On the Tails of Birds

What are the aerodynamic functions of birds' tails,
with their incredible diversity of form?

Adrian L. R. Thomas

Birds' tails vary more than their wings. Tails can develop enormous size and intricate elaborations in some sexually dimorphic species (Andersson 1994, Balmford et al. 1993a, 1994, Evans and Thomas 1992, Norberg 1995, Winquist and Lemon 1994). For example, the long-tailed widow bird *Euplectes progne*, a bird a little larger than a starling, has a tail more than 1 m long; the lyre-tailed nightjar *Uropsalis lyra* has a tail eight times as long as its body, giving it—in relative terms—the largest tail of any bird; and the marvelous spatule-tailed hummingbird *Loddigesia mirabilis* has a tail that is elongated into bizarre crossed wirelike structures with "flags" at the ends that are as long as its body (Figure 1). Other species, such as the spinetail swifts (*Neafrapus cassini*), have tails consisting of just a few spiny barbs.

Between these extremes, bird tails exhibit a wide range of morphologies (Figure 2; Norberg 1989, Thomas 1993a, Thomas and Balmford 1995). In this article, I describe recent work that uses aerodynamic analyses to investigate the evolutionary forces responsible for the morphologies of birds' tails.

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Aerodynamic considerations play a large role in determining the morphology of bird tails, but other factors—such as feeding style or vulnerability to damage—are also important

How birds use their tails

Watch any bird flying slowly, turning, or coming in to land, and you will see that the tail is an important part of its flight apparatus. During slow flight, a bird spreads its tail widely and lowers it at a large angle in the direction it is flying (Figure 3). As the bird accelerates, it gradually reduces its tail's angle in relation to airflow, and at higher speeds it furls its tail. A bird approaching a landing will often spread its tail widely (just as in slow flight), and as it enters the final stages of landing, it almost always angles its tail upward. This movement provides a control input to rotate the bird's body to a more vertical posture for the final flare, allowing it to slow and then stall its wings just as its feet touch down (Figure 4).

The way birds use their tails to control turning is most easily seen in buzzards or other large raptors circling and climbing in thermals (rising columns of hot air). Thermals are turbulent and bumpy, and to keep on course while circling, a buzzard has to constantly adjust its tail, twisting it one way and then the other.

At least three distinct aerodynamic functions have been identified for the tail. First, the tail can help maintain aerodynamic stability (like the horizontal and vertical tail surfaces of an aircraft). Second, the tail can be used to control the angle of attack of the wings and balance the pitching moments they generate. Third, the tail can produce substantial lift during acceleration, turning, and slow flight to augment that generated by the wings.

Stability and balance. The tail's role in maintaining stability and balance has been clearly demonstrated in wind tunnel studies. For example, Tucker (1992) trained a Harris hawk to glide at different speeds in a tilting wind tunnel. At high speeds, the bird flew with its wings flexed and swept slightly backward and its tail furled; this posture reduces drag. At lower speeds, the bird spread its wings widely; this moved their center of lift forward, in front of the bird's center of gravity. With the center of lift in front of the center of gravity, the bird would tumble over backwards at these lower speeds, so to maintain balance the Harris hawk generated lift with its tail.

The tail plays a similar balancing role in flapping flight. By analyzing how the tail muscles work in flight, Gatesy and Dial (1993) have shown that a bird generates substantial
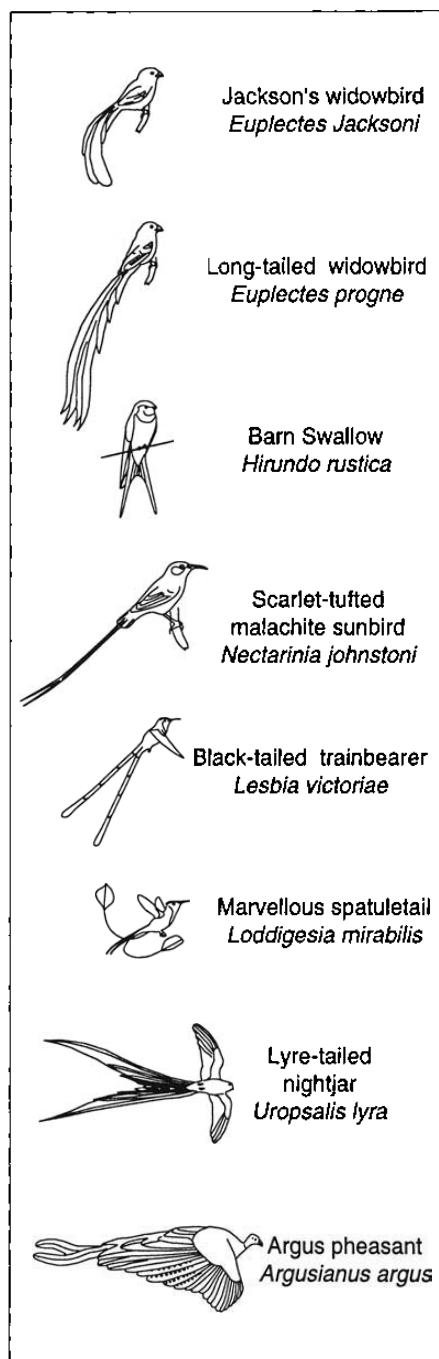
Figure 1. (above) Tails reach their most elaborate forms in the males of some sexually dimorphic species. The tails of the top four species have been shown to be involved in sexual selection—females of these species prefer males with the longest and most elaborate tails. Hummingbirds (e.g., the black-tailed trainbearer and marvelous spatuletail) exhibit more variety in tail form than any other group. The male lyre-tailed nightjar has the longest tail in relative terms—it may be more than eight times the length of the body. In terms of absolute size, the argus pheasant has the biggest tail—almost 2 m in length.

Figure 2. (below) Tails vary more than wings, even when sexual selection is not involved. The smallest tails are those of the spinetailed swifts, which, like woodpeckers, use their tails as a prop when climbing. Swifts are shown with their tails both opened and closed. The tails of seabirds (e.g., the albatross) and raptors (e.g., the condor and falcon) seem well suited for an aerodynamic function. However, the function of the relatively short, graduated tails of woodland birds (e.g., the magpie and the lesser spotted woodpecker), and the convergent evolution of comblike tail feathers in several species of birds that inhabit dense undergrowth (e.g., Des Mur's wiretail), remain a puzzle.
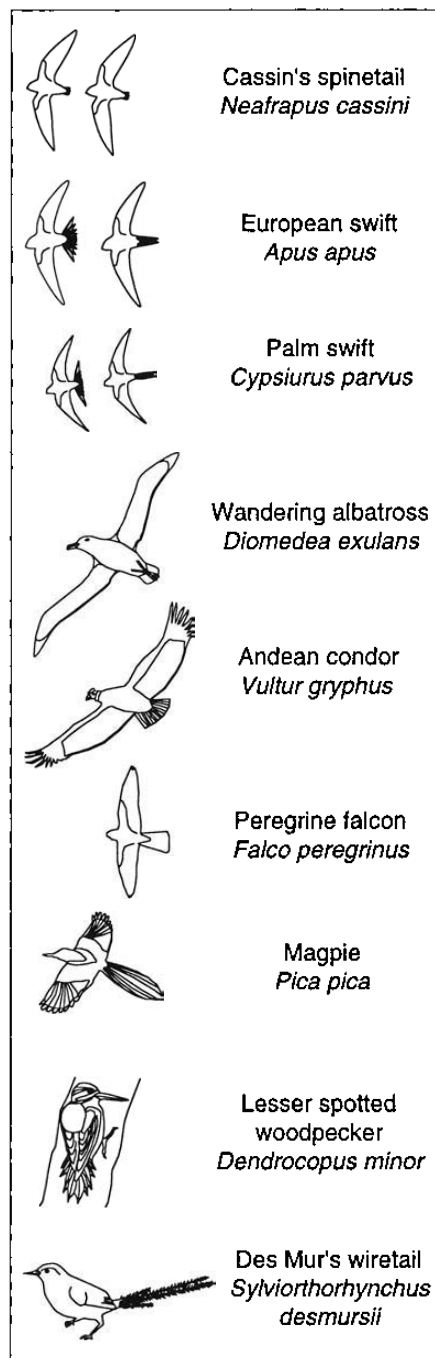
forces with its tail during takeoff and slow flight, when the tail is both flared and depressed in time with the wing beat. Once a bird is in level flight, it spreads its tail and holds it at a relatively constant angle to the airflow (see Figure 3).

Although the use of the tail in slow flight has been interpreted in terms of balance and stability, this role is necessary only because of the way birds hold their wings—specifically, because the bird's center of lift is forward of its center of gravity (Hummel 1992, Norberg 1994, Thomas 1993a). As a result of this design, birds have to generate both balancing and stabilizing lift with the tail when they are flying slowly. By using their tails to generate lift at low speed, birds can reduce the power needed for slow flight (see below; Norberg 1994, Thomas 1993b, Thomas and Balmford 1995).

Turning. To turn, a bird rolls to lean in the direction it wants to go—just like turning on a bicycle—and directs some component of lift in the direction in which it wants to turn. In a turn, the outer wing goes slightly faster than the inner wing, so the drag on the outer wing is slightly higher than on the inner wing. This increased drag could cause the bird to skid outward, away from the turn (the same effect happens in any aircraft). Therefore, to keep itself pointing in the direction it is going, the bird uses its tail as a rudder.

Besides functioning as a rudder, the tail has a second role during a turn or during accelerating flight. Both turning performance and acceleration depend on the maximum lift a bird can generate. For an aerial feeder, such as the swallow, the tighter it can turn, the more insects it can catch. In turning, as mentioned above, a component of lift acts to turn the bird. In accelerating, a bird must adjust its wingbeat so that a component of force acts in the direction in which it wishes to accelerate. The speed and tightness of a turn and the rate of acceleration, therefore, both depend on the total lift the bird can generate. Birds can also use the tail to generate lift additional to that of the wings—and this allows them to make tighter turns
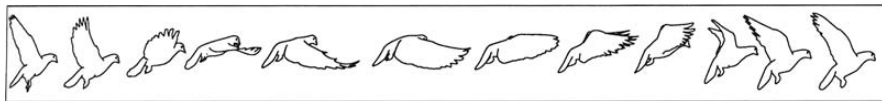
Figure 3. Slow flight in the pigeon (*Columba livia*). The tail is held spread and at a high angle of attack relative to the flight direction. Although the wings beat so that the wing tips almost touch at the ends of each stroke, the tail moves very little. During a downstroke of the wings, the tail is slightly depressed; during an upstroke, it is raised.

and increases their maximum rate of acceleration (Thomas 1993b).

The aerodynamics of the tail: force production

These observations on the role of the tail in stability, balance, and turning suggest that the tail is an important part of the bird's flight apparatus. However, to understand how birds' tails work and why different birds have tails of different shapes and sizes requires a model of the aerodynamics of the tail itself.

The aerodynamics of the tail have been modeled using slender lifting surface theory (Jones 1990, Katz and Plotkin 1991, Thomas 1993a). Aerospace engineers have used this theory to model delta-winged aircraft, such as the Concorde, the space shuttle, and F-16 fighter jets, and have tested this theory extensively. For simplicity, the model, as applied to bird tails, treats the tail independently of the wings and assumes that the flight speed is high enough to generate a steady airflow over the tail.

Any lifting surface (wings or tail) generates low pressure on its upper surface and high pressure on its lower surface. The high-pressure air constantly expands out from below the lifting surface, around the edges, and into the area of low pressure over the top surface. For a conventional high aspect-ratio wing (i.e., a long, narrow wing), this three-dimensional airflow—in which air spills out from the underside of the wing and flows onto its top surface—occurs only at the wing tips, where it forms wing tip vortices. The entire lifting surface of a bird's tail is effectively equivalent to the tips of a conventional high aspect-ratio wing. The airflow over the tail is, therefore, three-dimensional and is dominated by the transverse flow that moves around the leading edges from under the tail onto the top surface (Figure 5).

The pattern of flow in any transverse section across the tail will be exactly the same as in any other transverse section and will be entirely dominated by flow from the underside of the tail onto the top surface (Figure 5). However, in successive sections taken backward along the tail, as the span increases the scale of the flow increases. With the tail at a positive angle of attack, as the scale of the flow on the tail increases, the flow pattern simultaneously moves downward. The combination of the increase in scale and downward movement of the airflow accelerates a mass of air downward, creating the force (i.e., lift) generated by the tail. The magnitude of the aerodynamic force generated depends only on the increase in scale and downward movement of the airflow. The amount of downward movement is determined by the angle of inclination between the tail and the air through which it is moving (the angle of attack). The final scale of the flow is determined by the maximum continuous span of the tail.

Any tail section behind the point of maximum continuous span generates drag but does not produce lift (the flow effectively leaves the tail at the point of maximum width). Lift does not depend on the tail's shape, only on its maximum continuous span and angle of attack. However, the position of the center of lift of the tail does depend on tail shape. The center of lift is at the center of the lifting area of the tail (i.e., the approximately triangular area in front of the point of maximum span). The tail muscles of a long-tailed bird must therefore work harder than those of a short-tailed bird, even when their tails produce the same lift. However, the lift of a long tail has a greater lever arm through which it can act to turn the bird. Although the muscles of a long-tailed bird must work harder to support a given lift from the tail, that
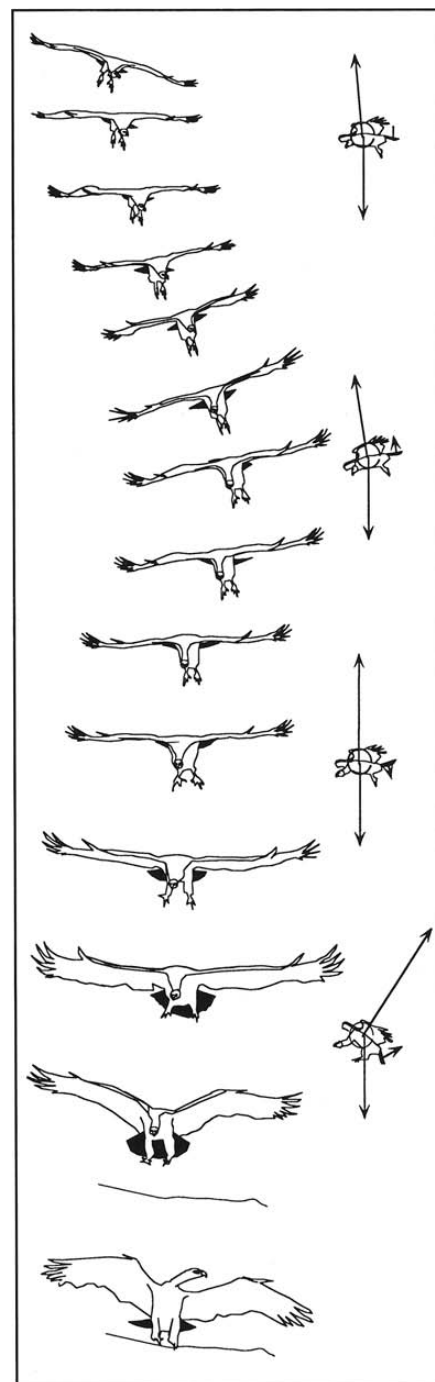

Figure 4. Final approach and landing in the white-backed vulture (*Gyps africanus*). The vulture uses its tail to control its direction of flight and the angle of its wings and body. During the final phases of the landing approach, the tail generates a downward force to rotate the body into a more vertical position. The wings then provide a braking force that slows the bird until it stalls just before landing. The drawings to the right of the bird illustrate the approximate directions and magnitudes of the forces produced by the wings and tails during the landing.

Figure 5. The aerodynamics of the tail. (a) The airflow in an imaginary stationary, ground-fixed, vertical plane (crosshatching) pierced by the tail is the same as the airflow around a two-dimensional flat plate moving perpendicular to its axis. (b) The flow in the plane an instant later has exactly the same pattern, but the scale is larger, that is, more mass is involved in the flow, and the position of the cut slice of the tail is lower (in the ground-based frame of reference). As a result, the increased mass of air has been accelerated downward, producing lift. (c) The lift distribution across any slice of the tail is U shaped, with most of the lift generated at the edges of the tail. (d) The lift distribution across the whole tail. Lift is not generated behind the point of maximum span because behind this point, the scale of the flow does not increase along the length of the tail and, therefore, no significant mass of air is accelerated downward.

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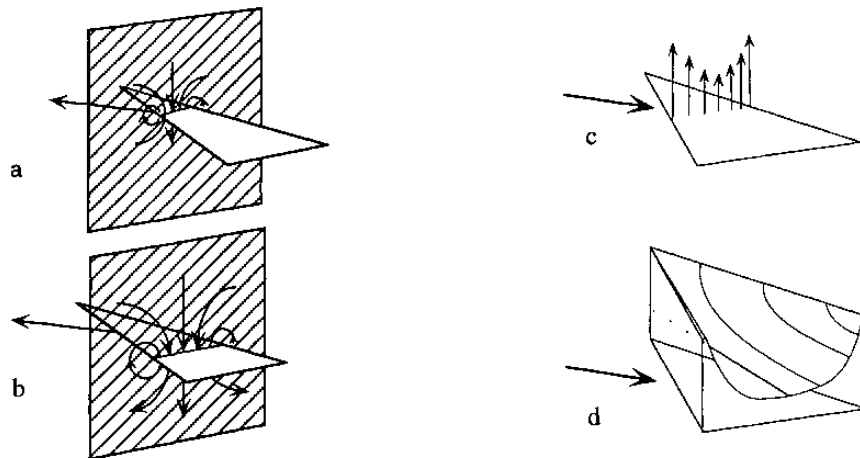
effort may be compensated for by the greater turning effect.

In addition to producing lift, the tail inevitably causes some aerodynamic drag. In almost all circumstances, the drag of the tail represents a cost to the bird. Two components of drag are relevant to the tail: induced drag (the cost of generating lift with the tail) and profile drag (the force generated by friction between the tail and air). Induced drag, which is unavoidable if the tail is to generate lift, depends only on the tail's angle of attack and the lift it generates. Profile drag depends on the morphology of the tail because the drag is proportional to the exposed surface area of the tail at any speed.

This model of tail aerodynamics accurately predicts the lift generated by the tail (Figure 6) at low angles of attack. At higher angles of attack, the flow separates over the top surface to form two large, detached vortices that increase the tail's lift (Figure 6). These vortices provide a means to generate sideways forces with the tail. By tilting the tail at an angle of roll relative to its flight direction, the bird can cause the vortex pattern to become asymmetric. This vortex asymmetry results in large rolling moments and considerable sideways force, exactly what the bird needs to control turning (Hummel 1978, 1992, Katz 1984). These asymmetric vortices are rela-

tively stable over low aspect-ratio tails (e.g., a buzzard's rounded tail) but become less stable on higher aspect-ratio tails (e.g., the kite's forked tail). The low stability of the vortices over a high aspect-ratio tail may explain why fork-tailed birds move their tails much more than other birds.

The aerodynamically optimum tail shape

The relationships between the shape and size of the tail and the aerodynamic forces it can produce make it possible to define an aerodynamically optimal tail—that is, the tail an aerodynamicist would design. Because lift and induced drag depend only on the tail's maximum continuous span, and because profile drag is proportional to tail area, the minimum drag is produced by a tail that is triangular when spread. A tail should be furled to reduce drag when lift is not required; an ideal tail—one that is triangular when spread—has a forked shape when furled because the inner feathers are shorter than the outer ones (Thomas 1993a, Thomas and Balmford 1995).

Increasing the length of the outer tail feathers relative to the inner ones increases the lift-to-drag ratio (which is a measure of the tail's aerodynamic efficiency in producing lift), so long as the outer tail feathers do not stick out beyond the trailing edge of the tail and it still forms a triangle when spread. In terms of lift-to-drag ratio, there is

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Figure 6. Accuracy and limitations of the aerodynamic model of the tail. (a) The model described in the text (solid line) and in Figure 5 accurately predicts tail lift coefficient (C_L) determined in the wind tunnel at low angles of attack, whereas values of C_L (circles) are higher than the model predicts at high angles of attack. Data from Katz and Plotkin (1991). (b) At high angles of attack, airflow over the tail separates to form leading edge vortices, which increases C_L. (c) If the tail is held at a large angle of attack and tilted sideways, the leading edge vortices adopt an asymmetric form, which generates large sideways forces. Birds can use these forces to control their direction during turns.

α (degrees)
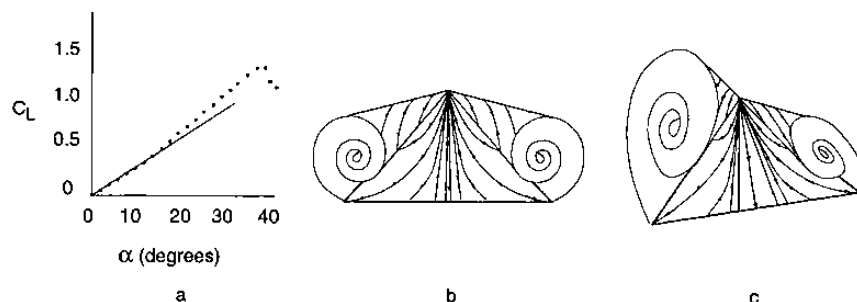
no defined optimum shape: a more deeply forked tail is always better (Figure 7). However, only the area of the tail in front of the point of maximum continuous width generates lift, and the lift acts through the center of that area. Comparing a deeply forked tail with a more shallowly forked tail, when both are spread to form triangles the center of area of the deeply forked tail (and, therefore, its center of lift) will be closer to the tail's base. If the two tails have the same maximum continuous span and act at the same angle of attack, then they will generate the same lift, but the shallowly forked tail will generate more drag and a larger turning moment because the lift is generated farther from the base of the tail.

Although the lift-to-drag ratio increases indefinitely as the tail becomes more deeply forked, the moment generated by the tail decreases and the moment-to-drag ratio (a measure of the tail's efficiency as a device for turning the bird and controlling the wings) has a defined optimum value (Figure 7). The aerodynamically optimum tail has outer feathers that are just slightly more than twice the length of its central feathers. The optimum tail therefore forms a triangular shape when spread by just over 120°. (This optimum tail is also the shape adopted by competition hang gliders; Nickel and Wohlfahrt 1994.)

Aerodynamics and natural selection

Aerodynamic performance can be measured in terms of a variety of factors, not all of which are compatible. For example, low wing loading (body mass per unit wing area) improves turning performance, whereas high wing loading increases flight speed (Norberg 1989, Vinh 1993). Different birds use flight for different purposes, and the strength of selection on a particular aspect of flight performance will depend on factors such as the bird's lifestyle, habitat, and foraging ecology (Thomas and Balmford 1995).

One fundamental measure of aerodynamic efficiency and performance is lift-to-drag ratio, which defines the glide angle (the distance a bird can glide from a given height). Birds
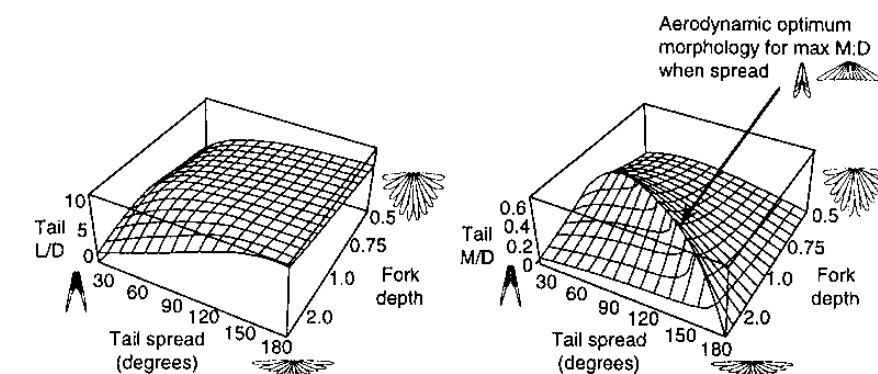

Figure 7. The effect of tail shape on its aerodynamic efficiency. (left) Lift-to-drag ratio (L/D) plotted against tail spread and morphology. The tail's efficiency in terms of lift-to-drag ratio is increased by spreading the tail and by making it more deeply forked. (right) Moment-to-drag ratio (M/D) plotted against tail spread and tail morphology. There is a discrete optimum tail morphology at which the outer feathers are twice as long as the inner feathers and the tail is spread to a triangular shape.
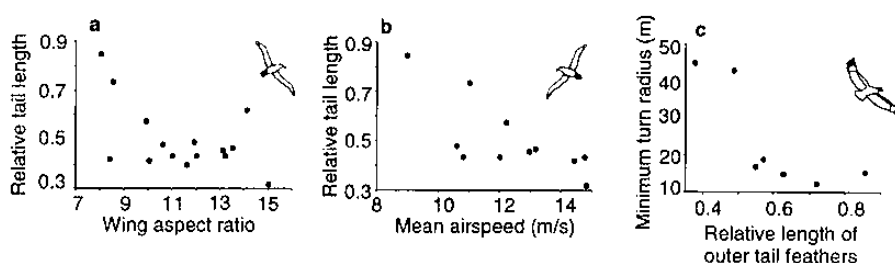

Figure 8. Correlations between tail morphology and measured flight performance. (a) Large seabirds that have higher aspect-ratio wings (long, thin wings) tend to have small tails (P < 0.05). (b) Large seabirds that fly faster have smaller tails (P < 0.01). (c) The raptors with the tightest turning circles tend to have the largest tails (P < 0.01).

adapted specifically and only for maximum lift-to-drag ratio, and for which stability is not a factor, should not have tails, because a single high aspect-ratio wing can achieve a higher lift-to-drag ratio than any combination of wings and tail (the materials used to add a tail could always be used more effectively to increase the span or aspect ratio of the wing). Similarly, for a given power, the minimum drag for a given lift determines a bird's maximum cruising speed. Even highly efficient tails decrease a bird's maximum lift-to-drag ratio and increase drag at high speeds relative to a single wing. Therefore, a bird selected exclusively for high-speed flight or exclusively for maximum lift-to-drag ratio should not have a tail.

Seabirds, because they have large foraging ranges, are likely to be under selection for high flight efficiency

and high flight speeds. They are also unlikely to encounter obstacles in the air, so they do not need great maneuverability. The procellariformes (albatrosses and petrels), large seabirds that fly at high speeds, have the high aspect-ratio wings required for high lift-to-drag ratios. By comparing relative tail size (corrected for differences in body size) of different seabirds with measured flight speed or aspect ratio (as an estimate of lift-to-drag ratio), it is clear that the fastest flying albatrosses, petrels, and birds with the highest aspect-ratio wings (Alerstam et al. 1993, Pennycuick 1982) do indeed have the smallest tails (Figure 8; Thomas and Balmford 1995). Although their tails are small relative to body size, even the wandering albatross still has a substantial tail. Possibly the tail is required for maneuverability as the bird turns,
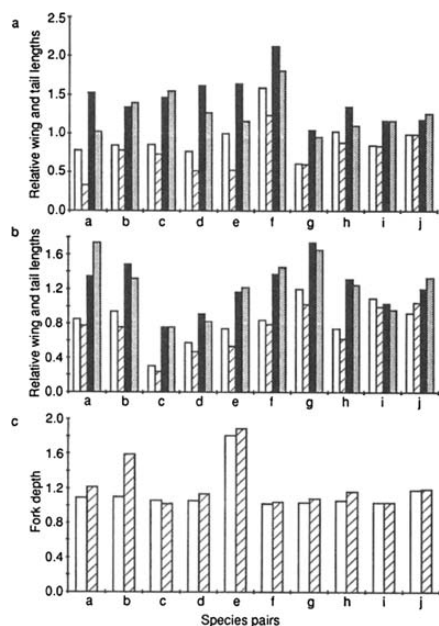
Figure 9. Comparative tests of predictions from aerodynamic theory. Pairs of closely related species that differed only in one variable (e.g., feeding strategy) were selected by independent ornithologists who were blind to the hypothesis to be tested. Measurements were normalized relative to body length. Values presented are means for ten males and ten females of each species (see Thomas and Balmford 1995 for details). (a) Turning ability is more important to an aerial-feeding bird than to one that feeds on the ground. Aerial-feeding birds have longer tails (white bars) than ground-feeding birds (striped bars; P < 0.01) and longer wings (black bars) than ground-feeding birds (stippled bars; P< 0.05). (b) In a cluttered environment, turning force (and therefore tail size) may be more important than efficiency. Birds with rounded tails have longer tails (white bars) if they inhabit cluttered woodland environments than if they live in open environments (striped bars; P < 0.05), but there is no difference in wing length (black versus stippled bars). (c) Deeply forked tails are likely to be more vulnerable to damage because the outer feathers are not as well supported by overlapping central feathers. In eight out of ten closely matched species pairs examined, fork-tailed birds from open environments (striped bars) have deeper forks than close relatives from woodland habitats (white bars; P < 0.01), even though tail length is not different. In one pair, the forks were the same length, and in another pair, the fork was deeper in the bird from the woodland habitat.

climbs, and dives during dynamic soaring and when "slope soaring" along the crests of waves. Alternatively, the tail may be important for maneuverability, not in flight but underwater, when the bird pursues squid and fish: The tail of the wandering albatross closely resembles the tails of diving ducks (and its very large webbed feet are also strikingly like a duck's, although much less sturdy). The albatross is usually portrayed as a master of the air (which it undoubtedly is), but it is also important to remember that it flies only to reach a foraging site. Once there, it must swim after its food.

Aerodynamic performance during turns—maneuverability and agility—is another aspect of flight performance that is a potential target of natural selection (Thomas and Balmford 1995). For instance, both aerial insectivores and woodland birds, which live in cluttered environments, must be under selection for turning ability. However, the selective pressures may be different for the two groups (Figure 9).

For aerial insectivores that feed in the open, away from clutter, two aspects of flight performance are important: efficient flight while searching for a prey item (fast flight will increase the amount of airspace searched per unit time) and maximum agility (to turn and capture detected prey). In addition, aerial insectivores should turn efficiently because any speed or altitude lost during the turn (due to drag) will either cost time in soaring or have to be made up by muscular effort. Aerial feeders that forage in the open therefore have the conflicting requirements of high aspect-ratio wings and high wing loading (for efficient high-speed flight) and of high aspect-ratio wings and low wing loading (for increased turning ability for successful prey capture). These conflicting requirements are resolved by having the wings needed for searching for prey (when the tail can be furled to reduce drag) and by having the tail needed to generate lift during turns (which effectively reduces wing loading). Across an array of unrelated bird families, aerial foragers that feed in the open have convergent morphologies: large, high aspect-ratio wings and large tails. Their tails closely approach the aerodynamic optimum shape for maximum moment-to-drag ratio—a forked tail with outer tail feathers twice as long as the central tail feathers (Thomas and Balmford 1995).

Whereas open habitat aerial foragers require efficient turning, woodland birds may require more sheer turning power, and efficiency is less important. Indeed, for woodland birds the tail's ability to withstand the inevitable abuse it will receive when bumping into twigs and branches may be more important than aerodynamic efficiency. Although a deeply forked tail is aerodynamically efficient, it also generates most of its force with the unsupported outer tail feathers, which are, therefore, particularly vulnerable to damage. A deeply forked tail will generate substantially less lift if the outer tail feathers are damaged because they alone define its maximum continuous width. When closely related pairs of species that differ only (in so far as is possible) in one characteristic are compared, the tails of aerial feeders are larger than those of terrestrial feeders (Figure 9). Such comparisons also reveal that woodland birds have larger tails than open-country birds; moreover, among fork-tailed birds, those from open country have more deeply forked tails than those that live in woodlands (Figure 9; Thomas and Balmford 1995).

These findings suggest that although aerodynamic considerations play a large role in determining the morphology of bird tails, other factors—such as feeding style or vulnerability to damage—are also important. Within the class of open-country aerial feeders, we find convergent evolution of the tail an aerodynamicist would design for birds that need a tail. This class of birds includes the spine-tailed swifts, which almost entirely lack a tail. Spine-tailed swifts roost on cliffs or rock walls, so they can drop to gain speed at takeoff and climb to lose speed for landing. Although their tiny tails may restrict them to a narrow range of flight speeds and probably do not allow them to take off from ground

level, they are among the most efficient flying birds when at their peak performance.

A major difference between the aerodynamic properties of the tail and the wings is their sensitivity to changes in shape. The aerodynamic performance of the wings is sensitive to small variations in morphology, but the tail can work reasonably well even when it differs substantially from its optimum form. As a result, the tail can generate lift at an angle of attack of up to 40°, whereas the wings stall at an angle of attack of approximately 15°. As the angle of attack of the tail changes, the lift produced by the tail changes slowly enough that variations in the flow direction at the tail—caused, for example, by the wings flapping—will have little effect on the lift generated by the tail.

A second consequence of the insensitivity of the tail to deviations from optimal morphology is that the tail does not need to be shaped as accurately as the wings (Figure 10). The developmental and genetic regulatory systems responsible for wing production are not perfect, and errors in development produce measurable levels of random asymmetry in both wings and tails (termed *fluctuating asymmetry*; Palmer 1996, Palmer and Strobeck 1986). Several studies have shown that the level of fluctuating asymmetry is higher in the tail than in the wings, and it has been suggested that the level of asymmetry in tail ornaments (see below) is even higher than in aerodynamically functional tails (Balmford et al. 1993b, Møller and Höglund 1991). This variation in the level of fluctuating asymmetry is likely to result from natural selection acting differently on wings, tails, and ornaments, according to their aerodynamic functions. The aerodynamic performance of wings is sensitive to their symmetry; this would create strong natural selection for wing symmetry. The aerodynamic performance of tails is less sensitive to their symmetry, and tail symmetry is, therefore, under weaker selection. This reduced selection could result in higher levels of tail asymmetry. Ornaments would be expected to have still higher asymmetry, because they are not aerodynamically
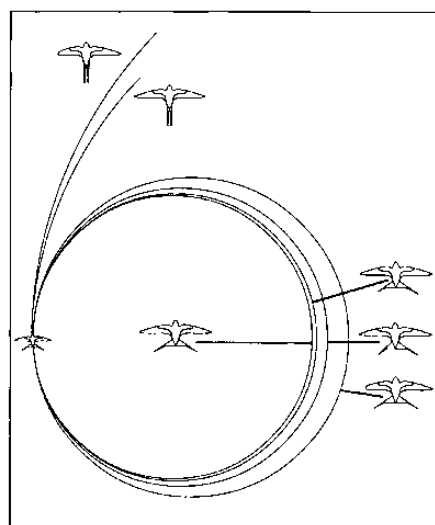

Figure 10. Turning circles for a swallow (drawn to scale with the circles at the left) of mass 0.025 kg, wingspan 0.35 m, outer tail feather length 0.1 m, and flight speed 5 m/s. The central circle is for a symmetrical swallow using its tail to generate lift. Moving outward from the center, successive circles show the effects of 2% asymmetries in the tail streamer (Figure 1; the tail streamer is the elongated bit on the swallow), in the maximum continuous span of the tail, and in the wings. The upper curves show the minimum turning circle for a swallow not using its tail, with (left) and without (right) 2% wing asymmetry.

functional (although they must cause drag, Figure 10; Thomas 1993b).

A third consequence of the tail's aerodynamic insensitivity to modifications is that selection against any tail modification, such as elongation, may be very weak. This weak selection may explain the widespread occurrence and repeated evolution of elaborate, costly tails.

Sexual selection and elaborate tail ornaments

Whereas most birds have tails that are well suited for aerodynamic function, in some species one sex—usually the males—have tails that no aerodynamicist would design. For example, the bizarre elongated tail of the scarlet tufted malachite sunbird (*Nectarinia johnstoni*; Figure 1) is costly to its bearer. Evans and Hatchwell (1992) manipulated the tails of male sunbirds by cutting the tail feathers and either shortening them by removing a few millimeters

from each tail feather, lengthening them by adding a few millimeters of tail feather from another bird, or cutting and regluing the tail feathers to provide a control for the manipulation. They determined the effect of the tail manipulations on flight by measuring how much time the manipulated males spent in flight and how effective they were at catching prey (hawking efficiency, or insects caught per chasing attempt). Males with elongated tails spent less time in flight, and were less successful at catching insects, than either control males or males with shortened tail feathers. The effect of lengthening the tail is not all that surprising, but Evans and Hatchwell also showed—astonishingly—that males with shortened tails were better at flying than control males. Males with shortened tails spent more time in flight and were better at catching insects after manipulation than they had been before!

The male scarlet tufted malachite sunbird's elongated tail is clearly an aerodynamically costly handicap. The aerodynamic and mechanical effects of the elongated tail feathers were due to two factors—the aerodynamic drag (up to 5% of the bird's total drag) and the inertia of the tail feathers (Evans and Thomas 1992). The inertial effect was particularly clear: Control manipulated birds, which had suffered a slight increase in the mass of their tail feathers (glue and a small splint of feather shaft), spent less time flying and were less able to catch insects than sham-manipulated birds.

To alleviate the costs of their elongated tails, male sunbirds have an increased wingspan (as compared with females or with males of related species with no tail ornament; Evans and Thomas 1992). This increase reduces the cost of flight enough to compensate for the tail ornament's drag at normal flight speeds (but not at high speed). Increasing the wingspan appears to be a widespread strategy to alleviate the aerodynamic costs of ornaments. Andersson and Andersson (1994) showed that for 14 species of widow birds and bishops (genus *Euplectes*), the sexual dimorphism in wing length between the sexes is related independently to sexual dimorphisms in
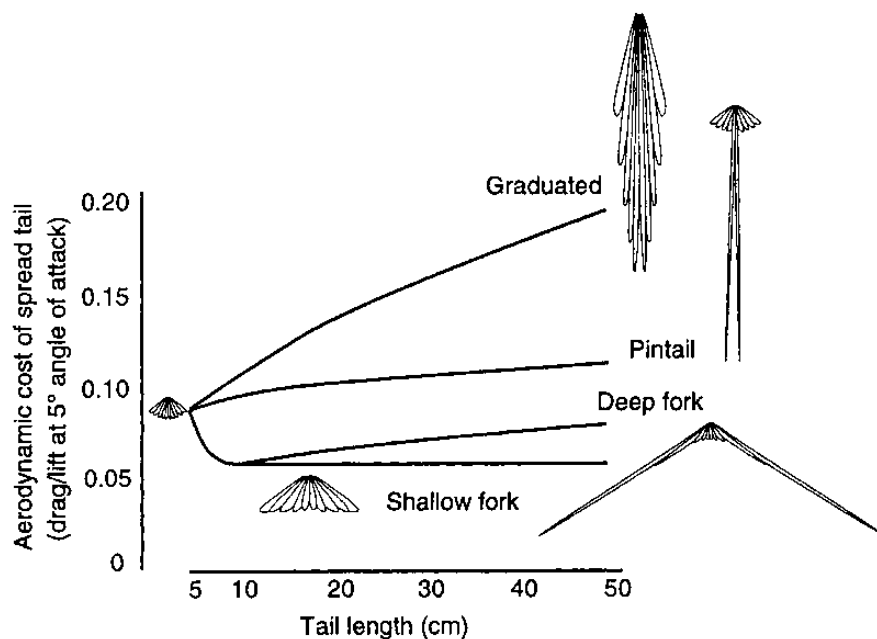
Figure 11. The aerodynamic cost (in terms of drag-to-lift ratio) of tails of different shapes changes as they become longer. The ancestral form of the tail (left) is assumed to be a rounded shape with feathers of equal size. The initial stages of elongation to form a forked tail are beneficial in terms of aerodynamic cost. If the tail acted as a signal, then elongation must be costly; otherwise, there is no way that an elongated tail could have an honest signaling function. Thus, this initial elongation could not be the result of selection for the tail to act as an honest signal of mate quality.

body size and in tail length, and to whether the males have display flights. This pattern of increased wing length to cope with the costs of elongated, elaborate tails seems to hold across a wide range of bird species: Variation in the sexual dimorphism in tail length is associated with corresponding variation in wing dimorphism. Furthermore, species with aerodynamically costly tails or that are particularly reliant on flight have particularly marked sexual dimorphism in wing length (Balmford et al. 1994).

Given the aerodynamic cost of elaborate tails, why do the males of some species develop them? Darwin (1871) suggested that ornaments develop in response to female mating preferences, and this has been confirmed by experimental manipulations (Andersson 1982, 1992, Møller 1988). A male with an elongated tail is a more attractive mate than one with a shorter tail. However, ever since Darwin first suggested that ornaments may have evolved in response to female mating preferences, scientists have disagreed about the underlying

mechanism. Theoretical analysis suggests that ornaments are likely to have evolved through either of two underlying mechanisms. One is a functional mechanism, in which ornaments evolve to act as signals of mate quality and females use the ornaments to choose the best mates. The other is a positive feedback mechanism (Fisherian runaway) inherent in the process of evolution, in which a preference for a particular character arises and the offspring of individuals possessing the preference are obviously likely to possess the genes responsible for both the preference and the preferred trait (Iwasa et al. 1991, Pomiankowski et al. 1991). Both character and preference are, therefore, likely to reinforce each other in a potentially explosive positive feedback or runaway evolution (see Andersson 1994 for a comprehensive review of sexual selection).

Distinguishing between the possible underlying mechanisms of sexual selection is notoriously difficult (indeed, the two may often act together). However, the two mechanisms make distinctly different pre-

dictions about the cost of ornaments during their evolution (Balmford et al. 1993a, Thomas 1993a). Ornaments that evolve through a signaling mechanism must be costly throughout their evolution. The cost prevents individuals of low quality from signaling that they are of high quality, because only high-quality individuals can afford the costs of the signal. Ornaments that evolved through the Fisherian runaway mechanism need not have any cost (although runaway evolution is likely to halt when the mating advantage of a particularly elaborate ornament is balanced by an equivalent disadvantage under natural selection).

To distinguish between the mechanisms of sexual selection on male tails, aerodynamic theory has been used to examine changes in the costs of elongated tails during their evolution (Thomas 1993a, b). As described earlier, the aerodynamic mechanism by which the tail generates lift means that lift is generated only by the part of the tail in front of the point of maximum width, whereas drag is generated by the entire tail area. Tail elongation that involves the central tail feathers will increase the tail's ability to produce drag but will not change its lift-generating properties. Tails with elongated central feathers (like the sunbird) or graduated tails in which all feathers are elongated (like the pheasant) are, therefore, costly throughout their evolution. By contrast, tail elongation that involves the outer tail feathers will increase the tail's lift-producing properties as well as its ability to produce drag. During the early stages of the evolution of a deeply forked tail, the elongation therefore improves the aerodynamic performance of the tail (Figure 11).

Elaborately elongated, deeply forked tails therefore fit well with Fisher's original model of the runaway process (Fisher 1930), in which he showed that sexual selection would proceed from a "kick start" through natural selection. In this process, the ornament-to-be was initially favored under natural selection, and females that preferred the ornament therefore had offspring that were not only attractive but also favored under natural selection. Fisher suggested that sexual selection acting through female preference would have sufficient

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momentum to carry ornamentation or elaboration beyond the point at which the ornament had any benefit under natural selection; indeed, he suggested that elaboration would proceed until the mating benefit of the ornament was balanced by its costs under natural selection.

The interaction between the wings and tail

So far, the tail has been modeled as if it acted independently of the wings, but in fact the airflows generated by both must interact. Pennycuick (1975) speculated that bird tails act as "split flaps": Tails increase the maximum lift coefficient of the wings and therefore improve performance in slow, turning, and/or accelerating flight. Using the aerodynamic theory of the interaction between the wings of a biplane, it is possible to show that this theory is indeed true (Figure 12; Thomas 1996b). The flow around the tail tilts the local flow around the wing, so that the wing operates in an airstream that is slightly rising and slightly accelerating relative to the flight direction. The resulting forward tilt of the wings' lift adds thrust. The wing has an opposite effect on the tail; that is, the resulting backward tilt of the tail lift adds drag. However, because the tail has a smaller span and is less efficient than the wing, and because the flow velocity will be slightly reduced at the tail, the drag or thrust on the tail is less than that on the wing. The two lifting surfaces therefore combine to create a greater force together than they would separately—a familiar mechanism to anyone who sails because the jib, or foresail, produces a greater force in combination with the mainsail than the sum of the forces generated by the two sails acting independently.

By using their horizonal tail surface to generate lift in this way, transport aircraft could reduce their total drag by approximately 5% at cruising speeds (Laitone 1978), with obvious economic implications. But for aircraft, the area of the tail is fixed, and the horizontal tail surface must always generate some drag. By contrast, birds can close their tails, reducing area and, thus, drag. At low speeds—when induced drag is

Figure 12. Airflow interactions between the wings and tail. Airflow over the tail inclines the local flow at the wings and slightly increases the flow velocity; thus, wing lift is increased and acts partly in a forward direction, and a component of thrust from the wings results. The wing has the opposite effect on the tail, but be-

cause the wing reduces the flow velocity at the tail, the reduction in the drag of the wings is greater than the increase in the drag of the tail.
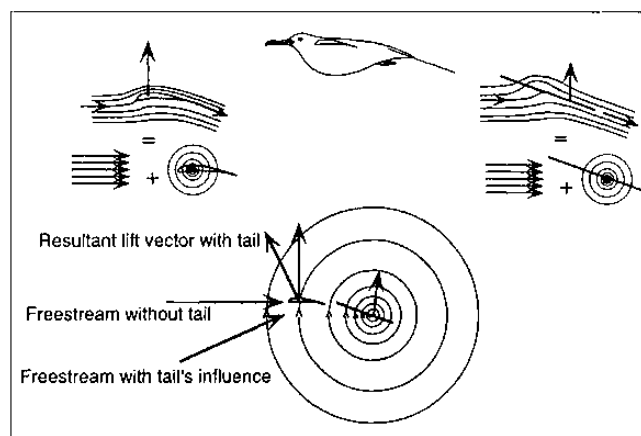
Figure 13. The influence of the swallow's tail on the power required for flight. At low speeds, the tail reduces power requirements by taking some of the load off the wings. At higher speeds, the bird can use the tail to generate useful lift (e.g., during a turn), but this increases drag. The absolute minimum power at any speed is achieved by adopting the morphology indicated by the dark line.
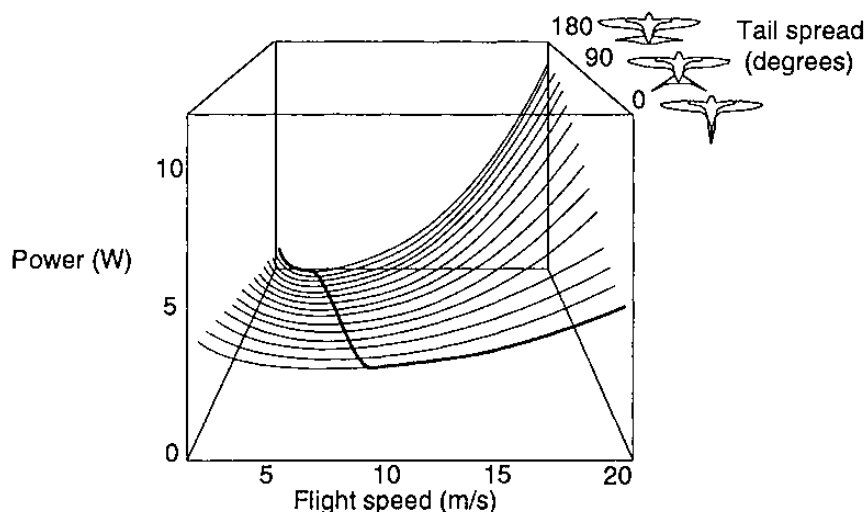
the major component of drag—birds could make substantial savings in induced drag by using their tails. As speed increases, the tail's profile drag increases, and at some speed the profile drag of the tail will be as large as the saving in induced drag due to the interaction between the wings and tail. At this and higher speeds, the bird should close its tail to reduce drag.

The tail's influence on flight power

Conventional models of bird flight ignore the tail. However, the tail of

most birds could generate as much as one-third of the total lift needed to support the bird's weight, and birds clearly use their tails during slow flight, when power requirements are high.

The simplest way to model the power consumption of a bird with a tail is to add the forces on the tail to the forces on the bird in flight using the conventional model of bird flight (see Pennycuick 1989 for a clear explanation of the model). The result of including the forces on the tail depends on how widely the tail is spread and on its angle of attack (Thomas 1996a). When the tail is completely closed, the single curve

represented by Pennycuick's model is recaptured. However, plotting power against both speed and tail spread for a single angle of attack gives a three-dimensional surface (Figure 13). At low speeds, the lift produced by the tail reduces the power requirements below the value predicted by Pennycuick's model, but at high speeds, the drag produced by a spread tail increases power requirements. During slow acceleration, a bird characterized by such a surface (i.e., all birds with tails) should continually change its tail morphology to maintain minimum power at all speeds. That is, it should effectively follow the lowest path (dark line) across the surface in Figure 13—near the back (widely spread tail) at low speeds, and moving to the front at some intermediate speed.

For birds with tails, the relationship between the power required to sustain flight and flight speed is broadly U shaped, but the details of the shape and the optimum flight speed depend on the morphology of the bird (Thomas 1996a, b). For a large-tailed bird, the power curve can become W shaped, with two local minimums (Figure 14). Overall, the minimum power always occurs with the tail spread widely; a second local minimum may occur at a slightly higher flight speed when the tail is furled. The speed that gives maximum range (the furthest distance the bird can fly on a given amount of energy) is found graphically by drawing the tangent from the origin to the curve. In Pennycuick's model, this point is well defined, because the power curve is strongly convex at its intercept with the tangent from the origin. Inclusion of the tail can make this interception point rather ill defined. In fact, including the tail in the power model often results in birds having a relatively low cost of transport over a very wide range of speeds because the tangent from the origin and to the power curve may be close to parallel over a wide speed range.

The pattern of variation in tail geometry with flight speed, as predicted both by including the tail in a model of the power required for flight and by considering the interactions between the wings and the tail, agrees well with that observed during normal free flight. Gatesy and Dial (1993) reported just such a pattern of tail use in pigeons (*Columba livia*), and Tucker (1992) found the same pattern of both wing and tail geometry in a gliding Harris hawk (*Parabuteo unicintus*).

Conclusions

Bird tails confer stability and control and provide a means of augmenting the lift of the wings to reduce the cost of low-speed flight and increase turning performance. Although the robust aerodynamic properties of the tail may be required for it to function close behind the flapping wings, the proximity between the wings and tail produces an interaction that may substantially reduce drag and could even increase the total lift the bird can generate. The tail may, therefore, allow birds to have the small wings needed for efficient, fast flight and, at the same time, to retain the ability to fly efficiently at low speeds and execute rapid maneuvers. The robustness of the tail's aerodynamic properties to variations in morphology may also imply that the shape of the tail, especially its trailing edge, is under relatively weak selection compared to the wings. This weak selection may explain why tails are often less perfectly formed than wings and why so many birds have evolved elaborate, elongated ornamental tails.

Although much has recently been learned about bird tails, many fundamental aerodynamic properties remain unexplained. In slow flight,

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Figure 14. The effect of the lift generated by the tail on the power required for flight. At low speeds, a widely spread tail can generate substantial lift, in addition to that generated by the wings, reducing the power required for flight. A bird such as the lyre-tailed nightjar (*Uropsalis creagra*), which has outer tail feathers that are longer than its wingspan, can fly with
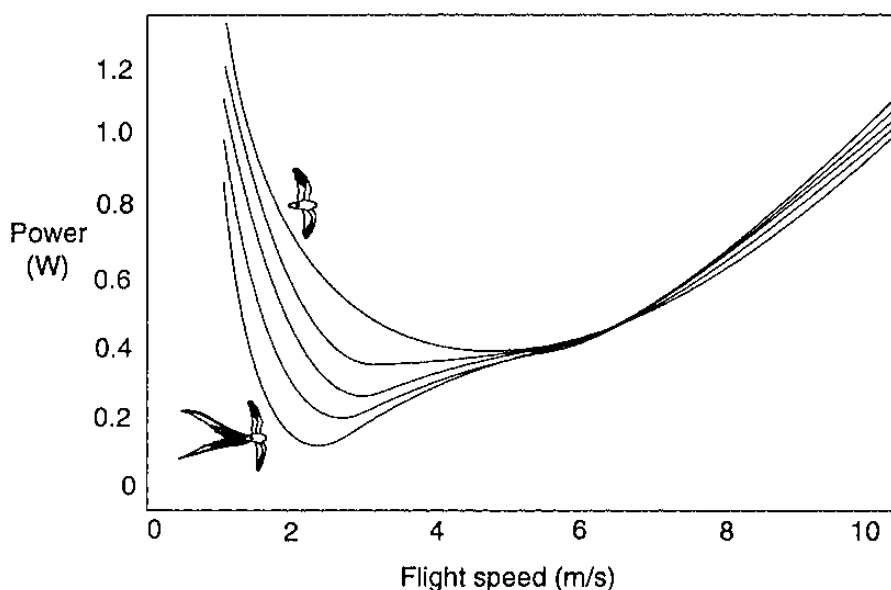
very low power at low speeds, because it uses its tail to generate lift and its wings to generate thrust. With tail length = 0 (top line), the classical solution (e.g., Pennycuick 1989) is recovered. In the classical case, two optimum speeds are well defined: the lowest point on the curve defines the flight speed at which power requirements are at a minimum, and the tangent from the origin defines a speed at which the range on a given amount of fuel is maximized. The lower curves represent the optimum use of tails of increasing length. When the influence of the tail is included, the shape of the line becomes more complex. When the tail is used, flight with minimum power requirements occurs at a lower speed, and a well-defined tangent between the origin and the power curve may not exist. These conclusions suggest that the maximum range that birds can achieve may vary little with speed.

the tail seems to be used like a rudder or paddle. The models I have described cannot deal with the unsteady flow that would be generated over the tail when a bird sweeps it sideways like a paddle. In fact, the aerodynamics of force generation by the kinds of movements that birds' tails perform during hovering flight represents an unsolved fundamental problem in aerodynamics. The aerodynamic forces generated by these kinds of motions have been found to exceed, by as much as an order of magnitude, the maximum force that conventional aerodynamic analyses would predict (Norberg 1989).

Similarly, the tail clearly has a function in maintaining stability, but nothing is known about the stability of birds: We do not even know if birds are aerodynamically stable or if they instead rely on neuromuscular control to stay in flight. Furthermore, tails show features consistent with detailed control of the flow and pressure differences over their surfaces. For example, the tail feathers of many fork-tailed birds, such as the swift (*Apus apus*), are emarginated (narrowing toward the tip). Such tail feathers separate toward their tips when large aerodynamic forces act on the tail, allowing air to "bleed through" from the high-pressure region below the tail into the low-pressure zone above it. This flow through the tail must affect the characteristics of the flow. The control of flow over delta wings (such as the tail) is the focus of much current aerodynamic research (Lee and Ho 1990). It seems likely that the study of the aerodynamics of such features of birds' tails can contribute to fundamental aerodynamics.

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