LUND UNIVERSITY

Power and Wake Dynamics of Hawkmoth Flight

Warfvinge, Kajsa

2019

[Link to publication]()

Total number of authors:
1

Power and Wake Dynamics of Hawkmoth Flight

KAJSA WARFVINGE

FACULTY OF SCIENCE | LUND UNIVERSITY

Power and Wake Dynamics
of Hawkmoth Flight

Kajsa Warfvinge

LUND
UNIVERSITY

DOCTORAL DISSERTATION

Faculty opponent

Assoc. Prof. Stacey A. Combes,
University of California, Davis

Author(s)
Kajsa Warfvinge

Title and subtitle
Power and wake dynamics of hawkmoth flight

Abstract

Aerodynamic theory states that the power required to fly is related to flight speed with a ∪-shaped curve. This has been shown in vertebrates, but insects have been proposed to have a flat, or J-shaped power curve. This means that hovering – flying at zero speed – is energy-efficient, which would explain why it is a relatively common flight mode in insects. In this thesis I show that some insects do, in fact, have a ∪-shaped power–speed relationship. I studied the flight of two hawkmoths (*M. sexta* and *M. stellatarum*) flying freely in a wind tunnel, and estimated aerodynamic power from the kinetic energy in the wake as well as from downwards velocities, using particle image velocimetry (PIV). In the first study, *M. sexta* flew at a range of speeds (1-4 ms^{-1}), and the resulting power curve constructed from the data was clearly ∪-shaped. In two separate studies I sampled the wake of *M. stellatarum* hovering, and flying at 1.5 ms^{-1}, respectively, and could show that hovering was a considerably more expensive mode of flight in this species.

   With knowledge of the power expenditure during flight one can estimate flight efficiency as well as predict certain characteristic flight speeds, which the animal should choose to optimize its flight depending on the task at hand. PIV is an impractical and expensive technique for estimating power, and so it is common, in *e.g.* migration studies, to simply use any of the available aerodynamic power models to acquire an estimate. Often these are based in aeroplane theory, and are seldom completely adapted to the special circumstances flyers operating at the scale of insects are exposed to. Here, I compared results from my power estimations with three models to evaluate the efficacy of this approach. I found that, while power in forward-flying *M. sexta* can be relatively accurately predicted by one model, its sensitivity to certain parameter choices makes predicting optimal flight speeds unreliable. A second model, specifically designed for insect hovering, severely overestimated power in hovering *M. stellatarum*.

   The taxa I have studied in this thesis – hawkmoths – are rare among the insects in that they can be easily positioned in a wind tunnel, as the nectar-feeding moths can be trained to feed from an artificial flower. As such, they can be studied when flying freely, but many other species require some form of tethering if we wish to study their flight. In tethered flight, the sensory feedback loop is corrupted, and so it is unclear how naturally a tethered insect flies. I compared kinematics and aerodynamic properties of the wake of *M. stellatarum* in free-flight as well as tethered, and found that tethered moths increased both their stroke amplitude and stroke plane angle. In addition, they had a less efficient flight.

Key words
insect flight, aerodynamics, wind tunnel, particle image velocimetry, tomo-PIV, power, *Manduca sexta*, *Macroglossum stellatarum*, hawkmoth

Classification system and/or index terms (if any)

Signature *KajsaWayh*

Date _____2019-05-08_____

DOKUMENTDATABLAD enl SIS 61 41 21

Power and Wake Dynamics of Hawkmoth Flight

Kajsa Warfvinge

LUND
UNIVERSITY

Cover illustration front: The large hawkmoth *Manduca sexta* searching for a feeder with its semi-extended proboscis (Credits: Anders Hedenström).

Cover illustration back: The hawkmoth *Macroglossum stellatarum* feeding from an artificial flower (Credits: Anders Hedenström).

CONTENTS

LIST OF PAPERS

I **The power–speed relationship is U-shaped in two free-flying hawkmoths (*Manduca sexta*)**

Warfvinge K, KleinHeerenbrink M, and Hedenström A
Journal of The Royal Society Interface, 2017. **14**, 20170372.

II **Hovering flight in hummingbird hawkmoths: wake dynamics and kinematics**

Warfvinge K, Johansson LC, and Hedenström A
(manuscript)

III **Hovering flight in hummingbird hawkmoths: aerodynamic power**

Warfvinge K, Johansson LC, and Hedenström A
(manuscript)

IV **Aerodynamic performance of hawkmoths is negatively affected by tethering**

Warfvinge K and Hedenström A
(manuscript)

Paper I is reproduced with permission of its publisher.

AUTHOR CONTRIBUTIONS

I   **KW** and AH conceived and designed the study. **KW** carried out the experiments and analysis, and drafted the manuscript. MKH and **KW** implemented the method for measuring aerodynamic power. All authors contributed to the final manuscript.

II **KW**, LCJ and AH conceived and designed the study. **KW** and LCJ carried out the experiments and analyses. **KW** drafted the manuscript. All authors contributed to the final manuscript.

III **KW**, LCJ and AH conceived and designed the study. **KW** and LCJ carried out the experiments. **KW** carried out the analyses and drafted the manuscript. All authors contributed to the final manuscript.

IV **KW** and AH conceived and designed the study. **KW** carried out the experiments and analyses and drafted the manuscript. Both authors contributed to the final manuscript.

Authors

Kajsa Warfvinge (KW), Anders Hedenström (AH), Marco KleinHeerenbrink (MKH), L. Christoffer Johansson (LCJ).

ADDITIONAL PUBLICATIONS

Wake analysis of aerodynamic components for the glide envelope of a jackdaw (Corvus monedula)

KleinHeerenbrink M, Warfvinge K, Hedenstrom A
Journal of Experimental Biology, 2016. **219**:1572–81.

Annual 10-Month Aerial Life Phase in the Common Swift Apus apus

Hedenström A, Norevik G, Warfvinge K, Andersson A, Bäckman J, Åkesson S
Current Biology, 2016. **26**:3066–70.

ABSTRACT

Aerodynamic theory states that the power required to fly is related to flight speed with a ∪-shaped curve. This has been shown in vertebrates, but insects have been proposed to have a flat, or J-shaped power curve. This means that hovering – flying at zero speed – is energy-efficient, which would explain why it is a relatively common flight mode in insects. In this thesis I show that some insects do, in fact, have a ∪-shaped power–speed relationship. I studied the flight of two hawkmoths (*M. sexta* and *M. stellatarum*) flying freely in a wind tunnel, and estimated aerodynamic power from the kinetic energy in the wake as well as from downwards velocities, using particle image velocimetry (PIV). In the first study, *M. sexta* flew at a range of speeds (1-4 ms^{-1}), and the resulting power curve constructed from the data was clearly ∪-shaped. In two separate studies I sampled the wake of *M. stellatarum* hovering, and flying at 1.5 ms^{-1}, respectively, and could show that hovering was a considerably more expensive mode of flight in this species.

With knowledge of the power expenditure during flight one can estimate flight efficiency as well as predict certain characteristic flight speeds, which the animal should choose to optimize its flight depending on the task at hand. PIV is an impractical and expensive technique for estimating power, and so it is common, in *e.g.* migration studies, to simply use any of the available aerodynamic power models to acquire an estimate. Often these are based in aeroplane theory, and are seldom completely adapted to the special circumstances flyers operating at the scale of insects are exposed to. Here, I compared results from my power estimations with three models to evaluate the efficacy of this approach. I found that, while power in forward-flying *M. sexta* can be relatively accurately predicted by one model, its sensitivity to certain parameter choices makes predicting optimal flight speeds unreliable. A second model, specifically designed for insect hovering, severely overestimated power in hovering *M. stellatarum*.

The taxa I have studied in this thesis – hawkmoths – are rare among the insects in that they can be easily positioned in a wind tunnel, as the nectar-feeding moths can be trained to feed from an artificial flower. As such, they can be studied when flying freely, but many other species require some form of tethering if we wish to study their flight. In tethered flight, the sensory feedback loop is corrupted, and so it is unclear how naturally a tethered insect flies. I compared kinematics and aerodynamic properties of the wake of *M. stellatarum* in free-flight as well as tethered, and found that tethered moths increased both their stroke amplitude and stroke plane angle. In addition, they had a less efficient flight.

SVENSK SAMMANFATTNING

Konsten att flyga har uppstått fyra gånger under evolutionens gång: hos fåglarna, fladdermössen, insekterna och de nu utdöda flygödlorna. En av dessa grupper – insekterna – har varit otroligt framgångsrik: insekter står för ungefär 80% av världens arter. Troligtvis har förmågan att flyga bidragit till deras framgång. Men trots att det finns många fördelar med att kunna flyga – man kan till exempel fly från potentiella fiender som saknar denna förmåga – är det ett väldigt energikrävande sätt att ta sig fram. Denna extra energi hade man annars kunnat lägga på andra viktiga aktiviteter, som exempelvis att producera avkomma, och därför ligger det i flygarens intresse att minimera flyktens energiåtgång. Detta kan djuret till exempel göra genom välja den energimässigt billigaste flyghastigheten. En människa som går gör av med mer energi ju snabbare den rör sig, och bör därför välja att gå väldigt långsamt om den vill spara energi. För ett flygande djur är det annorlunda: här säger fysiken att en medelsnabb hastighet är den minst energikrävande, och att djuret alltså bör välja denna om den vill hålla sig i luften med så liten energiåtgång som möjligt. Att ryttla, det vill säga stå stilla i luften, är däremot energimässigt dyrt; så även att flyga fort. Detta innebär att förhållandet mellan effekt (energi per tidsenhet) och flyghastighet teoretiskt kan beskrivas med en ∪-formad kurva. Inom insektforskningen har man dock länge trott att insekter faktiskt kan ryttla utan att göra av med mer energi än när de flyger medelfort, så att effektkurvan i stället är platt, eller har en J-form. Ett av syftena med denna avhandling har varit att ta reda på hur energiåtgången ser ut för insekter som flyger i olika hastigheter.

I mitt arbete har jag studerat två olika svärmare; tobakssvärmare och större dagsvärmare. Svärmare är ett släkte med nattfjärilar som är kända för sin goda flygförmåga. De lever på nektar som de suger upp med en lång snabel, samtidigt som de ryttlar framför en blomma. I labbet äter de även gärna sockerlösning från konstgjorda blommor, och man kan på så sätt enkelt studera deras flykt genom att placera matstationen framför sin mätutrustning. Jag har gjort experiment i en vindtunnel, och har på så sätt kunnat göra mätningar på både ryttlande och framåtflygande svärmare. I det senare fallet bestäms flyghastigheten av vindtunnelns flödeshastighet, medan djuret flyger på stället. I vindtunneln mäter vi luftens rörelser genom att släppa in mikroskopiska partiklar, och fotografera dessa när de lyses upp i ett laserskikt. Två kameror tar två bildpar i kort följd, och dessa jämförs sedan för att man ska kunna räkna ut hur luften rört sig mellan de två fotograferingsögonblicken. Detta sätt att mäta luftflöde kallas particle image velocimetry (PIV), och ger ett tvådimensionellt vektorfält med hastigheter i tre riktningar. Jag har även använt mig av tomografisk PIV, och har då fått fram hela volymer med flödeshastigheter genom att använda fyra i stället för två

kameror, samt ett tjockare laserskikt. Denna nya teknik har gjort att jag har kunnat ta fram väldigt detaljerade bilder av luftflödet som skapats av flygande svärmare – den så kallade vaken. Dessa bilder kan användas för att förstå hur olika delar av vingarna och vingslaget har bidragit till kraftbalansen. Jag har också utvecklat en metod för att räkna ut effekten från hastigheterna som uppmätts ur vaken. Jag har kunnat visa att det för båda mina studiarter är energimässigt billigast att flyga medelfort. Eftersom svärmare är väldigt beroende av att kunna ryttla (mina arter kan inte äta utan hjälp om de inte samtidigt flyger!) är det fascinerande att tänka att det samtidigt är väldigt dyrt för dem att göra detta.

Jag har mätt effekt med PIV, men detta är ett väldigt opraktiskt (och dyrt) tillvägagångssätt för de allra flesta som är intresserade av djurs energikonsumption. Därför är det vanligt att använda sig av aerodynamiska modeller för att i stället räkna ut hur mycket energi djuret borde göra av med. Många av dessa modeller är baserade på flygplansteori, men anpassade efter djur. Dock är det oerhört komplicerat att räkna ut exakt hur flödet rör sig runt flaxande vingar, och därför är de flesta modeller mycket förenklade. Eftersom insekter är väldigt mycket mindre än flygplanen som teorin är baserat på är det osäkert om det är lämpligt att använda dessa modeller för att uppskatta effekt hos insekter. Jag har därför jämfört mina uppmätta värden med modellerade sådana i både framåtflygande tobakssvärmare och ryttlande dagsvärmare. En modell designad för ryttlande insekter visade sig överskatta effekten hos dagsvärmarna i hög grad. Modellerad effekt hos framåtflygande tobakssvärmare låg däremot relativt nära de uppmätta värdena. Detta kan bero på att tobakssvärmare, med ett vingspann på cirka 10 cm, är stora insekter, och därför har en flykt som påminner mer om större djur än dagsvärmaren med sitt mindre än hälften så stora vingspann. En alternativ förklaring är att ryttlingsmodellen helt enkelt inte beskriver effekt hos svärmare särskilt bra.

Förutom att mäta och modellera energiåtgång, har jag utvärderat en metod som ibland används för att studera flygande insekter: att, istället för att låta djuret flyga fritt, fästa dess kropp på exempelvis en pinne. Insekten kan fortfarande flaxa med vingarna mer eller mindre obehindrat, men känner inga accelerationer från kroppen och får synintryck som liknar det den ser när den är stilla. Även om denna metod inte innebär att djuret flyger naturligt är den nödvändig för att kunna studera flykt hos vissa arter som inte är lika lätthanterliga som svärmare. För att undersöka vad metoden kan leda till för potentiella artefakter, lät jag dagsvärmare flyga fritt i vindtunneln, varpå jag fäste dem på en spik och lät dem flyga"en andra gång. När svärmarna var fastsatta ändrade de sättet de rörde sina vingar, och hade en energimässigt mindre effektiv flykt. Detta innebär att man bör undvika att använda denna metod om man specifikt är intresserad av att mäta energiåtgång hos insekter.

BACKGROUND

Before the invention of aircraft, humans were bound to the ground for hundreds of thousands of years by their lack of wings. Hence, it is natural for us to be fascinated by flying animals. Besides the mere appreciation of its beauty and astonishment of its ability to stay airborne, studying a bird, bat or insect can prompt many questions of how and why it does what it does. A songbird or monarch butterfly travels great distances during migration – how far can it reach? How soon can it arrive at its destination? A hawkmoth or hummingbird hovers in front of a flower in order to acquire nectar – how much energy does it need to gain from the food for it to be worth the effort?

These rather different questions are all related to energetics, and answering them requires knowledge about the power required to fly. Contrary to how the power required to walk scales with walking speed – where walking slowly can be done rather effortlessly, while running requires much more effort – a flying animal (or aeroplane) uses the least amount of power at an intermediate speed. Since the ability to manage one's energy reserves is extremely important for an individual's fitness, we can assume that there is a strong selection pressure for being able to choose the correct speed. This is of course especially important when there is a large difference in energy requirements between the most economical flight speed and the most expensive one. However, flight is generally a very expensive mode of transportation, and flight energy optimization has likely shaped the ecology for many flying species.

The optimal choice of flight speed varies between situations, and can be calculated if the relationship between flight speed and power required to fly is known. In the field of bird migration research, an aerodynamic power model first proposed by Pennycuick (1968) has been extensively used as a tool to predict an array of flight behaviours. Modified for vertebrate flight from helicopter theory, the model predicts a ∪-shaped relationship between flight speed and power required to fly. As we will see later in this text, insect flight may be less suited for aerodynamic models with their origin in aeroplane or helicopter theory, due to the very different scale these animals operate at. In fact, several computational fluid dynamic studies (where the air flow is computer-modelled around wings with more or less realistic kinematics) have suggested that a power curve for an insect might be more J-shaped, so that the power during hover is similar to the minimum power (fruit fly: Sun and Wu, 2003; bumblebee: Wu and Sun, 2005). In this thesis I have tried to answer the question of whether these types of aerodynamic models can be applied to insect flight by simultaneously

modelling and estimating, using flow visualization techniques, aerodynamic power. For the reader to be able to follow the theory behind the models, a short review of the general principles of flight is provided below. In addition, two important applications of the flight models will be expanded upon in this chapter: the prediction of flight behaviours (in the section *Optimal flight*) and estimations of flight efficiency (in *Flight energetics*).

General aerodynamic principles

A flying object, be it aeroplane or animal, needs to produce an upward force to counteract gravity in order to avoid accelerating towards the earth. To understand how the shape and angle of the wing accomplishes this, consider a fixed wing in a flow of constant speed. When air starts flowing over the wing, the flow on the downside, travelling a shorter way than that of the upper side, folds over the trailing edge and to the upper side of the wing. This develops into a vortex, the starting vortex, which is eventually shed from the trailing edge, and this leads to a stable flow. A vortex of equal magnitude, but opposite direction, is then bound to the wing (figure 1). This bound vortex is not the same particles flowing around the wing in a circle, since the free-stream velocity, (U_∞), is always higher than the circulation (Γ) of the vortex, but can be seen as differences in speed between the upper and lower side of the wing. More formally, the resulting air flow$= \Gamma + U_\infty$. As can be seen in figure 1, the circulation direction of the vortex above the wing is along the flow, which adds to the air speed, whereas circulation in the opposite direction below the wing decreases the air speed. Behind the wing, the circulation adds a downwards momentum to the air; the rate of which is a downward force. Since for every action there is an equal and opposite reaction (Newton, 1687), there is an upward force acting on the flying object – this is the lift that keeps it aloft.

Bound vortex

Resultant flow

Free flow
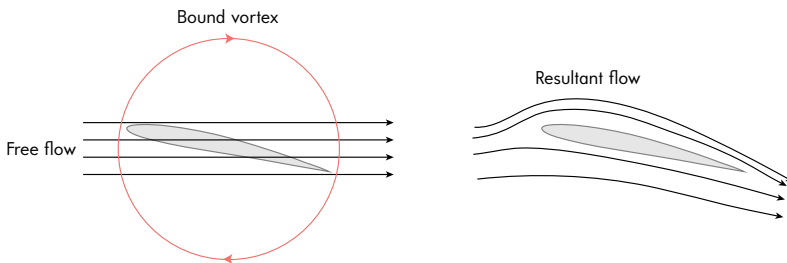
Figure 1. Free-stream velocity U_∞ and the circulation Γ of the bound vortex on the wing combine to produce the resultant flow as the wing moves through the air. As is indicated by the stream lines being closer together, the air moves faster than U_∞ on the upper side of the wing, while it moves slower than U_∞ on the lower side. The downwash can be seen in the rightmost part of the image.

In horizontal flight the upwards force completely balances the weight of the flier. In aerodynamics, we define the force perpendicular to the oncoming air as lift (L), and a consequence of producing lift is always that a (small) amount of backwards force has to be produced. This is called the induced drag (D_{ind}), and can be seen in figure 2 tilting the resultant force

backwards. At low speeds, more air needs to be deflected to create the same momentum, and this can be done by increasing the angle of attack of the wing. A result of this is that the force vector is tilted even more backwards, which means that induced drag increases as speed decreases.

Drag, in general, is defined as the force in line with the oncoming air. In addition to the induced drag, drag is created on the flier due to its shape as well as the friction between the flier and the air. When this type of drag originates on the body it is usually termed parasite drag (D_{par}), while profile drag (D_{pro}) originates on the wings. These drag components increase with speed, something that can be intuitively understood when considering the forces felt when biking in a headwind.
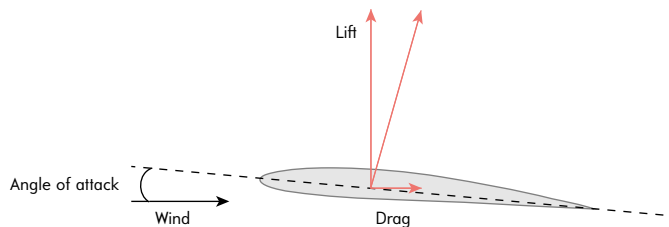
Figure 2. A wing in a steady flow, seen from the side. Lift and drag forces, as well as the resultant force are shown as red vectors. The angle of attack is defined as the angle between the wing and the air flow.

For the flier not to decelerate, drag needs to be counteracted by an opposing force, the thrust (T). In an aeroplane, thrust is created by the engines. A flying animal, lacking independent thrust production, needs other methods of compensating for the drag. When an animal is gliding, it uses its potential energy as a power source, but when not wanting to lose height, it has to flap its wings. Flapping the wings changes the angle of the relative wind that meets the wing, and this in turn changes the angle of the resultant force so that it, during downstroke, points slightly forward, producing thrust. It is only the thrust that requires energy from the animal or aeroplane. In steady (non-accelerating) flight, the thrust perfectly balances the drag, and so, to find out the energy requirements of the flying object one needs to have knowledge about the total drag; that is, the sum of the three main drag components. Multiplying the drag with the air speed gives the required power, which is the rate of energy spent. This can be done separately for each of the three components (D_{ind}, D_{par} and D_{pro}), and so power is often expressed as the sum of induced power (P_{ind}), parasite power (P_{par}) and profile power (P_{pro}). Logically, these also scale differently with flight speed (see details in *Modelling aerodynamic power*), which is what gives the power curve its ∪-shape (figure 3).

Optimal flight

I mentioned in the introduction that one of the benefits of being able to model power requirements is to be able to predict optimal flight behaviours and speeds. What, then, is
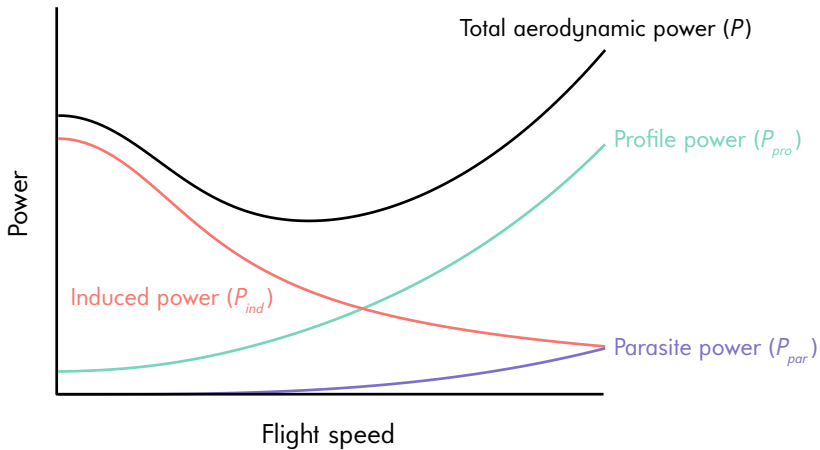
Figure 3. Example power curve visualizing how the contributions of the three power components – induced, parasite and profile power – change with speed. Morphometrics and kinematics of a hawkmoth was used to create the example. The relative magnitudes will certainly be different for a bird: there the parasite and profile power would be more similar in magnitude.

an optimal flight speed? This of course depends on multiple external factors, such as wind speed and direction. All things held constant, the task the animal is performing decides what "currency" should be optimised. For example, a skylark in display flight wishes to stay in the air for as long as possible for the minimum amount of effort, and should choose the speed that minimises power over time ("minimum power speed", U_{mp}) (Pennycuick, 1968). There exists such a non-zero speed because the power curve is ∪-shaped, and not *e.g.* linearly increasing with speed. In addition, the minimum power speed can be used by an animal whose objective is to climb as quickly as possible (Pennycuick, 1978). In this case a maximum amount of the available power can be spent on the ascent.

Should the animal instead aim to minimise power per distance flown, which is desirable during longer flights, the maximum range speed (U_{mr}) should be used (Pennycuick, 1968). This speed can be found graphically by drawing a line from the origin to the curve (see figure 4). U_{mr} is often associated with migration, but there are other aspects to consider when modelling migration flight. The animal could, to be able to hastily reach the breeding habitat, be more interested in minimising migration time than energy expenditure. Since a higher speed means more energy spent, additional stopover time to be able to replenish that energy needs to be added, and so the optimality criteria in this scenario becomes to minimise, per unit distance, the flight power plus the rate of energy accumulation in the stopover habitat (Hedenström and Alerstam, 1995). This can be seen graphically in figure 4 as the speed where the tangent drawn from minus the net energy rate touches the curve. This speed (U_{mt}) is always higher than U_{mr}.

It has become obvious that predicting any of these flight behaviours requires knowledge about the shape and magnitude of the power curve, which in itself can be rather sensitive to
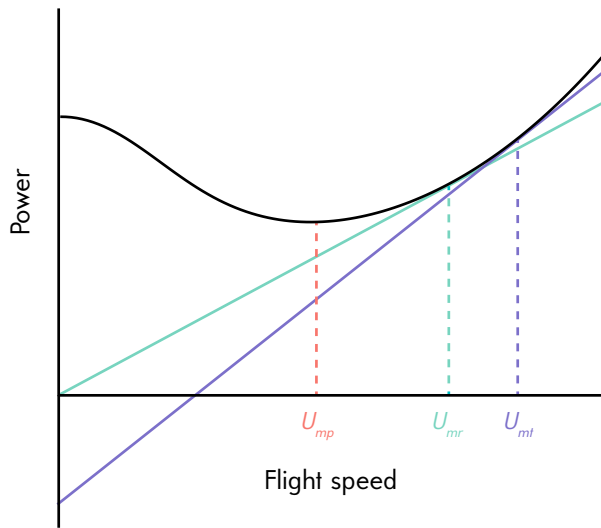
Figure 4. Characteristic speeds found graphically from a power curve: minimum power speed (U_{mp}), maximum range speed (U_{mr}) and migration flight speed (U_{mt}).

difficult to measure parameters, such as drag coefficients. However, there is an additional complication: the modelling is done on the level of aerodynamics – with the rate of energy that is added to the air – while the optimisation currency actually used by the animal is probably something like "perceived effort". Are these currencies interchangeable? As we will see, this is a rather complex question.

Flight energetics

Consider a male *Manduca sexta* hawkmoth, a species which I studied in paper I, searching for a female by means of a pheromone signal. The moth wants to be able to fly for as long as possible to maximise the chance of encountering a possible mate. Just prior to beginning the search, it has consumed a small amount of energy in the form of nectar. This energy is now stored as chemical energy, and the rate at which it depletes (the optimisation currency in this case) is often referred to as the metabolic power (P_{met}). The moth's flight muscles transform some of this power to mechanical power (P_{mech}) to be able to move the wings and produce flight forces, while some portion will be lost as heat (see figure 5). The ratio of P_{mech} to P_{met} can be seen as a measure of the efficiency of the flight muscles. It is not, however, directly a measure of the efficiency of the flight of the animal. This is because when flapping its wings, the moth needs to both move the air (the desired outcome) and accelerate and decelerate its wings (which could be considered "lost" energy). The power due to wing movements is termed inertial power (P_{acc}), while the rate of energy that is deposited into the air is the

aerodynamic power (P_{aero}), which is the focus of this thesis.
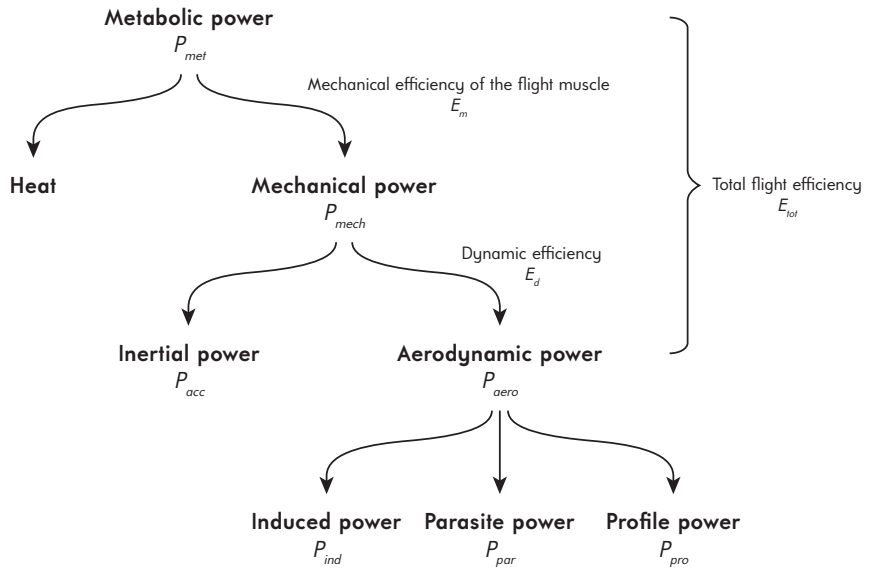
Figure 5. Energetics pathway for a flying animal, from metabolic energy input to the aerodynamic power components.

Consequently, our moth could economise its flight not only by tweaking aerodynamic parameters like drag coefficients, but have efficiently working flight muscles (E_m = muscle efficiency) and/or efficient translation of mechanical power to aerodynamic power (E_d = dynamic efficiency). For an estimation of E_m, one first needs to measure the P_{met}. Since the flight muscle used by *M. sexta* is assumed to work aerobically (Stevenson and Josephson, 1990), measurements of oxygen consumption or carbon dioxide release have been used multiple times for this purpose (hawkmoths: Bartholomew and Casey; Casey, 1978; 1976; fruit flies: Dickinson and Lighton, 1995; honey bees: Nachtigall *et al.*, 1989). Casey (1976) estimated that the moth in our example (with a body mass of around 2 g) generates approximately 0.4 W during hovering.

To get the efficiency of the flight muscles, we need to compare this value to P_{mech}. This can be measured with the work-loop technique, used by *e.g.* Stevenson and Josephson (1990) on *M. sexta* and Josephson (1997) on bumblebees. With this method, the flight muscles are stimulated with electrodes, and an ergometer measures the work done by the muscles. The power output can then be calculated as the product of the work and the cycle frequency. The work (and power) varies with muscle temperature as well as cycle frequency. In this manner, Stevenson and Josephson (1990) measured the maximum power available from the flight muscle of *M. sexta* to be approximately 90 $W\,kg^{-1}$ of muscle mass. This maximum could be found at a cycle frequency very close to the wingbeat frequency of the freeflying *M. sextas* in paper I: approximately 28 Hz. Assuming the flight muscle takes up between 21 and 34% of the total body mass of the moth (Marden, 1987; Stevenson and Josephson, 1990) this yields a maximum muscle efficiency of 10-15%, slightly lower than that of vertebrate

flight muscle (18-23%; Engel *et al.*, 2010). Similar values have been measured in fruit flies (Dickinson and Lighton, 1995). Worth noting when comparing muscle efficiencies of fruit flies and hawmoths are their different muscle types. While for example moths, locusts and dragonflies have so-called synchronous muscles that require one nerve impulse for each wingstroke, many other insect groups, such as flies, bumblebees and beetles have the more efficient asynchronous muscle that produces multiple contractions for each nerve impulse.

The next step in the energy pathway deals with how efficiently mechanical energy is translated into aerodynamic energy, represented in figure 5 as E_d. Sun and Wu (2003) showed that there exists a scaling relationship: smaller insects like fruitflies need to use more power to create aerodynamic forces (since the air is relatively "stickier" to them), while larger species like the hawkmoths have much larger inertial power requirements. This means that especially large species can benefit from elastically storing energy in the following way: At the start of each up- and downstroke the wings have to be accelerated, which requires energy, while the subsequent deceleration instead releases energy. This could theoretically be directly used to create aerodynamic forces, it could be stored as elastic energy, or be lost as heat. At least three possible mechanisms for elastic storage in insects have been proposed: the elastic protein resilin found in the cuticle of some insects (*e.g.* locusts; Jensen and Weis-Fogh, 1962), thick filaments inside the muscle itself (only asynchronous muscle, *e.g* fruit flies; Dickinson *et al.*, 2005) and cross-bridges between filaments, driven by temperature gradients in the muscle (hawkmoths; George *et al.*, 2013). While it has long been proposed (see *e.g.* Ellington, 1984c) that hawkmoths do save a significant amount of energy by means of elastic storage, it is not clear how much.

Finally, what is probably most interesting from the insect's point of view is the total efficiency of the flight: $E_{tot} = P_{aero}/P_{met}$. Aerodynamic power is usually only modelled, but in paper I I measured P_{aero} values of ~0.02 W, yielding a total flight efficiency of approximately 5% for *M. sexta*.

While it is, from a physiological point of view, interesting to know the efficiency of the muscles and the flight itself, most studies on this topic have unfortunately only been focussed on hovering flight. This opens the question of whether the animals operate equally efficient at all flight speeds. Returning to the moth in our example; since it wishes to maximise its air time, it chooses to fly at the speed that minimises the rate at which it consumes the nectar. If the efficiency of all the steps in the pathway pictured in figure 5 are, as has often been assumed, unaffected by flight speed, this speed would be exactly the U_{mp} found in the aerodynamic power curve in figure 4. An indication that the efficiency of at least some insects are speed-independent can be found when comparing the oxygen consumption measurements with kinematics-based aerodynamic models of bumblebees flying at 0-4 ms^{-1} (P_{met}: Ellington *et al.*, 1990; P_{aero}: Dudley and Ellington, 1990). In both instances, very flat and similarly shaped power "curves" were found. This is, however, the only time a metabolic power curve has been measured in an insect, and considering that bumblebees have asynchronous flight muscles, it is questionable to what extent this result can be extended to *e.g.* hawkmoths.

What's so special about insect flight?

Previously we imagined the flow around a wing as a steady free-stream flow superimposed on a constant, bound vortex. This is approximately true for aeroplane flight – in fact, the bound vortex is what leaves the wings as wingtip vortices and sometimes creates the characteristic trails that are left behind in the sky. When studying animal flight, a clearly more dynamic system, we often use a quasi-steady approach: we imagine the flow around a flapping wing as a series of moments where the flow is steady and unaffected by what came before. Doing this, we can measure the lift and drag coefficients on fixed wings at different angles of attack and model the flow around the moving wing using these numbers. However, this approach has proved somewhat unreliable for insect flight. This can be illustrated with the popular myth that claims that the bumblebee cannot fly (or, at least, that science fails to explain how). If quasi-steady analysis is conducted on a bumblebee, or, in fact, on many other insects, it will (if using steady-state estimates of parameters) not be able to explain how forces sufficient for lifting the animal are being produced. This is because several other lift-enhancing features are not accounted for with this simplified approach.

To better understand why a quasi-steady assumption may not be realistic, consider that a typical insect wingbeat consists of four phases: two translational (mid-downstroke and mid-upstroke) and two rotational phases (pronation; the transition between up- and downstroke, and supination; the transition between down- and upstroke). While the translational phases may or may not behave in line with the steady assumption, the rotations definitely do not. As the air to a small insect behaves relatively viscously (insects have a lower Reynolds number, Re, which is the ratio of inertial forces to viscous forces), it drags some air with the wings during rotation, which creates a force. This is similar to throwing a curve ball – the spin will give the ball some sideways force, making it curve. The direction of the force created by the wing rotation will depend on the timing. Dickinson *et al.* (1999) showed, using a mechanical model based on fruit fly morphology and kinematics, that a rotation slightly before the wing changes direction gives an upwards force, while a downwards force is created when the rotation happens after the change in direction.

The arguably most important unsteady effect is the leading-edge vortex, or LEV, illustrated in figure 6. Long known to be a lift-enhancing feature on delta winged aircraft (see *e.g.* Maltby *et al.*, 1965), it has been found accounting for a considerable part of the total lift production in hawkmoths (*M. sexta*: Bomphrey *et al.*, 2005; *Macroglossum stellatarum*: Johansson *et al.*, 2013) and further studied in bumblebees (Bomphrey *et al.*, 2009), dragonflies (Thomas *et al.*, 2004) and mechanical flappers based on wing shape and kinematics of hawkmoths (Berg and Ellington, 1997), fruit flies (Birch and Dickinson, 2001) and dragonflies (Lu and Shen, 2008). The idea that this is a mechanism found in all smaller, slow-moving animals is strengthened by the discoveries of a LEV in both bats (Muijres *et al.*, 2008) and birds (Muijres *et al.*, 2012) at low speeds.

The mechanism that causes the LEV on insect wings was first explained by Ellington *et al.* (1996) as a delayed stall, using smoke visualisations of the flow around *M. sexta* wings and a mechanical flapper. Under normal conditions, a wing that has a very large angle of
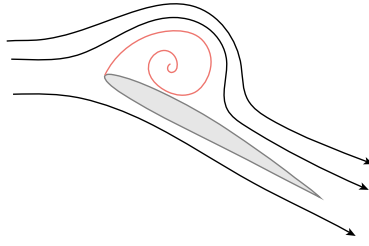
Figure 6. Flow over an insect wing at high angle of attack: a leading edge vortex (LEV) has formed at the front of the wing.

attack is stalled – the air detaches from the wing, which then loses most of its lift force and instead produces a large amount of drag. In insect flight, however, the stall process is delayed when a small vortex forms at the leading edge of the wing (the edge that meets the air), causing the air to reattach to the trailing parts of the wing, even at angles of attack large enough that the wing would normally stall. This way, the wing can more effectively impart downward momentum on the air than would be possible without the vortex. A LEV created by delayed stall grows during the wingstroke, and should, in theory, at some point shed from the wing, causing the wing to stall. However, this is not the case for insects (it would be very detrimental!), which has prompted several studies trying to explain the mechanism behind the stabilisation of the LEV; most suggesting that spanwise flow transports energy away from the LEV, preventing it from growing too large (Birch and Dickinson, 2001; Ellington *et al.*, 1996; Liu *et al.*, 1998).

Weis-Fogh (1973) described a more sparingly used lift-enhancing mechanism in the small, parasitic wasp *Encarsia formosa*: the clap-and-fling, where the two wings clap together at the end of upstroke followed by being rapidly flung apart. A variation is the clap-and-peel, where the wings are instead peeled apart, starting with the leading edge. This variant has been found in *e.g.* butterflies (Srygley and Thomas, 2002), damselflies (Marden, 1987), moths and tethered fruit flies (Ellington, 1984a). The main benefit has been proposed to be to rapidly increase circulation on the wings at the beginning of downstroke (Weis-Fogh, 1973) and/or produce a LEV (Lehmann *et al.*, 2005). Marden (1987) estimated the total muscle-mass-specific lift increase to be 25% in species utilising this mechanism. As the clap-and-fling produces a very short peak in force production, Lehmann *et al.* (2005) suggested that it is mainly a useful mechanism during manoeuvres.

THESIS AIMS

The main aim of this thesis was to evaluate the available methods of modelling aerodynamic power in insects. I have done this by estimating power from the wake while also performing the morphological and kinematic measurements required as input into the different models. The models I have reviewed are not necessarily the most realistic ones for predicting insect flight power – in fact they are all quasi-steady models, which we have already seen does not reflect insect flight well. The models are however relatively approachable as they do not require particularly elaborate measurements to be able to use. Additionally, they are "classic" models that have been used relatively ubiquitously in the literature, often with little or no evaluation. I have studied only hawkmoth flight, but none of the models are specific to moths.

All models I have evaluated require parameters that need to be experimentally estimated in order for the model to accurately predict aerodynamic power. Some of these estimations have been produced with tethered animals, but it has previously been unknown to what extent tethering affects the flight of insects. Therefore, a second aim of this thesis was to clarify the effects of tethering on kinematics, flight forces and, especially, energy efficiency in insect flight.

Finally, I aimed to determine whether insects can have a ∪-shaped power curve, something that is predicted by the aerodynamic models and would have great effects on the ecology of the animals.

METHODOLOGY

Study animals

In this thesis I have studied the flight of two species of hawkmoths; *Manduca sexta* and *Macroglossum stellatarum*.

About the species and genus

Hawkmoths, or *Sphingidae*, is a family of moths (*Lepidoptera*) well known for their excellent flight skills. Most species are nocturnal or crepuscular (primarily active during dusk or dawn), although some day-active species exist – for example *M. stellatarum*. Many hawkmoths, including both my study species, have a long proboscis with which they drink nectar while hovering in front of a flower. As a result, hawkmoths are very stable hoverers, and are sometimes mistaken for hummingbirds in the wild. The fact that they are nectar feeders may have helped in their popularity as research subjects, as it is relatively easy to control their position by providing a sugar solution in an artificial feeder. In addition to their skill in slow flight, hawkmoths can fly fast and for extended periods of time; some species (including *M. stellatarum*) even perform annual long-distance migrations. Hawkmoths have four wings, but are functionally two-winged as the larger forewing and smaller hindwing are coupled during flight.

With a wingspan of approximately 10 cm *M. sexta* (Carolina sphinx moth) is one of the largest hawkmoths. Native to the Americas, the species is considered a pest on *Solanaceous* plants, including tobacco and tomato. *M. sexta* is perhaps the most ubiquitously studied hawkmoth, and is a model organism across a variety of biological disciplines, such as muscle physiology, neurology and aerodynamics.

M. stellatarum (Hummingbird hawkmoth) is a smaller species whose flight has not been as well studied as that of *M. sexta*. It is distributed throughout Afro-Eurasia, but prefers warmer climates during breeding. Uniquely among its European relatives, the hummingbird hawkmoth winters in adult form.

Animal training

All individuals used in experiments were acquired as pupae from the Lund University Vision Group (*M. stellatarum*) and Swedish University of Agricultural Sciences (*M. sexta*). Both species are attracted to the color blue (Cutler *et al.*, 1995; Kelber, 1997), and were trained to feed from artificial, blue flowers that were filled with a 10-15% sugar solution. *M. sexta* requires olfactory stimuli to start their feeding behaviour (Kelber *et al.*, 2003), and so a drop of lavender oil was added to their food. Each moth was in turn let into a training cage and was not removed until it had located, and fed from, the feeder. During training the feeders were relatively large (see figure 7), but were gradually reduced in size to minimize the effect on the air flow in the wind tunnel during experiments.

When not used in experiments the *M. sexta* were kept in cloth cages approximately $0.4 \times 0.4 \times 0.4$ m in size. The lighting scheme in the cages was reversed, so that the crepuscular moths would only be active during work hours. The moths were occasionally rather active, and although the cages were made from a soft material, wing wear was difficult to completely avoid. Therefore the window for conducting experiments on this species was very limited.

M. stellatarum, on the other hand, could be kept completely inactive by being kept in small paper boxes, due to their day-active nature. No special light scheme was therefore necessary. In addition, the fact that the species winters in adult form allowed the moths to be stored in a refrigerator when longer breaks in experiments were necessary.

Figure 7. *M. stellatarum* feeding from a a large artificial flower during training.

The wind tunnel

The wind tunnel is a useful tool when studying flight, as it lets the animal stay in one place while the air moves over its wings and body. This makes it considerably easier to perform various measurements as it allows for an experimental setup fixed in place. Wind tunnels are widely used for studying the aerodynamics of aeroplanes, but very few wind tunnels designed for animal flight exist. One such tunnel is the Lund University wind tunnel (figure

8), in which all experiments in this thesis have been conducted. Being originally built for bird flight, the structure is rather large: 21 m long and 8 m tall. The tunnel is closed-circuit, meaning the air circulates around the length of the tunnel, as well as tiltable; however this feature has not been used in any of my experiments. For easy handling of the test subjects during experiments, the wind tunnel has an open test section 1.08 m in height and 1.20 m in width.

To be able to collect reliable data from wind tunnel experiments, it is important that the turbulence levels in the tunnel are low – in the tunnel used here they are less than 0.04% when the wind speed is 10 ms^{-1} (Pennycuick *et al.*, 1997). The low levels have been achieved by a combination of a honeycomb, wire mesh screens and a high contraction ratio. Passing through the honeycomb and screens, which are located in the widest section of the tunnel (approximately 14 m^2), forces the flow to become more laminar and reduces small-scale turbulence. Directly downstream, the tunnel contracts so that the cross-sectional area is 12.25 times smaller than at the widest section. This speeds up the air flow by a factor of 12.25. The residual turbulence is however not affected by the increase in speed, and so ends up a very small proportion of the flow in the test section.
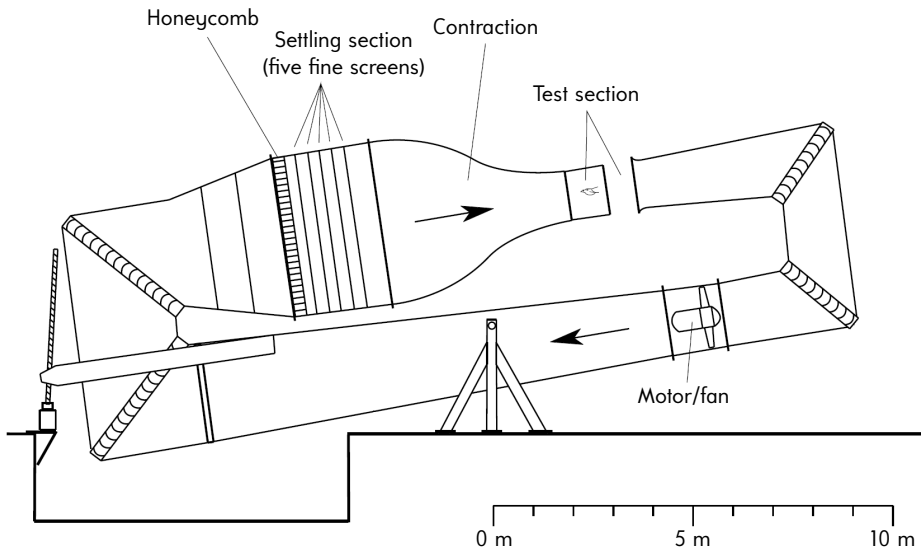
Figure 8. Lund University wind tunnel, after Pennycuick *et al.* (1997).

Working with insects in the tunnel

While the Lund University wind tunnel was designed with birds in mind, it is still possible to use for insect flight studies. Some practical details limits its convenience: First, the relatively large test section often made it difficult for the moths in my experiments to locate the feeder.

In the experiments with the smaller species *M. stellatarum*, the feeder was approximately 10 mm, which is less than 1% of the width, height and length of the test section. In the cases where a moth seemed unable to find the feeder, a larger, blue disk could be used to guide the individual to the correct location. Secondly, the openness of the test section proved to be impractical when working with very small animals with unpredictable flight behaviour. Thus, it was sealed with soft cloth, sometimes allowing for a researcher to have access to the animals by being partially sealed in (though without disturbing the flow).

A general issue with animals flying in a wind tunnel is that the unnatural setting may cause the flyer to behave differently than it would in the wild. Specifically, reaching the natural maximum flight speed is something that several studies (mainly on birds) have reported to be difficult (Engel *et al.*, 2010). In paper I, we may have to take this into consideration, as we explored nearly the full range of flight speeds in *M. sexta*. However, in none of the studies with *M. stellatarum* was the maximum flight speed of the moths reached during experiments.

One of the reasons why a wind tunnel is an unnatural environment is that the animal receives no visual feedback when flying. While Kern and Varjú (1998) have shown that visual feedback is important for the flight of hawkmoths, our study animals showed little difficulties flying stably in place in the tunnel at cruising speeds. For *M. stellatarum*, a slight alteration to the tunnel in the form of patterned paper covering the acrylic walls was needed to achieve a stable flight. This limited reflections from the lights as well as provided visual reference points. *M. sexta* flew naturally without any such measure.

Tethering

Fixing the study subject to a rigid or movable tether is a common practice in insect flight studies. While historically it has been common to simply glue the animal's abdomen to a metal rod, more complex and dynamic setups have since been developed. When using parameter values found in the literature in *e.g.* power models or efficiency estimations, some of these estimations will undoubtedly have been performed on tethered animals, but the effects of tethering have not before been fully investigated. Therefore I have dedicated a part of this thesis (paper IV) to evaluating the effects that tethering can have on kinematics and flight efficiency (using *M. stellatarum* as a study species). I employed a simple tethering technique, where the abdomen was glued to a small nail at the approximate angle with which it was normally held during forward flight. Flight was induced by lightly touching the posterior end of the abdomen, and recordings were made only in cases where the insect appeared to be flying naturally.

Flow visualization

Vortex wakes

From a previous chapter we know that a wing releases vortices in flight. These form a wake behind the flying animal, something that is often described as an aerodynamic footprint in the air. The wake holds information about the forces produced during flight, and can be studied to determine the magnitude of the forces as well as, in theory, the timing of vortex shedding. Kokshaysky (1979) visualized the first vortex wake from an animal by photographing well-lit clouds of sawdust, which he allowed small passerines to fly through. Later, smoke as well as helium-filled bubbles suspended in air have been used for visualizing the flow produced by flying animals (*e.g.* Spedding *et al.*, 1984). These early wake visualizations primarily showed two types of wakes: a vortex ring shed from each wingbeat (Grodnitsky and Morozov, 1993; Spedding, 1986) or wingstroke (Brodsky, 1991), and two continuously shed vortices released from the wing tips (Spedding, 1987). This was incorrectly interpreted as different "gaits", but as technology has progressed we have seen both continuously varying wake topologies (Spedding *et al.*, 2003) and significantly more complex structures than the ring. Figure 9 shows variations of the vortex ring model proposed for different taxa, with further details found in paper II.

Particle image velocimetry (PIV)

In recent times, particle image velocimetry (PIV) has been the primary method of visualizing wakes. In contrast to earlier methods, PIV allows for a quantitative as well as qualitative characterization of the wake. Since the first PIV study of freely flying animals – with a thrush nightingale (*Luscinia luscinia*) as the test subject (Spedding *et al.*, 2003) – numerous studies have used this method for estimating aerodynamic forces and flight performance in birds, bats and insects.

The principle behind PIV is as follows: The air is seeded with microscopic particles (in my experiments in the order of 10^{-6} m in diameter), and lit up in a thin sheet with a pulsing laser. The sheet is produced by letting a laser beam travel through one or more lenses, which allows the researcher to control its width and thickness. Cameras take two photos of the laser lit particles in quick succession, and by comparing these images we can deduce how the air moved in the elapsed time. This is done computationally in small windows across the image, and results in a vector field where each vector represents the air flow at one window position. Modern PIV systems generates 200-1000 such image pairs each second, and so these resulting vector fields may be stitched together to give a quasi-3D view of the wake. If one camera is used, only velocities in the plane can be measured. With a stereo-setup (two cameras) also out-of-plane velocities are obtained, although with less certainty than velocities in the measurement plane (Prasad, 2000). This is partly a general problem with stereoscopic images, and partly an effect of particles moving out of the measurement plane
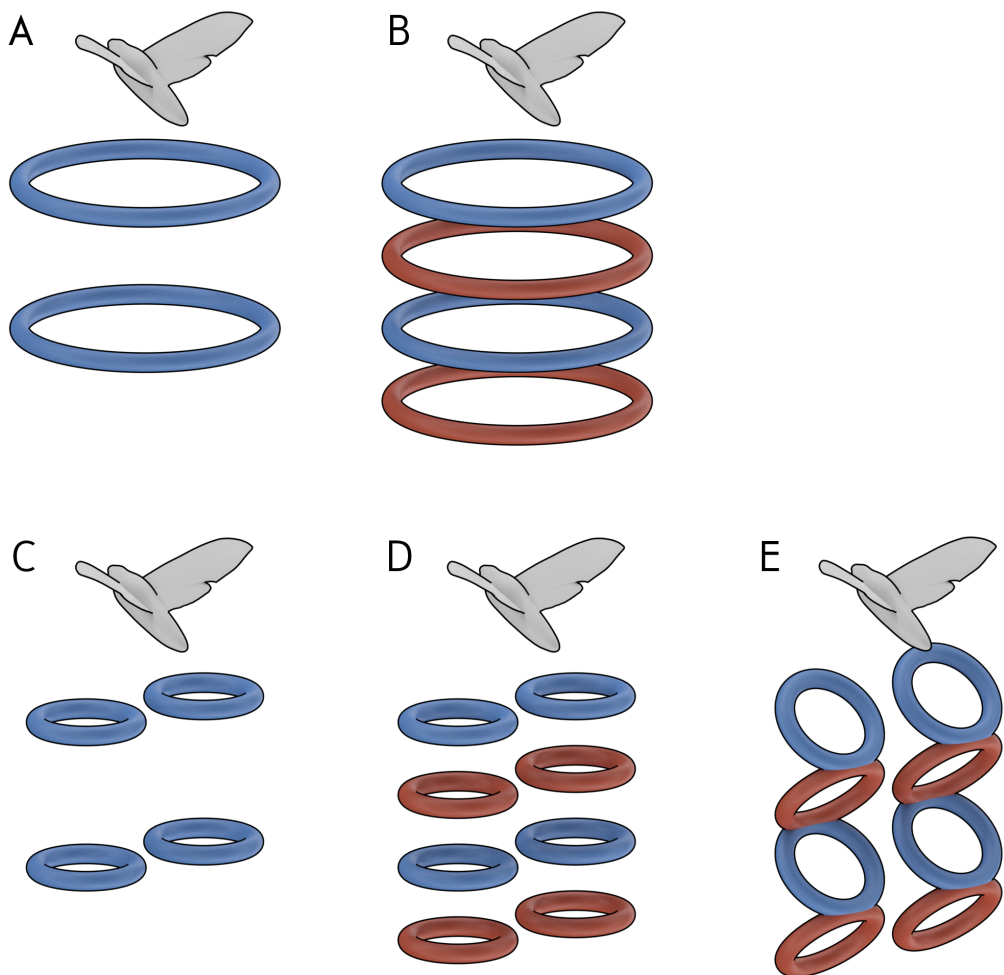
Figure 9. Cartoon representation of five different wake topologies. Blue vortex rings are created during downstroke, and red rings during upstroke. In C-E, each wing produced its own vortex ring. D and E are identical except for the fact that the rings produced during down- and upstroke are coupled in E.

when travelling in the out-of-plane direction.

Tomograpic PIV

The newest development in PIV systems is the tomographic (or "tomo-") PIV. Here, instead of using only one or two cameras to produce a 2D vector field, four or more cameras are used to produce a vector field with three dimensions. While stereo-PIV compares particle patterns

to find velocities, tomo-PIV first reconstructs the particles in 3D space, and subsequently performs the PIV calculations in small volumes across the larger 3D velocity field. As tomo-PIV typically deals with thicker laser sheets than stereo-PIV, particle loss is a lesser problem with this method. In addition, the extra cameras contribute to reducing some systematic errors and even though the process of reconstructing a 3D volume from photographs introduces another error source, tomo-PIV has been shown to produce more accurate results than stereo-PIV (Michaelis and Wieneke, 2008).

In principle, tomo-PIV eliminates the need to stack planes to form a quasi-volume as a true volume is already obtained. However, current technical limitations make it very difficult to produce volumes thicker than approximately 10 mm, and so some form of stacking of volumes or planes will still be required for the researcher to be able to visualize the wake of anything but the smallest insect. This is mainly due to a lack of light: when a light volume increases in thickness, the light gets weaker as it is less focussed. At the same time, the cameras need a longer focus range to be able to capture all particles, and this is achieved by decreasing the aperture. However, a smaller aperture lets less light into the camera, and so even a small increase in light sheet thickness can lead to a severe loss of light in the images. In paper I a 14 mm thick volume was achieved by bouncing a focussed laser beam between two mirrors to build up the volume (see figure 10). This was a rather impractical solution to the problem of light loss as the mirrors needed to be very exactly angled to avoid light loss, not accidentally touched, and very much in the area where the researchers needed to move during experiments. Therefore, this setup was – although producing excellent results – only used once. In papers II through IV, significantly thinner measurements volumes were used, without the aid of mirrors.

Other considerations when deciding whether to use a stero- or tomo-PIV setup are computer power (large tomo volumes require a large memory), time (tomo calculations are significantly slower) and quality of the raw data (tomo is more sensitive to an imperfect calibration of the system). As an example, the tomo-PIV dataset in paper I required three months of non-stop PIV calculations. This of course sets practical limits to the sample size if building a setup similar to ours.

Studying hovering flight with PIV

In forward flight in a wind tunnel, the vortices shed from the flyer's wings are carried with the wind towards a potential measurement plane downstream. In hovering flight, however, the wake moves downwards with its own induced velocity, and so a PIV setup for hovering flight needs to place a horizontal measurement plane below the animal (see figure 11). Components of the wake move with varying velocity, and as there is no free-stream flow to carry the shed wake away from the measurement area, the results can become very hard to interpret. To mitigate this problem, a very slow free-stream flow can be added, allowing the disturbed flow to leave the area of interest. Now, clearly the animal does not technically hover any more. However, Ellington (1984a) noted that kinematics of insects flying below a speed of 10% of the mean wingtip velocity are indistinguishable from those of true hovering, and in fact defined flight this slowly as hovering. In paper II and III I studied hovering flight
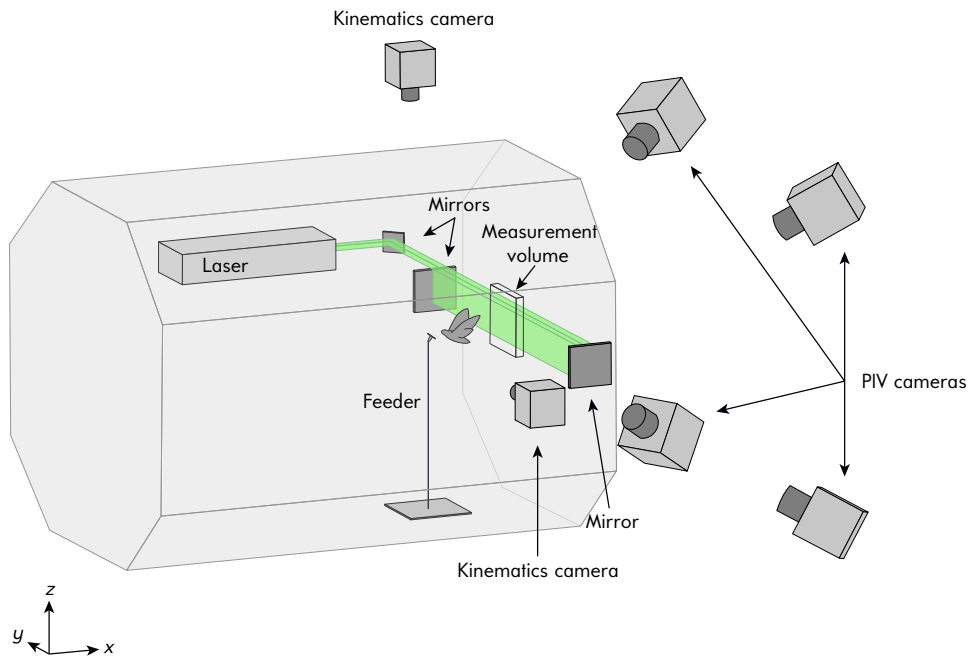
Figure 10. Experimental setup from paper I. Test section (1.2 m wide) of the Lund University wind tunnel, with a 14 mm thick measurement volume produced by bouncing laser light between two mirrors. Four PIV-cameras are pointed towards the volume to record particle images, and two kinematics cameras see the free-flying *M. sexta* from the side and above, respectively. The feeder is placed 190 mm from the laser sheet.

in *M. stellatarum*. In these studies, the wind tunnel had a free-stream flow of 0.2-0.3 ms^{-1}, which corresponds to less than 5% of the mean wingtip velocity of the moths.

Power estimations from the wake

Since the wake is the flyer's "aerodynamic footprint", information about flight forces and power can – in theory – be known by studying the wake. I used two different techniques to measure aerodynamic power from the wake, depending on whether the study animals were hovering or flying forward.
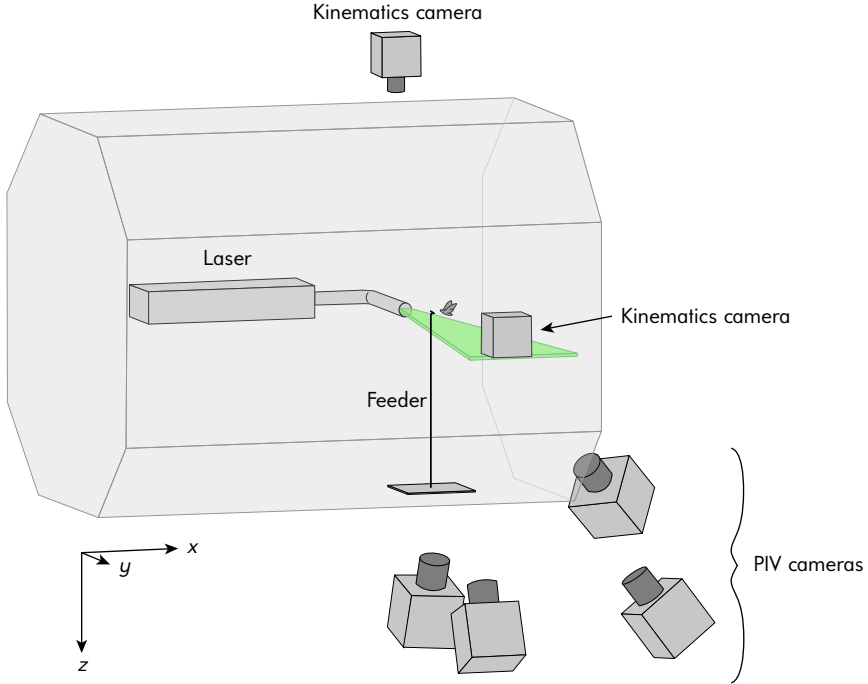
Figure 11. Experimental setup from papers II and III. A *M. stellatarum* is hovering in front of a feeder in the 1.2 m wide test section of the Lund University wind tunnel while two kinematics cameras are recording its flight. Simultaneously a PIV system, consisting of a laser, an aerosol generator (not in view) and four cameras, records the air flow below the moth.

Aerodynamic power in forward flight

In paper I and IV, where the moths were forward flying, power was defined as the rate of kinetic energy ($\dot{E}$) added to the air by the animal, and calculated as:

$$P = \frac{1}{2}\rho f \iiint \left(u^2 + v^2 + w^2\right)\left(1 + \frac{u}{u_\infty}\right)\mathrm{d}V,$$

following Drela (2009). Here, f is the wingbeat frequency and u, v and w are, respectively, the velocities parallel and perpendicular to the free-stream direction, and parallel to gravity. u_∞ is the free-stream velocity. The integral is evaluated over one wingbeat as well as the full cross-sectional area of the wind tunnel. It is certainly not feasible to produce a PIV measurement plane this large; in fact a PIV setup is usually little wider than the study animal's wingspan. This is because vorticity – which is often the property of the flow that is most interesting to the researcher – is confined to a limited area. The velocities induced

from the shed vortices (which is what we need for the power calculation) however covers a much larger area. To be able to know the full velocity field of the wind tunnel, a technique to extend the measured volume was developed, similar to a method in Busse *et al.* (2014). The method uses the relationship between the vorticity field ($\boldsymbol{\omega}$) – which we can fully know if we assume that the flow is irrotational outside our measurement area – and the stream function ($\boldsymbol{\psi}$), defined by the Poisson equation as:

$$-\boldsymbol{\omega} = \nabla^2 \boldsymbol{\psi}$$

After solving for the stream function (see further details in paper I), the velocity field ($\boldsymbol{u}$) could be calculated as the curl of the stream function:

$$\boldsymbol{u} = \nabla \times \boldsymbol{\psi}.$$

The method is easily validated, as we can compare the original measured velocity field to the part of the calculated velocity field that corresponds to the measurement volume.

Induced power in hovering

In paper III, induced power was calculated from the downwards velocities – or downwash – in the wake, similar to *e.g.* Håkansson *et al.* (2015):

$$P_{ind} = \frac{\rho}{2} \int\limits_{wb} \iint\limits_{A(t)} w(x, y, t)^3 \mathrm{d}x \mathrm{d}y \mathrm{d}t.$$

The integral was evaluated over the cross-sectional wake area (A) and the duration of a wingbeat ($t = 0 \rightarrow wb$). Here, we did not need to extend the velocity field, as downwash was already confined to the limits of the vortex wake. However, as there was a degree of noise in these measurements, the wake area had to be masked out in the velocity fields. This method is analogous to the actuator disk model discussed in the following section, but without assumptions about the shape of the wake or potential wake contraction (see paper III for further details).

Modelling aerodynamic power

The aerodynamic models I have evaluated in this thesis all have their origin in helicopter and aeroplane theory. Aerodynamics of these man-made objects are, compared to birds, bats and insects, well understood. Aeroplanes have fixed wings, and helicopter rotors have a predictable movement, making the corresponding models relatively simple. Animal flight,

however, is a complex and dynamic system. In addition, the air flow at these small scales (low Re) does not behave exactly like that around *e.g.* an aeroplane wing. Therefore, modifications must be made for the models to be useful. Before these can be discussed, I will introduce the aerodynamic concept of the actuator disk, which is the basis of most models of animal flight power.

Actuator disk

An actuator disk is an imagined, infinitesimally thin disk that produces lift by accelerating air from zero speed (far above the disk) to a speed w at the position of the disk, and finally to $2w$ far below the disk. This is visualized in figure 12 as a tube of downwards directed flow. As can be seen in the picture, the cross-sectional area of the tube contracts as air travel downwards. This is because the mass of air that passes through the disk each time unit stays constant, and so an increase in speed must be accompanied by a corresponding decrease in area. The air flow induced by the disk is uniform, which is the most efficient way of producing lift.
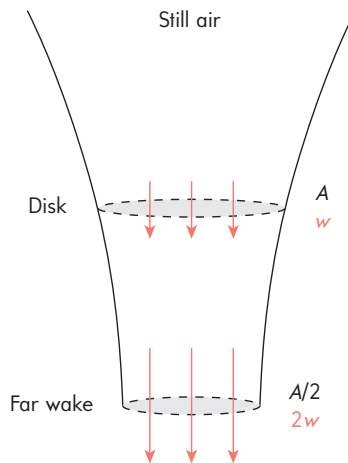
Figure 12. Depiction of an imagined actuator disk. Above the disk the air is still. The air is accelerated to w when it passes through the disk, and reaches a final velocity of $2w$ in the far wake. A the same time the cross-sectional area of the flow is decreased to half the disk area ($A/2$).

The mathematical concept of the actuator disk was first proposed as early as the 20th century as a simplification of the flow generated by rotating blades, and has been widely used to estimate induced power in helicopters. In its simplest form, it defines P_{ind} as a function of the air density (ρ), disk area (A) and downwards velocity (or downwash, w):

$$P_{ind} = 2\rho A w^3.$$

For a more thorough review of the actuator disk theory, refer to Gessow and Myers (1952).

Modifications for animal flight

The actuator disk model defines the minimum power that is needed to generate a certain lift force, but animal flight is never a perfect system. Therefore parameters describing deviations from the optimum must be introduced for the model to be useful for predictions about animal flight. In addition, the actuator disk only deals with induced power, and as we have seen previously, aerodynamic power (P) can be treated as a sum of three parts:

$$P = P_{ind} + P_{par} + P_{pro}.$$

Of these components, P_{ind} scales inversely with flight speed, while P_{par} and P_{pro} are often modelled to increase with the cube of the airspeed.

While parasite power is relatively simple to model – the body being more or less motionless in stable forward flight – profile power deals with flapping wings, which cannot easily be described by a simple mathematical expression. In one of the first attempts at modelling animal flight aerodynamics, Pennycuick (1968) approached this issue by making quite drastic simplifications, such as treating P_{pro} as a constant (see *e.g.* Pennycuick, 2008 for a justification). The purpose of this was to be able to predict flight power for any bird by inputting only a few morphological parameters such as wing span (b), wing area (S), wing chord (c) and weight (W). The model is available as downloadable software (Pennycuick, 2011), and has been widely used in bird migration research due mainly to its simplicity. The simplifications may or may not be realistic for bird flight, but it is unlikely that they reflect insect aerodynamics well (see paper I for a discussion on this).

Probably more realistic, but less straightforward to use, are versions of the actuator disk model that use kinematic (and sometimes aerodynamic) estimations to model profile power (see *e.g.* Willmott and Ellington, 1997). Both Pennycuick's model and the kinematics-based approach are applied to insect flight in paper I. While these models are mainly intended for forward flight (although they can be extended to zero speed with a modification to the calculation of induced power), a model specifically designed for insect hovering was developed by Ellington in a series of papers (see *e.g.* Ellington, 1984b,c). Here, the author deviates from the concept of a homogeneous downwash by instead assuming a pulsed flow, reflecting the pulsed nature of flapping wings. In paper III, I have studied power in hovering flight, and have compared my findings to Ellington's model.

RESULTS AND DISCUSSION

Wake dynamics

M. sexta and *M. stellatarum*, being relatively closely related species with superficially similar wingbeat kinematics, share the same fundamental features of the wake: Both shed strong tip vortices accompanied by weaker root vortices, the latter reflecting a loss of circulation over the body. Both species have an aerodynamically active upstroke, however this is always weaker than the downstroke. In paper I I studied *M. sexta* flying at a range of speeds (1-4 ms^{-1}), and noticed a clear trend where the upstroke appeared significantly weaker at lower speeds. This suggested that the large hawkmoth may have an almost completely inactive upstroke when hovering, something that is often associated with species with a more vertical stroke plane (see *e.g.* Ellington, 1984c). *M. sexta* has previously been described by Weis-Fogh (1973) as performing "normal hovering", meaning that the up- and downstroke contribute equally to weight support, and even though this claim has since been disproved (see *e.g.* Willmott and Ellington, 1997), a completely inactive upstroke in a hawkmoth would indeed be surprising. However, when studying wake dynamics in the smaller hawkmoth *M. stellatarum* (paper II), it was clear that at least this species utilizes the upstroke for weight support when hovering. Considering this, one could, in an alternative interpretation of the *M. sexta* results, explain the lack of upstroke vorticity at the lowest speeds with an increase in wake interactions when the speed is so low that the wing must pass through the wake shed by the previous half-stroke. However, I find this explanation less likely, as already the wakes at 2 ms^{-1} clearly show a decrease in upstroke vorticity compared with the downstroke, while still seeming similarly unaffected by wake interactions as the wakes at higher speeds.

The wake visualizations in this thesis have been produced with a significantly higher spatial and temporal resolution than previously visualized hawkmoth wakes. Thanks to technological advances like these, it has already been obvious that the vortex wakes of flying animals are much more complex than could be imagined when the first wake visualizations were produced decades ago. This is also the case for the wakes of hawkmoths. It is clear that the vortices shed from the wings and body of a hovering *M. stellatarum* show little resemblance to the "smoke-ring" like wake described by *e.g.* Grodnitsky and Morozov (1993). This could in principle make it difficult to defend the use of aerodynamic models that assume such a simple wake topology – at least without evaluation of these models.

Finally, thanks to the high resolution in the *M. sexta* wake visualizations, we could in paper I show a previously unknown feature of the moth's wake: the wing tip vortices are entwined with one or more additional vortex cores. As this has recently also been identified in the wakes of a locust (Henningsson *et al.*, 2015) and a bat (Johansson *et al.*, 2016), this might in fact be a common feature of tip vortices that we have not been able to discover until the resolution of PIV systems would allow so.

Wake evolution

In paper II I studied the evolution of the vortex wake as it travels towards the measurement plane after being shed from hovering *M. stellatarum*. Already at the near-wake measurement plane two wing lengths below the animal, we saw clear signs of wake interactions, and it was in many cases not possible to determine how and when the different vortex structures were produced. By the time the wake had reached the far-wake measurement plane approximately five wing lengths further down, almost no vortex structures could be identified in the wake. In addition, the cross-sectional area of the wake had increased, contrary to the expectation of a contracting wake. It is clear that it is crucial to place the measurement plane close to the animal when studying the timing of vortex shedding.

Modelling aerodynamic power

In paper I and paper III I have evaluated a few of the most commonly used animal flight power models by comparing their predictions to estimations from wake measurements. In the first paper, aerodynamic power measured from the wake of forward-flying *M. sexta* corresponded well with values modelled with morphological and kinematic data as input. In theory, this encourages using this type of model to estimate power for use in efficiency calculations or predictions of characteristic flight speeds. There is a caveat; this particular model requires estimations of an aerodynamic parameter – profile drag coefficient ($C_{D,pro}$) – which is available (but likely underestimated; see discussion in paper I) in the literature for *M. sexta*, but for few other species. Alternatively, the coefficient can be modelled for any insect (Ellington, 1984c), but this likely causes an even more severe underestimation. Additionally, another parameter, the induced power factor k is directly dependent on the somewhat arbitrary definition of the wake boundaries (see discussion in paper III). I evaluated the model with a range of parameter values for $C_{D,pro}$ and k found in the literature, and produced an envelope of possible power curves. While the model did in fact correspond well with my data in both magnitude and shape of the curve when average values of both parameters where chosen, the shape of the curve varied significantly when extreme values where chosen. Therefore it is difficult to defend the use of this type of aerodynamic model to predict characteristic flight speeds if these parameters are not first estimated with some degree of certainty. Efficiency estimations (see figure 5), however, are less sensitive to the shape of the power curve and so modelled aerodynamic power can be a reasonable substitute when

wake measurements are not practical. Of course, if the primary interest is if and how flight efficiency varies with flight speed, the same word of caution applies. Finally, Pennycuick's power model – which was originally intended for vertebrate flight – predicted wildly different characteristic speeds and should probably be avoided when estimating aerodynamic power in insect flight.

In paper III, I estimated induced power (P_{ind}) from the wake of hovering *M. stellatarum* and compared my findings to P_{ind} calculated with Ellington's model for hovering flight (Ellington, 1984b,c). The model consistently predicted a significantly higher induced power than the wake data produced, often more than double in magnitude. It is worth noting that also the results of this model are heavily influenced by a sometimes arbitrary choice of a parameter: Here, the upstroke is assumed to be either completely aerodynamically inactive or contributing as much to weight support as the downstroke. Based on measurements of the stroke plane angle I modelled the wake of hovering *M. stellatarum* as consisting of vortex rings shed only during downstroke. Wake visualizations in paper II however show that the species has a relatively active upstroke during hovering. As my aim was to evaluate the model used as originally intended – without any direct knowledge of the structures in the wake – I chose to follow Ellington's (1984b) rule which used a cut-off stroke plane angle of approximately 20 deg to decide between an active and inactive upstroke. Modelling the upstroke as active would have resulted in almost 30% lower induced power, showing that the choice of this parameter value should perhaps warrant more consideration than simply comparing the stroke plane angle to an arbitrary cut-off value. Nonetheless, in the case of *M. stellatarum* Ellington's model still overestimates P_{ind} with all iterations of the model.

Comparing the results from paper I and III, we can see that the power estimated from the wake corresponded well to modelled values for forward flying *M. sexta* but less well for hovering *M. stellatarum*. One explanation is of course that the model used in the forward flight experiments does a better job estimating aerodynamic power than Ellington's model for hovering flight. Alternatively, it may be a matter of scale. *M. sexta* is one of the largest insects, with a wingspan of approximately 10 cm, and as such is considerably more bird-like than its smaller cousin. Earlier in this text (*What's so special about insect flight?*) we have seen that insect flight does not adhere particularly well to the quasi-steady aerodynamic principles that these models assume. It is likely that *M. stellatarum* with its smaller size is subject to more viscous and unsteady effects than the large, fast-flying *M. sexta* (see *e.g.* Johansson *et al.*, 2013). Therefore, by extension, the models evaluated may be more suited for larger insects.

Finally it is worth noting that power models that have their basis in the actuator disk theory makes an assumption that has profound effects on the predicted power required to fly: As we saw in the *Methodology* section, the wake generated by an actuator disk contracts as it travels downwards, so that in the mature wake the cross-sectional area is half that of the area of the disk. In the actuator disk model, this is reflected in a factor 4 in the calculation of induced power. From papers II and III it is however clear that the wake of hovering *M. stellatarum* in fact expands rather than contracts. The mechanism behind the expansion is so far unknown. Independent of mechanism, however, this violates a fundamental assumption of the actuator disk model. Therefore it is probably unwise to predict aerodynamic power of very small insects with actuator disk based models without further investigation, unless one

is specifically interested in power at very high speeds, where this power component is small or negligible.

Aerodynamic performance

In paper I a power curve for *M. sexta* was produced from PIV-measurements of wake velocities, and it was clear from the data that the large moth has a ∪-shaped power curve. This was evidenced by the fact that the ∪-shape explained more of the variation in the power measurements than a straight line as well as had a lower AICc value (which indicates a better quality model). Insects have previously been believed to have either relatively flat power curves with little change in required power with flight speed, or J-shaped curves, which corresponds to a relatively effortless hovering (Ellington *et al.*, 1990). While I measured speeds between 1 and 4 ms^{-1} only, my data clearly suggested that insects in fact may be subject to the same issue as vertebrates, where hovering is a relatively expensive mode of flight. Interestingly, the first insect to show this is *M. sexta*, a species highly dependent on hovering for its intake of food. Further corroborating the prediction of an energy demanding hovering in hawkmoths is the comparison between power measurements in *M. stellatarum* in papers III and IV. In the first study I estimated induced power to be approximately 2.5 mW in hovering *M. stellatarum*, while the second study estimated total aerodynamic power to ca 1.5 mW in the same species flying at 1.5 ms^{-1}. As induced power is a subset of the total power, this is a clear indication that hovering is expensive also for the smaller hawkmoth.

Finally, in paper I I found that *M. sexta* in fact has a rather inefficient flight: merely 5-6% of the metabolic power available is used to produce aerodynamic forces. Corresponding values for birds and bats have been estimated to 3-33% (Videler, 2005) and 5.6-15% (Busse *et al.*, 2014; Norberg *et al.*, 1993), respectively.

Tethering

In paper IV a comparison between the kinematics and aerodynamics of tethered and free-flying *M. stellatarum* showed that tethering in fact affects both these aspects significantly. Tethered individuals had higher amplitude and a more vertical stroke plane angle than when free-flying. The response was however not stereotypic: While there was a noticeable between-individual variation in the increase in stroke plane angle, each individual increased its variation in amplitude when tethered. It is not likely that these changes are caused by a loss of the sense of flight speed (as suggested by Fry *et al.*, 2005), as the combination of an increase in both amplitude and stroke plane angle is not consistent with either slower or faster flight (based on kinematics of *M. sexta* in Willmott and Ellington, 1997).

Perhaps the most important finding was that tethered individuals had a lower lift:drag ratio (L:D) than when free-flying, meaning they were less aerodynamically efficient. This is

crucial to remember when tethering individuals specifically for the purpose of measuring efficiency parameters such as the induced power factor k. Often, researchers use weight support (lift/weight) as a control to judge whether the flight of a tethered animal is "natural". Interestingly, there was no statistically detectable difference in lift force between tethered and free-flying moths in my study, which unfortunately suggests weight support is a less useful criterion than previously believed.

CONCLUDING REMARKS

Energy efficiency

In this thesis I have shown that some insects – like birds – have a ∪-shaped power curve. Previous assumptions about a flat power curve in insects partly have their origin in studies of oxygen consumption, which essentially reflects metabolic power (P_{met}, see figure 5). Of course, none of the power curves constructed from data on metabolic power are from *M. sexta*, my study species, and so it is still unclear how my results relate to the other power components in the energetics pathway (figure 5). We can imagine two options: Firstly: the relatively flat metabolic power curves may correspond to similarly flat aerodynamic power curves in the species which have previously shown this (most famously, bumblebee; Ellington *et al.*, 1990). This would mean that the total flight efficiency (E_{tot}) is constant over all flight speeds. Alternatively, one can imagine a scenario in which a flat metabolic power curve is in fact common to most insects, including *M. sexta*. In that case, the effort required when flying at different speeds is constant even though the aerodynamically required power follows a ∪-shaped curve. The logical effect of this is that flight efficiency, rather peculiarly, is the lowest when flying at the minimum power speed. I encourage a future study which measures oxygen consumption in a hawkmoth flying at a range of speeds to shed a light on this question.

Modelling aerodynamic power

A relatively large portion of this work has been spent on attempting to clarify whether the currently available, quasi-steady aerodynamic power models can be applied to insect flight. This is of course an impossible undertaking, as insect flight is incredibly diverse. However, in paper II I show that a classic model of hovering flight (Ellington, 1984b,c) does not, in fact, predict aerodynamic power well in hovering *M. stellatarum*. This means that while the model may or may not perform well in predicting power in *some* species, it does not work for all insects. In contrast, a model aimed towards forward flight did in fact succeed rather well in predicting aerodynamic power in *M. sexta*, but making any general conclusions about the

model's usefulness in insect flight studies requires studies on other insect families. Specifically those interested in predicting flight speeds from power models should be cautious. Paper I shows that it is dangerous to rely on default parameter values when constructing a power curve, and so some effort needs to be spent on estimating coefficients such as the induced drag factor (k) and the profile drag coefficient ($C_{D,pro}$) as well as investigate the possibility that they do in fact vary with flight speed.

LIST OF SYMBOLS

A	Area
b	Wing span
c	Wing chord
$C_{D,\text{body}}$	Body drag coefficient
$C_{D,\text{pro}}$	Profile drag coefficient
D	Drag
D_{ind}	Induced drag (drag due to lift production)
D_{par}	Parasite drag (drag due to drag from the body)
D_{pro}	Profile drag (drag due to drag from the wings)
E	Energy
$\dot{E}$	Rate of energy = power
E_{dyn}	Dynamic efficiency
E_{mech}	Mechanical efficiency of the flight muscle
E_{tot}	Total flight efficiency
f	Wingbeat frequency
J	Advance ratio
k	Induced power factor
L	Lift
m	Body mass
P	Power
P_{acc}	Inertial power (power due to acceleration/deceleration of the wings)
P_{aero}	Aerodynamic power
P_{ind}	Induced power (power due to lift production)
P_{mech}	Mechanical power (power output of the flight muscles)
P_{met}	Metabolic power (power input)
P_{par}	Parasite power (power due to drag from the body)
P_{pro}	Profile power (power due to drag from the wings)
R	Wing length

Re	Reynolds number
S	Wing area
S_b	Frontal body area
T	Thrust
u, *v*, *w*	Velocity vectors in *x*, *y* and *z* direction.
U_∞	Free-stream velocity
U_{mp}	Minimum power speed
U_{mr}	Maximum range speed
U_{mt}	Migration speed
W	Body weight
x, *y*, *z*	Right-handed Cartesian coordinate system, where *x* is in stream-wise direction, *y* span-wise and *z* parallel to gravity
β	Body angle
Γ	Circulation
γ	Elevation angle
θ	Stroke plane angle
ρ	Air density
τ	Normalised time during a wingbeat
φ	Stroke amplitude
ψ	Stream function
ω	Vorticity, 2× the angular velocity of a fluid element

REFERENCES

Bartholomew, G. A. and Casey, T. M. 1978. Oxygen consumption of moths during rest, pre-flight warm-up, and flight in relation to body size and wing morphology. *The Journal of Experimental Biology* **76**, 11–25.

Berg, C. van den and Ellington, C. P. 1997. The three-dimensional leading-edge vortex of a 'hovering' model hawkmoth. *Philosophical Transactions of the Royal Society B: Biological Sciences* **352**, 329.

Birch, J. M. and Dickinson, M. H. 2001. Spanwise flow and the attachment of the leading-edge vortex on insect wings. *Nature* **412**, 729–733.

Bomphrey, R. J., Lawson, N. J., Harding, N. J., Taylor, G. K. and Thomas, A. L. R. 2005. The aerodynamics of Manduca sexta: digital particle image velocimetry analysis of the leading-edge vortex. *Journal of Experimental Biology* **208**, 1079–1094.

Bomphrey, R. J., Taylor, G. K. and Thomas, A. L. R. 2009. Smoke visualization of free-flying bumblebees indicates independent leading-edge vortices on each wing pair. *Experiments in Fluids* **46**, 811–821.

Brodsky, A. K. 1991. Vortex formation in the tethered flight of the peacock butterfly Inachis IO L. (Lepidoptera, Nymphalidae) and some aspects of insect flight evolution, 23.

Busse, R. von, Waldman, R. M., Swartz, S. M., Voigt, C. C. and Breuer, K. S. 2014. The aerodynamic cost of flight in the short-tailed fruit bat (Carollia perspicillata): comparing theory with measurement. *Journal of The Royal Society Interface* **11**, 20140147–20140147.

Casey, T. M. 1976. Flight energetics of sphinx moths: power input during hovering flight. *The Journal of Experimental Biology* **64**, 529–543.

Cutler, D. E., Bennett, R. R., Stevenson, R. D. and White, R. H. 1995. Feeding behavior in the nocturnal moth Manduca sexta is mediated mainly by blue receptors, but where are they located in the retina? *The Journal of Experimental Biology*, 1909–1917.

Dickinson, M. H., Lehmann, F.-O. and Sane, S. P. 1999. Wing Rotation and the Aerodynamic Basis of Insect Flight. *Science* **284**, 1954–1960.

Dickinson, M. H. and Lighton, J. R. B. 1995. Muscle Efficiency and Elastic Storage in the Flight Motor of Drosophila. *Science* **268**, 87–90.

Dickinson, M. et al. 2005. Molecular dynamics of cyclically contracting insect flight muscle in vivo. *Nature* **433**, 330–334.

Drela, M. 2009. AIAA 09-3762 Power balance in aerodynamic flows. en. In: *27th AIAA Applied Aerodynamics Conference June 22 – 25*. San Antonio, TX.

Dudley, R. and Ellington, C. P. 1990. Mechanics of Forward Flight in Bumblebees: II. Quasi-steady Lift and Power Requirements. *Journal of Experimental Biology* **148**, 53–88.

Ellington, C. P. 1984a. The Aerodynamics of Hovering Insect Flight. III. Kinematics. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **305**, 41–78.

Ellington, C. P. 1984b. The Aerodynamics of Hovering Insect Flight. V. A Vortex Theory. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **305**, 115–144.

Ellington, C. P. 1984c. The Aerodynamics of Hovering Insect Flight. VI. Lift and Power Requirements. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences* **305**, 145–181.

Ellington, C. P., Machin, K. E. and Casey, T. M. 1990. Oxygen consumption of bumblebees in forward flight. *Nature* **347**, 472–473.

Ellington, C. P., Berg, C. v. d., Willmott, A. P. and Thomas, A. L. R. 1996. Leading-edge vortices in insect flight. *Nature* **384**, 626–630.

Engel, S., Bowlin, M. S. and Hedenström, A. 2010. The Role of Wind-Tunnel Studies in Integrative Research on Migration Biology. *Integrative and Comparative Biology* **50**, 323–335.

Fry, S. N., Sayaman, R. and Dickinson, M. H. 2005. The aerodynamics of hovering flight in Drosophila. *Journal of Experimental Biology* **208**, 2303–2318.

George, N. T., Irving, T. C., Williams, C. D. and Daniel, T. L. 2013. The Cross-Bridge Spring: Can Cool Muscles Store Elastic Energy? *Science* **340**, 1217–1220.

Gessow, A. and Myers, G. 1952. *Aerodynamics of the Helicopter*. Frederick Ungar Publishing, New York, NY.

Grodnitsky, D. L. and Morozov, P. P. 1993. Vortex formation during tethered flight of functionally and morphologically two-winged insects, including evolutionary considerations on insect flight. *Journal of experimental biology* **182**, 11–40.

Håkansson, J., Hedenström, A., Winter, Y. and Johansson, L. C. 2015. The wake of hovering flight in bats. *Journal of The Royal Society Interface* **12**, 20150357.

Hedenström, A. and Alerstam, T. 1995. Optimal Flight Speed of Birds. *Philosophical Transactions: Biological Sciences* **348**, 471–487.

Henningsson, P. et al. 2015. The complex aerodynamic footprint of desert locusts revealed by large-volume tomographic particle image velocimetry. *Journal of The Royal Society Interface* **12**, 20150119.

Jensen, M. and Weis-Fogh, T. 1962. Biology and Physics of Locust Flight. V. Strength and Elasticity of Locust Cuticle. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **245**, 137–169.

Johansson, L. C., Engel, S., Kelber, A., Heerenbrink, M. K. and Hedenström, A. 2013. Multiple leading edge vortices of unexpected strength in freely flying hawkmoth. *Scientific Reports* **3**.

Johansson, L., Håkansson, J., Jakobsen, L. and Hedenström, A. 2016. Ear-body lift and a novel thrust generating mechanism revealed by the complex wake of brown long-eared bats (Plecotus auritus). *Scientific Reports* **6**.

Josephson, R. 1997. Power output from a flight muscle of the bumblebee Bombus terrestris. III. Power during simulated flight. *Journal of Experimental Biology* **200**, 1241–1246.

Kelber, A. 1997. Innate preferences for flower features in the hawkmoth Macroglossum stellatarum. *Journal of Experimental Biology* **200**, 827–836.

Kelber, A., Balkenius, A. and Warrant, E. J. 2003. Colour vision in diurnal and nocturnal hawkmoths. *Integrative and Comparative Biology* **43**, 571–579.

Kern, R. and Varjú, D. 1998. Visual position stabilization in the hummingbird hawk moth, Macroglossum stellatarum L. I. Behavioural analysis. *Journal of Comparative Physiology A* **182**, 225–237.

Kokshaysky, N. 1979. Tracing the wake of a flying bird. *Nature*, 146–148.

Lehmann, F.-O., Sane, S. P. and Dickinson, M. 2005. The aerodynamic effects of wing–wing interaction in flapping insect wings. *Journal of Experimental Biology* **208**, 3075–3092.

Liu, H., Ellington, C. P., Kawachi, K., Berg, C. v. d. and Willmott, A. P. 1998. A computational fluid dynamic study of hawkmoth hovering. *Journal of Experimental Biology* **201**, 461–477.

Lu, Y. and Shen, G. X. 2008. Three-dimensional flow structures and evolution of the leading-edge vortices on a flapping wing. *Journal of Experimental Biology* **211**, 1221–1230.

Maltby, R. L., Engler, P. B. and Keating, R. F. A. 1965. Some exploratory measurements of leading-edge vortex positions on a delta wing oscillating in heave. *Aeronautical Research Council, R & M* **3410**.

Marden, J. H. 1987. Maximum Lift Production During Takeoff in Flying Animals. *Journal of Experimental Biology* **130**, 235–258.

Michaelis, D. and Wieneke, B. 2008. Comparison between Tomographic PIV and Stereo PIV, 12.

Muijres, F. T., Johansson, L. C., Barfield, R., Wolf, M., Spedding, G. R. and Hedenström, A. 2008. Leading-Edge Vortex Improves Lift in Slow-Flying Bats. *Science* **319**, 1250–1253.

Muijres, F. T., Johansson, L. C. and Hedenström, A. 2012. Leading edge vortex in a slow-flying passerine. *Biology Letters* **8**, 554–557.

Nachtigall, W., Rothe, U., Feller, P. and Jungmann, R. 1989. Flight of the honey bee III. Flight metabolic power calculated from gas analysis, thermoregulation and fuel consumption. *Journal of Comparative Physiology B* **158**, 729–737.

Newton, I. 1687. *Philosophiae Naturalis Principia Mathematica*. London, UK.

Norberg, U. M., Kunz, T. H., Steffensen, J. F., Winter, Y. and Helversen, O. von 1993. The cost of hovering and forward flight in a nectar-feeding bat, Glossophaga soricina, estimated from aerodynamic theory. *Journal of Experimental Biology* **182**, 207–227.

Pennycuick, C. J. 1968. Power requirements for horizontal flight in the pigeon Columba livia. *Journal of Experimental Biology* **49**, 527–555.

Pennycuick, C. J. 2008. *Modelling the Flying Bird*. English. Elsevier, Oxford, UK.

Pennycuick, C. J. 2011. *Flight 1.24 [Computer software]*. 2011.

Pennycuick, C. J., Alerstam, T. and Hedenström, A. H. 1997. A new low-turbulence wind tunnel for bird flight experiments at Lund University, Sweden. *Journal of experimental biology* **200**, 1441–1449.

Pennycuick, C. J. 1978. Fifteen Testable Predictions about Bird Flight. *Oikos* **30**, 165–176.

Prasad, A. K. 2000. Stereoscopic particle image velocimetry. *Experiments in Fluids*, 103–116.

Spedding, G. R. 1986. The wake of a jackdaw (Corvus monedula) in slow flight. *The Journal of Experimental Biology*, 287–307.

Spedding, G. R., Rosén, M. and Hedenström, A. 2003. A family of vortex wakes generated by a thrush nightingale in free flight in a wind tunnel over its entire natural range of flight speeds. *Journal of Experimental Biology* **206**, 2313–2344.

Spedding, G. 1987. The wake of a kestrel (Falco Tinnunculus) in flapping flight. *Journal of Experimental Biology*, 59–78.

Spedding, G., Rayner, J. and Pennycuick, C. 1984. Momentum and energy in the wake of a pigeon (Columba livia) in slow flight. *The Journal of Experimental Biology*, 81–102.

Srygley, R. B. and Thomas, A. L. R. 2002. Unconventional lift-generating mechanisms in free-flying butterflies. *Nature* **420**, 660–664.

Stevenson, R. D. and Josephson, R. K. 1990. Effects of Operating Frequency and Temperature on Mechanical Power Output from Moth Flight Muscle. *Journal of Experimental Biology* **149**, 61–78.

Sun, M. and Wu, J. H. 2003. Aerodynamic force generation and power requirements in forward flight in a fruit fly with modeled wing motion. *Journal of Experimental Biology* **206**, 3065–3083.

Thomas, A. L. R., Taylor, G. K., Srygley, R. B., Nudds, R. L. and Bomphrey, R. J. 2004. Dragonfly flight: free-flight and tethered flow visualizations reveal a diverse array of unsteady lift-generating mechanisms, controlled primarily via angle of attack. *Journal of Experimental Biology* **207**, 4299–4323.

Videler, J. J. 2005. *Avian flight*. Oxford University Press, Oxford, UK.

Weis-Fogh, T. 1973. Quick Estimates of Flight Fitness in Hovering Animals, Including Novel Mechanisms for Lift Production. *Journal of Experimental Biology* **59**, 169–230.

Willmott, A. P. and Ellington, C. P. 1997. The mechanics of flight in the hawkmoth Manduca sexta. I. Kinematics of hovering and forward flight. *Journal of Experimental Biology* **200**, 2705–2722.

Wu, J. and Sun, M. 2005. Unsteady aerodynamic forces and power requirements of a bumblebee in forward flight. *Acta Mechanica Sinica* **21**, 207–217.

TACK!

Först, ett jättetack till mina handledare: **Anders**, du har en fantastisk förmåga att se det stora när andra bara ser detaljer. Hur många gånger har jag kommit till ditt kontor och sagt att jag inte alls förstår vad jag håller på med, varpå du berättat för mig exakt varför det faktiskt är väldigt intressant och varför alla i hela forskarvärlden kommer att jubla när de får se mina resultat? Många gånger. Du har peppat mig, gett mig bättre självförtroende, hjälpt mig att sätta min forskning i ett större sammanhang och stått ut med mig när jag haft en lite väl negativ attityd. Tack! **Christoffer**, jag har inte uttnyttjat din handledning tillräckligt, vilket är lite synd. Jag har varit inställd på att jag måste göra allt själv, vilket såklart inte stämmer. Men du har varit ovärderlig att diskutera de tekniska aspekterna av mitt arbete med, och din förmåga att förstå helt obegripliga vakbilder är verkligen imponerande. Tack för all hjälp!

Marco, without you I would have known nothing about aerodynamics and PIV. Basically, this thesis would've sucked. You said that without me you would still be in the wind tunnel trying to perfect the setup. Well, I would probably be in and out of the wind tunnel in two days time, with some truly subpar data. So I guess that makes us a good team! Thanks for all the fun times at the coffee bench, pub, ping pong table and long hours waiting for the DaVis self-calibration routine to finish. And, perhaps most of all, thanks for all the stroopwafels!

Tack till **Animal Flight Lab**: **Per**, för alla kul stunder i vindtunneln, och alla allvarliga eller mindre allvarliga snack om Tom Waits, barn och var man kan hitta endemiska fågelunderarter på Kanarieöarna. **Jonas**, för att det är nice med någon som delar mina lite mer nördiga intressen. Och för att du fixade ett schysst jobb till mig! **Lasse**, för att du alltid gjorde mig på bra humör, och för att du envist försökte lära mig danska. Det gick dock inte alls bra! Alla andra som kommit och gått, för att ni gjort forskningen lite mindre ensam.

Anna N., du är den mest entusiastiska person jag någonsin träffat. Du kommer att bli världens bästa lärare! Tack för att du gjort tiden på ekologihuset mycket roligare, och tack för att du vill vara min vän fast jag är så dålig på att svara på sms.

Anne, du är så cool! Tack för att du varit en sådan härlig kombination av polare, extramamma och administratörsguru.

Ganska länge hade jag ett eget kontor, och det var sjukt tråkigt. Så tack till mina roomies; **Lasse**, **Cecilia** och **Maja**, för att ni gjort mina arbetsdagar lite roligare!

Ibland är man inte på topp, och då är det skönt att ha folk omkring sig som kan hjälpa en att studsa tillbaka. Tack för allt stöd och pepp när jag behövde det som mest **Anders**, **Jan-Åke**, **Ingrid E**, **Dag H**, **Anne** och många andra.

Helena, jag har verkligen inte använt dina mentorskills tillräckligt mycket. Men jag har alltid känt att du varit på min sida. Tack för ditt stöd!

Almut, tack för all hjälp med insekterna, och för att du alltid visat intresse för min forskning!

Tack alla som förgyllt mina stunder i fikarummet: **Anna D**, **Elin**, **Katrine**, **Utku**, **Pablo**, **Fredrik**, **Jannie** och många andra.

Mamma, **pappa**, **Ida** och **Kristin** med familjer, tack för att ni är så härliga! And a very special thank you to **mamma** and **Mike**, who generously have dedicated many, many weekends to helping us with renovations and baby care, preventing me from going insane with stress.

Mikkel, min lilla ängel, du har ärligt talat inte hjälpt till särskilt mycket med den här avhandlingen. Men du har fyllt mitt liv med kärlek, och det är mycket bättre! Tack för att du är så himla go!

Till sist, **Mattias**, du är min (störiga) klippa. Utan dig finns det inte en chans i helvetet att den här avhandlingen hade blivit klar. Du peppar mig när jag saknar motivation, tröstar mig när jag mår dåligt, lyssnar intresserat när jag berättar om min forskning (haha) och påminner mig om att det faktiskt finns mycket viktigare saker i livet än avhandlingar. Tack!

List of Papers

I. **The power–speed relationship is U-shaped in two free-flying hawkmoths (*Manduca sexta*).** Warfvinge K, KleinHeerenbrink M, and Hedenström A. 2017. Journal of The Royal Society Interface. 14, 20170372.

II. **Hovering flight in hummingbird hawkmoths: wake dynamics and kinematics.** Warfvinge K, Johansson LC, and Hedenström A. (manuscript)

III. **Hovering flight in hummingbird hawkmoths: aerodynamic power.** Warfvinge K, Johansson LC, and Hedenström A. (manuscript)

IV. **Aerodynamic performance of hawkmoths is negatively affected by tethering.** Warfvinge K and Hedenström A. (manuscript)