation of a forked tail beyond the aerodynamic optimum shape, through sexual selection, it is the outer tail feathers that will be elongated. In contrast good genes theory is relatively indifferent to which feathers elongate, indeed as the outer tail feathers contribute disproportionately to lift they are initially the least costly feathers to elongate. The outer tail feathers are therefore the least likely to be elongated by sexual selection acting through the handicap principle. As with costs, because the initial female preference is essentially arbitrary, modern Fisherian models are indifferent to the pattern of feather elongation and can make no prediction.

If we take an arbitrary definition for a long tailed bird to be that it has a tail longer than its body, then there are 50 families of birds with long tailed species (Balmford *et al.* 1993). Seventeen of these families have forked tailed members, of which only five have any other type of long tail. There is only one family in which elongation has resulted in similar numbers of species with each tail type: the hummingbirds (trochilidae). In each of the other four families that have members with both forked and other types of elongated tails, the forked tail type is rare or unique and in each case the evolution of a long forked tail, and of other types of long tail occurs in distantly related species, and is likely to have occurred independently from separate short-tailed ancestors. In every family in which the forked tail type is the norm but sexual selection has resulted in at least some elongated tails (e.g. Fregatidae, Laridae, Hemiprocnidae, Hirundinidae) although the elongation of any of the tail feathers would be costly and could therefore act as an honest viability indicator, elongation invariably involves only the outer tail feathers. In many of these cases not only are the outer tail feathers elongated, but the central tail feathers are also reduced in length. This differen-

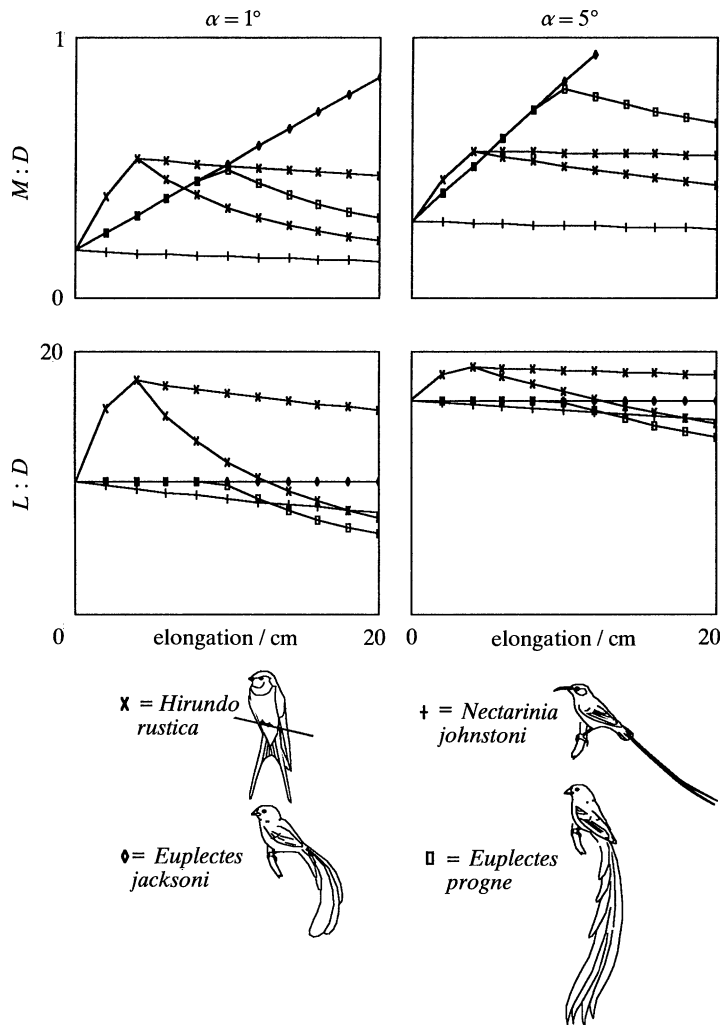


Figure 12. Costs of the sexually selected tails in terms of functional efficiency. The lift to drag ratio is a direct measure of efficiency. The ratio of tail moments to drag represents the cost of using the tail to turn. $M:D$ is not non-dimensional, so it may be more efficient to have a large tail to generate large tail moments.

tial pattern of modification acts to increase the apparent depth of the fork in the tail in precisely the same way that the initial evolution, under natural selection, of a forked tail would have done.

The swallow migrates from a Sub-Saharan wintering ground to European breeding areas. There is a cline in wing length in the swallow (and other migratory hirundines) that is correlated with migration range. Increasing wing length reduces the cost of flight, but also adversely affects agility. To maintain agility and manoeuvrability a bird with large wings will need a large tail (Thomas 1993). Assume that strength of sexual selection is constant, but the strength of natural selection for aerodynamic efficiency depends on migration distance (as evidenced by the cline in wing length) and consider birds with different migration ranges. If the tail extension is acting as a signal the size of the extension of the outer tail feathers should be either unaffected, or vary inversely with wing length (if sexual selection is constant, the cost of the signal should be constant). If the tail has evolved through Fisher's mechanism, the female preference is likely to be for the greatest length

of the outer feathers relative to the central tail feathers. The length of the tail streamer should therefore vary with wing length, but fork depth should be constant (if sexual selection is constant). The additional cost of the very long outer feathers of northern breeding birds might be compensated by reducing the width of the streamers. The patterns of tail elongation in the five specimens in the University Museum of Zoology at Cambridge support the Fisher hypothesis, but a detailed comparative test is required.

The slope of cost, in terms of drag, against elongation is positive for any form of tail elongation that increases tail area (figure 11). The gradient of the slope depends on the shape of the tail. Isometric elongation or elongation to form a graduated tail rapidly increases the area and cost of tail. A small increase in length represents a substantial increase in the cost of the tail, so these types may be relatively reliable signals of heritable male quality.

Among the widowbirds, the extreme cost of Jackson's widowbird's tail (which results from the huge increase in area when all 21 tail feathers are equally

elongated) is probably only bearable because Jackson's widowbird does not perform a flight display. If it flies at all, the flight of Jackson's widowbird in nuptial plumage is slow and laboured (Anderson 1992). The long tailed widowbird displays its tail in flight. Male long tailed widowbirds have a substantially increased wingspan and wing area and the resulting reduction in the cost of flight may compensate, at least partially, for the cost of the tail. In addition because the full elongation of the tail is restricted to the central tail feathers, the area of the tail of *Euplectes progne*, which may be more than 50 cm long, is actually less than the area of the 21 cm long tail of Jackson's widowbird.

The slopes of cost against elongation are much lower for the narrow extensions of a forked tail or pintail. The effectiveness of these types of tail as a signal depends critically on the impact of flight efficiency on fitness. In birds like the swallow that feed on the wing and have extensive migrations, even a small extension of the tail can have significant costs. In birds that are less constrained by selection for flight efficiency the effects of environmental variation on health – noise in the signal – is likely to swamp the effects of heritable variations in intrinsic quality. If they act as signals, the length of an elongated forked tail or pintail may not be a particularly reliable indicator of heritable male quality. Another cue, such as symmetry, might be required (see Møller 1992, 1993; but also Balmford & Thomas 1992).

The aerodynamic drag, and therefore cost, of an elongated tail is proportional to its area. In species with elongated forked tails, the width of the outer tail feathers is often considerably reduced, so that in some species the terminal section of the outer tail feathers is reduced to a bare, wire like shaft (e.g. wire tailed swallow *Hirundo smithii*). This reduction in width has no consequences for an elongated tail evolved through a Fisherian mechanism. If the tail is required to act as a signal, reduction in width represents a form of cheating because of the relationship between the drag coefficient and length of the tail elongation (equations 12 to 15). The drag coefficient is inversely proportional to the square root of the Reynolds number, and the Reynolds number is proportional to the length of the tail. So for tail elongations of the same area, a long thin elongation has lower drag than a short wide elongation. An empirical examination of female preference for the width of tail elongations is lacking and might be revealing. In assessing the cost of a tail, tail area will almost always be a more reliable cue than tail length.

The aerodynamics of a slender lifting surface like the bird's tail are robust to changes in shape. The tail can still generate useful lift even when its shape is far from the aerodynamic optimum. The tail, particularly in its aft sections, may therefore be relatively free from natural selection for aerodynamic performance. The rare occurrence of elaborate wings, as opposed to tails, is at least in part due to the much more tightly defined aerodynamic optimum morphology for a high aspect ratio wing. Tail elaboration does incur a cost, and the magnitude of the cost of a tail that an individual bird is able to bear will depend on how important flight is

for that bird. Thus the seed eating widowbirds are able to afford much more expensive tails than the sunbird which either hawks for insects or feeds on nectar. In turn the sunbird is able to afford a more expensive tail than the aerial feeding swallow. The patterns of feather elongation, and the evolutionary trajectories of cost against elongation suggest that graduated tails and pintails could have evolved by either Fisherian or viability indicator mechanisms, but in pintailed birds (especially those that are not strongly constrained by selection for aerodynamic efficiency) the elongated central tail feathers may not be a very effective means of honestly signalling heritable male quality. The initial evolution of long forked tails was probably driven by natural selection for aerodynamic efficiency, and manoeuvrability. Elongation beyond the naturally selected aerodynamically optimum shallow forked tail is likely to have occurred by the classic Fisherian mechanism.

(c) Peak and off-peak performance: optimization of a bird's tail

The aerodynamic properties of the tail seem very well suited to its function as a control surface. To what extent is the morphology of the tail a compromise between selection for aerodynamic efficiency, the constraints of evolutionary history and selection for characteristics other than aerodynamics?

The highest lift to drag ratio – the most efficient flight – is achieved by a planar, high aspect ratio wing with an elliptic planform and a streamlined cambered aerofoil section. Any modification to the wing, such as adding a body, or a tail, must reduce its efficiency. In flight, when generating lift, a cambered planar high aspect ratio wing is stable in roll and yaw (at least neutrally stable) but is unstable in pitch. If the wing is set at an angle of attack then it will generate lift, and a nose down pitching moment. To counteract the pitching moment generated by the wings an equal and opposite moment must be generated. This balancing moment can be produced by positioning the centre of gravity of the body behind the centre of lift, by reflex camber in the aerofoil, or by using a separate control surface.

Insects, bats, and most birds and aircraft have the centre of gravity positioned close to or just behind the centre of lift of the wings. Balance is thus achieved, but at only one flight speed and lift coefficient because the position of the centre of pressure of a cambered wing depends on the angle of attack. This single point of balance can be stable, if the centre of gravity is sufficiently low for bodymass to act as a pendulum (as in paragliders). In most flying animals, and aircraft, pendulum stability is local and weak or neutral. Any disturbance from equilibrium is likely to be divergent (Thomas 1993). Obviously no animal or aircraft can normally fly in this state and an additional form of pitch control is required.

Bats and insects do not have a separate tail. Pitch is controlled by modifying the position of the centre of lift of the wings relative to the centre of gravity. This can be done either by moving the wings relative to the

body (Norberg 1976), or in four winged insects, by generating differential lift on the fore and hind wings. Alternatively the pitching moment generated by the wings can be balanced by reflex camber: where the trailing edge is tilted upwards and generates a downwards force (Pennycuik 1975; Norberg 1976, 1989). Any of these modifications will increase drag and reduce the efficiency of flight.

Aircraft characteristically control pitch by using small, high aspect ratio, horizontal tail surfaces mounted at end of a long fuselage. The long moment arm provided by the fuselage means that a small lift force from the tail is sufficient to produce a large pitching moment. The area and drag of the tail can then be small, but is always present as a cost.

The centre of gravity of an aircraft is normally set so that when the wings are operating at their most efficient lift coefficient, the pitching moment generated by the wings is balanced so that the tail generates minimum drag. This gives the peak performance of the aircraft. Peak performance may be optimized to give the maximum range, maximum speed, or maximum cruise duration, depending on the operation the aircraft is designed for. Off-peak performance describes the width of the performance envelope – the range of possible flight conditions – and is in essence a measure of versatility. The optimization of aircraft design is analogous to the effect of natural selection on an animal's flight morphology.

A specialized aircraft, such as a high performance glider, is designed to have a very high peak performance. In the glider the peak performance is centred around the speed that gives the maximum lift to drag ratio, and best glide angle. Performance falls off rapidly away from this speed; there is only a narrow performance envelope. The off-peak performance of a specialized aircraft is therefore relatively poor. In contrast a general purpose aircraft has a lower peak performance, but has good off-peak performance, and is able to fly at a wide range of speeds and lift coefficients. Because a good off-peak performance requires flight at a range of lift coefficients, it also requires a tail that can generate sufficient force to control large moments from the wing. Thus a good off-peak performance requires a large tail area relative to the wing area, while a high peak performance requires a relatively small tail, because of drag.

The avian tail has a variable area, a variable aspect ratio and a variable orientation relative to the body. Unlike the tail of an aircraft it is mounted near to the trailing edge of the wing. When the bird wishes to generate large pitching moments it can spread its tail. During fast flight or gliding, when reducing drag may be more important, the tail can be closed. When substantial lift and pitching moments need to be generated the tail can be spread.

To what extent does the morphology of the avian tail represent a global optimum for aerodynamic function as a control surface? Should we expect to see aircraft with bird-like tails? If we assume selection acts only for the aerodynamic efficiency of the tail, there is a global optimum shape for the avian tail that is a consequence of the increase in lift and the reduction in

the moment arm of the tail as aspect ratio increases. The stability boundaries for flow over the tail shown in figure 9 also constrain the optimum shape, because as aspect ratio increases the angle of attack at which stall occurs decreases. If the flow is considered to be stable only up to 15° angle of attack, then the optimum spread for the tail is just 120° at an aspect ratio of approximately 2.5, and the tail should have a triangular planform. The central tail feathers will then be approximately half the length of the outer tail feathers and the tail will be strongly forked when closed.

To determine whether this optimum tail morphology is a global optimum for a pitch control surface it must be compared with the other options for pitch control. Because the moment arm of a tail is much greater than that of a reflexed section of a wing, and the tail does not adversely affect the aerodynamic properties of the wing, the tail can be a more efficient pitch control than reflex camber.

The remaining comparison is between the avian tail and a high aspect ratio tail mounted at the end of a boom, as in an aircraft (the term bird could, in general, be inserted in the following section wherever the term aircraft is used). Consider the tail of a high performance glider. A typical, if rather elderly, glider is the Slingsby 'Prefect'. This has a tail area of 2.7 m^2 15% of the wing area, and a tail moment arm of 3.5 m. The tail has a flat Göttingen 417 section, which would achieve a maximum operating lift coefficient of about 1.2. At 10 m s^{-1} (close to stalling speed, the comparisons are qualitatively similar at any speed) the glider's tail could produce a moment of 680 Nm. For the optimum avian tail, described above, to produce the same moment it would have to have a maximum continuous width of 5.25 m. The moment arm of the avian tail would be only 1 m. To produce the same moment as the glider's tail the avian tail would have to produce 3.5 times the lift: almost 50% of the lift produced by the glider's wings. Effectively the maximum lift coefficient of the whole aircraft would be increased by almost a third. The maximum lift coefficient determines the minimum possible speed for flight, and also the manoeuvrability (defined as the minimum turning radius) of an aircraft, or animal, and this increase in the maximum lift coefficient may be a significant advantage of the avian tail (Maynard Smith 1952). When widely spread the leading edges of the avian tail come close to the trailing edge of the wings to form a slotted arrangement. With the right slot geometry a further substantial increase in the maximum lift coefficient of the whole aircraft might be possible (theoretically up to $C_l = 4\pi$ (Smith 1975)). The two types of tail differ in the drag they would generate. When generating maximum lift, the avian tail would generate almost seven times as much drag as the glider's horizontal tail surface. This reduces to a factor of five if the drag generated by the tail boom, and vertical tail surface of the glider are included in the drag of the glider's tail. With the glider trimmed to fly at maximum lift to drag ratio with the pitching moments balanced, so no force is required from the tail, if the avian tail could be closed to an apical angle

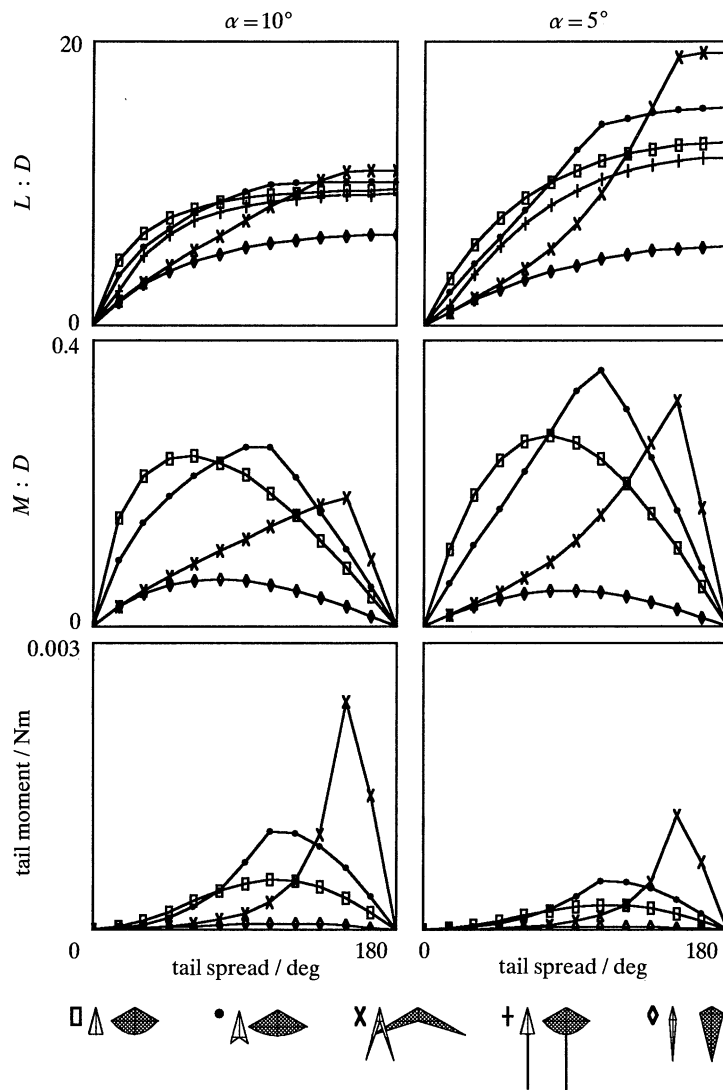


Figure 13. Variation in the lift to drag ratio, moment to drag ratio, and pitching moment generated by the tail, as the tail spreads. Incident flow velocity = 5 m s^{-1} . The peak performance of forked tails is very much higher than that achieved by any other tail shape, but only when the tail is spread. In normal cruising flight, when the tail is closed, the forked tails shown here achieve a lower lift to drag ratio than the other tail types, but can still produce higher turning moments. The optimum shape for aerodynamic efficiency is intermediate between the two forked tails, as is shown by the moment to drag ratios. The graduated tail has an almost flat relationship between performance and spreading angle, this therefore represents a very forgiving type of tail. This type of tail is common in birds that do not fly a lot.

of 30° it would generate less than half the drag of the glider's tail. Swifts and terns are able to close the tail so that the inner feathers are completely covered by the outer tail feathers, and effectively form a streamlined fairing over the rear of the body. In this state the drag of an avian tail would be significantly less than the drag of the glider's tail boom alone, and the avian tail should really be considered as a means of reducing drag by streamlining the body. In addition, by saving the mass and moment of inertia of the tail boom, the pitch response would be improved. The drag of the glider's tail represents about 10% of total drag of the glider when it is flying at its maximum lift to drag ratio. Using an avian tail would reduce the total drag of the glider by at least 5%, at the maximum lift to drag speed. With an avian tail the glider could fly at a higher overall lift coefficient. The stalling speed, and

manoeuvrability of the glider would both be significantly improved.

The use of an avian tail would improve the aerodynamic performance of a glider, but at the cost of a reduction in stability. To achieve the benefits of the avian tail an aircraft (or bird) must be trimmed so that when flying at its maximum lift to drag ratio the nose-down pitching moment generated by the wings is balanced by positioning the centre of gravity aft of the centre of lift. At lower speeds with the centre of pressure in front of the centre of gravity the tail must produce a nose down pitching moment, and the aircraft would be unstable in pitch. At higher speeds, the centre of lift would move back behind the centre of gravity, the tail must then produce a nose up pitching moment, and the aircraft would become stable in pitch. This pattern of stability (similar to that of a

bicycle) gives certain advantages in that manoeuvrability is maintained at low flight speeds (unstable aircraft are more manoeuvrable) but would mean that the pilot would have to maintain constant active control at low speeds to avoid crashing (again much like a cyclist).

Tucker (1992) finds that the area of the tail of a Harris' hawk (*Parabuteo unicinctus*) varies from 10% in fast flight to 20% of the wing area in slow flight. Harris' hawk is a thermal soaring bird. It has a relatively large tail, and a best lift to drag ratio of only 10.9. Off-peak performance is probably more important than peak performance for this species (Tucker & Heine 1990). In the wandering albatross (*Diomedea exulans*) the tail area is only 5% of the wing area when spread, and 3% when closed (areas measured from the outlines in Pennycuik (1982)). Peak lift to drag in the wandering albatross is 23.2 (Pennycuik 1982). The peak performance of the wandering albatross is very much higher than that of the Harris' hawk, but the small tail suggests it has a much narrower performance envelope. The sizes of the tails of birds are comparable or smaller than the typical size of a glider's elevator. As the wings can also be used for control in birds, the tail is not the only control surface, and can be smaller than would be required for a conventional aircraft.

Any change in the lift distribution across the wings and body of a bird should result in a change in the flow field behind the bird. Flow visualizations of the wakes of freely gliding birds do not detect the presence of a separate wake for the body (Spedding 1987a; Thomas 1993). This suggests that the bound circulation on the body is the same as the bound circulation at the wing root, so that the body is generating lift as if it were a smooth continuation of the wing. To maintain circulation on the body it must have a degree of camber, and this could best be induced by the tail. The effect is that a gliding bird is best considered as a simple planar wing with a smooth loading distribution, in most cases not significantly different from the ideal elliptic loading. Parasite drag in free gliding flight might therefore be extremely low. Measurements of the drag of dead birds must therefore be treated with extreme caution (Tucker 1990).

Although there is a global optimum shape for the tail if selection acts purely on the aerodynamics of the tail, selection may often be acting in favour of quite different characteristics. Consideration of the moment to drag ratio for the different tails illustrated in figure 13 shows that while the forked tail has a better lift to drag ratio than any other type, other factors may be relevant. A forked tail is particularly vulnerable to damage, because only a few feathers extend to the tips, and these are relatively unsupported. Damage to a forked tail is likely to be to the outer tail feathers, both because these extend beyond the rest of the tail, and because the tail is likely to be widely spread in the final desperate manoeuvres before a crash. Because only a few feathers extend to the tips of the fork, if these feathers are damaged, the maximum continuous width of the tail is reduced, reducing the lift it can generate. If the damage is asymmetric, as it is likely to

be, the flow pattern over the tail will be affected, and the tail must be held at an angle of roll, if the bird is to fly in a straight line. The result will therefore be a reduction in manoeuvrability. A tail with feathers of equal length or a graduated tail is much less vulnerable to damage. If selection on a simple tail favours an increase in the forces the tail can produce, but also requires the tail to be damage resistant, then the optimum solution may be simply to enlarge the tail isometrically.

Selection for the best lift to drag ratio of the tail will always tend to produce a triangular planform with a straight trailing edge. If selection favours an increased lift to drag ratio of the bird as a whole, then because the forces needed to balance a bird gliding at maximum lift to drag ratio are likely to be small (assuming the centre of gravity is positioned to this effect), the straight trailing edge might be best achieved at a relatively low spreading angle. In the vulture shown in figure 11, the outer tail feathers are 32 cm long, and the central feathers are 30 cm. This extremely shallow fork gives a straight trailing edge at an angle of spread of 40°, corresponding nicely to the tail spread seen in cross country glides, when the maximum lift to drag ratio is achieved. At 10° angle of attack and 15 m s⁻¹ this tail would generate a pitching moment of 1.5 Nm which corresponds very well with the requirements for control in a bird of this size. Similar criteria may determine the tail shape in many species, where selection is acting not for the best lift to drag ratio when the tail is fully spread to generate maximum force, but for the best lift to drag ratio in straight level flight, either flapping or gliding.

The peak performance of the optimum forked tail is high, but off-peak performance is low. When a forked tail is not spread, it generates little lift (but also little drag). The flow over a forked tail is also rather less stable than over a lower aspect ratio tail. It can only operate within a narrow range of angles of attack. This may be why birds with forked tails move their tails in a twitchy manner, constantly spreading and twisting them. A lower aspect ratio tail has a better off-peak performance. Although the area elongated beyond the point of maximum width does not contribute to lift, and so cannot actively contribute to stability, it does contribute drag. The effect of this drag will be to increase stability passively in much the same way as the fletchings on an arrow (Hummel 1992). A bird that requires considerable stability in flight – especially if it does not fly very much – may therefore benefit from the passive stability caused by a graduated tail.

Although selection may act to favour other tail shapes, the slender lifting surface theory shows that the forked tail is the aerodynamically optimum morphology for an avian tail. Comparison with the high aspect ratio tail of a glider suggests that the optimum avian tail may be a global optimum as a flight control device.

ALRT is supported by the SERC. I am grateful to Dave Harper, Alexandra Gampel, Georgia Mason, Peter Northcott, Sandy Willmott and Thomas Wolf for their comments

on the manuscript, and to Charlie Ellington for entertaining discussions on the subject. I am also grateful to an anonymous referee whose detailed comments led to a substantial improvement in the final version.

REFERENCES

- Anderson, J.D. 1991 *Fundamentals of aerodynamics*, 2nd edn. New York: McGraw-Hill.
- Andersson, M. 1982 Female choice selects for extreme tail length in a widowbird. *Nature, Lond.* **299**, 818–820.
- Andersson, S. 1992 Lek mating and sexual selection in Jackson's widowbird (*Euplectes jacksonii*). Ph.D. thesis, University of Gatedburg, Sweden.
- Andersson, S. 1992 Female preference for long tails in lekking Jackson's widowbirds: experimental evidence. *Anim. Behav.* **43**, 379–399.
- Balmford, A. & Thomas, A.L.R. 1992 Swallowing ornamental asymmetry. *Nature, Lond.* **359**, 487.
- Balmford, A. Thomas, A.L.R. & Jones, I.L. 1993 Aerodynamics and the evolution of long tails in birds. *Nature, Lond.* (In the press.)
- Borodulina, T.L. 1951 Ekolova-funktsional'noye znachiye khvosta ptits. (Eco-functional aspects of bird tails) *Dokl. Akad. Nauk SSSR* **71**, 959–962.
- Brown, R.H.J. 1953 The flight of birds. II. Wing function in relation to flight speed. *J. exp. Biol.* **30**, 90–103.
- Cone, C.D. 1962 The theory of induced lift and minimum induced drag of nonplanar lifting systems. **NASA TR R-139**.
- Darwin, C. 1871 *The descent of man and selection in relation to sex*. London: John Murray.
- Evans, M.R. & Hatchwell, B.J. 1992a An experimental study of male adornment in the scarlet-tufted malachite sunbird: I the role of pectoral tufts in territorial display. *Behav. Ecol. Sociobiol.* **29**(6), 413–419.
- Evans, M.R. & Hatchwell, B.J. 1992b An experimental study of male adornment in the scarlet-tufted malachite sunbird: II the role of the elongated tail in mate choice and experimental evidence for a handicap. *Behav. Ecol. Sociobiol.* **29**(6), 421–427.
- Evans, M.R. & Thomas, A.L.R. 1992 The aerodynamic and mechanical consequences of elongated tails in the scarlet tufted malachite sunbird: Measuring the cost of a handicap. *Anim. Behav.* **43**, 337–347.
- Fisher, R. 1930 *The genetical theory of natural selection*. Oxford: Clarendon Press.
- Grafen, A. 1990a Sexual selection unhandicapped by the Fisher process. *J. theor. Biol.*, **144**, 473–516.
- Grafen, A. 1990b Biological signals as handicaps. *J. theor. Biol.* **144**, 517–546.
- Hamilton, W.D. & Zuk, M. 1982 Heritable true fitness and bright birds; a role for parasites? *Science, Wash.* **218**, 384–387.
- Hummel, D. 1978 On the flow formation over a slender thin wing at large angles of attack. Paper no. 15 in 'High angle of attack aerodynamics'. **AGARD CP-247**.
- Hummel, D. 1992 Aerodynamic investigations on tail effects in birds. *Z. Flugwiss. Weltraumforsch.* **16**, 159–168.
- Jones, R.T. 1946 Properties of low aspect ratio pointed wings above and below the speed of sound. **NACA TR 835**.
- Jones, R.T. 1980 Wing flapping with minimum energy. *Aeronaut. J.* **84**, 214–217.
- Jones, R.T. 1990 *Wing theory*. Princeton University Press.
- Katz, J. 1984 Lateral aerodynamics of delta wings with leading edge separation. *AIAA Jl.* **22**(3), 323–328.
- Klatz, J. & Plotkin, A. 1991 *Low speed aerodynamics: from wing theory to panel methods*. New York: McGraw-Hill.
- Lande, R. 1980 Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* **34**, 292–305.
- Lande, R. 1981 Models of speciation by sexual selection on polygenic traits. *Proc. natn. Acad. Sci. U.S.A.* **78**, 3721–3725.
- Lighthill, J. 1986 An informal introduction to fluid mechanics. *IMA Monogr. Ser.* **2**.
- Maynard Smith, J. 1952 The importance of the nervous system in the evolution of animal flight. *Evolution* **6**, 127–129.
- Maynard Smith, J. 1991 Theories of sexual selection. *Trends Ecol. Evol.* **6**, 146–151.
- Møller, A.P. 1988 Female choice selects for male sexual tail ornaments in the monogamous swallow. *Nature, Lond.* **332**, 640–642.
- Møller, A.P. 1989 Viability costs of male tail ornaments in a swallow. *Nature, Lond.* **339**, 132–135.
- Møller, A.P. 1992 Female swallow preference for symmetrical male ornaments. *Nature, Lond.* **357**, 238–240.
- Møller, A.P. 1993 Female preference for apparently symmetrical ornaments in the barn swallow *Hirundo rustica*. *Behav. Ecol. Sociobiol.* (In the press.)
- Norberg, U.M. 1976 Some advanced flight manoeuvres of bats. *J. exp. Biol.* **64**, 489–495.
- Norberg, U.M. 1989 *Vertebrate flight: mechanics, physiology, morphology, ecology and evolution*. Heidelberg: Springer Verlag.
- Padian, K. 1988 The flight of pterosaurs. *Nat. Hist.* **97**(12), 58–65.
- Polhamous, E.C. 1971 Prediction of vortex characteristics by a leading edge suction analogy. *J. Aircraft* **8**(4), 193–199.
- Pennycuik, C.J. 1968 A wind-tunnel study of gliding flight in the pigeon *Columba livia*. *J. exp. Biol.* **49**, 509–526.
- Pennycuik, C.J. 1971a Gliding flight of the white-backed vulture *Gyps africanus*. *J. exp. Biol.* **55**, 13–38.
- Pennycuik, C.J. 1971b Control of gliding angle in Ruppell's griffon vulture *Gyps ruppellii*. *J. exp. Biol.* **55**, 39–46.
- Pennycuik, C.J. 1975 Mechanics of flight. In *Avian Biology*, vol. 5 (ed. D. S. Farner & J. R. King), pp. 1–75. London: Academic Press.
- Pennycuik, C.J. 1982 The flight of petrels and albatrosses (Procellariiformes), observed in South Georgia and its vicinity. *Phil. Trans. R. Soc. Lond.* **B 300**, 75–106.
- Pennycuik, C.J. 1989 *Bird flight performance: a practical calculation manual*. Oxford University Press.
- Shanks, R.E. 1963 Low subsonic measurements of static and dynamic stability derivatives of six flat plate wings having sweep angles from 70 to 84 degrees. **NASA TN D-1822**.
- Spedding, G.R. 1987a The wake of a kestrel (*Falco tinnunculus*) in gliding flight. *J. exp. Biol.* **127**, 45–57.
- Spedding, G.R. 1987b The wake of a kestrel (*Falco tinnunculus*) in flapping flight. *J. exp. Biol.* **127**, 59–78.
- Spedding, G.R., Rayner, J.M.V. & Pennycuik, C.J. 1984 Momentum and energy in the wake of a pigeon (*Columba livia*) in slow flight. *J. exp. Biol.* **111**, 81–102.
- Smith, A.M.O. 1975 High lift aerodynamics. *J. Aircraft* **15**(6), 501–530.
- Thomas, A.L.R. 1993 The flow field on the wings and in the wake of free flying birds. *Math. Rev.* (In the press.)
- Thomas, A.L.R. 1993 The aerodynamic stability of flying animals. (In preparation.)
- Tucker, V.A. 1987 Gliding birds: the effect of variable wing span. *J. exp. Biol.* **133**, 33–58.
- Tucker, V.A. 1990 Body drag, feather drag and interference drag of the mounting strut in a peregrine falcon, *Falco peregrinus*. *J. exp. Biol.* **149**, 449–468.
- Tucker, V.A. 1992 Pitching equilibrium, wing span and

tail span in a gliding Harris' Hawk, *Parabuteo unicinctus*. *J. exp. Biol.* **165**, 21–43.

Tucker, V.A. & Heine, C. 1990 Aerodynamics of gliding flight in a Harris' hawk, *Parabuteo unicinctus*. *J. exp. Biol.* **149**, 469–489.

Zahavi, A. 1975 Mate selection – a selection for a handicap. *J. theor. Biol.* **53**, 205–214.

Received 19 May 1992; accepted 20 October 1992; finalized typescript received 8 February 1993