Catching the invisible - aerodynamic tracks and kinematics of bat and bird flight

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Catching the Invisible:

Aerodynamic Tracks and Kinematics of Bat and Bird Flight

Catching the Invisible:

Aerodynamic Tracks and Kinematics
of
Bat and Bird Flight

Marta Wolf

Akademisk avhandling, som för avläggande av filosofie doktorsexamen vid naturvetenskapliga fakulteten vid Lunds Universitet, kommer att offentligen försvaras i Blå Hallen, Ekologihuset, Sölvegatan 37, torsdagen den 14 maj, 2009, klockan 09.00.

Fakultetens opponent: Sharon M. Swartz, Associate Professor, Dept. Ecology and Evolutionary Biology, Brown University, Providence, USA

Avhandlingen kommer att försvaras på engelska.

Dissertation

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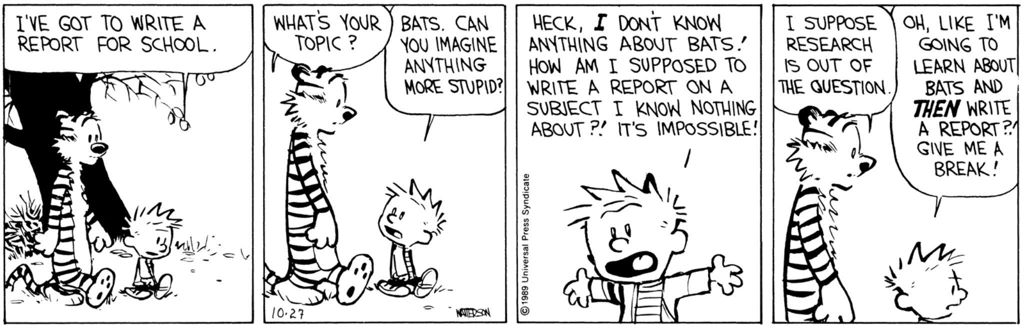
I'VE GOT TO WRITE A REPORT FOR SCHOOL.
WHAT'S YOUR TOPIC?
BATS. CAN YOU IMAGINE ANYTHING MORE STUPID?
10·27
WATTERSON
HECK, *I* DON'T KNOW ANYTHING ABOUT BATS! HOW AM I SUPPOSED TO WRITE A REPORT ON A SUBJECT I KNOW NOTHING ABOUT?! IT'S IMPOSSIBLE!
© 1989 Universal Press Syndicate
I SUPPOSE RESEARCH IS OUT OF THE QUESTION.
OH, LIKE I'M GOING TO LEARN ABOUT BATS AND **THEN** WRITE A REPORT?! GIVE ME A BREAK!

Contents

This thesis is based on the following papers:

Paper I is reprinted with the permission from Science and paper II with permission from The Company of Biologists Limited

Aerodynamics of vertebrate flight

> Man must rise above the Earth – to the top of the atmosphere and beyond – for only thus will he fully understand the world in which he lives.
>
> *Socrates*

Photo 1. Together with the jackdaws that I hand raised, Merlin to the left and Freja to the right.

Introduction and background

This thesis is about the flight of vertebrates and the studies of different modes of flight. Flight has always fascinated mankind and the phenomenon of flight has been observed and admired throughout the history. Active flight has evolved independently three times in the 500 million years of vertebrate history (in Pterosaurs, birds and bats) (Thewissen and Babcock, 1992; Ji et al., 1998; Simmons et al., 2008) and at least once among invertebrates (insects) (Dudley et al., 2007). Animal flight was probably the inspiration for our early attempts to fly and it was long covered in mystery until the technology and deeper understanding of principles of physics allowed us to make useful progress. A new era in aeronautical science had begun.

Among animals flight is the most expensive means of locomotion per unit time and yet used by many different species and with a large variation in the different flight modes (Norberg, 1990). In order to understand the properties of vertebrate flight, some knowledge of basic physical principles and parameters is needed.

Basic Flight Physics

In order to stay airborne a flying animal has to produce **lift** (see Glossary) and **thrust** to balance weight and **drag** (Figure 1). Lift is a positive force, perpendicular to the direction of the air meeting the wing, generally directed upwards, and created by the difference in air pressure above and underneath the wing. The air moving over the wing separates at the leading edge and as the air moves faster over the upper surface of the wing than under the wing, a pressure difference is created. This pressure difference causes lift, which counteracts the animal's weight that is pulling the animal downward (Pennycuick, 1975; Vogel, 1994; Anderson, 2007). Lift will vary with several different factors and e.g. changing the **angle of attack** of the wing and thus increasing the surface of the bottom of the wing, will affect the velocity of the air flowing over the wing and lead to an increased lift production (Vogel, 1994; Alexander, 2003). The lift production will also increase with increasing flight speed and a higher **camber** or area of the wing, and thus the majority of the lift is produced by the innermost part of the wing, where the area is largest (Pennycuick, 1989; Vogel, 1994; Alexander, 2003). However in flapping flight more lift is produced further out on the wing as the outer part of the wing has a higher velocity than the inner part. (Pennycuick, 1989; Vogel, 1994; Anderson, 2007).

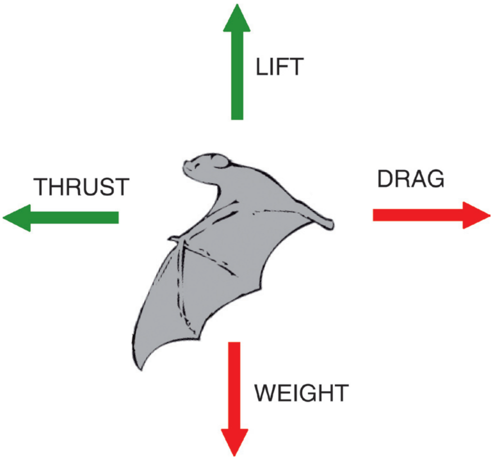

Figure 1. Forces acting on a flying animal.

A flying animal experiences drag that is simply put an air resistance. The larger the surface exposed to the air, the higher the drag. Also drag increases with increasing flight speed. In order to move forward steadily and overcome drag, a flying animal must produce thrust otherwise it will start loosing altitude, which is usually seen in gliding animals. In powered flight, the animal creates thrust and lift by flapping the wings and thereby tilting the lift generated forwards (Vogel, 1994; Alexander, 2003).

The energy cost in terms of mechanical power required to sustain horizontal flapping flight is equal to the total drag experienced by the flying animal times speed:

$$P = DU, \tag{1}$$

where P is the total power, D is the total drag and U is airspeed. There are different components of drag associated with the production of lift, the wings and the body, and therefore the total power is a sum of four power components related to these (Pennycuick, 1989; Norberg, 1990):

$$P = P_{ind} + P_{pro} + P_{par} + P_{iner}, \tag{2}$$

where P_{ind} is the induced power, P_{pro} is the profile power, P_{par} is the parasite power and P_{iner} is the inertial power. Induced power is due to the induced drag which is a consequence of generating wing tip vortices. As the flapping wing is moving forward it creates an induced downwash, deflecting the airstream that moves over the wing, and causing the resultant lift vector to tip backwards. This power component is largest at hovering and low forward flight speeds and decreases with increasing flight speed (Pennycuick, 1975; Norberg, 1990). Profile power is difficult to calculate or estimate and is associated with overcoming the drag acting on the wings as they are swept through the air. This component is dependent on the size, smoothness and shape of the wing surface, as well as the **Reynolds number**. Profile power increases with increasing flight speed (Norberg, 1990; Vogel, 1994).

Glossary

Angle of attack: the angle between the chord of a wing and the velocity meeting the wing. 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 divided by the mean chord.
Camber: the curvature of an airfoil, calculated as the maximum height of the airfoil relative to the chordline divided by the chord.
C_D – drag coefficient is a dimensionless quantity describing the resistance of an object moving through a fluid. It varies with the shape of the object and Reynolds number and is calculated as $C_D = D/(\rho A U^2/2)$, where D is drag, ρ is the density, A is the reference area and U is the flight speed.
DPIV – digital particle image velocimetry, a method for measuring the velocity of the flow by seeding it with buoyant particles and capturing images of the illuminated flow within short time interval. By tracking the movement of the particles between images, flow properties such as velocity and vorticity can be calculated.
Drag: the aerodynamic force in the same direction as the velocity.
Induced velocity: the velocity induced by an object to the surrounding fluid.
Lift: the aerodynamic force that is created, normal to the flow, by the action of an object.
Maximum range speed: the flight speed relative to the air resulting in minimum energy cost per unit distance covered; given by the condition $dP/dU = P/U$, where P is power required to fly and U is the airspeed.
Minimum power speed: the flight speed relative to the air with lowest rate of energy requirement; given by the condition $dP/dU = 0$.
Reynolds number: a dimensionless number describing the relative importance of inertial forces to viscous forces and thus properties of the flow defined as $Re = Uc/\nu$, where U is the flight speed, c is the mean chord length and ν is the kinematic viscosity. For flying vertebrates Re ranges between 10^3 and 10^5.
Span ratio: the ratio between the wingspan at mid-upstroke and mid-downstroke
Strouhal number: a dimensionless number defined as: $St = fA/U$, where f is wingbeat frequency, A is the tip-to-tip amplitude of the wing and U is the flight speed. Strouhal number describes the growth and shedding of vortices and can serve as a predictor of unsteadiness of the flow.
Thrust: the aerodynamic force created to propel the animal forward and overcome the drag.
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 loading: a ratio between the weight of the animal and the wing surface area
Wake loading: is the ratio between the weight of the flying animal and the horizontally projected area of the wake calculated as $Q_{wake} = W/S_e = \rho\Gamma f$, where W is the weight of the animal, S_e is the horizontally projected area of the wake, ρ is the density, Γ is the circulation and f is the wingbeat frequency. Cost of generating lift, the induced power, is proportional to the square of as Q_{wake}.

The third power component is the parasite power, used to overcome the friction and pressure drag of the body. It is proportional to the frontal body area and also increases with increasing flight speed. Thus a streamlined body well aligned with the flow will minimize this power component. The **body drag coefficient** ($C_{D,par}$), involved in parasite power, has previously been estimated, using frozen bird bodies, to a value between 0.2 for large birds and 0.5 for smaller birds (Tucker, 1973; Pennycuick et al., 1988; Maybury, 2000). Values of a similar magnitude have also been reported for live birds. Ward et al. (2001) estimated $C_{D,par}$ to be 0.26 for starlings and values of a similar magnitude has been demonstrated, for birds of a similar size, by Hedenström and Liechti (2001), who looked at the maximum dive speeds of passerines. The forth component of total mechanical power required is the inertial power. This is the power associated with accelerating and decelerating the wing during every wing stroke. The inertial power is considered to be very low at medium and fast flight speeds, because at the end of a stroke the wing inertia is converted into aerodynamic work (Pennycuick, 1975; Norberg, 1990, Hedrick et al. 2004). At very low flight speeds and during hovering flight, inertial power may play an important role (Norberg, 1990).

The different components of power required can be summarized in a U-shaped power curve (Figure 2). At the low flight speed the highest cost is due to the production of lift. At higher flight speeds, as drag on the wing and body increases, more power goes into generating thrust (Pennycuick, 1975). From this power curve a number of ecologically important flight speeds can be derived. **Minimum power speed** (U_{mp}) is the speed at which the animal flies "cheapest", i.e. the power consumption per unit of time is lowest (Alexander, 2003; Biewener, 2003). It has been shown that displaying skylarks (*Alauda arvensis*) use this speed to stay aloft as long as possible (Hedenström and Alerstam, 1996). **Maximum range speed** (U_{mr}) is the speed at which an animal can fly greatest distance at a minimum energy cost. This is the speed that bird should use during migration (Norberg, 1990; Alexander, 2003; Biewener, 2003).

Methods used

Wind tunnel

To study the detailed aerodynamics of flight in free flying animals in their natural surroundings is very hard. The animals are often moving fast in three dimensions, they can often be far away and the natural conditions, such as wind speeds, temperature and pressure, are hard to measure precisely as they can vary with altitude, distance, etc. These are just some of the reasons that make the wind tunnel a perfect tool for studying animal flight. Greenwalt (1961) was the first to apply a

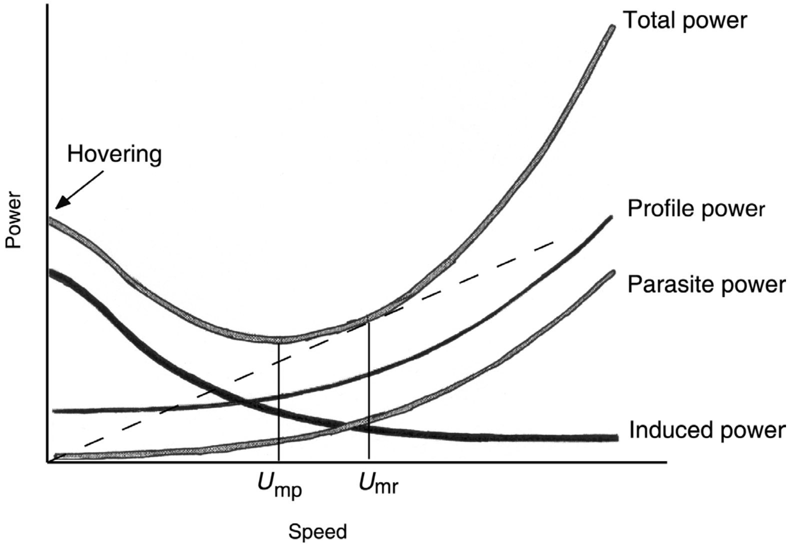

Figure 2. The U-shaped power curve of flight. At hovering the cost of producing lift is the highest. As the flight speed increases, induced power decreases and profile and parasite drag increase. Minimum power speed, U_{mp}, is the speed where the flight cost is at minimum and maximum range speed, U_{mr}, is where the flying animal can cover most distance at the minimum cost.

wind tunnel for studying animal flight. Probably the most important aspect of using a wind tunnel to study flight is the possibility to vary airspeed. This makes it possible to study the gradual changes in the aerodynamics systematically with changing flight speed and allows for repeatable conditions during experiments. Wind tunnels are common tools today for engineers to study aerodynamic properties of airplanes, cars and other vehicles, but there are still just a few wind tunnels used for animal flight, and thus there are also a limited number of good studies of animal flight using wind tunnels.

The Lund wind tunnel is a closed circuit wind tunnel, which means that the air is circulating continuously (Figure 3). The entire structure is 21 m long, stand 8 m above the floor and is 4.2 m wide. The air is produced by a fan and travels through the wind tunnel, passing corners and diffusers, which decrease the turbulence. The widest part of the tunnel, with a cross sectional area of almost 14 m, is the settling section. It contains multiple screens that make the airflow as smooth as possible. Afterwards the air goes through the contraction chamber, which accelerates the air by a factor of approximately 12. The contraction ratio is one of the most important features of the wind tunnel as the greater the contraction ratio, the lower the turbulence of the flow is. After going through the contraction chamber the air flows through the test section where the animals are flying and towards the bellmouth (Pennycuick et al., 1997; Spedding et al., 2009). The wind tunnel in Lund has a very low and evenly distributed turbulence across the test section, which makes it particularly suitable for studying animal flight. The opening, just after the test section of the wind tunnel gives a quick access to the flying animals as well as helps to remove the streamwise pressure gradients. The entire wind tunnel can be tilted between +8° and –6° degrees, to simulate descending and climbing flight, and the air speed in the wind tunnel is carefully monitored and can be varied from 0 to 38 m/s. (Pennycuick et al., 1997; Spedding et al., 2009).

High-speed cameras

In the lab we can use high speed cameras to record the movement of flying animals and thus

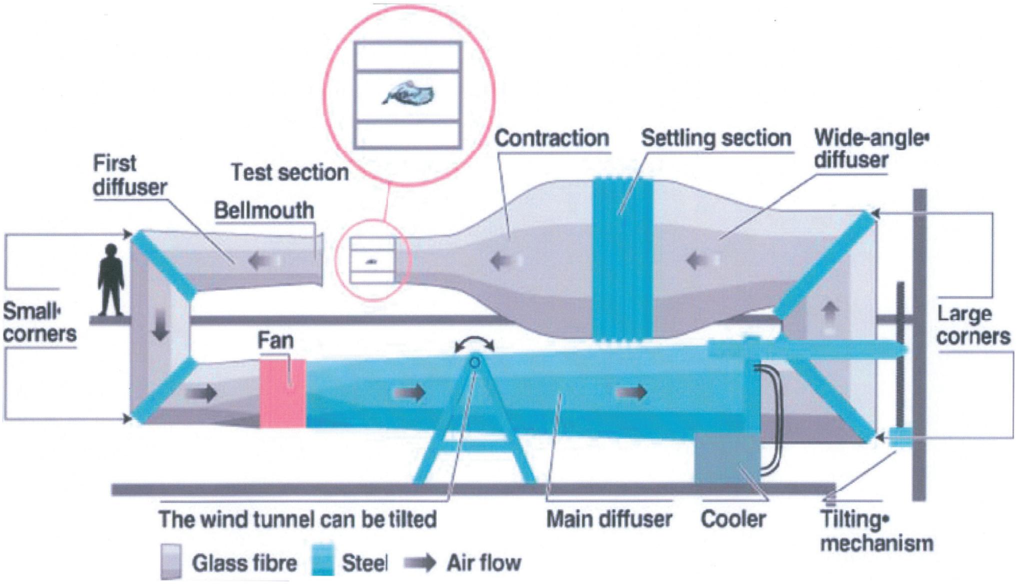

Figure 3. Lund wind tunnel. The direction of the air movement is shown by arrows. The test section can easily be accessed by an opening just in front of the bellmouth and the Plexiglas-walls of the test section allow for free placing of high speed cameras. The entire structure can be tilted to simulate climbing or descending flight.

look at the changes of different kinematic parameters with flight speed. A high speed camera usually takes 250–500 frames per second during our studies of animal flight, compared to the 25 frames per second used for a movie or television playback. Flying animals move their wings very fast and it is only with high speed cameras that we can observe this motion (Figure 4). The data for kinematic studies can be collected without intrusive procedures, simply by tracking a number of coordinates on the wings and body of the animal and following how their movement changes across flight speeds. Kinematic measurements have a long history of detailed studies and a number of bat species (e.g. Norberg, 1976a, b; Aldridge, 1986, 1987; Lindhe-Norberg and Winter, 2006; Swartz et al., 2006), but particularly birds have been studied so far (e.g. Brown, 1953; Tobalske and Dial, 1996; Hedrick et al., 2002; Rosén et al., 2004, 2007). However it is first during the last 10–15 years that digital high speed cameras have been used for studying kinematics.

One of the potential problems working with high-speed cameras is the need for light, particularly when filming dark object such as bats and many species of birds. Filming requires very bright light to be able to see details of the wings, which is problematic as bats are nocturnal and many of the birds try to escape the bright light as well. In the lab we use a system for filming in infra red light, consisting of two cameras equipped with filters to remove the light from the visible range. This allows us to study kinematics simultaneously with the studies of the flow that require dark conditions. This system has been used for studying the kinematics of flight of *Glossophaga soricina* bats, described in detail in paper III and also used for papers I, II and IV. For the kinematic study of bounding flight in paper V I used visible light conditions and a different set of high speed cameras filming at 250/500 frames per second.

High speed cameras provide a very powerful tool for analyzing flight, although the procedure is extremely time-consuming for large sets of data. Every marker you choose to follow on the flying animal has to be followed from two or more views, over a substantial number of frames. The coordinates for that marker are digitalized manually, a prolonged and tedious process. This explains why studies of animal flight are usually based on just a few study objects – the time constrains, difficulties with the training of animals etc. do not allow for large numbers of individuals.

Flow visualization

Flow visualization can be used to study the wake and thus the airflow behind a flying animal.

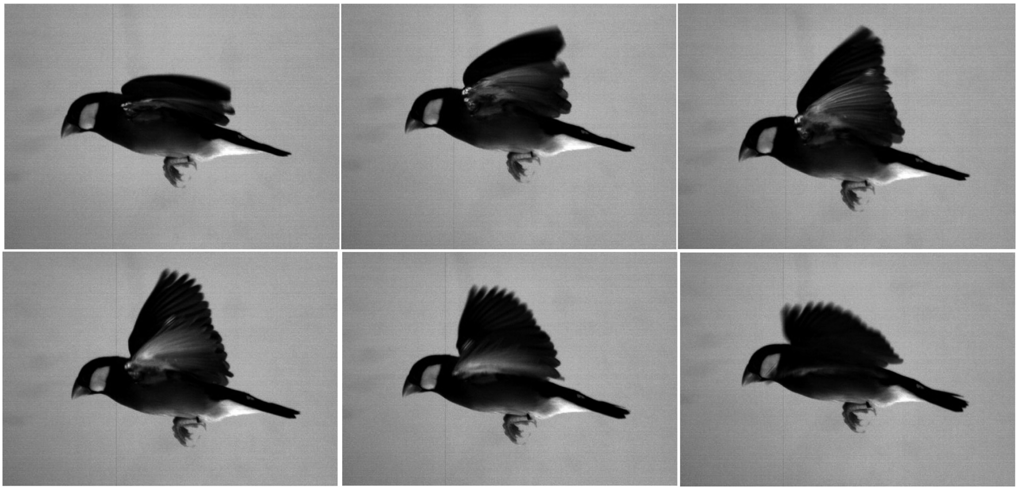

Figure 4. An example of frames taken with a high speed camera of a flying Java sparrow (*Padda oryzivora*). Frame rate is 250 frames per second, flight speed 8 m/s. The six frames here correspond to 0.020s.

When a flying animal moves its wings, the forces generated leave an aerodynamic 'footprint' in the form of **vortex** structures in the wake. The geometry and **vorticity** from these vortices can be used to estimate the aerodynamic forces and how they change with flight speed. Researches have been trying to use flow visualization and studies of vortex wakes of flying animals since the 1970's and to develop models of animal flight (Kokshaysky, 1979; Rayner, 1979a, b; Spedding et al., 1984; Rayner et al., 1986; Spedding, 1986, 1987). Most of the earlier studies used helium-filled soap bubbles that were illuminated with flashguns fired in short intervals. By taking sequential stereo photographs of the bubbles, it was possible to follow the movement of the bubbles and identify the discrete vortices. A significant improvement in the field came with the development of a new method: Digital Particle Image Velocimetry (**DPIV**). This method is based on seeding the air in the wind tunnel with fine fog particles, which are illuminated with a very bright light sheet generated by a laser. A digital camera synchronized with the laser takes pairs of images with a very short time interval between consecutive exposures. These images are then used to track the movement of groups of fog particles between the images, using a correlation routine. The displacement is then used to create flow maps with vector fields that describe the direction and magnitude of the flow across the image (Figure 5). The application of this technique in studies of vertebrate flight is quite recent and thus the number of animal studies performed is limited, however an increasing number of studies of bird flight have emerged in the last few of years (Spedding et al., 2003; Warrick et al., 2005;

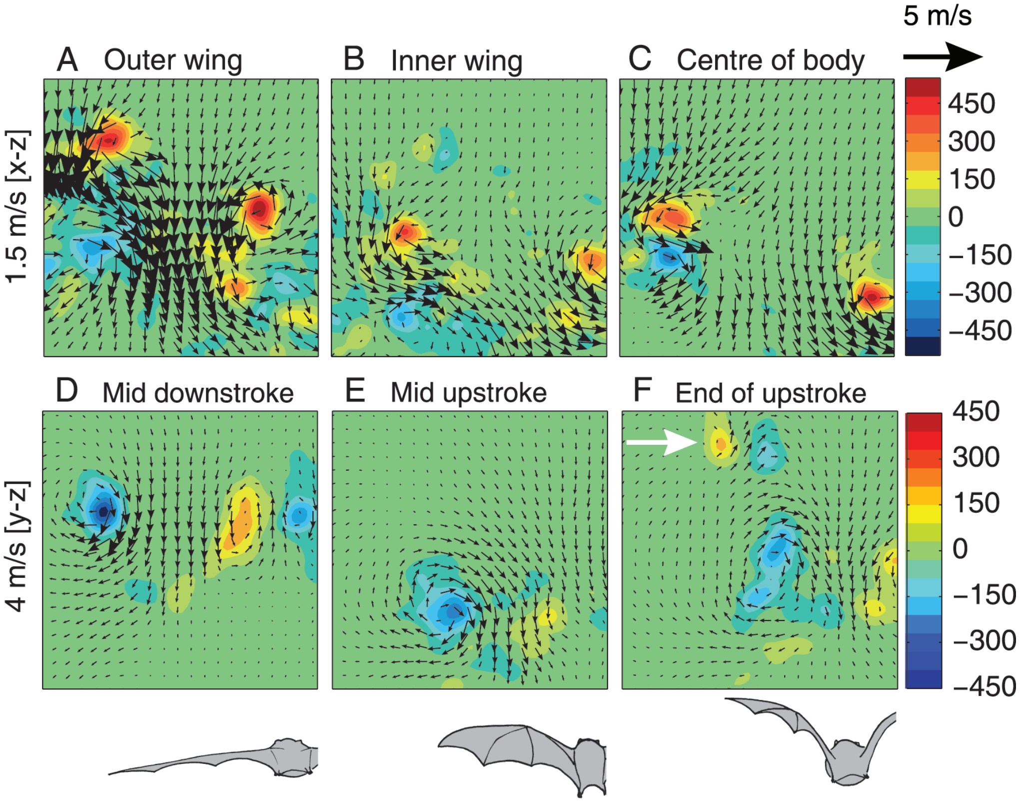

Figure 5. An example of the wake flow fields for the flight of *Glossophaga soricina* bats. Near wake in the streamwise plane (A–C) and transverse plane (D–F). A–C show the flow at different positions of the wing and body. D–F show different phases of a wingstroke. From. Hedenström et al. (2007) (Paper I).

Hedenström et al., 2006; Rosen et al., 2007; Henningsson et al., 2008). The number of bat species studied are still limited, with only three species studied this far, of which one is the species in Paper I and II (Tian et al., 2006; Hedenström et al., 2009a; Hubel et al., 2009).

Powered flight of vertebrates – bats and birds

Birds and bats are the two extant vertebrate groups that use powered flight and thus represent two independent evolutionary pathways leading to the same result – active flapping flight. Clearly, both birds and bats must be considered as successful vertebrate groups as the abundance of species is high in both bats and birds. There are more than 10000 species of birds and about 1100 species of bats, with bats representing 20% of all mammal species (Speakman, 2001; Hedenström et al., 2009b). As flight is such an expensive means of locomotion it is expected to require morphological adaptations in muscles, skeleton, body size and wing shape (Norberg, 1990; Swartz et al., 1992, 2006). Bats and birds show a number of similarities in their functional morphology, e.g. lighter skeleton, thin-walled bones, rigid leading edge of the wing and similar wing shape (Figure 6) (Rayner, 1988; Norberg, 1990; Swartz et al., 1992; Dudley et al., 2007). Both bats and birds have generally a low body mass compared to other vertebrates, although birds can reach a body mass one order of magnitude higher than bats (Rayner, 1988; Hedenström et al., 2009b). But the main difference is the morphology of the wing itself. Birds have more rigid wings covered with feathers and bats have wings with elastic membranes stretched over the elongated fingers of the hand. In slow flight birds can separate their primary feathers during the upstroke, allowing the air to pass through and thus making the upstroke aerodynamically inactive (Norberg, 1976a, b; Tucker, 1993). The membranous wings of bats have a large number of independently controlled joints, which allow the dramatic changes of the wing shape needed to perform fast manoeuvres (Swartz et al., 2006; Swartz and Middleton, 2008). Although the bats cannot make lifting surfaces inactive as birds can, they can use a lifting upstroke by twisting part of the wing and flipping the wing upside down (Norberg, 1976a; von Helversen, 1986; Hedenström et al., 2007). During slow flight the wing goes through a pitching rotation at the top and bottom of a stroke, so that the hand wing is flipped upside down. As the wing moves upwards and backwards relative to the still air during the upstroke, it generates a forward and upward force i.e. thrust and lift (Hedenström et al., 2007).

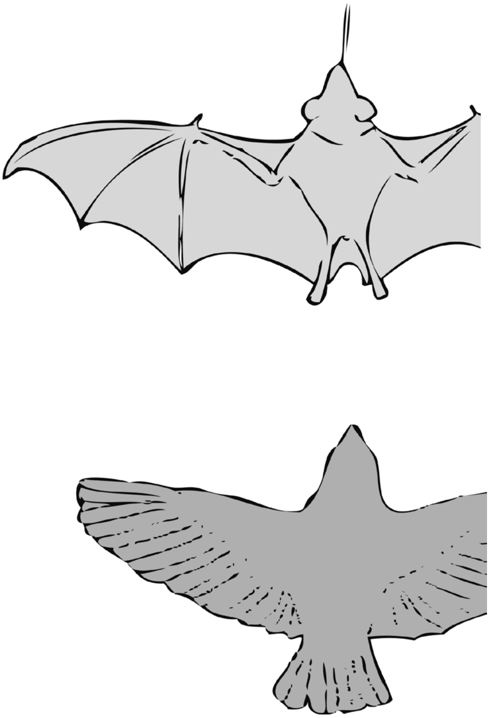

Figure 6. A simplified, comparative view over a bat and a bird wing. Top view of a nectarivorous bat (*Glossophaga soricina*) and a Java sparrow (*Padda oryzivora*)

The wake of flapping flight in birds has been studied previously and revealed many novel findings about the underlying aerodynamics. It has been previously argued that birds, in analogy with terrestrial animals, use two distinct gaits in flapping flight: a closed vortex loop gait and a continuous trailing vortex gait (Rayner, 1986). This is however not supported by studies of bird flight over a wide range of flight speeds, which show that the vorticity and circulation varies continuously over flight speeds (Spedding et al., 2003; Hedenström et al., 2006). At low speeds the bird is generating closed vortex loops, but as the speed increases the proportion of the upstroke contributing to the weight support is increasing, thus generating a more continuous wake pattern. As the flight speed increases even more there is a further gradual change in the vortex pattern towards continuously trailing vortices throughout the wingbeat (Figure 7) (Spedding et al., 2003). This is also supported by analysis of wing beat kinematics for several bird species that display a similar, gradual variation over flight speed (Tobalske and Dial, 1996; Tobalske et al., 1999; Rosén et al., 2004, 2007)

Although the flight kinematics have been studied for a number of bat species there has only been one study of the wake properties until recently (Rayner et al., 1986, but see Tian et al., 2006 for some preliminary results). This study was conducted using stereo-photogrammetry and helium filled bubbles as tracer particles, and claimed that the bats exhibited two separate wing beat gaits. At slow speed the bats were reported to have an inactive upstroke (i.e. no lift production) with a single vortex loop shed as a result of the downstroke. At higher speeds aerodynamic lift was produced during the upstroke and an undulating vortex pair was shed from the wingtips (Rayner et al., 1986). We studied the vortex wake of *G. soricina* bats, flying at a range of speeds between 1 and 7 m/s, from a streamwise and transverse plane, and found that there were a number of characteristics in the wake properties that differed from these early models of bat flight. Our results are presented in papers I and II. The bats generated quite a complex wake, with two separate vortex loops, one from each wing, at all investigated flight speeds (Figure 8). There was also a systematic variation in circulation of the start/stop vortices along the wingspan, and we found that the bats produced lift during the upstroke at all investigated speeds, except for a transition speed at 2–3 m/s, when the backward speed of the wing is the same as the forward flight speed. In Paper II we observed a novel vortex wake at 2 m/s, with two consecutive start vortices but only one stop vortex. At this flight speed the upstroke is more or less vertical relative to the still air (Lindhe Norberg and Winter, 2006), and the upstroke generates thrust or negative thrust but no lift (Paper II). At speeds 3–7 m/s the downstroke generates a strong start vortex and a weaker stop vortex, more diffuse closer to the body. During the upstroke, the wing is flexed at first but extends at the end of upstroke, which leads to a difference in the circulation on the hand wing (outer) and arm wing (Papers I and II). The wing thus generates weight support throughout the upstroke, except for the outer wing at the end of upstroke, generating a negative lift (Papers I and II). In papers I and II we also examined the wake of *G. soricina* in a transverse plane and found wing root vortices as well as the expected wing tip vortices. The wing root vortices were present at all investigated flight speeds (Papers I and II), indicating the formation of separate vortex loops for each wing. The formation of two separate rings is most likely caused by the differences in the flow properties between

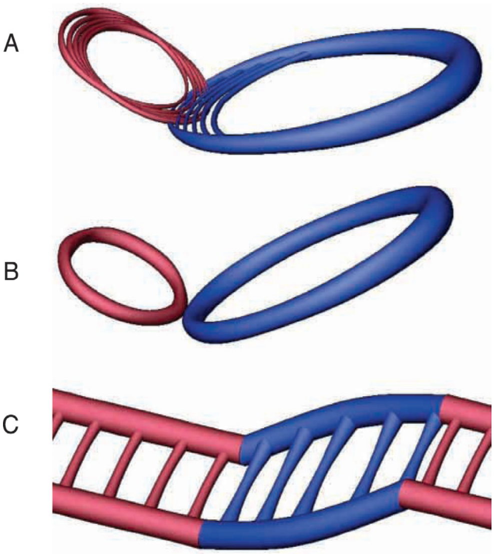

Figure 7. A summary of an idealized and simplified view of three wake patterns of bird flight for thrush nightingale (*Luscinia luscinia*), at slow (A), medium (B) and high (C) flight speed. The three samples do not represent discrete wake topologies and the transition from one to another is gradual. The tubes represent constant vorticity magnitude, and are coloured blue or red according to whether they originated with down- or upstroke. The wakes are rescaled to occupy the same length, but in practice the high-speed pattern occupied almost three times that of the low speed wake. From Spedding et al., 2003.

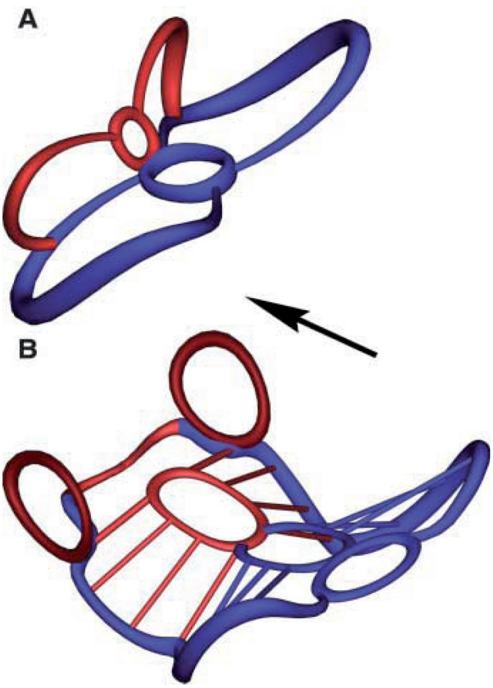

Figure 8. Cartoon of the slow (A) and (B) medium speed wakes of bat flight, for *Glossophaga soricina* bats. Blue denotes vortex structures originating from the downstroke; red from upstroke. The arrow indicates the flight direction. The wake at higher flight speeds displayed a longer wavelength but was otherwise the same. From Hedenström et al., 2007 (Paper I).

the outer and the inner parts of the wing due to rotational motion of the flapping wing. The speed of the inner wing is quite low compared to the outer wing and the circulation over the wing may also vary with camber, and local twist of the wing (Paper II). Another reason for the separate rings may be the form of the body of bats. Bats have a more blunt body than birds with morphological structures, such as the leaf-nose or the ears which can potentially disturb the flow over the body. This would make the lift production by the body less likely and thus more difficult for the flow over the wings to connect and create a unified vortex structure (Paper IV)

Our results show that the wakes of bats and birds differs quite dramatically and suggests that the flight of bats is governed by unsteady flight mechanics, at low flight speeds. Unsteady flow is generally created by turbulence in the bound vortex, i.e. the vortex over the wing. The flow over flapping wings is disturbed by the motion of the wing itself and the distortion increases with the flapping speed of the wing (Norberg, 1990; Anderson, 2007). The notion of unsteady mechanisms is also supported by our study of the detailed wing beat kinematics of bats presented in Paper III. We collected the kinematic data simultaneously with the wake measurement and found that the kinematics varied continuously across flight speeds and reflected the properties of the wake. However, there were several differences in the kinematics of bats compared with birds. The values of **span ratio** were much higher than reported for most birds, close the values reported for the rigid wings of swifts (Henningsson et al,. 2008). This indicates that the bats flex the wings to a less degree that birds, probably to avoid looser membrane that could increase drag and decrease lift production (Paper III). The angle of attack varied over the course of a wingbeat, which has also been shown for other bat and bird species (Hedrick et al., 2002; Swartz et al., 2006). At low speeds the changes in angle of attack ranged from –70° to 60°, over the course of a wingstroke (Paper III). These values are high, comparable to those of hummingbirds (Tobalske et al., 2007), and much higher than those found for engineered airfoils, which usually operate at angles of attack between 0–15°. The camber of the wing varied throughout the wingbeat, which has also been shown for other bat species by Swartz et al. (2006). The camber for the bat wings was higher than normally found for wings with steady flow, however similar values have been found by Muijres et al. (2008) in flow visualisation directly over a bat wing. The camber was highest at mid-upstroke at the lowest flight speed and decreased with increasing forward flight speed. The high values of angle of attack, camber and **Strouhal number** together with the wake geometry, all point to that the flight of bats is governed by unsteady high-lift mechanism at low flight speeds. This is also confirmed by recent findings of a leading-edge vortex in *G. sorcina* bats flying at low speeds (Muijres et al., 2008).

In paper IV we compared quantitative measures of the circulation in the far wake between three bird species and one bat species. We found several differences between birds and bats in the

Photo 2. Capturing bats in mist nets in, Venezuela, Morrocoy area. Florian Muijres to the right. *Photo by Martin Pedersen, March, 2008.*

regulation of the circulation and in the way that the wake pattern changes with speed, indicating that birds have a more continuous change of the circulation during a wingbeat and that bat wings exhibit a relatively higher circulation throughout a larger proportion of the wake. We also found that the bats had a higher normalized **wake loading** based on the start vortex, which points to a relatively small wake area associated with a high acceleration of the air. Higher acceleration of the air results in a relatively higher induced power and thus less efficient lift generation. This indicates that bats have a less aerodynamically economic flight than birds. No differences have been found in studies of metabolic power in bats and birds (Speakman and Racey, 1991; Winter and von Helversen, 1998), which suggests differences also in conversion efficiency. Less economic flight of bats could help explain the difference in maximum size of bats compared to birds and the absence of long-distance migration among bats.

Intermittent flight

Who flies intermittently?

Due to the high cost of flight it is not surprising that there is a high selective pressure for energy saving flight patterns to evolve, such as using external natural forces for soaring or flying intermittently. When an animal flies intermittently the active flapping phases are interspersed with pauses. There are two different types of intermittent flight: flap-gliding or undulating flight and flap-bound-

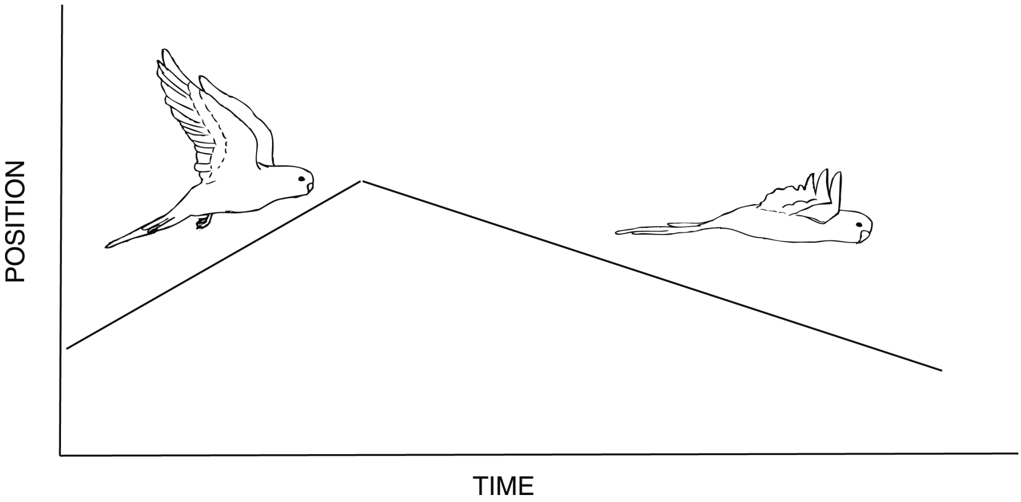

Figure 9. A representative view of undulating flight. After a period of flapping the bird stretches out the wings and glides and as it glides it looses altitude due to drag.

ing or bounding flight. Undulating flight (Figure 9) is widespread among birds and most birds that can glide also engage occasionally/regularly in flap-gliding. This flight mode is most common among birds of intermediate size, with relatively long wings, low **wing loading** and/or high **aspect ratio**, e.g. gulls. Small birds, having short, rounded wings glide rather poorly, and are therefore less adapted for flap-gliding (Rayner, 1985; Tobalske and Dial, 1996; Rayner et al., 2001).

Undulating flight is also found among bats. Megachiropterans, i.e. larger species of bats, at times soar, glide or flap-glide but only one species of microchiropteran bats has been documented to do so (Thomas et al., 1990). The European pipistrelle bat (*Pipistrellus pipistrellus)* has been shown to flap-glide frequently while foraging (Thomas et al., 1990). The glides are always of short duration, and can be compared to a period of one or two wingbeats. A plausible reason for this short duration can be that, while gliding, the bats do not use echolocation and are therefore 'blind' during this period. Thomas et al. (1990) suggested that as the bats are gliding the flight muscles are not active and therefore do not contract and compress the thorax which in turn influences the respiratory cycle so that echolocation is either not possible or not as intense. Since bats rely on the echolocation to orient and locate prey, they may be constrained from gliding more frequently or longer. It is possible that other microchiropterans also use undulating flight, but there has been no evidence of that except for occasional anecdotal observations (Thomas et al., 1990). This may be partially due to the trade-off between gliding and echolocation. Another explanation may be that other microbats may be hindered from flap-gliding by their wing design, since their wings have lower aspect ratio, which would give poorer gliding performance than wings of high aspect ratio (Rayner, 1977; Thomas et al., 1990; Rayner et al., 2001).

Bounding flight (Figure 10) has only been observed in birds. One potential reason for the lack of this flight behaviour among bats is most likely the wing morphology of bats. The membranous wings would be quite difficult to fold during the bounding phase. Also, the bounds would last longer than the short glides observed in bats, and thus the problem with echolocation ability would be even larger in bounding flight than in undulating flight (Rayner et al., 2001). Bounding flight is commonly used by small birds, with maximum weight of about 250 g, but some medium-sized birds also flap-bound (e.g. magpies and woodpeckers). Flap-bounding birds generally have wings with large area and low wing loading, relatively low aspect ratio and rounded wing tips (Rayner, 1977, 1985; Tobalske et al., 1999; Rayner et al., 2001; Alexander, 2003).

Power and intermittent flight

In the non-flapping phase of undulating flight the bird extends its wings and glides but it does not produce mechanical work to move forward. Instead, it uses the loss in altitude and thus potential energy to overcome drag and cover forward distance. The active flapping phase is then used to gain altitude. Consequently the only mechanical work is done during the second phase. However, the bird needs to maintain a force on its wings (static muscle work) during the non-flapping phase to balance the lift force that is pushing the wing upwards (Rayner, 1985; Norberg, 1990; Rayner et al., 2001). Still, undulating flight demands less mechanical power compared to steady level flight. Rayner (1977, 1985) showed that flap-gliding is especially energetically appealing at low to moderate speeds, below the maximum range speed. Undulating flight is thus most likely to be used during short flights or slow flights and in situations when the bird is not under pressure to minimize the flight time (Rayner, 1985). At high speeds, the profile drag increases and the cost of generating thrust in order to climb during the flapping phase becomes too high, so that continuous flapping is more profitable (Norberg, 1990; Tobalske et al., 1999; Rayner et al., 2001). In the non-flapping phase of bounding flight the bird folds its wings and then performs a bound during which it continues climbing through the air for a short period of time and then starts to fall. There is no mechanical power produced during the bound, which was demonstrated by Tobalske and Dial (1994), who showed that the flight muscles were inactive during the bounds in budgerigars (*Melopsittacus undulatus*). When the bird reaches a minimum altitude, it extends and elevates the wings and starts to flap. Thus the flap-bounding cycles follow a repeated, sinusoidal, often predictable patterns and variations in altitude. This is sometimes even be used by field ornithologists for identification of species (Ward-Smith, 1984a, b; Tobalske, 1995; Rayner et al., 2001; Biewener, 2003). Since profile drag increases with increasing speed, folding the wings and flap-bounding would require less mechanical power at higher speeds (DeJong, 1983; Ward-Smith, 1984a, b; Tobalske et al., 1999; Tobalske, 2001). As the speed increases the induced drag becomes less important for the total drag acting on the bird. At the same time profile drag accounts for a larger proportion of the total drag. If the speed is high enough the reduction in profile drag, due to bounding, will compensate for the induced drag (Norberg, 1990; Alexander, 2003). Rayner (1977, 1985) calculated that this is the case only at speeds greater than the maximum range speed (> $1.2U_{mr}$), when flap-bounding would become

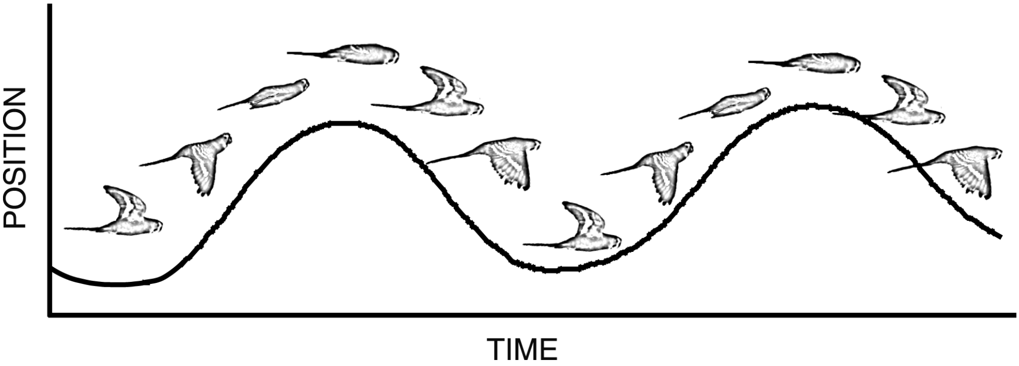

Figure 10. A representative view of a bounding flight cycle. The bird flaps the wings and gains altitude. During the bound, the bird folds its wings, loses altitude and then, as it stretches out its wings and begins to flap, it starts to climb upwards through the air.

advantageous. Hedenström and Alerstam (1992) showed that migrating siskins (*Carduelis spinus*) and other small, migrating birds, fly at speed that exceed their estimated U_{mr} and radar observations show that many small birds use bounding flight while migrating (Bäckman and Alerstam, 2003).

Problems with bounding flight

The energy savings during undulating flight seem quite clear; however, several bird species have been shown to use bounding flight at speeds much lower than predicted. There are two main hypotheses trying to explain this phenomenon. The fixed-gear hypothesis concerns the muscle efficiency and disregards bounding flight as an energy saving mechanism. To control power output from the muscles a bird can do either of three things: it may vary contraction rate (strain rate or wingbeat amplitude and frequency), it may recruit different proportions of the flight muscles or it may introduce intermittent rest periods, while keeping contraction rate almost constant and recruiting practically all of the muscle (Rayner, 1985; Norberg, 1990). It has been agued that small birds often have simpler muscle and that the wingbeat kinematics are invariant, which forces them to flap-bound (Rayner, 1985). Later it has been shown that there is a variation in the kinematics so that small birds are not restricted to fixed power outputs per wingbeat, as stated by the fixed-gear hypothesis (Tobalske, 1995,; Tobalske et al., 1999). Tobalske (2001) suggested that small birds use intermittent bounds at low speeds, due to wing design, rather than muscle composition. Birds with wings of higher aspect ratio, e.g. budgerigars, can flap-glide at low speeds and flap-bound at high speeds. Small birds with wings of low aspect ratio can not glide efficiently or vary wingbeat kinematics as dramatically as larger birds with wings of higher aspect ratio can (Tobalske, 2001). Thus, they are constrained to flap-bound also at low speeds (Tobalske et al., 1999; Tobalske, 2001).

The second hypothesis trying to explain the use of bounding flight at low speeds is the body-lift hypothesis, which says that during the bounding phase the bird generates a vertical, upward directed lifting force, body-lift, which partially supports the body weight of the bird. Body lift was first demonstrated using plaster casts of birds by Csicsáky (1977) and has later been shown for flying zebra finches (*Taenopygia guttata*) and starlings (*Sturnus vulgaris*) (Tobalske et al., 1999, 2009; Rayner et al., 2001). The values of body lift have been estimated to approximately 15–20% of weight and, although body lift of that size may give enough power savings at intermediate flight speeds, it is not enough to explain bounding flight as an energy saving mechanism at low speeds (Tobalske et al., 1999, 2009; Rayner et al., 2001).

In Paper V, I investigated bounding flight of budgerigars and Java sparrows (*Padda Oryzivora*) to see how the production of body lift varies with the differences with wing morphology and how the wingbeat kinematics varies over the speed range investigated (8–13 m/s). I found that both species produced body lift at all investigated flight speeds, which was approximately of the same size as previously found for other species. The wingbeat kinematics varied with flight speed, which argues against the fixed-gear hypothesis. However, Java sparrows showed a co-variation in amplitude and frequency indicating a restriction in the power output. This difference may be caused by the differences in the wing morphology between budgerigars and Java sparrows. I was also able to use horizontal accelerations during the bounding phase to investigate the body drag coefficient and found it to be in the range between 0.2 for and 0.5, which agrees with findings on other species (Paper V, Tucker, 1973; Pennycuick et al., 1988; Maybury, 2000).

It seems that the use of bounding flight cannot be explained only as an adaptation to reduce energy. It is possible that the benefits from flap-bounding are in reality a mixture of energetic advantages and morphological constrains.

Concluding remarks and summary

This thesis concerns the flight of vertebrates, particularly the flight of bats and intermittent flight of birds. It also compares some of the factors concerning the differences between the flight of bats and birds, and the underlying aerodynamics. In the first three papers we have described the characteristics of flight for small, nectivorous bats, *G. soricina*, flying in a wind tunnel over a wide range of speeds. Paper I describes the wake structure of flying bats, revealing novel structures not previously seen in neither birds nor bats, such as e.g. individual vortex loop for each wing, and a rather complex wake pattern. In paper II we analysed the wake of *G. soricina* further and compared the near and far wake measurements in the wind tunnel. We could show that, the strength of start and stop vortices does not differ significantly between the near and far wake, but there is a risk of missing details of the wake morphology by only looking at the far wake. The wake evolves and deforms over time as it moves further away from the animal and some vortex structures may move out of view, which could lead to oversimplified view of the wake. Paper III concerns the kinematics of flying *G. soricina* bats and ties the wingbeat kinematics together with the observed wake, collected simultaneously. The wingbeat kinematics showed a gradual variation over flight speed which reflects the continuous change in wake geometry. The notion of presence of high-lift mechanism at low flight speeds, suggested by the wake structure and measured circulation, was also supported by the wingbeat kinematics. In Paper IV we compared quantitative measures of the circulation of the wake of the bat *G.soricina* with the wakes of three bird species. Our results showed differences in how the circulation was regulated and how the wake pattern changed in birds and bats. The lower values of normalized wake loading indicate that bats have less economic flight due to higher induced drag.

Paper V concerns bounding flight of birds and presents the results of a wind tunnel study of bounding budgerigars and Java sparrows. I found that both birds produced body lift at all investigated flight speeds, supporting part of the body weight. There were however several differences between the two species that may be caused by the differences in the wing morphology. Budgerigars, having relatively high aspect ratio wings are able to flap-glide at low flight speeds, and the proportion of time spent bounding was low at first but increased rapidly over the range of flight speeds investigated. Java sparrows, having low-aspect-ratio wings are not able to glide efficiently and thus the increase in the time spent bounding was much lower than in the budgerigars. I was also able to estimate the drag coefficient (C_{Db}) during bounds and found it to be large at lower speeds due to the high body angle during bounds, but close to 0.2 at higher speeds, when body posture became more horizontal.

To fully understand ecology and behaviour of animals we have to understand the underlying mechanisms and factors involved. Choices of flight speed will influence metabolism and migratory behaviour, wing structure influences the successful outcome of aerial predator-prey interactions, manoeuvrability or the distance an animal can migrate. All of these factors play roll in the evolution of flight and can help explain how the differences between aerial animals developed over time. Technological advances have opened up new possibilities regarding what can be studied. For example, there are still only few studies present using DPIV and high speed kinematics and in order to draw more general conclusion about birds or bats we need to investigate more species representing a wider size and morphology range. Future studies will also need to couple the aerodynamics with morphological data in comparative analyses. The rapid improvement of technology and methods available for aerodynamic studies opens new possibilities for future projects and every new study performed awakens new questions.

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Flygande vertebrater och aerodynamik

Flykt och bakomliggande aerodynamik har alltid fascinerat människor. Det är det dyraste sättet att förflytta sig på och samtidigt har flygförmågan utvecklats oberoende av varandra fyra gånger inom djurriket, hos insekter, fåglar, fladdermöss och de nu utdöda pterosaurs. Fortfarande är det dock mycket vi inte vet eller förstår vad gäller flykt. Min avhandling är bara en liten pusselbit som jag hoppas kommer att bidra till ökad förståelse och kanske avslöja åtminstone en del av hemligheter bakom fåglarnas och fladdermössens flygförmåga.

Flykt och energi

För att en fågel ska flyga framåt måste den skapa tillräckligt med energi för att övervinna två krafter: gravitation och luftmotstånd. Gravitationen, som drar fågeln nedåt, motverkas av lyftkraften medan luftmotståndet motverkas av drivkraften. Båda dessa krafter produceras av fågelns vingar (se figur 1, inledning).

Vid låga hastigheter är det mest kostsamt för fågeln att producera energin för att stödja sin kroppsmassa. Samtidigt så blir luftmotståndet på kroppen och vingarna allt större med ökande hastighet, vilket innebär att det krävs mer energi för att flyga framåt. Dessa två kostnader bildar tillsammans en U-formad effektkurva för flykt (se figur 2, inledning). Ur denna kurva kan man dra slutsatser om att det finns vissa hastigheter som är speciellt viktiga ur ekologisk synpunkt. ”Minimum power speed”, $U_{mp,}$ är den hastigheten då det är billigast att flyga och används bl. a. av lärkor som flyger i cirklar under uppvisning. ”Maximum range speed”, U_{mr}, är den hastigheten då en fågel kan flyga längst sträcka till lägsta energikostnad och det har visats användas av flera fågelarter under migration.

Detta är bara en liten inblick i fåglarnas flygmekanik. Det finns många fler faktorer som måste undersökas för att få en mer fullständig bild av djurens flygenergibudget. Alla förändringar av flyghastigheten ändrar inte bara energiproduktionen utan även vingarnas rörelse och utseendet av de luftvirvlar som produceras av fågeln och dess vingar. Fåglarna använder även olika energibesparande flygtekniker och användandet av dessa påverkas också av flyghastigheten. Allt detta kommer i sin tur att inverka på bl. a. fåglarnas migration, annat beteende och ekologi.

Vindtunnel och teknik

Vindtunnel är ett unikt hjälpmedel för att studera flygförmågan. Framförallt utgör den en kontrollerad miljö och ger även möjligheten att påverka ett flertal parametrar, som t ex flyghastigheten eller sjunkhastighet. Detta medför att man kan få en mycket bra bild av de krafter som påverkar det flygande djuret, vilket annars är svårt, om ej omöjligt, att uppskatta ute i fält. Med hjälp av höghastighetskameror kan man följa det flygande djurets rörelser och studera det noggrant bild för bild. Detta kan senare användas för djupare analys av djurets kinematik, dvs. kroppens och vingarnas rörelse, och förhoppningsvis ge en bättre förståelse av flygmekanik.

För att bättre förstå flykt använder vi oss även av flödesvisualisering, vilket innebär att man studerar de luftvirvlar som uppkommer till följd av fågelns eller fladdermössens rörelser. Luftvirvlarna varierar i storlek och form beroende på djurets flygsätt och flyghastighet. Genom att fylla vindtunnel med finkornig dimma och belysa den med laser kan vi ta bilder av de små rökpartiklarna, med kort tidsintervall mellan bilderna. Därefter kan man följa de individuella partiklarnas rörelser och skapa sig en bild av hur virvlarna formas och förflyttar sig, vilket gör att man kan se hur luftflödet påverkas av vingarna och dra slutsatser om de krafter som skapas. Resultat från flödesvisualiseringsexperiment kan alltså användas för att skapa nya teoretiska flygmodeller. Hittills har dock sådana flödesvisualiseringsförsök gjorts endast för ett fåtal fågelarter och nu har vi även undersökt luftflödet bakom flygande fladdermöss. För att formulera nya säkra och allmänna modeller och kontrollera alla hittills framtagna teorier, krävs studier av många olika fågelarter, jämförelser mellan fåglarnas och fladdermössens flygsätt samt sammanställningar av olika flygsätt som t ex glidflykt, bågflykt eller ryttling.

Fladdermöss

Fåglar och fladdermöss är de enda nu levande ryggradsdjuren som använder sig av aktiv flykt som innebär att de flaxar med vingarna för att skapa lyftkraft. Fåglar och deras flygförmåga har studerats en hel del och på senare åren har den tekniska utvecklingen gjort det möjligt att granska flygförmågan mer ingående än tidigare. Den troliga anledningen till varför forskning om fåglar har varit så vida sprid jämfört med fladdermöss, är främst att de är lättare att observera i och med att de är dagaktiva, de har haft bättre rykte om sig och det har länge funnits ornitologer som bidragit med mycket kunskaper. Fladdermössen har länge betraktats som ”mörkrets djur” och många människor är rädda för dem. De är svårare att hålla i fångenskap och när det gäller vindtunnelstudier så är de svårare att motivera till att flyga. De svenska arterna av fladdermöss är alla insektätande och vill alltså helst jaga sin mat, vilket försvårar uppsättning av experiment. Genom att vi kunde använda tropiska, nektarätande fladdermöss har vi fått möjligheten att studera deras flygförmåga under mer kontrollerade former, då djuren kan matas med nektarlösning och därmed flyga i en förutsägbar och återkommande position i vindtunneln. I de två första manus presenteras resultat av flödesvisualiserings studier som har visat att det finns väsentliga skillnader mellan fladdermössens och fåglars flygförmåga och underliggande aerodynamik.

Vid låga flyghastigheter kan fladdermössen vrida vingen så att den i princip vänds upp och ner. Detta försvinner när flyghastigheten ökar så att flygsättet börjar likna alltmer fåglarnas flygsätt. Dock kvarstår det en väsentlig skillnad. När vingen övergår från nedslag till uppslag genererar vingspetsen en virvel med negativ lyftkraft medan en virvel med positiv lyftkraft uppstår nära kroppen. Det innebär att fladdermusens vingar genererar var sin luftloop med en virvel vid spetsen och en vid kroppen. När fåglar flyger producerar deras vingar en enda sammanhållen luftloop över båda vingarna (se figur 7 och 8 i inledningen). I det tredje manuset presenteras noggrant hur fladdermössens kinematik varierar med ökande flyghastigheter. Genom att följa en mängd parametrar över ett brett spann av flyghastigheter kan man se förändringar i vingarnas och kroppens rörelse. Samtidigt så kopplar vi kinematik och de förändringar vi ser, till förändringar vi kan se i vaken, dvs. flödet bakom den flygande fladdermusen. De kvalitativa skillnaderna i flödet över fåglarnas och fladdermössens vingar utforskas vidare i det fjärde manuset. Där presenterar vi tydliga olikheter mellan de båda djurgrupperna och som kan hjälpa att i framtiden bättre förstå evolutionen av djurens flygförmåga.

Bågflykt

Eftersom det är så dyrt att flyga är det rimligt att det ska finnas ett starkt selektionstryck på att utveckla energibesparande flygmekanismer. Många fågelarter använder bl.a. glidflykt och naturkrafter från omgivningen som t ex luftvirvlar, vindar och markeffekt. En annan strategi är att använda oregelbunden flykt, då fågeln omväxlande flaxar med vingarna och pausar. I pauserna kan fågeln antingen glidflyga eller lägga ihop vingarna och ”studsa”. Det sistnämnda flygsättet kallas för bågflykt och används av många småfåglar. Det är framför allt fåglar som väger mindre än 250g och har rundade, korta vingar som använder sig av bågflykt. Man har länge undrat varför fåglar använder sig av detta ganska underliga flygsätt.

Teoretiskt borde fåglarna använda sig av glidflykt vid låga hastigheter medan bågflykt är först lönsamt vid höga hastigheter, då ökad hastighet också ökar luftmotståndet vilket då motverkas genom att fälla ihop vingarna. Dock ger detta en mycket förenklat bild av verkligheten. Ett flertal fågelarter använder bågflykt vid hastigheter mycket lägre än de som förutsägs av modeller och många fågelarter använder båda glidflykt och bågflykt fast vid olika flyghastigheter.

Det finns olika hypoteser som försöker förklara detta men ingen verkar kunna helt klargöra bågflyktens användning. Under mina försök att studera bågflykt i vindtunnel har jag tittat på bågflykt hos undulater, javafinkar och grönsiskor, med varierande resultat. Det har varit svårt att träna fåglarna till att flyga ”rätt” dvs. på ett naturligt sätt. I det sista manuset presenterar jag dock mina resultat från studier med höghastighetskameror. Jag har kunnat se att under bågflyktfasen, då en fågel inte använder sina vingar, lyckas den ändå skapa en lyftkraft som kan stödja omkring 20% av dess kroppsvikt. Även om det inte förklarar helt varför fåglar använder bågflykt vid låga hastigheter, så är denna lyftkraft tillräcklig för att förklara bågflykt vid de mellersta hastigheterna. Mina försök att lösa gåtan bakom bågflykt har alltså inte lyckats helt även om jag har lärt mig mycket om fåglarnas kapacitet att manövrera och anpassa sig till nya situationer man skapar i vindtunnel.

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List of my contributions to the papers.

Paper I. This study was planned together with my supervisors: Anders Hedenström and Christoffer Johansson. I collected all of the data with some help from CJ and Rhea von Busse. I analyzed parts of the data. The results were discussed by all of us. I participated in the writing of the paper.

Paper II. This study was planned together with my supervisors. I collected all of the data with some help from CJ and RvB. I analyzed parts of the data. The results were discussed by all of the authors. I participated in the writing of the paper.

Paper III. I planned the study together with my supervisors. I collected all of the data with help from RvB. I analyzed all the data with some help from CJ and wrote the paper.

Paper IV. This paper is based on the data collected for Paper I&II and on previously published bird data provided by A.H. I analyzed part of the data and participated in the writing process.

Paper V. I planned these experiments with my supervisor, A.H. I collected all of the data, analyzed the data and wrote the paper.