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Proc. R. Soc. Lond. B 1993 **254**, 181-189
doi: 10.1098/rspb.1993.0144

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The aerodynamic costs of asymmetry in the wings and tail of birds: asymmetric birds can't fly round tight corners

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SUMMARY

Asymmetry in the wings and tails of birds is an unusual trait in that, because of their aerodynamic function, the optimum phenotype for the trait is known: perfect symmetry. There is considerable variation from this optimum both within and between species. Here I use simple aerodynamic theory to predict the aerodynamic costs of asymmetry in the wings and tail, and to examine the relation between the length of the wings or tail, and the cost of given amounts of absolute asymmetry (equal to a given fixed length) and relative asymmetry (asymmetry equal to a given proportion of the length of the wings or tail). The aerodynamic analysis shows that wing asymmetry is much more costly than tail asymmetry, and asymmetry in the aerodynamically functional parts of the tail is more costly than asymmetry in ornaments such as tail streamers. The cost of wing asymmetry and of asymmetry in aerodynamically functional parts of the tail is unaffected or decreases with trait length. In contrast, the aerodynamic cost of asymmetry in tail ornaments increases with trait size. Much of the pattern of variation in the level of fluctuating asymmetry in the wings and tail can thus be explained by natural selection for aerodynamic efficiency.

1. INTRODUCTION

Fluctuating asymmetry (FA) is defined as small non-directional random deviations from perfect symmetry in an otherwise bilaterally symmetric trait. The level of FA in a trait may indicate genetic, developmental or environmental stress (Reeve 1960; van Valen 1962; Palmer & Strobeck 1986). In particular, in several species the level of FA has been shown to reflect the level of homozygosity and imbalance in the genome (Mather 1953; Thoday 1955; Jones 1987; Leary & Allendorf 1989; but see Clarke *et al.* 1992). Directional selection has been shown to result in increased FA (Thoday 1955; Leary & Allendorf 1989). FA seems to be the result of errors in developmental regulation, and a low level of FA in a population could indicate that population has high viability and the ability to cope with environmental stress.

These features of FA are potentially very useful in the study of sexually selected ornaments (Møller 1990, 1992; Møller & Höglund 1991; Thornhill 1992*a, b*). Ornaments, such as the elongated tails of birds, are thought to have evolved under the influence of directional sexual selection and can be costly (Møller 1989; Evans & Thomas 1992).

It might be possible to examine a species and use the ornamental trait involved in mate choice, e.g. a long tail, to select the most preferred individuals, and then use FA as an independent means to determine whether the preference is based on a trait that is arbitrary or is actually an honest signal of mate quality. If the trait is an honest signal then individuals with a high signalling intensity, e.g. a very long tail, should also have high

viability (either heritable or direct), and the population of individuals that signal at high intensity should therefore have low FA. A negative correlation between trait elaboration (signalling intensity) and FA could therefore be evidence that a trait functions as an honest signal of mate quality. If the trait is arbitrary, a simple analysis would not suggest any particular pattern of FA against trait length (Møller & Höglund 1991; Balmford *et al.* 1993*b*).

Negative correlations between trait size and asymmetry have been demonstrated in several characters that are thought to be under directional sexual selection, and this has been taken as evidence in favour of the sexual selection hypothesis of FA (Møller & Höglund 1991). However, in the absence of any specific theoretical analysis of the aerodynamic costs of asymmetry, it is impossible to make any predictions regarding the patterns of asymmetry that should be expected as a result solely of natural selection. Here I use aerodynamic theory to predict the costs of asymmetry in the wings and tails of birds, and to predict the variations in those costs with trait size.

2. THEORETICAL ANALYSIS

Aerodynamic forces on the wings are calculated by using classical aerodynamic theory (Anderson 1991; Katz & Plotkin 1992). The aerodynamic forces on the tail are calculated by using a lifting surface model (Thomas 1993). This model has been shown to predict accurately the properties of the avian tail (Balmford *et al.* 1993*a*).

Asymmetry could have a direct effect on the power

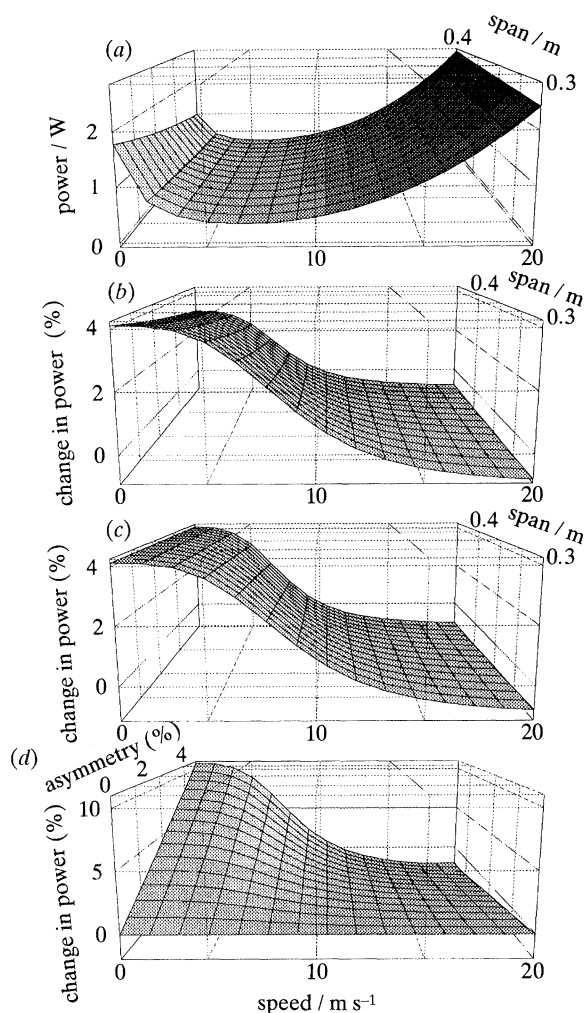


Figure 1. The effect of wing asymmetry on the power required for flight. Power is calculated by using the momentum jet model (Pennycuick 1989). The bird is assumed to balance out asymmetry by flexing its longer wing reducing overall wing span. The wings have a high aspect ratio so mean wing chord is not affected by asymmetry. Increased asymmetry therefore reduces both span and area equally. The graphs illustrate the relation between asymmetry, span and power for an individual bird with different wing spans. With constant mean chord, increasing span increases the aspect ratio so the effect of increasing aspect ratio is also illustrated. The cost of asymmetry is quite sensitive to aspect ratio, which varies here from 7.5 at span = 0.3 m to 10 at span = 0.4 m. (a) The effect of variation in speed and span on power. At low speeds the power required for flight is inversely proportional to wingspan. At very high speeds the increase in wing area that is associated with an increase in wingspan results in an increase in power requirements. (b) As wing span increases the cost of a constant absolute asymmetry decreases (asymmetry = 0.006 m is modelled here, 2% of the shortest modelled span). Note the different scale of the vertical axis. (c) The cost of 2% relative asymmetry is independent of wing span. (d) Change in power caused by wing asymmetry. Note the change in the scale of the vertical axis. A 5% asymmetry can require more than 10% increase in power at low speeds, but can also give a small reduction in power at the highest speeds, because of the reduction in area. Over the normal range of flight speeds asymmetry is costly, the cost being proportional to the asymmetry at any given speed.

required for flight if asymmetry reduces the effective wingspan, or alters the lift distribution on the wings (which must inevitably reduce the aerofoil efficiency). Pennycuick's momentum jet model is used to estimate the power required for flight (Pennycuick 1975). A detailed and explicit description of the model is provided by Pennycuick (1989). Norberg (1990) gives a critical analysis of the limitations of this most simple and general model of animal flight, and it is her recipe for the model that is used here.

The aerodynamic calculations are constructed in such a way as to give the absolute minimum value of the various aerodynamic costs of asymmetry. The predicted values may not accurately reflect the true cost of asymmetry, but the qualitative relations between asymmetry, trait length and aerodynamic costs will be accurately determined. I use the barn swallow (*Hirundo rustica*) as an example species throughout the calculations. The results are not qualitatively affected by the choice of species (A. L. R. Thomas, unpublished results).

3. ASYMMETRY IN THE LENGTH OF THE WINGS

Wing asymmetry is a difference in wing length. Absolute asymmetry is a given difference in length between the left and right wing. Relative asymmetry is defined as the absolute trait asymmetry divided by the mean trait length. In the calculations I give relative asymmetry as absolute asymmetry equal to a given percentage of wing length.

Birds have high aspect ratio wings, that is, a high ratio of wing span to mean chord (typically ≥ 4). As a result of this long thin shape, a small wing asymmetry has a direct effect on wingspan but does not have a significant effect on the mean chord of the wing. The change in area resulting from a small change in asymmetry can be estimated as the product of the mean chord and absolute wing asymmetry. The shape of the wings and the position at which the asymmetry is introduced (for example, wing root or wing tip) is unimportant provided the wings have a high aspect ratio.

Wing asymmetry has three major effects: the total span may be affected, unbalanced rolling and yawing moments are generated, and turning performance is impaired.

In a symmetric animal there are no net rolling or yawing moments in steady flight. The centre of lift and drag of the two wings is halfway between the wingtips. With an asymmetric wing the centres of lift and drag are offset from the body axis. Birds generally have a lift to drag ratio of at least 10. The rolling moment from lift asymmetry is therefore much more important than the yawing moment resulting from drag. With lift L , wing asymmetry (a) gives a rolling moment (M_a) of magnitude

$$M_a = La/2. \quad (1)$$

The moment generated by wing asymmetry is independent of the length of the wings, and depends only on the total force generated by the wings, and the asymmetry.

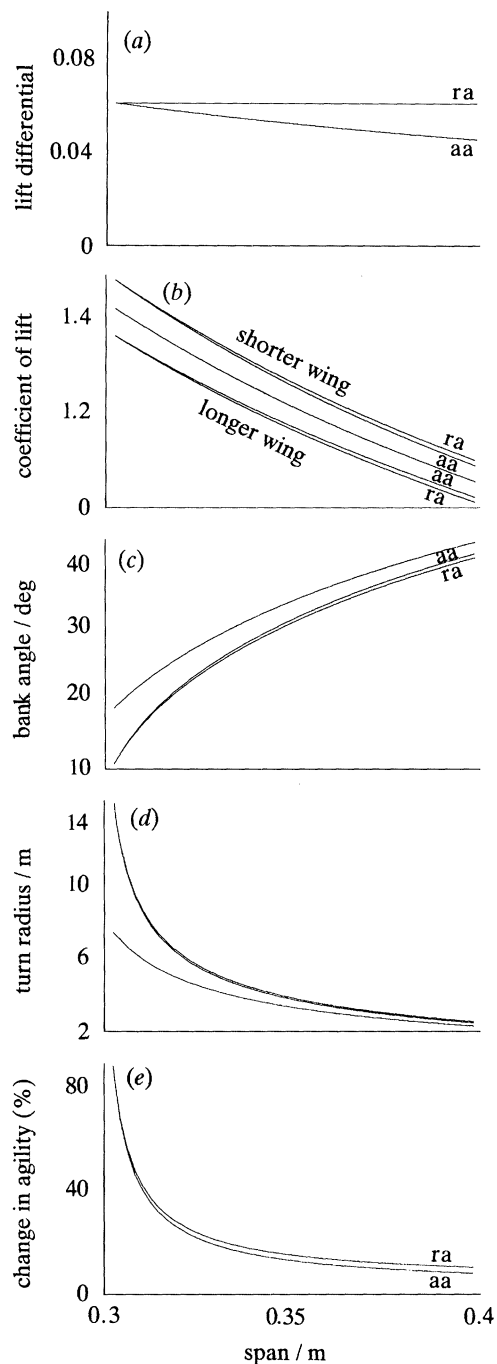


Figure 2. Asymmetry affects almost all aspects of aerodynamic performance; $ra = 2\%$ relative asymmetry, $aa = 0.006$ m absolute asymmetry (i.e. 2% of the smallest span). (a) The lift differential needed to balance asymmetry is proportional to asymmetry divided by span. The cost of absolute asymmetry therefore decreases with span. (b) The lift differential (a) is most economically generated by increasing the lift coefficient on the shorter wing, and decreasing the lift coefficient on the longer wing. At 5 m s^{-1} the wings are operating at close to their maximum steady-state lift coefficient. The central line shows the lift coefficient for symmetric wings, the upper two lines are the lift coefficient for the shorter wing, and the lower lines the lift coefficient of the longer wing. In the case of absolute asymmetry, the lift coefficient on both longer and shorter wings tends towards the symmetric wing value as the wings get longer. (c) The increased lift coefficient (Cl) on the shorter wing limits turning performance. Bank angle (Φ) = $\text{ArcCos}(Cl/Cl_{\text{max}})$. In the Reynolds number range for birds the steady-state lift coefficient cannot greatly exceed 1.5. Flight speed during

To offset the rolling moment generated by wing asymmetry, a bird could flex its longer wing to the same length as the shorter wing. The wing span would then be shortened by an amount equal to the asymmetry. The cost of flight is inversely related to span over the normal range of flight speeds, so this solution is costly (see figure 1; see also Pennycuik 1975, 1989; Norberg 1990).

Alternatively, to balance asymmetry, a bird could adjust the spanwise distribution of lift, either by altering the camber (aerofoil section) or angle of attack of the two wings independently. The shorter wing has to generate increased lift equal to $(1+k)/2 Mg$ (where k is the lift differential), and the longer wing reduced force equal to $(1-k)/2 Mg$. The two add up to the weight (mass M times the acceleration due to gravity g). As the centre of lift is roughly halfway along each wing ($(b-a)/2$ and $(b+a)/2$), where b is the span, the moment due to differential lift is

$$[(1+k)/2] Mg[(b-a)/4] - [(1-k)/2] \times Mg[(b+a)/4] = M_a. \quad (2)$$

Combining equations (1) and (2) and rearranging for the lift differential (k) needed to balance a given wing asymmetry gives

$$k = 3a/b. \quad (3)$$

The lift differential to offset a given absolute asymmetry is inversely proportional to span. The effect of given relative asymmetry is independent of span. At a given span the effect of asymmetry is proportional to the asymmetry (figure 2). An asymmetric spanwise distribution of lift must reduce the aerofoil efficiency of the wings (Anderson 1991).

Whether the lift differential is achieved by altering the angle of attack of the wings or by altering the aerofoil section, the result is an increase in the lift coefficient on the shorter wing. In steady flight the wings operate well below their maximum lift coefficient, so the increased lift coefficient could be easily achieved; this is not true in turning or accelerating flight.

To accelerate or turn, a bird has to increase the force generated by its wings, and reconfigure the wingbeat so that the mean force vector acts at an angle relative to the flight path. The force generated by the wings can then be resolved into vertical and horizontal components. The vertical component ($L \cos \Phi$) balances the bird's weight. The horizontal component, ($L \sin \Phi$),

turn = 5 m s^{-1} . (d) Manoeuvrability is defined in terms of turn radius. The lines for absolute and relative asymmetry are superimposed. Turn radius $r = V^2/g \tan(\Phi)$. (e) Agility is defined as the time to make a turn. Here the percentage increase in time for a turn of 90° at 5 m s^{-1} is illustrated ($t = (\pi/2r)/V$). As the mass of the bird is held constant (0.026 kg), the lift coefficient required for steady flight decreases as the wings get longer. The effect of asymmetry on turning performance therefore reduces as wing length increases. Agility also increases with flight speed, and the effect of asymmetry on agility (but not manoeuvrability) will be smaller at higher speeds, because the lift coefficient for steady flight is smaller at higher speeds.

provides the force to accelerate the bird in a straight line ($L \sin \Phi = MA$, where A is the acceleration) or around a turn ($L \sin \Phi = MV^2/r$, where V is the flight velocity and r is the turn radius). The bird can accelerate faster, or make a tighter turn, by increasing $L \sin \Phi$, but a limit is imposed by the maximum lift coefficient the birds wings can sustain: if the bird tried to turn a tighter corner it would stall.

The minimum radius turn a bird can make is determined by the difference between the absolute maximum lift coefficient and that needed to support weight. Asymmetry drastically reduces turning performance, whether the bird shortens its longer wing, or increases the lift coefficient on its shorter wing (figure 2). Even a small decrease in turning performance can have dramatic consequences on foraging success (see, for example, Evans & Thomas 1992).

Wing asymmetry also results in yawing moments. The two wings have different areas, and therefore generate different drags. In flapping flight this yawing moment may be balanced: the longer wing generates greater thrust. Furthermore, if the bird should choose to balance the rolling moment that results from asymmetry by increasing the lift on its shorter wing, the induced drag of that wing must increase. Compensating for the effect of an asymmetric lift distribution therefore reduces the effect of an asymmetric distribution of drag.

In addition to its aerodynamic effects, wing asymmetry will affect wing inertia. The power required to overcome inertia has generally been considered to be significant only in hovering and very slow flight, but Norberg (1990) and Norberg *et al.* (1993) suggest that it can be a major component of power in small bats even at minimum power speed. Norberg finds inertial power requirements are roughly proportional to wing span. If asymmetry reduces span it could therefore reduce power requirements at low speeds, but the mechanical system responsible for flapping the wings relies on symmetry for efficient function (Norberg 1990). There will be a residual torque, and uneven strain, on the muscles and skeleton of the bird as a result of asymmetry. The cost of such a small but steady strain is unknown.

4. TAIL ASYMMETRY

Tail asymmetry affects the flow field over the tail, generates rolling and yawing moments, and if asymmetry changes the area or maximum width of the tail it will directly affect the lift and drag of the tail.

The effect of asymmetry depends on how widely the tail is spread. In fast flight the tail is furled, and generates little or no force, acting mainly to damp pitching oscillations. Asymmetry could then only have an effect if it alters the total area, and therefore drag, of the tail.

To generate aerodynamic forces the tail is spread. The aerodynamic force generated by the tail depends on the square of its maximum continuous width (Thomas 1993). The maximum width of the tail is in most cases defined by the spread of the outermost tail feathers. In a forked tail the maximum spread is

defined entirely by these outermost feathers, so asymmetry will have greater effect on a forked tail than any other tail type (Balmford & Thomas 1992). Other types of tail are less efficient than the forked tail but are also more stable and more resistant to damage (Thomas 1993).

During slow flight, and turning flight, the tail is widely spread and augments the lift generated by the wings. By taking some of the load off the wings the tail can substantially improve both agility and manoeuvrability, and can reduce the cost of low-speed flight. If asymmetry reduces the width of the tail it will adversely affect all of these components of aerodynamic performance (figure 3).

Even if the tail area and maximum tail width are unaffected by asymmetry, tail asymmetry is costly. As with wing asymmetry, tail asymmetry results in rolling and yawing moments. However, the geometry of the tail is such that the moment arm of the force generated by asymmetry depends on the position of the asymmetry.

Asymmetry in the central tail feathers only affects forces on the centreline of the body, and therefore results in little turning force. Likewise, when the tail is furled the lateral moment arm of any force generated by asymmetry, and the resultant turning moment, is small.

When the tail is spread, asymmetry can result in forces offset substantially from the centreline. The resulting moment (M_t) can be counteracted most efficiently by a differential lift and thrust from the wings;

$$[(1+k_t)/2]F(b/4) - [(1-k_t)/2]F(b/4) = M_t. \quad (4)$$

F represents the force to be offset to compensate for the moment generated by the tail. This force is either the total drag or the total lift of the bird. Simplifying and rearranging for the force differential k_t gives

$$k_t = 4M_t/bF. \quad (5)$$

The denominator of the right-hand side is the product of the total aerodynamic force generated by the wings (lift or drag) and the wing span. The tail force due to asymmetry will always be less than the total force generated by the wings, and the moment arm of the force resulting from tail asymmetry will always be less than the wing span, so the value of k_t will be small.

Tail asymmetry could alternatively be offset by flying with the tail tilted at an angle to generate the required balancing roll or yaw moments (Thomas 1993). The tail has a lower lift to drag ratio than the wings, and the offset force from the tail would be small relative to total lift or drag, so the value of k_t would be much higher. The tail is tilted to initiate turning manoeuvres, and to control sideslip during a turn (Thomas 1993). If the tail had to be tilted to maintain straight flight, this would reduce the range of force it could produce, and therefore impair turning performance. Using the wings to balance tail asymmetry is much cheaper than using the tail.

Asymmetry in the wings is costly because it affects their aerodynamic performance. The same is true for

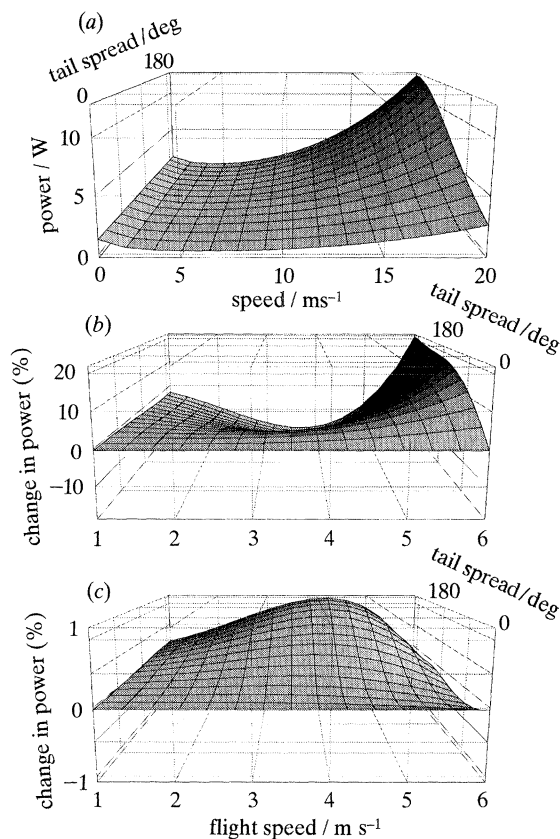


Figure 3. The effect of tail asymmetry on the power required for flight. The effect of the tail on aerodynamic performance is described in detail elsewhere (Thomas 1993, A. L. R. Thomas, unpublished results). The contribution of the lift and drag of the tail to the total power required for flight is calculated here by combining the power for flight (Pennycuik 1989) with the power required by the tail (Thomas 1993)

$$P_t = U \left(\frac{2 K \{ \sqrt{[(Mg - L_t)^2 + (D_{\text{par}} + D_{\text{pro}} + D_i + D_p)^2]} \}^2}{\rho U^2 \pi b^2} + D_{\text{par}} + D_{\text{pro}} + D_i + D_p \right),$$

where P_t is the power required for flight, U is the velocity, K is the aerofoil efficiency, M is the body mass, g is acceleration due to gravity, L_t is tail lift, D_{par} is parasite drag, D_{pro} is profile drag, D_i is induced drag of the tail, D_p is profile drag of the tail, ρ is air density, b is span. Profile and parasite drag are calculated by the methods described in Norberg (1990), the lift and drag of the tail are calculated by the methods described in Thomas (1993). The tail modelled here has 5 cm central feathers and 10 cm outer feathers: the aerodynamically optimum forked shape. Tail angle of attack is 10 deg. (a) The tail can flatten the power curve, and extend the lower range of speeds a bird can attain. At high speeds the drag of the tail increases the power requirement dramatically, so the tail should be furled in fast flight. (b) The tail only reduces the power required for flight over a narrow range of speeds. Note the change in the scales of the vertical and horizontal axes. (c) Asymmetry is assumed to reduce the span of the tail and therefore reduces drag slightly, and lift substantially. Tail asymmetry particularly increases the power required by the tail in the speed range where the tail most reduces the power required for flight. Note that the magnitude of the effect of tail asymmetry on power is very much less than the effect of wing asymmetry.

the aerodynamically functional parts of the tail, and asymmetry in the lifting part of the tail is particularly costly (Balmford & Thomas 1992). Asymmetry in the non-functional parts of the tail introduces an asymmetry in drag, and, although much less costly than asymmetry affecting the aerodynamically functional parts of the tail, this asymmetry will have aerodynamic costs.

The moment arm of the drag of an asymmetric elongated tail feather is given by the lateral distance between the centreline of the bird and the centre of area of the projecting part of the feather. This distance (z_a) depends on how widely the tail is spread, and on the lengths of the asymmetric feathers:

$$z_a = R \sin(\Delta/2), \quad (6)$$

where R is the length of the feathers would have if symmetric, and Δ is the angle of spread of the tail.

The moment will be the product of equation (6) and the change in drag due to asymmetry. As we are considering a small asymmetry in a single pair of tail feathers, and the width of a tail feather is invariably much less than its length, the area is proportional to the asymmetry. As an ornamental tail feather is effectively a thin flat plate aligned with the flow, the drag at any given speed will be proportional to the exposed surface area of the feather.

From equations (5) and (6) it is clear that the effect of asymmetry in the tail will increase as tail length increases, as tail spread increases, and that asymmetry will be more important in outer than central tail feathers.

The aerodynamic cost of both relative and absolute tail asymmetry increases with tail length, but the cost of relative asymmetry increases exponentially. The cost of absolute tail asymmetry increases linearly over the naturally occurring range of tail lengths, and reaches an asymptote at extreme (theoretically infinite) tail lengths (figure 4).

The aerodynamic mechanism responsible for the lift of the tail (Thomas 1993) is different from that acting on the wings, and the details of the aerodynamics of flow over the tail are important in determining the moments resulting from asymmetry in lift.

At high angles of attack the flow over the leading edge of the tail separates forming detached leading edge vortices. These leading edge vortices stabilize the flow increasing the range of performance and lift coefficient of the tail. Although the vortices stabilize the flow over the tail, they are themselves rather unstable. Asymmetry in the angle of the trailing edge to the freestream direction can result in an early onset of vortex breakdown, so the tail can suffer a sudden asymmetric stall at a relatively low angle of attack. Vortex instability and vortex breakdown result in high drag, and can lead to large yawing and rolling forces. The existence of these forces has been confirmed in several windtunnel studies (Lee & Ho 1990; Hummel 1992). Specific numerical models can predict the forces accurately, but a simple general theoretical model is lacking.

Several features of the avian tail seem to be designed to increase the stability of the leading edge vortices.

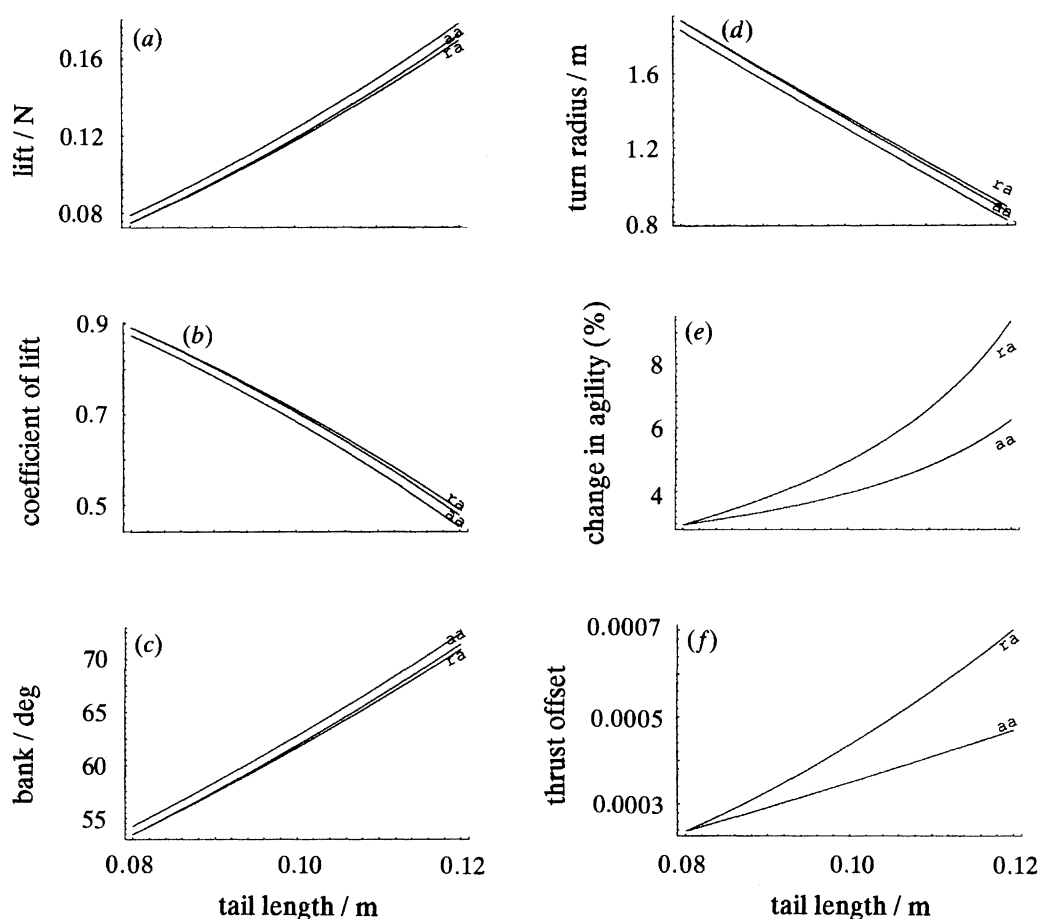


Figure 4. Tail asymmetry affects lift, drag and turning performance; $ra = 5\%$ relative tail asymmetry, $aa = 0.004$ m absolute tail asymmetry. The tail is assumed to be generating lift so angle of attack = 10° , flight speed = 5 m s^{-1} and tail spread = 120° throughout. Central tail feather length is half the outer feather length giving the aerodynamically optimum fork-shaped tail in all symmetric cases. (a) If asymmetry reduces the maximum span of the tail it reduces the lift the tail can produce. Both absolute and relative asymmetry are most costly in a long tail than in a short tail (b) The tail removes some of the load from the wings at low speeds. The wing lift coefficient at 5 m s^{-2} is therefore reduced substantially (compare figures 1 and 5). (c) Bank angle at 5 m s^{-1} with the influence of the tail. The tail augments the lift of the wings and can therefore substantially improve turning performance. If asymmetry affects the lift generated by the tail it impairs turning performance. (d) Manoeuvrability is adversely affected by tail asymmetry. The cost of asymmetry increases with tail length. Asymmetry has a similar effect on agility. (e) Percentage change in agility induced by an asymmetry which affects the lift generated by the tail. The effect of both relative and absolute asymmetry on agility increases with tail length. A small change in the lift generated by the tail can have a substantial effect on the turning performance of a bird, because tight turns require both wings and tail to operate at the limit of their aerodynamic capabilities. (f) Asymmetry has a substantial effect even if it occurs in a part of the tail that is not aerodynamically functional. The yaw moment contributed by the difference in drag between the streamers on the ends of the outer tail feathers of a male swallow is proportional to the asymmetry in streamer length. The shape of the relation would be the same for any other bilaterally paired feather ornament, such as the pectoral tufts of sunbirds (e.g. *Nectarinia johnstonii*, *N. famosa*) or the elongated wing feathers of the pennant winged nightjar (*Semiopterus longipennis*). The cheapest way for the bird to compensate for the yaw moment generated by asymmetric drag is to introduce a differential in the thrust generated by the left and right wings. As tail length increases, thrust differential needed to balance relative asymmetry increases exponentially. The thrust differential to balance 0.004 m absolute tail asymmetry also increases rapidly over the range of tail lengths examined here (which coincide with the natural variation in length). At extreme (theoretically infinite) tail lengths the moment generated by absolute tail asymmetry must reach an asymptote.

The transverse curvature of the tail can control vortex formation and induced drag. The emarginated outer tail feathers of many birds may reduce the pressure gradient at the trailing edge, delaying vortex breakdown. Alternatively, by blowing air into the leading edge vortices, they may increase the effective span and reduce induced drag: similar mechanisms have been shown to increase the performance of delta-winged aircraft (Lee & Ho 1990). This is an area in which the aerodynamics of birds' tails may be far in advance of

aircraft design (Thomas 1993); further investigation is to be desired.

5. DISCUSSION

Both tail and wing asymmetry increase the cost of flight and reduce flight performance (figure 5). The aerodynamic mechanisms responsible for lift on the wings and tail are quite different, resulting in quite different relations between trait length and asymmetry.

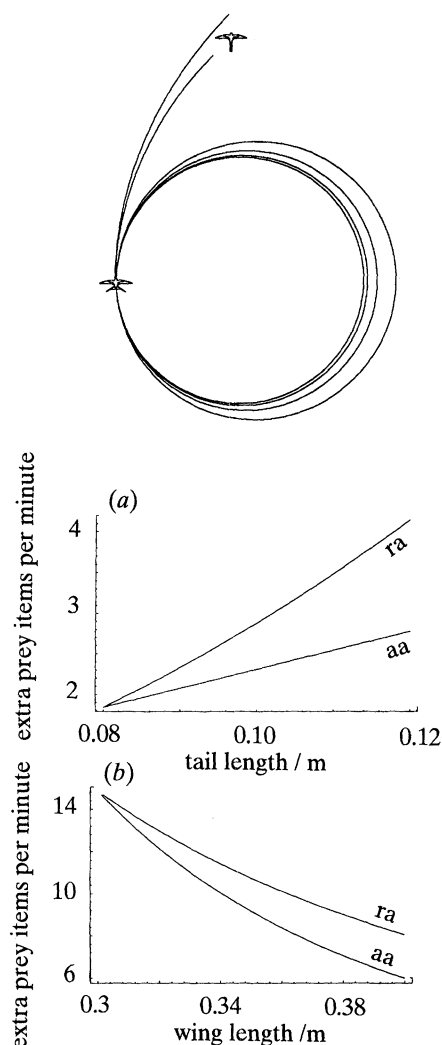


Figure 5. The upper drawing shows, to scale, a swallow with 35 cm wing span and 10 cm outer tail feathers. The circles show, to the same scale, the minimum radius circle this bird could fly with both wings and tail spread to generate maximum lift at 5 m s^{-1} flight speed. The smallest circle could only be achieved by a bird with both symmetric wings and a symmetric tail. The two intermediate circles are the tightest turns that a swallow with tail asymmetry could make; the inner of the two shows the effect of asymmetry in the streamers, the outer the effect of asymmetry in the lifting parts of the tail. The outer circle is the tightest turn for a bird with a symmetric tail but 2% asymmetry in the wings. The upper two curves are the lines followed during the first 45 deg of the tightest turn that could be made without using the tail by a symmetric swallow (inner curve) and a swallow with 2% wing asymmetry (outer curve). The lower two graphs show the number of prey items that an asymmetric swallow would have to catch during every minute of flight to compensate for the increase in the power needed for flight as a result of asymmetry. (a) The effect of 5% relative asymmetry, and 0.004 m absolute tail asymmetry. (b) The effect of 2% relative asymmetry and 0.006 m absolute wing asymmetry. The following assumptions are made in calculating the number of prey that would need to be consumed: prey mass = 10 mg, prey energy content = 1.2 J, assimilation efficiency = 70%, muscle efficiency = 10%, flight speed = 5 m s^{-1} . Bryant and Turner (1992) found swallow mean prey size = $6.01 \pm 5.6 \text{ mg}$, and a bolus brought back to feed nestlings contained 18.1 ± 14.1 insects. Swallows took 2.40 ± 1.64 min foraging time to collect this bolus, but, as they were presumably also feeding themselves at the same time, the

The flow over a high aspect ratio wing is essentially two dimensional, and lift on the wings results from vertical movements of the air with no significant sideways motion outside the wingtip vortices. The wings generate lift proportional to their area (Anderson 1991). This has the result that the cost of asymmetry in the wings becomes smaller as the wings get longer.

In contrast, the flow over the tail contains substantial components of sideways motion, and these transverse flows are ultimately responsible for the lift of the tail. The transverse flow over the tail results from the increasing width of the tail in the freestream direction, and the lift of the tail depends on the square of the maximum tail span (Lee & Ho 1990; Thomas 1993). Tail asymmetry that reduces the maximum width of the tail reduces the lift generated by the tail: asymmetry in the outer tail feathers is therefore particularly costly.

Many birds have elaborate tail streamers, rackets and plumes which cannot be considered to be aerodynamically functional (Balmford *et al.* 1993; Thomas 1993). Asymmetry in these types of ornament is nevertheless costly because it results in an asymmetry in drag which generates a turning moment. To balance this turning moment most efficiently the bird can induce a differential in the thrust of the left and right wings, but balance can only be achieved at the penalty of increased drag, and reduced performance in turning and accelerating flight. The drag generated by such ornaments will depend on their surface area and, to some extent, on their shape. The moment arm depends on the length of the ornament. Therefore the cost of asymmetry in an ornament such as a tail streamer increases with both the size of the asymmetry and the ornament's length.

Birds could use a variety of techniques to reduce the impact of asymmetry. For example, the rolling moment generated by asymmetric wings could be counter-balanced by generating a rolling moment with the tail, although this would increase the drag of the tail. Furthermore, because the tail is generating a rolling moment it will also generate a yawing moment which must also be balanced somehow if the bird is to maintain steady flight. Birds are best considered as unified lifting surfaces (Thomas 1993). Changes in the aerodynamic forces on one part of the animal can affect the aerodynamics of all the other parts. Therefore the cost of asymmetry can only be redistributed, not removed.

Recent interest in FA has been aroused because the level of FA in a population is apparently correlated with the fitness of that population (Palmer & Strobeck 1986; Jones 1987). If elaborate sexually selected ornaments have evolved as honest signals of male quality, then the individuals signalling at the highest intensity (e.g. those with the longest tails) must be of the highest quality. A population of such individuals

bolus brought back for the young can only give an indication of the spare foraging capacity for a swallow. By comparison it would seem that even very small amounts of asymmetry results in a substantial energetic strain.

should exhibit low FA. Alternatively, elaborate sexually selected ornaments may have evolved through an arbitrary preference and Fisherian runaway process. In this case the mechanism of evolution itself does not require any correlation between the degree of elaboration of the ornament and individual quality. A population of individuals with a high degree of trait elaboration (again the longest-tailed individuals) would not be expected to have any particular level of FA.

The competing models of the mechanism underlying sexual selection can lead to different predictions of the relation between trait elaboration (signal intensity) and FA (Møller 1990, 1992, Møller & Höglund 1991; Thornhill 1992*a, b*). The signalling model predicts a negative correlation between trait elaboration and FA, but the arbitrary preference model predicts no relation. A trait evolved through an arbitrary preference might be expected to show the U-shaped relation between FA and trait elaboration that is seen in most morphological traits (Palmer & Strobeck 1986).

The use of FA as a test of the mechanisms underlying the sexual selection of ornaments relies on the independence of FA as a measure of fitness. If FA is itself the subject of selection (either natural or sexual), and especially if the strength of that selection varies with trait elaboration, then the use of FA as a test of mechanism becomes of doubtful value. Direct sexual selection for symmetric mates with a high degree of trait elaboration could occur through an arbitrary preference mechanism, in which case FA in the trait would not be a good indication of fitness. If the expression of a sexually selected trait has reached an equilibrium level (defined as a level at which sexual selection for elaboration and natural selection against the costs of an elaborate trait are equal and opposite), or if natural selection directly penalizes asymmetry, then FA can no longer provide a qualitative test of models of sexual selection. Kirkpatrick & Ryan (1991) and Balmford & Read (1991) have pointed out that in a population at equilibrium, whether a trait has evolved through an arbitrary preference or as an honest signal, the highest-quality individuals will have the highest degree of trait elaboration (because the highest-quality individuals must signal most intensely, or alternatively can afford the greatest degree of elaboration of an arbitrary trait). FA cannot, therefore, be used to distinguish qualitatively between the competing models of the evolution of elaborate ornaments if the ornament is costly, and exaggeration of the ornament is limited by natural selection (i.e. the trait is at equilibrium).

Møller (1993*a*) provides evidence that female swallows (*Hirundo rustica*) discriminate against apparently asymmetric males. It is unlikely that female swallows actually select for symmetry. It follows from the definition of FA that most individuals of any genotype that exhibits FA will be symmetrical no matter what the actual level of FA is. The symmetry of an individual is therefore unlikely to be a good indicator of quality. However, high asymmetry has all the characteristics of an honest signal of low quality. Møller (1993*a*) has shown that female swallows in the

Chernobyl area discriminate against males with an aberrant outer tail feather morphology that they are unlikely ever to have previously encountered. Discrimination against unusual morphologies could be sufficient to explain female discrimination against highly asymmetric males, and would enable females to avoid low viability mates. Thus, despite the action of sexual selection on symmetry, it may still be possible to use FA to distinguish between models of sexual selection.

The analysis presented here and recent experimental evidence show that asymmetry impairs flight performance (Møller 1990). The aerodynamic costs of asymmetry suggest that natural selection may be responsible for a large part of the pattern of fluctuating asymmetry. If the aerodynamic cost of asymmetry is important, levels of FA should depend on the importance of flight. Balmford *et al.* (1993*b*) found that, as the importance of flight to a species increases, the FA in the wings and tails of that species decreases.

Tail asymmetry is much less costly than wing asymmetry, and comparative studies have shown higher levels of FA in tails than in wings (Møller & Höglund 1991; Balmford *et al.* 1993*b*). In fact, the low costs of modifications to the tail may be why the tail is so often elaborated (together with the fact that tail elaboration makes a bird look larger). The cost of asymmetry in the parts of the tail that are not aerodynamically functional should be lower than for either the wings or lifting parts of the tail. Balmford *et al.* (1993*b*) found that species with aerodynamically functional forked tails had significantly lower FA than species with graduated tails or pintails. In parts of the tail that are not aerodynamically functional the cost of asymmetry should increase with trait length, whereas in aerodynamically functional parts of the tail the cost should be independent or decrease with length. Møller & Höglund (1991) did find a negative relation between trait length and FA in birds with ornamental tails. However, in a very large survey of long-tailed birds, Balmford *et al.* (1993) failed to find any consistent negative relation between trait length and asymmetry.

The level and pattern of FA found in comparative studies is entirely consistent with the qualitative pattern expected under the action of natural selection against asymmetry. A quantitative analysis would be needed to determine the level of asymmetry expected at any given trait length under natural selection; deviation from this quantitative pattern could result from sexual selection. Both natural selection and sexual selection can determine the level of FA and the relation between trait elaboration and FA in a species. If FA is to be used to distinguish between the competing models of the mechanism of sexual selection, it is essential to determine the relative contributions of both natural selection and sexual selection to the distribution of FA.

This work was funded by the SERC and DSS. Alexandra Gampel, Sandy Willmott, Ian Hartley and Nick Davies made valuable contributions to the manuscript.

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Received 9 August 1993; accepted 21 September 1993

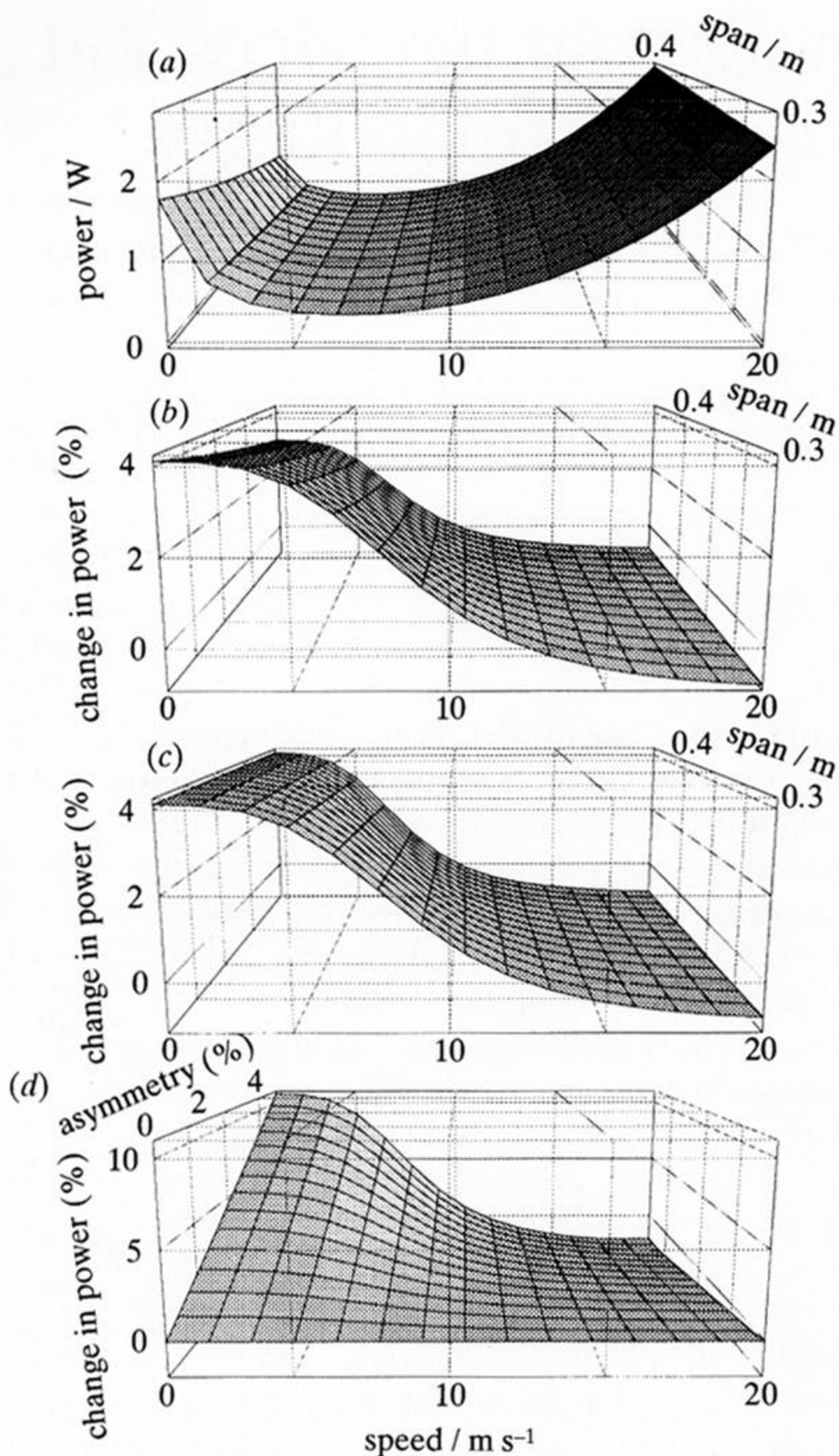


Figure 1. The effect of wing asymmetry on the power required for flight. Power is calculated by using the momentum jet model (Pennycuik 1989). The bird is assumed to balance out asymmetry by flexing its longer wing reducing overall wing span. The wings have a high aspect ratio so mean wing chord is not affected by asymmetry. Increased asymmetry therefore reduces both span and area equally. The graphs illustrate the relation between asymmetry, span and power for an individual bird with different wing spans. With constant mean chord, increasing span increases the aspect ratio so the effect of increasing aspect ratio is also illustrated. The cost of asymmetry is quite sensitive to aspect ratio, which varies here from 7.5 at span = 0.3 m to 10 at span = 0.4 m. (a) The effect of variation in speed and span on power. At low speeds the power required for flight is inversely proportional to wingspan. At very high speeds the increase in wing area that is associated with an increase in wingspan results in an increase in power requirements. (b) As wing span increases the cost of a constant absolute asymmetry decreases (asymmetry = 0.006 m is modelled here, 2% of the shortest modelled span). Note the different scale of the vertical axis. (c) The cost of 2% relative asymmetry is independent of wing span. (d) Change in power caused by wing asymmetry. Note the change in the scale of the vertical axis. A 5% asymmetry can require more than 10% increase in power at low speeds, but can also give a small reduction in power at the highest speeds, because of the reduction in area. Over the normal range of flight speeds asymmetry is costly, the cost being proportional to the asymmetry at any given speed.

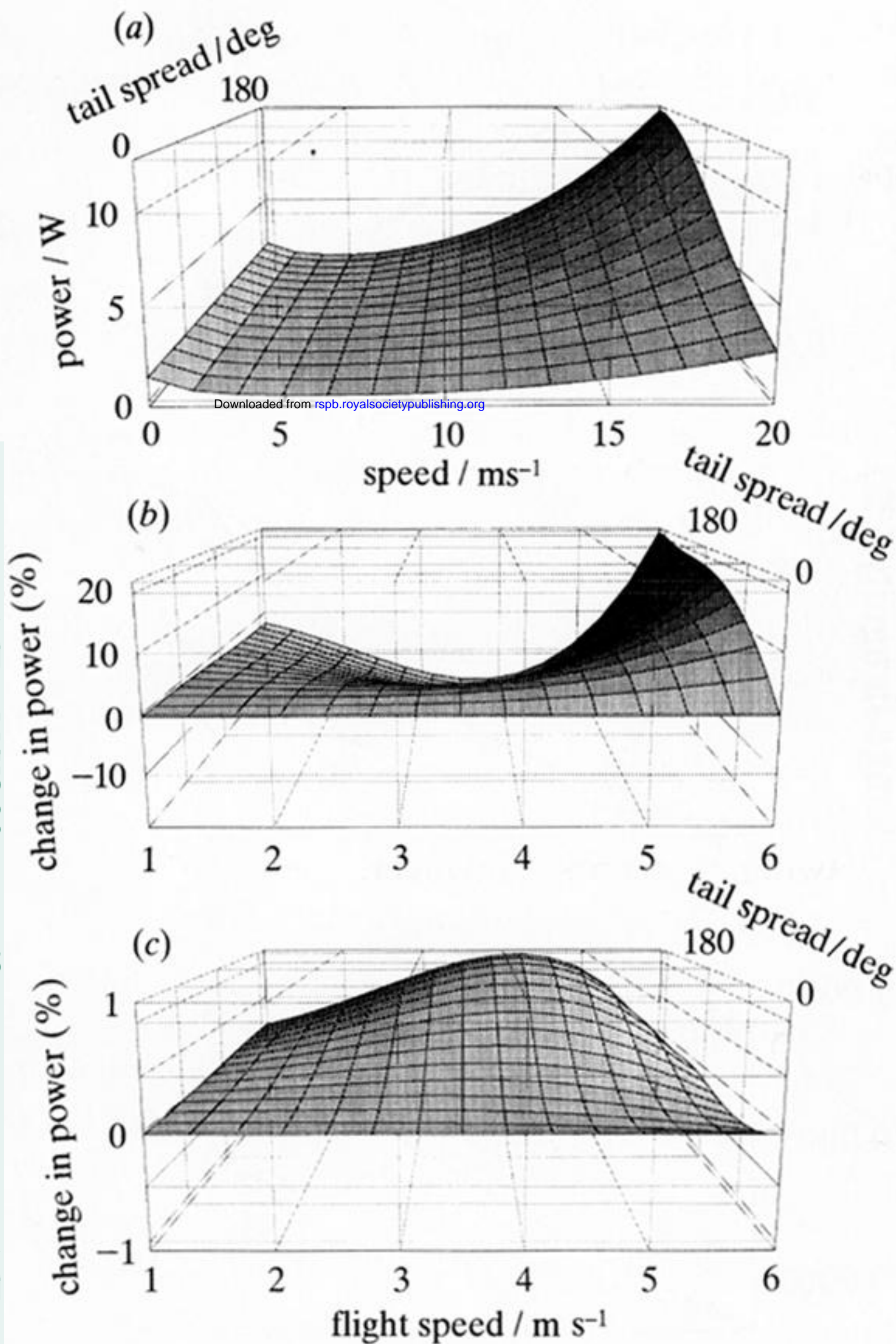


Figure 3. The effect of tail asymmetry on the power required for flight. The effect of the tail on aerodynamic performance is described in detail elsewhere (Thomas 1993, A. L. R. Thomas, unpublished results). The contribution of the lift and drag of the tail to the total power required for flight is calculated here by combining the power for flight (Pennycook 1989) with the power required by the tail (Thomas 1993).