

# Aerodynamics, evolution and ecology of avian flight

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Animal flight poses intriguing questions about biological adaptation, from how flight could have evolved to the morphological and physiological designs that enable flight to occur. Aerodynamic theory provides ecologists with a useful tool for understanding the basic physics of flight, but analysing flapping flight aerodynamics in birds is difficult, with interesting physiological complications. Recent research, using sophisticated techniques, has generated new and exciting insights about the evolution of flight, the function of tails and the ecological adaptations to a flying lifestyle.

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The ability to fly is the key adaptation that has made birds so successful. They can travel long distances in a short time and can therefore exploit the best seasons for reproduction and survival. Migratory nonstop flights can be >10 000 km – by far surpassing the performance of any man-made vehicle of a similar size. By adopting an aerodynamic approach, borrowed from engineering and modified to apply to animals, it is now possible for biologists to address fundamental questions about flight in birds, bats and insects. From aerodynamic theory, we can not only calculate the flight range of birds, their optimal migration strategy and the most appropriate flight speed, but we can also examine the evolutionary design of their morphology. Aerodynamics also provides a tool for understanding how flight could have evolved in birds, bats and even in fossil pterosaurs, where it is virtually the only approach available to examine flight design. Research about animal flight is a truly interdisciplinary field, combining both biology and physics. Here, I briefly introduce the essential elements of current aerodynamic theory and discuss some recent research about the evolution of flight and the aerodynamic function of bird tails. Because of the breadth of the topic, I focus on studies related to birds, even though research on bat and insect flight is advancing at an equally rapid pace.

## The aerodynamic theory of bird flight

In steady forward-flapping flight, all physical forces are in equilibrium (i.e. there is no net acceleration); LIFT (see Glossary) balances weight and thrust balances DRAG. However, this applies to means of the forces only, because the INSTANTANEOUS FORCE acting on a beating wing is an inherently dynamic AERO-ELASTIC phenomenon. The continuously changing WING PLANFORM, twist, rotation speed and the elastic deformation of feathers during a wing beat make calculating instantaneous forces virtually impossible.

There are two main approaches for modelling aerodynamics of flight (Fig. 1). The first is to estimate the local force acting on a wing-strip (or blade element) and to integrate (or sum) the result over the wingspan. It is assumed that the instantaneous forces on the wing in unsteady motion are equal to those in steady flow at the same local speed and ANGLE OF ATTACK (the QUASI-STEADY ASSUMPTION) [1–3]. The second approach takes advantage of the fact that flapping wings deform the 'fluid' around them, and the aerodynamic force on the wing is associated with the IMPULSE of the wake MOMENTUM change. Hence, from the topology and kinetic energy deposited in the wake of the flying animal, lift and drag can be calculated [4–7]. This 'VORTEX wake' approach neatly circumvents the problems of wing beat kinematics, but cannot offer instantaneous wing force resolution. The choice of model approach therefore depends on the question addressed and the time resolution required.

Both approaches converge on the estimation of three main drag components: induced, profile and parasite drag (Box 1). The sum of these multiplied by the forward velocity through the air gives the power required to fly in steady level motion (Box 1). In a simple and widely used flight model [8,9], the variable nature of the aerodynamic force during flapping is ignored and the bird is represented by a circular disk with the wingspan as the diameter, and the body is represented by its projected frontal area and mass (Box 1). This approach is, in principle, a vortex wake model with an infinitely thin vortex sheet enclosing a core jet of downward-deflected air. Because the bird morphology is represented by its wingspan and weight only, the same aerodynamic characterization will be obtained for quite different birds if the wingspans and weights are the same.

For ecologists, the  $P(V)$  function (the so-called power curve) describing the power required to fly ( $P$ ) in relation to forward speed ( $V$ ) is perhaps the most useful result from aerodynamic analysis (Box 1). The U-shaped power curve has an analytical appeal, but its empirical validity has been surprisingly difficult to establish [10]. Much of the work on the ecology and evolution of flight stems from the power curve and, therefore testing the validity of the aerodynamic theory empirically is a high priority. One source of disagreement reported between theory and data is that most empirical studies involve measurements of the metabolic rate (power input) of flight in relation to speed [10,11], whereas the aerodynamic  $P(V)$  function

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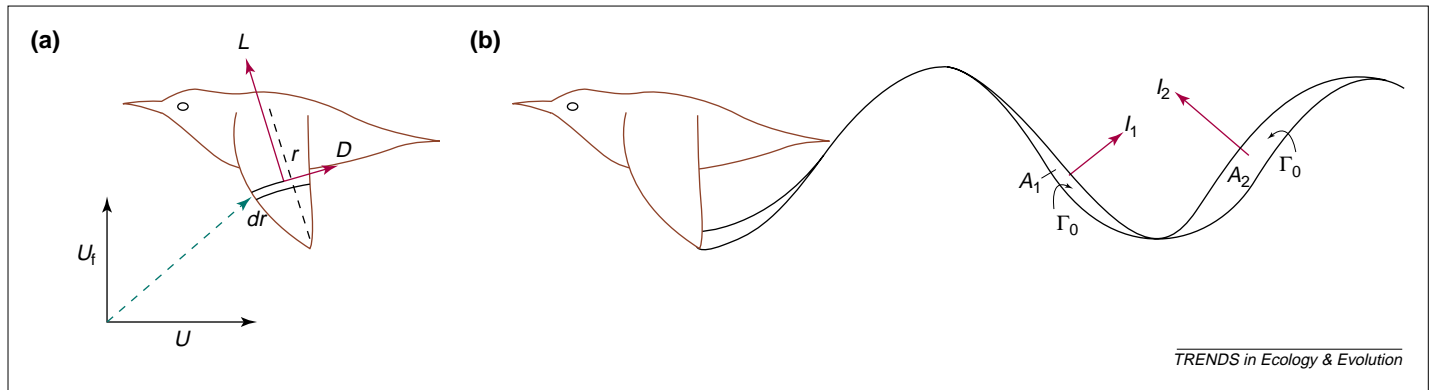


Fig. 1. The two alternative approaches for analyzing aerodynamic forces of a flying bird. (a) Aerodynamic forces, lift ( $L$ ) and drag ( $D$ ), are calculated for thin wing sections of width  $dr$ . The local incident velocity at a wing section depends on the forward velocity ( $U$ ) and the velocity of the wing section due to its rotation ( $U_t$ ) at span  $r$ . Provided that 3D effects can be ignored the local section lift and drag are calculated for all wing positions during a wing beat. The mean lift and drag are obtained by the summation (or integration) of vertical and horizontal components of wing section lift and drag over the wingspan during one wing beat. (b) Alternatively, the mean aerodynamic forces can be calculated from properties of the wake. At cruising speed the bird sheds undulating wing-tip vortices with constant circulation  $\Gamma_0$ . The different segments of the wake associated with the upstroke and downstroke will enclose different areas,  $A_1$  and  $A_2$ , which determines the associated impulses,  $I_1$  and  $I_2$ , as indicated. The aerodynamic forces can then be obtained from the impulses. For details about the two approaches see [3].

refers to the mechanical power output. Power output appears to be more difficult to measure than is power input, judging by the number of published studies. The logic for measuring metabolic rate rather than mechanical power is the assumption of a constant conversion efficiency across speeds, which might be questionable [12]. One could argue that what matters from an ecological viewpoint is the power input relationship with speed, because this involves the actual energy cost that the animal must pay. The results from metabolic studies differ greatly, regarding, for instance, the shape of the curve, probably because of differences relating to wind-tunnel turbulence, measurement technique and speed range investigated, and so we would never be able to generalize from such data.

For questions relating to the evolution of flight and manoeuvrability, the mechanical  $P(V)$  curve is the relevant one, because, for example, it gives the power required for take off at the MINIMUM POWER SPEED. Measurements of mechanical power output do however converge on the general U shape [13,14], but the final validation (and revision) of the aerodynamic theory of birds and bats is still needed. Until then, we will continue to use the current flight model for qualitative inferences, but any quantitative claims should always be treated with some caution.

#### Evolution of flight

Aerodynamic theory offers perhaps the only way to recreate the likely sequence of events in the evolution of a flapping wing from a forelimb with no locomotory function in a small bipedal dinosaur. There are two competing theories for the evolution of flight: the arboreal (trees-down) scenario and the cursorial (ground-up) scenario [15]. The arboreal theory assumes that flight evolved in animals that climbed

trees or rocks, from which they launched themselves as parachuters or gliders into the air, whereas the ground-up scenario imagines proavis (i.e. the ancestor of birds) as a running MANIRAPTOR that leapt to catch flying insects. Selection for increased control and stability [16] favoured adaptations for lift on the forelimbs. Both camps in this controversy have used aerodynamic modelling to support their arguments [16–19].

It is easy to envisage how flapping flight could have developed in a gliding animal [17], thus favouring the arboreal scenario. In the cursorial scenario, flight has to evolve against gravity, which is considered a problem. However, if proavis was running and leaping to catch prey, it could have first evolved gliding flight from its highest position back to the ground, which, in turn, transformed into flapping flight by the gliding–flapping scenario. Even though this argument saved the cursorial scenario, other problems remain; for example, that speed is reduced when leaping compared with continuous running. Hence, if proavis ran to escape predators or to catch prey, running–leaping would reduce its performance [18]. In a more recent hypothesis, proavis was an ambush predator that pounced on prey and therefore evolved adaptations for controlling wing manoeuvrability [20].

Recent fossil finds of feathered dinosaurs [21] again increased the credibility of the cursorial theory, because they provided evidence that birds definitely evolved from a cursorial maniraptor. These finds also resolved the issue of whether feathers are unique to birds and whether they evolved as an adaptation for flight or for some other function (such as insulation). Because feathers pre-date flight, the aerodynamic design of flight feathers, involving asymmetric vanes and AIRFOIL profile [22], is thus an exaptation [23]. However, the evolutionary scenario remains to be understood from an aerodynamic perspective.

#### Archaeopteryx: analysing the flight of a fossil

The arboreal scenario can easily explain how take off was accomplished and how an incipient wing would have gradually improved flight performance, although the feathered dinosaurs favour the cursorial hypothesis. For take off from the ground, proavis would have needed to reach a sufficiently high forward speed on the runway [which is given by the minimum power speed of the power curve (Box 1)].

### Box 1. Mechanics of powered bird flight

Power ( $P$ ) required for flight in relation to forward speed ( $V$ ) is obtained from the sum of three main drag components: induced, parasite and profile drag.

#### Induced power

A simple approach to calculate induced drag [ $a$ ] represents the bird as a circular disk ( $S_d$ ) with the wing span ( $b$ ) as diameter, which in aeronautical terms is an ACTUATOR DISK that produces an induced downwards velocity to the air flowing through it. The mass flow through the wing disk is the volume flow,  $S_d = \pi b^2/4 \times$  forward speed ( $V$ )  $\times$  air density ( $\rho$ ), and written as  $S_d V \rho$ . By multiplying the mass flow (unit  $\text{kg s}^{-1}$ ) by the speed acquired in the far wake ( $2v_i$ , where  $v_i$  is the induced velocity of the flow at the wing disk) we get the force by which the bird is pushing on the air to support its weight as  $mg = 2v_i S_d V \rho$ . This can be rearranged to determine the induced velocity as  $v_i = mg/(2S_d V \rho)$ . Power is force  $\times$  speed and the power required to generate the induced velocity, or equivalently to generate a sufficient lift to balance the weight, is the induced power (Eqn I):

$$P_{ind} = \frac{k(mg)^2}{2S_d V \rho} \quad [\text{Eqn I}]$$

where  $k$  is the induced power factor that accounts for deviations from the ideal elliptic lift distribution.  $k$  is usually set to 1.2 for flapping flight [ $a$ ].

#### Parasite power

Parasite drag is the drag of the body isolated from the wings and is calculated as (Eqn II):

$$D_{par} = \frac{1}{2} \rho S_b C_{D,par} V^2 \quad [\text{Eqn II}]$$

where  $S_b$  is the body frontal area and  $C_{D,par}$  is a dimensionless drag coefficient. Parasite drag occurs mainly because the body causes an increase of pressure in front of it, which tends to decelerate oncoming flow. A large frontal area causes a relatively high drag, whereas a slim and streamlined body allows oncoming air molecules to flow past more easily resulting in low drag. Typical values of  $C_{D,par}$  are in the range 0.1–0.4 [ $b$ – $d$ ]. The parasite power  $P_{par}$  is simply parasite drag  $\times$  forward speed as (Eqn III):

$$P_{par} = \frac{1}{2} \rho S_b C_{D,par} V^3 \quad [\text{Eqn III}]$$

#### Profile power

The wings also cause profile drag in addition to the induced drag associated with lift generation. If the wings are held in a position so that they do not generate any lift, they will still produce pressure and friction drag, which is the profile drag that the flight muscles must overcome to rotate the wings for flapping. In flapping flight, the magnitude of the profile drag depends on both the rotation speed of the wings, which changes along the wingspan from zero at the wing root to maximum at the wing tip, and the forward speed [ $e$ ]. There is a tradeoff between the profile drag coefficient (decreasing with increasing forward speed) and the profile drag owing to forward speed, resulting in a near-constant profile power in the range of typical cruising speeds [ $e$ ,  $f$ ]. Profile power ( $P_{pro}$ ) is provisionally calculated as (Eqn IV):

$$P_{pro} = X P_{am} \quad [\text{Eqn IV}]$$

where  $X$  is a constant (1.2) and  $P_{am}$  is the minimum of the sum of induced and parasite power. At fast speeds, the profile power will increase with speed in a similar way as the parasite power and so this approximation cannot be extrapolated outside the range in which it is valid.

#### Mechanical power of bird flight

The total mechanical power ( $P_{mech}$ ) required to fly is (Eqn V):

$$P_{mech} = P_{ind} + P_{par} + P_{pro} \quad [\text{Eqn V}]$$

which is a function of forward speed, bird morphology and air density. The metabolic power input ( $P_{flight}$ ) is usually calculated as (Eqn VI):

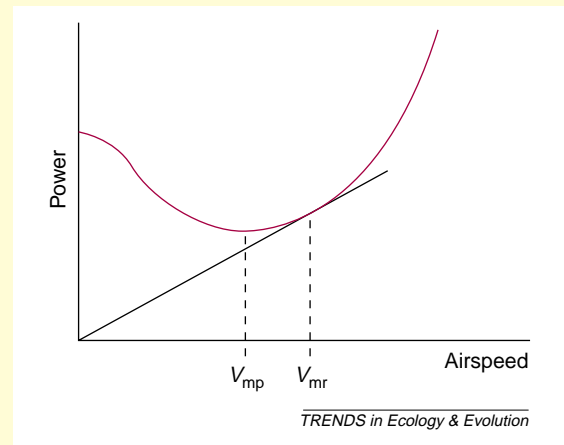


Fig. 1. The mechanical power versus airspeed relationship for a bird in forward flapping flight. It is relatively costly to hover and fly slowly, and there is a minimum power speed ( $V_{mp}$ ). The maximum range speed ( $V_{mr}$ ) can be estimated by drawing a tangent to the power curve as shown.

$$P_{flight} = R\eta^{-1}(P_{ind} + P_{par} + P_{pro}) + P_{bmr} \quad [\text{Eqn VI}]$$

where  $P_{bmr}$  is the basal metabolic rate,  $R$  is an overhead cost of elevated respiration and blood circulation costs during flight and  $\eta$  is the conversion efficiency. A power curve is shown in Fig. 1 with two characteristic speeds indicated. The minimum power speed  $V_{mp}$  is obtained from  $dP/dV=0$ , and is the speed that would keep the bird airborne for the maximum duration using only the take-off fuel store. By dividing power (dimension energy/time) with speed (distance/time) we get the dimension energy/distance, and by minimizing the power: speed ratio with respect to flight speed ( $dP/dV = P/V$ ) we obtain the maximum range speed  $V_{mr}$ . Graphically  $V_{mr}$  can be found by drawing a tangent from the origin to the power curve (Fig. 1).

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This problem was analysed recently for *Archaeopteryx*, the oldest known bird, living 150 million years ago [24]. The literature about this fossil is huge, and controversy still rages regarding the species flight capability [15]. The main problem is that the estimated top running speed of *Archaeopteryx* is  $2 \text{ ms}^{-1}$ , whereas the speed required for take off is at least  $6 \text{ ms}^{-1}$ , thus making it impossible for *Archaeopteryx* to have been able to take off from the ground [18].

Using estimated morphology for *Archaeopteryx*, Burgers and Chiappe [25] modelled the force dynamics from standstill through a take-off run (Fig. 2). At speed  $V=0$ , the weight is balanced by an equal and opposite force on the feet. When starting to run, the hind limbs produce forward propulsion and, by flapping the wings simultaneously, the feet generate a forward thrust that increases the acceleration. The wings also generate lift force, but, during running, this is residual lift, because it does not act on the bird, but relieves the hindlimbs

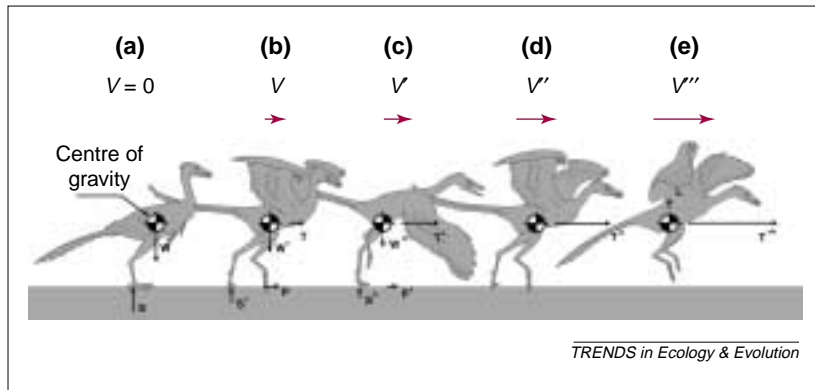


Fig. 2. Net forces on *Archaeopteryx* during a take-off run. The forward speed vectors ( $V$  to  $V''$ ) indicate the incremental velocity. (a) At standstill, the hindlimbs support the total weight  $W$  by an opposite and equal force  $S$ ; (b) initially, during the take-off run, the hindlimbs produce a forward propulsion  $P$  and, when the wings start to flap, they produce a thrust  $T$ . Because of residual lift  $L$ , the hindlimbs need to supply a reduced upwards force  $S'$  to balance the smaller net weight  $W'$ . This is the vertical force migration; (c) thrust is gradually increasing and becomes more important than the hindlimb propulsion  $P'$ , whilst  $W''$  and  $S''$  are further reduced as result of the vertical force migration. The shift of the forward force from hindlimb propulsion to thrust from the wings is the horizontal force migration; (d) just before lift off, the horizontal force migration is completed and  $P'$  has disappeared. The only net force acting on *Archaeopteryx* is thrust  $T''$ . The vertical force migration is also completed and the residual lift  $L$  translates into useful lift that exerts work on the bird, lifting it upwards. Residual lift refers to the fact that, during the take-off run, when  $L < mg$  lift does not act as a net force and therefore does not exert any work on the bird. Reproduced, with permission, from [25].

from 'weight support' and so the vertical force on the feet is reduced. This is the 'vertical force migration' from the hind limbs to the wings, and the reduced weight support causes a further acceleration by this feedback, which in turn increases the residual lift on the wings and hence the acceleration. Similarly, there is a 'horizontal force migration' from hind limb propulsion to increasing wing thrust during the taxiing run (Fig. 2). Taken together, the flapping wings increase acceleration and the top running speed from a mere  $2 \text{ ms}^{-1}$  to  $7.8 \text{ ms}^{-1}$  when lift equals weight, and thus *Archaeopteryx* would have taken off from the ground, with the help of flapping wings. Even though it is based on assumed morphology and weight, this aerodynamic model shows that *Archaeopteryx* could have used powered flight and was probably quite an advanced flyer. One can also envisage that feathered and winged dinosaurs [21] could have likewise increased their running speed by using wing thrust, and that bird flight therefore evolved from the ground up.

#### The function of bird tails

The aerodynamic theory outlined in Box 1 considers only the wings and body, and assumes that tails are more or less inactive when furled in cruising flight. Even a casual observer, however, will notice the continuous spreading and twisting of, for example, the tail of a red kite *Milvus milvus* during flight, suggesting that there is some aerodynamic benefit from the tail. But what that function is remains largely an open question. It has long been presumed that the tails of birds act as a control surface in a similar way as an aircraft tail, mainly to support PITCH control [8,26]. *Archaeopteryx* had quite a sturdy tail (Fig. 2) that might

have had this function [27], but, in modern birds, tails are typically much smaller and have disappeared altogether in fruit bats and pterosaurs [8]. A bird can still fly quite well even if its tail is lost, whereby stability and control of flight are achieved solely by the wings.

#### The slender wing theory of bird tails

In the 1990s, A.L.R. Thomas and co-workers developed an aerodynamic model for bird tails based on the slender-wing theory [28]. The first main application was to explain tail elongation in birds, which was believed generally to be the outcome of sexual selection [29,30]. Slender-wing theory provided a tool for comparing the lift and drag generated by tails of varying shapes (Box 2). The lift generated from a tail is proportional to its maximum continuous span, whereas drag is related directly to its total surface area. Any area protruding beyond the line of maximum span therefore adds drag but no lift. When comparing the lift:drag ratio among different shaped tails, it appeared that elongation of pintail and graduated tails is always costly (decreasing lift:drag), whereas elongation in forked tails is advantageous initially; however, further elongation beyond the point of maximum continuous span is also costly [31]. Long pintails and graduated tails are most likely to be the outcome of sexual selection, because any elongation is costly, but forked tails could well be a result of natural selection. These hypotheses received support from comparative studies [31,32]. In a recent wind-tunnel study, Evans *et al.* [33] tested the prediction of wing span reduction and tail position in relation to the forward speed of barn swallows *Hirundo rustica* according to the combined bird plus tail theory [34]. Wingspan decreased with speed, and the tail spread and angle of attack changed in qualitative agreement with the theory, but the quantitative disagreement was so large that the validity of the theory could be questioned.

#### The barn swallow as a model species for analysing tail function

The barn swallow is a model for studies of sexual selection [30]. In the wake of new theory about bird tail aerodynamics, it was natural, therefore, for studies to focus on this species. Norberg [35] suggested a novel aero-elastic mechanism, which proposed that the elongated tail streamers of barn swallows could bend in the airflow, causing the proximal parts of the outer tail feathers to droop passively, thereby attaining a function as FLAPS. Supposedly, this helps to increase tail lift during foraging-turning manoeuvres. Such a function for the tail streamers casts doubts on the streamers as being a product purely of sexual selection. Evans and Thomas [36] also worked out testable predictions about tail length and flight behaviour, which were tested using swallows and martins [37–39]. The studies indicated that the length of streamers is a compromise between natural and sexual selection. Sand martins *Riparia riparia* with experimentally elongated outer tail feathers

## Box 2. Slender wing theory of bird tail aerodynamics

The aerodynamics of bird tails have been modelled using slender wing theory [a,b]. The tail is considered to be a thin flat delta-shaped wing of low ASPECT RATIO  $AR$  (span squared divided by wing area) at an angle of attack  $\alpha$  (Fig. 1). The angle at the apex can be changed according to whether the tail is furled or spread, which will change the maximum span of the tail. Using 2D wing theory, Thomas [b] derived that lift for such a shape is (Eqn I):

$$L = (\pi/4)\rho\alpha V^2 b_{\max}^2 \quad [\text{Eqn I}]$$

where  $\rho$  is air density,  $V$  is forward speed and  $b_{\max}$  is the span at the widest point of the tail. The induced drag, which occurs because the aerodynamic force is tilted backwards because of the induced downwash, is (Eqn II)

$$D_i = (1/2)L\alpha \quad [\text{Eqn II}]$$

and the profile drag comprises skin friction ( $D_f$ ) and pressure drag ( $D_p$ ) (Eqn III,VI):

$$D_f = (1/2)\rho V^2 S_w C_{Df} \quad [\text{Eqn III}]$$

$$D_p = (1/2)\rho V^2 S_f C_{Dp} \quad [\text{Eqn IV}]$$

where the reference area  $S_w$  is the wetted area (twice the wing planform area),  $S_f$  is the projected frontal area (increases with  $\alpha$ ), and  $C_{Df}$  and  $C_{Dp}$  are dimensionless force coefficients. The skin friction drag will typically dominate and  $D_p$  can usually be neglected. The area and maximum span of the tail depend on tail shape and spread angle. The slope of the lift coefficient against angle of attack ( $\pi/2AR$ ) for bird tails is small compared with high aspect ratio wings ( $2\pi$ ), which means that the lift generated is less sensitive to small changes of  $\alpha$ . In addition to lift and drag the theory can be used to evaluate quantities such as pitching moment and stability in relation to tail morphology and asymmetry [b,c]. A consequence of this theory is that if the tail has a surface area that is distal to the point of maximum span, such that when the tail is graduated, as in a magpie, this area will not contribute to lift but only to drag. Hence, such tails will be more costly than tails where the trailing edge is where the tail has maximum span. The whole-bird aerodynamics has also been modelled by

(thus mimicking the early stage of swallow streamer elongation) caught smaller and less profitable prey than did controls, indicating a cost of elongation [40]. By contrast, similar tail manipulations in house martins *Delichon urbica* resulted in improved manoeuvrability [41]. Further experimental evidence is needed to settle the debate concerning the relative importance of natural and sexual selection behind the current length of swallow tail streamers [40–42].

### Tail and bird together

Most birds have rather short triangular tails when spread. The slender-wing theory of bird tail aerodynamics (Box 2) considers the tail in isolation, but when attached to a bird, the tail is influenced by the time-varying wake of flapping wings and the flow over the body. It is reasonable to assume that body, wings and tail morphology have evolved in concert. Modelling the interaction between the wings and tail suggest that the induced drag of the wing–tail combination is lower than that for the wings alone [43]. A tail thus enables the bird to have wings that are optimized for cruising speed (with the tail furled to minimize drag) and, at low speeds, the spread tail reduces induced drag during manoeuvring and turning flight. Observations show that tails are maximally spread at low speeds and then become furled increasingly with increasing speed [26,44].

A team led by J.M.V. Rayner has provided fresh insights about the aerodynamic function of bird tails on the basis of wind-tunnel measurements of starling

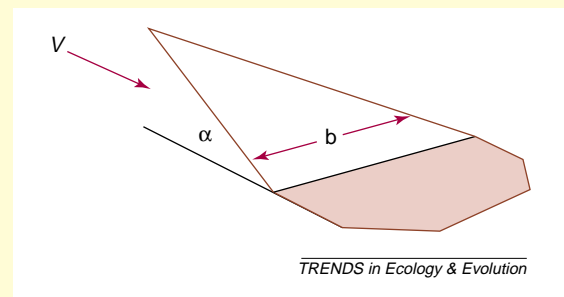


Fig. 1. A hypothetical bird tail showing a triangular shape to the line of maximum span and an aft area (shaded) beyond this line. The tail lift depends on the maximum span and the angle of attack ( $\alpha$ ). The shaded area does not contribute to lift but generates drag.

combining slender wing theory for tail with the flight mechanical theory outlined in Box 1 [d].

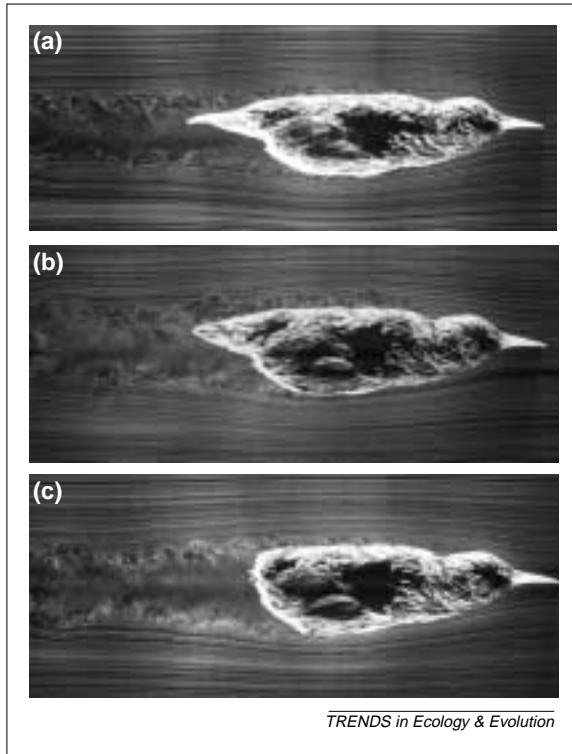
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*Sturnus vulgaris* bodies [45,46]. Wingless starling bodies were mounted on a force balance to measure the effect of the tail on lift generated by the body and tail combinations. Lift was more or less independent of tail-spread angle at a speed of  $4.9 \text{ ms}^{-1}$  and a  $15^\circ$  attack angle [46]. In addition, lift was significantly less than that predicted by the slender-wing theory. These results show that the tail and body cannot be considered in isolation, and that the conjectured function of the tail as an induced drag-reducing flap might be incorrect.

Aeronautical engineers know that the drag of AXISYMMETRICALLY SHAPED objects, such as cylinders, can be reduced by placing a SPLITTER PLATE in the wake centreline downstream from the body. This might reduce the interaction between the shear layers on opposite sides of the body, thus affecting the shedding of wake vortices. Maybury and Rayner [45] hypothesized that the typical avian tail might act as a splitter plate even when furled, as in cruising flight, with the adjacent tail covert feathers forming a wedge that reduces drag further. Drag was measured on dead birds with complete (but furled) tails, with shortened tails, and with tail and coverts completely removed [45]. As predicted, the parasite drag of the body–tail combination was lowest with an intact tail. Removing tails increased drag by up to 25%. The aerodynamic mechanism was checked by elegant-flow visualization (Fig. 3), showing that the diameter of the turbulent wake is increased when the tail and coverts are absent (drag is directly proportional to the width of the turbulent wake). These studies therefore indicate that

Fig. 3. Flow visualization around mounted wingless starling bodies using the smoke-wire technique in a wind tunnel at  $9 \text{ ms}^{-1}$ . (a) The bird with intact tail and covert feathers; (b) tail feathers protruding beyond ventral coverts are trimmed to the same length as coverts; (c) tail feathers, ventral and dorsal covert feathers removed. The height of the wake increases from (a) to (c). The dorsal boundary layer also becomes increasingly turbulent in (b) and (c) compared with the intact tail-body configuration in (a). Reproduced, with permission, from [45].



typical bird tails act as splitter plates with a primary function of reducing the parasite drag of the body rather than the induced drag of the wings. However, these results come from dead birds without wings. In

live birds, the flapping wings add dynamic complexity to the body–wing–tail interference. The next step will be to disentangle this dynamic problem, perhaps by using a mechanic model flapper [47] or a live bird.

### Ecology of flight

A U-shaped power–speed relationship (Box 1) immediately suggests ecologically significant or ‘optimal’ flight speeds that should be selected depending on what currency is being optimized. The speed of minimum power ( $V_{mp}$ ) is optimal if flight endurance is important without the need to account for distance, whereas the MAXIMUM RANGE SPEED ( $V_{mr} > V_{mp}$ ) is associated with the minimum energy cost per unit distance. Birds seem capable of adjusting their airspeed as if they were aware of  $V_{mp}$  and  $V_{mr}$  [e.g. skylarks *Alauda arvensis* adjust their airspeed during song flight ( $V_{mp}$ ) versus migratory flight ( $\geq V_{mr}$ )] [48]. If birds are minimizing the overall migration time, they should fly slightly faster than  $V_{mr}$  because the energy lost on flight in relation to  $V_{mr}$  will be compensated for by the time gained at the next stopover [49]. In natural situations, the expected difference in relation to  $V_{mr}$  is small, and it remains to be shown whether the higher flight speed is used by time-minimizing migrants. Central-place foragers should likewise fly faster than  $V_{mr}$  if maximizing the rate of food transport to young or to a cache [49,50].

Adaptive speed adjustment can also be derived for several external factors. For example, flight speed should increase with altitude, because of the reduced air density [51],  $V_{mr}$  should increase when flying into headwinds and decrease when flying with tailwinds [51], and speed should increase with increasing angle of side wind (track-heading) if maintaining a constant track over the ground [52].

The best choice of flight mode, such as thermal soaring or powered flapping flight, can be analysed on the basis of the  $P(V)$  curve (Box 1) and cross-country soaring theory [9,53]. At some body size, it pays to switch from flapping to soaring flight migration, provided that there are some average expected thermal conditions for both an energy and time-saving migration strategy. Selection would then favour increasing body size once a bird species has evolved a soaring migration habit, whereas flapping flight will favour reduced body size [54]. These general predictions could be tested by comparative data. Aerodynamic theory has also been used recently for analysing evasive flight responses to predators and the effect of moult gaps on flight performance [55].

### Conclusions and prospects

Since the development of flight mechanics for birds and bats in the 1960s, there has been a steady growth in applying the aerodynamic theory to evolutionary and ecological questions (e.g. C.J. Pennycuik’s 1989 book *Bird Flight Performance* [9] has now been cited >340 times). Aerodynamic theory relating to animals has generated numerous predictions about

### Glossary

**Actuator disk:** inserts momentum at a certain rate into a downward airstream.

**Aero-elastic:** effect of aerodynamic forces on elastic materials and structures exposed to an airflow.

**Airfoil:** a section of a wing (profile) that can produce circulation in its vicinity without actually rotating.

**Angle of attack:** the angle of the chord axis of a wing in relation to the flight path. The induced velocity reduces the local angle of attack to the effective angle of attack.

**Aspect ratio:** a shape index for a wing calculated as the wing span squared divided by wing area.

**Axisymmetrically shaped:** symmetrical with respect to an axis.

**Circulation:** a measure of the intensity of an irrotational vortex, defined as the product of the circumference and tangential velocity of the vortex. Lift is directly proportional to the circulation

**Drag:** the aerodynamic force parallel to the direction of velocity.

**Flap:** a special high-lift device that can be used to extend the leading edge of a (usually) wing.

**Impulse:** the change in momentum of a particle or a volume of fluid.

**Instantaneous force:** momentarily magnitude of a time varying force.

**Lift:** the force that is created by the action of an airfoil normal to the flow.

**Maniraptor:** advanced carnivorous dinosaur with short forelimbs that walked or ran on strong hind legs.

**Maximum range speed:** the flight speed relative to the air resulting in minimum energy cost per unit distance; given by the condition  $dP/dV = P/V$ .

**Minimum power speed:** the flight speed relative to the air with lowest rate of energy requirement; given by the condition  $dP/dV = 0$ .

**Momentum:** the product of mass and velocity.

**Quasi-steady assumption:** the instantaneous forces on a flapping wing are assumed to be the forces that the wing would experience in steady motion at the same instantaneous velocity and angle of attack.

**Pitch:** rotation of the body’s longitudinal axis in the nose-up or nose-down sense.

**Splitter plate:** a thin plate inserted downstream from a body that physically divides the wake, and usually reduces the rate at which vortices are shed.

**Vortex:** a package, usually in the form of a cylinder, of rotating fluid (A smoke ring is a typical vortex ring).

**Vorticity:** calculated as twice the angular velocity of a fluid element at a point in space or, more formally, the circulation around an infinitesimal circuit divided by the area of that circuit.

**Wing planform:** the shape outline of a wing as projected upon a horizontal plane.

morphological adaptations and flight behaviour [51,56] and many of these have, at least qualitatively, withstood empirical tests. Perfect agreement between predictions and measured quantities is expected only if the theory is perfect and additional assumptions concerning, for example, optimization currencies are correct. This is unlikely ever to be the case in a field such as biology. Aerodynamics is often used as a baseline theory in combination with ecological considerations, and so a secondary optimality theory has been constructed [57]. Needless to say, if there are uncertainties in the aerodynamic theory, the derived properties will at best be correct qualitatively. It is therefore important to refine our understanding of flapping flight mechanics. To this end, specially crafted low turbulence wind tunnels will be the most useful tools [58], because both aerodynamic and physiological properties can be measured simultaneously. The conversion of metabolic power (fuel consumption) to useful mechanical power output is usually assumed to be constant (Box 1). Recent studies indicate that conversion efficiency might change with flight speed and even body mass within a species [12,59], which, if proven to be general, will affect predictions about flight behaviour. These issues

will be resolved only when metabolic rate (power input) and mechanical power output are measured simultaneously on the same bird. The drag coefficient of bird bodies (Box 1) is probably much lower than was previously found from measurements on frozen bodies in wind tunnels [60], but the true range of the body drag coefficient for live birds is still unknown [61].

New techniques for visualizing the vortex wakes of freely flying birds should be deployed in wind tunnels [62]. Former wake visualization experiments enabled the bird to select the speed. Although these experiments were very informative [7,63], we do not know how the wake topology and momentum change over a range of speeds. When such data become available, a more realistic characterization of wake topologies and VORTICITY and CIRCULATION will emerge, which, in turn, are fundamental to the development of the next generation of flight models. Field studies of flight behaviour using radar and satellite telemetry will provide information about flight ranges and migration speeds that are important to our appreciation of what live animals can actually achieve. The fantastic feats of migratory birds, stooping falcons or displaying snipes will remain the fuel for our imagination.

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# Are populations of coral reef fish open or closed?

Camilo Mora and Peter F. Sale

Dispersal plays a crucial role in several aspects of the biology, management and conservation of many species, including coral reef fish and other demersal marine organisms with pelagic larval stages. To know the origin of propagules that replenish benthic populations is a major challenge, yet, whereas earlier studies emphasized the broadly extensive dispersal of reef fish larvae, recent publications have emphasized the extent to which these larvae succeed in returning to their natal populations. Here, we critically analyse the evidence concerning the dispersal of coral reef fish, and conclude that: (1) at present, the extent to which reef fish populations are open or closed must be regarded as unknown; and (2) further improved research is likely to confirm that larval dispersal structures populations into more or less open populations depending on the particular attributes of species, physical oceanographical systems in which they occur and the scale at which the question is posed.

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DISPERSAL (see Glossary) is one of the most important life-history traits involved in species evolution and persistence [1–4]. It is also the primary determinant of CONNECTIVITY among local populations, which is a vital parameter for conservation strategies based on protected areas [5]. In addition to the intrinsic importance of dispersal for fundamental science, recent evidence of impacted fish stocks [6] and our growing awareness of coral reef degradation by human activity and climate warming [7] highlight the need for accurate understanding of dispersal. For demersal and benthic marine organisms with

pelagic larval stages, delineating patterns of dispersal remains a major challenge, both because the dispersing organisms are minute and difficult to track, and because dispersal is driven by multiple complex factors. Because of the potential for transport of propagules by currents, early work assumed that larval dispersal was largely passive, with an extent that was dependent on patterns of water movement and duration of larval life. Thus, local populations were expected to be replenished largely by larvae derived from elsewhere [5,8].

Fish of coral reefs typically have larval lives that are measured in weeks or months, but their larvae are capable behaviorally of participating actively in their own dispersal [9–14]. These attributes are compatible with various patterns of dispersal [11], but ecologists of reef fish have increasingly tended to emphasize that fish larvae remain in the vicinity of the natal reef [15–17]. Whereas the view in the late 1970s was that reef-fish populations were broadly open, the consensus has shifted to view them as substantially closed [15–22]. This change relies on a variety of evidence, including physical oceanography near reefs [16], larval behavior [9], tagging studies [18–19] and genetic patchiness among geographically separate populations [2,23]. It is also supported by some recent models of dispersal [22], and conforms to theoretical expectations that marine populations must achieve CLOSURE by

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