

HOW NATURAL SELECTION SHAPES BIRDS' TAILS

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Abstract.—Birds differ widely in the shape and size of their tails, yet until recently nearly all attempts to understand this morphological diversity have focused exclusively on the role of sexual selection for elaborate tail ornaments. In contrast, here we use aerodynamic models and comparative data to examine the extent to which natural selection can explain observed variation in avian tail morphology. A tail reduces a bird's overall lift-to-drag ratio (L/D), but the tail is important in maintaining stability over a range of flight speeds and in generating lift to help with turning and slow flight. As predicted, we found that large, open-country birds selected for high L/D have relatively short tails. Conversely, birds that need high maneuverability in order to feed aerially or avoid collisions in cluttered environments have longer tails. One prediction not supported by our data is that tails should also be elongated in species that need supplementary lift in order to wind-hover. Tail shape can also be important, particularly in aerial hawkers that rely on high agility to obtain their food. We found that, as expected, such birds generally have long, deeply forked tails capable of generating maximum turning moments for a given drag. Understanding the various ways in which natural selection acts on tail morphology provides an essential baseline from which to investigate how sexual selection has gone on to modify further the shapes of birds' tails.

Recent developments in our understanding of the aerodynamic properties of birds' tails suggest a discrete optimum shape. When spread out, forked tails with outer feathers roughly twice as long as inner feathers give a high ratio of lift to drag (L/D) and generate a greater turning moment for a given drag than any other tail shape; forked tails also have very low drag when they are closed (Thomas 1993a). Nevertheless, birds' tails vary considerably in both shape and size, and many deviate substantially from this optimum form.

The most extreme tail morphologies incur considerable aerodynamic cost and are often associated with marked sexual dimorphism (Evans and Thomas 1992; Balmford et al. 1993b, 1994; Winquist and Lemon 1994). In some species, experiments have shown that intersexual selection is responsible for these examples of pronounced tail elaboration (Andersson 1982; Møller 1988; Andersson 1992). However, in most bird species lacking forked tails there is no morphological or behavioral evidence to suggest that this is due to sexual selection.

Much of this unexplained diversity in avian tail morphology may be due to

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natural selection. Work on birds' wings shows that selection for fast flight favors a reduction in wing area, while selection for high maneuverability leads to increased wing area (Norberg 1989; Thomas 1993*b*). In the same way, tail morphology can be expected to deviate from that associated with maximum L/D if other aerodynamic properties are more closely targeted by natural selection. Here we use theory to predict how tail size and shape should vary as a result of selection for different components of flight performance. We then test the validity of our predictions using comparative morphological data.

THE AERODYNAMIC PROPERTIES OF BIRDS' TAILS

In order to understand the selection pressures acting on the avian tail it is necessary to review its aerodynamic properties (for a detailed analysis see Thomas 1993*a*, 1993*b*; for definitions of all key terms, see the appendix). The tail, like any object in a moving fluid, experiences forces due to the viscosity and the changes in pressure that result when the free flow of surrounding air is disturbed by moving around the tail. The sum of all the forces generated by the flow over the tail is conventionally resolved into two components (see fig. 1*A*): lift, defined as a force perpendicular to the direction of flow of the free airstream, and drag, defined as a force aligned with the free airflow. These forces act through a point defined as the aerodynamic center of the tail, whose position determines both the turning moment the tail can generate and the moment the tail muscles must control.

Lift

Birds' tails are low-aspect-ratio lifting surfaces that generate lift by an aerodynamic mechanism that is quite unlike that acting on a conventional wing (for detailed derivations see Jones 1990; Thomas 1993*a*). Whereas flow over a high-aspect-ratio wing is dominated by components moving around the wing in the direction of the free airstream, the flow over the avian tail is highly three-dimensional and is dominated by air flowing out around the edges of the tail from the lower to the upper surface. The tail can therefore generate lift only if it increases in width along the direction of flow, so that the mass of air flowing out around the edges of the tail increases along its length. A parallel-sided or tapering section of the tail behind the point of maximum tail width generates no lift—only drag. Thus, while the magnitude of the lift generated by a high-aspect-ratio wing is proportional to its area, the magnitude of the lift generated by a tail is determined by its maximum continuous span (b_{\max} ; see fig. 1*B*) and is independent of tail area (Thomas 1993*a*). At a given angle of attack (α , in radians), air density (ρ), and freestream velocity (U), the lift generated by the tail (L) is given by

$$L = \frac{\pi}{4} \rho \alpha U^2 b_{\max}^2. \quad (1)$$

Moments

The lift of the tail and the distance between its aerodynamic center and apex (its joint with the body) in turn set the moment that must be opposed by the tail

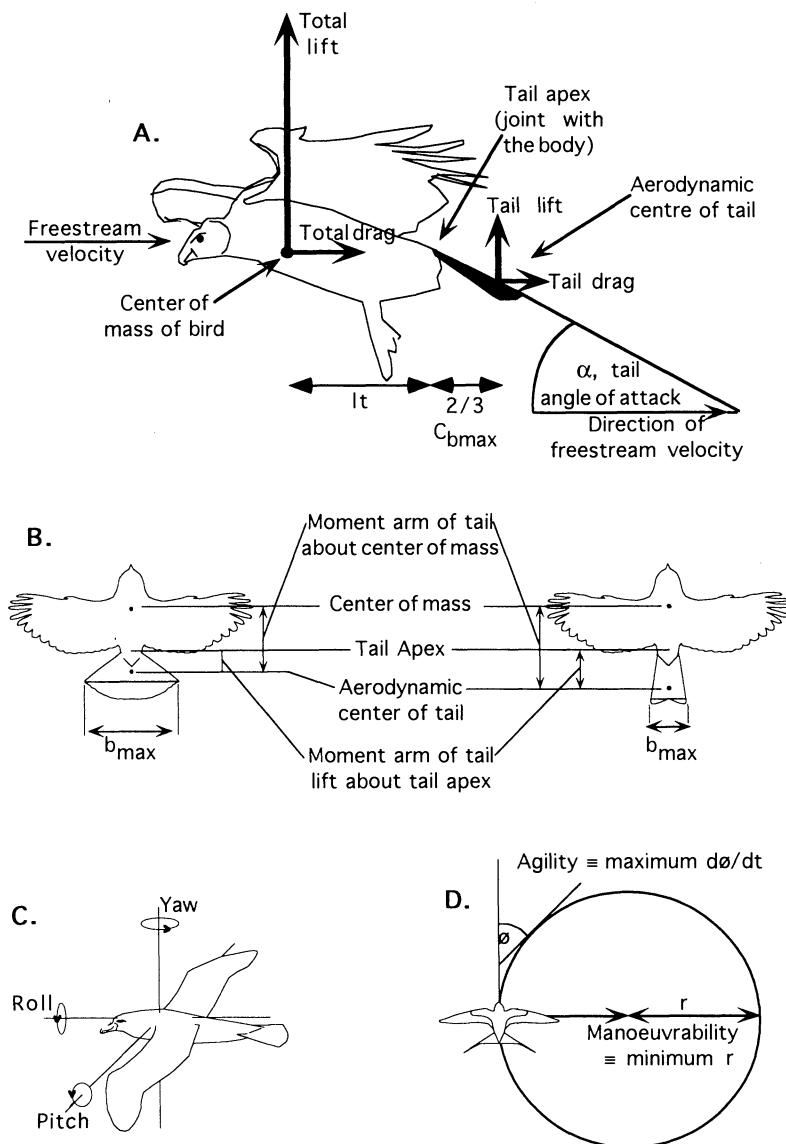


FIG. 1.—Illustrations of aerodynamic terms used in the text and defined in the appendix. *A*, Lift, drag, and angle of attack of a bird's tail. The forces generated by the tail supplement those of the wings. *B*, The lift generated by the tail is set by b_{max} , its maximum continuous span. The moments generated by the tail are set by the tail lift and the distances between its aerodynamic center and either the tail apex or the center of mass of the bird. *C*, A bird can rotate about any of three axes. The tail is used to control pitch and, to a lesser extent, yaw and roll. *D*, Maneuverability and agility are two distinct components of turning ability. Agility is defined as the maximum rate of turning and usually involves high-speed flight. Maneuverability is defined as the minimum turning radius. Maximum maneuverability occurs at low speeds.

musculature. For a symmetrical triangular tail the aerodynamic center can be shown to be at the center of area, which is at a position on the midline, two-thirds of the way from the apex of the tail to its trailing edge (see Katz and Plotkin 1991, p. 213, for derivation). For tails that deviate substantially from a triangular shape, the drag of the area behind the point of maximum span will contribute a very small component of vertical force that will move the center of lift slightly aft, but lift is typically at least an order of magnitude larger than drag, so this effect can be neglected (to a first approximation; see Thomas 1993a). For a tail of any shape, the moment generated by the tail about its apex (M_{apex}) and which must be counteracted by the tail's musculature is therefore given by

$$M_{\text{apex}} = L \frac{2}{3} C_{b\text{max}}, \quad (2)$$

where the moment arm is two-thirds of the distance ($C_{b\text{max}}$) from the apex of the tail to the point of maximum continuous span (Thomas 1993a).

The turning moment that a tail can provide to turn the bird about its center of mass has a greater moment arm—in this case it is the sum of $\frac{2}{3} C_{b\text{max}}$ and the distance from the center of mass to the apex of the tail (l_t). The tail moment about the bird's center of mass (M_{cg}) is thus

$$M_{\text{cg}} = L(l_t + \frac{2}{3} C_{b\text{max}}). \quad (3)$$

Because moments depend on $C_{b\text{max}}$ as well as lift, two tails with identical maximum spans but different lengths generate the same lift, but the longer tail requires more force from its muscles and also generates a greater moment to turn the bird.

Drag

The aerodynamic cost of the tail is drag. The total drag of the tail is the sum of induced drag, associated with accelerating air to generate lift, and profile drag, which results from the viscous interactions between the tail and the air (see Anderson 1991). Provided the flow does not separate from the tail's surface, the component of profile drag associated with pressure changes in the flow around the tail is included in the tail's induced drag (D_i):

$$D_i = \frac{1}{2} L \alpha \quad (4)$$

(Katz and Plotkin 1991, p. 212; Thomas 1993a). Because induced drag is proportional to lift, it cannot be avoided if the tail is to do useful work.

The remaining component of the tail's profile drag is that due to skin friction (D_f). This is generated under any flight conditions, depends on the area (S) of the tail, and is given by

$$D_f = \frac{1}{2} \rho U^2 S C_{d_f} \quad (5)$$

(Anderson 1991). The drag coefficient (C_{d_f}) of the tail has been shown to be very close to that given by the drag of a thin flat plate (Evans and Thomas 1992), and

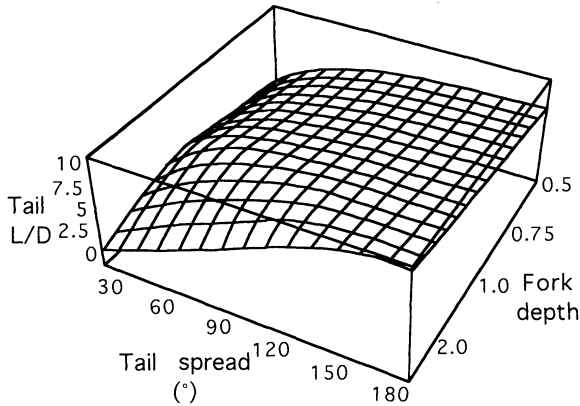


FIG. 2.—The effect of tail shape and spread on L/D . For deeply forked tails (fork depth >2.0) L/D can be very high when the tail is widely spread, but it is relatively low when the tail is not spread. Graduated tails (fork depth <1) are less sensitive to either shape or spread but are also less efficient.

for the purposes of the present article this can be assumed to be constant between species. Thus, the only morphological way a bird can reduce the profile drag of its tail is by reducing tail area.

The Aerodynamically Optimum Tail

Because profile drag is proportional to the area of a bird's tail but lift and induced drag are dependent only on its maximum continuous span, the maximum lift for any given drag is produced by a spread, triangular tail. When such a tail is furled (as it would be to reduce drag whenever maximum lift is not required), it will adopt a forked shape. The lift-to-drag ratio increases indefinitely with increasing fork depth, defined as the ratio of outer to central tail feather length (fig. 2). This means that deeper forks generate greater L/D , but there is no discrete optimum fork depth. In contrast, there is a single optimum yielding the best moment-to-drag ratio (M_{cg}/D), defined by the increase in L/D and decrease in moment arm as fork depth increases (fig. 3). This optimum shape has outer feathers that are just slightly more than twice the length of the central feathers; it therefore forms a triangular planform when tail spread just exceeds 120° . As an aside, it is no coincidence that under selection for performance in competition, hang-glider designs have converged on exactly the same optimum shape (Nickel and Wohlfahrt 1994).

While these aerodynamic properties define an aerodynamically optimum shape for birds' tails, they have no bearing on how big tails should be. In fact, a bird selected solely for maximum L/D and which needs to fly at just one speed should have no tail at all, since highest overall L/D is achieved by a single high-aspect-ratio wing (see Anderson 1991). Understanding why birds do have tails and why these vary in size as well as shape requires more detailed consideration of their function.

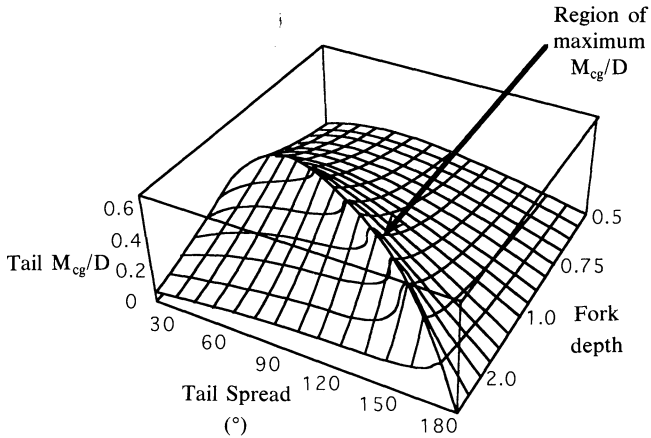


FIG. 3.—The effect of tail shape and spread on moment-to-drag ratio (M_{cg}/D). There is a discrete optimum tail morphology—a forked tail with fork depth ≈ 2.0 —which gives maximum M_{cg}/D .

THE AERODYNAMIC FUNCTION OF BIRDS' TAILS

Why Does a Bird Need a Tail?

The avian tail has two aerodynamic functions. First, it helps to maintain stability and control the angle of attack of the wing, thereby enabling the bird to fly at more than one speed. Second, the tail can contribute lift, supplementing that generated by the wings. This additional lift could be important in two particular situations: in turning, and during very slow flight.

Control and Stability

When generating lift, a cambered planar high-aspect-ratio wing is stable in roll and yaw, but is unstable in pitch (see fig. 1C) and generates a nose-down pitching moment (Anderson 1991; Thomas 1993a). To counteract the pitching moment from the wings an equal and opposite moment must be generated. This can be produced by positioning the center of mass of the body behind the center of lift, but this will achieve balance only at one flight speed. Obviously a bird cannot be restricted to just one speed of flight, so some form of control is required. By using the tail as a separate control surface, birds can provide the forces needed to hold the wing at a high angle of attack for slow flight and at a low angle of attack for high speed flight. Tails therefore provide for flexible flight behavior.

Additional Lift for Turning and Very Slow Flight

Aspects of aerodynamic performance such as rate of acceleration, turning circle, rate of turning, minimum flight speed, and power requirements at minimum flight speed all depend on the maximum lift a bird can generate. At any speed, a bird's wings can generate a fixed maximum lift. Experiments confirm that the tail can generate important additional lift (Hummel 1992; Norberg 1994); in swallows, this can equal one-third of body mass at a 5-m/s flight speed (Thomas 1993b).

This extra lift generated by the tail is important in determining turning performance. Turning ability can be described in terms of two properties: agility and maneuverability (see fig. 1D). These have different definitions and require rather different design features in both birds and aircraft. Maneuverability is defined as minimum turning radius, which is maximized by flying at low speeds (see Thomas 1993b for derivation). In contrast, agility is defined as the maximum speed with which an animal can change direction, and is associated with fast flight (Thomas 1993b).

The additional lift generated by the tail could also be valuable during slow flight (Thomas 1993b; Norberg 1994; A. L. R. Thomas, unpublished manuscript). In gliding flight at very low speed the lift generated by the bird drops below that needed to support its weight, and the bird stalls. In flapping flight, power requirements increase dramatically as speed drops. Both problems could be solved by increasing the size of the wings, but at the cost of increased drag at high flight speeds. The tail offers a better solution to this problem—at low speeds it can be spread to generate lift, thereby reducing both stalling speed and the power required for flapping flight (Thomas 1993b; A. L. R. Thomas, unpublished manuscript). At high speeds the tail can be furled so that it causes very little drag.

Thus, tails act as control devices maintaining stability and as lifting surfaces to enhance maneuverability, agility, and low-speed flight. The relative importance of these different functions will in turn determine both the size and shape favored by natural selection.

PREDICTED TAIL MORPHOLOGY UNDER NATURAL SELECTION

1. Tail Morphology under Selection for Increased Lift-to-Drag Ratio

A bird's maximum L/D determines its best glide angle and its maximum range and is therefore an obvious potential target for natural selection. Maximizing overall L/D could be achieved in two ways: by maximizing L/D of the tail itself by having a deeply forked tail (see above), or by minimizing tail area and hence tail drag. According to this latter argument, in birds adapted for maximum L/D there should be directional selection toward tail reduction. Selection to maximize L/D will be most pronounced in birds adapted for high-speed flight (because the drag of the tail increases as the square of flight speed) and in those species that fly long distances to feed or migrate (Pennycuik 1972; Kerlinger 1989; Gudmundsson et al. 1991). However, the extent of tail reduction will be counterbalanced by selection for control, stability, and maneuverability, all of which require a large tail (see below) and which are likely to be particularly important in birds that fly slowly or are at risk of crashing because they inhabit cluttered environments. This assessment leads to three testable predictions:

PREDICTION 1a. Tail length should decrease relative to body length as L/D increases. In practice, L/D has rarely been measured directly, but is known to exhibit a close positive relationship with the aspect ratio of a bird's wings (Pennycuik 1972, 1982). We can therefore use aspect ratio as a proxy for L/D , and we predict that as aspect ratio increases, relative tail length should decrease.

PREDICTION 1b. Relative tail length should decrease with increasing flight speed.

PREDICTION 1c. Birds that migrate long distances should generally have shorter tails than species that migrate less far.

Note that because all tail feathers add to the drag of the tail, these three predictions all deal with the length of the longest tail feathers, regardless of whether these extend beyond b_{\max} .

2. Tail Morphology under Selection for Maneuverability

Maneuverability depends on maximum lift and is therefore proportional to the area of the wings and to the maximum continuous span of the tail. Thus, selection for maneuverability should favor an increase in tail size (and in particular in the length of the outer tail feathers, which set b_{\max}) and a similar increase in the size of the wings. How selection for maneuverability influences tail shape is less easy to predict. Maneuverability is maximized by flying at low speeds, close to the point of stall (Thomas 1993b). In slow flight, profile drag is relatively low (eq. [5]), so selection for a deep fork with high L/D may not be strong. Moreover, the flow over a deep fork is very sensitive to changes in angle of attack, and therefore prone to stalling (Thomas 1993a). These considerations suggest that as the need for maneuverability increases, tail and wing size should increase, but selection on tail shape may be weak. High maneuverability is important in birds that fly in cluttered environments and that feed on the wing from fruit or flowers or by hawking or gleaning insects. From this analysis we can generate four predictions:

PREDICTION 2a. For birds with similar tail shapes, maneuverability should increase as the outer tail feathers become longer relative to body length.

PREDICTION 2b. Both outer tail feathers and wings should be longer in aerial feeders than in terrestrial species.

PREDICTION 2c. The relative length of the outer tail feathers should be greater in birds that live in cluttered environments than in those from more open habitats. Differences in wing length between open and cluttered environments are more difficult to predict, because while longer wings enhance maneuverability, increased span might make a woodland bird more vulnerable to collisions with vegetation.

PREDICTION 2d. In birds selected for high maneuverability, tail shape should be only weakly constrained by selection for high L/D . This prediction is unlikely to hold in many aerial foragers, because these often require high agility as well as maneuverability (see below). However, selection for high L/D is likely to be weak in those species that require high maneuverability because they inhabit cluttered environments. Thus, among those birds that have forked tails, we predict that fork depth will be lower in species from cluttered habitats.

3. Tail Morphology under Selection for Agility

Like maneuverability, agility will be increased by extending the maximum continuous span and hence the length of the tail. However, unlike maneuverability, agility is maximized by flying fast and is therefore far more strongly impaired by drag. Thus, selection for agility favors tails that can generate maximum L/D and M_{cg}/D . As discussed above, such tails have a triangular shape when spread and

form a deep fork (with fork depth ≈ 2.0) when closed. Selection for high agility will be most pronounced in aerial hawkers. This is because in these species, the rate of prey encounter increases with flight speed, but prey can be captured only if the bird can then turn quickly enough that its flight path intercepts that of its prey. Increasing agility therefore expands the cone-shaped volume in front of an aerial hawker within which items can be captured. In the absence of published estimates of agility, a directional test of this hypothesis is difficult, but one simple prediction is as follows:

PREDICTION 3. Aerial hawkers should exhibit convergent tail morphology and have long tails with outer feathers roughly twice as long as central feathers.

4. Tail Morphology under Selection for Slow or Hovering Flight

All birds have to fly slowly in order to land or take off, and the cost of slow flight is high. By augmenting the lift of the wings, the tail can reduce both stalling speed and the power required for slow flapping flight. Selection for low-speed flight should favor a tail with long outer feathers (and thus high b_{\max}), but because profile drag is low in slow flight, tail shape need not be tightly constrained. The effects of selection for slow flight are most likely to be seen in birds that wind-hover (i.e., that hold station over a spot on the ground by flying slowly into the wind), either when hunting or when singing above their territories. We can therefore make a single prediction:

PREDICTION 4. Wind-hovering species should have relatively longer outer tail feathers than species that wind-hover less or not at all.

METHODS FOR TESTING PREDICTIONS

We tested our predictions in two main ways. For those tests that required specific aerodynamic measurements (such as flight speed), we simply took morphological data on all species for which the relevant information was available in the literature. The relative lack of aerodynamic data meant that we then treated each species as an independent point in subsequent analyses, assuming that within an order, interspecific or intergeneric differences in tail morphology were not confounded by problems of phylogeny.

For other predictions for which we could obtain all necessary information from museum specimens, we controlled for the potentially confounding effects of common ancestry using Felsenstein's pairwise comparative method (Felsenstein 1985). Pairs of species from different families or subfamilies were chosen for us by ornithologists unaware of the prediction being tested. The members of each pair were from the same family and differed in the variable (such as habitat type) whose putative effect we were examining, but were matched as closely as possible for tail shape and any other ecological or behavioral variables that might confound our interpretation of tail morphology. For example, we compared male, female, and average tail morphology across five sets of matched pairs, yet Wilcoxon signed-rank tests showed these matched species differed significantly from one another (at $P < .05$) in body length in just one of these 15 comparisons. This is

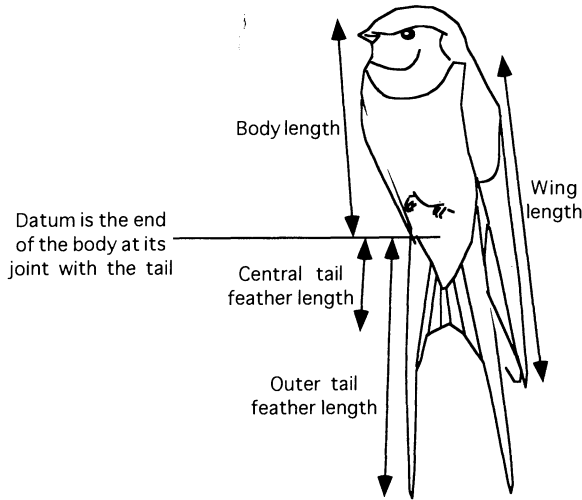


FIG. 4.—Morphological measurements used in the comparative tests

approximately what one would expect from chance alone, indicating that consistent, gross differences in body size did not confound our pairwise comparisons.

For each species we recorded tail shape (defined as forked if the outer tail feathers were longer than the inner feathers or graduated if the inner feathers were longer). Using three fully molted males and females, we then carried out the following standard measurements: body length, left and right wing length, and the lengths of the left and right outermost and innermost tail feathers (fig. 4). Measurements were made with vernier calipers to ± 0.1 mm (if < 100 mm) or with a metal rule to ± 1 mm (if > 100 mm). The repeatability of our measures was consistently high (see Balmford et al. 1993a). For every specimen we calculated inner and outer tail feather length and wing length (defined as the mean of the relevant left and right measures). To compare morphology across species, we also calculated relative tail length (the mean length of the longest pair of tail feathers divided by body length), relative outer tail feather length (outer tail feather length divided by body length), relative wing length (wing length divided by body length), and fork depth (for birds with forked tails only, defined as the ratio of outer to inner tail feather length).

RESULTS AND DISCUSSION OF TESTS

1. Tail Morphology under Selection for Increased Lift-to-Drag Ratio

PREDICTION 1a. Relative tail length should decrease as aspect ratio increases. Published estimates of wing aspect ratio were available for 15 species of procelariiform seabirds (Pennycuik 1982; Alerstam et al. 1993). When we measured the mean relative tail length of three male and three female specimens of each

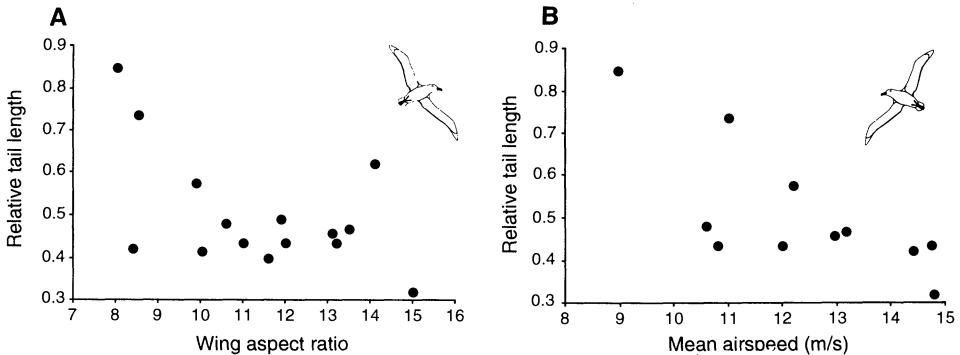


FIG. 5.—The relative tail length of procellariiform seabirds in relation to their wing aspect ratio (A) and their mean airspeed (B). Relative tail lengths are the mean of male and female values; aspect ratios and airspeeds are taken from the literature (Pennycuick 1982; Alerstam et al. 1993) and averaged if more than one value is available.

species, we found that, as predicted, relative tail length decreased with increasing wing aspect ratio (fig. 5A; Pearson product-moment correlation: $r = -0.53$, $N = 15$, $P < .05$; in these and all other tests of predictions, we cite one-tailed P values because our predictions are unidirectional; note also that here we used the average of mean male and mean female relative length because aspect ratio figures were not sex specific). This relationship was associated with variation in body size. Within this particular sample, tail length exhibited negative allometry (regression of \log_{10} [tail length] on \log_{10} [body length] yielded $r^2 = 0.80$, $N = 15$, $P < .001$; slope = 0.68 ± 0.09 ; $H_0: \beta = 1.00$, $t = 3.65$, $df = 13$, $P < .01$); hence, relative tail length decreased with increasing body length ($r = -0.61$, $N = 15$, $P < .05$). In contrast, aspect ratio increased with body length ($r = 0.93$, $N = 15$, $P < .001$). Controlling for body size by first performing a regression of tail length on body length, we found no evidence that residual variation in tail length was correlated with aspect ratio (residual tail length vs. aspect ratio: $r = 0.17$, $N = 15$, NS). It is tempting to argue, therefore, that the observed negative relationship between relative tail length and aspect ratio arises simply as a nonselected consequence of allometry. However, tail length does not consistently exhibit negative allometry in other groups (see below and Balmford et al. 1994), and in the absence of any obvious scaling explanation for an inevitable decrease in relative tail length with body size, we instead suggest that the allometry observed in the Procellariiformes is adaptive and arises in part because large seabirds are selected for maximizing L/D .

Data on aspect ratios were also available for 12 species of raptors (Kerlinger 1989). In this case there was no indication that either relative tail length or aspect ratio varied with body size (relative tail length vs. body length: $r = -0.25$, $N = 12$, NS; aspect ratio vs. body length: $r = 0.00$, $N = 12$, NS). However, the taxa examined did differ in their use of maneuverability during foraging (Pennycuick 1972; Brown et al. 1982). Selection for increased tail size to enhance maneuverability (see below) therefore confounds the relationship between relative tail

TABLE 1
RELATIVE TAIL AND WING LENGTH DATA FOR MATCHED PAIRS OF LONG- AND
SHORT-DISTANCE MIGRANTS

	RELATIVE TAIL LENGTH			RELATIVE WING LENGTH		
	Males	Females	Both	Males	Females	Both
Long-distance migrant:						
1. <i>Myiarchus crinitus</i>	1.26	1.29	1.27	1.26	1.30	1.28
2. <i>Riparia riparia</i>	.98	1.03	1.00	1.77	1.90	1.83
3. <i>Anthus hodgsoni</i>	.92	.88	.90	1.13	1.07	1.10
4. <i>Oenanthe oenanthe</i>	.83	.88	.86	1.27	1.36	1.31
5. <i>Phoenicurus phoenicurus</i>	.87	.90	.88	1.07	1.13	1.10
6. <i>Toxostoma rufum</i>	1.27	1.25	1.26	.98	1.04	1.01
7. <i>Troglodytes aedon</i>	1.07	.99	1.03	1.13	1.10	1.11
8. <i>Vireo bellii</i>	.99	.99	.99	1.14	1.11	1.13
9. <i>Emberiza hortulana</i>	.94	1.13	1.04	1.16	1.34	1.25
10. <i>Carpodacus erythrinus</i>	1.03	.97	1.00	1.38	1.33	1.36
Short-distance migrant:						
1. <i>Myiarchus tyrannulus</i>	1.16	1.15	1.16	1.14	1.15	1.14
2. <i>Riparia paludicola</i>	.89	.95	.92	1.71	1.75	1.73
3. <i>Anthus spinoletta</i>	.95	.88	.92	1.12	1.13	1.12
4. <i>Oenanthe lugens</i>	.86	.90	.88	1.23	1.31	1.27
5. <i>Phoenicurus ochruros</i>	1.06	.91	.99	1.32	1.18	1.25
6. <i>Toxostoma longirostre</i>	1.37	1.25	1.31	1.07	.99	1.03
7. <i>Thryothorus ludovicianus</i>	.96	1.05	1.01	1.05	1.11	1.08
8. <i>Vireo huttoni</i>	1.03	1.09	1.06	1.21	1.28	1.25
9. <i>Emberiza cirrus</i>	1.08	.94	1.01	1.12	.97	1.04
10. <i>Carpodacus mexicanus</i>	1.11	1.10	1.11	1.31	1.25	1.28

NOTE.—Paired birds are preceded by the same number.

length and aspect ratio in raptors, which may explain why no clear pattern emerged ($r = 0.11$, $N = 12$ species, NS).

PREDICTION 1b. Tail length should decrease with increasing flight speed. Airspeeds have been recorded for several procellariiform seabirds (Pennycuik 1982; Alerstam et al. 1993). Measurements of these species confirmed our prediction and revealed a clear negative correlation between mean relative tail length (taken across both sexes) and mean airspeed (fig. 5B; $r = -0.74$, $N = 11$ species, $P < .01$). This association could again potentially be explained as an artifact of allometry. Our fast-flying species were generally large (correlation between mean airspeed and body length: $r = 0.67$, $N = 11$, $P < .05$), and residual tail length (controlling for body length) was unrelated to airspeed ($r = -0.41$, $N = 11$, NS). Alternatively, fast flight might provide an (additional) adaptive explanation for why negative allometry of tail length occurs among the Procellariiformes.

PREDICTION 1c. Long-distance migrants should have shorter tails than birds that migrate less far. We tested this idea by measuring relative tail length in 10 pairs of closely-related species. Each pair was drawn from a different family or subfamily and contained a long- and a short-distance migrant. When we compared relative tail length across each of these species pairs, we found no evidence that species that migrated farther had relatively short tails (table 1; Wilcoxon tests comparing mean relative tail length across 10 matched pairs: for males, $T^+ =$

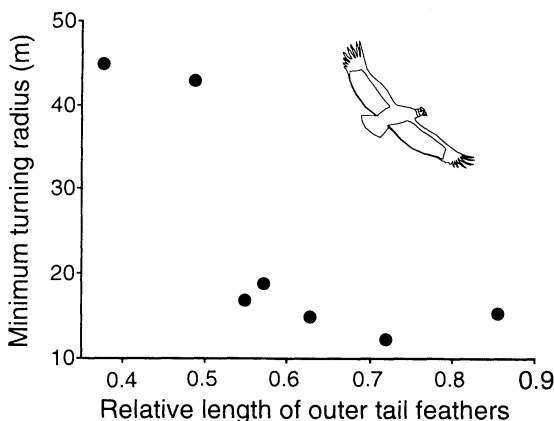


FIG. 6.—The minimum turning radius of raptors vs. the relative length of their outer tail feathers. Turning circle data are from Kerlinger (1989); relative outer tail feather lengths are again the mean of male and female values.

35, NS; for females, $T^+ = 31$, NS; for both sexes combined, $T^+ = 31$, NS). This result may have been confounded by other differences in flight behavior within our pairs, because we also failed to find support in this data set for the well-established link between wing length and migration distance (comparisons of relative wing length: for males, $T^+ = 31$, NS; for females, $T^+ = 38$, NS; for both sexes combined, $T^+ = 36$, NS).

To sum up this section, comparative data supported two of our three predictions. Although we found no evidence that tail length is reduced in long-distance migrants, we did find that large seabirds that fly fast and have high-aspect-ratio wings also have relatively short tails.

2. Tail Morphology under Selection for Maneuverability

PREDICTION 2a. Maneuverability should increase with increasing outer tail feather length. We could find turning circle data for only seven species. These were all soaring raptors (Kerlinger 1989). When these were measured, we found that, as predicted, minimum turning radius was indeed negatively correlated with relative outer tail feather length (fig. 6; $r = -0.78$, $N = 7$ species, $P < .05$). This result confirms that relatively long tails are associated with high maneuverability, but is potentially confounded by variation in body length. Although relative tail length was unrelated to body size in a larger set of raptors (see above), in this reduced sample, outer tail feather length exhibited negative allometry (regression of \log_{10} [outer tail feather length] on \log_{10} [body length] yielded $r^2 = 0.58$, $N = 7$, $P < .05$; slope = 0.49 ± 0.16 ; $H_0: \beta = 1.00$, $t = 3.19$, $df = 5$, $P < .05$). Relative outer feather length thus decreased with body length ($r = -0.80$, $N = 7$, $P < .05$), while minimum turning radius increased ($r = 0.82$, $N = 7$, $P < .05$). Residual outer tail feather length (controlling for body length) was unrelated to turning radius ($r = -0.48$, $N = 7$, NS). Once again, therefore, the observed support for our prediction could be a fortuitous consequence of allome-

TABLE 2

RELATIVE OUTER TAIL FEATHER AND WING LENGTH DATA FOR MATCHED PAIRS OF AERIAL AND NONAERIAL FEEDERS

	RELATIVE OUTER TAIL FEATHER LENGTH			RELATIVE WING LENGTH		
	Males	Females	Both	Males	Females	Both
Aerial feeder:						
1. <i>Hydrobates pelagicus</i>	.84	.72	.78	1.63	1.42	1.52
2. <i>Surnia ulula</i>	.87	.83	.85	1.38	1.31	1.34
3. <i>Aquila chrysaetos</i>	.84	.88	.86	1.43	1.50	1.47
4. <i>Thalasseus sandvicensis</i>	.78	.77	.77	1.72	1.53	1.62
5. <i>Glareola pratincola</i>	.98	1.01	1.00	1.61	1.68	1.64
6. <i>Pterophanes cyanopterus</i>	1.63	1.56	1.59	2.17	2.07	2.12
7. <i>Ceryle rudis</i>	.60	.61	.61	1.03	1.05	1.04
8. <i>Muscicapa striata</i>	1.07	.99	1.03	1.40	1.30	1.35
9. <i>Nectarinia amethystina</i>	.90	.80	.85	1.22	1.13	1.17
10. <i>Dendroica coronata</i>	.99	.99	.99	1.20	1.16	1.18
Nonaerial feeder:						
1. <i>Puffinus puffinus</i>	.32	.33	.33	1.01	1.05	1.03
2. <i>Strix aluco</i>	.81	.74	.78	1.43	1.37	1.40
3. <i>Aquila clanga</i>	.73	.73	.73	1.56	1.54	1.55
4. <i>Larus fuscus</i>	.49	.53	.51	1.30	1.25	1.28
5. <i>Cursorius cursor</i>	.50	.53	.52	1.09	1.23	1.16
6. <i>Patagonia gigas</i>	1.24	1.25	1.24	1.81	1.82	1.81
7. <i>Melidora macrorrhina</i>	.63	.57	.60	1.00	.92	.96
8. <i>Phoenicurus phoenicurus</i>	.87	.90	.88	1.07	1.13	1.10
9. <i>Anthreptes longuemareii</i>	.84	.84	.84	1.19	1.15	1.17
10. <i>Seiurus aurocapillus</i>	1.03	.94	.99	1.29	1.22	1.26

NOTE.—Paired birds are preceded by the same number.

try. However, changes in body size per se do not explain the underlying relationship between tail length and maneuverability, and we suggest instead that in our sample, smaller raptors have relatively long outer tail feathers as an adaptation to enhance their maneuverability.

PREDICTION 2b. Both wings and outer tail feathers should be longer in aerial than in terrestrial feeders. We assessed this prediction by comparing tail and wing length across pairs of close relatives, one of which feeds on the wing while the other feeds on the ground, while perched, or while swimming. We found that the relative length of outer tail feathers was indeed greater in aerial feeders (table 2; Wilcoxon tests across 10 pairs: for males, $T^+ = 52$, $P < .01$; for females, $T^+ = 54$, $P < .01$; for both sexes, $T^+ = 55$, $P < .01$). Maneuverability in aerial feeders may also be enhanced by longer wings, since our measurements revealed a somewhat weaker tendency for relative wing length to increase in more aerial species (for males, $T^+ = 43$, $P < .10$; for females, $T^+ = 45$, $P < .05$; for both sexes, $T^+ = 45$, $P < .05$).

PREDICTION 2c. The relative length of outer tail feathers should be greater in birds from cluttered environments. Comparing pairs of species from closed and more open habitats, we found that among birds with graduated tails, those from cluttered environments had longer outer tail feathers than their open-habitat rela-

tives (table 3; Wilcoxon tests comparing relative tail length across 10 matched pairs: for males, $T^+ = 54$, $P < .01$; for females, $T^+ = 45$, $P < .05$; for both sexes, $T^+ = 50$, $P < .05$). This was not the case among 10 pairs of fork-tailed species (for males, $T^+ = 30$; for females, $T^+ = 37$; for both sexes, $T^+ = 30$, all NS), but in this group increased environmental clutter is associated with other predicted changes in tail morphology (see below).

Tail elongation in woodland birds could conceivably arise because such species have shorter wings in order to avoid collisions (see above) and so need longer tails to compensate for the loss of lift from their wings. However, we found no evidence that relative wing length differed between birds from cluttered and more open environments, either among species with graduated tails (males: $T^+ = 30$; females: $T^+ = 31$; both sexes: $T^+ = 24$, all NS) or among those with forks (males: $T^+ = 37$; females: $T^+ = 30$; both sexes: $T^+ = 28$, all NS; see table 3). Thus, differences in wing length do not confound our observation that the relative length of outer tail feathers increases with environmental clutter.

PREDICTION 2d. Fork depth should be lower in species from cluttered habitats. We tested this by calculating the ratio of outer to inner feather length for our 10 pairs of species from cluttered and more open environments. We found that, as predicted, fork depth was consistently lower in birds from cluttered environments (table 4; for males, $T^+ = 48$, $P < .05$; for females, $T^+ = 50$, $P = .01$; for both sexes, $T^+ = 51$, $P < .01$). This observation therefore supports the idea that tail shape is less constrained by selection for high L/D in species requiring high maneuverability, but also has another possible explanation. Of all tail types, forks are especially vulnerable to damage. The distal portions of their outer feathers receive little support from other feathers, particularly when the tail is widely spread—as is likely during the last maneuvers before a crash. Moreover, any damage sustained by a fork will probably be asymmetrical and will affect feathers involved in producing lift; thus, the lift generated by the tail will decrease, and remaining lift will be distributed asymmetrically, which will result in a considerable loss of maneuverability and agility (Møller 1991; Balmford and Thomas 1992; Thomas 1993*b*). The need to avoid damage will select against pronounced (and hence unsupported) forks in birds exposed to a high risk of crashing and therefore provides a plausible alternative explanation for the decrease in fork depth in species from cluttered as opposed to open environments.

Summarizing our results on maneuverability, we found that birds with long outer tail feathers are relatively maneuverable. Birds requiring high maneuverability for aerial foraging have relatively long outer tail feathers. Last, the need for high maneuverability in woodland birds is associated with elongated outer feathers in species with graduated tails, and with the predicted decrease in fork depth in species with forked tails.

3. Tail Morphology under Selection for Agility

PREDICTION 3. Aerial hawkers should generally have long forked tails with outer feathers roughly twice as long as inner feathers. Assessments of tail morphology across a suite of taxonomically distant hawkers provided clear though circumstantial support for this prediction. We found that in eight different families, aerial

TABLE 3
RELATIVE OUTER TAIL FEATHER AND WING LENGTH DATA FOR MATCHED PAIRS OF BIRDS FROM
CLUTTERED AND OPEN ENVIRONMENTS

	RELATIVE OUTER TAIL FEATHER LENGTH			RELATIVE WING LENGTH		
	Males	Females	Both	Males	Females	Both
Graduated tails:						
Cluttered environment:						
1. <i>Surnia ulula</i>	.87	.83	.85	1.38	1.31	1.34
2. <i>Buteo lineatus</i>	.95	.94	.94	1.47	1.48	1.48
3. <i>Aix sponsa</i>	.32	.28	.30	.73	.80	.76
4. <i>Dendragapus canadensis</i>	.54	.62	.58	.90	.92	.91
5. <i>Columba palumbus</i>	.77	.71	.74	1.20	1.12	1.16
6. <i>Cuculus saturatus</i>	.79	.89	.84	1.31	1.42	1.37
7. <i>Caprimulgus europaeus</i>	1.27	1.13	1.20	1.73	1.74	1.74
8. <i>Melanerpes carolinus</i>	.69	.79	.74	1.26	1.36	1.31
9. <i>Toxostoma longirostre</i>	1.14	1.05	1.09	1.07	.99	1.03
10. <i>Euphagus carolinus</i>	.98	.86	.92	1.26	1.14	1.20
Open environment:						
1. <i>Asio capensis</i>	.82	.74	.78	1.73	1.75	1.74
2. <i>Buteo jamaicensis</i>	.75	.78	.76	1.28	1.36	1.32
3. <i>Anas strepera</i>	.24	.25	.24	.79	.73	.76
4. <i>Lagopus mutus</i>	.49	.44	.47	.84	.80	.82
5. <i>Columba livia</i>	.53	.53	.53	1.20	1.24	1.22
6. <i>Cuculus canorus</i>	.76	.83	.79	1.43	1.47	1.45
7. <i>Caprimulgus aegyptius</i>	1.06	.99	1.02	1.69	1.62	1.65
8. <i>Melanerpes uropygialis</i>	.65	.59	.62	1.31	1.19	1.25
9. <i>Toxostoma lecontei</i>	1.04	.95	.99	.99	.92	.96
10. <i>Euphagus cyanocephalus</i>	.99	1.08	1.04	1.27	1.38	1.33
Forked tails:						
Cluttered environment:						
11. <i>Chlorostilbon mellisugus</i>	.84	.76	.80	1.40	1.33	1.37
12. <i>Eurystomus glaucurus</i>	.90	.82	.86	1.46	1.36	1.41
13. <i>Tyrannus couchii</i>	1.21	1.16	1.18	1.38	1.31	1.34
14. <i>Lullula arborea</i>	.79	.75	.77	1.37	1.29	1.33
15. <i>Psalidoprocne pristoptera</i>	1.62	1.38	1.50	1.95	1.80	1.87
16. <i>Prunella modularis</i>	1.01	.87	.94	1.05	.94	.99
17. <i>Phoenicurus phoenicurus</i>	.87	.90	.88	1.07	1.13	1.10
18. <i>Dicrurus ludwigii</i>	1.16	1.13	1.15	1.19	1.20	1.19
19. <i>Emberiza aureola</i>	.84	.86	.85	1.04	1.00	1.02
20. <i>Acanthis flammea</i>	1.04	1.12	1.08	1.25	1.34	1.30
Open environment:						
11. <i>Chlorostilbon aureoventris</i>	1.00	.90	.95	1.38	1.40	1.39
12. <i>Coracias caudata</i>	1.32	1.25	1.29	1.19	1.15	1.17
13. <i>Tyrannus verticalis</i>	1.05	1.12	1.09	1.31	1.39	1.35
14. <i>Alauda arvensis</i>	.86	.86	.86	1.32	1.28	1.30
15. <i>Pseudhirundo griseopyga</i>	1.50	1.29	1.39	1.74	1.56	1.65
16. <i>Prunella collaris</i>	.82	.82	.82	1.11	1.13	1.12
17. <i>Oenanthe oenanthe</i>	.83	.88	.86	1.27	1.36	1.31
18. <i>Dicrurus adsimilis</i>	1.21	1.18	1.20	1.38	1.24	1.31
19. <i>Emberiza hortulana</i>	.94	1.13	1.04	1.16	1.34	1.25
20. <i>Acanthis flavirostris</i>	.97	.95	.96	1.11	1.12	1.12

NOTE.—Paired birds are preceded by the same number.

TABLE 4

FORK DEPTH FOR MATCHED PAIRS OF FORKED-TAILED BIRDS FROM
CLUTTERED AND OPEN ENVIRONMENTS

	FORK DEPTH		
	Males	Females	Both
Cluttered environment:			
1. <i>Chlorostilbon mellisugus</i>	1.13	1.05	1.09
2. <i>Eurystomus glaucurus</i>	1.12	1.09	1.10
3. <i>Tyrannus couchii</i>	1.07	1.06	1.06
4. <i>Lullula arborea</i>	1.04	1.05	1.05
5. <i>Psalidoprocne holomelaena</i>	1.89	1.73	1.81
6. <i>Prunella modularis</i>	1.02	1.02	1.02
7. <i>Phoenicurus phoenicurus</i>	1.03	1.03	1.03
8. <i>Dicrurus ludwigii</i>	1.06	1.05	1.06
9. <i>Emberiza aureola</i>	1.03	1.02	1.03
10. <i>Acanthis flammea</i>	1.20	1.17	1.18
Open environment:			
1. <i>Chlorostilbon aureoventris</i>	1.30	1.12	1.21
2. <i>Coracias caudata</i>	1.61	1.57	1.59
3. <i>Tyrannus verticalis</i>	1.02	1.02	1.02
4. <i>Alauda arvensis</i>	1.14	1.12	1.13
5. <i>Pseudhirundo griseopyga</i>	1.96	1.82	1.89
6. <i>Prunella collaris</i>	1.04	1.05	1.04
7. <i>Oenanthe oenanthe</i>	1.10	1.05	1.08
8. <i>Dicrurus adsimilis</i>	1.17	1.15	1.16
9. <i>Emberiza hortulana</i>	1.02	1.04	1.03
10. <i>Acanthis flavirostris</i>	1.19	1.19	1.19

NOTE.—Paired birds are preceded by the same number.

TABLE 5

CONVERGENT TAIL MORPHOLOGY IN AN ARRAY OF TAXONOMICALLY DISTANT HAWKERS

FAMILY	SPECIES MEASURED	RELATIVE TAIL LENGTH			FORK DEPTH		
		Males	Females	Both	Males	Females	Both
Fregatidae	<i>Fregata magnificens</i>	1.27	1.25	1.26	2.14	2.22	2.18
Accipitridae	<i>Chelictinia ricourii</i>	1.54	1.39	1.46	1.95	1.70	1.83
Glareolidae	<i>Glareola pratincola</i>	.98	1.01	1.00	1.82	1.87	1.85
Lariidae	<i>Sterna melanogaster</i>	1.15	1.33	1.24	2.23	2.25	2.24
Apodidae	<i>Apus apus</i>	.99	.90	.94	1.78	1.76	1.77
Hemiprocridae	<i>Hemiprocne comata</i>	1.10	1.24	1.17	2.12	1.96	2.04
Coraciidae	<i>Coracias abyssinica</i>	1.93	1.88	1.90	1.91	1.91	1.91
Hirundinidae	<i>Pseudhirundo griseopyga</i>	1.50	1.29	1.39	1.96	1.82	1.89

foragers all had relatively long tails (approaching or exceeding body length) associated with low sexual dimorphism and a fork depth close to 2.0 (see table 5).

4. Tail Morphology under Selection for Slow or Hovering Flight

PREDICTION 4. Wind-hoverers should have longer outer tail feathers than relatives that wind-hover less. Our ornithologists could find only nine matched pairs

TABLE 6

RELATIVE OUTER TAIL FEATHER AND WING LENGTH DATA FOR WIND-HOVERERS AND RELATIVES THAT WIND-HOVER LESS OR NOT AT ALL

	RELATIVE OUTER TAIL FEATHER LENGTH			RELATIVE WING LENGTH		
	Males	Females	Both	Males	Females	Both
Wind-hovers more:						
1. <i>Thalassoica antarctica</i>	.39	.42	.41	1.16	1.23	1.20
2. <i>Asio flammeus</i>	.71	.70	.71	1.52	1.47	1.50
3. <i>Elanus caeruleus</i>	.69	.74	.72	1.42	1.57	1.49
4. <i>Buteo lagopus</i>	.80	.82	.81	1.48	1.56	1.52
5. <i>Falco tinnunculus</i>	.96	.89	.93	1.51	1.47	1.49
6. <i>Larus minutus</i>	.70	.69	.69	1.63	1.56	1.59
7. <i>Chlidonias nigra</i>	.68	.75	.72	1.73	1.81	1.77
8. <i>Ceryle rudis</i>	.60	.61	.61	1.03	1.05	1.04
9. <i>Alauda arvensis</i>	.86	.86	.86	1.32	1.28	1.30
Wind-hovers less or not at all:						
1. <i>Fulmarus glacialisoides</i>	.41	.40	.41	1.25	1.13	1.19
2. <i>Asio capensis</i>	.82	.86	.84	1.73	1.75	1.74
3. <i>Rostrhamus sociabilis</i>	.86	.84	.85	1.68	1.62	1.65
4. <i>Buteo jamaicensis</i>	.75	.78	.76	1.28	1.36	1.32
5. <i>Falco naumanni</i>	.87	.85	.86	1.60	1.54	1.57
6. <i>Rissa tridactyla</i>	.51	.52	.51	1.27	1.25	1.26
7. <i>Clidonias leucopterus</i>	.60	.67	.64	1.69	1.81	1.75
8. <i>Chloroceryle inda</i>	.48	.56	.52	.84	.95	.89
9. <i>Chersophilus duponti</i>	.72	.62	.67	1.05	.96	1.01

NOTE.—Paired birds are preceded by the same number.

of species that differed in their use of wind-hovering. These provided no evidence in support of our prediction. We found that both the relative length of outer tail feathers and relative wing length were similar in species that wind-hover and those that wind-hover less or not at all (table 6; comparisons of relative outer tail feather length: for males, $T^+ = 31$, NS; for females, $T^+ = 32$, NS; for both sexes, $T^+ = 32$, NS; comparisons of relative wing length: for males, $T^+ = 27$, NS; for females, $T^+ = 33$, NS; for both sexes, $T^+ = 30$, NS). The lack of any relationship here is puzzling. There are two obvious possibilities. The aerodynamic theory may be wrong, but the fact that the same theory accurately predicts tail morphology in other circumstances in which maximizing additional lift is at a premium (turning flight) suggests this is unlikely. An alternative is that variation in the wind-hovering behavior of our species does not lead to strong differences in the selection pressures acting on tail morphology.

CONCLUDING REMARKS

The comparative data reported here support many of the predictions of our aerodynamic analyses, suggesting that much of the diversity seen in avian tail morphology reflects how natural selection for differing aspects of flight performance varies with ecology. For instance, even highly efficient tails decrease a

bird's overall lift-to-drag ratio, which explains why tail length is reduced in large-bodied open-country species selected for high L/D or high-speed flight. In contrast, in closed environments, avoiding collisions may be more important than efficient flight per se. Thus, woodland birds generally have long tails, which enhance maneuverability, and those with forked tails tend to have shallower forks, which are less efficient but more resistant to damage. Last, birds that forage on the wing in open environments rely on high agility to obtain their food. Agility is maximized by having an aerodynamically efficient tail, which presumably explains the convergent evolution of relatively deep forks across a wide array of aerial hawkers. One key prediction of our model that was not supported by the comparative data was that birds needing additional lift in order to wind-hover should have elongated tails and wings. This negative result may have arisen because in practice, species can never be perfectly matched for all variables, so that pairwise tests are only sensitive to selection pressures that are strong enough to overwhelm other confounding influences.

Unlike birds' wings, tails have often been selected for additional functions other than simply optimizing aerodynamic performance. Both wings and tails vary widely in size and shape depending on which aspects of flight are most closely targeted by natural selection. However, tails usually generate substantially less lift than wings, and their aerodynamic performance is far more robust to deviations from any given optimum morphology. As a result, tail size and shape commonly reflect nonaerodynamic selection pressures. For instance, tails are sometimes co-opted to perform additional biomechanical functions, such as acting as props for use in climbing (Norberg 1989). More generally, we suggest that the ability of tails to maintain aerodynamic function while deviating substantially from optimum flight morphology also explains why, unlike wings, birds' tails have so commonly been the subject of elaboration through sexual selection.

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APPENDIX

DEFINITIONS OF THE MAIN AERODYNAMIC TERMS USED IN THE TEXT

Aerodynamic center: the point at which all aerodynamic forces acting on a body can be considered to act

Agility: the maximum rate at which a bird can turn

Aspect ratio: the nondimensional measure of body shape, calculated as $\text{span}^2/\text{area}$; sailplanes have high-aspect-ratio wings while the Concorde has low-aspect-ratio wings

Center of mass: the point about which all the mass in a body is evenly distributed; for a bird in steady flight its center of mass and aerodynamic center are by definition coincident

Drag: the component of the total aerodynamic force generated by a body that is aligned with the freestream velocity

Drag coefficient: a dimensionless measure of the ability of a body to generate forces in the direction of the freestream velocity; it is high for a parachute and low for a streamlined body

Freestream: the airflow that would exist in the absence of the bird and does exist away from the influence of the bird

Freestream velocity: the speed and direction the airflow would have in the absence of the bird

Lift: the component of the total aerodynamic force generated by a body that is perpendicular to the freestream velocity

Maneuverability: the minimum turning radius that can be achieved by a bird in flight

Tail moments: the products of the lift generated by the tail and the distance between its aerodynamic center and either its apex or the bird's center of mass

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