

Bird or bat: comparing airframe design and flight performance

Anders Hedenström¹, L Christoffer Johansson¹ and Geoffrey R Spedding^{2,3}

¹ Department of Theoretical Ecology, Ecology Building, SE-223 62 Lund, Sweden

² Department of Aerospace and Mechanical Engineering, University of Southern California, Los Angeles, CA 90098-1191, USA

E-mail: anders.hedenstrom@teorekol.lu.se

Received 14 August 2008

Accepted for publication 28 January 2009

Published 4 March 2009

Online at stacks.iop.org/BB/4/015001

Abstract

Birds and bats have evolved powered flight independently, which makes a comparison of evolutionary 'design' solutions potentially interesting. In this paper we highlight similarities and differences with respect to flight characteristics, including morphology, flight kinematics, aerodynamics, energetics and flight performance. Birds' size range is 0.002–15 kg and bats' size range is 0.002–1.5 kg. The wingbeat kinematics differ between birds and bats, which is mainly due to the different flexing of the wing during the upstroke and constraints by having a wing of feathers and a skin membrane, respectively. Aerodynamically, bats appear to generate a more complex wake than birds. Bats may be more closely adapted for slow maneuvering flight than birds, as required by their aerial hawking foraging habits. The metabolic rate and power required to fly are similar among birds and bats. Both groups share many characteristics associated with flight, such as for example low amounts of DNA in cells, the ability to accumulate fat as fuel for hibernation and migration, and parallel habitat-related wing shape adaptations.

(Some figures in this article are in colour only in the electronic version)

1. Introduction

Active flapping flight has evolved on three occasions among the vertebrates: in birds, bats and the extinct *Pterosaurs*. Among the extant groups, birds originate from theropod dinosaurs (Ji *et al* 1998) and bats originate from mammalian insectivores (Simmons and Geisler 1998). The oldest bird, *Archaeopteryx*, had already evolved capacity for flight about 150 million years ago. The oldest known fossil bats, *Icaronycteris index* and *Onychonycteris finneyi*, exhibit most features of modern bats already more than 50 million years ago, while the history of bats is probably not very much older than this (Jepsen 1970, Springer *et al* 2001, Simmons *et al* 2008). Hence, birds had much longer time to evolve into efficient flyers than did bats. However, considering that bats have

remained relatively unchanged for the last 50 million years, the difference in age between birds and bats is unlikely to explain the differing flight adaptations among the two groups.

In this paper we will compare birds with bats and pay special attention to flight performance. These two taxa represent independent evolutionary pathways leading up to active flight, thus having solved the same (or similar) problems of aerodynamics. However, the associated adaptations are slightly different. It is therefore of interest and potentially informative to make this comparison. The idea of comparing birds with bats is not new (e.g. Jepsen 1970), but with recent research progress, we may shed some new light on this classical comparison by focusing on the implications of recent flight performance measurements. This paper is therefore not intended as an exhaustive review of the subject but represents a particular selection of some aspects of flight performance that we find interesting and where there is some quantitative information available. The presentation requires

³ Present address: Department of Mechanical and Aeronautical Engineering, University of Pretoria, 0002 Pretoria, South Africa.

Table 1. List of symbols.

Symbol	Meaning
b	Wing span
b_d	Wing span during mid-downstroke
b_u	Wing span during mid-upstroke
c	Wing chord
f	Wingbeat frequency
g	Acceleration due to gravity
r'	Normalized turn radius
r_{\min}	Minimum turn radius
AR	Aspect ratio
C_L	Lift coefficient
I	Moment of inertia
L'	Span-specific lift
M	Body mass
P	Mechanical power
P_{in}	Power input
P_{ind}	Induced power
P_{max}	Maximum power available
P_{out}	Power output
P_{par}	Parasite power
P_{pro}	Profile power
Q	Wing loading
R	Span ratio ($= b_u/b_d$)
Re	Reynolds number
S	Wing area
U	airspeed
U_{char}	Characteristic flight speed
U_{max}	Maximum sustainable speed
U_{mp}	Minimum power speed
U_{mr}	Maximum range speed
U_{∞}	Free-stream flow speed
α	Angle of attack
β	Coefficient of parasite power
γ	Coefficient of profile power
η	Energy conversion efficiency
ϕ	Angle of bank
θ	Stroke plane angle
κ	Coefficient of induced power
ν	Kinematic viscosity
ρ	Air density

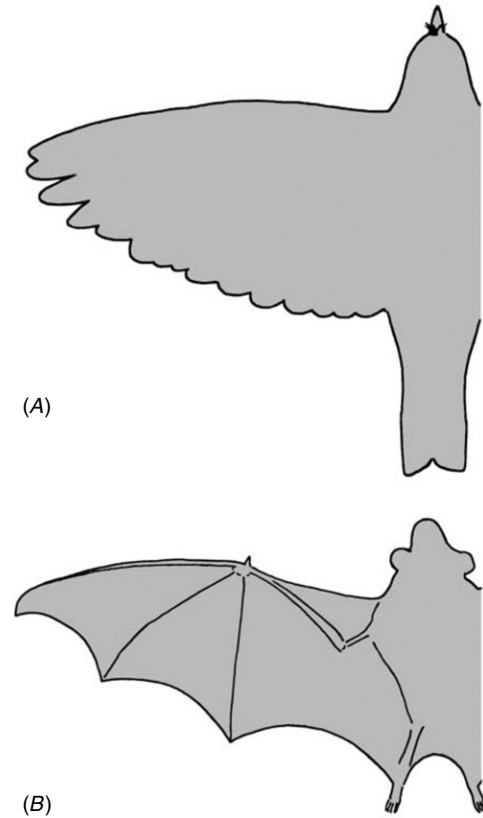


Figure 1. Top view wing planform of (A) a small passerine bird, wood warbler *Phylloscopus sibilatrix* (body mass 9 g), and (B) a nectarivorous Pall's long-tongued bat *Glossophaga soricina* (body mass 12 g). The wing semi-span ($b/2$) is shown.

the introduction of a number of symbols, which are listed and defined in table 1.

2. Functional morphology

2.1. Body size and wing morphology

The body mass range extends one order of magnitude higher in birds than bats, with the heaviest extant flying birds reaching about 15 kg, while the largest bat is about 1.5 kg. The smallest bird and bat are both about 2 g. This is an interesting difference calling for an evolutionary explanation. Since the physical constraints on flight performance are similar among birds and bats, any differences regarding the flight apparatus and wing design ought to be due to evolutionary constraints or adaptation to specific flight behaviors and ecology. Even if birds and bats show great similarities in overall wing size and shape, there are more subtle differences (Norberg 1981). On average, in bats wing span variation in relation to body mass shows near isometric scaling as $b \propto M^{0.32}$ (Norberg and Rayner 1987), while in birds it shows a more pronounced allometric scaling

as $b \propto M^{0.39}$ (Rayner 1988). The same holds for wing area scaling in relation to body mass as $S \propto M^{0.64}$ in bats and $S \propto M^{0.72}$ in birds, respectively (Norberg and Rayner 1987, Rayner 1988). Comparing wing loading ($Q = mg/S$) among similar sized birds and bats suggests that bats have lower wing loading than birds (Norberg 1986), and therefore should have a better maneuverability than birds (see below). The aspect ratio (AR) is a shape index calculated as wing span squared divided by the wing area, where high values signal long and slender wings and low values denote short and broad wings. The aspect ratio varies more among birds than bats, so that birds occupy a somewhat larger range than do bats. Among birds higher aspect ratio wings are common while bats have generally broader wings (Rayner 1988), but there are notable exceptions such as in the molossid bats with a swift-like open-air feeding niche (Norberg and Rayner 1987).

Figure 1 shows the wing outline of a small passerine bird species, wood warbler *Phylloscopus sibilatrix* and a Pallas's long-tongued bat *Glossophaga soricina* as an illustration of bird and bat wings. The bird is a rather 'standard' migratory passerine of low-aspect-ratio wings ($AR = 4.7$), while the bat is a hovering specialist ($AR = 6.3$). The bat wing has a leading edge membrane between the shoulder and first digit framed by the humerus and radius/ulna (figure 1), which can be lowered as a leading edge flap (McCormick 1995) to increase the camber (curvature) of the wing, possibly to enhance the lift

(Norberg 1990). The same function may be attributed to the narrow membrane between the second and third digits, which is kept rigid by a special arrangement of ligaments and the bending of the third digit metacarpophalangeal joint (Norberg 1969). The angle between this surface and the rest of the outer wing increases during the downstroke, thereby increasing the camber of the outer wing (R von Busse *et al* in preparation). Increased camber in bats may also be obtained by the lowering of the fifth digit. The bird wing is equipped with an alula, a small winglet attached to the 'thumb', which is thought to work as a slot increasing the lift. The primary feathers of the hand wing can also be separated, resulting in a slotted wing tip, increasing efficiency by reducing the induced drag (Tucker 1993). Note also the differing shape of the trailing edge between the bird and bat wing (figure 1). Another notable feature, in this case, is the lack of a tail in this bat species, which actually has an indentation ('negative' tail) between the legs (figure 1). However, there is a great deal of variation regarding tail morphology among bat species, where often a short tail that protrudes beyond the wing trailing edge is found (Norberg 1990).

The moment of inertia is a measure of the mass distribution along the wing and determines the resistance against accelerating the wings about an axis. Bat wings generally have lower moment of inertia than bird's wings (Kirkpatrick 1990, 1994, Thollesson and Norberg 1991, Van den Berg and Rayner 1995), which means that the mass of bat wings is concentrated nearer to the body than in birds. It is generally assumed that the work required to accelerate the wings at the beginning of the down-/upstroke is recovered as aerodynamic work when decelerating the wings at the end of half-strokes (e.g. Pennycuik (1975), Pennycuik *et al* (2000)). Hedrick *et al* (2004) estimated inertial power in cockatiels *Nymphicus hollandicus* and found support for this notion, except that all of the upstroke inertial power was not converted into aerodynamic work. In the bat *G. soricina*, Norberg *et al* (1993) estimated that during hovering inertial power dominated the total mechanical power output, while at forward speed it represented about 30%. On the basis of these limited measurements, it is unwise to draw any conclusions about possible differences between birds and bats regarding inertial power.

2.2. Flight muscles

The main flight muscle depressing the wing during the downstroke is the pectoralis muscle in both groups, but the relative mass tends to be larger in birds compared with bats (Vaughan 1970). However, bats have a set of 17 muscles involved in the wingstroke that are active either during the downstroke (4 muscles) or the upstroke (7 muscles), or that are bifunctional (6 muscles) (Hermanson and Altenbach 1983). The function of the second most important flight muscle in birds, supracoracoideus, is replaced by several smaller muscles in bats. The main function of supracoracoideus in birds is probably to rotate, not elevate as previously thought, the wing during the upstroke (Poore *et al* 1997, Tobalske and Biewener 2008). For a detailed description of flight muscle systems in both birds and bats, see Norberg (1990).

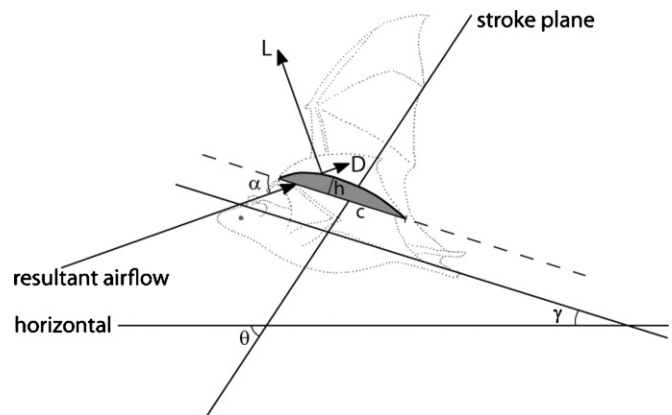


Figure 2. A bat wing and wing profile with some basic aerodynamic definitions. The symbols are as follows: L is lift, D is drag, c is chord line, h is maximum distance from the chord line to the dorsal wing surface (camber can be expressed as h/c), angle of attack (α), stroke plane angle (θ) and body tilt angle (γ).

3. Flight

The mechanics and cost of flight are traditionally studied by a few different approaches: kinematics, measurement of muscle work and recording of the action of the wings on the surrounding airflow. The interpretations of results obtained from any of these approaches should converge as they represent different descriptions of the same phenomenon. In the following paragraphs we summarize some important results obtained by these three approaches.

3.1. Kinematics

Kinematics deal with the movements of wings, body and tail in the flying animal, where typical descriptors are wingbeat frequency (f), wingbeat amplitude, stroke plane angle, wing tip path, wing twist, angle of attack and camber (figure 2). Wing twist refers to a rotation of the chord along the span allowing for a passive adjustment of the effective angle of attack changes along the span. Usually kinematics studies are limited to a few of these descriptive metrics, while those difficult to measure but of great potential aerodynamic relevance are often left out (such as angle of attack, wing camber and wing twist). Several of these parameters are beginning to become recordable in wind tunnel facilities thanks to stereo high-speed video (for example Hedrick *et al* 2002) and the use of stereo photogrammetry of surfaces for measurement of camber and wing twist.

A fundamental and easy to measure component of kinematics is the wingbeat frequency, which depends on the force required to accelerate the wing and that available from the flight muscles. Pennycuik (1996) listed variables likely to influence the wingbeat frequency (body mass, wing span and area, moment of inertia, air density and acceleration due to gravity) and performed a multiple regression analysis on field observations of a range of species to estimate the exponents conforming to a dimensionally correct combination of variables. This analysis yielded the following formula

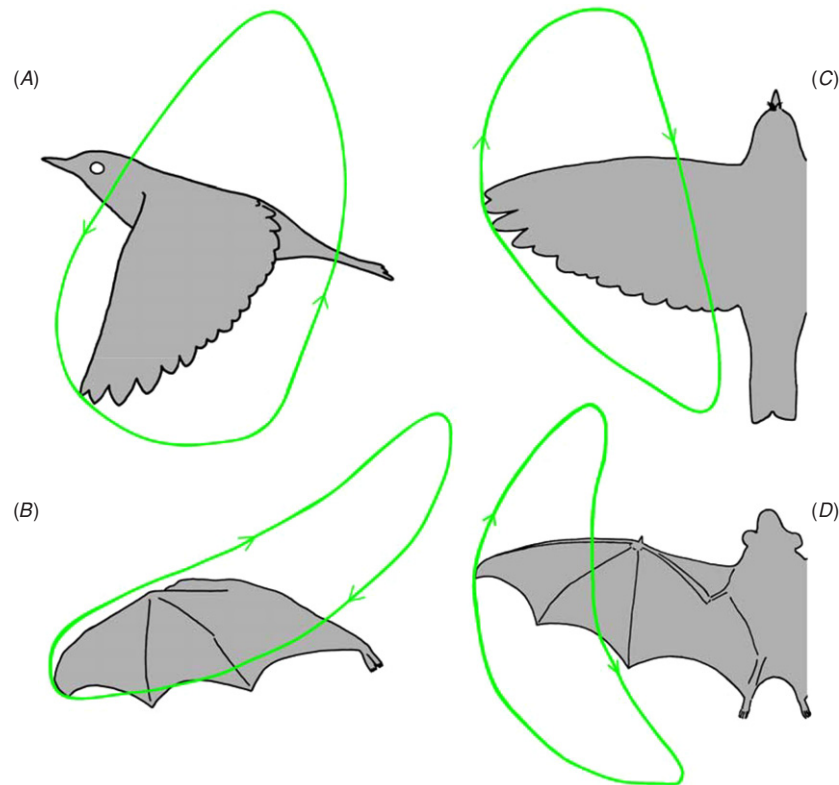


Figure 3. Typical wing tip paths during one wingbeat for a passerine bird and a small bat seen in the side view (A, B) and the top view (C, D). The arrows indicate the direction of the wing tip during the wingbeat.

for wingbeat frequency as (see table 1 for definition of the symbols)

$$f \propto (Mg)^{1/2} b^{-17/24} S^{-1/3} I^{-1/8} \rho^{-3/8}.$$

In isometrically scaled birds this formula collapses into $f \propto M^{-1/6}$, which means that f decreases as the animal gets larger when compared at some equivalent characteristic flight speed. In birds this formula enjoyed a good fit with measurements of free-flying birds, and also in bats there is a negative slope across a range of body masses (Bullen and McKenzie 2002). The data available do not suggest that f differs much when comparing birds and bats of the same size.

Wingbeat frequency may also change within an individual as it changes mass, which occurs during fuel accumulation before migratory flight or hibernation, during pregnancy (bats) or egg-laying (birds), or when flying at different airspeeds. The expected relationship of mass change within an individual at some equivalent characteristic speed is $f \propto M^{1/2}$ (Pennycuick 1996), which was the case also in a real thrush nightingale *Luscinia luscinia* (Pennycuick *et al* 1996). Artificial loads added to long-eared bats *Plecotus auritus* yielded increased wingbeat frequency (Hughes and Rayner 1991), also in accord with the prediction.

The wingbeat frequency determines the rate of work by the flight muscles. However, the variation of f with airspeed is problematic since the mechanical work depends on other factors as well. Variation of f according to a U-shaped function in relation to speed (Pennycuick *et al* 1996, Park *et al* 2001) has been interpreted as reflecting the variation

in power required to fly (see below). However, estimated speeds of minimum power output and speed of minimum f did not coincide in two bird species (Tobalske *et al* 2003a), and so birds may modulate power in other ways than only changing f . Several bird species show rather constant f across airspeeds (Rosén *et al* 2004, Hedenström *et al* 2006, Tobalske *et al* 2007), while bats mainly show a decrease in f from hovering ($U = 0 \text{ m s}^{-1}$) and with increasing airspeed (Schnitzler 1971, Bullen and McKenzie 2002, Lindhe Norberg and Winter 2006), without an increase in f at high speeds.

The wing trajectory throughout a wingbeat determines the aerodynamic force production mainly via the wing planform, angle of attack and local airspeed. Therefore, much effort has been invested in the description of wingbeat patterns. The standard approach is high-speed stereo-photogrammetry of animals flying in a wind tunnel to achieve 3D coordinates of morphological or artificial landmarks, such as the wing tip, the wrist and wing root (Hedrick *et al* 2002). The dynamics of camber, the chordwise curvature of the wing, has rarely been obtained (but see Bilo (1971a) and Pennycuick (1971) for exceptions). There are plenty more studies of birds than bats across a range of speeds, and therefore we will only mention some characteristic differences between birds and bats.

The wing-tip path as seen from the side typically follows an ellipsoid curve, where the downstroke path is anterior to that of the upstroke in birds and vice versa in bats (figure 3), although at certain speeds the wing tip may follow nearly the same path on down-/upstroke. Even if not generalizable to all species of bats and birds, this pattern is consistent

with observations in the bats *Plecotus auritus*, *G. soricina* and *Leptonycteris curasoae* (Norberg 1975c, Lindhe Norberg and Winter 2006, own unpublished data), and in several bird species including *Columba livia*, *Pica pica*, *Hirundo rustica* and *Selasphorus rufus* (Tobalske and Dial 1996, Park *et al* 2001, Tobalske *et al* 2007). During the downstroke, the wing tip moves downward and forward relative to the body. During hovering and slow forward flight the stroke plane (the direction of the long axis of the ellipsoid; figure 3) is tilted at a rather small angle or even aligned with the horizontal, while this angle increases with increasing airspeed until the stroke plane becomes almost perpendicular to the horizontal at fast speeds. During the upstroke, at slow speed, the wing tip is brought backward in relation to the body, and below a certain speed this speed is higher than the forward flight speed resulting in a stroke-reversal or ‘backward-flick’ (Brown 1951, Norberg 1975c, Tobalske *et al* 2003a, 2003b, Lindhe Norberg and Winter 2006). This reversal is most pronounced at the outer (hand) part of the wing, and an aerodynamic force, generating thrust and weight support, may result due to the local speed at the wing (Bilo 1971a). During hovering, birds may separate their primaries to allow airflow through, resulting in a ‘feathered’ (inactive) upstroke (Norberg 1975a), while in hummingbirds having relatively stiff wings the upstroke produces a significant amount (25%) of total weight support (Warrick *et al* 2005). Bats do not have the option of making the lifting surface inactive to the same degree as birds, but employ a lifting upstroke with the wing inverted and appropriate camber of the wing membrane in hover and slow forward speed (Norberg 1975b, Helvesen 1986, Aldridge 1987b, Hedenström *et al* 2007). The angle of attack varies from large positive to negative during a stroke cycle (Hedrick *et al* 2002), with particularly high values in hummingbirds and bats (Norberg 1975b, Tobalske *et al* 2007), which are beyond the values where flow separates in fixed wings. The house sparrow *Passer domesticus*, however, showed low local angles of attack consistent with quasi-steady-state aerodynamics throughout the stroke cycle (Bilo 1971a, 1971b). At cruising speeds the local angle of attack of the inner wing is typically positive at all times for birds (Bilo 1971a, 1971b, Hedrick *et al* 2002), which is consistent with continuous force production.

The span ratio ($R = b_u/b_d$) measures the degree of wing flexing during the upstroke and is proportional to the asymmetry in force production between downstroke and upstroke. In hummingbirds $R \approx 1$ and decreases marginally with airspeed, while some non-passerine species also show decreasing trends but starting at values about 0.6–0.8 at slow airspeed (Tobalske *et al* 2007). This is also the case for the barn swallow *Hirundo rustica* and swift *Apus apus* (Park *et al* 2001, Henningsson *et al* 2008), which are species of relatively high-aspect-ratio wings. In other passerines, where bounding or intermittent flight is common, R shows increasing trends from values about 0.2–0.4 at slow airspeed (Rosén *et al* 2004, Tobalske *et al* 2007), suggesting an increasing importance of the upstroke as a generator of weight support as flight speed increases. In the bat *G. soricina*, R is relatively high at 0.6–0.7 with no or little change across airspeeds (Lindhe Norberg and Winter 2006, M Wolf *et al* unpublished data).

3.2. Aerodynamics

The relative contribution of viscous and inertial forces can be characterized by a dynamic similarity index, which in fluid dynamics is the Reynolds number defined as

$$Re = \frac{Uc}{\nu}, \quad (1)$$

where U is speed relative to the medium (air in our case), c is a characteristic length (typically the mean wing chord) and ν is the kinematic viscosity. Re varies between approximately 10^3 to 10^5 in birds and bats.

When viewed in chordwise cross-section, wings of birds and bats show an asymmetric shape with a convex (cambered) dorsal side and a concave ventral side (figure 2), with a higher degree of camber in bats due to their thin skin membrane. The significance of this shape (camber) of bird wings was recognized already by Lillienthal (1889) (see Liu *et al* (2006) for more recent quantitative measurements). When the wing is positioned at some angle of attack (α) with respect to the free-stream velocity (U_∞), it will generate a lift force normal to U_∞ . The capacity of the wing to generate lift is described by the non-dimensional lift-coefficient (equation (5a) for an implicit definition). For fixed wings under quasi-steady conditions, i.e. as when mounted in a wind tunnel at a fixed α and allowing initial transient phenomena to vanish, the maximum lift-coefficient at animal-like Reynolds numbers is about 1.6 (Laitone 1997, Lyon *et al* 1997 Rosén *et al* 2007, Spedding *et al* 2008). In a gliding jackdaw *Corvus monedula* and a gliding squirrel *Glaucomys volans*, the estimated lift coefficient was higher than this value at 2.1 (Rosén and Hedenström 2001, Bishop 2006). In animal flapping, flight steadiness is never the case since the wings rotate, flex, twist and deform continuously throughout the stroke cycle. Therefore, it is notoriously hard to estimate or measure instantaneous forces of flapping animal flight.

One approach, the blade-element method, for obtaining the lift throughout a whole wingbeat cycle is to divide the wing into chordwise strips and calculate the lift and drag for each strip separately at all stages of the wingbeat (Weis-Fogh 1972, Norberg 1990). The results from each strip are then summed along the wing span and instances of the stroke cycle to obtain the total lift and drag. Although this method is rather cumbersome, it has nevertheless been applied to some birds and bats (e.g. Bilo 1971a, Weis-Fogh 1972, Norberg 1975a, Watts *et al* 2001). When applied to a hovering pied flycatcher *Ficedula hypoleuca*, the average lift coefficient required to support the weight was estimated to 5.3 (Norberg 1975a), which violates the quasi-steady assumption. Hence, animal wings can develop lift forces by some unsteady aerodynamic effects, of which there are a few alternatives (Sane 2003, Lehmann 2004).

According to wing theory, the lift per unit span can be written as

$$L' = \rho U \Gamma, \quad (2)$$

where Γ is the circulation associated with lift. Kelvin’s theorem says that when lift (hence the associated circulation) changes on a wing, a transverse vortex will be shed into

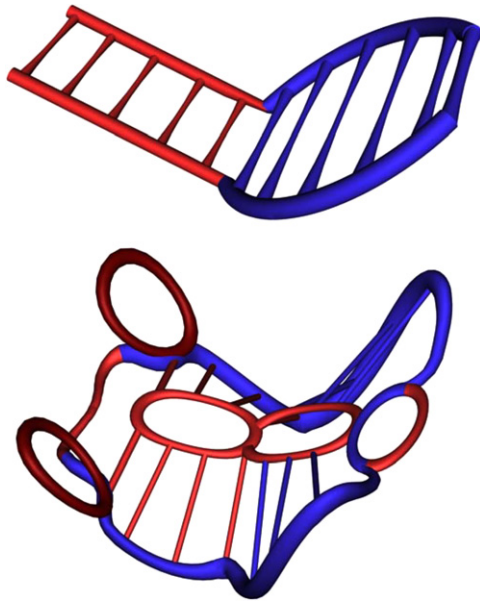


Figure 4. Cartoon representation of wake geometry for (A) bird and (B) bat. The blue colour refers to structures generated during the downstroke, while red colour indicates structures generated during the upstroke. The thickness of the tubes illustrates in schematic the magnitude of the circulation. Based on Spedding *et al* (2003) and Hedenström *et al* (2007).

the wake of the same circulation but of opposite sign, corresponding to the change of lift. These vortices shed into the wake can be studied by an experimental approach, digital particle image velocimetry (DPIV, Raffel *et al* 1997), by which the velocity field can be visualized and measured using laser illuminated smoke particles. Circulation is obtained by integrating the vorticity, ω , which is a measure of the direction and magnitude of the local rotation of the fluid and defined as twice the local angular velocity, over a surface S . Formally circulation is thus obtained as $\Gamma = \int_S \omega \cdot dS$. Information about the geometry, vorticity distribution and circulation allows inferences about the time history and magnitude of the aerodynamic forces. This method has proved useful when studying freely flying birds and bats in wind tunnels (Spedding *et al* 2003, Warrick *et al* 2005, Hedenström *et al* 2007).

In slow flight ($\sim 4\text{--}5\text{ m s}^{-1}$) birds generate vortex loops from the downstroke, while the upstroke is more or less aerodynamically inactive. At cruising speeds ($\geq 7\text{ m s}^{-1}$) there are trailing wing-tip vortices throughout the down- and upstroke with low-amplitude cross-stream vortices shed throughout the stroke cycle (figure 4(A)). Although only two bat species have been studied so far (*G. soricina*, *L. curasoae*; Hedenström *et al* 2009), the results show some striking differences between birds and bat wakes (figure 4). A main difference is that bats appear to have a stream-wise vortex shed also from the wing base, giving rise to a vortex loop being shed behind each wing (figure 4(B)). Also, at the transition between up-/downstroke smaller vortex loops are shed from the outer wing (seen as red loops in figure 4(B)), inducing an upward directed flow and therefore some small negative lift (Johansson *et al* 2008).

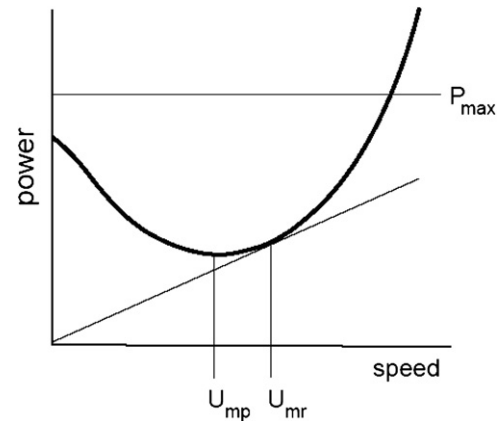


Figure 5. A generic power curve (power as a function of airspeed) for a vertebrate with speeds of minimum power (U_{mp}) and maximum range (U_{mr}) indicated. P_{max} is the maximum power available from the flight muscles. Based on Pennycuik (1975).

The circulation of wake vortices varies continuously from high values at slow speed to low values at high speed in both birds and in the bat *G. soricina* (Rosén *et al* 2007, Hedenström *et al* 2007), suggesting a smooth change in aerodynamic force generation across the speed range. Measures of normalized circulation can be interpreted as time-averaged lift coefficients, and the values suggest that time-averaged C_L exceed 2 in birds and even higher in *G. soricina* at slow ($1\text{--}3\text{ m s}^{-1}$) forward speed (Hedenström *et al* 2007, Rosén *et al* 2007). These observations confirm previous estimates deduced from kinematics (Norberg 1975a, 1975b). It therefore appears that birds and bats use some high-lift mechanism at slow speeds (see Lehmann (2004)). Recent experiments with *G. soricina* demonstrate that a leading edge vortex is attached throughout most of the downstroke, contributing about 40% of the lift generated (Muijres *et al* 2008). An equivalent has not yet been found in birds, but the appropriate experiments have not been conducted either.

3.3. Power required for flight

3.3.1. Power curve. Flight mechanical theory suggests a functional relationship between (mechanical) power required to fly (P) in relation to airspeed (U) according to the equation

$$P(U) = P_{ind} + P_{par} + P_{pro}, \quad (3)$$

where the three terms on the right-hand side represent induced, parasite and profile power, respectively (figure 5). Induced power arises due to the generation of trailing wing-tip vortices, parasite power is due to the drag of the body and profile power is due to the drag of the wings. Each of these terms vary according to airspeed in different ways, with $P_{ind} = \kappa U^{-1}$, $P_{pro} = \beta U^3$ and $P_{par} = \gamma U^3$, with κ, β, γ representing different morphological and physical properties of the wings and the air combined into these constants (Pennycuik 1975, Hedenström 2002). Even if P_{pro} strictly is an increasing function of airspeed, Pennycuik (1975) noted that as the local speed increases over the wing, the lift coefficient and associated profile drag coefficient decrease, thereby canceling

the effect since profile power is a function of both speed and profile drag coefficient. Therefore, P_{pro} is usually taken as nearly constant in the range of cruising speeds of birds (Pennycuik 1975, 2008). The sum of the three power terms result in an overall U-shaped relationship between mechanical power required to fly and airspeed (figure 5). Note that inertial power is neglected in this case (Pennycuik 2008). Now, how does this theory fare when confronted with data?

A range of different approaches have been attempted to measure the power-speed relationship in birds, but only one method has been applied to bats. The main methods can be divided into three categories: (I) metabolic measurements, (II) measuring forces applied by flight muscles and deriving a work loop and (III) measuring momentum change in the wake. Metabolic measurements can be made by some different approaches, such as analyzing oxygen extraction (or CO₂ production) sampled by attaching a mask to the flying animal (Tucker 1968, Winter *et al* 1998). This method requires tubing to lead the air to the gas analyzer with obvious problems of restricting the movement and increased drag of tubes and mask. An alternative approach is the doubly labeled water method (Kvist *et al* 2002, Engel *et al* 2006), which requires comparatively long continuous flights of several hours. A main problem with metabolic measurements is that they actually measure the whole-animal metabolic rate (or power input; P_{in}), while the mechanical power curve of equation (3) refers to mechanical power output (P_{out}). With the additional assumption of a constant energy conversion efficiency ($\eta = P_{\text{out}}/P_{\text{in}}$), metabolic measurements should however reflect the overall shape of the mechanical power curve. This method has been used a number of times on birds in wind tunnels with mixed results (Butler and Bishop 2000). A few studies have shown a clear U-shape between flight metabolic rate and airspeed (Tucker 1968, Rothe *et al* 1987, Bundle *et al* 2007), while others show a more or less flat relationship (e.g. Engel *et al* 2006). As mentioned before, a potential problem could be non-invariant conversion efficiency, but this would require a reduced efficiency at intermediate speeds, which are the speeds where birds most frequently fly, for the metabolic curve not to be U-shaped. However, the characteristic U-shape has occurred on so many occasions that its existence should not be disputed. In bats only four species have been studied in wind tunnels over a range of speeds and they all show, if not acute, at least shallow U-shaped relationships between metabolic rate and airspeed (Thomas 1975, Carpenter 1986). The only other measurements of flight metabolic rate refer to small bats flying in a room at unknown speed (Speakman and Racey 1991, Winter and Helsen 1998). In one species, *G. soricina* (body mass 11.9 g), the metabolic rate was measured at 1.88 W by means of fast-response respirometry when hovering ($U = 0 \text{ m s}^{-1}$) at a feeder, which was only 1.2 times higher than at (unknown) forward flight speed (Winter 1998). This suggests a shallow left-hand side of a U-shaped power curve.

The second (II) approach uses either surgically attached strain gauges to measure force variation applied by the flight muscles to the humerus (Dial *et al* 1997, Hedrick *et al* 2003, Tobalske *et al* 2003a) or sonomicrometry for measuring muscle shortening during contraction in combination with

in vitro calibration (Askew and Ellerby 2007). The force-length relationship gives a ‘work-loop’ representing net positive work (Biewener 2003), which multiplied by wingbeat frequency gives power. These measures are thought to be close to mechanical power output and hence should be more suitable for testing the theory. The few studies carried out thus far on birds show clearly U-shaped power curves (Tobalske *et al* 2003, Hedrick *et al* 2003, Askew and Ellerby 2007)

Finally, the third (III) approach would quantify the rate of kinetic energy actually deposited as wake vortices (see above), which at least in theory should match the prescribed power output from equation (1). There are still many problems with this approach, such as a correct 3D description of the wake topology and an accurate measurement of the momentum transfer, why this method still needs refinement before it can deliver a mechanical power curve.

3.3.2. Mass-dependent power. Power required to fly is mass dependent, and comparing a series of isometrically scaled ideal birds (*sensu* Pennycuik 1975), it can be derived that

$$P \propto M^{7/6}, \quad (4)$$

where M is body mass and P is power output as before. The power required for an ideal bird is the sum of the induced and profile powers, which is the power required to fly having a perfectly streamlined body supported by an ideal actuator disk, hence neglecting any drag from flapping the wings. Thus, if regressing log-transformed data of P against M (or plotting data in a diagram with logarithmic axes), the slope will represent the exponent of proportionality (4). In birds such analyses have been done on a number of occasions using different data selections from the literature, where a recent analysis obtained an exponent of 0.87 based on literature data (McWilliams *et al* 2004). This exponent was significantly lower than the prediction of 7/6. Using a subset of published studies of laboratory measurements only (with the majority being wind tunnel measurements) yield $P = 56.0 M^{0.75}$ ($N = 20$) (figure 6), which is also significantly lower than 7/6 (Hedenström 2008). The few studies of bats refer to both hovering and forward flight (figure 6), but there was no significant difference between hovering and forward flight (Winter and Helsen 1998). The combined hovering and forward flight data yield $P = 55.7 M^{0.80}$ ($N = 13$) for bats, displaying an exponent significantly lower than 7/6 just as in birds. However, comparing the body mass flight power scaling among birds and bats shows almost identical relationships (figure 6), and the small differences between groups in both slope and intercept are not significant statistically ($P > 0.05$).

Similarly, it can be predicted that power required to fly in relation to mass changes within an individual is expected to be

$$P \propto m^{7/4},$$

which may be expected during periods of pregnancy, fuel accumulation, or fuel consumption during long-distance migratory flights. Only few studies have addressed this question, one in bats and two in birds, with the result that the scaling exponent did not differ from that expected in pregnant *G. soricina* (Voigt 2000), while it was significantly less than

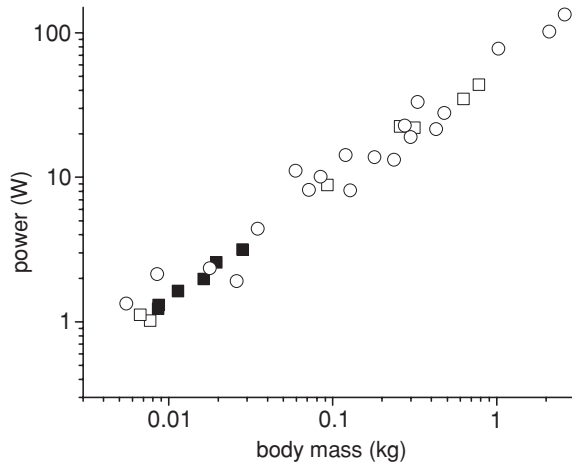


Figure 6. Metabolic rate in relation to body mass for birds and bats. Open circles show measurements of birds, filled squares show measurements obtained during hovering in bats and open squares refer to forward flight in bats. Regressions on \log_e -transformed data were for birds (\pm SE): $\ln P = 4.02 (\pm 0.10) + 0.75 (\pm 0.040) \ln M$, and for bats $\ln P = 4.02 (\pm 0.048) + 0.80 (\pm 0.013) \ln M$. Data from Thomas (1975), Carpenter (1985, 1986), Speakman and Racey (1991), Winter and Helversen (1998), and Hedenström (2008). The following species were included; birds: *Anser indicus*, *Branta leucopsis*, *Anas crecca*, *A. rubricaps*, *Melospittacus undulatus*, *Colibri thalassinus*, *C. coruscans*, *Columba livia*, *Calidris canutus*, *Larus atricilla*, *L. delawarensis*, *Falco sparverius*, *F. tinnunculus*, *Corvus ossifragus*, *C. cryptoleucus*, *Luscinia luscinia*, *Sturnus vulgaris*, *S. roseus*, *Hirundo rustica*, *Coccythraustes vespertinus*; bats: *Phyllostomus hastatus*, *Pteropus gouldii*, *P. poliocephalus*, *Eidolon helvum*, *Hypsognathus monstrosus*, *Pipistrellus pipistrellus*, *Plecotus auritus*, *Choeronycteris mexicana*, *Glossophaga mexicana*, *G. commissarisii*, *G. longirostris*, *G. soricina*, *Hylonycteris underwoodi*, *Leptonycteris curasoae*.

expected in red knots *Calidris canutus* at different fuel loads but not different from the expected value in a thrush nightingale *Luscinia luscinia* (Hedenström 2003a).

To conclude, even if based on limited data, the data available do not suggest that flight metabolic rates differ to any significant degree between birds and bats.

3.4. Flight performance

3.4.1. Speed. At steady level flight, the lift balances the weight according to the following equation:

$$Mg = L = \frac{1}{2} \rho S C_L U^2, \quad (5a)$$

which after rearrangement can be written as

$$U = \sqrt{\frac{2Mg}{S\rho C_L}}, \quad (5b)$$

where symbols are as defined in table 1. From this equation, it is straightforward to derive that, in a sequence of geometrically similar birds or bats, the airspeed is expected to vary according to

$$U_{\text{char}} \propto M^{1/6}, \quad (6a)$$

or

$$U_{\text{char}} \propto Q^{1/2}, \quad (6b)$$

where U_{char} is some characteristic speed and $Q = Mg/S$ is the wing loading, which is the only variable in equation (5b) for constant ρ and C_L flight. Airspeed may vary in the same species depending on the ecological context, such as display versus migratory flight (Hedenström and Ålerstam 1996), but cruising flight during migration or commuting flight between a roost and foraging areas should be near the maximum range speed U_{mr} . However, effects such as differences between energy and time-selected migration, climbing or descending flight, load lifting and other situations should modify the airspeed selected (Hedenström and Ålerstam 1995).

Variation of airspeed among birds is only partially explained by body mass and wing loading, with significant effects also from wing shape (aspect ratio) and phylogenetic group (Ålerstam *et al* 2007). Cruising airspeeds among a set of 138 species measured with radar varied from 6.7 m s^{-1} to 23.6 m s^{-1} across a range of body masses from 9 g to 10 kg (Ålerstam *et al* 2007). The overall scaling equation based on body mass was $U = 15.9 M^{0.13}$ (Ålerstam *et al* 2007), with a scaling exponent significantly lower than the expected exponent of $1/6$ (~ 0.17). Also, the scaling exponent for the relationship against wing loading was lower than the expected value of 0.5 at $U = 4.3 Q^{0.31}$ (Ålerstam *et al* 2007). Comparable high-quality data for freely flying bats are not available, with one study reporting speeds from four species, ranging in mass between 9 g and 24 g measured in a flight corridor, resulting in the scaling equation $U = 20 M^{0.23}$, with an exponent not significantly different from the expected value of $1/6$ (Winter 1999). The range of average speeds for these bats was $6.5\text{--}8.6 \text{ m s}^{-1}$, while the top speed of *G. soricina* reached 10.5 m s^{-1} (Winter 1999). However, another study of freely flying bats across the size range $0.05\text{--}0.7 \text{ kg}$ yielded a speed range $4.7\text{--}8.3 \text{ m s}^{-1}$ and the scaling equation $U = 8.4 M^{0.08}$ (Bullen and McKenzie 2002), which is significantly lower than the expected $1/6$. A study of commuting bats over distances up to 30 km obtained a mean speed of 8.2 m s^{-1} (Sahley *et al* 1993), while high-altitude free-tailed bats *Tadarida brasiliensis mexicana* moved at 11.1 m s^{-1} (Williams *et al* 1973). Measurements from larger bats in the field are absent, whereas a wind tunnel study of *Pteropus gouldii* at body mass 0.78 kg and wearing a respirometry mask yielded a maximum speed of 10 m s^{-1} (Thomas 1975). On balance, the flight speed of bats is much less studied than those of birds, but the few data available for free-flying bats suggest that they generally fly slower than birds. This conclusion should however be considered as provisional before more data on bat flight speeds have been obtained.

3.4.2. Maneuvering. One aspect of maneuverability is the ability to make a tight turn, often a deciding feat for an aerial hawk or when escaping from an attacking predator (Hedenström and Rosén 2001). When observing foraging bats using a bat detector one can often see them making a sharp turn simultaneously as they emit a ‘feeding buzz’, i.e. the accelerated echolocation calls as they detect and close in on the targeted prey. The minimum turn radius in gliding flight at a given angle of bank (ϕ) is

$$r_{\text{min}} = \frac{mg}{S} \cdot \frac{2}{\rho g C_L \sin \phi}, \quad (7)$$

where C_L is the lift coefficient and other symbols as defined in table 1. The absolute minimum turn radius is thus obtained when banking at 90° (when $\sin \phi = 1$). From equation (7), it is clear that wing loading ($Q = mg/S$) determines turn radius, which was experimentally confirmed among small bat species (Aldridge 1987b). Since bats have lower wing loading than birds of the same body mass (Norberg 1986), they should be able to make tighter turns than birds, but finding quantitative and comparable data is not simple. If one calculates a normalized turning radius, $r' = r/b$, then $r' \approx 1$ for both birds and bats in right angle turns (Warrick and Dial 1998, Hedrick and Biewener 2007, Iriarte-Díaz and Swartz 2008), but $r' \approx 0.1$ for smaller bats confronted with 360° (Aldridge 1987b). The number of wingbeats required to make a turn also appear to depend more on the experimental configuration rather than showing any systematic difference between birds and bats. The minimum turn radius also depends on the maximum achievable lift coefficient and bats have been shown to be able to increase C_L substantially at low speed using unsteady mechanisms (Muijres *et al* 2008). As previously noted, birds have yet to be tested in this.

3.4.3. Gliding and soaring flight. Gliding flight performance is conveniently recorded as the ratio between forward (U) and vertical velocity (U_z), which is the same as the ratio between lift and drag, $L:D$ (Pennycuik 1975). If $L:D$ is reasonably high, the use of thermal convection or slope lift for cross-country soaring becomes an alternative strategy to flapping flight. The reason is that metabolic rate in gliding flight is much less than in flapping flight, and even if the cross-country speed is reduced during soaring, the energy savings outweighs the loss in speed (Pennycuik 1975). In larger birds, soaring on migration may even be the best strategy from a time-minimization perspective (Hedenström 1993). Cross-country soaring is most common among relatively large birds, such as many raptors and storks. Also corvids show gliding flight performance on par with that of raptors, such as for example the jackdaw *Corvus monedula* (body mass = 0.18 kg, $AR = 6.0$) with a maximum $L:D$ of 12.6 (Rosén and Hedenström 2001). The slightly smaller dog-faced bat *Rousettus aegyptiacus* (body mass = 0.12 kg, $AR = 5.4$) had an estimated maximum $L:D$ of 6.8 in a wind tunnel (Pennycuik 1971). Hence, the bat showed inferior gliding flight performance compared with the jackdaw, which is probably explained by the jackdaw's higher AR and its slotted wing tips. It should be noted that this comparison between two species may not adequately represent a general difference between birds and bats, but until more data are obtained this is the only comparison available. The gliding flight performance in large bats may approach that of birds, as indicated by their wing morphology and calculated glide performance (Lindhe Norberg *et al* 2000).

4. Summary of comparisons

We have described a number of flight-related properties in birds and bats. In several cases, there is a lack of relevant quantitative data for one of the groups, in most cases for bats. It appears that studies of bat flight are now being published

Table 2. Comparison of some selected properties between birds and bat as described in the main text. '=' indicates that birds and bats show similar values and '≠' indicates that they differ in this property.

Property	Birds	=/≠	Bats
Body mass (kg)	0.002–15	≠	0.002–1.5
Aspect ratio	3–15	≈	5–14
Wing loading ($N\ m^{-2}$)	4–160	≠	4–60
Span ratio	0.2–1	≠	~0.7
Wing-tip path ^a	Anticlockwise	≠	Clockwise
Vortex wake	See figure 5(A)	≠	See figure 5(B)
High lift ($C_L > 1.6$)	yes	=	Yes
Power curve	U-shape	=	U-shape
Power scaling (W)	$56 M^{0.75}$	=	$55.7 M^{0.80}$
Flight speed ($m\ s^{-1}$)	$15.9 M^{0.13}$	≠	$8.4 M^{0.08}$

^a As seen from the side along the span.

at an increased rate (e.g. Tian *et al* 2006, Hedenström *et al* 2007, Iriarte-Díaz and Swartz 2008, Johansson *et al* 2008, Muijres *et al* 2008), and hopefully some of the unbalanced comparisons will become more meaningful in the near future. As a summary and to provoke further discussion and research a selection of comparisons are shown in table 2.

5. Discussion

Birds and bats exhibit many convergent adaptations to aerial locomotion, but also some notable differences due to their independent evolutionary history and perhaps diverging ecological niches. Bats occupy a reduced morphological range compared with birds and pterosaurs (Rayner 1988, McGowan and Dyke 2007), suggestive of some factor(s) constraining the morphological design. As bats and birds evolved flight independently, we may ask if they acquired flight along the same evolutionary scenario or differently. The two competing theories about evolution of vertebrate flight are the 'trees-down' and 'ground-up' scenarios, where the trees-down scenario is usually thought of as a route via an initial gliding stage. The debate about these questions has a long history, but recent fossil records of feathered dinosaurs (Ji *et al* 1998), believed to be close relatives to the bird ancestor, suggest that birds evolved flight according to the ground-up scenario (see Hedenström (2002) for a summary). Dial (2003) proposed an alternative hypothesis for the evolution of avian flight by observing that some precocial species perform a 'wing-assisted incline running' to reach elevated refuges. This behavior directs the aerodynamic force toward the substrate and thereby improves adherence. Also juveniles show this behavior before having attained flight capacity to improve their climbing performance, and Dial (2003) suggests that it could represent an evolutionary pathway leading to powered flight. However, bats probably evolved flight according to the trees-down scenario, presumably with an intermediate gliding flight stage (Simmons and Geisler 1998). A spectacular fossil of the most primitive bat found thus far indicates that bats evolved flight before they acquired echolocation (Simmons *et al* 2008) because ear morphology suggests that this bat lacked an ability to echolocate.

Both birds and bats must be considered as evolutionary relatively successful vertebrate groups with more than 10 000 and 1100 species, respectively, with bats representing 20% of all mammal species. Flight is the common attribute that likely facilitated the dispersal and spread by birds and bats into new continents and habitats where further ecological adaptations and diversification could take place.

Locomotion by powered flight is associated with a very high metabolic rate that comes with morphological and physiological adjustments, such as high affinity for oxygen uptake by the blood and energy accumulation. For long-distance uninterrupted flight, fat is the best energy substrate available as it gives the highest mass-specific energy density of available substrates (Jenni and Jenni-Eiermann 1998). In birds fat metabolism is turned on very soon after the commencement of flight (Jenni-Eiermann *et al* 2002), ensuring efficient energy usage. Bats likewise accumulate fat as energy reserve before periods of hibernation (e.g. Davis 1970, Kunz *et al* 1998) or migration (Fleming and Eby 2003). Hence, fat is the currency that transports the animal in space (migration) or time (hibernation). Why hibernation is the dominating strategy in bats and migration in birds for escaping periods of resource scarcity in temperate regions remains a challenging research question.

Long-distance migration is well developed in many bird species and is associated with adaptations for efficient migration (Alerstam *et al* 2003), involving fast fuel (fat) accumulation, efficient flight and navigation. Even if flight is very expensive measured as metabolic rate, the cost of transport ($C = P/mgU$) evaluates favorably when compared with locomotion by running (e.g. Pennycuik 1992). Hence, it is relatively cheap to move unit mass over unit distance when flying mainly because of the relatively high speed compared with running. Swimming is however cheaper still (Pennycuik 1992). Both the proportion of species that migrates and the migration distance in those species are lower in bats than in birds, and there are no examples of long-distance inter-continental migrations among bats (Fleming and Eby 2003). A part explanation for this difference could be found in the cost of transport (C), which likely is higher in bats due to their lower flight speeds when compared with birds. It was however found above that the flight metabolic rate did not differ much between birds and bats, but in this comparison the flight speed was not controlled for. It may be that bats generate more drag than birds, for example as a consequence of their more complex vortex wakes (Hedenström *et al* 2007), protruding ears due to their echolocation system and perhaps due to generally less streamlined bodies than birds. This would select for reduced flight speeds, because drag increases with speed squared, and hence an increased overall cost of transport. Bats, on the other hand, may have an enhanced maneuverability than birds and are adapted for slow flight aerial hawking for insects (e.g. Jones and Rydell 2003).

There are many other parallels between birds and bats that are related to the 'flight syndrome', i.e. the suite of adaptations related to aerial locomotion. These include wing morphological adjustments in birds and bats of different flight ecology, such as higher aspect ratio wings in migrants and

open-air foragers (e.g. Norberg and Rayner 1987, Mönkönen 1995, Fleming and Eby 2003). Another feature refers to the amount of DNA in cells, which has been found to be reduced in birds and bats compared with other animals (Hughes and Hughes 1995, Van den Bussche *et al* 1995). It has been suggested that there is a physiological connection and that flight favors a reduced amount of DNA in cells. However, although this characteristic is correlated with an aerial life-style, flightless dinosaurs also had a low DNA content in cells (Organ *et al* 2007). Therefore, the causality of this correlation needs to be better understood.

Birds' feathers become worn by wear and tear, and the feather shafts loose flexural stiffness and aerodynamic efficiency by repetitive bending during wing flapping (Weber *et al* 2005). This is the reason why birds must replace their flight (and body) feathers at regular intervals by a process called moult, which is energetically costly due to synthesis of new feather material and because flight capacity is reduced due to temporary wing gaps (Hedenström 2003b). In most birds, moult does not overlap with other energetically demanding processes such as breeding and migration. Hence, the design option of having feathers made of dead keratinous material that must periodically be renewed has life-history consequences for birds. In bats, the skin membrane is maintained and repaired continuously, presumably with a much lower impact on the scheduling of life-history events in the annual cycle. The ecological significance of this difference between birds and bats remains however little understood.

Can one say that birds are better adapted for flight than bats or vice versa? We do not think so because birds and bats have evolved completely independently to the present point. Overall, they are adapted to different ecological tasks, limited mainly by different evolutionary constraints, but with ample overlap concerning, for example, foraging technique and migration. Hence, there are both convergences and divergences regarding their design. A comparative study of bird and bat adaptive design in their evolutionary and ecological context is far from complete, as should be clear from the present paper. However, with rapid methodological developments regarding aerodynamic studies, there are hopes for improved analysis regarding, for instance, the bird and bat wing designs and their aerodynamic performances.

Acknowledgments

This manuscript benefited from constructive comments from two referees. This study was supported by the Swedish Research Council, and AH's position as a Royal Swedish Academy of Sciences Research Fellow is supported by a grant from the Knut and Alice Wallenberg Foundation.

References

- Aldridge H D J N 1987a Body accelerations during the wingbeat in six bat species: the function of the upstroke in thrust generation *J. Exp. Biol.* **130** 275–93

- Aldridge H D J N 1987b Turning flight of bats *J. Exp. Biol.* **128** 419–25
- Alerstam T, Hedenström A and Åkesson S 2003 Long-distance migration: evolution and determinants *Oikos* **103** 247–60
- Alerstam T, Rosén M, Bäckman J, Ericson P G and Hellgren O 2007 Flight speeds among bird species: allometric and phylogenetic effects *PLoS Biol.* **5** e197 doi: 10.1371/journal.pbio.0050197
- Askew G N and Ellerby D J 2007 The mechanical power requirements of avian flight *Biol. Lett.* **3** 445–8
- Biewener A A 2003 *Animal Locomotion* (Oxford: Oxford University Press)
- Bilo D 1971a Flugbiophysik von Kleinvögeln: I. Kinematik und Aerodynamik des Flügelabschlages beim Haussperling (*Passer domesticus* L.) *Z. Vergl. Physiol.* **71** 382–454
- Bilo D 1971b Flugbiophysik von Kleinvögeln: II. Kinematik und Aerodynamik des Flügelaufschlages beim Haussperling (*Passer domesticus* L.) *Z. Vergl. Physiol.* **76** 426–37
- Bishop K L 2006 The relationship between 3-D kinematics and gliding performance in the southern flying squirrel, *Glaucomys volans* *J. Exp. Biol.* **209** 689–701
- Brown R H J 1951 Flapping flight *Ibis* **93** 333–59
- Bullen R D and McKenzie N L 2002 Scaling bat wingbeat frequency and amplitude *J. Exp. Biol.* **205** 2615–26
- Bundle M W, Hansen K S and Dial K P 2007 Does the metabolic rate-flight speed relationship vary among geometrically similar birds of different mass *J. Exp. Biol.* **210** 1075–83
- Butler P J and Bishop C M 2000 Flight *Sturkie's Avian Physiology* ed G C Whittow (New York: Academic) pp 391–435
- Carpenter R E 1985 Flight physiology of flying foxes, *Pteropus poliocephalus* *J. Exp. Biol.* **114** 619–47
- Carpenter R E 1986 Flight physiology of intermediate-sized fruit bats (Pteropodidae) *J. Exp. Biol.* **120** 79–103
- Davis W H 1970 Hibernation: ecology and physiological ecology *Biology of Bats* vol 1 ed W A Wimsatt (New York: Academic) pp 265–300
- Dial K P 2003 Wing-assisted incline running and the evolution of flight *Science* **299** 402–4
- Dial K P, Biewener A A, Tobalske B W and Warrick D R 1997 Mechanical power output of bird flight *Nature* **390** 67–70
- Engel S, Biebach H and Visser G H 2006 Metabolic costs of avian flight in relation to flight velocity: a study in Rose Coloured Starlings (*Sturnus roseus*, Linnaeus) *J. Comp. Physiol. B* **176** 415–27
- Fleming T H and Eby P 2003 Ecology of bat migration *Bat Ecology* ed T H Kunz and M B Fenton (Chicago: University of Chicago Press) pp 156–208
- Hedenström A 1993 Migration by soaring or flapping flight in birds: the relative importance of energy cost and speed *Phil. Trans. R. Soc. B* **342** 353–61
- Hedenström A 2002 Aerodynamics, evolution and ecology of bird flight *Trends Ecol. Evol.* **17** 415–22
- Hedenström A 2003a *Twenty-Three Testable Predictions about Bird Flight Avian Migration* ed P Berthold, E Gwinner and E Sonnenschein (Berlin: Springer) pp 563–82
- Hedenström A 2003b Flying with holey wings *J. Avian Biol.* **34** 324–7
- Hedenström A 2008 Power and metabolic scope of bird flight: a phylogenetic analysis of biomechanical predictions *J. Comp. Physiol.* **194** 685–91
- Hedenström A and Alerstam T 1995 Optimal flight speed of birds *Phil. Trans. R. Soc. B* **348** 471–87
- Hedenström A and Alerstam T 1996 Skylark optimal flight speeds for flying nowhere and somewhere *Behav. Ecol.* **7** 121–6
- Hedenström A, Johansson L C, Wolf M, von Busse R, Winter Y and Spedding G R 2007 Bat flight generates complex aerodynamic tracks *Science* **316** 894–7
- Hedenström A, Muijres F, von Busse R, Johansson C, Winter Y and Spedding G R 2009 High-speed stereo DPIV measurement of wakes of two bat species flying freely in a wind tunnel *Exp. Fluids* at press, doi:10.1007/s00348-009-0634-5
- Hedenström A and Rosén M 2001 Predator versus prey: on aerial hunting and escape strategies in birds *Behav. Ecol.* **12** 150–6
- Hedenström A, Rosén M and Spedding G R 2006 Vortex wakes generated by robins *Erithacus rubecula* during free flight in a wind tunnel *J. R. Soc. Interface* **3** 263–76
- Hedrick T L and Biewener A A 2007 Low speed maneuvering flight of the rose-breasted cockatoo (*Eolophus roseicapillus*): I. Kinematics and neuromuscular control of turning *J. Exp. Biol.* **210** 1897–911
- Hedrick T L, Tobalske B W and Biewener A A 2002 Estimates of circulation and gait change based on a three-dimensional kinematic analysis of flight in cockatiels (*Nymphicus hollandicus*) and ringed turtle-doves (*Streptopelia risoria*) *J. Exp. Biol.* **205** 1389–409
- Hedrick T L, Tobalske B W and Biewener A A 2003 How cockatiels (*Nymphicus hollandicus*) modulate pectoralis power output across flight speeds *J. Exp. Biol.* **206** 1363–78
- Hedrick T L, Usherwood J R and Biewener A A 2004 Wing inertia and whole-body acceleration: an analysis of instantaneous aerodynamic force production in cockatiels (*Nymphicus hollandicus*) flying across a range of speeds *J. Exp. Biol.* **207** 1689–702
- Helversen O von 1986 Blotenbesuch bei Blumfledermäusen: Kinematik des Schwirrfluges und Energiebudget im Freiland *Bat Flight, Biona Report 5* ed W Nactigall (Berlin: Gustaf Fischer) pp 107–26
- Henningson P, Spedding G R and Hedenström A 2008 Vortex wake and flight kinematics of a swift in cruising flight in a wind tunnel *J. Exp. Biol.* **211** 717–30
- Hermanson J W and Altenbach J S 1983 The functional anatomy of the shoulder of the pallid bat, *Antrozous pallidus* *J. Mammal.* **64** 62–75
- Hughes A L and Hughes M K 1995 Small genomes for better flyers *Nature* **377** 391
- Hughes P M and Rayner J M V 1991 Addition of artificial loads to long-eared bats *Plecotus auritus*: handicapping flight performance *J. Exp. Biol.* **161** 285–98
- Iriarte-Díaz J and Swartz S 2008 Kinematics of slow turn maneuvering in the fruit bat *Cynopterus brachyotis* *J. Exp. Biol.* **211** 3478–89
- Jenni L and Jenni-Eiermann S 1998 Fuel supply and metabolic constraints in migrating birds *J. Avian Biol.* **29** 521–8
- Jenni-Eiermann S, Jenni L, Kvist A, Lindström Å, Piersma T and Visser G H 2002 Fuel use and metabolic response to endurance exercise: a wind tunnel study of a long-distance migrant shorebird *J. Exp. Biol.* **205** 2453–60
- Jepsen G L 1970 Bat origins and evolution *Biology of Bats* vol I ed W A Wimsatt (New York: Academic) pp 1–64
- Ji Q, Currie P P, Norell M A and Ji S-A 1998 Two feathered dinosaurs from northeastern China *Nature* **393** 753–61
- Johansson L C, Wolf M, Busse R von, Winter Y, Spedding G R and Hedenström A 2008 The near and far wake of Pallas' long tongued bat (*Glossophaga soricina*) *J. Exp. Biol.* **211** 2909–18
- Jones G and Rydell J 2003 Attack and defense: interactions between echolocating bats and their insect prey *Bat Ecology* ed T H Kunz and M B Fenton (Chicago: University of Chicago Press) pp 301–45
- Kirkpatrick S J 1990 The moment of inertia of bird wings *J. Exp. Biol.* **151** 489–94
- Kirkpatrick S J 1994 Scale effects on the stresses and safety factors in the wing bones of birds and bats *J. Exp. Biol.* **190** 195–215
- Kunz T H, Wrazen J A and Burnett C D 1998 Changes in body mass and fat reserves in pre-hibernating little brown bats (*Myotis lucifugus*) *Ecoscience* **5** 8–17

- Kvist A, Lindström Å, Green M, Piersma T and Visser G H 2002 Carrying large fuel loads during sustained bird flight is cheaper than expected *Nature* **413** 730–2
- Laitone E V 1997 Wind tunnel tests of wings at Reynolds numbers below 70 000 *Exp. Fluids* **23** 405–9
- Lehmann F O 2004 The mechanisms of lift enhancement in insect flight *Naturwissenschaften* **91** 101–22
- Lillienthal D 1889 *Der Vogelflug als Grundlage der Fliegkunst* (Berlin: R. Gärtners Verlagsbuchhandlung)
- Lindhe Norberg U M, Brooke A P and Trewhella W J 2000 Soaring and non-soaring bats of the family Pteropodidae (flying foxes, *Pteropus* spp.): wing morphology and flight performance *J. Exp. Biol.* **203** 651–64
- Lindhe Norberg U M and Winter Y 2006 Wing beat kinematics of a nectar-feeding bat, *Glossophaga soricina*, flying at different flight speeds and Strouhal numbers *J. Exp. Biol.* **209** 3887–97
- Liu T, Kuykendoll K, Rhew R and Jones S 2006 Avian wing geometry and kinematics *AAAA J.* **44** 954–63
- Lyon C A, Broeren A P, Giguere P, Gopalathnam A and Selig M S 1997 *Summary of Low-Speed Airfoil Data* vol 3 (Virginia Beach, VA: Soartech Pub)
- McCormick B W 1995 *Aerodynamics, Aeronautics, and Flight Mechanics* (New York: Wiley)
- McGowan A J and Dyke G J 2007 A morphospace-based test for competitive exclusion among flying vertebrates: did birds, bats and pterosaurs get in each other's space *J. Evol. Biol.* **20** 1230–6
- McWilliams S R, Guglielmo C, Pierce B and Klaassen M 2004 Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective *J. Avian Biol.* **35** 377–93
- Mönkönen M 1995 Do migrant birds have more pointed wings? A comparative study *Evol. Ecol.* **9** 520–8
- Muijres F T, Johansson L C, Barfield R, Wolf M, Spedding G R and Hedenström A 2008 Leading-edge vortex improves lift in slow-flying bats *Science* **319** 1250–3
- Norberg U M 1969 An arrangement giving a stiff leading edge to the hand wing in bats *J. Mammal.* **50** 766–70
- Norberg U M 1975a Aerodynamics, kinematics, and energetics of horizontal flapping flight in the long-eared bat *Plecotus auritus* *J. Exp. Biol.* **65** 179–212
- Norberg U M 1975b Hovering flight in the pied flycatcher (*Ficedula hypoleuca*) *Swimming and Flying in Nature* vol 2 ed T Y-T Wu, C J Brokaw and C Brennen (New York: Plenum) pp 869–81
- Norberg U M 1975c Aerodynamics of hovering flight in the long-eared bat *Plecotus auritus* *J. Exp. Biol.* **65** 459–70
- Norberg U M 1981 Allometry of bat wings and legs and comparison with bird wings *Phil. Trans. R. Soc. B* **292** 359–98
- Norberg U M 1986 Evolutionary convergence in foraging niche and flight morphology in insectivorous aerial-hawking birds and bats *Ornis Scand.* **17** 253–60
- Norberg U M 1990 *Vertebrate Flight* (Berlin: Springer)
- Norberg U M, Kunz T H, Steffensen J F, Winter Y and Helsen O 1993 The cost of hovering and forward flight in a nectar-feeding bat, *Glossophaga soricina*, estimated from aerodynamic theory *J. Exp. Biol.* **182** 207–27
- Norberg U M and Rayner J M V 1987 Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation *Phil. Trans. R. Soc. B* **316** 335–427
- Organ C L, Shedlock A M, Meade A, Pagel M and Edwards S V 2007 Origin of avian genome size and structure in non-avian dinosaurs *Nature* **446** 180–4
- Park K J, Rosén M and Hedenström A 2001 Flight kinematics of the barn swallow (*Hirundo rustica*) over a wide range of speeds in a wind tunnel *J. Exp. Biol.* **204** 2741–50
- Pennycuik C J 1971 Gliding flight of the dog-faced bat *Rousettus aegyptiacus* observed in a wind tunnel *J. Exp. Biol.* **55** 833–45
- Pennycuik C J 1975 Mechanics of avian flight *Avian Biology* vol 5 ed D S Farner, J R King and C Parkes (New York: Academic) pp 1–75
- Pennycuik C J 1992 *Newton Rules Biology: A Physical Approach to Biological Problems* (Oxford: Oxford University Press)
- Pennycuik C J 1996 Wingbeat frequency of birds in steady cruising flight: new data and improved predictions *J. Exp. Biol.* **199** 1613–8
- Pennycuik C J 2008 *Modelling the Flying Bird* (London: Academic Press)
- Pennycuik C J, Hedenström A and Rosén M 2000 Horizontal flight of a swallow (*Hirundo rustica*) observed in a wind tunnel, with a new method for directly measuring mechanical power *J. Exp. Biol.* **203** 1755–65
- Pennycuik C J, Klaassen M, Kvist A and Lindström Å 1996 Wingbeat frequency and the body drag anomaly: wind-tunnel observations on a thrush nightingale (*Luscinia luscinia*) and a teal (*Anas crecca*) *J. Exp. Biol.* **199** 2757–65
- Poore S O, Sánchez-Haiman A and Goslow G E J 1997 Wing upstroke and the evolution of flapping flight *Nature* **387** 799–802
- Raffel M, Willert C and Kompenhans J 1997 *Particle Image Velocimetry: A Practical Guide* (Berlin: Springer)
- Rayner J M V 1988 Form and function in avian flight *Curr. Ornithol.* **5** 1–66
- Rosén M and Hedenström A 2001 Gliding flight in a jackdaw: a wind tunnel study *J. Exp. Biol.* **204** 1153–66
- Rosén M, Spedding G R and Hedenström A 2004 The relationship between wingbeat kinematics and vortex wake of a thrush nightingale *J. Exp. Biol.* **207** 4255–68
- Rosén M, Spedding G R and Hedenström A 2007 Wake structure and wingbeat kinematics of a house-martin *Delichon urbica* *J. R. Soc. Interface* **4** 659–68
- Rothe H-J, Biesel W and Nachtigall W 1987 Pigeon flight in a wind tunnel: II. Gas exchange and power requirements *J. Comp. Physiol. B* **157** 99–109
- Sahley C T, Horner M A and Fleming T H 1993 Flight speeds and mechanical power outputs of the nectar-feeding bat, *Leptonycteris curasoae* (Phyllostomidae: Glossophaginae) *J. Mammal.* **74** 594–600
- Sane S P 2003 The aerodynamics of insect flight *J. Exp. Biol.* **206** 4191–208
- Schnitzler H-U 1971 Fledermäuse im Windkanal *Z. Vergl. Physiol.* **73** 209–21
- Simmons N B and Geisler J H 1998 Phylogenetic relationships of *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* to extant bat lineages, with comments on the evolution of echolocation and foraging strategies in Microchiroptera *Bull. Am. Mus. Nat. Hist.* **235** 1–182
- Simmons N B, Seymour K L, Habersetzer J and Gunnell G F 2008 Primitive early Eocene bat from Wyoming and the evolution of flight and echolocation *Nature* **451** 818–22
- Speakman J R and Racey P A 1991 No cost of echolocation for bats in flight *Nature* **350** 421–3
- Spedding G R, Hedenström A, McArthur J and Rosén M 2008 The implications of low-speed fixed-wing aerofoil measurements on the analysis and performance of flapping bird wings *J. Exp. Biol.* **211** 215–23
- Spedding G R, Rosén M and Hedenström A 2003 A family of vortex wakes generated by a thrush nightingale in free flight in a wind tunnel over its entire natural range of flight speeds *J. Exp. Biol.* **206** 2313–44
- Springer M S, Teeling E C, Madsen O, Stanhope M J and de Jong W E 2001 Integrated fossil and molecular data reconstruct bat echolocation *Proc. Natl. Acad. Sci.* **98** 6241–6
- Thollessen M and Norberg U M 1991 Moments of inertia of bat wings and body *J. Exp. Biol.* **158** 19–35

- Thomas S P 1975 Metabolism during flight in two species of bats, *Phyllostomus hastatus* and *Pteropus gouldii* *J. Exp. Biol.* **63** 273–93
- Tian X, Iriarte-Diaz J, Middleton K, Galvano R, Israeli E, Roemer A, Sullivan A, Song A, Swartz S and Breuer K 2006 Direct measurements of kinematics and dynamics of bat flight *Bioinsp. Biomim.* **1** S10-8
- Tobalske B W and Biewener A A 2008 Contractile properties of the pigeon supracoracoideus during different modes of flight *J. Exp. Biol.* **211** 170–9
- Tobalske B W and Dial K P 1996 Flight kinematics of black-billed magpies and pigeons over a wide range of speeds *J. Exp. Biol.* **199** 263–80
- Tobalske B W, Hedrick T L and Biewener A A 2003b Wing kinematics of avian flight across speeds *J. Avian Biol.* **34** 177–84
- Tobalske B W, Hedrick T L, Dial K P and Biewener A A 2003a Comparative power curves in bird flight *Nature* **421** 363–6
- Tobalske B W, Warrick D R, Clark C J, Powers D R, Hedrick T L, Hyder G A and Biewener A A 2007 Three-dimensional kinematics of hummingbird flight *J. Exp. Biol.* **210** 2368–82
- Tucker V A 1968 Respiratory exchange and evaporative water loss in the flying budgerigar *J. Exp. Biol.* **48** 67–87
- Tucker V A 1993 Gliding birds: reduction of induced drag by wing tip slots between the primary feathers *J. Exp. Biol.* **180** 285–310
- Van Den Berg C and Rayner J M V 1995 The moment of inertia of bird wings and the inertial power requirement for flapping flight *J. Exp. Biol.* **198** 1655–64
- Van Den Bussche R A, Longmire J L and Baker R J 1995 How bats achieve a small C-value: frequency of repetitive DNA in *Macrotus Mamm. Genome* **6** 521–5
- Vaughan T A 1970 The muscular system *Biology of Bats* vol 1 ed W A Wimsatt (New York: Academic) pp 139–94
- Voigt C C 2000 Intraspecific scaling of flight power in the bat *Glossophaga soricina* (Phyllostomidae) *J. Comp. Physiol. B* **170** 403–10
- Warrick D R and Dial K P 1998 Kinematic, aerodynamic and anatomical mechanisms in the slow, maneuvering flight of pigeons *J. Exp. Biol.* **201** 655–72
- Warrick D R, Tobalske B W and Powers D R 2005 Aerodynamics of the hovering hummingbird *Nature* **435** 1094–7
- Watts P, Mitchell E J and Swartz S M 2001 A computational model for estimating the mechanics of horizontal flapping flight in bats: model description and validation *J. Exp. Biol.* **204** 2873–98
- Weber T P, Borgudd J, Hedenström A, Persson K and Sandberg G 2005 Resistance of flight feathers to mechanical fatigue covaries with moult strategy in two warbler species *Biol. Lett.* **1** 27–30
- Weis-Fogh T 1972 Energetics of hovering flight in hummingbirds and in *Drosophila* *J. Exp. Biol.* **56** 79–104
- Williams T C, Ireland L C and Williams J M 1973 High altitude flights of the free-tailed bat, *Tadarida brasiliensis*, observed with radar *J. Mammal.* **54** 807–21
- Winter Y 1998 Energetic cost of hovering flight in a nectar-feeding bat measured with fast-response respirometry *J. Comp. Physiol. B* **168** 434–44
- Winter Y 1999 Flight speed and body mass of nectar-feeding bats (Glossophaginae) during foraging *J. Exp. Biol.* **202** 1917–30
- Winter Y and Helversen O von 1998 The energy cost of flight: do small bats fly more cheaply than birds? *J. Comp. Physiol. B* **168** 105–11
- Winter Y, Voigt C and von Helversen O 1998 Gas exchange during hovering flight in a nectar-feeding bat *Glossophaga soricina* *J. Exp. Biol.* **201** 237–44