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Aerodynamic performance in bat flight

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AERODYNAMIC PERFORMANCE IN BAT FLIGHT

Aerodynamic performance in bat flight

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Abstract

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Among other things, we found hovering bats to have asymmetrical wingbeats with regard to up- and downstroke, discovered new levels of complexity in the wakes of large-eared bats, quantified the aerodynamic consequences of large ears in bat flight, and we devised a new method for automatically reconstructing the wing shapes of flying animals.

Key words
Leptonycteris yerbabuenae, Plecotus auritus, Glossophaga soricina, PIV, aerodynamics, wing morphology, aerodynamics, bats, wind tunnel, animal flight

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Aerodynamic performance in bat flight

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Till mamma och pappa.

Content

List of papers

I.   Jonas Håkansson, Anders Hedenström, York Winter, och Christoffer Johansson. (2015) The wake of hovering flight in bats. J. R. Soc. Interface 12: 20150357. doi: 10.1098/rsif.2015.0357.

II.   L. Christoffer Johansson, Jonas Håkansson, Lasse Jakobsen, och Anders Hedenström. (2016) Ear-body lift and a novel thrust generating mechanism revealed by the complex wake of brown long-eared bats (Plecotus auritus). Sci. Rep. 6, 24886; doi: 10.1038/srep24886.

III.   Jonas Håkansson, Lasse Jakobsen, Anders Hedenström och L. Christoffer Johansson. (Manuscript) Aerodynamic consequences of large ears in bat flight.

IV.   Jonas Håkansson, Anders Hedenström, Lasse Jakobsen and L. Christoffer Johansson. (Manuscript) A method for reconstructing wing shape in animal flight.

Author contributions

I. A.H. and J.H.; J.H. carried out the experiments. J.H., A.H. and L.C.J. analysed the data and drafted the manuscript. All authors gave final approval for publication.

II. L.C.J., J.H., L.J. and A.H. contributed to the planning of the study. L.C.J., J.H., L.J. and A.H. performed the experiments. L.C.J. conducted the analyses and drafted the paper. L.C.J., J.H., L.J. and A.H. contributed critical revision of the manuscript.

III. L.C.J., J.H., L.J., and A.H. contributed to the planning of the study. All authors performed the experiments on *P. auritus*. J.H. analysed bodydrag. L.C.J. and calculated total mechanical energy in the wakes. Data for *G. soricina* was acquired for a previous study (F. T. Muijres, L. C. Johansson, Y. Winter and A. Hedenström (2011). Comparative aerodynamic performance of flapping flight in two bat species using time-resolved wake visualization. Proc. R. Soc. Interface. 8, 1418-1428.) and was analysed anew for this study. J.H. wrote first draft of manuscript. L.C.J., J.H., and A.H. contributed critical revision of the manuscript.

IV. L.C.J. and J.H. planned the study. All authors performed the experiments. L.C.J. wrote the first version of the method, J.H. and L.C.J. revised and refined the method. J.H. drafted the manuscript. J.H., A. H. and L.C.J. contributed critical revision of the manuscript.

Abstract

Bats are the only mammals capable of flight, and they are the only animal flyers that are mammals. This thesis focuses on the latter of those facts, and investigates how bats fly, from an aerodynamic perspective. The data on which this thesis is based were generated by examining the airflows beneath and behind bats flying in a wind tunnel, and by examining their wing kinematics manually and automatically, using high-speed cameras. We analysed the data by writing computer scripts and interfaces that calculated forces, powers, efficiencies, and kinematical and morphological parameters.

Among other things, we found hovering bats to have asymmetrical wingbeats with regard to up- and downstroke, discovered new levels of complexity in the wakes of large-eared bats, quantified the aerodynamic consequences of large ears in bat flight, and we devised a new method for automatically reconstructing the wing shapes of flying animals.

Introduction

Birds are the most specious land vertebrates (May 1988), and among mammals, bats are the second most specious group, only outnumbered by rodents (Hedenström & Johansson 2015). Add to this that insects, most of them flying, constitute most of the described species on Earth (May 1988), and you have a strong argument for powered flight being an evolutionary highly successful mode of locomotion.

The ability to fly allows animals to use food sources otherwise unavailable to them, escape predators, and migrate great distances. This makes understanding animal flight an important part of understanding the success of the four groups of animals (insects, pterosaurs, birds, and bats) evolved to perform this impressive feat (Norberg 1990).

Humans have long been fascinated by flight, which has led to the scientific research that allowed us to take to the skies using aeroplanes (Pennycuick 2008). Originally, human flight was inspired by flying animals, but once our understanding of the physics of flight increased, theories and aeronautic models were developed and researchers started applying the theories to animals (Pennycuick 2008). Here I continue that tradition by applying aerodynamic models when investigating bat flight.

The fascination with bats stretches well beyond the limits of academia, and one does not have to search human culture for long to encounter bats. It might be their nocturnal lifestyle, the fact that some of them drink blood or their slightly demonic appearance that makes bats able to stir our imagination so. That is probably part of the reason why bats are a common theme in vampire lore, and it is certainly why the character Bruce Wayne based his alter ego, the superhero Batman, on these animals (Miller & Mazzucchelli 2007).

Bats have more practical relevance for us as well, they are important to humans as pollinators (Fleming et al. 2009), as vectors of zoonotic diseases (Gatherer 2014; Schneider et al. 2009), and as inspiration for small-scale air vehicles (Swartz et al. 2007; Yusoff et al. 2013). Understanding them is therefore (and for a number of other reasons as well) very important to us. Bats are of great interest to me. In part since they, like me, are mammals, but, to a greater degree because I think that they, rivalled by the pterosaurs, are simply the most beautiful, fascinating, and cool animal fliers.

Bat flight and lifestyle

In order to fly, two forces have to be counteracted, namely weight and drag. The weight results from the gravitational pull from the earth on the flyer and the drag results from friction and pressure on the flyer as it moves through the air (Anderson 2011). To counteract these forces, the flyer has to produce lift and thrust. An aeroplane wing produces lift by accelerating the air it passes through downwards, which gives rise to a force on the wing and the engine produces the thrust necessary to counteract the drag on the aeroplane. Animal flyers have to use their wings to produce both the lift and the thrust necessary for flight. They accomplish this by flapping their wings, producing forces approximately perpendicular to the direction the wing moves through the air.

The forces the wings produce are mirrored in the air they move through as an aerodynamic wake. This wake consists of added momentum to the air, which takes the shape of a series of vortex structures (Rayner et al. 1986; Spedding et al. 1984; Pennycuick 1988). Since the momentum is preserved (Benson 2008), one way of studying animal flight is by inspecting these vortex structures (Muijres et al. 2008; Pournazeri et al. 2012; Henningsson et al. 2008; Fuchiwaki et al. 2013; Hedenström et al. 2007; Spedding et al. 2003). Through a number of studies, a general description of the aerodynamic wake of bats has taken shape (Hedenström and Johansson 2015). At cruising speed, farthest to the right and farthest to the left the tip vortices, originating from the wingtips and being shed throughout the wingbeat can be seen (Tian et al. 2006; Hedenström et al. 2007). Wing tip vortices occur in fixed wing flight as well as in flapping flight. They occur as a result of the pressure beneath the wing being higher than above it, causing air below the wing to curl up around the wing tip (Anderson 2011). In flapping flight, the tip vortices follow the same path as the tip of the wing (Hedenström et al. 2007). In bats, the wings produce significantly more lift than the body region and in the intersection between wing and body, this gradient causes vortices known as root vortices, that spin in the opposite direction compared to the tip vortices, to shed (Hubel et al. 2012; Hedenström et al. 2007). The root vortices shed primarily during the downstroke as that is when the lift production of the wings is greatest, and therefore when the difference between lift production of the body and the wings is greatest. In fast flight, at the end of the upstroke, the hand wing sheds a vortex known as the reversed vortex dipole (Hedenström et al. 2007; Muijres, Johansson, et al. 2011), which contributes negatively to weight support production in exchange for higher thrust production (Muijres, Johansson, et al. 2012; Johansson et al. 2008). In slow flight and hovering, the lack of forward speed compels the bat to move its wings in a more complicated manner, twisting it upside down to so that the leading edge meets the airflow (Von Busse et al. 2012). The description of aerodynamic wakes in bat flight was prior to this thesis limited to forward flight in bats with rather small ears (Hubel,

Hristov, et al. 2010; Muijres et al. 2014; Muijres et al. 2008; Muijres, Bowlin, et al. 2011). In paper I, we added to the knowledge of the aerodynamics of hovering flight in bats. We determined the wake topology beneath a hovering bat and measured the mechanical power, i.e. the rate at which the bats transferred energy to the air. In paper II, we examined the structure of the wake behind a large-eared bat, *Plecotus auritus*, over a range of speeds to see how ears may influence the wake structure. We also described details of bat wakes and a novel thrust generating mechanism. In paper III we examined the quantitative aspects of flight with large ears by comparing the drag produced by the body (including the head and ears) of *P. auritus* and the mechanical power in the wake to that of a smaller-eared species, *G. soricina*.

Bat ecomorphology

Bats can be found across the globe, except in the polar areas (Simmons 2005). Although the majority of species feed on insects, we also find fruit, nectar, pollen, and, as mentioned, blood on the menu (Norberg & Rayner 1987). Accordingly, bats can be divided into groups based on feeding strategy. Any subdivision will, however, contain a degree of subjectivity, but grouping bats in this manner can yield ecologically as well as functional morphologically interesting insights (Fenton & Bogdanowicz 2002; Norberg & Rayner 1987). Gardiner et al. (2011) divided bats into four feeding groups related to aerial behaviour: commuting bats, slow-hawking bats, fast-hawking bats, and gleaning bats. Commuting bats commute between roost and feeding sites, where they feed on pollen, nectar, fruit, or blood, depending on the species. Slow-hawking bats catch insects in flight, on the wing, often in vegetation, while fast-hawking bats also catch insects in flight, but do so while flying in open areas and at higher speeds than slow-hawkers. Finally, gleaning bats catch insects on leaves, often while hovering. On the basis of this grouping, Gardiner et al. (2011) were able to statistically infer trends with regards to the relationship between morphology and foraging style. In general commuting bats tend to have small ears and short tail; slow-hawking bats have long tails and broad wings; fast-hawking bats have slender wings and small ears; and gleaning bats have large ears, broad wings, and long tails with pronounced tail membranes. Understanding the aerodynamics of bat flight involves understanding the aerodynamic implications of the variation in morphology between feeding groups. Papers II and III add to this knowledge, being the first studies to examine the aerodynamics of gleaning bats using modern flow measurements.

Echolocation and aerodynamic implications

Bats forage in the darkness of the night and while birds use vision for navigating and finding prey, bats use echolocation (Lee et al. 1992). Bats that forage in open air use echolocation predominately for prey detection, whereas bats that forage in cluttered environments rely on echolocation for both spatial orientation and food acquisition (Schnitzler et al. 2003). Bats that use a gleaning foraging strategy, i.e. catching insects on leaves in the foliage, tend to have larger ears (Gardiner, Codd, et al. 2011; Norberg 1986). The benefit of large ears in gleaning bats is quite clear, large ears amplify sound at frequencies below 15 kHz (Obrist et al. 1993), and insects rustling in the leaves generate most sound in the frequency close to 10 kHz (Goerlitz et al. 2008). Larger ears are also quite simply able to intercept a larger portion of incoming sound waves, with positive consequences for both echolocation and passive listening (Obrist et al. 1993). In addition, directionality, i.e. the ability to determine which direction a sound is coming from also improves with ear size (Zhao et al. 2003). The implication seems to be that, with regards to echolocation and passive listening, most bats would benefit from having large ears. Large ears, however, have consequences for the aerodynamics of the bat (Voigt & Lewanzik 2012). Norberg (1976) suggested that only slow flying bats can have large ears, since the parasite drag, i.e. drag originating from the ears, body, and other parts of the animal traditionally not thought to contribute to lift or thrust production (compare to the fuselage of an aeroplane), is simply too large at higher speeds.

Bats have been found to have lower aerodynamic efficiency than birds (Johansson et al. 2010; Muijres, Johansson, et al. 2012). The difference has been partly attributed to the ears of the bats resulting in reduced body lift and increased drag (Johansson et al. 2010; Muijres, Johansson, et al. 2012). For paper III, we thus hypothesized that large ears increase the parasite drag of the bat by increasing the body frontal area and making the bat less streamlined. The aerodynamic consequences of bat ears had prior to papers II and III only been studied indirectly (by inspecting wakes of bats with relatively small ears) (Johansson et al. 2010; Muijres, Johansson, et al. 2012) or by using simplified physical models of large-eared bats (Gardiner et al. 2008; Vanderelst et al. 2015). The usefulness of using static models is limited by their inability to take the flapping of the wings into consideration, especially so in cases where only the body and heads of the bats were modelled (Vanderelst et al. 2015). In papers II and III we address these concerns by qualitatively and quantitatively investigating how large ears affects the aerodynamics of bat flight.

Bat wings

Bats, birds, and insects (that fly) are similar in the sense that they all rely on flapping their wings for producing both weight support and thrust. The apparatus for doing so, though, differs greatly. Insect wings are composed of a thin membrane supported by veins, allowing the insect to control the wing mainly at the point of attachment to the thorax (Walker et al. 2014). Bat and bird wings, in comparison, are composed of altered vertebrate forelimbs, allowing for control of the shape of the wings by active means, more so in the bat than in the bird (Pennycuick 2008; Hedenström & Johansson 2015). Bird wings are composed of reduced forelimbs covered in specialised flight feathers. Feathers are made of dead keratinous material (Hedenström et al. 2009) and are therefore only controlled at the point of attachment to the bird. Birds are able to morph their wings in flight by flexing the joints in the wing to alter its span and area (Tucker 1987). Bats have wings composed of a thin membrane stretched over elongated finger bones (Norberg 1990; Hedenström & Johansson 2015; Swartz & Konow 2015). This configuration allows the bat to actively alter the morphology of the wing in flight to a high degree. The size and shape of wings, the surface area, wing span, camber (the curvature of the wing profile), angle of attack (i.e. the angle between the wing chord and the relative air velocity), and twist (the variation in angle of attack along the wing span) are all parameters that influence the aerodynamic properties of the wing, and the flexible structure of the vertebrate wings allows these parameters to be altered dynamically throughout the wingbeat (Von Busse et al. 2012). The high degree of morphing ability makes studying bat wings more challenging than other groups.

One aspect that separates bat wings from all the wings of the other extant groups of flying animals is that bat wings are highly compliant (Von Busse et al. 2012; Hedenström & Johansson 2015; Swartz 1997; Cheney et al. 2014; Galvao et al. 2006). Compliant aerofoils have aerodynamic properties that rigid wings lack. For example, compliant wings have been found to produce more lift at low speeds and at high angles of attack compared to rigid wings, possibly due to a passive increase in wing camber as response to wing loading (Song et al. 2008). However, compliant wings also produce more drag than rigid wings, possibly due to the aforementioned increase in camber and also because of compliant aerofoils being more prone to flutter than rigid wings (Tucker 1990; Hays et al. 2012). The increase in drag production related to compliant wings can be somewhat mitigated by strategies for stiffening the wing (Cheney et al. 2014). Bats have muscles pulling the wings tense, as well as trailing edge tendons (Norberg 1972), possibly allowing the bat to decrease the tendency of the wing to flutter (Cheney et al. 2014). The properties mentioned here all make studying the shape of bat wings in flight very interesting, but also challenging, since the wings morph and fold in complex ways, requiring advanced experimental setups for accurate measurements. In order to accomplish

such measurements, in paper IV, we developed a method for reconstructing the three-dimensional shape of a wing in flight. We tested the method by reconstructing the wings of bats in flight and used the reconstruction to measure aerofoil parameters along the wingspan.

Animals studied

Lesser long-nosed bat, *Leptonycteris yerbabuenae*

Leptonycteris yerbabuenae is the study species of paper I. It is a medium sized bat, weighing approximately 20 to 30 g, with a wingspan of 30 to 35 cm. Its wings are rather slender and it has an aspect ratio (wingspan divided by wing chord) of around 7. Of the four feeding categories mentioned earlier *L. yerbabuenae* is classified as a commuter, since it travels between roosts and foraging sites directly (Gardiner, Codd, et al. 2011). The bat's habitat is mainly situated in Mexico, but reaches southern Arizona and south-western New Mexico to the north, and Guatemala to the northeast. These bats migrate annually, spending the summer in the northern parts of its range and the winter in the southern parts and its annual migration range can be as long as 1,800 km (Wilkinson & Fleming 1996). On top of migrating an impressive distance, with bat standards, it is also able to engage in hovering flight, a skill that allows it to feed on the nectar of cactus flowers (Muijres 2011; Cole & Wilson 2006).

The aerodynamics of *L. yerbabuenae* has been extensively studied (Muijres, Spedding, et al. 2011; Muijres, Johansson, et al. 2011; Muijres, Johansson, et al. 2012; Muijres, Henningsson, et al. 2012; Muijres et al. 2014), but paper I is the first time the details of its wake in hovering flight has been researched.

Brown long-eared bat, *Plecotus auritus*

Plecotus auritus is the study species of paper II, III, and IV. It is a rather small bat, weighing around 10 g, and it has a wingspan close to 30 cm. Its wings are long but relatively broad, giving it an aspect ratio of around 6. Of the four feeding categories *P. auritus* is classified as a gleaner, since it feeds mainly by picking insects from foliage. It travels short distances, spending most of its time foraging within a 1.5 km radius from its roost site (Entwistle et al. 1996; Andersson & Racey 1991). It is found throughout Europe (Spitzenberger et al. 2006), and is one of the most common bat species in Sweden (Rydell 1989). *P. auritus* has very large ears. This

is believed to aid its capacity for echolocation, but more importantly, the large ears make it very good at passive listening (Gardiner et al. 2008).

The aerodynamics of *P. auritus* has been studied before (Norberg 1976b; Norberg 1976a; Harbig et al. 2013; Gardiner, Dimitriadis, et al. 2011; Gardiner et al. 2008), but prior to paper II and III, it had not been studied using modern wake measurement techniques such as particle image velocimetry (PIV).

Pallas' long-tongued bat, *Glossophaga soricina*

Glossophaga soricina is one of the study species of paper III. It is close to *P. auritus* in size, weighing around 10 g, and has a wingspan of around 25 cm. Its wings are smaller and more slender than those of *P. auritus*, and it has an aspect ratio of approximately 6.4. It lives in tropical rainforests in South and Central America and feeds on nectar, which it metabolizes at a rate comparable to hummingbirds (Voigt & Speakman 2007), i.e. very quickly for a mammal. Although it does not travel as large distances as *L. yerbabuenae*, it is still classified as a commuting bat (Gardiner, Codd, et al. 2011). *G. soricina* has a varying foraging range, with some individuals using a feeding strategy that involves defending a small feeding patch of 1.5 to 4 ha, while others use a strategy of visiting several different feeding patches over an area of 35 to 51 ha (Society & Lemke 1984).

The aerodynamics of *G. soricina* has been studied before (Johansson et al. 2008; Wolf et al. 2010; Muijres, Johansson, et al. 2011; Muijres et al. 2008; Hedenström et al. 2007), but here we make the first power estimates from modern wake measurements in this species.

Experimental setup and procedure

Wind tunnel

The experiments were performed in the Lund University low-turbulence wind tunnel (Pennycuick et al. 1997). It is a closed circuit wind tunnel with a partly open experimental section, meaning we, the researchers using it, have the ability to easily interact with the animals and the measurement equipment while doing experiments (Fig. 1). The test chamber of the wind tunnel has an octagonal cross-sectional area. Its walls are composed of exchangeable sheets of acrylic glass or wood, which are attached between steel girders. The construction allows for convenient mounting of measurement equipment, such as particle image velocimetry cameras, kinematics cameras, infrared barrier for automated feeding, and feeding tubes.

Animal training

In paper I, the bats (*L. yerbabuenae*) were trained to fly in the desired manner, i.e. to hover in front of a feeding tube. We used an automatic feeder for dispensing a droplet of honey water when the bats had hovered for a short period, and increased the period gradually, thereby teaching the bats to hover for longer and longer periods. During wind tunnel experiments, the bats resided in the settling chamber of the wind tunnel, and when they wanted to eat, they flew out in the test section, made a U-turn, and approached the feeding tube. Their access to food was limited prior to experiments, making them more motivated to feed during experiments.

In paper II, III, and IV we trained *P. auritus* bats to fly at a range of speeds in front of a feeder holding a mealworm. During the experiments, one researcher handled the bat and then let go of it so that it flew at the mealworm, while another researcher activated the data acquisition. These bats too, had limited access to food prior to experiments to make them more motivated to feed during experiments.
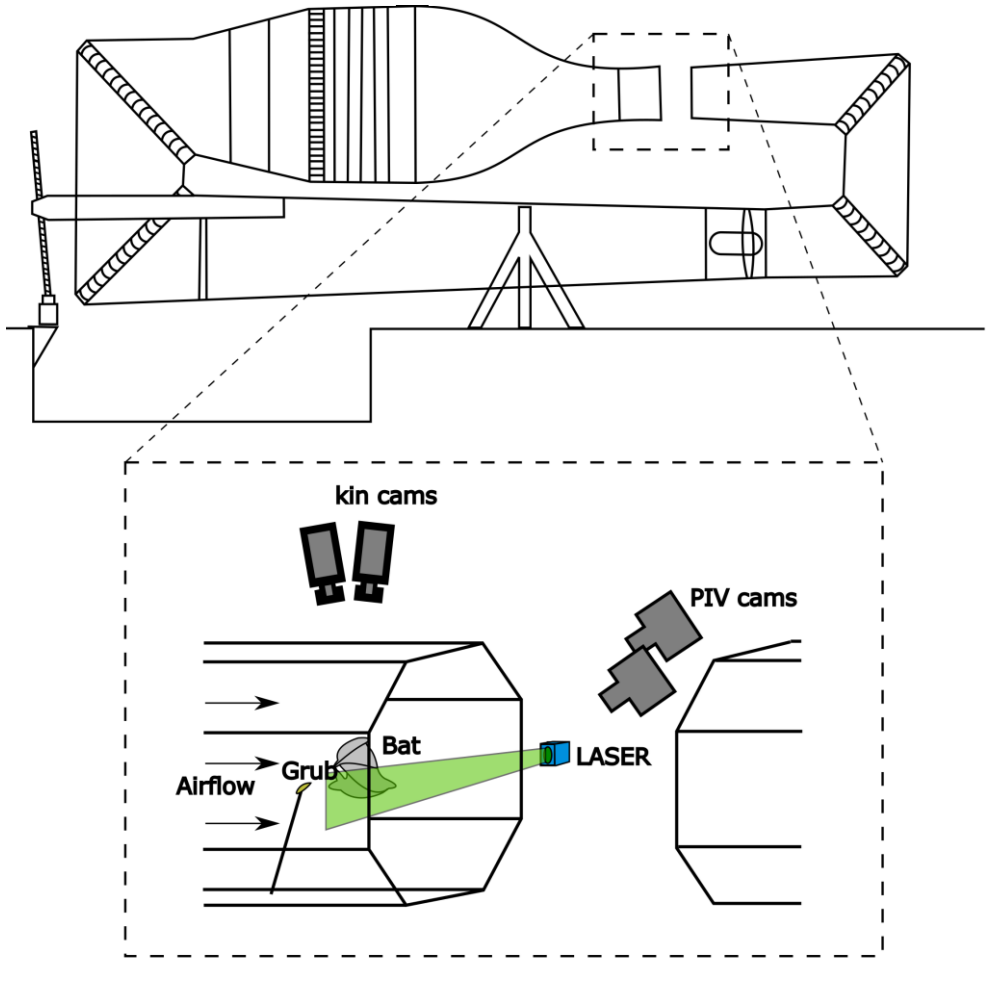
Figure 1.
Illustration of wind tunnel and setup. Kinematic cameras (kin cams) film the animal as it approaches a food source (honeywater or mealworm, a.k.a. "grub") and the flow is measured by calculating the displacement of fog particles in the laser sheet, filmed by PIV cameras.

For paper III, we used data from previous studies on *G. soricina*, a smaller-eared species, for comparing the aerodynamics of a small-eared species to that of a larger-eared species, i.e. *P. auritus*. The data was captured in 2008 (Muijres, Johansson, et al. 2011), and the bats were trained in a manner similar to what is described for *L. yerbabuenae* above.

Flow measurements

Particle Image Velocimetry (PIV) is a method for obtaining quantitative measures of fluid movement in a measurement plane. The method requires the wind tunnel to be filled with fog particles which are then illuminated, by a laser beam (LPY732 laser, Litron Lasers Ltd, Rugby, England for paper I, LDY304PIV laser, Litron Lasers Ltd, Rugby, England for paper II & III) that is spread into a sheet through a lens. One or more cameras (two High-SpeedStar3 CMOS-cameras for paper I, two LaVision Imager pro HS 4M cameras for paper II and III) capture images of the fog particles. The cameras take pairs of images within short succession, a number of times per second (200 for the *L. yerbabueanae* and *G. soricina* data, 640 for the *P. auritus* data). For each pair of images, a correlation routine is used to determine the displacement of the illuminated fog particles between the first and the second image, and thereby the displacement of the air. The displacement of the air, together with the time difference between the consecutive images allows for calculations of the velocity of the air over the measurement area. Using two or more cameras that are calibrated for stereo vision allows the air displacement perpendicular to the laser sheet to be calculated. Stereo PIV can thereby yield a three-dimensional description of the airflow in the measurement plane. For this study, we used the software DaVis (DaVis from LaVision, v. 7.2.2 for paper I, v. 8.1.5 for paper II and III) for controlling the setup and processing the raw images into useable data. After processing in DaVis, the data was in the form of matrices of velocity vectors that we could import into MATLAB (MathWorks Inc.) and perform the necessary calculations on.

Aerodynamic estimates

The particle image velocimetry setup used for papers I, II, and III, resulted in matrices of velocity vectors. In order to derive the force, energy, power, and efficiency of the wake, we therefore wrote custom scripts and interfaces that implement mathematical models of fluid dynamics.

Aerodynamic force

The most important aspect of flight is to remain airborne, which is achieved by accelerating air downwards. In doing so, an equal but opposite force acts upon the flyer, matching the force of gravity and thereby preventing the flyer from accelerating towards the ground. The second most important aspect of flight is the ability to move forward through the air. Moving forward through the air results in a drag force acting on the animal which it needs to counteract. The animal accomplishes this by accelerating air backwards, which causes the air to push the flier forward with a force called thrust. With the PIV measurement plane oriented perpendicular to the freestream airflow, the vertical component of the force produced, L_v, can be estimated from the PIV vector fields by integrating over the in plane vorticity, ω, i.e. the curl of the velocity field ($\omega = \nabla \times (v, w)$, where v and w are the in-plane components of the velocity vector), in the measurement plane according to:

$$L_v = \rho U_\infty \iint\limits_{wake\ area} \omega \cdot b(y) \cdot dA, \tag{1}$$

where U_∞ is the airspeed relative to the flyer, ρ is the density of the air, $b(y)$ is the horizontal distance to the centre of the wake, and dA is the area elements of the cross-section of the wake. Since we assumed bilateral symmetry in the wake, we measured half the wake in the experiments and doubled the resulting force. This allowed for higher resolution than what would have been achieved had we instead measured the whole wake.

In stable flight, the force generated by the wings needs to balance the weight and drag acting on the animal, as its speed would otherwise change. The drag force acting on a forward flying animal is the sum of the induced drag, D_{ind} the profile drag, D_{pro}, and the parasite drag, D_{par} (Norberg 1990). Induced drag arises from the process of altering the airflow in order to generate lift. Profile drag is the sum of the pressure drag and the friction drag of the wings, where the pressure drag is dependent on the shape of the wings and the friction drag is dependent on its surface area. Parasite drag is the drag that the less aerodynamically active parts of the animal or plane produces, including the body, the landing gear of a plane, the feet of a bird, or the ears of a bat (Anderson 2011).

In paper III, we used a wake deficit model for calculating the parasite drag force of freely flying bats, D_{par}. A wake deficit model is a method for calculating drag force of an object as the change in momentum flux in the air before it reaches the animal to after it has passed it:

$$D_{par} = \rho \iint_{\substack{body\,wake \\ area}} u(y,z) \cdot (U_\infty - u(y,z)) dA, \tag{2}$$

where $u(y,z)$ is the streamwise velocity component in the wake at position (y,z). The equation is easier understood if one considers that the product of the airspeed of the wake, the area of the wake, and the air density results in the mass rate of air passing through the plane of measurements. Multiplying this mass rate by the difference in speed gives us the change in momentum rate between before and after the object in question, which equals the drag force experienced by the object. In classical aerodynamics, the parasite drag of a flying animal can be calculated as:

$$D_{par} = \frac{\rho U_\infty^2 S_b C_{D,par}}{2}, \tag{3}$$

where S_b is the body frontal area of the flyer defined as the cross sectional area perpendicular to the airflow (Norberg 1990), and $C_{D,par}$ is the parasite drag coefficient, which represent the streamlining of the body, where a lower value represents greater streamlining.

Induced drag can be viewed as the result of adding kinetic energy to the wake when producing lift (von Busse et al. 2014). In paper III, we therefore calculated the induced drag as:

$$D_{ind} = \frac{1}{2}\rho \iint\limits_{wake\ area} (v(y,z)^2 + w(y,z)^2)\, dA, \qquad (4)$$

where $v(y,z)$ is the in-plane horizontal velocity component and $w(y,z)$ the vertical velocity component (compare to the textbook definition of kinetic energy: mass $\cdot$ speed^2/2 (Benson 2008)).

The last drag component, the profile drag of a flapping wing is very difficult to measure directly, since it is directed parallel to the relative air speed over the wing, which varies in a very complex manner during flapping flight. We therefore refrained from measuring the profile drag directly in the papers of this thesis.
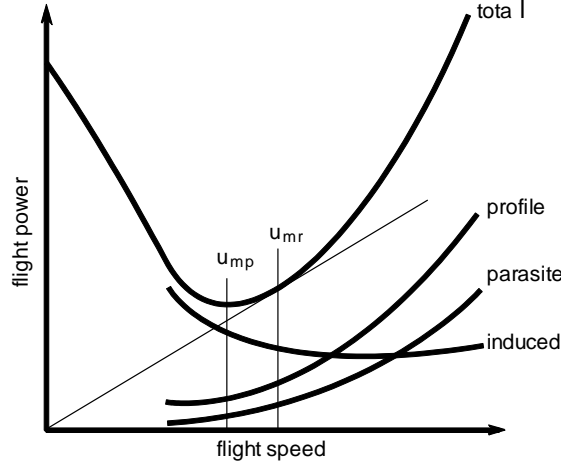
Aerodynamic power

The aerodynamic forces the animal has to produce to fly cost energy. The energy cost per unit of time is given by the power, which is defined as the product between force and speed (Benson 2008). The flying animal produces power by acting on the air to produce thrust and weight support, according to:

$$P = U_\infty \cdot D_{total}, \qquad (5)$$

where D_{total} is the sum of induced drag, profile drag, and parasite drag.

At slow flight speeds, the animal passes a smaller volume of air, and therefore has to accelerate the air to a higher downward speed in order to produce enough weight support to remain airborne (Pennycuick 2008), resulting in high levels of induced power. The parasite power, as well as the profile power, depend on the flight speed cubed, which leads to a the power increasing rapidly at higher speeds (Anderson 2011). At intermediate flight speeds, induced power is lower than at slow speed, and parasite and profile power are lower than at fast speed. Since the total mechanical power of flight is the product of total drag (see equation (5)) and flight speed, this gives rise to a U-shaped power curve when we plot the mechanical power against flight speed (Fig. 2). From the power curve ecologically relevant speeds can be inferred (Norberg 1990). The minimum power corresponds to the minimum power speed, the speed at which the flyer extends the minimal amount of energy per unit of time. If we draw a tangent to the power curve that crosses origin, the speed at the intersection between the tangent and the curve is the speed at which the animal is able to fly the largest distance per unit of energy, the maximum range speed.

Figure 2.
The aerodynamic power plotted against flight speed. The lines show how the total power (total), and the different power components, which are profile power (profile), parasite power (parasite), and induced power (induced), vary across flight speed. The U-shape of the curve is caused by the fact that flying slowly is aerodynamically demanding, since having a lower forward speed means the flyer encounters a smaller volume of air and has to accelerate this air to a higher downward speed to produce enough lift than what it would have had to if it had been flying faster and by the fact that drag forces (parasite and profile drag) increase with the forward flight speed raised to the power of two. The minimum value in power corresponds to a speed, u_{mp}, which is the minimum power speed, i.e. the speed at which the animal expends the minimum amount of energy per unit of time. The speed corresponding to the intersection between a straight line from origo tangential to the total power curve, u_{mr}, is the maximum range speed, which is the speed at which the animal is able to fly the longest distance per unit of energy.

Total mechanical power can also be seen as the kinetic energy per unit time added to the wake (von Busse et al. 2014). This can be estimated from the measurements of the velocity distribution in the wake. For best results, the energy of the entire wake should be calculated. An approximation of the whole wake area can be achieved by assuming the flow outside the area of measurement to be irrotational, which allows for reconstructing it (von Busse et al. 2014). The procedure is described in the supplement to paper III, but in short it uses the vorticity in the measurement plane to extend the velocity field beyond the measurement plane, all the way to the wind tunnel walls (by solving the Poisson's equations for the velocity potential). We can then estimate the mechanical power as:

$$P = \frac{1}{2}\rho U_\infty \iint_{\substack{wake \\ area}} |(\boldsymbol{u}(y,z) - U_\infty)^2|dA, \qquad (6)$$

where $\boldsymbol{u}(y,z)$ is the velocity vector at position *(y,z)*. We used this in paper III for calculating total mechanical power in the wakes of *P. auritus* and *G. Soricina*. Additionally, we calculated parasite power and induced power by multiplying parasite drag and induced drag by flight speed, resulting in:

$$P_{par} = \rho U_\infty \iint\limits_{\substack{body\,wake \\ area}} u(y,z) \cdot (U_\infty - u(y,z)) dA, \tag{7}$$

and:

$$P_{ind} = \frac{1}{2} \rho U_\infty \iint\limits_{wake\,area} (v(y,z)^2 + w(y,z)^2)\, dA. \tag{8}$$

Power calculations are a bit different for hovering flight and I cover that in the following section.

Actuator disk model

The actuator disk theory of flight is a theory that models a flying machine or animal as a disk through which a downward fluid speed is induced, thereby giving rise to a corresponding lift force on the flyer. Actuator models of flight have been proven suitable for analysing hovering flight, which makes sense considering their origin in the theory of helicopter flight (Gessow & Myers 1952). Central to the theory is the idea of a rotor or pair of wings accelerating air through an imagined circular disk, the so-called actuator disk, with a radius equal to the rotor radius or half the wing span of the pair of wings (Ellington 1978). Hovering flight can be seen as a special case where the airspeed is equal to zero and the lift force (in the absence of air speed, defined as the aerodynamic force antiparallel with the gravitational pull of the Earth) balances the weight of the animal.

The theory makes a number of unrealistic assumptions, sacrificing physical realism for simplicity and usability. These assumptions are the following: the air is assumed to be completely still far above the actuator disk and to accelerate uniformly as to achieve a specific speed at the moment of reaching the actuator disk, this acceleration is assumed to be constant over time, and the area of the disk is assumed to be circular.
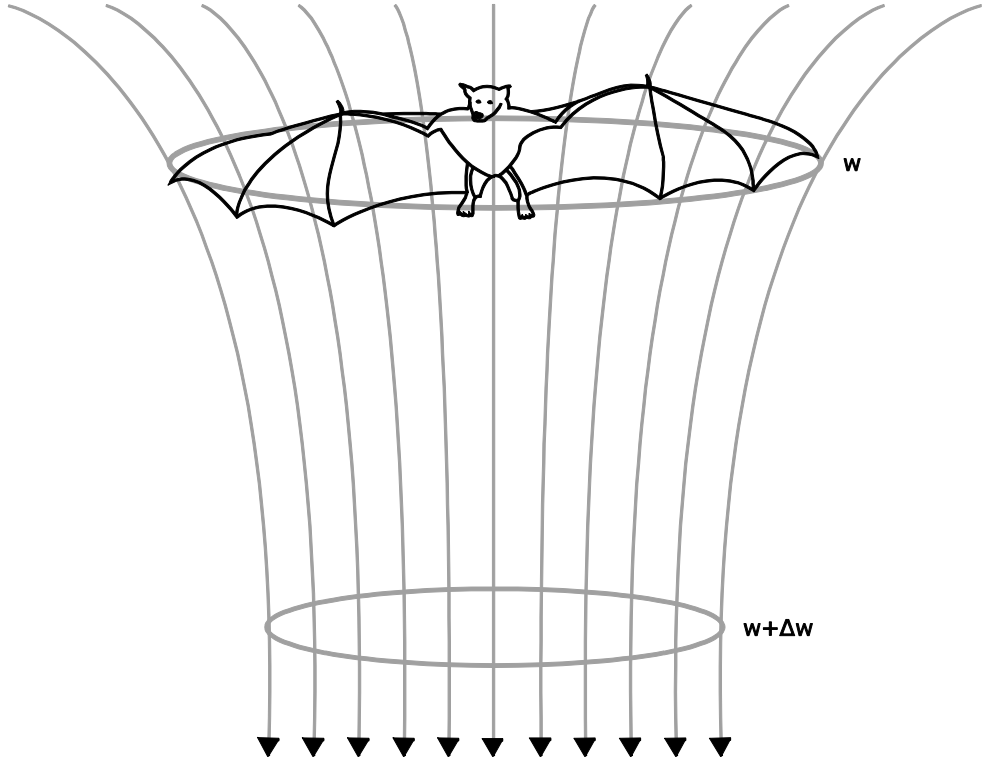
Figue 3
An illustration of the actuator model of hovering flight. At the actuator disk, the downwash speed is *w*, as it reaches the far wake, the speed has increased to *w* + *Δw* and the wake area has contracted.

The vertical component of the air velocity will be zero far above the disk, at the disk it will assume the so-called induced velocity, and far below in the mature wake, the speed will be double the induced velocity (Gessow & Myers 1952). The reason for the far wake speed being double the induced velocity is derived below.

The air accelerated through the disk will have a mass, *m* as follows:

$$m = \rho S w \Delta t, \qquad (9)$$

Where ρ is the density of the air, S is the surface area of the actuator disk, *w* is the vertical speed to which the air is accelerated as it passes through the actuator disk and Δt is the time it takes for the air to pass from above the actuator disk to below the actuator disk (Fig. 3).

Newton's second law of motion states that the external force on an object is equal to the product of the mass of the object and its acceleration. The lift force on the animal can therefore be expressed as:

$$L = m \cdot a = \rho S w \Delta t \cdot a, \tag{10}$$

where a is the acceleration of the air during the time Δt. The product of the acceleration and the time during which it acts is the change in speed. Since the air starts out with a speed of zero, the product of the acceleration a and the time Δt is equal to the speed the air has as it reaches below the actuator disk, since we are interested in how this speed differs from the induced speed, we will define it as follows:

$$\Delta t \cdot a = w + \Delta w, \tag{11}$$

which gives that

$$L = m \cdot a = \rho S w (w + \Delta w). \tag{12}$$

We can find Δw by considering the kinetic energy of the air. The product of the force a body produces and its speed gives its power. The power times the time it is applied gives the change in kinetic energy, ΔKE. The power supplied to the air is therefore equal to its change in kinetic energy divided by the time during which the power is applied. Since the air starts out with zero speed, the change in kinetic energy is simply the kinetic energy it has attained as it reaches below the actuator disk. Therefore:

$$w \cdot L = P = \frac{\Delta KE}{\Delta t} = \frac{m(w + \Delta w)^2}{\Delta t \cdot 2} = \frac{\rho S w \cdot (w + \Delta w)^2}{2}, \tag{13}$$

$$w \cdot L = \rho S w^2 (w + \Delta w) = \frac{\rho S w \cdot (w + \Delta w)^2}{2} \implies \tag{14}$$

$$\implies w = \frac{w + \Delta w}{2} \iff \tag{15}$$

$$\iff \Delta w = w. \tag{16}$$

That is to say, the speed of the air has doubled once it reaches below the actuator disk, and the lift force the animal produces can be expressed as:

$$L = m \cdot a = 2 \cdot \rho S w^2,$$ (17)

and the power the animal applies to the air as it accelerates it, the induced power, can be expressed as:

$$P_i = 2 \cdot \rho S w^3.$$ (18)

For paper I, the actuator disk theory was modified for increased physical accuracy. The basic idea of the bat accelerating the air through an area was kept, but the area was not assumed to be circular but rather defined as the area at which the downward airspeed deviated from the background speed, measured without a bat in the wind tunnel. We measured the downward airspeed over the whole area, rather than assuming it to be uniform (constant over the whole wake area). The instantaneous lift was then calculated using an alternative form of equation (17):

$$L(t) = 2 \cdot \rho \iint_{S_w(t)} w(x, y, t)^2 dA,$$ (19)

where $S_w(t)$ is the wake area at time t, and $w(x,y,t)$ the induced downwash speed at position (x, y) at time t. The average lift over a wingbeat was then calculated by taking the average of $L(t)$ over the period of the wingbeat.

We calculated the instantaneous induced aerodynamic power by modifying equation (18):

$$P_i(t) = 2 \cdot \rho \iint_{S_w(t)} w(x, y, t)^3 dA.$$ (20)

The average induced power over a wingbeat was then calculated by taking the average of $P_i(t)$ over the period of the wingbeat.

In paper I, we did not measure the vertical speed component at the actuator disk, since the bat itself occupied that position. Instead we measured the vertical speed component in the mature wake below the bat, where it has doubled in speed (see equations (13) to (16)) and where the wake area has contracted by 50% (since the

momentum is conserved, double the speed leads to half the area). This has implications for how the equations are formulated, but the physics they describe are the same. See paper I for details.

Results and discussion

Hovering flight

In paper I we examined the aerodynamics of hovering flight in *L. yerbabuenae*. We found our bats to produce the majority of the weight support during the downstroke, but the upstroke was also active and produced weight support. We showed this by visualising the flow field below the hovering bats, which showed that they generate lift producing structures originating from the upstroke. The structures formed during the upstroke were, however, weaker than the downstroke structures. Prior studies have suggested hovering bats to produce weight support during the upstroke (Norberg 1976b), but paper I is the first study to use modern flow visualisation techniques to confirm this.

Hovering flight in animals is classified in two groups, avian and normal hovering (Rayner 1979). Avian hovering is associated with a shedding of one vortex loop, or a pair of vortex loops (one for each wing), per downstroke, and for using the upstroke to recover for another downstroke. Normal hovering is thought to produce two vortex loops, or pair of vortex loops, during each wingbeat as both the up- and downstroke produce one vortex loop, or a pair of vortex loops, each (Pournazeri et al. 2012; Rayner 1979). Avian hoverers therefore produce weight support during the downstroke alone, whereas normal hoverers produce weight support during both downstroke and upstroke (ideally at a ratio of 1:1, but I believe this ideal to be mostly theoretical). Our result from hovering bats did not confirm fully to either model. I suggest the reason for bat's deviation from the two established models of hovering flight to be the fact that their wings are composed of membranes that are attached along the whole body, from shoulder to feet. During the upstroke in avian hovering, the feathers are rotated around their lengthwise axis to a low angle of attack relative to the air flow, resulting in a largely inactive upstroke (Norberg 1985; Muijres et al. 2012). Bats (as well as insects and pterosaurs) are unable to accomplish this type of inactive upstroke since their wings are built in a completely different manner. During normal hovering in insects and hummingbirds, the animal supinates its wing to a great degree during the upstroke, in effect turning it upside down (Altshuler & Dudley 2003; Tobalske et al. 2007). The great degree of supination is achievable, in part, by the wing having a rather small area of attachment to the body of the animal, allowing it to rotate at the point of attachment.

Bats (and I expect some pterosaurs to have been limited in a similar matter) are unable to rotate their wings freely, since the wing is attached along the whole body of the bat. In this way, the wing structure of bats prevent them from hovering according to any of the two proposed models, and they have to instead perform rather complex wing movements to produce enough weight support for hovering flight. Hovering bats are able to achieve a large degree of supination at the distal parts of the wings by reducing the span during the upstroke, but since the inner part of the wing is attached to the body and is not rotated, it is unable to efficiently produce lift.

We also showed our bats to produce a pair of bilateral vortex loops per wingbeat, one ring per wing, during hovering. Generating two vortex loops is less aerodynamically efficient than generating one larger one, since two rings increase the variance in the downwash, pushing it further form the theoretical ideal of a uniform downwash (Henningsson et al. 2011). The added energetic cost of producing two vortex loops is detrimental to the performance of the bat. I therefore expect the production of two vortex loops to be an unavoidable consequence of the morphology of the bat, possibly caused by the body disrupting the flow, or an adaptation conferring some advantage to the bat. Generating two vortex loops rather than a single large one has been proposed as a way of increasing manoeuvrability by improving the flyers ability to produce left-right asymmetries in force production (Pournazeri et al. 2012; Wolf et al. 2013). Enhanced ability to manoeuvre would be beneficial to an animal that moves between flowers to feed (Bomphrey et al. 2009), such as *L. yerbabuenae*. In paper II the wake of *P. auritus* flying at 1 m/s was shown to, at least in some of the sequences, produce a single vortex loop for the wing pair during the downstroke. *P. auritus* feeds by picking insects of leaves in cluttered habitats, a feeding strategy that I judge as even more dependent on ability to manoeuvre. At this stage, I therefore view the bilateral vortex loops in the wake of hovering *L. yerbabuenae* as a consequence of the body disrupting the flow rather than an adaptation for increasing manoeuvrability, but further research is needed to answer this question definitely.

In addition to qualitatively assessing the wake structure, we also used a variation on the actuator disk model to obtain measures of the induced lift force and power production over time. We found a lift force production of 108% of the weight of the bat and we found the induced power to be approximately 0.4 W. Our calculated induced power was slightly above 80% of what Dudley and Winter (2002) found by using a model for hovering insect flight developed by Ellington (Ellington 1984a; Ellington 1984b; Ellington 1984c; Ellington 1984d; Ellington 1984e; Ellington 1984f) to calculate the power requirements of hovering flight in *L. curasoe* (synonymous with *L. yerbabuenae*, Cole & Wilson 2006). The similarity in induced power to a prior study of on the same species, as well as the close to 100% weight

support that we found makes me confident that we managed to capture the entire wake of the bat.

A previous study (Muijres, Spedding, et al. 2011) examined induced power in *L. yerbabuenae* over a speed range of 2 to 7 m/s and found the induced power at 2 m/s to be approximately 0.43 W, i.e. slightly higher than what we found at hovering flight. I can imagine two possible explanations for this. The first one is that the difference is caused by differences in method or some type of measurement error. A more interesting possibility is that the induced power has a local maximum at around 2 m/s. In a study of the kinematics of flight for *L. yerbabuenae* (Von Busse et al. 2012) suggested that the bats had a harder time flying at this speed than at slower or higher speeds. If there is a local maximum of induced power at around 2 m/s, it could indicate that this flight speed constitutes an awkward transition from hovering to forward flight at which neither flight style is optimal. Were this the case, then the shape of the power curve for these bats would perhaps be better describes as W-shaped rather than U-shaped. Until a more conclusive study is performed, these musing should, however, be considered speculations.

Hovering flight is interesting from a biological perspective since it allows animals to exploit food sources otherwise unavailable to them. *L. yerbabuenae*, for instance, feeds by hovering in front of cacti flowers by licking the nectar (Cole & Wilson 2006). *P. auritus*, on the other hand, hovers in dense vegetation in which it picks insects from leaves (Andersson & Racey 1991; Rydell 1989). Determining the degree to which these sorts of differences in ecology between different hovering species of bats translates to differences in aerodynamics of hovering motivates further investigation. For instance, does the larger tail membrane of *P. auritus* (and other bats of similar morphology) affect the hovering wake structure in a discernible manner? Does the need for passive listening, and the need to not scare off prey animals impose restrictions on the manner in which gleaning bats hover? These and other questions show that paper I is far from the final word on the aerodynamics of hovering flight in bats, even if it is an important step on the way.

Flying with large ears

For papers II and III, we investigated the relationship between large external ears, aerodynamics and flight efficiency in live bats flying in a wind tunnel. In paper II we inspected the wakes of large-eared bats, *P. auritus* flying at 1 to 5 m/s. We found the ears to produce wake structures suggestive of lift generation that interacted with the wing root vortices, and thereby reduced the inner wing lift generation, suggesting a complex effect on efficiency of flight for the bat. The interaction between the aerodynamic structures originating from the ears and the wing root

vortices highlights a drawback of previous studies on model bats (Gardiner et al. 2008; Vanderelst et al. 2015), since the model bats lacked wings and thereby neglected the ear-wing interactions.

In paper III, we measured the body drag production from *P. auritus* and compared it with that of *G. soricina*. We found both bats to have higher body drag than assumed in the literature. In addition, we found *P. auritus* to have a significantly higher body drag coefficient than *G. soricina*. The effect of the larger tail membrane of *P. auritus* on the body drag coefficient cannot be properly separated from that of the ears, but previous studies point towards little influence on the body drag by the tail membrane (Gardiner, Dimitriadis, et al. 2011; Hubel et al. 2016). We therefore conclude that the difference in ear size as the most likely explanation for the difference in body drag coefficients. One apparent consequence of a higher body drag coefficient is a reduction in maximum flight speed. In our study we observed that *P. auritus* was unable to fly faster than 5 m/s, whereas *G. soricina* was able to fly as fast as 7 m/s in the same wind tunnel, in agreement with expectations. We know from earlier studies that ear size correlates with foraging strategy in bats where large eared bats prefer slow flight (Gardiner, Codd, et al. 2011; Fenton 1972; Norberg & Rayner 1987), and paper III clarifies this eco-morphological relationship with quantitative aerodynamic data.

Paper II showed the body region of *P. auritus* to generate substantial downwash, indicating that the body produces lift. In paper III, we compared the body lift of *P. auritus* to that of *G. soricina* and found *P. auritus* to produce significantly more relative body lift than *G. soricina*. Once again, we cannot determine whether or not this is a consequence of the larger ears of *P. auritus* or of its more pronounced tail membrane compared to *G. soricina*, but prior studies have not shown the tail membrane to contribute to lift production in model bats (Gardiner, Dimitriadis, et al. 2011). Neither have live bats been shown to produce any wake structures indicative of increased lift attributed to the tail in forward flight (Tatjana Y Hubel et al. 2016). The downwash of a flying animal tends to be reduced behind the body, i.e. between the points of attachment of the wings, indicating a reduction of the lift production over the body compared to over the wings (Muijres et al. 2012). A uniform downwash speed distribution is energetically optimal (Pournazeri et al. 2012), but bats have been shown to have a more noticeable downwash reduction behind the body than birds. This suggests less efficient lift production for bats than for birds, which is reflected in a lower span efficiency in bats compared to birds (Muijres, Johansson, et al. 2012). The bat's broad, blunt, less streamlined body with external ears and a noseleaf has been suggested as explanation for this, since it may reduce the lift generating ability of the body (Johansson et al. 2010; Muijres, Johansson, et al. 2012). Large ears have, however, been suggested to be able to produce extra lift (e.g. Norberg & Rayner 1987), which could possibly counteract the downwash reduction, and studies on model bats have supported this notion

(Gardiner et al. 2008; Vanderelst et al. 2015). The results from papers II and III, provide further corroboration of this idea by showing an increase in body lift production for freely flying large-eared bats compared to smaller-eared species. By producing lift of their own, the large ears of *P. auritus* potentially mitigate some of the drag cost they cause by reducing the amount of lift the bat needs to produce by flapping its wings. The body lift-to-drag ratio, a measure of aerodynamic efficiency of the body (calculated by dividing the body lift by the body drag), was not significantly different between *P. auritus* and *G. soricina*. This suggests that even though the larger ears of *P. auritus* increase drag, the extra lift compensates so that they do not significantly lower the aerodynamic efficiency of the bat body at the ecologically relevant flight speeds.

In paper III we quantified the mechanical power from the wake of *P. auritus* and compared it with that of *G. soricina* to get a quantitative measure of the aerodynamic consequences of the large difference in ear size. The power is predicted to follow a U-shaped curve with flight speed (von Busse et al. 2013; Pennycuick 2008; Heerenbrink et al. 2015), but previous attempts to measure the power from the wake did not clearly support a U-shaped relationship between mechanical power and flight speed (von Busse et al. 2014), possibly due to methodological difficulties. We found the power curves of *P. auritus* and *G. soricina* to exhibit the U-shape (e.g. Fig. 2) predicted by theory. To remove scaling effects, we compared the measured power with model predictions (Heerenbrink et al. 2015). Despite that aerodynamic factors that we measured (i.e. body drag) deviated from assumptions used in the model (see paper III for details), our measured total mechanical power conformed very well to theoretical predictions for *G. soricina*. The measured power for *P. auritus* was consistently above model predictions, suggesting a higher body drag. This leads me to believe that the theoretical models of flight (i.e. Heerenbrink et al. 2015) do well at predicting the total energetic requirements of flight, i.e. the sum of the power components, but that the details, i.e. the additional drag of large ears and the proportions of the power components needs further examining.

In paper II, we found the wake of *P. auritus* to be more complex than what previous studies on bat wakes have shown but to still largely conform to the established description of bat wakes (Hubel, Riskin, et al. 2010; Hubel et al. 2012; Hedenström et al. 2007; von Busse et al. 2014; Muijres, Johansson, et al. 2011; Johansson et al. 2008). Paper II thus, corroborates existing models of wake patterns in bat flight, and increases the applicability of these models to an additional foraging group, i.e. gleaning bats. Bat wakes have long been known to be more complex than those of birds (Hedenström et al. 2007), and paper II reveals them to be even more complex than previously thought. We judge the revealed complexity to, in part, be a consequence of the morphology of *P. auritus*, which has larger ears than any bat previously examined in PIV studies. However, we also believe the discovered complexity to be a consequence of the unprecedented recording resolution of the

setup. We revealed spiralling vortex structures around the wing tip vortex, which are caused in part by the wing tip vortex of one wingbeat not diminishing before the next wingbeat, but rather remaining and getting mixed up with the wingtip vortex of the next wingbeat. These results indicate that the circulation around the wing does not necessarily go to zero at the transition between up- and downstroke as assumed by earlier studies of force generation (Hedenström et al. 2007, Johansson et al. 2008). Additional spiralling structures, representing changes in the circulation around the wing, also rotate around the wing tip vortex. This shows that circulation changes continuously throughout the wingbeat, unlike what is assumed in traditional models of low-speed aerodynamics.

Flying slowly makes it more challenging to stay aloft, but also to manouver. In paper II, we found the bats to perform a wing pitch manoeuvre at the end of the upstroke during slow flight (i.e. 1 to 2 m/s), which we interpreted as a thrust generating mechanism at the cost of negative weight support. The speed range around 2 m/s has been suggested to be challenging for bats (Von Busse et al. 2012), and generating additional thrust could be a means of coping with this difficulty since the upstroke generates little lift at this speed range and an increased thrust production during the upstroke frees the downstroke to be used mainly for lift production. Another explanation is that the wing pitch, which occurs at the hand wing, is used for generating yaw and pitch and thereby increase manoeuvrability, which would be desirable when, for instance, preying on insects in foliage. The described mechanism shows the need for alternative mechanisms to control flight during varying flight conditions and highlights the need for further studies of how animals control their flight in different situations.

Wing surface reconstruction

Flapping flight involves a lot more than just moving the wings up and down. An actively flying animal has to continuously rotate and morph its wings throughout the wingbeats in order to generate thrust and lift (Alexander & Taliaferro 2015). A topic for researchers of animal flight is therefore to relate the aerodynamic efficiency and wake patterns of an animal to how it moves and morphs its wings (Wolf et al. 2010; Hubel, Hristov, et al. 2010). Examining the movement of animal wings has traditionally involved manually tracking movement on parts of the wings of animals (Von Busse et al. 2012; Wolf et al. 2010; Altshuler et al. 2012; Aldridge 1986; Norberg & Winter 2006), a process that is time consuming, subject to human error, and which yields relatively sparse (i.e. low resolution) data.

In paper IV, we devised a method by which the surface of an animal in flight can be reconstructed as a digital three-dimensional representation to get around these

problems. Although methods for automatically constructing the surface of an animal exists (eg. Heinold et al. 2016; Koehler et al. 2012; Bergou et al. 2011; Wolf & Konrath 2015), none of them were deemed suitable for our needs. Our requirement was a method that did not involve manually tracking points on the wing, that did not require us to paint markers or alter the animal in any way, which worked on animals lacking easily discernible patterns, and that could be used simultaneously with our particle image velocimetry (PIV) system for flow measurements. The method we developed accomplish our goals by relying on cross correlation of a random dot pattern of red laser light projected onto the animal. By using light of an alternative wavelength for the laser dots compared to the laser used by the PIV system, the light of the two systems can be separated using optical filters.

Our method provides a non-intrusive way of measuring the surface of an animal in flight alongside measurements of airflow. In addition, our method is highly automated, significantly lowering the amount of manual work required for calculating relevant morphological parameters. We achieved a satisfying degree of accuracy with our method, the root mean square error of the triangulated three-dimensional coordinates compared to a test case (a flat plate) was below 0.6 mm, which is comparable to existing alternative methods (Deetjen et al. 2017; Heinold et al. 2016; Koehler et al. 2012). We tested our method further by reconstructing the surface of a *P. auritus* during four phases of the wingbeats and measuring morphological parameters. The reconstructed surface of the *P. auritus* was detailed enough for morphological features such as ears, feet, and thumb (first digit) to be easily identifiable. Since our setup used two cameras calibrated for stereo vision, the wings need to be in view of both cameras simultaneously for successful reconstruction, which was not always the case during the more complex wing configurations (e.g. when the wing was folded or shadowed by the body). This issue can, however, be resolved by increasing the number of cameras, or potentially by the use of strategically positioned mirrors.

On the reconstructed wings we measured aerodynamically relevant morphological parameters, such as camber (curvature of the wing profile) and wing twist along the length of the wing. The parameters we measured aligned relatively well with previous studies (Pennycuick 1973; Von Busse et al. 2012; Wolf et al. 2010), and our continuous distribution of parameters along the length of the wings allowed us to reveal nuances in the variation of these parameters previously unseen. One example of the nuances previously undiscussed is how the flexibility of the membrane of the inner wing leads to a lower camber than than at the fifth digit and at the wingbase, resulting in a camber "wave" along the length of the wing.

Our method allows for detailed, quantitative, comparisons between in-flight morphology and wake structures, which can be used for improving our knowledge of how animals dynamically alter their shape to tackle the varying aerodynamic

challenges an airborne lifestyle entails. This involves both studies related to how animals control their aerodynamics, such as leading edge vortices (Muijres et al. 2008; Muijres et al. 2014), and how animals generates manoeuvres (Ros et al. 2011; Bergou et al. 2015). In addition to direct correlation between experimental data on morphology and aerodynamics, methods for reconstructing the three-dimensional shape of bats during flight can also improve robotic models of bat flight, e.g. (Yin et al. 2016) and computational modelling of bat flight (Wang et al. 2015; Viswanath et al. 2014).

Concluding remarks

Given continued efforts to describe the wakes of flying bats (e.g. Papers I, II, and III), future researchers will have a database allowing them to investigate the connection between morphology and aerodynamics statistically, which will improve our understanding of how different aspects of bat morphology relate to aerodynamic capabilities such as flight efficiency, flight control, manoeuvring flight, and flight speed. This will improve not only our understanding of the evolution of eco-morphological relationships among bats, but also our library of biological solutions to aerodynamic challenges by the use of membranous wings, which can inspire development of micro air vehicles.

This thesis adds hovering flight to the modes of flight in bats researched using modern flow measurement techniques (paper I). Additionally, it increases the number of species, and also foraging groups, that have been researched using modern flow measurement techniques, adding new information to how bats produce aerodynamic forces and adding solidity to our current understanding of how bats fly (Paper II). My research also sheds new light on the aerodynamic consequences of flying with big ears (Paper III), an area so far mostly covered by comparing bat morphology to bat ecology, or by constructing simplified models of bats and testing their aerodynamic properties. Lastly, my research has helped develop a method for constructing a three-dimensional representation of bat wings in flight, thereby allowing us to follow the dynamics of the aerodynamically relevant aspects of its shape during flight.

Research remains to be done on the areas covered in this thesis. Hovering flight in bats needs more attention, since so far only one species has been studied using modern flow measuring techniques and the generality of those results needs to be investigated by studying hovering flight in more species from more feeding categories. The aerodynamics of flying with large ears also needs further investigation. Not only to answer questions relating to how ear size affects bats of different feeding ecology, but also to separate the aerodynamics effects of large ears from those of large tail membranes. A natural next step would be to quantitatively compare the aerodynamics of bats with large ears and large tail membranes to those with large ears and small tail membranes or small ears and large tail membranes.

The results from paper II shows that we are now able to describe details of the wake that warrants studies of aerodynamic control and variation between individuals.

Together with the method developed in paper IV for reconstructing the wing surface, we should now be able to research the relationship between wing dynamics and force production to a finer degree than what has previously been done, with implications not only for the study of bat flight, but also for that of birds and insects.

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Populärvetenskaplig sammanfattning

Den här avhandlingen handlar om aerodynamik hos fladdermöss. Det vill säga, hur fladdermöss skapar de krafter som låter dem flyga, hur de påverkar luften för att åstadkomma detta, och hur deras vingar rör sig när de gör det.

Tack vare förmågan att flyga kan djur utnyttja annars otillgängliga födoämnen, undfly rovdjur, och övervintra i varmare trakter. Fördelarna med flygning blir än mer uppenbara när man tänker på att flygning utvecklats minst fyra gånger i djurriket – hos insekter, reptiler, fåglar, och däggdjur.

Arbetet jag har utfört under min tid som doktorand har till stor del varit relaterat till att räkna ut hur mycket energi det kostar fladdermöss att flyga. Jag har gjort flödesmätningar i luften bakom, eller under, fladdermöss. På detta vis har jag kunnat se hur mycket fladdermössen påverkar luften de flyger i, vilket i sin tur tillåtit mig räkna ut hur mycket energi fladdermöss tillför luften de flyger i.

Artikel I handlar om, *ryttling*, det vill säga stillastående flygning, hos *Leptonycteris yerbabuenae*, som är en nektarätande fladdermus. Ryttling hittar vi exempel på hos kolibrier, insekter, och fladdermöss, och även hos helikoptrar. För att förstå varför stillastående flygning är så intressant behövs kunskap om hur vingar fungerar. En vinge skapar lyftkraft genom att röra sig genom luften och tillföra den rörelsemängd nedåt (om den flyger framåt). När ett djur flyger framåt så passerar det en stor mängd luft som det kan påverka för att producera krafter. Ett djur som ägnar sig åt stillastående flygning rör sig inte genom luften på samma sätt, utan måste istället röra vingarna genom luften desto mer. Det är detta behov av att röra vingarna mer som gör stillastående flygning så energikrävande, och därför särskilt intressant.

I artikel I använde vi flödesmätningar under ryttlande fladdermöss för att undersöka hur mycket energi de tillförde luften, hur mycket lyftkraft de producerade under upp- respektive nedslaget, och vilka aerodynamiska virvlar den stillastående flygningen gav upphov till under fladdermusen. Vi var de första att använda modern flödesmätningsteknik för att undersöka ryttling hos fladdermöss, och därför även de första att kunna besvara frågan om vilken typ av aerodynamiska virvlar de producerar när de flyger på detta vis. Vi fann att stillastående fladdermöss producerar lyftkraft även under uppslaget, dock inte i samma utsträckning som insekter och kolibrier. Vi fann även att varje vinge producerar en individuell aerodynamisk virvel, och att de teoretiska modeller man tidigare använt för att skatta

hur mycket energi en ryttlande fladdermus tillför luften var förhållandevis korrekta, men att de möjligen underskattade energin något.

Många fladdermöss är nattaktiva. För att kunna orientera sig i mörkret använder de sig av ekolokalisation. Ekolokalisation bygger på att fladdermusen producerar ett högfrekvent ljud med sina stämband, varpå den sedan lyssnar till ekot från detta ljud, och då kan uppfatta hur ljudet studsat mot olika föremål. Med hjälp av ekolokalisation kan fladdermöss orientera sig i mörker, och det hjälper vissa insektsätande fladdermöss att lokalisera bytesdjur. För att kunna lyssna väl behöver fladdermusen yttre öron som förstärker de inkommande ljuden. Yttre öron förbättrar även fladdermusens förmåga att lyssna efter bytesdjur som prasslar i löv, eller gör ljud på andra sätt. De yttre öronen sticker dock ut från kroppen och påverkar fladdermusens aerodynamik, särskilt om de är stora. Exakt hur öronen påverkar aerodynamiken är inte helt klart. De borde ge upphov till extra vindmotstånd, men det finns även forskning som tyder på att de kan producera extra lyftkraft.

I artikel II undersökte vi de aerodynamiska spåren bakom en långörad fladdermus, *Plecotus auritus*. Vi fann att öronen och kroppen gav upphov till virvlar som tyder på att det skapas lyftkraft av kroppen och öronen. Detta betyder att öronen kanske inte är ett så stort hinder för fladdermusens flygning som man tidigare trott. Tack vare ny och förbättrad mätapparatur fann vi dessutom tidigare osedda detaljer i de aerodynamiska virvlar som fladdermusen producerar, såsom mindre virvelstrukturer som roterade kring de större virvlarna och ett nytt sätt för fladdermöss att producera aerodynamisk kraft i flygriktningen under uppslaget vid långsam flygning.

Artikel III går än djupare in på de aerodynamiska konsekvenserna av stora öron och undersöker kvantitativt hur stora öron påverkar motståndskraften som fladdermöss möter när de flyger, samt hur detta påverkar hur mycket energi fladdermöss behöver tillföra luften för att flyga. I studien undersökte vi de kvantitativa konsekvenserna på motståndskraft, lyftkraft, och energikostnad vid flygning med stora öron genom att jämföra mätningar på en art med stora öron, långörad fladdermus, och en art med små öron, *Glossophaga soricina*. Vi fann att stora öron ger upphov till betydligt mer luftmotstånd, men att de även tycks producera mer lyftkraft än mindre öron. Det luftmotstånd vi uppmätte från kroppen på en flygande fladdermus, både med stora och små öron, var betydligt högre än vad man tidigare antagit, vilket antyder att kostnaden för att flyga med stora öron är betydande.

Artikel IV beskriver en metod som vi utvecklat för att räkna ut den tredimensionella formen på ett djurs vingar under flygning. Metoden bygger på att filma djuret under flygning med två höghastighetskameror samtidigt som vi projicerar ett slumpmässigt mönster av prickar på djuret via laserljus. Med hjälp av de projicerade prickarna kan sedan den tredimensionella formen på djurets vingar härledas via automatisk mönsterigenkänning och triangulering. En av metodens främsta styrkor

är att den går att använda samtidigt som vi genomför mätningar av flödet fladdermusen producerar i luften. Detta gör det möjligt att jämför hur ett djur påverkar luften det flyger samtidigt med hur det rör sina vingar. Vi testade metoden genom att använda den på en långörad fladdermus som flög i vår vindtunnel. Med hjälp av metoden kunde vi se hur formen på fladdermusens vingar varierade längs vingspannet på ett sätt som påverkar vingarnas förmåga att skapa lyftkraft.

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Paper I

Paper II

Paper III

Paper IV