How does the morphology of gleaning bats constrain their locomotor performance?

A thesis submitted to the University of Manchester for the degree of Doctor of Philosophy in the Faculty of Life Sciences.

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Abstract

Abstract for the Thesis "How does the morphology of gleaning bats constrain their locomotor performance?" submitted by James Gardiner for the degree of PhD in the Faculty of Life Sciences at the University of Manchester in September 2011.

Bats are one of the most numerous and diverse orders of mammals. This diversity is reflected in the wide range of bat morphologies. The relationship between bat foraging behaviours, flight styles and wing shapes has been well studied. Little research, however, has focused on other features of bat morphology, such as ear and tail membrane size, and how variations in these affect a bat's locomotion. Indeed, knowledge on this topic has at best been speculative. In this thesis, I provide insight into the trade-offs and relationships that exist between less studied aspects of bat morphology, and their foraging and locomotion, with focus on the group of bats referred to as gleaners.

In this thesis I use a model bat in wind tunnel tests to demonstrate that the long ears of some bat species have profound implications for their aerodynamic performance, and their energetics. A trade-off, however, is likely to exist, since the long ears provide a foraging benefit, which may balance the additional flight cost of the large ears. Additionally, bats may be able to minimise the flight cost of their ears through appropriate ear positioning. Using data collected from museum specimens I also demonstrate that other features of bat morphology, particularly the tail membrane, are good indicators of foraging strategy. Gleaning bats are identified as the group with the largest ears, whilst commuting bats have the shortest tail membranes. The energetic implications of these variations in morphology were then investigated using a theoretical model. The theoretical model suggested that tail morphology, as well as ear morphology, was likely to have a profound effect on flight performance in bats

In contrast to bird tails the aerodynamic function of bat tail membranes is not well understood. Accordingly, I investigated bat tail membrane aerodynamics empirically using a model suspended in a wind-tunnel and from this was able to present the first evidence that bat tail membranes fulfil an important flight control function. Although bats primarily fly, certain species, such as the gleaning bats, spend a significant proportion of their foraging time on or near the ground and vegetation, landing to capture prey. Several gleaning species are also documented as frequently jumping from the ground back into flight. Research, however, on bat jumping had previously concentrated on the unusual vampire bats. I, therefore, present further data on bat jump performance and show that no-ecological trend is present, with body mass being the best indicator of performance. No correlation between foraging habit and take-off performance suggested that flight so dominates bat morphology and locomotor performance that other modes of locomotion tend to be derivative.

The findings of the thesis presented here, provide important insights into the relationships that exist between gleaning bat morphology, locomotor performance and foraging strategy. Areas for future research are also identified.

Declaration

No portion of the work referred to in the thesis has been submitted in support of an application for another degree or qualification of this or any other university or other institute of learning.

Signature:

Date:

Copyright Statement

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Publications

Refereed articles

Gardiner, J. D. & Nudds, R. L. (2011) No apparent ecological trend to the flight-initiating jump performance of five bat species. *Journal of Experimental Biology* **214**, 2182-2188.

Gardiner, J. D., Dimitriadis, G., Codd, J. R. & Nudds, R. L. (2011) A potential role for bat tail membranes in flight control. *PLoS ONE* **6**, e18214.

Gardiner, J. D., Codd, J. R. & Nudds, R. L. (2011) An association between ear and tail morphologies of bats and their foraging style. *Canadian Journal of Zoology* **89**, 90-99.

Nudds, R. L., Gardiner, J. D., Tickle, P. G. & Codd, J. R. (2010) Energetics and kinematics of walking in the barnacle goose (*Branta leucopsis*). *Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology* **156**, 318-324.

van Casteren, A., Codd, J. R., Gardiner, J. D., McGhie, H. & Ennos, A. R. (2010) Sonation in the male common snipe (*Capella gallinago gallinago* L.) is achieved by a flag-like fluttering of their tail feathers and consequent vortex shedding. *Journal of Experimental Biology* **213**, 1602-1608.

Gardiner, J., Dimitriadis, G., Sellers, W. & Codd, J. (2008) The aerodynamics of big ears in the brown long-eared bat *Plecotus auritus*. *Acta Chiropterologica* **10**, 313-321.

Katzner, T. E., Lai, C. H., Gardiner, J. D., Foggin, J. M., Pearson, D. & Smith, A. T. (2004) Adjacent nesting by Lammergeier *Gypaetus barbatus* and Himalayan Griffon *Gyps himalayensis* on the Tibetan Plateau, China. *Forktail* **20**, 94-96.

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As always my family have been unshakeably supportive of my studies. I am exceptionally thankful to them all and feel very blessed.

Organisation of Thesis

Here, I present my PhD thesis in the Alternative Format for examination at the University of Manchester. The thesis is structured so that each of the four research chapters presented, on which I am the first author, have been published in a a peer-reviewed journal. The thesis also includes a general introduction and a general discussion, with references at the end of each section. Due to the collaborative nature of the research presented here, the author contributions for each journal article are presented below.

Chapter 2

Gardiner, J., Dimitriadis, G., Sellers, W. & Codd, J. (2008) The aerodynamics of big ears in the brown long-eared bat *Plecotus auritus*. *Acta Chiropterologica* **10**, 313-321.

I carried out all the research and analysis for this article, which was based on an original idea I had developed. I also wrote the journal article. Prof Greg Dimitriadis provided both facilities and support for the wind tunnel experiments as well as editorial advice. Drs Bill Sellers and Jonathan Codd, helped develop the initial idea and provided editorial advice on the manuscript.

Chapter 3

Gardiner, J.D., Codd, J.R. & Nudds, R.L. (2011a) An association between ear and tail morphologies of bats and their foraging style. *Canadian Journal of Zoology* **89**, 90-99.

I carried out all the research and data analysis for this article, which was based on a follow up idea from Chapter 2. I wrote the research article. Dr Jonathan Codd helped to develop the idea and analysis. He also edited the manuscript prior to submission. Dr Robert Nudds helped with the data analysis and provided editorial support.

Chapter 4

Gardiner, J.D., Dimitriadis, G., Codd, J.R. & Nudds, R.L. (2011b) A Potential Role for Bat Tail Membranes in Flight Control. *PLoS ONE* **6**, e18214.

I carried out the research, data analysis and manuscript writing for this article. Prof Greg Dimitriadis provide facilities for conducting the experiments and technical support. Drs Jonathan Codd and Robert Nudds provide editorial support for the writing of the article. Robert Nudds also helped with the statistical analysis.

Chapter 5

Gardiner, J.D. & Nudds, R.L. (2011) No apparent ecological trend to the flight-initiating jump performance of five bat species. *The Journal of Experimental Biology* **214**, 2182-2188.

I carried out the research and data analysis for this paper, based on an idea I developed. I wrote the journal article. Dr Robert Nudds, provided the video footage used and helped with both the data analysis and manuscript writing.

Chapter 1

General Introduction

Origins of bats

Bats (Chiroptera) are one of only three vertebrate groups to evolve powered flight, along with the birds and the extinct pterosaurs (Norberg, 1990). The Mammalia, including bats, separated from other vertebrate groups around 200 million years ago (Figure 1) but did not become the dominant terrestrial order until after the Cretaceous-Tertiary mass extinction event, when a rapid and extensive radiation of species occurred (Pough *et al.*, 2002). The ancestor of bats during this period was likely to have been a small arboreal insectivore feeding in the canopy (Altringham, 1996).

Bats are thought to be monophyletic (Liu *et al.*, 2001, Murphy *et al.*, 2001). The monophylogeny of bats, however, has been strongly debated, particularly because a variety of morphological differences between the two suborders of bats are known (Pettigrew *et al.*, 1989, Altringham, 1996). Indeed, some researchers propose that the mega-bats (Pteropidae) are more closely related to primates, than to all the other bats. The mega-bat/primate link was initially championed by Pettigrew (1986) in research that showed the pattern of neural connections between the retina and the brain of mega-bats was similar to primates and different from all other vertebrates including the micro-bats. Flight, therefore, potentially had evolved twice in mammals (mega and micro-bats), and the mega-bats are 'flying primates'. More recent DNA phylogenies, however, have tended not to support the 'flying primate' theory and have placed bats away

from the primates (Liu *et al.*, 2001, Murphy *et al.*, 2001). Current consensus places bats as most closely related to the carnivorans, perissodactyls and artiodactyls (Liu *et al.*, 2001, Murphy *et al.*, 2001).

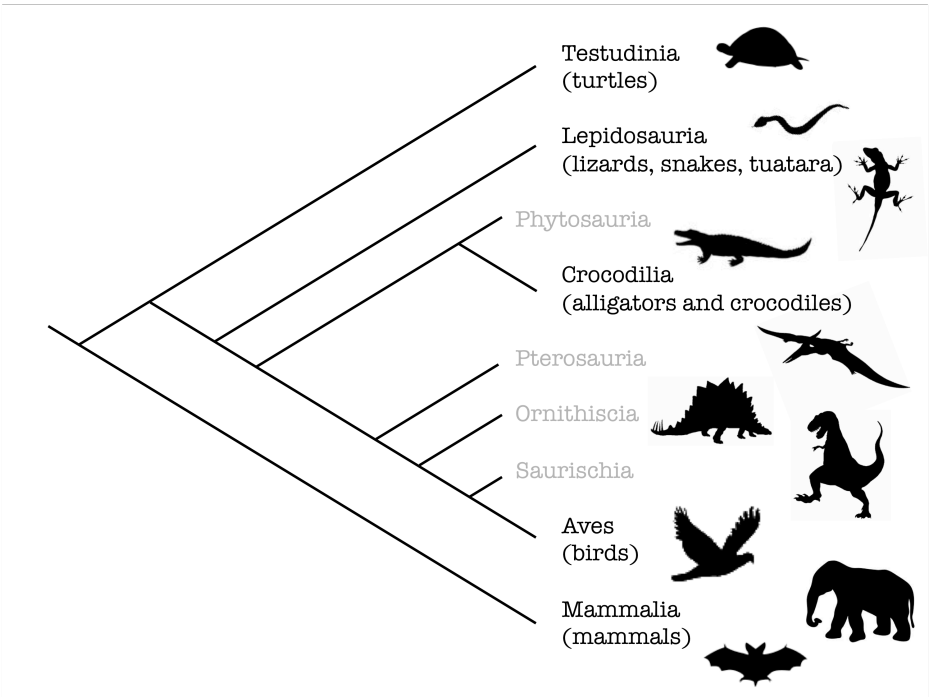


Figure 1 - Phylogenetic relationship between mammals and other vertebrate groups, including the other groups to have evolved powered flight, the pterosaurs and the birds. Orders shown in grey are extinct. (modified from Pough *et al.*, 2002)

Evolution of bat flight

Whilst most mammal groups are terrestrial, gliding flight has evolved as a form of locomotion approximately nine times in the mammals (Dudley *et al.*, 2007) across a wide range of orders including the flying squirrels (Rodentia), flying lemurs (Dermoptera) (Figure 2) and the marsupial sugar gliders (Diprotodontia). Only bats, however, have made the transition to true flight probably separating from their sister mammalian groups during the Paleocene

(Teeling *et al.*, 2005). Indeed, many of the earliest bat fossils from Eocene deposits are remarkably similar to their modern counterparts (Jepsen, 1966), suggesting proto-bats evolved significantly earlier. Whilst there have been several competing theories advanced for the evolution of both bird and insect flight, most researchers agree that bats have evolved flight ability from an arboreal gliding ancestor (Norberg, 1990, Altringham, 1996, Bishop, 2008). The ground-up theory for the evolution of bird flight (Ostrom, 1974, Caple *et al.*, 1983) has never been seriously considered for bats, since this would require a running take-off and the anatomy of bats (the wing membrane is attached to the hind legs) makes this highly unlikely. Nevertheless the transition from arboreal gliders to powerful flyers required dramatic changes in wing morphology and a stepwise evolutionary model for this transition can be difficult to envisage (Bishop, 2008). This is particularly because most extant gliding animals don't flap their membranes and bats are rarely seen gliding, with the exception of some larger mega-bats (Norberg *et al.*, 2000). Many gliders, however, share morphological similarities with bats that are associated with gliding and flight, and help to provide some clues to the ancestor of bats. Indeed, so many adaptations are shared between Dermopterans (Figure 2) and bats that they were originally believed to be sister taxon until molecular phylogenies (Liu *et al.*, 2001, Murphy *et al.*, 2001) failed to support a link. Some of these shared morphological features include a propatagium (flap of skin membrane in front of the main wing), the hind-legs being incorporated into the wing and webbing between the fingers (Altringham, 1996). With this basic dermopteran glider

planform, only the progressive extension of the fingers would be required to produce a wing not too dissimilar to that of bats.

Another potential hurdle in the evolutionary pathway to bat flight is the development of the flapping wing stroke (Bishop, 2008). Several studies have shown that even low-amplitude flapping may help to provide useful aerodynamic forces (in particular thrust), possibly improving the performance of a glide, whether in terms of flight distance, speed or manoeuvrability (Norberg, 1985, Nudds & Dyke, 2009). This is particularly pertinent, when recent studies revealed that gliding mammals constantly move their limbs in flight (Bishop, 2008). These limb movements are correlated with body rotation and are thought to be important in flight stability. We can begin to envisage a step-by-step evolutionary model based on these findings. Whereby, with each progressive finger extension wing area is gained, providing improved lift production. Simultaneously, the small flaps gain amplitude and become more than just flight control, but actually help to lengthen the flight path. Until, however, a fossil proto-bat is found to help confirm or disprove existing models, the debate on the evolution of flight in bats is set to continue.

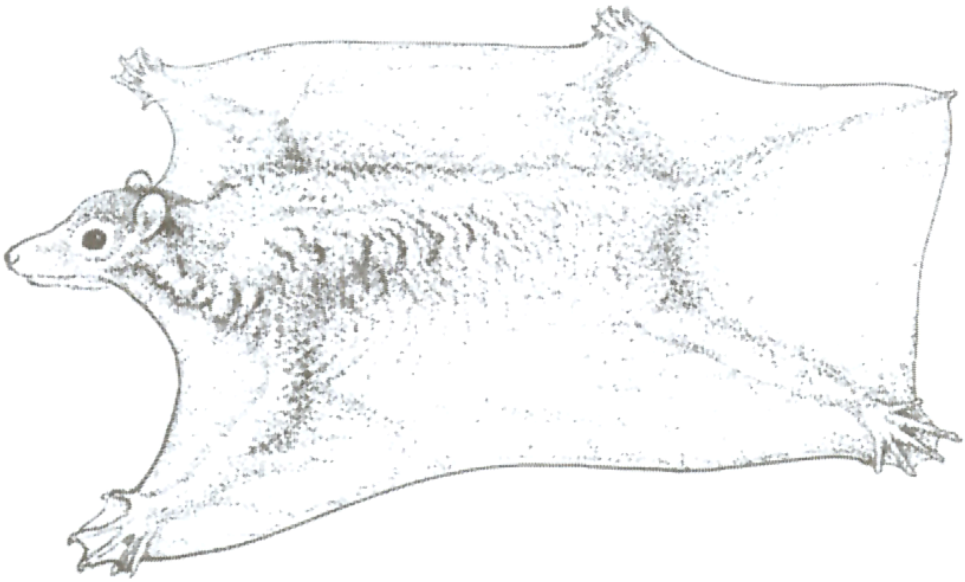


Figure 2 - A gliding dermopteran, the Malayan colugo (*Cynocephalus variegatus*), showing some of the morphological adaptations shared with bats such as the webbed fingers, and the hind legs and tail being incorporated into the wing membrane. (from Altringham, 1996)

Physiological adaptations for flight

Flight is both an energetically expensive and a cheap form of locomotion; depending on the metric used. In absolute terms (i.e. per unit time) flight is more energetically demanding than running (Thomas, 1987). Per unit distance travelled, however, flight is cheaper than terrestrial locomotion (Schmidt-Nielsen, 1972). Furthermore, flight is fast. For example, gliding is typically five times faster than terrestrial locomotion for animals of comparable size (Altringham, 1996). Increasing speed allows volant animals to exploit larger foraging areas, migrate over longer distances and fly over large geographical barriers. A particularly illuminating example of this is bar-headed geese migrating across one of the largest mountain ranges in the world; the Himalayas (Hawkes *et al.*, 2011). With the many advantages that flight affords animals it is

pertinent to ask why flight has only evolved in three vertebrate lineages (one of which is now extinct). The answer is in part due to the large morphological and physiological demands that flight places on an animal. Since flight is energetically expensive per unit time, the demands for efficient cardiac and respiratory systems are high. Without these the flight muscles would not be supplied with the necessary oxygen and fuel. Bats cope with this demand in part by increasing the size of the heart and lungs compared to a similarly sized terrestrial mammal (Maina, 2000). Furthermore, the respiratory system is refined so that it is efficient in oxygenating the blood. For example, the blood gas barrier in the lungs is remarkably thin for a mammal, the haemoglobin concentration of the blood is high and the lungs and muscles are well supplied with capillary vessels (Maina, 2000). Furthermore, the digestive, nervous and sensory systems have also been modified to cope with flight. Reducing weight is a key adaptation for efficient flight; bat intestines show modifications that facilitate the rapid absorption of nutrients thus reducing flying time with any additional load (Makanya *et al.*, 1997). The nervous system has also evolved to cope with the demands of controlling flight (Maynard Smith, 1952) such as processing a constant stream of sensory information being provided by unique adaptations such as the microscopic hairs which give feedback on the airflow conditions over the wing surface (Zook, 2005, Dickinson, 2010). One of the most discussed sensory adaptations that bats have evolved is echolocation, which not only allows them to orientate in complete darkness but is also essential for prey capture. Echolocation is hypothesised to have evolved due to the aerial dominance of diurnal raptorial birds and the associated predation risk

(Speakman, 2001). Being able to forage at night, therefore, reduced this predation risk and avoided potential food competition. Indeed, the thermal soaring in island dwelling mega-bats shows that in the correct ecological context, bats have no difficulty in adapting to a diurnal lifestyle (Norberg *et al.*, 2000). Fundamentally echolocation works by the bat listening to the returning echoes of its own frequently emitted high-pitched calls. The bat analyses these echoes and gains spatial information to help it navigate and identify food sources. Although this sounds simple enough, the complexity of the calls and the level of information the bats seem to gain from their echoes is truly remarkable and an area of extensive research (see Norberg, 1990, Altringham, 1996, Neuweiler, 2000).

Wing shape and aerodynamics

The most visually striking adaptation for flight, however, is the hand-wing of bats. Although the wings of pterosaurs, birds, bats and indeed insects are all anatomically different (Figure 3), they serve the same purpose of producing aerodynamic forces. The starting point for the explanation of the generation of aerodynamic forces on a wing is a simplified version of Bernoulli's equation

$$P + \tfrac{1}{2}\rho V^2 = \text{constant}$$

where for an ideal fluid (i.e. no viscosity and incompressible), P is the pressure, ρ is the fluid density and V is the fluid's velocity. Bernoulli's equation indicates that the faster a fluid flows the lower its pressure. An aerofoil shape is, designed so that the air on the upper surface is travelling faster than the air on the lower surface. A pressure difference, therefore, is created and a force is produced.

Most of this force is directed against gravity and called lift. Another way of visualising this process is that an aerofoil is designed to deflect air downwards. An equal and opposite force, therefore, must act on the wing deflecting it upwards, which is called lift (Figure 4). This explanation of the production of aerodynamic forces on a wing using Bernoulli's equation is necessarily a simplification of the actual complex aerodynamic phenomena that occur. A more comprehensive description of the theory of wing aerodynamics is beyond the scope of this thesis it can, however, be found in many excellent textbooks (for example Anderson, 2007).

Lift production is the most obvious requirement for flight since it keeps the animal aloft. The generation of lift, however, always results in the production of drag and therefore the animal must also be able to produce thrust to overcome the drag. Animals typically flap their wings asymmetrically (i.e. partially fold wings on the upstroke) to produce the necessary thrust (Rayner, 1987); some, however, make use of thermals and slopes to save the costs of continuous flapping (Tennekes, 1997).

When steady-state conditions are assumed to prevail the aerodynamics of animal wings can be approximated by theories developed for aircrafts. A key example of this approach is the 'momentum jet' model used to calculate the power required for an animal to fly. Pennycuick first applied this approach to animal flight in his classic article on the power required for flight in a pigeon (Pennycuick, 1968). Pennycuick's (1968) model calculates how both the power required to produce both lift and thrust (to overcome drag) vary with the flight speed of the animal. The total required aerodynamic power is a summation of

three components, the induced, the profile and the parasite powers. The induced power

$$P_{\text{ind}} \propto \frac{M}{b^2 V}$$

where P_{ind} is the induced power, M is the animal's mass, b is the animal's wingspan and V is the flight velocity is associated with lift production and decreases as flight velocity increases. The profile power

$$P_{\text{pro}} \propto SV^3$$

where P_{pro} is the profile power and S is the animal's wing area, and the parasite power

$$P_{\text{par}} \propto S_{\text{b}} V^3$$

where P_{par} is the parasite power and S_{b} is the animal's frontal area, are associated with the drag of the wings and body respectively, and both increase with flight velocity. The total aerodynamic power curve, therefore, forms the classic U-shape (Pennycuick, 1968) (Figure 5). This theoretical curve is useful since it predicts the optimal flight speeds animals would be expected to use in various ecological scenarios such as foraging or migrating. These flight speeds include the minimum power speed (the flight speed that requires the lowest aerodynamic power) and the maximum range speed (the flight speed at which the furthest distance can be travelled for least power). Predictions of these flight speeds can then be tested against empirical data from the field (Grodzinski *et al.*, 2009, Henningsson *et al.*, 2009). In general the overall trends predicted by the theoretical models tend to be supported by the empirical data. The exact values,

however, tend not to match as well due to unknown errors and factors in both the models and empirical data.

Much animal aerodynamics analysis still relies on assumptions of steady state conditions and this approach has some limitations, particularly at lower flight speeds and during hovering, where unsteady effects can become extremely important (Norberg, 1976a, Hedenström *et al.*, 2007, Muijres *et al.*, 2008, Wolf *et al.*, 2010). For example, it is often quoted that a bumblebee is too heavy to fly, since classical aerodynamic analysis shows it is impossible for their tiny wings to produce enough lift. This is clearly not true, and the discrepancy comes about due to unsteady aerodynamics effects such as delayed stall, which can massively increase the lift generated on small insect wings (Dickinson *et al.*, 1999, Wu, 2011). The limitations of classic aerodynamics have led many animal flight researchers to use theories based on the production of vortex wakes, since these theories match more closely what is observed in wind-tunnel studies. A comprehensive discussion of the mathematics of vortex wake theory and it application to animal flight is beyond the scope of this thesis, but can be found in Norberg (1990).

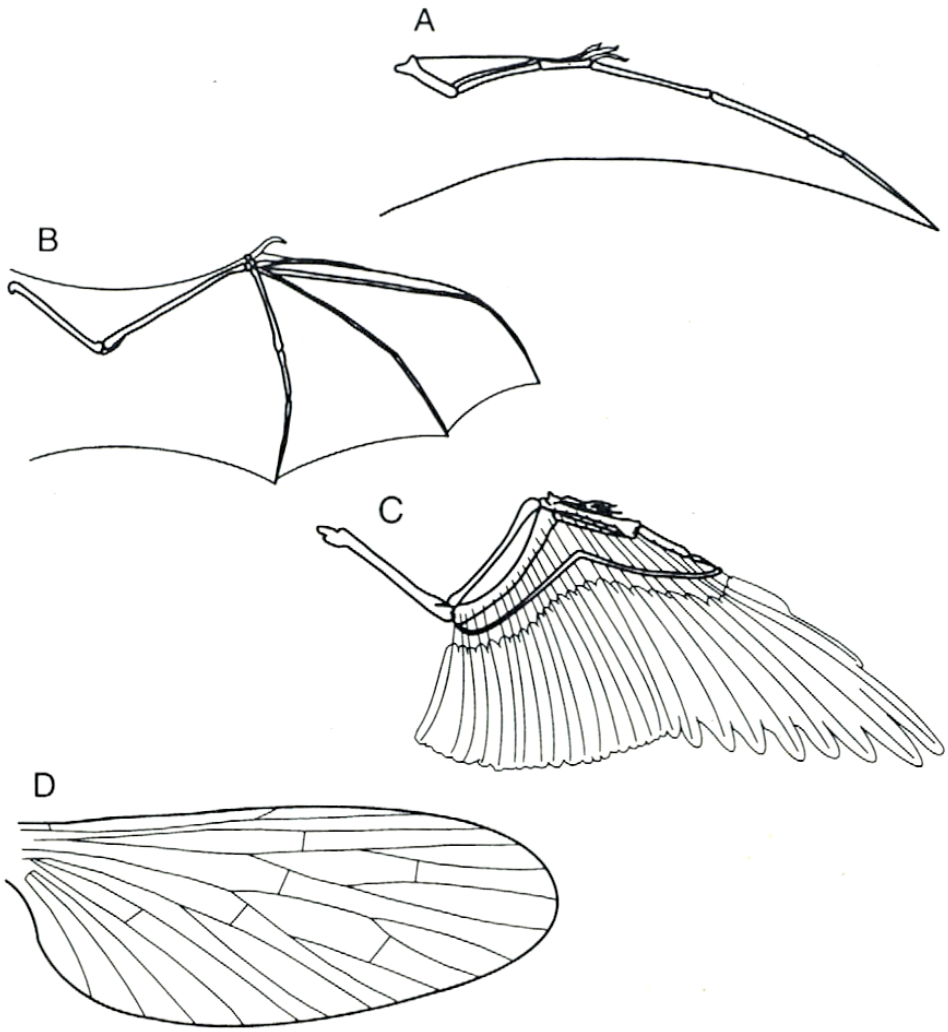
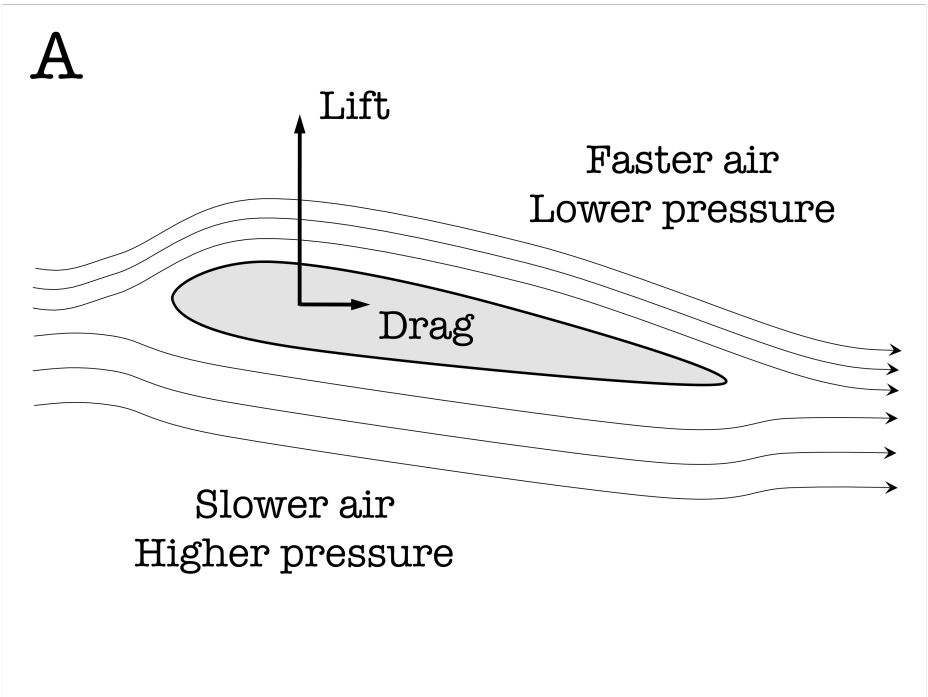


Figure 3 - Comparison of wing anatomies, showing main skeletal supports and morphological features. A: Pterosuar, B: Bat, C; Bird, D: Insect. (from Alexander, 2002)



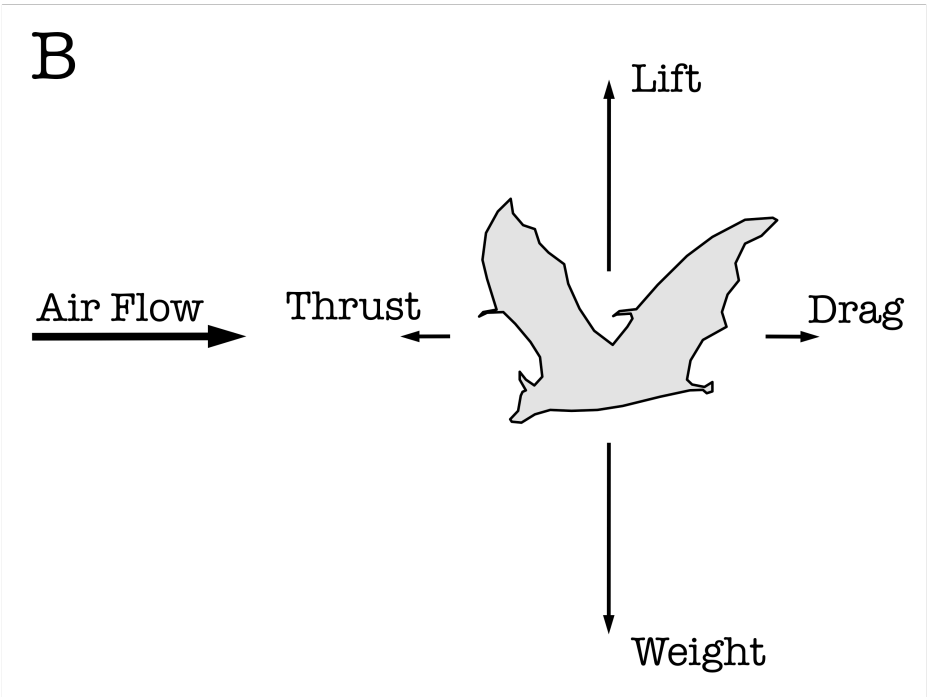


Figure 4 - A: Cross section of an aerofoil showing the generation of lift according to Bernoulli's equation. Faster moving air on the upper surface has a lower pressure than the slower moving air below. The pressure difference produces lift, as well as some drag. B: Average forces of a bat during level flapping flight. Average lift over a wing beat counteracts weight. Thrust also produced by the flapping wing counteracts drag.

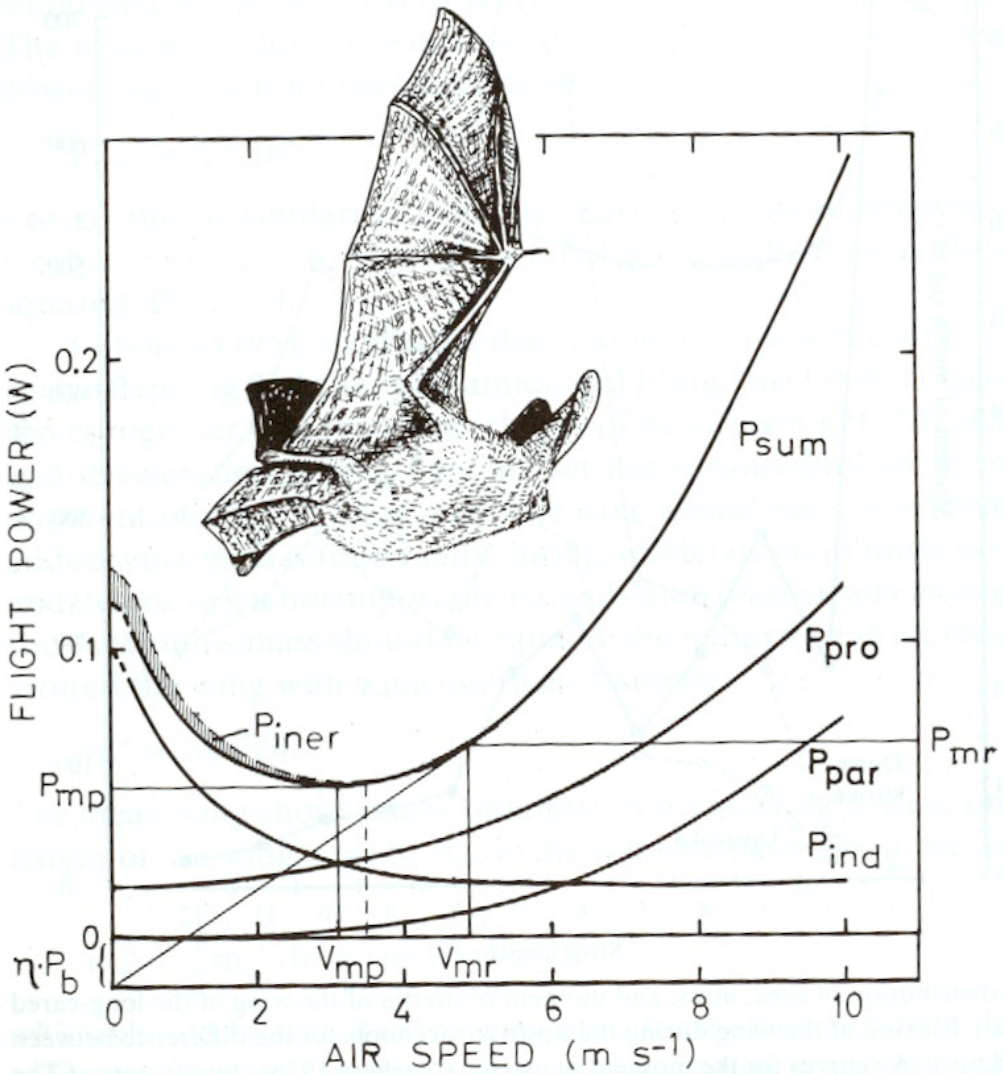


Figure 5 - Power curves for *Plecotus auritus*. P_b represents the resting metabolic rate and is set to zero at bottom of diagram. P_{sum} is the total aerodynamic power made up of P_{ind} the induced power, P_{par} the parasitic power and P_{pro} the profile power. P_{iner} is the inertial power associated with flapping the wings. P_{mr} and V_{mr}; and P_{mp} and V_{mp} are the powers and flight speeds of the maximum range and minimum power respectively. (from Norberg, 1990)

Morphological variation of bat wings

Flight is undoubtedly one of the key components in the success of bats. At around a thousand species, bats make up approximately one fifth of all known mammals (Nowak, 1994, Altringham, 1996). Compared to other forms of locomotion flight allows bats to quickly and easily exploit new niches and cross-geographical barriers such as mountain ranges and stretches of ocean. For example, New Zealand has only two species of native land mammals, both bats (Altringham, 1996), which probably arrived via a long flight over the ocean. Bats success is reflected in their huge diversity of diets and habitats. Whilst most species are hawking insectivores, more unusual diets include fish, scorpions, nectar, other bats and blood (Nowak, 1994). The only terrestrial habitats that bats don't tend to occupy are the polar regions, although some species do spend the summer north of the Arctic Circle (Altringham, 1996) Bats therefore present a fantastic study group for investigating how ecological pressures shape a basic mammalian blueprint in a plethora of different morphological and physiological solutions. Indeed, the morphological variation of bats is often much larger than it would appear at first glance. Whilst all bats have to conform to a basic wing shape that makes flight possible, within this envelope there is substantial variation. The variation in wing shape is typically a trade-off between aerodynamic performance to aid foraging and energetic demands (Fenton, 1972, Baagøe, 1987, Norberg & Rayner, 1987, Norberg, 1995). In general faster flying hawking bats tend to have longer thinner wings (referred to as high aspect ratio wings) and a higher wing loading (i.e. the ratio of body mass to wing area is high). Slower-flying bats have shorter broader wings (low aspect ratio) and lower

wing loadings (Figure 6). Some subtler specialisations of the wing include broad wing tips in species that forage close to vegetation improving manoeuvrability (Thollesson & Norberg, 1991). There is even some evidence that the height the wing bones protrude from the wing surface may vary between species and relate to their aerodynamics and foraging behaviour (Bullen & McKenzie, 2007).

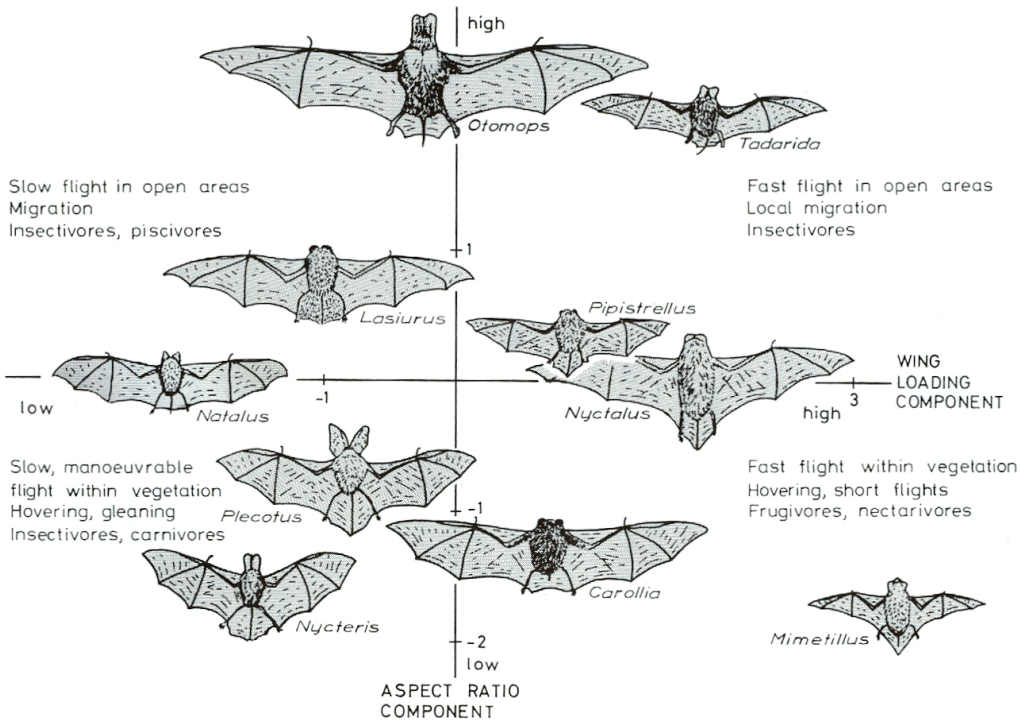


Figure 6 – Principal component analysis showing the relationship between two aspects of wing morphology, the aspect ratio and wing loading. Bats with long thin wings (high aspect ratio) and high wing loading (high ratio of weight to wing area) tend to forage in a similar style, using high-speed fight to catch insects on the wing. Bats with shorter, broader wings and lower wing loadings tend to forage amongst vegetation, gleaning insects from surfaces. (from Norberg, 1987)

Ecology, morphology and locomotion

It is no surprise that wing shape relates to foraging behaviour and therefore flight style, since wings are the most obvious aerodynamic surfaces of bat morphology. It is not only wing shape, however, that is implicated in these trade-offs. Features such as the feet, the ears, the tail membrane and even the fur have all been suggested as correlating with flight style and foraging behaviour (Fenton, 1972, Bullen & McKenzie, 2001, Fenton & Bogdanowicz, 2002, Bullen & McKenzie, 2008). In this thesis the trade-offs between the morphology, ecology and locomotor performance of one group of bats, the gleaners, are the central theme. Particular attention is paid to features of external morphology such as the tail and ears (Figure 7), which are not typically associated with locomotor behaviours, yet may have profound implications on the flight performance of the bats.

Gleaning bats have evolved to collect food from surfaces such as vegetation, walls, spider webs and the ground. Interestingly, although gleaning bats do echolocate, many species don't rely on it for foraging. Instead, the bats use sounds generated by the movement of their prey (Swift, 1998). This passive listening foraging style has led to the evolution of one of the most striking features of many gleaning bats morphology; their enormous ears. The brown long-eared bat (*Plecotus auritus*) for example, has ears that are almost as long as its forearms (Figure 8). The aerodynamic implications of such large ears have often been suggested, with two possible hypotheses put forward. The first hypothesis is that the ears produce additional drag and therefore increase the energetic demands on the bat (Fenton, 1972, Norberg, 1976b). The second

hypothesis is that the ears produce additional lift and act as 'canard' wings in front of the main wings, improving control and manoeuvrability (Bullen & McKenzie, 2001). The additional lift may even support the weight of the bat's head in flight (Vaughan, 1966). Testing these two hypotheses formed the starting point for this PhD thesis and is presented in Chapter 2, which is a reprint of Gardiner *et al.* (2008). The paper uses a simplified physical wind-tunnel model of *P. auritus* and a small force balance to measure the aerodynamic forces generated by the bat model's large ears in a variety of positions. The study found that the bat model's ears produced significant lift and drag, however were unlikely to be important in flight control (i.e. not canard wings).

The conclusions from Chapter 2, made it clear that the external morphology of gleaning bats had profound implications for their aerodynamic performance, their foraging style and energetic costs. Several features of bat morphology had been identified as correlating with foraging strategy, in particular ears and tail membranes (Fenton, 1972, Lawlor, 1973, Norberg & Rayner, 1987, Bullen & McKenzie, 2001). A comprehensive study of the relationship between bat external morphology and foraging style, however, had not been undertaken to date. Furthermore, the energetic implication of variations in morphological features such as ears and tails was unknown. Chapter 3 of this PhD thesis which is a reprint of Gardiner *et al.* (2011a), therefore, identifies the features of bat morphology that are most prominent in distinguishing between foraging styles. The energetic implications of variations in the most prominent morphological features are then modelled using Pennycuick's power curves model (Pennycuick, 1968), as was discussed above. Chapter 3 shows that ears

and tail membranes are morphological features that correlate well with foraging strategies. Gleaning bats have the longest ears and commuting bats the shortest tails. Chapter 3 also indicates the variations in ear and tail length of bat species have profound energetic implications.

In Chapter 3, the tail membrane of bats was identified as potentially fulfilling an important aerodynamic role. The aerodynamic function of bird tails is one of the most well researched and hotly debated topics in vertebrate flight (Thomas, 1993, Norberg, 1994, Thomas, 1996, Evans & Thomas, 1997, Maybury & Rayner, 2001, Maybury *et al.*, 2001, Evans *et al.*, 2002, Evans, 2003). A similar study investigating the role of bat tails, however, had not been conducted and our understanding of their flight function was at best speculative. Using a similar approach to Chapter 2, an aerodynamic model testing bat tail function is presented in Chapter 4 of this thesis, which is a reprint of Gardiner *et al*. (2011b). The study focused on testing the hypothesis that bat tails may contribute additional lift and be important for flight stability and control. Chapter 4 showed that the tail membrane of the model bats had a large impact on the pitching moment produced, suggesting therefore a role for tail membranes in bat flight control. Chapter 4 also highlighted the importance of the bat model's leg position on the camber of the inner wing surface which strongly influences the level of lift produced.

Although flight is the principal mode of locomotion for all species of bats. They all have to be capable of at least some terrestrial or arboreal locomotion for the purposes of roosting and mating. Some species are particularly proficient at terrestrial locomotion. For example, the vampire bat (*Desmodus rotundus)* is

often cited as being extremely agile on the ground, running and jumping with ease (Altenbach, 1979, Schutt *et al.*, 1997, Riskin & Hermanson, 2005, Riskin *et al.*, 2006). In general, gleaning bats, spend more time on or near the ground than aerial insectivores. A good jumping ability to get back into flight, therefore, is more likely to be have evolved in gleaning bats than other species. Testing this hypothesis is the basis of Chapter 5, a reprint of Gardiner & Nudds (2011). The paper compares video footage of several species of bats jumping against their foraging behaviours. The relationship between body size and jump performance is also investigated, since body size is one of the key morphological variations between all animals. Chapter 5, showed that contrary to expectations no relationship between jump performance and foraging style could be found. Body size was well correlated with jump performance, with larger bats producing higher forces, larger take-off speeds and higher jumps. It was concluded that flight so dominates the evolution of bat arm morphology and musculature, secondary locomotor modes such as jumping tend to be derivative.

The overall aim of this thesis is summarised by its title "How does the morphology of gleaning bats constrain their locomotor performance?" Indeed, the form and function of animal morphology is one of the key questions in evolutionary biology, and this thesis attempts to advance our knowledge of one area of this broad question: the relationship between the morphology of bats that forage in a gleaning style and their ecology, locomotion and physiology. The thesis focuses on aspects of morphology not typically studied such as the ears and tail membrane. Furthermore, it is not only flight performance that is considered but also other forms of locomotion such as jumping.

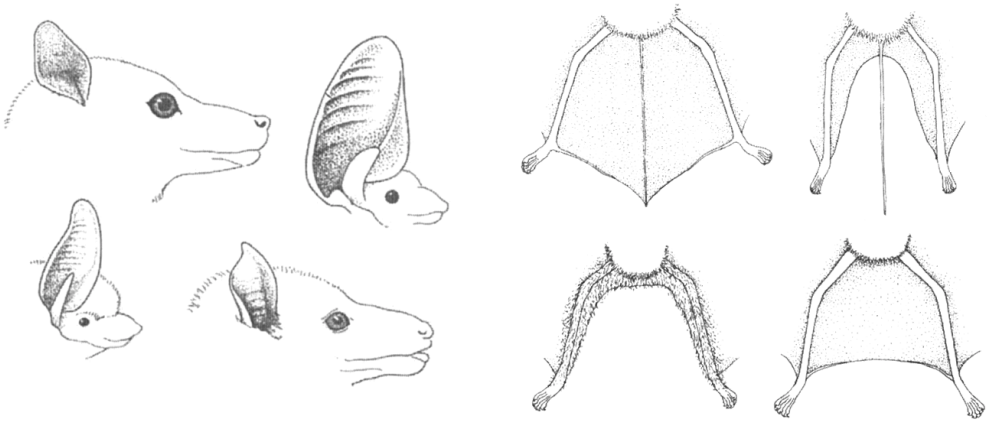


Figure 7 – Variations in bat ear and tail morphology, showing the large differences that occur not only in size, but also shape. (adapted from Altringham, 1996)

Figure 8 - Long-eared bat (*Plecotus auritus*) with ears erect, highlighting their enormous ears that can be as long as their forearm. (from Swift, 1998)

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Chapter 2

The aerodynamics of big ears in the brown long-eared bat *Plecotus auritus*

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The aerodynamics of big ears in the brown long-eared bat *Plecotus auritus*

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Wings are the most obvious adaptation bats have for powered flight and differences in wing morphology are known to correlate with flight behaviour. However, the function(s) of ancillary structures such as the ears and tail, which may also play an important role during flight, are less well understood. Here we constructed a simplified model of a bat body with ears based upon morphological measurements of a brown long-eared bat (*Plecotus auritus*) to examine the aerodynamic implications of flying with large ears. The forces and moments produced by the model were measured using a sensitive 6-component force and torque balance during wind tunnel testing. The large ears of the model bat produced positive lift as well as positive drag of the same order of magnitude. At small ears angles (0° to 10°), increasing the angle of the ears resulted in an increase of the lift-to-drag ratio. At higher ear angles (> 10°) separation of the flow occurred which caused a large decrease in the lift-to-drag ratio produced. To maximise the benefit from the ears (i.e., lift-to-drag ratio) our model predicts that a horizontal free flying *P. auritus* should hold its ears at an approximate angle of 10°. The results of the pitching moment coefficient are inconclusive in determining if the large ears are important as flight control structures. The additional drag produced by the ears has consequences for the foraging behaviour of *P. auritus* with reductions in its flight speed and foraging range.

Key words: Chiroptera, flight, ear, aerodynamics, *Plecotus auritus*

Introduction

Variation in the shape and size of the wings has a clear relationship with feeding preferences in bats. A bat with a high wing loading (high ratio of body mass to wing area) and high aspect ratio wings (long and thin) is likely to use fast foraging flight in open areas whilst catching insects from the air, whereas a bat with a low wing loading and low aspect ratio wing is more likely to use slow flight amongst vegetation whilst gleaning insects from surfaces (Baagøe, 1987; Norberg, 1987; Norberg and Rayner, 1987). Bats are also distinguished by differences in the ears and tail which may also have an important influence on the aerodynamics of flight (Fenton, 1972; Bullen and McKenzie, 2001). Although these studies have suggested that ancillary structures play an important role in the aerodynamics of flight, no direct measurements of the forces and moments have been made.

The brown long-eared bat (*Plecotus auritus*) is a common European species that is remarkable for the very large size of its ears (length 29–41 mm) which are almost the same length as its forearms (34–42 mm — Altringham, 2003). For such structures to have evolved there must be a significant benefit. For example, it has been shown that bats with long ears are superior at avoiding thin wires stretched across their flight paths when compared to other bats with smaller ears (Griffin, 1958). Behavioural studies of *P. auritus* lead to similar conclusions about their hearing ability, since they often emit very quiet or no echolocation calls whilst gleaning prey, relying instead upon passive listening (Anderson and Racey, 1991). Furthermore studies of the acoustic properties of the outer ear have shown that the large ears possessed by many gleaning species are particularly sensitive at low frequencies, which aid prey detection by passive listening (Coles *et al*., 1989; Obrist *et al*., 1993). However, not all gleaning species adopt this technique, some species such as *Myotis nattereri* have been observed to carry on echolocating whilst gleaning and to make little use of prey-generated sounds (Swift and Racey, 2002). Therefore the large ears of *P. auritus* may have evolved to be highly effective at detecting prey-generated sounds, particularly the initial detection of faint sounds which

may be missed by other gleaning bats (Coles *et al.*, 1989).

Large ears are often thought to be of aerodynamic significance during the flight of these bats and are suggested to have both potentially positive and negative effects. For example, having big ears may have a detrimental effect on flight performance and contribute significantly to the drag of the animal (Fenton, 1972; Norberg, 1976*b*). This increased drag from the ears may result in a reduction in the flight speed of the bats and may only be affordable to bats with low wing loading (Norberg, 1976*b*). The reduction in flight speed maybe a key factor which limits *P. auritus* foraging range (Swift, 1998). This suggestion is strengthened by research showing that most *P. auritus* roosts are found close (less than 0.5 km) to deciduous woodland (Entwistle *et al.*, 1997), their preferred foraging habitat (Entwistle *et al.*, 1996). Another possible aerodynamic consequence of having large ears is that they generate additional lift (Vaughan, 1966; Fenton, 1972; Bullen and McKenzie, 2001). There are several suggestions as to the advantage of any additional lift being produced by the ears. Firstly it is thought that the additional lift may be important in supporting the bat's head during flight (Vaughan, 1966), this is likely to be more significant for bats in comparison to birds as a bat's head makes up a larger proportion of its overall weight. Secondly it is suggested that the additional lift produced by the ears may mean they act as flight control structures analogous to the canard wings of aircraft located in front of the wings (Bullen and McKenzie, 2001). Canard wing structures reduce the adverse effects of stalling and also contribute to the positive lift being generated by the wings (Stinton, 2001). Therefore, the large ears of some bats may not have the expected detrimental effect on flight performance.

Morphological characteristics of the ears are useful parameters in identifying the agility of bats (Bullen and McKenzie, 2001). Agile bats tend to have the smaller ears, perhaps because large ears are impractical for high speed turns whilst catching insects in the air. Among all the extant bat species large ears are most commonly associated with gleaning bats, which are known to require slower manoeuvrable flight (Wilson, 1973; Norberg and Rayner, 1987). Furthermore, bats with similar ear to forearm length ratios occupy the same foraging niches worldwide (Fenton, 1972) meaning they are all likely to experience similar aerodynamic costs or benefits.

The aerodynamics of flying animals is intrinsically linked to their energetic expenditure during flight. Therefore the aerodynamic effect of ancillary structures like the ears, should they be producing increased drag and lift, must also have energetic implications which will directly impact the behaviour of these animals. If the ears do produce substantial additional drag then the energetic cost of flight for the bat will also be increased (Norberg, 1976*b*). Bats with larger ears tend to have larger than expected hearts, possibly due to overcoming the increased energetic cost of the drag produced by the ears (Canals *et al.*, 2005). However, the larger heart may also be related to additional factors, for example it is know that some species of long-eared bats can hover (Norberg, 1976*a*), which is more energetically expensive than forward flight (Norberg *et al.*, 1993). Conversely if the large ears of bats are in fact having a positive effect on the aerodynamics of these bats by, for example, producing additional lift, then they may in fact reduce the energetic expenditure of the bat, since the lift produced will offset the energetic cost of supporting the bats head in flight (Vaughan, 1966). Building simple models is commonly used to assess the aerodynamics of flight (e.g., Maybury and Rayner, 2001; Maybury *et al.*, 2001) and these models can help us to understand the possible ecological significance of morphological variations. Here we investigated the impact of large ears on the aerodynamics of flight in *P. auritus*.

Materials and Methods

Morphological Measurements and Model Construction

Morphological measurements of the ears and bodies of *P. auritus* were collected from dried specimens at the University of Manchester Museum (UK). All measurements (body size, length, width and depth of ears) were taken using digital callipers, (16EX 150 mm Prod No: 4102400, Mayr GmbH, Berlin, Germany). A simplified wooden model was then constructed and used in wind tunnel testing. The model was designed at 2:1 scale from preliminary results which indicated that a scaled up model would experience aerodynamic forces that could be measured using a sensitive 6-component aerodynamic balance. To ensure that the flow around the model is similar to the flow around a bat in flight, Reynolds number, Re, must be of the same order of magnitude for both situations. Reynolds number is defined as: $Re = \rho Ud/\mu$ (where ρ is the density of the air, U the free stream airspeed, d a characteristic length and μ the viscosity of the air). Our model was scaled at 2:1 (i.e., much less than an order of magnitude) therefore scaling will not have a significant impact on the flow, for example drag coefficients are fairly constant between Reynolds numbers of 10^4 to 10^5 (based on diameter — Vogel, 1994). The Reynolds number for our model during testing was approximately between 20,000 and 50,000 (based on model width). The ears of the model were

constructed from thin aluminium sheet and attached to the smoothed wooden body of the model via terminal blocks to allow the angle of the ears to be adjusted (Fig. 1). All voids in the model were filled with plasticine to ensure that they didn't interfere with the flow. Although simplified, the model allows the aerodynamics of the ears to be studied in isolation from the rest of the bat. Furthermore testing of hypothetical situations not observed in nature is also possible (Koehl, 2003).The body of the bat was included in the model since this was considered to be an integral part of the aerodynamics of the ears. Simple wind tunnel models are a commonly used and experimentally validated approach when investigating many features of flight including the aerodynamics of complaint wing membranes (Galvao *et al.*, 2006; Song and Breuer, 2007).

Force and Moment Measurements

The bat model was attached to a 6-component NANO-17 Force Torque transducer (ATI Industrial Automation). The assembly (Fig. 2) was mounted via a support onto a mast in an experimental wind tunnel housed at the Université de Liège, Belgium. The working area of the tunnel is 2 × 1.5 m. Fibreboard plates were used to attach the support and model to the force balance. The support was designed to be thin so as not to produce a large flow disturbance.

The angle of the ears relative to the body (θ) was adjusted set with a large protractor, using the back surface of the ears and the upper surface of the body as references. The angle of the body relative to the oncoming wind (φ) (also referred to as the angle of attack) was set using a large adjustable spirit level held vertically against the support (Fig. 2).

Data were logged from the force balance for three seconds at a sampling rate of 64 Hz. These data were then averaged over the three seconds to give the steady forces and moments measured by the balance. All force and moments were measured relative to zero airspeed. The wind speeds for testing (4–8 m/s) correspond to the range of natural commuting flight speeds recorded for *P. auritus* (Baagøe, 1987; Howard, 1995). The actual wind speed in the test section of the wind tunnel was measured using a pitot tube, since the nominal wind speed was set across the fan section of the wind tunnel. Lower wind speeds could not easily be obtained due to unstable flow conditions at wind speeds below 4 m/s in the wind tunnel. The ear angle of the model was adjusted to six positions ranging from 0° to 60° (relative to the body of the model). The body angle of the model was adjusted to four positions ranging from 0° to 20° (relative to the airflow). The test angles were chosen to reflect the angles that the ears are held at during unrestrained flight, based upon photographs from flight studies of *P. auritus* (Norberg, 1976*b*).

Calculation of Lift, Drag and Pitching Moment Coefficients

The force balance can measure six components of force and moment (namely, lift drag, side-force, pitching moment, rolling moment and yawing moment), however, only three of these components are important for the present application. These are the lift, drag and pitching moment around the balance's point of attachment to the model. As the model was designed to be symmetric and was installed with nearly zero roll and yaw angles, the side force, rolling and yawing moments were negligible.

As the angle of the body was tilted relative to the flow so were the axes of the force balance (Fig. 3). Therefore, to allow the calculation of the lift, drag and pitching moment coefficients, the data from the force balance had to be transformed from body axes to horizontal and vertical axes. The relations used to transform the forces output by the force balance into lift and drag relative to the ground are shown in equations 1 and 2 (where L is the lift, D the drag, F_z the force in the z-direction, F_x the force in the x-direction and φ the angle of the body to the wind).

$$L = F_z\cos\varphi - F_x\sin\varphi \quad (1)$$

$$D = F_x\cos\varphi + F_z\sin\varphi \quad (2)$$

The pitching moment was unaffected by the change in the body angle therefore no correction was applied to it. From the lift, drag and pitching moment, the lift, drag and pitching moment coefficients were calculated. These are defined in equations 3, 4 and 5, where C_L is lift coefficient, C_D is drag coefficient, C_M is pitching moment coefficient, M is the pitching moment around the model's support (defined positive nose down), S is a reference area and c a reference length.

$$C_L = \frac{L}{\frac{1}{2}pU^2S} \quad (3)$$

$$C_D = \frac{D}{\frac{1}{2}pU^2S} \quad (4)$$

$$C_M = \frac{M}{\frac{1}{2}pU^2Sc} \quad (5)$$

The reference area was defined as the area of the plan view of the model bat and the reference length was defined as the

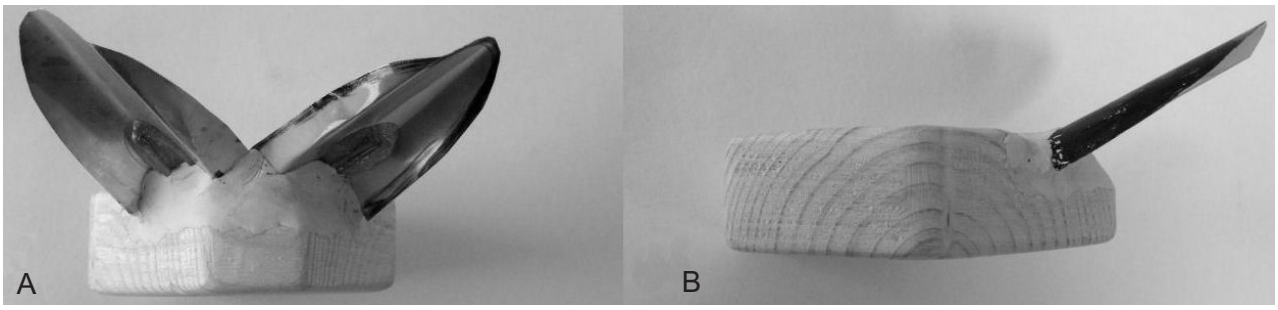

FIG. 1. Two views of the completed *P. auritus* model for wind tunnel testing. (A) Frontal view showing ear details. (B) Lateral view

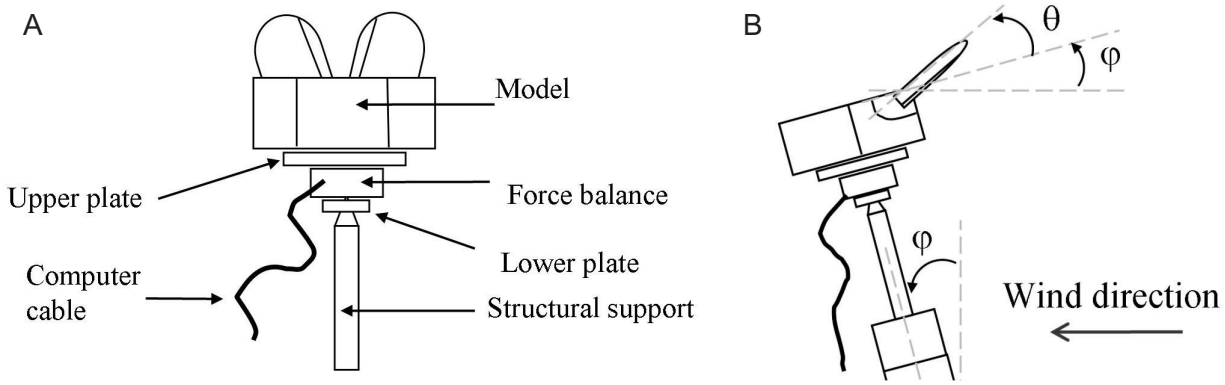

FIG. 2. Experimental set up in wind tunnel of *P. auritus* model. (A) Locations of model, structural supports, force balance and mounting plates. (B) Definition of ear angle and body angle for model testing relative to wind direction

combined length of the body and ears of the model (at 0° ear angle).

The lift to drag ratio for the bat model was also calculated as this gives a good indication of the overall aerodynamic performance. The lift to drag ratio is equal to the ratio of lift coefficient to the drag coefficient and can be calculated using equations 3 and 4.

Forces Experienced by a Bat in Flight

To test if the lift and drag measured on the bat model would be significant to *P. auritus* in flight, the actual lift and drag forces experienced was calculated. Since the lift and drag coefficient are dimensionless and flow similarity was ensured between the model and real bat in flight, the aerodynamic coefficients for both situations should be similar. Therefore, by rearranging equations 3 and 4 the lift and drag forces on a bat in flight can be calculated.

Assuming that a bat would fly in a position generating the maximum lift-to-drag ratio, the lift and drag coefficients for this ear and body angle were selected. The lift and drag forces where then calculated for a range of natural flight speeds (Baagøe, 1987) and compared against the average body weight (body mass × 9.81) for *P. auritus* (Altringham, 2003).

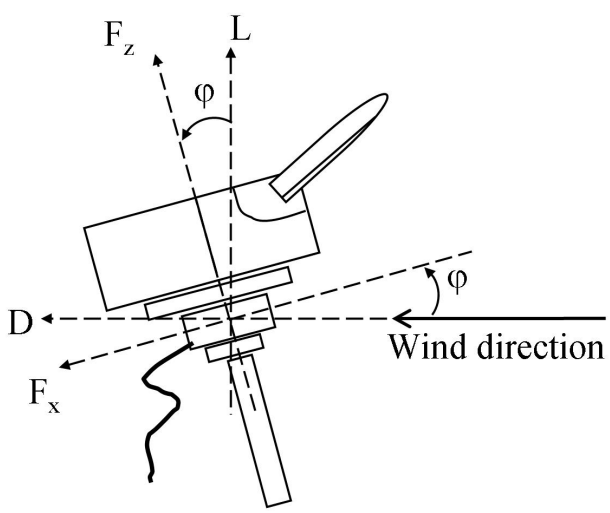

FIG. 3. Force balance axes (F_x and F_z) relative to lift (L) and drag (D) for experimental set up of model *P. auritus* in the wind tunnel

Flow Visualisation

Flow visualisation was used to observe the flow structure around the model. The bat model was set at a body angle of 0° and an ear angle of 30°. The wind tunnel was then run at a nominal wind speed of 10 m/s. Smoke was passed over the model and illuminated using the Particle Image Velocimetry (PIV) system's lasers. The laser plane could be traversed across the span of the model, thus illuminating different sections of the flow. Photographs and videos were recorded using a digital camera (Olympus Camedia C-350).

RESULTS

For all ear and body angles tested the bat model generated a positive lift coefficient, positive drag coefficient and a negative (nose-up) pitching coefficient. The pitching moment coefficient was found to vary little with the ear and body angles tested and consistently assumed a value of -0.4 (Fig. 4)

However, both the lift and drag coefficients showed interesting variations with the changing ear and body angle of the model (Figs. 5 and 6). Initially increasing ear angle results in an increase in the lift produced before a clear drop in lift coefficient at higher ear angle, for all airspeeds (Fig. 5). The ear angle that corresponds to this drop is 10° for low body angles and 5° for high body angles. The drop is less prominent at nominal airspeeds higher than 6 m/s. Furthermore increasing the body angle causes a reduction in the lift produced by the model for all ear angles.

The general trend is for drag coefficient measurements to increase as ear and body angles on

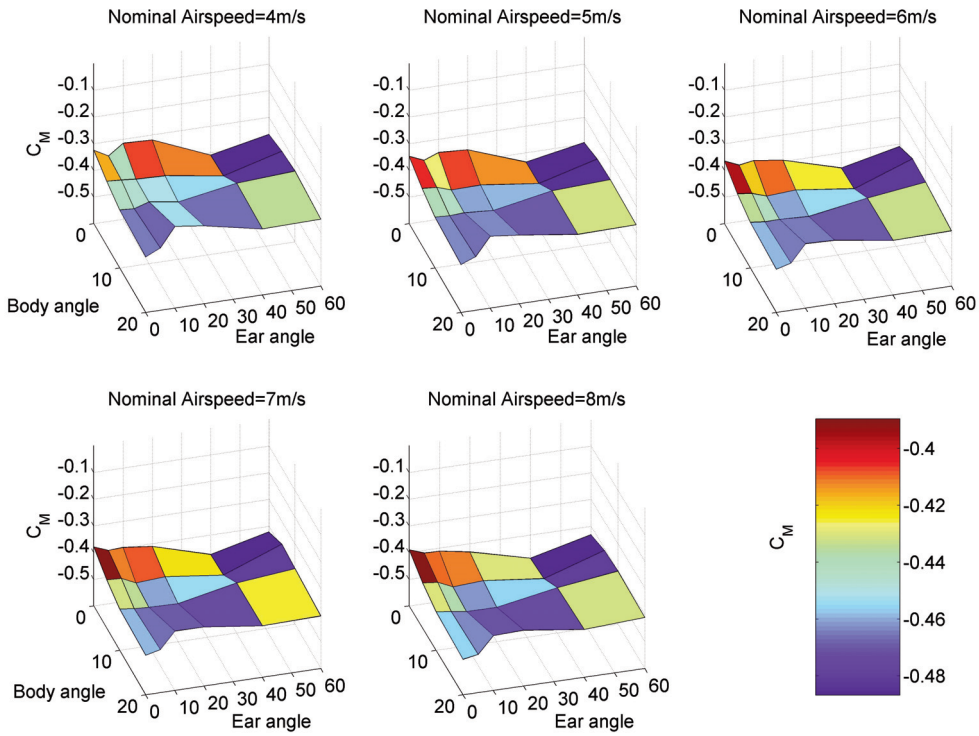

FIG. 4. Effect of ear angle and body angle on pitching moment coefficient (C_M) calculated for model *P. auritus* in wind tunnel tests at five set speeds

the model are increased (Fig. 6). However, the rise in drag coefficient is sharper at low ear angles (between 0° and 10°) when the body angle is larger than 5°. The highest drag is obtained at 0° body angle and 60° ear angle. The ear angle that tends to give the lowest drag is 0°.

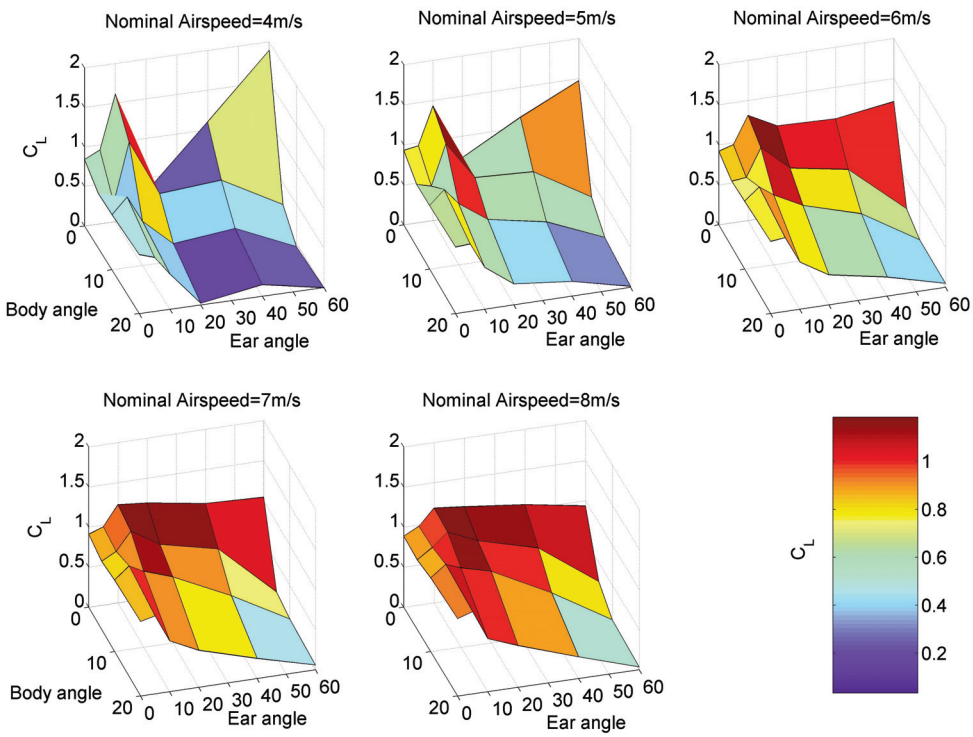

FIG. 5. Effect of ear angle and body angle on lift coefficient (C_L) calculated for model *P. auritus* in wind tunnel tests at five set speeds

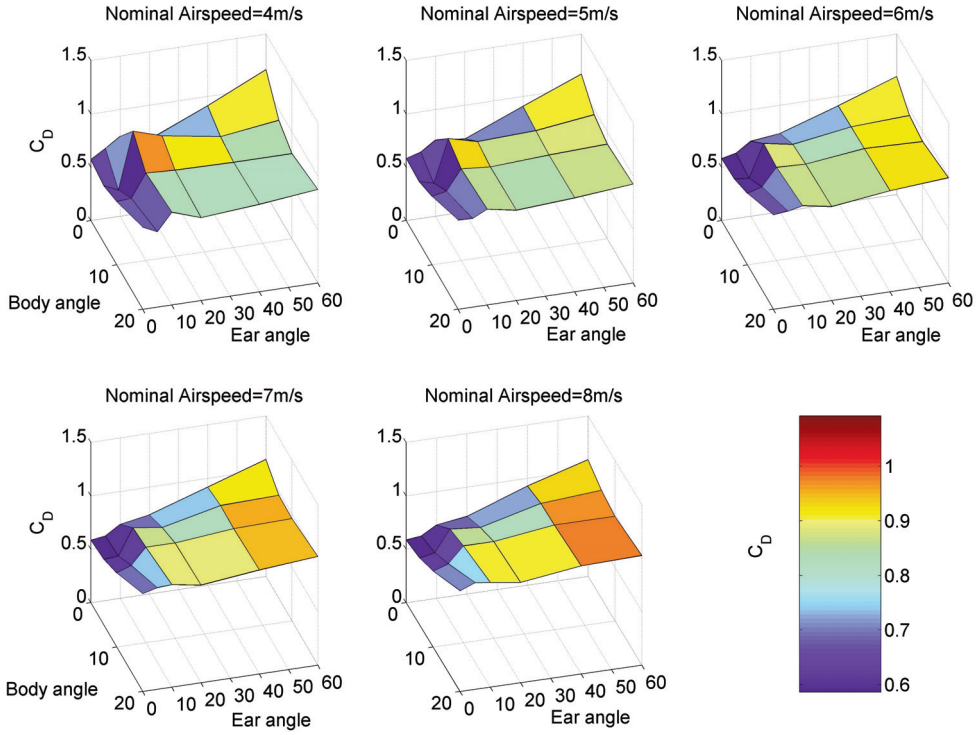

FIG. 6. Effect of ear angle and body angle on drag coefficient (C_D) calculated for model *P. auritus* in wind tunnel tests at five set speeds

The lift-to-drag ratio (Fig. 7) shows similar trends as the lift coefficient with an increase initially as ear angle increases before a sudden drop at higher ear angles. For all body angles and airspeeds, the lift-to-drag ratio reaches a maximum value at ear angles between 5° and 10° degrees. The maximum lift to drag ratio occurs at 10° ear angle for the 0° body angle, whereas for the other three body

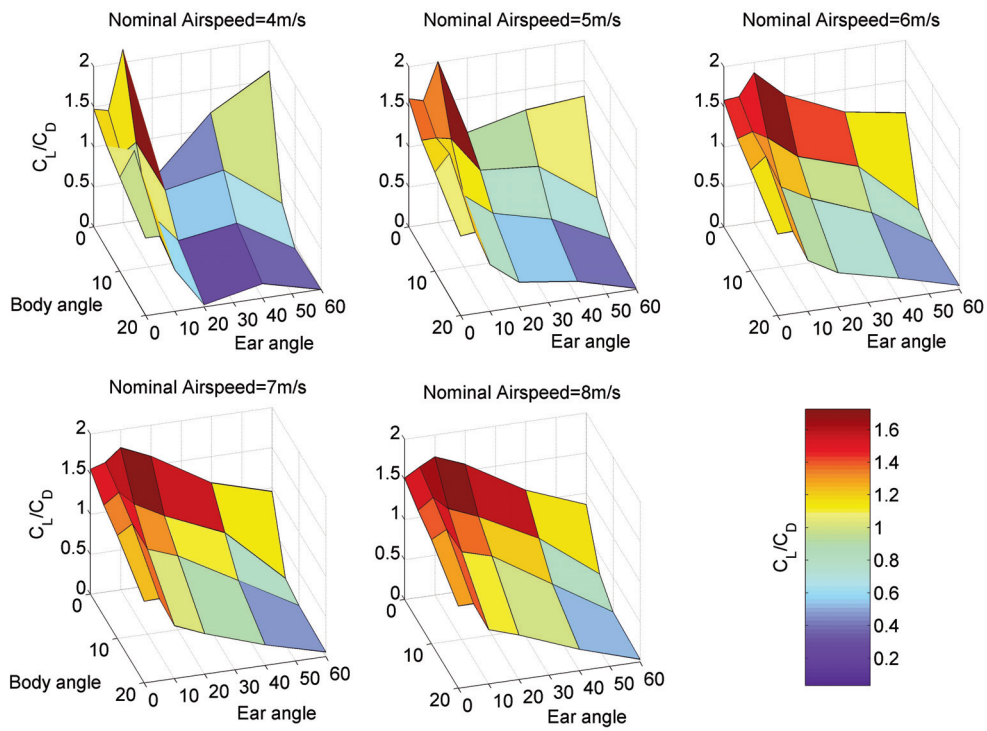

FIG. 7. Effect of ear angle and body angle on lift-to-drag ratio (C_L/C_D) calculated for model *P. auritus* in wind tunnel tests at five set speeds

angles the maximum occurs at 5° ear angle. It can also be seen that, for all ear angles, the lower the body angle the higher the lift to drag ratio, with 0° body angle producing the highest ratios.

Results from the flow visualisation test (Fig. 8) of the model bat set with an ear angle of 30° and a body of 0° show that the smoke above the model has an upwards velocity component behind the ears. This phenomenon is referred to a flow separation or stalling.

Forces Experienced by a Bat in Flight

The calculations of the force coefficient for the model show that the model produces the maximum lift-to-drag ratio of 2.16 at a body angle of 0°, an ear angle of 10° and a nominal airspeed of 4 m/s (Fig. 7). The lift and drag coefficients for the model in this position are 1.62 and 0.75 respectively. These results allow the calculation of the forces experienced by a bat in flight (Fig. 9). As speed increases the magnitude of the lift and drag also increase. The 7 m/s flight speed the ear and body combination would provide approximately half the lift required to keep a *P. auritus* in flight. The drag at this speed would also be approximately a third of the bat's body weight in Newtons (calculated as body mass (kg) × 9.81). At a flight speed of 9 m/s the ear and body combination is providing enough lift to support the entire bats body weight, although a significant amount of drag is also being produced.

Discussion

The bat model results show the forces generated by the ear and body combination of the model bat will have a significant aerodynamic impact on *P. auritus* flight and therefore must be considered when discussing the overall aerodynamics of the bat. At the higher range of natural flight speeds for

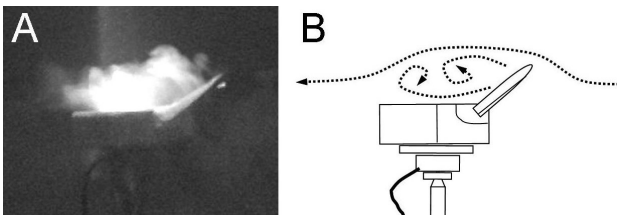

Fig. 8. (A) Selected frame from PIV laser flow visualisation showing illuminated smoke in span-wise strips over the model. The model is set with a body angle of 0° and an ear angle of 30°. Nominal airspeed set at 10 m/s. (B) Schematic diagram to illustrate flow structure in frame A

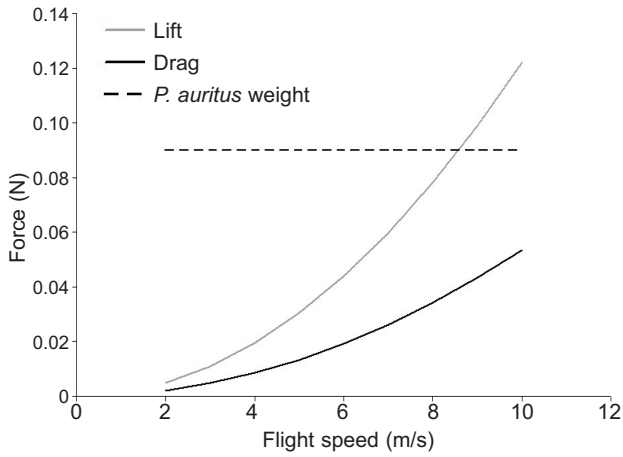

Fig. 9. Calculation of model predicted vertical lift and drag forces that would be experienced by *P. auritus* in flight from its ear and body combination, with an ear angle of 10° and body angle of 0°. Body weight for *P. auritus* calculated in Newtons as mass (kg) × 9.81

P. auritus the body and ears are accounting for all the lift required to support the body weight. Although these results may be artificially high due to the bluff nature of the body of the model, the results from our wind tunnel testing confirm, as suggested from previous studies (Vaughan, 1966; Fenton, 1972; Norberg, 1976*b*; Bullen and McKenzie, 2001), that the lift and drag forces produce by the body and ears have an impact on *P. auritus* aerodynamics. Furthermore the calculations of the lift-to-drag ratio show that adjusting the positioning of the ear and body of the model caused large variations in the ratio calculated. At low ear angles the lift-to-drag ratio of the model increases with ear angle until about 10° (Fig. 7). At higher ear angles (> 10°) the lift-to-drag ratio drops abruptly, suggesting that the flow over the ears stalls. This suggestion is reinforced by the flow visualisation images (Fig. 8), which clearly show an area of separated flow behind the ears at an ear angle of 30°. Flow separation causes an abrupt drop in lift coefficient and rise in drag coefficient. Interestingly increasing the body angle does not seem to follow the same pattern as the ear angle but seems to always cause a reduction in the lift-to-drag ratio produced. This is probably due to the bluff nature of the body, where any increase in body angle will produce a larger increase in drag than lift.

The lift-to-drag ratio is one of the most important aerodynamic variables for a flying animal, since it must generate sufficient lift whilst not generating excessive drag. Therefore, the energetic cost of flight will be minimised. The results of the present

experimental work indicate that if a bat wishes to generate the maximum lift-to-drag ratio in its body-ear combination then it should fly with its body in a horizontal position and hold its ears at an angle of attack of approximately 10º, although the bat's wings will also have a large influence on the body angle adopted. However, it should be noted that a bat might not necessarily wish to generate the maximum lift to drag ratio, but one that produces sufficient lift, whilst minimizing drag. It is interesting to note that in photographs of *P. auritus* in slow horizontal flight (Norberg, 1976*b*), the angle adopted by the ears is fairly shallow around 20º to 30º to the horizontal. Although this angle is larger than predicted by the model it shows that shallow ears angles are likely to be important to *P. auritus* to minimise the energetic cost. The higher angles seen in the photographs may be due to the ability of the real ears to maintain attached flow to higher ear angles than the model bat's ears. This may be because the ears of a real bat are more compliant than a model; therefore stalling is delayed through the shape changes of the ear caused by aerodynamic loading. This softened stalling behaviour is thought to be a property of bat's wing membranes (Song and Breuer, 2007). Wing membrane skin has specific material properties which can be related to flight (Swartz *et al.*, 1996).

The pitching moment coefficient measurements demonstrate that body angle and ear angle have little effect on the pitching moment coefficient generated and therefore the longitudinal stability of the bat, was found to be largely unaffected by the angle of the ears. This may be due to the simplicity of the model which is likely to be bluffer than an actual bat's body. Therefore, the increased drag and additional lift produced by the bluff body may have hidden the control effectiveness of the ears. However, due to the limited effect of ear angle on the pitching moment generated, our bat model does not support the theory that large ears behave as flight control structures (Bullen and McKenzie, 2001). However future, more detailed models and field studies may further elucidate the effect of ears on flight control and stability.

Plecotus auritus is a small, insectivorous bat species, which is well known to use gleaning as a prey capture method (Anderson and Racey, 1991). Gleaning is a hunting method that requires slow and manoeuvrable flight, which these bats species are suitably adapted to use (Norberg and Rayner, 1987). For example wings with low aspect ratios and low wing loadings. In addition gleaning bats often possess large ears (Wilson, 1973) thought to aid prey capture by passive listening. It is unsurprising that large ears are associated with bats that use slow flight, since any additional ancillary structure is likely to increase the drag upon the bat. The model results presented here demonstrates that the large ears of *P. auritus* do contribute to the aerodynamic cost of flight by producing additional drag. This additional drag can have significant consequences since drag increases as the square of flight speed therefore; a small increase in flight speed can lead a significant increase in the energetic demand which may limit the flight speed of *P. auritus* (Norberg, 1976*b*). Bats with larger ears tend to have larger hearts, the results from our study suggests this may, in part be due to overcoming the increased energetic demand caused by the large drag producing ears (Canals *et al.*, 2005).The limit in flight speed suggested would result in a limit upon the foraging range of the bats and therefore provide a tangible explanation for why these bats roost close to suitable feeding habitat (Entwistle *et al.*, 1997).

The evolution of the large ears of *P. auritus* appears to be a trade-off between two competing factors. The increased sensitivity of the ears in detecting the low frequency prey-generated sounds whilst gleaning insects (Coles *et al.*, 1989), particularly insects undetectable to other gleaning species (Swift and Racey, 2002), must be balanced with a requirement to limit the detrimental impact of the increased drag produced by the large ears. A comparative study investigating both the acoustic and the aerodynamic performance of various ear morphologies would further understanding of trade-offs in bat morphology. It is expected that bats which fly faster will have evolved ears that limit aerodynamic cost, but also have reduced acoustic sensitivity. One interesting possibility is that *P. auritus* hold their ears at lower angles during commuting flight than during foraging. This would ensure that hearing ability is maximised for effective prey capture when foraging, whereas in commuting flight the ears do not cause too high an energetic demand. *P. auritus* are also known to fold their down ears during roosting (Swift, 1998), but ear folding has never been suggested to occur during flight.

Acknowledgements

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Chapter 3

An association between ear and tail morphologies of bats and their foraging style

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An association between ear and tail morphologies of bats and their foraging style

James D. Gardiner, Jonathan R. Codd, and Robert L. Nudds

Abstract: Most studies relating bat morphology to flight ecology have concentrated on the wing membrane. Here, canonical variance analysis showed that the ear and tail morphologies of bats also strongly relate to foraging strategy, which in turn is correlated with flight style. Variations in tail membrane morphology are likely to be a trade-off between increases in the mechanical cost of flight and improvements in foraging and flight performance. Flying with large ears is also potentially energetically expensive, particularly at high flight speeds. Large ears, therefore, are only likely to be affordable for slow foraging gleaning bat species. Bats with faster foraging flight styles tend to have smaller ears, possibly to cut the overall drag produced and reduce the power required for flight. Variations in the size of ears and tail membranes appear to be driven primarily by foraging strategy and not by body size, because the scaling relationships found are either weak or not significant. Ear size in bats may be a result of a trade-off between acoustic and aerodynamic performance.

Résumé : La plupart des études qui relient la morphologie des chauves-souris à leur écologie du vol se sont intéressées principalement à la membrane de l'aile. Notre analyse de variance canonique montre que les morphologies des oreille et des queues des chauves-souris est fortement reliée à la stratégie de recherche de nourriture, elle-même en corrélation avec le style de vol. Les variations dans la morphologie de la membrane caudale représentent vraisemblablement un compromis entre les accroissements des coûts mécaniques du vol et les améliorations de la performance de la recherche de nourriture et du vol. Le vol avec de grandes oreilles peut aussi être coûteux en énergie, particulièrement aux vitesses de vol élevées. Il est donc vraisemblable que seules les chauves-souris à vol lent qui recherchent leur nourriture par glanage peuvent se permettre de grandes oreilles. Les espèces dont le style de vol de recherche de nourriture est plus rapide possèdent des oreilles plus petites, probablement pour réduire la traînée totale produite et diminuer la puissance requise pour le vol. Les variations dans la taille des oreilles et des membranes caudales semblent s'expliquer principalement par la stratégie de recherche de nourriture et non par la taille corporelle, puisque les relations de cadrage trouvées sont ou bien faibles ou non significatives. La taille de l'oreille chez les chauves-souris peut être le résultat d'un compromis entre les performances acoustique et aérodynamique.

[Traduit par la Rédaction]

Introduction

The shape and size of a bat's wings are known to relate to their foraging strategy (Fenton 1972; Baagøe 1987; Norberg and Rayner 1987). Ears (Vaughan 1966; Bullen and McKenzie 2001) and tail membranes (Lawlor 1973; Norberg 1990) are also thought to have a significant effect on the flight and foraging performance of bats. Like the wings, ear and tail morphologies are highly variable between families and correlate, at least qualitatively, with foraging strategy (Fenton 1972; Lawlor 1973; Norberg and Rayner 1987; Bullen and McKenzie 2001; Fenton and Bogdanowicz 2002).

Tail membranes

Tails are known to be an important aid during the locomotion of many vertebrates (Demes et al. 1996; Essner 2002; Jusufi et al. 2008). In particular, the aerodynamic functions of bird tails during flight are well established (Thomas 1993; Norberg 1994; Evans et al. 2002; Sachs 2007). Bat tail membranes are likely to share some functional similarities with bird's tails. For example, both bat tail membranes (Lawlor 1973; Norberg and Rayner 1987; Bullen and McKenzie 2001) and bird tails (Maybury and Rayner 2001) are thought to contribute to lift generation during flight. There are, however, important differences because the tail membrane of bats is an extension of the wing surface between the hind legs of the bat and does not form a separate lifting surface. The tail membrane, therefore, cannot be analysed as a delta wing following previous studies of the aerodynamic function of bird tails (Thomas 1993; Evans 2003).

Stabilizing flight is thought to be a key function of bird tails (Thomas and Taylor 2001; Sachs 2007), helping the bird to maintain its flight course even when disturbances occur (e.g., a large gust of wind). The tail membrane of bats may play a similar stabilizing role. Flying animals can achieve stability either passively through stabilizing morphological features (e.g., a large drag producing tail will im-

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prove stability) or actively through flapping of the wings (Taylor and Thomas 2002; Hedrick et al. 2009; Dickson et al. 2010). In general, however, a trade-off exists between flight stability (particularly passive stability) and control because excessive stability will tend to inhibit agility and manoeuvrability. Indeed, modern birds and bats are more inherently unstable than their ancestors, thereby improving manoeuvrability and agility, as their nervous and sensory systems have evolved to cope with the demands of active flight control (Maynard Smith 1952). We would therefore expect tail morphology to correlate strongly with flight style, which in turn is likely correlated with foraging ecology.

Ears

Bats exhibit diverse ear morphology and some species, such as the brown long-eared bat (*Plecotus auritus* (L., 1758)), have enormous ears (Figs. 1*a*, 1*b*). The effect of flying with large ears is unclear. Some studies speculate that during flight large ears may have a detrimental effect on flight performance by increasing drag (Fenton 1972; Norberg 1976). Alternatively, large ears may in fact be beneficial during flight, acting as canard structures (small lifting surfaces in front of the main wings) producing additional lift and contributing to flight control (Bullen and McKenzie 2001). Wind-tunnel tests on a simple model of *P. auritus* indicated that the ears do produce significant lift, as well as drag, especially at higher flight speeds (Gardiner et al. 2008). Bat ear morphology seems to correlate with foraging strategy (Fenton 1972; Norberg and Rayner 1987), yet the implications of this morphological variations on flight performance remain unclear.

Study outline

Although, previous studies have related wing morphology to foraging behaviour and flight style (e.g., Norberg and Rayner 1987), similar examinations of ear and tail morphologies are generally lacking. Accordingly, here using morphometric and comparative analyses, the ear and tail morphologies of bats were compared with foraging strategies. Additional flight structures and the main characteristics of wing morphology were also included in a canonical variance analysis (CVA) to confirm that tails and ears are predominant in defining foraging strategy. Finally, the consequences of possessing large ears and tail membranes were calculated using Pennycuick's (1968) classic theoretical power curve models and the morphology of *P. auritus* as an exemplar.

Materials and methods

Bat morphology

Data were collected from 98 museum specimens representing 12 of the 17 extant bat families (Nowak 1994). Morphological measurements (Fig. 1*a*) of ear length and width, thumb, forearm, lower leg, foot, calcar, and tail membrane lengths were collected using a pair of Mayr digital callipers (16EX 150 mm; product No. 4102400; Mayr GmbH, Mauerstetten, Germany). Data on wingspan, wing area, and body mass were taken from Table 1 of Norberg and Rayner (1987). Mean wing chord was calculated as wing area / wingspan. Bats were assigned to one of four foraging styles, based on descriptions of their feeding behaviour, diet, and flight style (Norberg and Rayner 1987; Nowak 1994; Altringham 1996; Fenton and Bogdanowicz 2002). The foraging style groupings used were

(1) Commuting: bats that generally commute directly between roosts and foraging sites (e.g., nectar- and fruit-feeding bats). Vampire bats (Desmodontinae) were also included in this group.
(2) Slow-hawking: bats that catch insects on the wing often among vegetation (e.g., most horseshoe bat species (Rhinolophidae)). This group also included bats that feed over water, taking insects and fish while on the wing.
(3) Fast-hawking: bats that use faster and more direct flight to forage in open areas (e.g., free-tailed bats (Tadarida)).
(4) Gleaning: bats that take food (e.g., insects and vertebrates) from the ground or vegetation, often while hovering (e.g., the ghost bat, *Macroderma gigas* (Dobson, 1880)).

The morphological measurements and the foraging strategy grouping of each bat are listed in supplementary Table S1.[3]

Statistical analysis

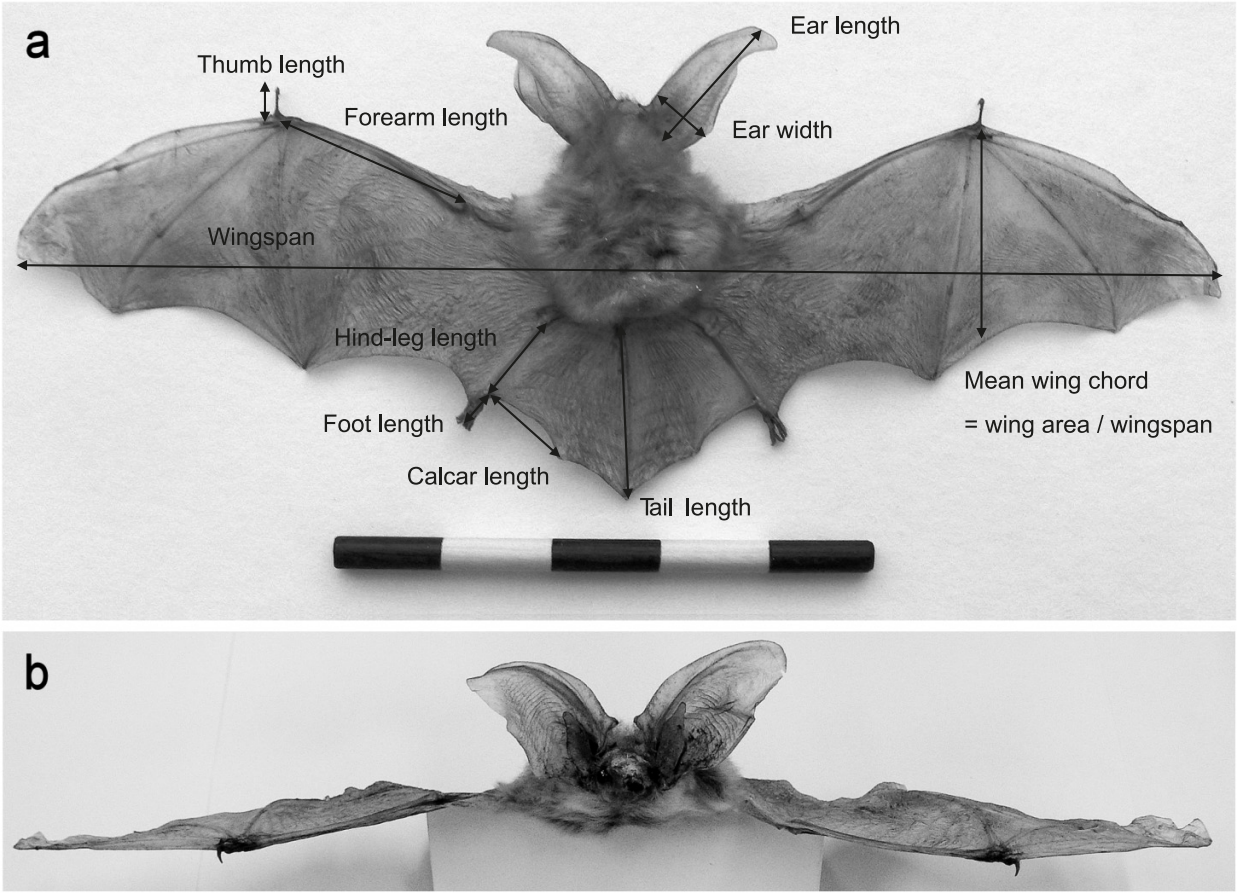
CVA was used to determine the morphological features that were most strongly related to foraging group. CVA maximizes the variation between groups relative to the variation within groups (Campbell and Atchley 1981). To correct for body size, all the morphological measurements were scaled by the cube root of the species' body mass. CVA was performed using SPSS version 14.0 (SPSS Inc., Chicago, Illinois, USA).

The BRUNCH algorithm in CAIC (Purvis and Rambaut 1995) was then used to determine whether the differences observed in the CVA remained after controlling for the confounding effects of common ancestry. Independent contrasts derived from CAIC were tested using one-sample Student's *t* tests to establish if scaled ear length in the gleaning bats was significantly different from all other bats (the three remaining foraging groups collated into a single group) and if scaled tail length in commuting bats was significantly different from all other bats (the three remaining foraging groups collated into a single group). Teeling et al. (2005) was used to construct the phylogenetic tree for the bat families (Hipposideridae was also included as a separate family from Rhinolophidae). Where further detail of relationships between genera was required, Simmons (2000) was used (for the phylogeny used in the analyses see supplementary Fig. S1).[3]

The lengths of bat ears and tail membranes should scale isometrically with body mass ($\propto M^{1/3}$) if ears and tails perform a similar mechanical function for all bat sizes (Schmidt-Nielsen 1984). In this study isometric scaling acts as the null hypothesis, because it is predicted that both ears and tail membranes will not be solely determined by body mass, but other ecological factors will contribute. CAIC (Purvis and Rambaut 1995) was used to determine the scal-

[3] Supplementary Table S1 and Fig. S1 are available on the journal Web site (http://cjz.nrc.ca).

Fig. 1. Dorsal (*a*) and frontal (*b*) views of an example dried museum bat specimen (brown long-eared bat, *Plecotus auritus*, from Manchester Museum) showing ancillary flight structures and measurements collected; ear length and width (upper ear surface), thumb length (edge of wing membrane to tip of nail), forearm length, lower leg length, foot length, calcar length (a small bone that runs from the ankle along the rear edge of the tail membrane), and tail membrane length (excluding caudal vertebrae beyond the edge of the tail membrane). Wingspans and wing areas were taken from Norberg and Rayner (1987). The large increase in frontal area caused by the long ears of this specimen can also be seen. Scale bar = 100 mm.



ing exponents of ear and tail lengths against *M*. Contrasts of $\log_{10}$(ear length) and $\log_{10}$(tail membrane length) were calculated against $\log_{10}$(body mass) using the CRUNCH algorithm in CAIC (Purvis and Rambaut 1995). Regression analyses were then performed on both data sets of length versus body mass contrasts. The regression lines passed through the origin as is appropriate when using contrasts calculated with CAIC. The resultant slopes were then tested using one-sample Student's *t* tests to determine whether they differed significantly from both 0 (i.e., no relationship between variables) and 0.33 (i.e., isometric scaling). An exponent indicating isometry and a high r^2 (low variation around the regression line) would be indicative of a similar structural function for the ears or tail membranes across bat body sizes, i.e., trait size variation was determined primarily by body size.

Calculating the mechanical flight costs of possessing a tail membrane and ears

The effect of both large ears and tail membranes on the classic U-shaped mechanical flight power curve (Pennycuick 1968) was calculated using morphological data collected for *P. auritus* (supplementary Table S1),[3] because this species has both large ears and a tail membrane. Simplifying assumptions are inherent in the estimation of the power curve because existing methods are based on application of fixed-wing aircraft aerodynamics to animals and do not take into account the complex and unsteady aerodynamics of flapping wings. Furthermore, even slight variations in application of the simplifying assumptions such as how to include bat tail membrane area in the model (see below) can influence the resulting power estimates. Nevertheless, power curves do capture some of the fundamental physics of flight such as the rapid increase in drag at higher speeds and are commonly used for understanding the energetics of flight (e.g., Grodzinski et al. 2009; Henningsson et al. 2009). Furthermore, power curves are a valuable technique for investigating the effects of changes in morphology and for the development of testable hypotheses (Hedenström 2009), particularly when investigating the relative effects of changes in a single variable and not absolute values of mechanical power. The total mechanical power curve for a flying animal is the summation of the induced power, the parasite power, and the profile power. Here the calculation methods and constants described by Norberg (1990) were used.

The induced power (the work rate needed to produce a

vortex wake for lift and thrust) was calculated using two separate versions of the equation, as the influence of a tail membrane on the induced power is unclear. Firstly, the conventional form of the equation was used

$$[1a] \qquad P_{\text{ind}} = \frac{2k(Mg)^2}{\rho V \pi b^2}$$

where P_{ind} is the induced power, k is the induced drag factor (which is generally given the value 1.2 for animal flight calculations), M is the body mass, g is the gravitational acceleration constant, ρ is the density of air, V is the flight speed, and b is the wingspan of the bat. This version of the equation assumes that the only morphological dimension that affects the induced power is the wingspan and is unaffected by the changes in the wing surface area caused by a large tail membrane. It is plausible, however, that a tail membrane increases lift production and therefore reduces induced power. To account for this, eq. 1*a* can be rewritten as

$$[1b] \qquad P_{\text{ind}} = \frac{2k(Mgc)^2}{\rho V \pi S^2}$$

where wingspan b has been replaced by mean wing chord c (assumed to be constant, as the tail membrane is a continuation of the wing surface behind the body) and wing area S. The tail membrane is included as part of the wing area, as it is often considered to be a continuation of the wing membrane and flaps in synchrony with the wings during flight (Norberg 1990).

The profile power (the work rate needed to overcome the profile drag of the wings) was calculated using

$$[2] \qquad P_{\text{pro}} = \tfrac{1}{2}\rho V^3 C_{\text{Dpro}} S$$

where P_{pro} is the profile drag, C_{Dpro} is the profile drag coefficient set at 0.02 (Norberg 1990), and S is the wing area. The parasite power (the work rate needed to overcome pressure and friction drag of the body) was calculated from

$$[3] \qquad P_{\text{par}} = \tfrac{1}{2}\rho V^3 C_{\text{Dpar}} S_{\text{b}}$$

where P_{par} is the parasite power, C_{Dpar} is the parasite drag coefficient set at 0.1 (Norberg 1990), and S_{b} is the frontal area. Having larger ears significantly increases the frontal area of a bat (Fig. 1*b*). Frontal area is more than double for *P. auritus* at an ear angle of 30° compared with the frontal area with the ears removed (supplementary Table S1).[3] It is thought, however, that positioning the ears at a suitable angle of attack may minimize the aerodynamic drag of large ears (Gardiner et al. 2008). Therefore, the lower estimate of 50% increased frontal area due to large ears was used in the calculation of parasite power. The aerodynamic performances were analysed for four alternative morphologies:

(1) *Plecotus auritus* with both large ears and tail membrane.
(2) *Plecotus auritus* with ears only (no tail membrane). The tail membrane area was removed from the wing area used in calculations of profile power.
(3) *Plecotus auritus* with a tail only (no ears). The increased frontal area due to large ears was removed from the calculation of parasite power.
(4) *Plecotus auritus* with no ears or tail.

The maximum range speed for a particular morphology was calculated by plotting a line from the origin to the tangent of the total power curve (Pennycuick 1968; Hedenström 2009).

Results

Ecological correlates of the size of ears and tails

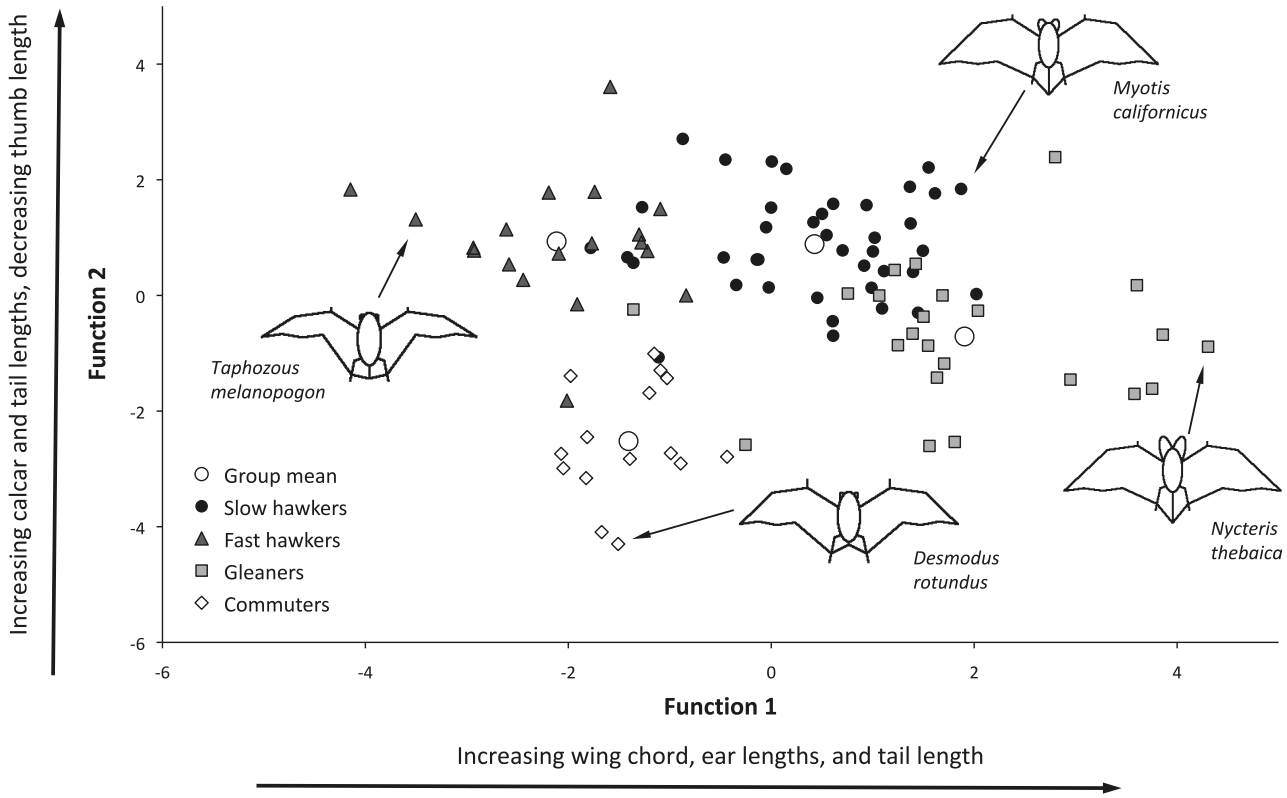
The CVA showed clustering within the data corresponding to the foraging strategies (Fig. 2). Significant differences were found between the group means (Wilks' $\lambda = 0.075$, $p < 0.001$). Canonical discriminant function 1 accounted for 49.5% of the variance, function 2 accounted for 37.5%, and function 3 accounted for 13.0%. The discriminating variables that had the highest correlations with each discriminant function were as follows: wing chord, ear length, and tail length with function 1; calcar length, tail length, and thumb length with function 2; and ear length and ear width with function 3. Hence, the flight structures (other than the wings) showing the greatest specificity to foraging strategy (i.e., those occurring in function 1) were ear and tail lengths. As expected in a biological data set, areas of overlap are present between all the groups and a number of outlier species are also present.

The contrasts calculated using the BRUNCH procedure of CAIC showed that scaled ear length was significantly longer in gleaning bats when compared with all other bats (mean contrast = 0.0119, $t_{[8]} = 2.472$, $p < 0.05$). Scaled tail length was also found to be significantly shorter in commuting bats when compared with all other bats (mean contrast = –0.0324, $t_{[3]} = -3.922$, $p < 0.05$). Ear length scaled predictably with body mass and the scaling exponent did not differ significantly from the exponent predicted for isometry (0.33) (Fig. 3*a*). The low r^2 value (0.2085), however, suggested that much of the variation in ear length was due to factors other than body size. In contrast, no relationship was found between tail length and body mass (Fig. 3*b*).

Aerodynamic consequences of tails and large ears

The flight power curves (Figs. 4*a*, 4*b*) both predict that at higher flight speeds (i.e., greater than the maximum range speed), large ears and a large tail membrane increase the mechanical power required for flight. This predicted increase in mechanical flight power requirements at higher speeds is due to two effects: the increase in parasitic power caused by large ears and the increase in profile power caused by the tail membrane increasing the overall wing area. Because of differences, however, in which assumptions you accept for defining the induced power equation (eqs. 1*a*, 1*b*; see the Materials and methods section), the flight curves at lower speeds are more complex. If eq. 1*a* is accepted (only total wingspan affects induced power), then adding a tail membrane to the bat planform does not affect the induced power curve (Fig. 4*a*). Therefore, removing both the tail membrane and the large ears result in an increased maximum range speed (Fig. 4*a*) and approximately a 10% reduction in the associated total mechanical flight power at the maximum range speed (Fig. 4*a*). At lower flight speeds, between the minimum power speed and the hovering flight speed (0 m/s), the effect of large ears and a tail membrane on the total mechanical flight power becomes negligible

Fig. 2. A plot of functions 1 and 2 of a canonical variate analysis (CVA) of ancillary flight structure morphology in bats. Bats are grouped by their general foraging strategy; commuting bats (n = 15), slow-hawking bats (n = 41), fast-hawking bats (n = 19), and gleaning bats (n = 23). The large open circles indicate the mean of each group. Function 1 was primarily correlated with wing chord, ear length, and tail length, whereas function 2 was correlated with calcar length, tail length, and thumb length. A sketch of a representative species from each group is shown to highlight differences in the morphologies of the wings and ancillary flight structures.



(Fig. 4*a*). If eq. 1*b* is accepted (a larger overall wing area will help reduce induced power), then adding a tail membrane to the planform results in a reduction in induced power requirement because the tail area is included as part of the overall wing area (Fig. 4*b*). As a consequence of the tail area effect, the planform with both large ears and a tail membrane actually has a reduced mechanical power requirement at its maximum range speed (Fig. 4*b*) compared with the planform with no ancillary structures. Furthermore at the minimum power speed and below, the tail membrane reduces the overall mechanical power required for flight (Fig. 4*b*).

Discussion

Ear length and tail membrane length strongly correlate with foraging group (Fig. 2), with the largest ears being found in gleaning bats and the shortest tails in commuting bats. Furthermore, these variations in ear and tail morphologies potentially have implications for the bat's flight energetics, because they affect the shape and magnitude of predicted mechanical flight power curves (Figs. 4*a*, 4*b*).

The foraging groups used in this study represent broad specializations in foraging ecology for bats. They are by no means mutually exclusive and therefore regions of overlap and outlying species are to be expected and were accordingly found in the CVA (Fig. 2). Overlap and outlying species may be due to limited information about true foraging methods or plasticity in their foraging styles (Altringham 1996). The outliers in the CVA (Fig. 2) also tend to show one or more features that are markedly different from typical insectivorous bat morphologies. For example, the California myotis bat (*Myotis californicus* (Audubon and Bachman, 1842)) (Fig. 2) has small but obvious external ears, long broad wings, and a fairly substantial tail membrane; typical for a slow-hawking insectivorous bat. In contrast, the Egyptian slit-faced bat (*Nycteris thebaica* E. Geoffroy, 1818) that appears on the far right of the CVA has very long ears, which are particularly suited to the passive listening method of foraging (Coles et al. 1989; Obrist et al. 1993) used by this species, which mainly eats scorpions collected from the ground (Nowak 1994). Another outlying species, the common vampire bat (*Desmodus rotundus* (E. Geoffroy, 1810)) occupies the lowest point of the CVA (Fig. 2), and has a highly unusual foraging strategy, a combination of flying then crawling along the ground, to feed on the blood of large sleeping mammals (typically domestic cattle) (Nowak 1994). Therefore, it is no surprise that *D. rotundus* is an outlier in the CVA; with very long thumbs, small ears, and a small tail membrane, it has a suite of novel morphological adaptations.

In addition to ear and tail lengths, wing chord was identified in the CVA as important for distinguishing between the foraging groups. Previous studies have also shown that wing parameters are useful for distinguishing between foraging strategies (Baagøe 1987; Norberg and Rayner 1987; Bullen

Fig. 3. Ear length (*a*) and tail length (*b*) contrasts against body mass contrasts calculated using the crunch procedure of CAIC (Purvis and Rambaut 1995). A regression line (solid line) significantly different from 0 was found for the relationship between ear length and body mass ($y = x^{0.263 \pm 0.132}$, $t = 3.985$, $n = 61$, $r^2 = 0.2085$, $p < 0.001$). Broken lines represent the 95% confidence limits and show the slope of the regression line was not significantly different from 0.33. No relationship ($y = x^{0.18 \pm 0.134}$, $t = 0.269$, $r^2 = 0.018$, $p = 0.789$) was found between tail length contrasts and body mass contrasts. The outlying contrast (α) is a result of the two representatives of the *Hipposideros* genus having an order of magnitude difference in their body masses.

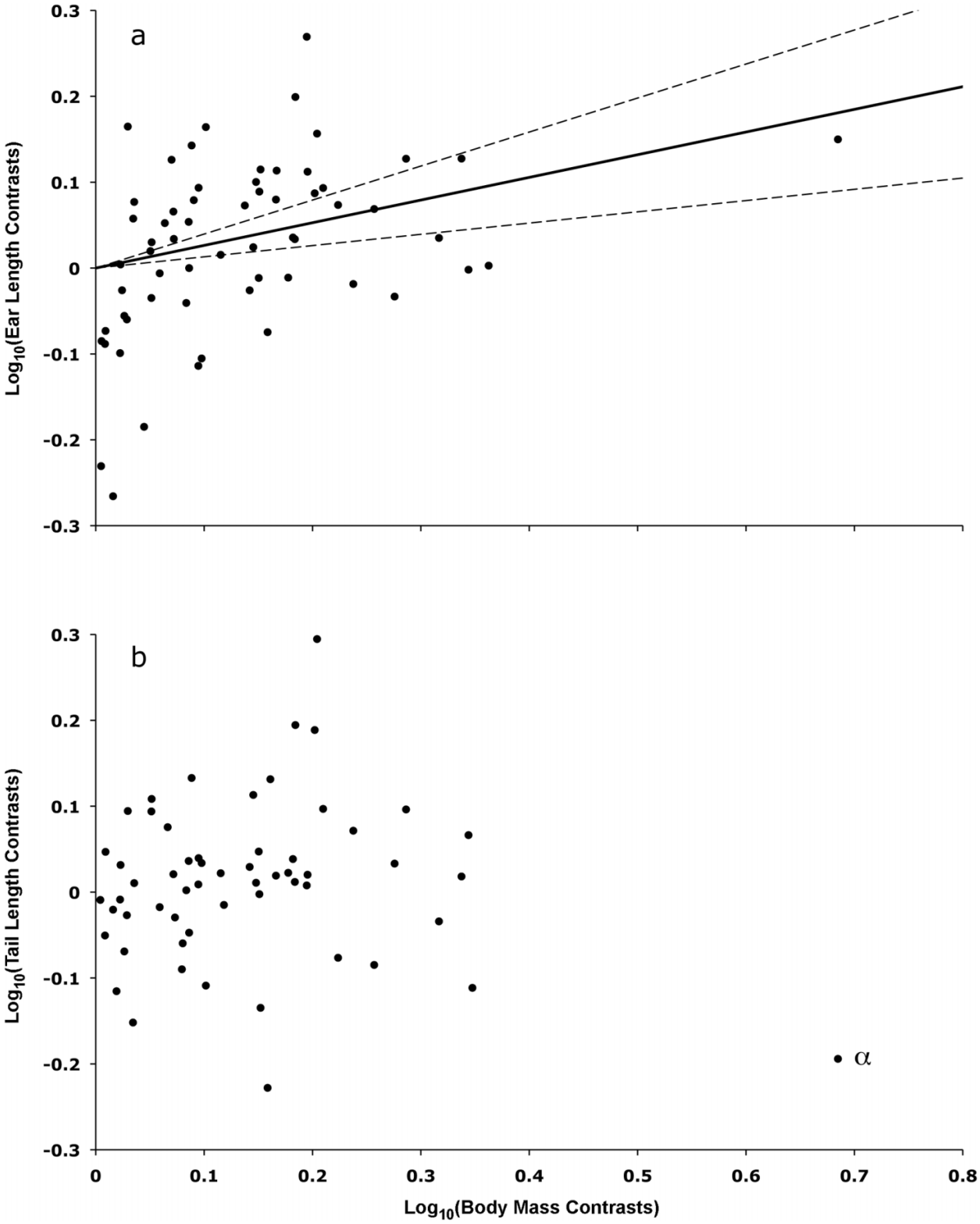
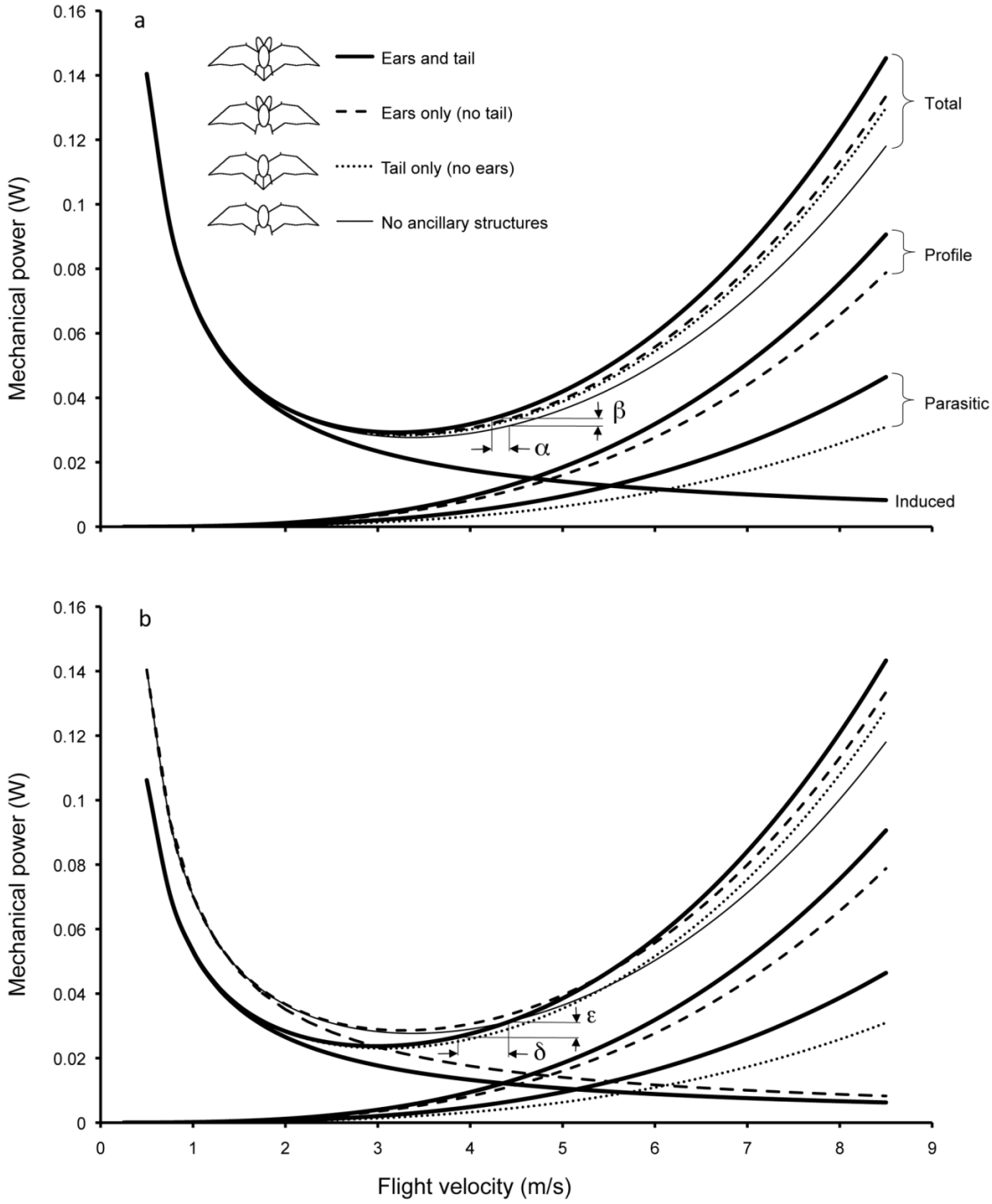


Fig. 4. The U-shaped mechanical flight power curves for four hypothetical bat planforms (based on brown long-eared bats, *Plecotus auritus*), with two variations (*a* and *b*) of the equation defining induced power. (*a*) Removal of the tail membrane results in a drop in the profile power. Removal of the large ears results in a drop in parasite power. Removal of both tail membrane and ears causes an increase in the maximum range speed (α) and an associated drop of approximately 10% in the total flight power required (β). At flight speeds lower than the minimum power speed, the aerodynamic cost of having large ears and a tail membrane becomes negligible. (*b*) At higher flight speeds, the inclusion of a tail membrane on the planform increases the power required for flight. At lower speeds, however, the tail reduces the induced power requirement and therefore also the total power curve. At the minimum power speeds, the planform with no ancillary structures, while still at a higher flight speed (δ), has a greater total power requirement (ε).



and McKenzie 2001). Surprisingly, wingspan was not identified as a particularly important distinguishing feature between foraging groups, suggesting that in bats, variations in wing morphology, and therefore flight performance, are more dependant upon wing area and the aspect ratio than on wingspan.

The lack of a scaling relationship between the tail membrane length of bats and their body mass was unexpected (Fig. 3*b*) and suggests that features other than body size strongly influence the size of tail membranes in bats. This does not mean that body size has no influence over tail length in bats, rather that other ecological requirements

(such as roosting behaviour or foraging style) tend to mask the size trend.

Depending of which assumptions are accepted in the definition of the induced power for the flight power curves (eqs. 1*a*, 1*b*), the presence of a tail membrane on a *P. auritus* planform may reduce or indeed increase the predicted mechanical power required for flight (Figs. 4*a*, 4*b*). At high flight speeds, for eqs. 1*a* and 1*b*, the tail membrane increases the overall mechanical flight power curve, which may help to explain the smaller tail membranes of faster flying commuting and fast-hawking bats. At lower speeds (i.e below minimum power speed), a tail membrane may either reduce the predicted mechanical power (Fig. 4*b*) or have little affect (Fig. 4*a*). At the maximum range speed, however, the effect of the tail membrane is difficult to clarify. For both versions of the curves, the presence of a tail membrane reduced predictions of the maximum range speed (Figs. 4*a*, 4*b*), but this may be accompanied by either an increase or decrease in predicted mechanical power (Figs. 4*a*, 4*b*). It must be noted, however, that the current understanding of the aerodynamics of the tail membranes of bats is limited, and although Pennycuick's model is helpful for producing hypotheses, its resolution is often questioned especially at lower flight speeds. Nevertheless, the tail membrane size is likely to be the result of a trade-off between energetic costs (Figs. 4*a*, 4*b*) and ecological or aerodynamic (manoeuvrability) benefits. For example, the tail membrane functions as an insect catching pouch in some species (Webster and Griffin 1962). It is also likely that a tail membrane improves a bat's flight control (Lawlor 1973; Norberg and Rayner 1987), possibly by increasing the overall camber of the wings (i.e., like a wing flap) (Norberg 1990), which in turn improves manoeuvrability (Baagøe 1987; Stockwell 2001). Increased camber would be beneficial to both hawking bats making rapid changes in direction to intercept aerial prey and gleaning bats manoeuvring among cluttered vegetation. Despite its importance for some species, the tail membrane is clearly not an essential component of bat flight, because many fruit bats fly with no tail membrane present and presumably control their flight through wing adaptations alone. Rather, the tail membrane appears to be an important adaptation to enhance flight performance of bats that require additional agility and manoeuvrability.

Although a scaling relationship, not significantly different from isometry, was found between ear length and body mass, the broad 95% confidence limits of the regression line (Fig. 3*a*) and the very low r^2 value (0.2085) indicated that other features of bat ecology such as foraging strategy and acoustic requirements also help to determine ear length. It maybe that one ear size is optimal for acoustic performance, and if the case, then selection pressure for acoustic performance would be expected to push towards equal absolute ear size across bat size. Large ears, however, are predicted to increase the mechanical cost of flight (Figs. 4*a*, 4*b*), particularly at higher speeds, and therefore variations in ear morphology are likely to be driven in part by the need for bats to reduce the cost of flight. Gleaning bats that have the longest ears are likely to incur the greatest ear aerodynamic cost, especially at higher flight speeds. The foraging style of gleaning bats, however, means that they spend a large proportion of their time flying at or below the minimum power speed while using their large ears to passively listen for prey (Coles et al. 1989; Obrist et al. 1993). At these low flight speeds, the energetic cost of having larger ears all but disappears (Figs. 4*a*, 4*b*) and may be ameliorated through appropriate positioning of the ears (Gardiner et al. 2008). Nevertheless, large ears may limit the length of time a long-eared bat is able to spend flying at higher flight speeds and therefore limit its foraging range (Swift 1998).

Non-gleaning bats have significantly shorter ears; possibly because at higher flight speeds, enlarged ears would incur excessive energetic costs (Figs. 4*a*, 4*b*). The foraging strategy of fast-hawking bats, for example, means that they spend the majority of flight time at the maximum range speed (Norberg and Rayner 1987). Similarly, commuting bats may also need to reduce flight costs by having smaller ears, particularly if distances between roost and feeding sites are large. Therefore, a trade-off between the benefits of large ears for food location and smaller ears to reduce flight costs ensues. In addition, large ears are an important adaptation to pick up the low frequency noise of insects rustling on vegetation (Coles et al. 1989; Obrist et al. 1993) and are not necessarily beneficial for echolocating insects in flight.

Conclusions

Here we have demonstrated that morphological features other than the wings of bats, in particular ears and tail membranes, may be important in determining the overall aerodynamic performance and energetic costs of bats. Furthermore, the variation in size of these ancillary flight structures appears to be strongly determined by ecological factors and not primarily body mass.

The energetic cost for a bat flying with a large tail membrane is complicated. At high flight speeds, it is likely to increase the power requirements, whereas at slower flight speeds, it may reduce the cost. A trade-off is predicted to exist between the aerodynamic and the ecological functions of a tail membrane. The lack off tail membranes in large commuting bats may be to help reduce flight costs, as sufficient flight control can be obtained through wing adaptations alone.

Flying with large ears is expected to increase the energetic cost of flight for a bat, and therefore only likely to be affordable to species with slower foraging flight speeds, such as gleaning species. At higher flight speeds, the trade-off between aerodynamic efficiency and improved foraging ability is thought to result in these bats having smaller ears to reduce the drag produced.

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Chapter 3 - Appendix

Supplementary Data

Table S1 and Figure S1

Supplementary data

Table S1. Morphological measurements and foraging strategies of bats. Data on total mass, wingspan, and wing area taken from Norberg and Rayner (1987), whereas data on foraging group (based on foraging strategy, flight style, and diet) taken from Norberg and Rayner (1987), Nowak (1994), Altringham (1996), and Fenton and Bogdanowicz (2002).

											Length (m)						
Family	Species	Foraging group	Total mass (kg)	Wingspan (m)	Wing area (m^2)	Mean wing chord (wing area / wingspan); (m)	Aspect ratio (wing $area^2$ / wingspan)	Wing loading (total mass × gravitational accleration / wing area); (N/m^2)	Ear length (m)	Ear width (m)	Thumb	Forearm	Hind leg	Foot	Calcar	Tail (to edge of membrane)	Museum
Rhinopomatidae	*Rhinopoma hardwickei (Rhinopoma cystops)*	Fast hawker	0.0163	0.28	0.0114	0.0407	6.8772	14.0266	0.00945	0.00858	0.00583	0.05229	0.02585	0.01045	0.00000	0.00774	Liverpool
Emballonuridae	*Rhynchonycteris naso*	Slow hawker	0.0039	0.239	0.0088	0.0368	6.4910	4.3476	0.00640	0.00398	0.00424	0.03518	0.01539	0.00695	0.01787	0.02573	Natural History Museum (NHM)
Emballonuridae	*Saccopteryx bilineata*	Slow hawker	0.0075	0.275	0.0125	0.0455	6.0500	5.8860	0.00568	0.00489	0.00576	0.04740	0.01811	0.01048	0.02136	0.02945	NHM
Emballonuridae	*Taphozous flaviventris*	Fast hawker	0.045	0.489	0.0304	0.0622	7.8658	14.5214	0.00947	0.00967	0.00900	0.07671	0.03060	0.01561	0.02263	0.02679	NHM
Emballonuridae	*Taphozous longimanus*	Fast hawker	0.0282	0.39	0.0155	0.0397	9.8129	17.8479	0.00658	0.01081	0.00730	0.05560	0.02036	0.01235	0.01700	0.02135	NHM
Emballonuridae	*Taphozous melanopogon*	Fast hawker	0.0391	0.385	0.0148	0.0384	10.0152	25.9170	0.00540	0.00889	0.00680	0.05790	0.02512	0.01241	0.01719	0.02344	NHM
Emballonuridae	*Taphozous perforatus*	Slow hawker	0.0188	0.326	0.0142	0.0436	7.4842	12.9879	0.00852	0.00833	0.00729	0.06059	0.02244	0.01304	0.01561	0.02018	NHM
Nyteridae	*Nycteris grandis*	Gleaner	0.032	0.38	0.0277	0.0729	5.2130	11.3329	0.01582	0.01800	0.01125	0.06206	0.03772	0.01410	0.02184	0.04671	NHM
Nyteridae	*Nycteris hispida*	Gleaner	0.008	0.266	0.0146	0.0549	4.8463	5.3753	0.01351	0.01280	0.00500	0.03962	0.01833	0.00860	0.01306	0.03800	NHM
Nyteridae	*Nycteris macrotis*	Gleaner	0.0115	0.288	0.0159	0.0552	5.2166	7.0953	0.01928	0.01541	0.00862	0.04578	0.02140	0.01160	0.01510	0.04101	NHM
Nyteridae	*Nycteris thebaica*	Gleaner	0.011	0.307	0.0171	0.0557	5.5116	6.3105	0.02310	0.01746	0.00623	0.04266	0.02248	0.00936	0.01387	0.04302	Liverpool
Megadermatidae	*Macroderma gigas*	Gleaner	0.123	0.66	0.0717	0.1086	6.0753	16.8289	0.03290	0.03066	0.01368	0.10205	0.03814	0.03186	0.02279	0.04860	NHM
Megadermatidae	*Lavia frons*	Gleaner	0.026	0.34	0.0213	0.0626	5.4272	11.9746	0.01829	0.01774	0.00674	0.06063	0.03163	0.01545	0.01358	0.04469	NHM
Rhinolophidae	*Rhinolophus darlingi*	Slow hawker	0.011	0.295	0.0138	0.0468	6.3062	7.8196	0.01146	0.01079	0.00372	0.04477	0.01451	0.00980	0.00980	0.02278	NHM
Rhinolophidae	*Rhinolophus euryale*	Slow hawker	0.0109	0.285	0.0132	0.0463	6.1534	8.1007	0.01213	0.01356	0.00423	0.04325	0.01682	0.00880	0.00955	0.01930	NHM
Rhinolophidae	*Rhinolophus ferrumequinum*	Gleaner	0.0226	0.332	0.0182	0.0548	6.0563	12.1816	0.01311	0.01176	0.00482	0.05296	0.02112	0.01293	0.01378	0.03405	NHM
Rhinolophidae	*Rhinolophus fumigatus*	Slow hawker	0.0129	0.333	0.0165	0.0495	6.7205	7.6696	0.01274	0.01432	0.00439	0.04985	0.02069	0.01061	0.01022	0.02043	NHM
Rhinolophidae	*Rhinolophus hildebrandti*	Slow hawker	0.0243	0.407	0.0243	0.0597	6.8168	9.8100	0.01669	0.01989	0.00554	0.06039	0.02836	0.01325	0.01702	0.03875	Liverpool
Rhinolophidae	*Rhinolophus hipposideros*	Slow hawker	0.0068	0.231	0.0094	0.0407	5.6767	7.0966	0.00847	0.00904	0.00309	0.03332	0.01551	0.00839	0.00829	0.02473	Liverpool
Rhinolophidae	*Rhinolophus megaphyllus*	Slow hawker	0.0098	0.281	0.013	0.0463	6.0739	7.3952	0.01101	0.01254	0.00398	0.04396	0.01753	0.00809	0.01057	0.01857	NHM
Rhinolophidae	*Rhinolophus swinnyi*	Slow hawker	0.007	0.268	0.0109	0.0407	6.5894	6.3000	0.00771	0.01027	0.00310	0.04088	0.01615	0.00806	0.01050	0.02032	NHM
Hipposideridae	*Hipposideros cineraceus*	Slow hawker	0.0038	0.245	0.0079	0.0322	7.5981	4.7187	0.00846	0.01271	0.00266	0.03338	0.01446	0.00612	0.00680	0.02098	NHM
Hipposideridae	*Hipposideros commersoni*	Slow hawker	0.089	0.654	0.0556	0.0850	7.6927	15.7031	0.01687	0.01212	0.00862	0.08698	0.03561	0.01576	0.01158	0.00858	NHM
Hipposideridae	*Triaenops persicus (Triaenops afer)*	Slow hawker	0.0109	0.293	0.0116	0.0396	7.4008	9.2180	0.00513	0.00714	0.00490	0.05141	0.01669	0.00785	0.00911	0.02350	NHM
Phyllostomidae	*Micronycteris megalotis*	Gleaner	0.0071	0.231	0.0095	0.0411	5.6169	7.3317	0.01154	0.00984	0.00502	0.03355	0.01530	0.00908	0.01042	0.01932	NHM
Phyllostomidae	*Macrotus californicus*	Gleaner	0.0141	0.295	0.0136	0.0461	6.3989	10.1707	0.02114	0.01770	0.00616	0.04932	0.02092	0.01147	0.01057	0.02575	NHM
Phyllostomidae	*Macrotus waterhousii*	Gleaner	0.0095	0.34	0.0128	0.0376	9.0313	7.2809	0.01650	0.01578	0.00712	0.05273	0.02049	0.01265	0.01124	0.02179	NHM
Phyllostomidae	*Phyllostomus discolor*	Commuter	0.0422	0.416	0.0262	0.0630	6.6052	15.8008	0.01066	0.01170	0.00782	0.05951	0.02311	0.01365	0.01063	0.01881	NHM
Phyllostomidae	*Phyllostomus hastatus*	Gleaner	0.107	0.562	0.0417	0.0742	7.5742	25.1719	0.01592	0.01273	0.01071	0.07592	0.02730	0.01719	0.02368	0.04486	NHM
Phyllostomidae	*Trachops cirrhosus*	Gleaner	0.0438	0.422	0.0281	0.0666	6.3375	15.2910	0.00918	0.01240	0.01125	0.05326	0.02174	0.01655	0.01177	0.02067	NHM
Phyllostomidae	*Chrotopterus auritus*	Gleaner	0.0809	0.539	0.0532	0.0987	5.4609	14.9178	0.02421	0.02310	0.01743	0.07783	0.03443	0.02164	0.02630	0.04337	NHM
Phyllostomidae	*Vampyrum spectrum*	Gleaner	0.158	0.676	0.0844	0.1249	5.4144	18.3647	0.02708	0.02413	0.02301	0.09910	0.04855	0.02423	0.02842	0.07303	NHM
Phyllostomidae	*Glossophaga soricina*	Commuter	0.0106	0.252	0.0099	0.0393	6.4145	10.5036	0.00469	0.00651	0.00537	0.03594	0.01394	0.00896	0.00640	0.01278	NHM
Phyllostomidae	*Anoura geoffroyi*	Commuter	0.0141	0.282	0.0111	0.0394	7.1643	12.4614	0.00661	0.00642	0.00548	0.04243	0.01468	0.00968	0.00000	0.00000	NHM
Phyllostomidae	*Lichonycteris obscura*	Commuter	0.0065	0.224	0.0076	0.0339	6.6021	8.3901	0.00504	0.00710	0.00556	0.03406	0.01237	0.00761	0.00732	0.01442	NHM
Phyllostomidae	*Choeronycteris mexicana*	Commuter	0.0182	0.3	0.013	0.0433	6.9231	13.7340	0.00707	0.00784	0.00577	0.04475	0.01572	0.00953	0.00739	0.01014	NHM
Phyllostomidae	*Carollia perspicillata*	Commuter	0.0191	0.316	0.0165	0.0522	6.0519	11.3558	0.00993	0.00920	0.00711	0.04014	0.01818	0.00998	0.00641	0.01337	Liverpool
Phyllostomidae	*Sturnira lilium*	Commuter	0.015	0.281	0.0121	0.0431	6.5257	12.1612	0.00549	0.00793	0.00793	0.03648	0.01513	0.01029	0.00000	0.00000	NHM
Phyllostomidae	*Uroderma bilobatum*	Commuter	0.0154	0.307	0.015	0.0489	6.2833	10.0716	0.00740	0.00876	0.00787	0.04232	0.01649	0.00991	0.00611	0.00818	NHM
Phyllostomidae	*Chiroderma villosum*	Commuter	0.0229	0.32	0.0161	0.0503	6.3602	13.9534	0.00740	0.00941	0.01028	0.04647	0.01753	0.01103	0.00786	0.00658	NHM
Phyllostomidae	*Artibeus jamaicensis*	Commuter	0.047	0.42	0.0277	0.0660	6.3682	16.6451	0.00835	0.00892	0.00940	0.06300	0.02437	0.01343	0.00753	0.00611	NHM
Phyllostomidae	*Artibeus lituratus*	Commuter	0.0596	0.448	0.033	0.0737	6.0819	17.7175	0.00959	0.00963	0.01165	0.07290	0.02878	0.01857	0.00865	0.01007	NHM
Phyllostomidae	*Desmodus rotundus*	Commuter	0.0285	0.366	0.02	0.0546	6.6978	13.9793	0.00675	0.00784	0.01385	0.06121	0.02794	0.01586	0.00000	0.00519	NHM
Phyllostomidae	*Diaemus youngi*	Commuter	0.0361	0.419	0.0206	0.0492	8.5224	17.1913	0.00575	0.00974	0.01009	0.05170	0.02075	0.01754	0.00000	0.00800	NHM
Phyllostomidae	*Diphylla ecaudata*	Commuter	0.0329	0.356	0.019	0.0534	6.6703	16.9868	0.00190	0.00801	0.00923	0.05168	0.01779	0.01536	0.00351	0.00000	NHM
Natalidae	*Natalus stramineus (Natalus mexicanus)*	Gleaner	0.0039	0.24	0.0099	0.0413	5.8182	3.8645	0.00699	0.00736	0.00482	0.03674	0.01826	0.00645	0.01645	0.04014	NHM
Thyropteridae	*Thyroptera discifera*	Slow hawker	0.0031	0.211	0.0075	0.0355	5.9361	4.0548	0.00571	0.00668	0.00268	0.03341	0.01534	0.00564	0.00990	0.02705	NHM
Thyropteridae	*Thyroptera tricolor*	Slow hawker	0.0035	0.224	0.0083	0.0371	6.0453	4.1367	0.00442	0.00537	0.00168	0.03641	0.01699	0.00448	0.00980	0.01968	NHM
Vespertilionidae	*Myotis adversus*	Slow hawker	0.0103	0.292	0.0127	0.0435	6.7137	7.9561	0.00950	0.00824	0.00590	0.04231	0.01900	0.01189	0.01759	0.03030	NHM
Vespertilionidae	*Myotis albescens*	Slow hawker	0.0059	0.23	0.0077	0.0335	6.8701	7.5168	0.00640	0.00556	0.00454	0.03275	0.01203	0.00774	0.01805	0.02358	NHM
Vespertilionidae	*Myotis californicus*	Slow hawker	0.0042	0.22	0.0086	0.0391	5.6279	4.7909	0.00755	0.00855	0.00398	0.03218	0.01435	0.00656	0.01800	0.02684	NHM
Vespertilionidae	*Myotis dasycneme*	Slow hawker	0.0114	0.271	0.0108	0.0399	6.8001	10.3550	0.01046	0.00562	0.00631	0.04212	0.01723	0.01240	0.01891	0.03033	NHM
Vespertilionidae	*Myotis daubentoni*	Slow hawker	0.007	0.248	0.0098	0.0395	6.2759	7.0071	0.00576	0.00603	0.00478	0.03402	0.01962	0.00913	0.01997	0.01932	Liverpool
Vespertilionidae	*Myotis emarginatus*	Slow hawker	0.0067	0.235	0.0093	0.0396	5.9382	7.0674	0.00775	0.00770	0.00565	0.03984	0.01830	0.00935	0.01682	0.02862	NHM
Vespertilionidae	*Myotis evotis*	Slow hawker	0.0073	0.265	0.0118	0.0445	5.9513	6.0689	0.01442	0.01059	0.00440	0.03681	0.01720	0.00729	0.01464	0.02494	NHM
Vespertilionidae	*Myotis lucifugus*	Slow hawker	0.0071	0.237	0.0093	0.0392	6.0397	7.4894	0.00832	0.00635	0.00423	0.03724	0.01745	0.00820	0.01437	0.02685	NHM

Vespertilionidae	*Myotis myotis*	Gleaner	0.0265	0.383	0.0233	0.0608	6.2957	11.1573	0.01749	0.01292	0.00948	0.05722	0.02348	0.01415	0.01971	0.03488	Liverpool
Vespertilionidae	*Myotis oxygnathus (Myotis myotis oxygnathus)*	Slow hawker	0.021	0.369	0.0204	0.0553	6.6746	10.0985	0.01306	0.01128	0.00916	0.05559	0.02369	0.01395	0.02105	0.04697	NHM
Vespertilionidae	*Myotis mystacinus*	Slow hawker	0.0054	0.213	0.0075	0.0352	6.0492	7.0632	0.00689	0.00539	0.00510	0.03250	0.01511	0.00592	0.01490	0.02672	NHM
Vespertilionidae	*Myotis nattereri*	Gleaner	0.007	0.268	0.0113	0.0422	6.3561	6.0770	0.00824	0.00610	0.00479	0.03850	0.01630	0.00796	0.01345	0.02871	Manchester
Vespertilionidae	*Myotis nigricans*	Slow hawker	0.0042	0.21	0.0068	0.0324	6.4853	6.0591	0.00695	0.00573	0.00415	0.03364	0.01478	0.00533	0.01634	0.02922	NHM
Vespertilionidae	*Myotis tricolor*	Slow hawker	0.016	0.344	0.0191	0.0555	6.1956	8.2178	0.01093	0.01025	0.00657	0.05006	0.01914	0.00997	0.01806	0.03968	NHM
Vespertilionidae	*Myotis yumanensis*	Slow hawker	0.0052	0.203	0.0065	0.0320	6.3398	7.8480	0.00707	0.00603	0.00494	0.03397	0.01318	0.00769	0.01665	0.02357	NHM
Vespertilionidae	*Lasionycteris noctivagans*	Slow hawker	0.0106	0.289	0.0127	0.0439	6.5765	8.1879	0.00584	0.00889	0.00535	0.03934	0.01578	0.00852	0.01203	0.02888	NHM
Vespertilionidae	*Pipistrellus hesperus*	Slow hawker	0.0044	0.19	0.0063	0.0332	5.7302	6.8514	0.00654	0.00766	0.00370	0.03133	0.01345	0.00720	0.01554	0.02425	NHM
Vespertilionidae	*Pipistrellus kuhli*	Slow hawker	0.0047	0.185	0.0054	0.0292	6.3380	8.5383	0.00546	0.00704	0.00353	0.03056	0.01346	0.00647	0.01530	0.02949	NHM
Vespertilionidae	*Pipistrellus nanus*	Slow hawker	0.005	0.206	0.0058	0.0282	7.3166	8.4569	0.00510	0.00681	0.00263	0.02852	0.01140	0.00529	0.01390	0.03122	Manchester
Vespertilionidae	*Pipistrellus pipistrellus*	Slow hawker	0.0052	0.218	0.0063	0.0289	7.5435	8.0971	0.00546	0.00505	0.00352	0.03101	0.00842	0.00566	0.01064	0.01828	Manchester
Vespertilionidae	*Pipistrellus rusticus*	Slow hawker	0.005	0.218	0.007	0.0321	6.7891	7.0071	0.00390	0.00552	0.00356	0.02995	0.01007	0.00871	0.01440	0.02082	NHM
Vespertilionidae	*Pipistrellus subflavus*	Slow hawker	0.0051	0.237	0.009	0.0380	6.2410	5.5590	0.00471	0.00497	0.00524	0.03210	0.01588	0.00744	0.01491	0.02855	NHM
Vespertilionidae	*Scotozous dormeri (Pipistrellus dormeri)*	Fast hawker	0.0078	0.256	0.0084	0.0328	7.8019	9.1093	0.00735	0.00689	0.00488	0.03400	0.01210	0.00603	0.01295	0.02620	NHM
Vespertilionidae	*Nyctalus leisleri*	Fast hawker	0.0169	0.26	0.0086	0.0331	7.8605	19.2778	0.00755	0.00941	0.00456	0.04583	0.01499	0.00954	0.01612	0.03408	NHM
Vespertilionidae	*Nyctalus noctula*	Fast hawker	0.0265	0.344	0.0161	0.0468	7.3501	16.1469	0.00465	0.00985	0.00573	0.05061	0.01796	0.01062	0.02162	0.03983	Manchester
Vespertilionidae	*Eptesicus fuscus*	Slow hawker	0.0159	0.325	0.0166	0.0511	6.3630	9.3963	0.00806	0.00862	0.00496	0.04606	0.01687	0.00851	0.01623	0.03279	NHM
Vespertilionidae	*Eptesicus nilssonii*	Slow hawker	0.0092	0.272	0.0112	0.0412	6.6057	8.0582	0.00619	0.00703	0.00685	0.03720	0.01540	0.00998	0.01162	0.03022	NHM
Vespertilionidae	*Eptesicus serotinus*	Slow hawker	0.0223	0.341	0.018	0.0528	6.4601	12.1535	0.00945	0.00908	0.00768	0.05207	0.02096	0.01165	0.01982	0.03286	NHM
Vespertilionidae	*Mimetillus moloneyi*	Fast hawker	0.0088	0.18	0.0048	0.0267	6.7500	17.9850	0.00564	0.00682	0.00353	0.02840	0.01008	0.00660	0.01032	0.02261	NHM
Vespertilionidae	*Chalinolobus gouldii*	Slow hawker	0.0153	0.331	0.014	0.0423	7.8258	10.7209	0.00448	0.01028	0.00607	0.04331	0.02089	0.00862	0.01548	0.03634	NHM
Vespertilionidae	*Nycticeinops schlieffeni*	Fast hawker	0.005	0.224	0.0073	0.0326	6.8734	6.7192	0.00310	0.00471	0.00485	0.03101	0.01120	0.00567	0.00867	0.02627	Liverpool
Vespertilionidae	*Scotophilus heathi*	Fast hawker	0.0345	0.425	0.0225	0.0529	8.0278	15.0420	0.00773	0.00816	0.00602	0.05888	0.02164	0.01229	0.01973	0.04366	NHM
Vespertilionidae	*Lasiurus cinereus*	Fast hawker	0.033	0.398	0.0196	0.0492	8.0818	16.5168	0.00503	0.01401	0.00953	0.05657	0.02167	0.01230	0.01936	0.03415	NHM
Vespertilionidae	*Lasiurus borealis*	Fast hawker	0.0167	0.281	0.0117	0.0416	6.7488	14.0023	0.00317	0.00660	0.00652	0.03706	0.01588	0.00793	0.01318	0.03248	NHM
Vespertilionidae	*Barbastella barbastellus*	Slow hawker	0.0103	0.258	0.0111	0.0430	5.9968	9.1030	0.00693	0.00961	0.00563	0.03593	0.01662	0.00672	0.01708	0.03143	Manchester
Vespertilionidae	*Plecotus auritus*	Gleaner	0.009	0.267	0.0124	0.0464	5.7491	7.1202	0.02696	0.01624	0.00522	0.03581	0.01781	0.00692	0.01138	0.03248	Manchester
Vespertilionidae	*Plecotus austriacus*	Gleaner	0.01	0.276	0.0124	0.0449	6.1432	7.9113	0.02748	0.01943	0.00551	0.03598	0.01730	0.00822	0.01993	0.03756	Liverpool
Vespertilionidae	*Miniopterus inflatus*	Fast hawker	0.0125	0.29	0.0097	0.0334	8.6701	12.6418	0.00576	0.00914	0.00476	0.04921	0.01763	0.00906	0.01930	0.04296	Liverpool
Vespertilionidae	*Kerivoula argentata*	Slow hawker	0.01	0.301	0.0149	0.0495	6.0806	6.5839	0.00876	0.00856	0.00534	0.03654	0.01360	0.00707	0.01896	0.03242	NHM
Vespertilionidae	*Antrozous pallidus*	Gleaner	0.0173	0.357	0.021	0.0588	6.0690	8.0816	0.01939	0.01556	0.00812	0.05561	0.02201	0.01019	0.01339	0.03323	NHM
Vespertilionidae	*Nyctophilus geoffroyi*	Gleaner	0.008	0.276	0.0109	0.0395	6.9886	7.2000	0.01465	0.01411	0.00535	0.03397	0.01498	0.00765	0.01175	0.03321	NHM
Vespertilionidae	*Nyctophilus gouldi*	Gleaner	0.0112	0.311	0.0141	0.0453	6.8596	7.7923	0.01433	0.01167	0.00559	0.03925	0.01683	0.00792	0.01445	0.03052	NHM
Vespertilionidae	*Nyctophilus timoriensis*	Gleaner	0.0095	0.294	0.014	0.0476	6.1740	6.6568	0.01421	0.01141	0.00428	0.03478	0.01534	0.00577	0.01218	0.03108	NHM
Mystacinidae	*Mystacina tuberculata*	Commuter	0.0135	0.274	0.0108	0.0394	6.9515	12.2625	0.01131	0.00886	0.00544	0.03996	0.01484	0.00892	0.01124	0.01181	NHM
Molossidae	*Tadarida aegyptiaca*	Fast hawker	0.0159	0.354	0.013	0.0367	9.6397	11.9984	0.01114	0.01302	0.00699	0.04761	0.01462	0.00938	0.01658	0.01794	NHM
Molossidae	*Tadarida fulminans*	Fast hawker	0.033	0.457	0.016	0.0350	13.0531	20.2331	0.00790	0.01303	0.00496	0.05438	0.01619	0.00851	0.01622	0.00628	NHM
Molossidae	*Otomops martiensseni*	Fast hawker	0.0355	0.467	0.0234	0.0501	9.3200	14.8827	0.02405	0.01477	0.00838	0.06960	0.02581	0.01116	0.02473	0.01969	NHM
Molossidae	*Eumops perotis*	Fast hawker	0.0535	0.446	0.0209	0.0469	9.5175	25.1117	0.02008	0.02629	0.01183	0.07473	0.02337	0.01266	0.02414	0.02309	NHM
Molossidae	*Molossus molossus (Tadarida molossa)*	Fast hawker	0.0162	0.294	0.0099	0.0337	8.7309	16.0527	0.00551	0.00837	0.00362	0.03636	0.01288	0.00752	0.00912	0.02207	Liverpool
Molossidae	*Molossus sinaloae*	Fast hawker	0.0238	0.328	0.0133	0.0405	8.0890	17.5547	0.00457	0.00898	0.00676	0.04836	0.01596	0.00953	0.01828	0.02229	NHM

Frontal area of Manchester Museum *Plecotus auritus* specimen (measured using digitised photographs).

	Frontal area (m^2)
Ears at an angle of 30°	0.001767
No ears	0.000847

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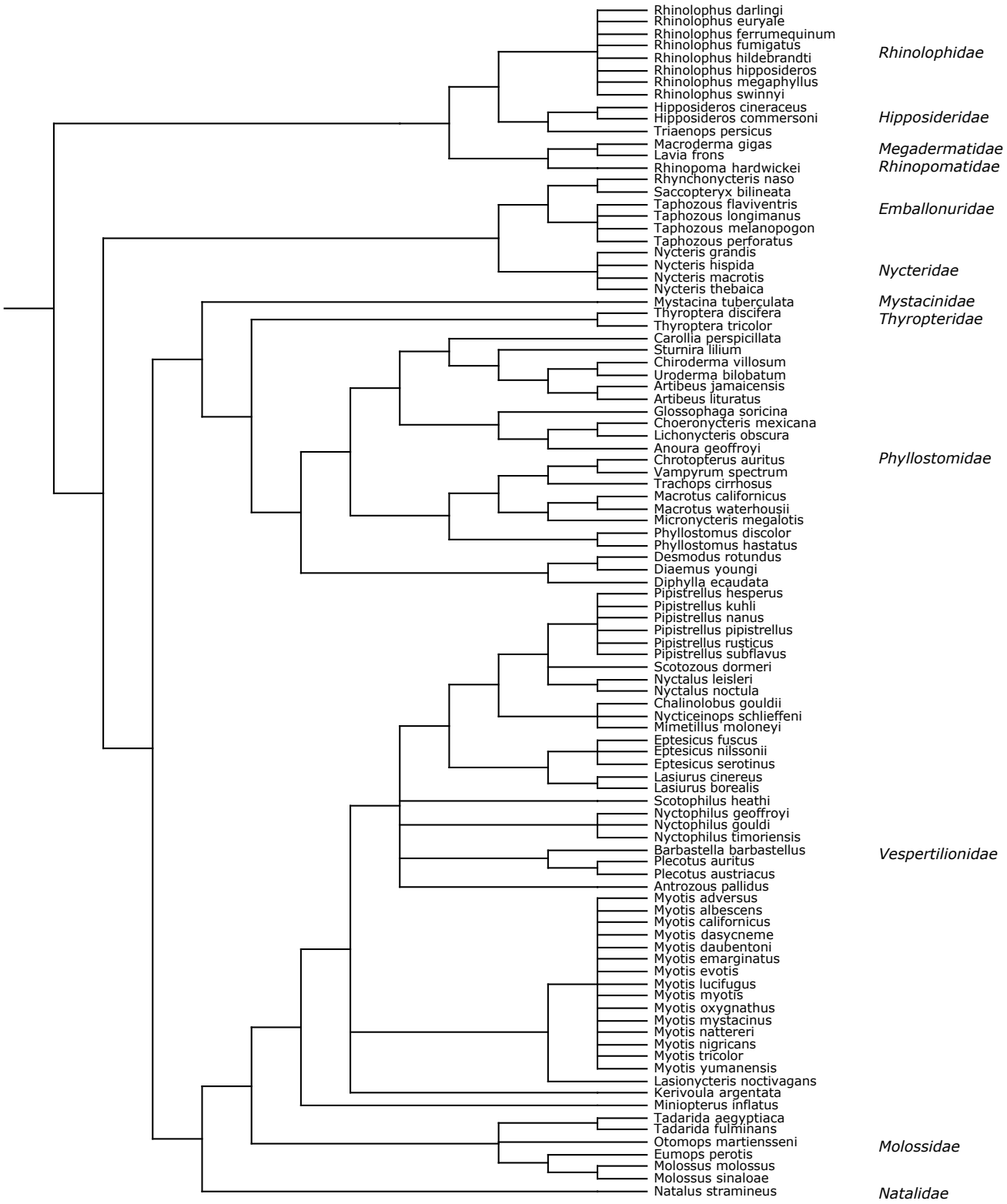
Fig. S1. Phylogenetic tree used in CAIC.



Chapter 4

A Potential Role for Bat Tail Membranes in Flight Control

Gardiner, J.D., Dimitriadis, G., Codd, J.R. & Nudds, R.L. (2011) A potential role for bat tail membranes in flight control. *PLoS ONE* **6**, e18214.

A Potential Role for Bat Tail Membranes in Flight Control

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Abstract

Wind tunnel tests conducted on a model based on the long-eared bat *Plecotus auritus* indicated that the positioning of the tail membrane (uropatagium) can significantly influence flight control. Adjusting tail position by increasing the angle of the legs ventrally relative to the body has a two-fold effect; increasing leg-induced wing camber (i.e., locally increased camber of the inner wing surface) and increasing the angle of attack of the tail membrane. We also used our model to examine the effects of flying with and without a tail membrane. For the bat model with a tail membrane increasing leg angle increased the lift, drag and pitching moment (nose-down) produced. However, removing the tail membrane significantly reduced the change in pitching moment with increasing leg angle, but it had no significant effect on the level of lift produced. The drag on the model also significantly increased with the removal of the tail membrane. The tail membrane, therefore, is potentially important for controlling the level of pitching moment produced by bats and an aid to flight control, specifically improving agility and manoeuvrability. Although the tail of bats is different from that of birds, in that it is only divided from the wings by the legs, it nonetheless, may, in addition to its prey capturing function, fulfil a similar role in aiding flight control.

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Introduction

In recent years it has become established that bird tails have important effects upon their flight. For example, bird tails are known to produce lift during flight [1,2]. Bird tails also appear to reduce body drag, by acting as a splitter plate [3] that reduces flow separation behind the body, essentially making the body more streamlined [4]. Furthermore, sufficient flight stability is essential for all flying animals and bird tails are thought to be a key component for overall flight stability [5,6,7]. Bird tails are also thought to be important for flight control, particularly during take-off and landing when the tail is fanned out and the angle of attack increased, augmenting lift production, improving manoeuvrability and possibly reducing wing stall [8,9].

In contrast to birds, relatively little research has investigated the aerodynamic function(s) of a bat's tail membrane (uropatagium). Although previous authors have hypothesised that bat tail membranes perform similar aerodynamic functions to bird tails [9,10,11,12], empirical tests of bat tail aerodynamics have yet to be undertaken. Other studies of bat flight have found marked differences between bat and bird aerodynamics [13], meaning there are potentially significant functional differences between the tails of bats and birds. For example bats seem to generate more complex aerodynamic wakes than birds [14].

Of the 17 families of bats [15] only one family, the old world fruit bats (Pteropodidae), have no real tail membrane. The tail membrane is an extension of the skin between the hind limbs often incorporating the tail vertebrae (Figure 1A). This membrane is usually supported at its rear edge by a thin structure called the calcar, which extends from the ankle joint. The calcar is thought not only to provide structural support for the tail membrane, but also to allow the tail to form a larger aerodynamic surface than if the trailing edge was unsupported [11]. The morphology of the tail is highly variable between species of bats and typically correlates with their foraging style [16]. Insectivorous bats often have long and broad tail membranes that they use as pouches to aid in the capture of insects during flight [17], whereas many nectivorous and frugivorous bats have very reduced tail membranes.

Current understanding of the flight aerodynamics of animal tails is polarised. For example, although delta-wing theory has been used to predict tail performance in birds [8], more recent work [1,18] suggests this approach is not entirely valid. In bats the tail forms a continuation of the wing membrane (separated by the leg bones) and not a separate lifting surface, therefore, delta wing theory is definitely not applicable. The fact that theoretical approaches based upon aircraft aerodynamics are inadequate when investigating vertebrate tail aerodynamics emphasises the need for new approaches. Accordingly, here we present the first experimental study into the function of bat tails using a wind-tunnel model based on a brown long-eared bat (*Plecotus auritus*). The use of simple physical modelling in biomechanics is a valuable technique as it allows variables to be manipulated in a manner not possible using comparative *in vivo* methods. This approach also allows the performance consequences of each variable to be thoroughly explored [19]. Creating simple models is a well-accepted technique, which has been widely used to gain valuable insights into the flight performance of vertebrates [20,21,22,23]. Furthermore, simple models do not necessarily lead to simple or limited conclusions; for example Taylor et al. [21] used a simple flapping flat plate in a wind tunnel to show that the Strouhal number that all flying and swimming animals cruise at is associated with high power efficiency.

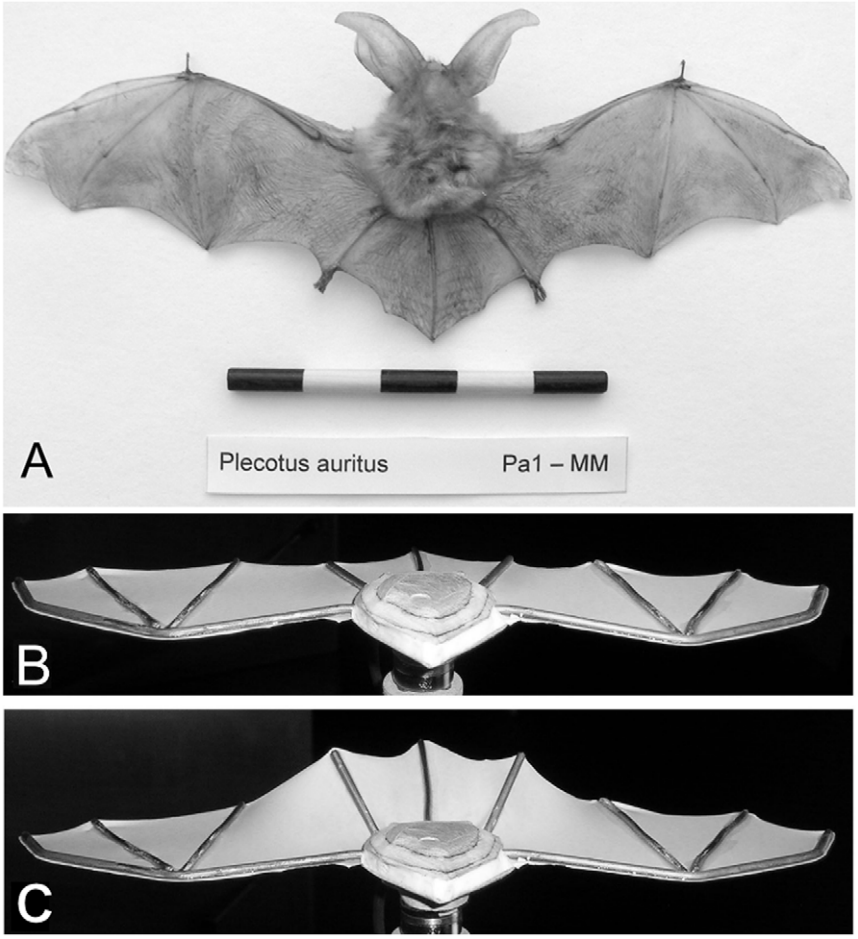

Figure 1. *Plecotus auritus* specimen and the completed wind-tunnel model. A: Dried *P. auritus* bat specimen upon which the bat model was based (Scale bar = 100 mm). B and C: Completed bat model at the extremes of the leg positions (B: Leg angle (β) = 0°, C: Leg angle (β) = 60°), showing the effect on the tail membrane angle of attack and the increased wing camber (termed leg-induced wing camber). Leg angle adjustments were made via small screw mountings hidden within the body of the model. The model was mounted upside down in the wind-tunnel to minimise the aerodynamic effect of the wake from the support, since the tail is then deflected away from the support, instead of towards. Note that the large ears of *P. auritus* were excluded from the model, since this investigation was primarily concerned with the aerodynamics of the tail membrane.
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The bat model presented here is necessarily a simplification of a real bat in flight, representing a small gliding bat in steady state aerodynamic conditions. At first glance this may appear at odds with bat biology as most bat species, with the exception of some large bats [24,25] and the small insectivorous *Pipistrellus pipistrellus* [26], are thought to flap their wings continuously during flight. However, a fixed-wing gliding model can still extend our current understanding of bat flight. Spedding et al. [27] showed that predictions based upon fixed wing data agree well with quantitative observations of flapping flight in birds and that this approach "shows the simplest tenable baseline approximation, upon which more complex and realistic theories might be constructed". In many ways, therefore, a simple model has advantages over more complicated models by virtue of its simplicity, since this allows any shortcomings in the model to be more easily identified and accounted for. Indeed, the aerodynamic forces and wake produced on an inaccurate flapping model are likely to be more misleading than helpful. We therefore err on the side of simplicity with a gliding bat model that is intended to generate hypotheses for later testing in the field and use our model to provide the first experimental data on the aerodynamic significance of the tail membrane of bats.

Materials and Methods

Morphological measurements and model construction

A model for wind tunnel testing was created using detailed morphological measurements taken from a reference specimen held at the Manchester Museum (Manchester, UK) of a brown long-eared bat (*P. auritus*, Figure 1A). *Plecotus auritus* is a slow flying, highly manoeuvrable species which gleans prey from amongst vegetation [28,29]. All morphological measurements from the museum specimen were taken using digital calipers (16EX 150 mm Prod No: 4102400, Mayr GmbH, Berlin, Germany). The posture of the preserved *P. auritus* specimen, from which the measurements where taken, represents a typical method of stretching out wings of both bird and bats in the field for calculating wing span and area. The model, therefore, provides our best possible representation of the posture of a gliding bat, in the absence of detailed *P. auritus* flight footage, and is consistent with previous work on vertebrate aerodynamics (see Table 1 for model dimensions). The frame of the model was constructed out of plywood, with stiff steel wire to represent the arm, wing, leg and tailbones of the bat. A sheet of 0.1 mm thick latex, cut from a large Semperguard latex glove (Semperit Technische Produkte

G.m.b.H, Vienna, Austria), was then stretched over the model frame and glued to the sheet with Cyanoacrylate. Once the glue had dried the model frame was cut out, leaving the stretched latex to form the wings and tail membrane of the bat model (Figure 1B). Latex sheeting was used since this could be tensioned before attachment to the frame, therefore reducing the chance of the trailing edge of the wing fluttering during testing. The latex membrane on the final model was strained approximately 55% in the span-wise direction and 11% in the chord-wise. This corresponds to a pre-stress of approximately 1.0 MPa in the span-wise direction and 0.6 MPa chord-wise, assuming plane stress conditions, a Young's modulus of 1.2 MPa and a Poisson's ratio of 0.5. The actual membrane tension used by these bats during flight is currently unknown, consequently here we made the tension across the membrane as uniform as possible using the materials and methods available to us. One advantage of our modelling technique was that we were able to alter the model as required and in ways not possible with a real bat to ask specific 'what if' questions. For example, the tail membrane of the model could be cut out resulting in a morphology that is similar to some nectivorous bats belonging to the Phyllostomidae family, to allow a comparison of the effects of flying with and without a tail membrane. Adjustments to the angle of the tail membrane were made by changing the leg angles via screw fittings hidden within the body of the model. Adjusting the leg positions not only repositioned the tail membrane but also locally changed the camber and angle of attack of the inner surface of the wing (the plagiopatagium) (Figure 1C). Henceforth, we term this effect 'leg-induced wing camber'. Before wind tunnel testing the corners of the model were rounded and any voids filled with modelling clay to minimise unwanted aerodynamic effects. The large ears of *P. auritus*, which have previously been shown to play a significant role in the aerodynamics of these bats [30] were excluded from the model, as this research focused specifically on the aerodynamics of the tail membrane and therefore it was desirable to avoid interference effects between the ears and tail. Furthermore removing the ears from the model results in a morphology that closely represents a broad range of insectivorous bats, extending the potential relevance of the experimental results.

Force and moment measurements

The force and moment measurements were made using a 6-component force torque transducer (Nano-17, ATI Industrial Automation, USA). Prior to testing the calibration of the transducer was checked using small weights applied in the direction of each axis. Data was acquired using a National Instruments card (Austin, Texas, USA) plugged into a desktop computer. The transducer is manufactured to be accurate down to increments of 0.0125 N (forces) and 0.0625 Nmm (torques). The bat model was mounted onto the transducer via small wooden discs and a thin structural support. This arrangement was then attached to the mast of the wind tunnel at the Université of Liège, Belgium. The wind tunnel working section area of 2×1.5 m is significantly larger than the bat model, removing the potential for unwanted aerodynamic effects induced by the tunnel walls [31]. The bat model was mounted upside-down so that the tail was deflected away from the structural support as opposed to towards it and therefore the effect of the wake from the structural support on the tail membrane aerodynamics was minimised (Figure 1C). The leg angle (β) was set relative to the body and the body angle (φ) was set relative to the oncoming air stream (Figure 2). All angles were set using a large adjustable spirit level, held against the model or support. Data were collected for a model with a tail membrane at leg angles of 0° to 60° in steps of 5° for four separate body angles: -5°, 0°, 5° and 10°. Data were also collected for the same model with the tail membrane removed at 0° and 5° body angles for all leg angles above. The recorded wind speed for all tests fell within the range of 8.6 m/s to 9.3 m/s (Reynolds number range of 2.6×10^4 to 2.8×10^4) determined using a pitot tube, which is at the higher end of the natural flight speeds of many insectivorous bats [32]. Although higher than the typical foraging flight speed recorded for *P.auritus* (around 3 m/s) [28], it is comparable to estimates of the commuting speed (6 m/s) in this species [29]. Testing the model at a higher speed has a two-fold benefit. Firstly, the noise/signal ratio received by the force torque transducer is improved, reducing errors and secondly the wind tunnel struggles to produce consistent flow conditions at speeds lower than those tested. Importantly as there is not a significant difference between the Reynolds number of the model testing and that of the natural flight of *P. auritus* the aerodynamic coefficients (i.e. lift coefficient) measured in the wind tunnel will also be applicable to the natural flight of *P. auritus*. Indeed, aerodynamic coefficients are often quoted as being relevant over Reynolds numbers of several orders of magnitude [4]. See Barlow et al. [31] for a complete discussion of the applicability of wind-tunnel test data to real world scenarios, and the importance of maintaining dynamic similarity (i.e. maintaining a constant Reynolds number at low wind speeds).

Table 1. Dimensions of wind-tunnel *Plecotus auritus* model, with and without the tail membrane present, showing that removal of the tail membrane reduces the wing area and average wing chord of the model and increases the aspect ratio.

Variable	Model configuration	
	Tail membrane present	Tail membrane removed
Wingspan (m)	0.267	0.267
Wing area (m^2)	0.0124	0.0108
Aspect ratio	5.7	6.6
Average wing chord (m)	0.0465	0.0404

doi:10.1371/journal.pone.0018214.t001

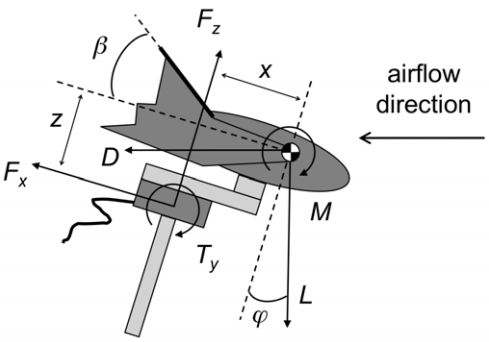

Figure 2. Schematic of the experimental set-up. The relationship between transducer forces and torques (F_x, F_z and T_y) and lift (*L*), drag (*D*) and pitching moment, due to the body angle (φ) is illustrated. The leg angle (β) and the position of the centre of mass relative to the transducer (*x* and *z*) are also shown. Note that the lift force (*L*) is downwards and the pitching moment (*M*) is clockwise since the model is mounted upside-down.
doi:10.1371/journal.pone.0018214.g002

Data were recorded for two hundred samples at a rate of 64 Hz and averaged to give a steady-state reading. The lift and drag readings were corrected at each body angle, to ensure that they were relative to the incoming wind direction using the following equations:

$$L = -F_z\cos\vartheta - F_x\sin\vartheta \quad (1)$$

$$D = -F_z\sin\vartheta + F_x\cos\vartheta \quad (2)$$

Where L is the lift, D the drag, F_x and F_z the transducer forces and φ the body angle (Figure 2). The pitching moment (defined as nose up positive) was relocated from the force torque transducer to the centre of mass of the bat model using

$$M = T_y + F_z x + F_x z \quad (3)$$

Where M is pitching moment, T_y the transducer torque, x and z the location of the centre of mass of the bat relative to the transducer (Figure 2). The location of the centre of mass of the bat model relative to the force balance was calculated by firstly weighing the model. Then the model was attached to the transducer and force and torque measurements taken at several different body angles whilst the tunnel was turned off. These measurements were then used to set up simultaneous equations, which were solved to find the centre of mass of the model, relative to the transducer (i.e. x and z). The location of the centre of mass on the bat model corresponded well with methods used to estimate the centre of mass of live bats [12]. The lift, drag and pitching moment were converted into non-dimensional aerodynamic coefficients using the following equations:

$$C_L = \frac{L}{\frac{1}{2}\rho V^2 A} \quad (4)$$

$$C_D = \frac{D}{\frac{1}{2}\rho V^2 A} \quad (5)$$

$$C_M = \frac{M}{\frac{1}{2}\rho V^2 A c} \quad (6)$$

Where C_L, C_D and C_M are the lift, drag and pitching moment coefficients respectively, ρ is the air density, V the air speed, A the wing area and c the average wing chord. Finally the lift to drag (L/D) ratio of the model was calculated for each test position since this ratio gives a good indication of overall aerodynamic performance.

Statistical analysis

ANCOVA was used to determine whether the different model configurations (body angles of 0 and 5°, and with, and without a tail membrane present) changed the relationship between aerodynamic parameters and leg angle. Tukey's post hoc tests were used to indentify specific differences between the four model configurations used. All statistical tests were preformed using the statistics toolbox for MATLAB® R2009a (MathWorks, Natick, Massachusetts, USA).

Results

During wind tunnel testing little aero-elastic deformation of the model's latex wing membranes or wing struts was observed. There was also no obvious fluttering of the trailing edge of the membrane. The only deformation of the latex membrane observed was the local increase in wing camber (leg-induced wing camber) due to the repositioning of the legs (Figure 1C), previously discussed in the methods.

The C_L and C_D produced by the bat model with a tail membrane follow similar general trends with body angle and leg angle (Figure 3A and B). As leg and body angle increased C_L and C_D also increased. An ANCOVA (Figure 4A) confirmed that C_L increased with both leg angle (β) and also changed with bat model configuration (body angle and presence/absence of the tail membrane), and the incremental change (i.e. the slope) in C_L with leg angle differed between the model configurations (leg angle: $F_{1,44} = 521.53$, $p<0.001$; configuration: $F_{3,44} = 88.18$, $p<0.001$; configuration*leg angle: $F_{3,44} = 16.11$, $p<0.001$). Furthermore, it is clear from Figure 4A and was confirmed by Tukey's post-hoc test, that the relationship between C_L and leg angle was similar for the model with and without a tail membrane; only body angle had an effect. The C_L produced by the bat model is, therefore, increased by both leg angle and body angle, but the removal of the tail membrane has no impact.

The C_D was always positive and tended to increase with body and leg angle (Figure 3B). ANCOVA showed that there was no difference in the slopes of C_D against leg-angle for any of the model configurations (configuration*leg angle: $F_{3,44} = 2.29$, $p = 0.0916$). Accordingly, simplifying the ANCOVA to assume parallel lines (i.e., no difference in slopes) showed that C_D increased with leg angle and changed with model configuration (leg angle: $F_{1,47} = 1130.68$, $p<0.001$; configuration: $F_{3,47} = 87.36$, $p<0.001$). Figure 4B shows, and Tukey's post hoc test confirmed, that contrary to the limited effect on the C_L, C_D is increased by the removal of the tail membrane from bat model. The C_D, therefore, increases with both increasing leg angle and body angle, and further increases with the removal of the tail membrane from the model.

The L/D ratio (Figure 3C and 4C) has a more complex relationship with body and leg angle. These data were not analysed with an ANCOVA since the L/D ratio is derived from both the C_L and C_D, which are have already been analysed. It is apparent, however, that the highest L/D ratio was produced at approximately a body angle of 5° and a leg angle of 20°.

Decreasing body angle and increasing leg angle caused the pitching moment coefficient to decrease (Figure 3D). This does not mean, however, that the pitching moment coefficient tended to zero, in fact it became negative (i.e. a higher nose-down pitching moment) at the lowest body and highest leg angles. An ANCOVA showed that the pitching moment coefficient differed between model configurations and increased with leg angle, and the incremental change in pitch moment coefficient with leg angle also differed between model configurations (configuration: $F_{3,44} = 218.75$, $p<0.001$; leg angle: $F_{1,44} = 111.93$, $p<0.001$; configuration*leg angle: $F_{3,44} = 12.23$, $p<0.001$). Removal of the tail membrane from the model has a profound affect on the pitching moment produced. (Figure 4D). Tukey's post hoc test of

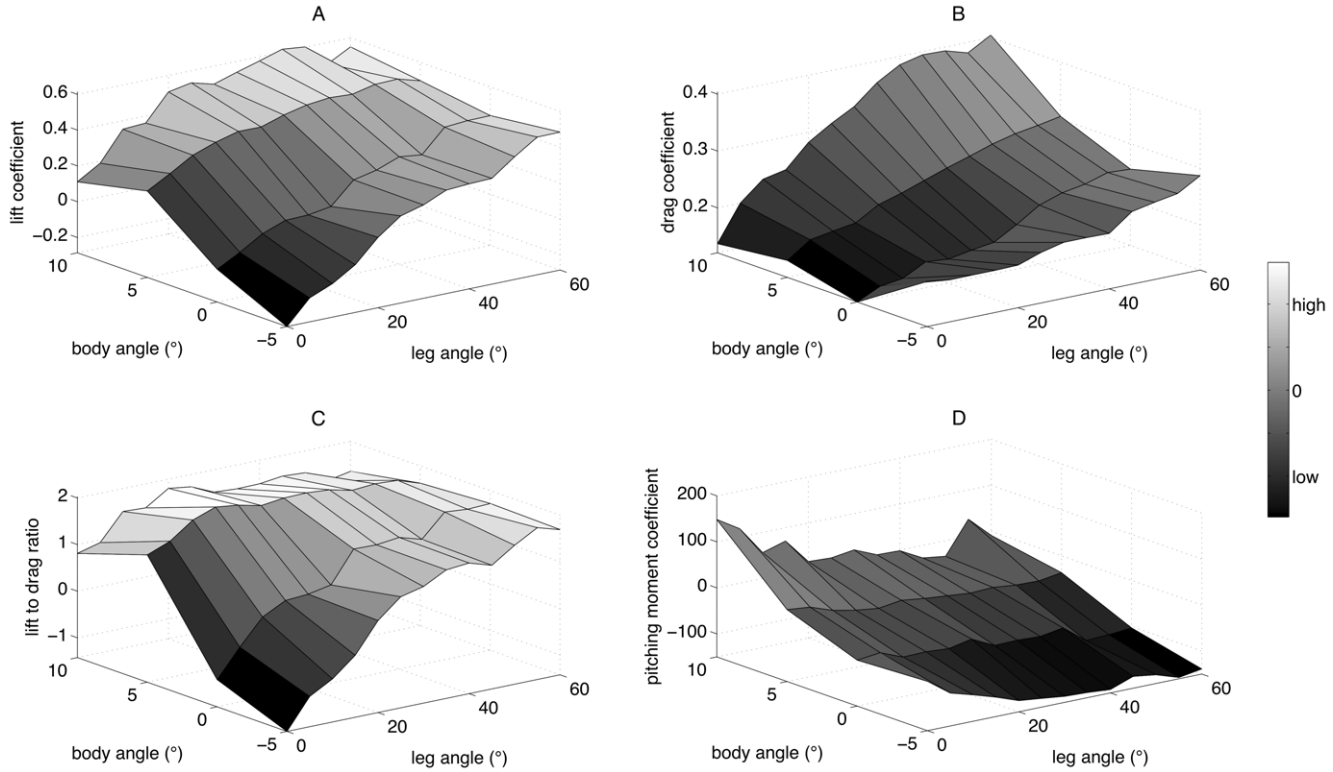

Figure 3. Aerodynamic force and moment coefficients produced by the bat wind-tunnel model. Effect of both leg angle and body angle on the lift coefficient (A), drag coefficient (B), lift to drag ratio (C) and the pitching moment coefficient (D) generated by the bat model with tail membrane present during wind-tunnel tests. Darker grey indicates lower values, while lighter grey higher values.
doi:10.1371/journal.pone.0018214.g003

the original ANCOVA showed that removing the tail membrane substantially reduced the level of nose-down pitching produced by the bat model.

Discussion

Changes in leg angle had a significant impact on the aerodynamic performance of the bat model (Figure 3). These leg angle induced aerodynamic effects are likely to be due to two main factors; increased leg-induced wing camber (i.e. locally increased camber and angle of attack of the inner wing surface of the model) and an increase in the angle of attack of the tail membrane. Both have a different impact on the bat model's aerodynamics and therefore different implications for *P. auritus* flight performance.

One of the most critical issues of flight performance is the trade-off between stability and manoeuvrability [33]. The pitching moment coefficient results (Figure 3D) are important in defining the model's stability. First, for almost all leg angles the pitching moment coefficient around the centre of gravity increases with body angle. This means that the bat model is statically unstable. Consider the case where a bat is in equilibrium, i.e. the pitching moment is zero ($M = 0$) and lift equals weight ($L\text{-}W = 0$). Then in general, a statically stable bat would be defined by

$$\frac{dM}{d\vartheta} < 0 \tag{7}$$

(i.e. the slope of the equation describing the relationship between the pitching moment coefficient and body angle should be negative). In this statically stable case, an increase in body angle due to, for example atmospheric turbulence will be corrected by an accompanying decrease in pitching moment and the bat will return to equilibrium position. However, the results of the pitching moment (Figure 3D) for the bat model clearly demonstrate that

$$\frac{dC_M}{d\vartheta} > 0 \tag{8}$$

i.e. the slope of the relationship between pitching moment coefficient (and therefore the pitching moment) and body angle is positive. In this case any increase in body angle will tend to be exacerbated by the increase in pitching moment, which will in turn increase body angle further making the bat model statically unstable. Second, the pitching moment results show that the slope of the surface is not significantly affected by the leg angle (Figure 3D). In other words, leg angle doesn't change the degree of instability of the bat model. The main effect of leg angle is to decrease pitching moment at all body angles. This is consistent with aerodynamic theory, which states that increasing wing camber causes increasing nose-down pitching moment, i.e. a negative nose-up moment [34]. Interestingly the inclusion of a tail membrane on the model exacerbates the increases with body angle of the pitching moment produced by the model (Figure 4D). Therefore, equation 8 would predict the model with a tail membrane is more unstable than the model without a tail membrane. In many ways this is counterintuitive since an aerodynamically active surface behind the centre of mass,

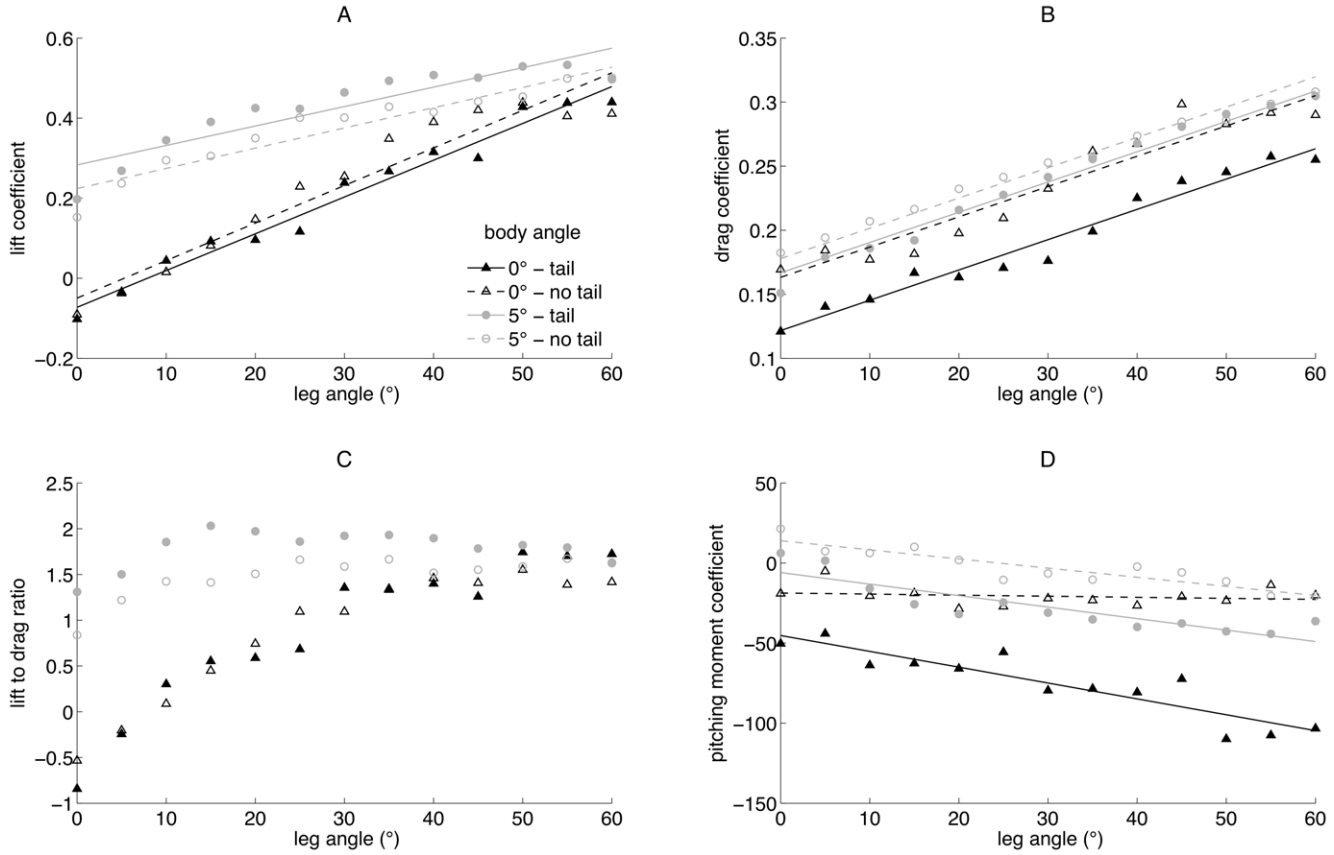

Figure 4. Comparison of the bat model's aerodynamic coefficients with and without a tail membrane. Lift coefficient (A), drag coefficient (B), lift to drag ratio (C) and pitching moment coefficient (D) produced by bat model for two body angles (0° and 5°) at all leg angles, with and without a tail membrane. Solid lines represent model with tail membrane. Dashed lines represent model without tail membrane. Black lines are for body angle of 0° and grey lines for 5°.
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generally aids stability. The tail membrane of bats, however, is not a separate aerodynamic surface but rather an extension of the wing membrane separated only by the leg bones, and therefore cannot be considered as a separate aerodynamic surface.

The most obvious explanation for the static instability of the bat model is that the centre of pressure of the wing (the point where the aerodynamic forces act) lies in front of the centre of mass. Of course, real bats can flap and deform their wings in a complex manner [35] and small modifications of the sweep angle of the wing could shift the position of the centre of pressure behind the centre of mass and thus produce a statically stable configuration [24,36]. Nevertheless, the centre of mass of the model is consistent with estimates for real bats [12] and suggests a gliding *P. auritus* configuration is statically unstable. A lack of static stability is not necessarily undesirable. Acrobatics aircraft are often neutrally stable (on the border between static stability and instability) as this increases their flight agility and the ability of the pilot to perform stunts [37].

Repositioning the tail membrane by increased leg angle, increases the pitching moment coefficient produced by the model, compared to the model without a tail membrane (Figure 4D). Therefore, the tail membrane could be an important structure for improving manoeuvrability and agility of *P. auritus*, particularly around the pitch axis. The wings of bats are well positioned to produce the necessary rolling and yawing moments around the centre of mass required for many manoeuvres [38]. However, wings are poorly positioned to produce large pitching moments around the centre of mass, since the quarter lifting line of a wing (i.e. the line which the lift force acts through) lies close to the pitching axis, which passes through the centre of mass [5]. This is a desirable scenario for most steady state horizontal flight, when average pitching moment over several flaps will tend to zero. However, during manoeuvres, a large pitching moment may be desirable so that the lift and thrust force can quickly be redirected and a turn made. Indeed, studies of manoeuvring bats have shown that the manoeuvres involve complex kinematics and changes around more than just the roll axis [38,39]. Roll acceleration is clearly important for initiating and completing manoeuvres and several taxa that forage close to vegetation (for example *Eptesicus nilssoni* and *Pipistrellus pipistrellus*) have specialisations in wing morphology, such as broad wing tips, to enhance the aerodynamic rolling moment generated by their wings [40]. However, during the banked phase of a turn the control of both the yawing and pitching moment (in addition to the rolling moment) will be essential if the manoeuvre is to be completed successfully. Therefore, possibly one of the important functions of a bat tail membrane (and indeed bird tails) is to control the pitching moment produced around the centre of mass, allowing control of the orientation of the lift forces and therefore more precise manoeuvres.

Removing the tail membrane from the bat model has no significant impact on the C_L produced by the model (Figure 4A). This suggests for the aerodynamic features tested on the bat model that the leg-induced wing camber is a more important feature than

the angle of attack of the tail membrane for controlling the level of lift produced. This doesn't mean the tail membrane has no role in affecting lift production; rather that the leg-induced wing camber seems to have a more significant effect. This is a slightly surprising result since bird tails clearly do have an important lifting function, particularly at lower speeds [1,2], and a similar role had been hypothesised for the bat tail membrane [9,10]. However, a bird can easily change the area of its tail by fanning out feathers, therefore changing its aerodynamic function to suit the current flight speed. For example, when birds come in to land they fan out their tail and increase its angle of attack, whereas during faster flight the tail is generally more furled [9]. For bats changing the area of their tail membrane to suit different flight speeds is not such a simple task; perhaps they can achieve some level of tail area control by appropriate positioning of their hind legs, however this remains to be tested. Furthermore, since leg position will influence both the positioning of tail membrane and the amount of leg-induced wing camber, it is impossible for the bat to manipulate the aerodynamics of one without affecting the other. In this sense the name tail membrane is perhaps a misnomer, since although the membrane encompasses the tail vertebrae, it is more akin to a wing flap.

The presence of a tail membrane on the model bat was shown to reduce the C_D produced (Figure 4B). Suggesting that tail membrane may act as a splitter plate, streamlining the body of the bat, as has been suggested previously for bird tails [3]. Furthermore, this potential drag reduction role may help to explain why many bat species that lack a large tail membrane, still posses small fringes of skin around the back of the body and legs.

Increasing leg-induced wing camber via appropriate leg positioning impacts the lift and drag coefficients produced by the bat model (Figure 3). The control of wing camber in flying bats is clearly important for controlling the magnitude of the lift and drag produced and is known to vary in a complex manner across the wing surface during each stroke [41]. Furthermore, camber has long been recognised in the aircraft aerodynamic literature as a key parameter in the aerodynamic performance of aircraft wings. Therefore, it is not surprising that the ability of bats to camber their wing surface is also recognised to have a distinct impact on their flight performance and foraging behaviour [32,42]. Indeed, it is not only the control of wing camber, but the deformation of the flexible membrane in response to aerodynamic loads, that has been shown to affect a bat's aerodynamic performance [22,43]. This automatic cambering behaviour of the wing skin is thought to delay the onset of stall [44]. Very little aero-elastic deformation of the latex membrane, however, was observed on the wind tunnel model tested here. The level of camber present on a bat's wing has a critical impact on its aerodynamic performance and our model results show that bats may partly control their wing camber through appropriate positioning of the legs.

Compared to experimental results of the gliding flight of live birds and bats in wind tunnels, the model's gliding performance is poor. The lift to drag ratio of the model doesn't get higher than around 2 (Figure 3C), whereas the dog-faced bat *Rousettus aegyptiacus* reached a maximum of 6.8 during glide tests in a tilting wind-tunnel [24]. This is not surprising since the bat model is necessarily a simplification of live bats and only the function of the tail membrane (and not the wings) was being investigated. Furthermore, the model was designed to enable testable hypotheses to be generated rather than provide quantitative aerodynamic performance parameters for a gliding bat planform.

Given that tails appear to improve flight performance of *P. auritus* it is interesting that many species of fruit bats lack a tail membrane. Fruit bats, however, are unlikely to require a high level of flight performance since the vast majority of their foraging time is spent either climbing in the trees, or in direct flight between roosts and foraging areas. The additional control of pitching moment and hence flight performance that the model tests indicate repositioning a tail membrane produces (Figure 4) may not therefore be required for foraging fruit bats. Therefore, other ecological pressures such as roosting behaviour [11] may dictate the presence or absence of the tail membrane. Aerial insectivores, on the other hand, require high levels of flight performance since they catch prey on the wing or amongst the clutter of vegetation. For the gleaning and slow flying hawking bats, manoeuvrability (i.e. the ability to perform tight turns) is a key factor that will influence foraging success. Manoeuvrability is likely to be best in bats possessing the lowest wing loading and an ability to sustain high C_L [45]. Therefore having a large tail membrane is likely to confer several key flight benefits. For example, the increase in wing area provided by having a tail membrane will reduce wing loading and therefore potentially improve manoeuvrability. A large tail membrane will also potentially offer a foraging advantage for bats that use the tail membrane as an insect capturing pouch [17], presenting a large area with which to snare prey. The data here highlights a potential role for the tail membrane in flight control, however whether this role is the primary function of the tail or a secondary function to improving prey capture is difficult to clarify. High speed footage of bats using their tail in flight and for prey capture may help distinguish between these functions. Altering the positioning of the hind legs potentially allows additional control of the wing camber for all bat species and therefore afford bats a level of either passive or active control of the lift and drag forces. Birds, on the other hand, are limited in their ability to adjust wing camber since feathers are relatively stiff structures and are not connected to the hind legs or tail.

Our model data here presents the first experimental evidence for a flight function of the bat tail membranes and provides a foundation for future research efforts. It would, for example, be very interesting to study whether bats actively control their leg position during flight as the model results suggests since potentially this is similar to a bird's control of tail position and furl which allows them to actively influence their aerodynamic performance. The alternative to active control is passive positioning of the legs and tail membrane driven by the inherent aerodynamic and inertial loads from the wings and body of the bat. From the results of the *P. auritus* model we conclude that the tail membrane of many bats (since many have wings and tails morphologically similar to *P. auritus*) has a flight control function and hypothesise that:

1. bats will actively control leg position (and hence tail position and leg-induced wing camber), since this will allow greater control over their flight and consequently, their foraging performance.
2. bats will rapidly reposition their legs and tail, coincident with aerial manoeuvres.
3. bats with the longest legs and largest tail membranes will be the most manoeuvrable.

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Author Contributions

Conceived and designed the experiments: JDG GD. Performed the experiments: JDG GD. Analyzed the data: JDG RLN. Contributed reagents/materials/analysis tools: GD JRC. Wrote the paper: JDG RLN GD JRC.

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Chapter 5

No apparent ecological trend to the flight-initiating jump performance of five bat species

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RESEARCH ARTICLE

No apparent ecological trend to the flight-initiating jump performance of five bat species

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SUMMARY

The jump performance of five insectivorous bat species (*Miniopterus schreibersii*, *Myotis blythii*, *Myotis capaccinii*, *Myotis myotis* and *Rhinolophus blasii*) was filmed using a high-speed camera. All study bats jumped using a similar technique, with the wing musculature providing the force. The bats jumped off the wrist joint of their wings, typically with their feet already off the ground. Contrary to expectations, jump performance did not correlate with ecology and was instead strongly determined by body size. In general, the larger bats produced more jump force, left the ground at higher speeds and jumped higher than the smaller bats. The differences in force production disappeared when the data were corrected for body size, with the exception of *Myotis capaccinii*, which produced significantly less force. Scaling of jump performance with body size measured here was compared against two existing muscle performance scaling models. The model suggesting that muscle contraction velocity is proportional to muscle length was better supported than that based on muscle cross-sectional area. Both models, however, failed to accurately predict the scaling of jump forces, with the slope of the relationship being significantly steeper than predicted, highlighting the need for further investigations of vertebrate muscle performance scaling. The results of this study indicate that a bat's jumping ability is a secondary locomotor ability that uses the strongly selected-for flight apparatus with no apparent ecological trend present, i.e. flight so dominates bat locomotor morphology that other locomotor abilities tend to be derivative.

Key words: biomechanics, jumping, muscle, scaling, take-off.

INTRODUCTION

The ability to take-off is crucial for all volant animals, as this marks the transition from terrestrial, arboreal or aquatic to aerial locomotion. For many species of bat, taking-off is not particularly challenging, as they roost in caves, attic spaces or trees and only need to drop into space to initiate flight. Indeed, landing upside-down on a horizontal surface is the real acrobatic challenge they face (Riskin et al., 2009). Several bat species, however, spend a significant proportion of their foraging time on the ground (Altringham, 1996; Riskin et al., 2006; Schutt et al., 1997) and must become airborne again with gravity working against them. Furthermore, all bats can potentially crash onto the ground and an ability to quickly return to flight will improve their survival chances, particularly as the terrestrial crawling ability of most bats seems to be poor because of their modified hindlegs (Riskin et al., 2005). Although a number of bat species are known to jump into the air, only two studies, and then concerning only one species (the vampire bat, *Desmodus rotundus*), have quantitatively investigated this behaviour in bats (Altenbach, 1979; Schutt et al., 1997).

In general, however, animal jumping is well studied, occurring in a wide range of species from tiny insects to large vertebrates (e.g. Alexander, 1995; Caple et al., 1983; Demes et al., 1996; Gabriel, 1984; Harris and Steudel, 2002; James et al., 2007; Schutt et al., 1997; Toro et al., 2003). A jump (as opposed to continuous hopping) is generally considered to be a single discrete kinematic event. This allows the animal's mechanical performance to be relatively easily parameterised (i.e. jump distance or height, take-off speed, jump force). Specialist jumping species typically have several adaptations that improve their performance: both leg length and the musculature associated with jumping are increased (Gabriel, 1984; James et al., 2007). In addition, keeping weight at the extremities of the legs to a minimum and having additional leg joints allows further improvements in jump performance (Alexander, 1995). Humans roll onto the ball of their foot during a jump, allowing the section of foot between the heel and the ball to act as an additional leg segment (Alexander, 1995). Many specialist jumpers also employ energy storage mechanisms. Small insects often make use of a catapult-type mechanism, deforming an elastic structure to store energy before releasing a 'catch' to propel them through the air (Alexander, 2003). Larger vertebrates, however, rely on counter-movement prior to the jump to stretch tendons, thus storing energy, which is released during the jump (Alexander, 2003). Even humans (non-specialist jumpers) make use of tendon stretching counter-movement to improve jump height (James et al., 2007).

The jumping technique used by bats is unusual amongst vertebrates because the power is generated by the forelimbs instead of the hindlegs (Schutt et al., 1997). In contrast, birds generate approximately 80–90% of their take-off speed from their hindlegs, with the wings continuing the initial movement generated by the legs (Earls, 2000). Bats, however, possess extensively modified hindleg and pelvic bones (Neuweiler, 2000; Riskin et al., 2005), which have left them with relatively poor terrestrial locomotion. Many bat species are documented as landing on the ground during foraging, and then resuming flight once the prey is captured (e.g. Arlettaz, 1996; Bell, 1982; Fiedler, 1979; Siemers and Ivanova, 2004; Vaughan, 1976), but it is their forelimbs and powerful wing

musculature that generate the necessary forces to propel them back into the air, the hindlimbs only being used to orientate the body over the pectoral limbs, which generate the jump force (Schutt et al., 1997). The vampire bat *D. rotundus* is considered to be one of the most agile bats on the ground. Therefore, perhaps unsurprisingly, previous studies investigating bat jumping have tended to focus on *D. rotundus* (Altenbach, 1979; Schutt et al., 1997). Schutt and colleagues found that *D. rotundus* typically generates a force of 6.51 times their body weight, giving them a take-off speed of 2.38 m s^{-1} (Schutt et al., 1997). The unique foraging ecology of *D. rotundus* (feeding on the blood of larger mammals) could influence its jumping performance and it may not, therefore, be a good exemplar of all bat species. A study by Siemers and Ivanova comparing the take-off times of three Rhinolophidae species, *Rhinolophus blasii*, *R. euryale* and *R. mehelyi*, however, did not detect any ecological trend in jump performance even though *R. blasii* spends significantly more time on the ground than the other two species (Siemers and Ivanova, 2004). In quantifying take-off performance, the study used the time taken to cover a given distance, which perhaps lacked the resolution necessary to identify any interspecific ecologically driven differences in take-off performance. Therefore, a more comprehensive study is required before uniformity (no ecological trend) in ground take-off performance in bats may be concluded.

The aim of our study was to determine whether a bat's foraging behaviour affects its jump performance. We hypothesised that gleaning bats would have a better jumping ability (i.e. higher jumps made at faster speeds and higher jump forces) than hawking bats as they spend a larger proportion of their time on or near the ground catching their prey. In addition, we investigated the scaling of jump performance in bats and compared this with the theoretical scaling models of Hill (Hill, 1950) and Richard and Wainwright (Richard and Wainwright, 1995).

MATERIALS AND METHODS

Filming of bat jumps

Bats were caught using a harp trap on three separate evenings (24 August 2006, 25 August 2006 and 25 August 2007) as they exited a roosting cave at Maronea, Rhodope Prefecture, Greece. The bats were then released onto a flat platform (±5 deg) from which they could take-off. The bats were escaping from their captors and therefore it was assumed that they would be performing their take-off with maximal performance. To encourage the bats to leave the platform in a perpendicular direction to the camera view, a white sheet was hung behind the platform; this also improved the visibility of the bat in the footage. The platform was illuminated using floodlights (Nightsearcher, Portsmouth, UK). The take-off jumps were filmed using a Trouble Shooter camera (Fastec Imaging, San Diego, CA, USA), running at either 125 or 250 frames s^{-1} (Fig. 1). Before the jump the forearm length and body mass (M_b) of the bat were measured.

Study species

Data were collected from five species of bat.

Myotis blythii, Tomes 1857 (N=5) and *Myotis myotis*, Borkhausen 1797 (N=12), two closely related large bat species. Both of these bats have flexible foraging strategies including ground gleaning and

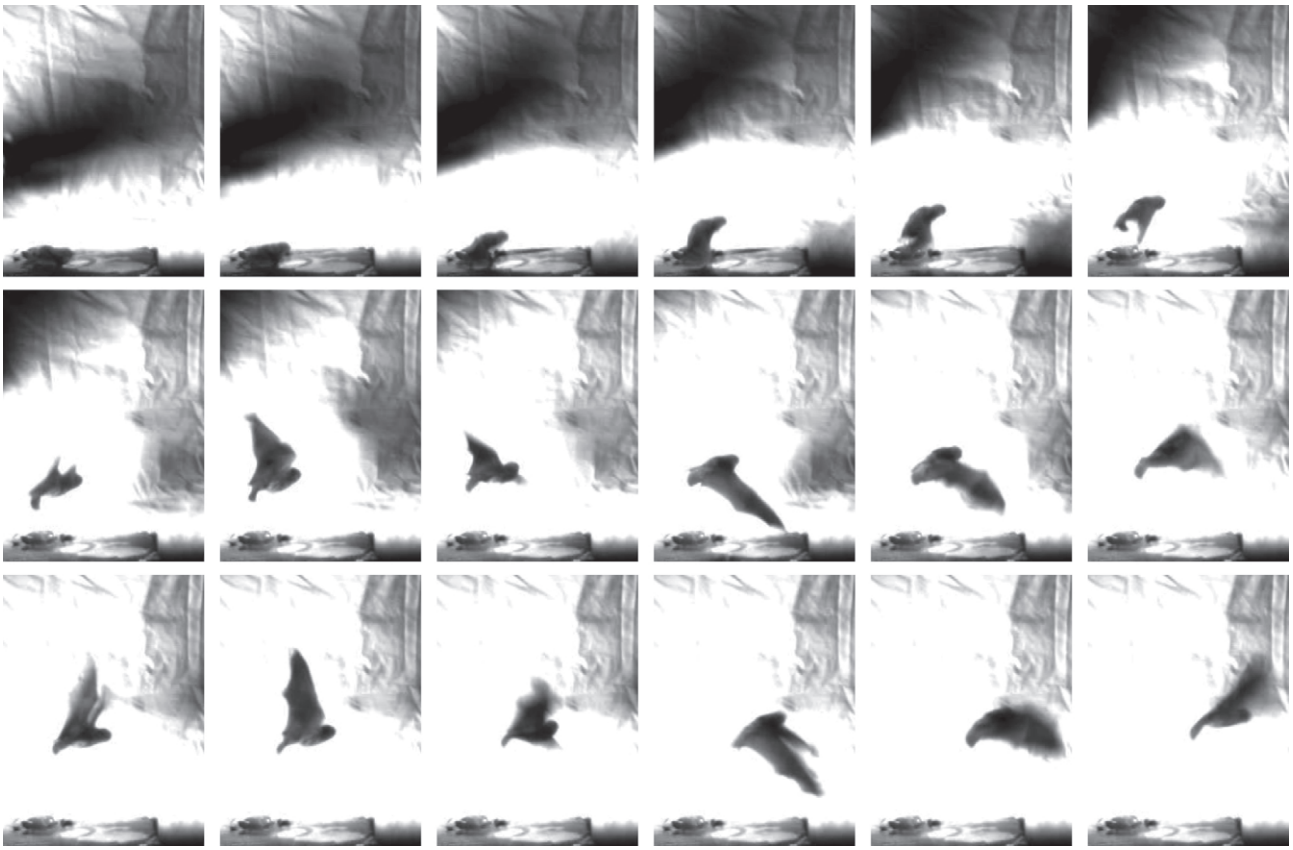

Fig. 1. Selected frames from high-speed video footage of *Miniopterus schreibersii* jumping from a platform to initiate flight. The use of the forearms to generate the force of the jump is clearly visible. Also note that the first wing beat after jumping tends to have a reduced amplitude, compared with a more typical wing beat. Frames are 16 ms apart.

aerial hawking, depending on the availability of food (Arlettaz, 1996). These bats were predicted to have intermediate jumping performance compared with the other species because they are able to glean prey from the ground.

Myotis capaccinii, Bonaparte 1837 (*N*=15), a much smaller bat, with a highly specialised trawling foraging behaviour, gaffing insects and small fish from the surface of ponds (Aihartza et al., 2008). *Myotis capaccinii* was predicted to have poor jumping performance because it is a specialist trawler.

Miniopterus schreibersii, Kuhl 1817 (*N*=17), which forages at high altitudes, hawking insects in flight (Norberg and Rayner, 1987). *Miniopterus schreibersii* was predicted to have the poorest jump performance, as it specialises in hawking insects out of the air.

Rhinolophus blasii, Peters 1866 (*N*=6), a small, ground-gleaning species, sometimes even pursuing prey items across the ground (Siemers and Ivanova, 2004). *Rhinolophus blasii* was predicted to perform the best in the jumping experiments because of its frequent ground gleaning.

Video analysis

Video footage of the bats jumping to initiate flight was digitised using Tracker 3.10 (Brown, 2009). The shoulder joint of the bat was tracked as a proxy for the centre of mass (CoM) of the bat. Although not ideal, given a bat's CoM is known to vary in location throughout locomotor activities such as flight (Iriarte-Diaz and Swartz, 2008), this gave the best consistently viewable landmark close to the CoM. The timing of key events in each jump was recorded: the start of the jump (first frame showing vertical movement), the wrist joint leaving the ground (signalling the end of the jump) and the start of both first and second downstrokes. Video footage was scaled and rotated relative to the vertical using a checkerboard and a plumb line. Any footage in which the bat obviously jumped towards or away from the camera, or was obscured, making tracking difficult, was disregarded.

Data analysis

All subsequent data and statistical analyses were performed using Matlab® R2007a (The MathWorks Inc., Natick, MA, USA). The data were smoothed using a fourth-order Butterworth filter with a cut-off frequency of 12.5 Hz. The cut-off frequency was selected by plotting the residuals (i.e. a measure of the difference between the smoothed data and the original) over a large range of potential cut-off frequencies for the data of the first few jumps analysed. The cut-off frequency that was the best compromise between maximising noise reduction and minimising the signal distortion (that all smoothing introduces) was selected [see p. 42 of Winter (Winter, 1990)]. The following kinematic variables (Fig. 2) were then calculated for each bat from the smoothed data: take-off angle (deg; the angle travelled by the bat above horizontal between the start of the jump and the wrist leaving the ground, which was calculated from the slope of a linear least-squares fit to the data); jump height (m; defined as the height above ground obtained at the start of the first downstroke, as this marks the transition between the bat being a projectile and actively flying); maximum take-off speed ($\mathrm{m\,s^{-1}}$; between the start of the jump and the wrist leaving the ground); and jump force, which was calculated as:

$$F = M_\mathrm{b}\sqrt{a_\mathrm{h}^2 + (a_\mathrm{v} + \boldsymbol{g})^2}\ , \qquad (1)$$

where F is jump force (N), M_b is body mass (kg), a_h is horizontal acceleration ($\mathrm{m\,s^{-2}}$), a_v is vertical acceleration ($\mathrm{m\,s^{-2}}$) and $\boldsymbol{g}$ is gravitational acceleration ($\mathrm{m\,s^{-2}}$). The maximum value between the start of the jump and the onset of the first downstroke was then taken as the jump force. The ratio of jump force to the bat's weight was also calculated.

As the velocities and accelerations are derived from the estimated position of the CoM, the process of video digitisation may introduce error into the estimates of kinematic variables. Digitising video footage is dependent upon the selection of a reliable landmark on the animal (in this case the shoulder joint). To estimate the error

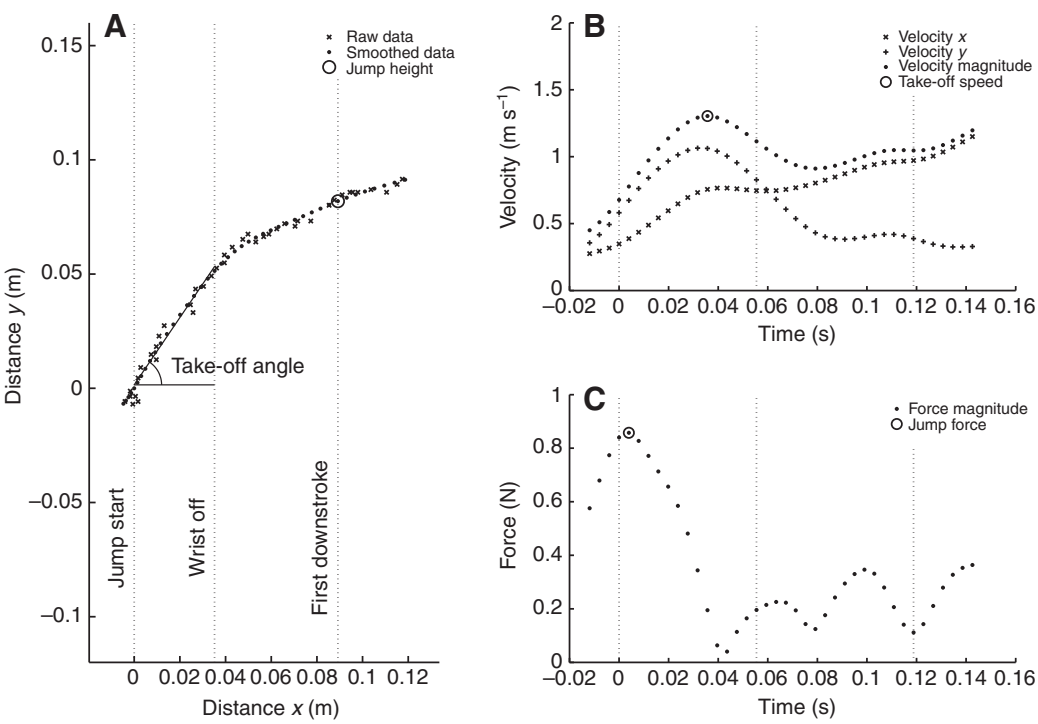

Fig. 2. Example kinematic data from a *Myotis myotis* jump. (A) Raw and smoothed positional data of the bat's centre of mass (CoM). Definitions of take-off angle and jump height are also indicated. (B) Velocity of the bat's CoM, including the point taken as representative of the bat's take-off speed. (C) Force acting upon the bat's CoM, including the point taken to be the bat's jump force. All plots are shown with vertical dashed lines to indicate key events in the jump sequence. From left to right, the lines signify the jump start, wrist off the ground and the first downstroke.

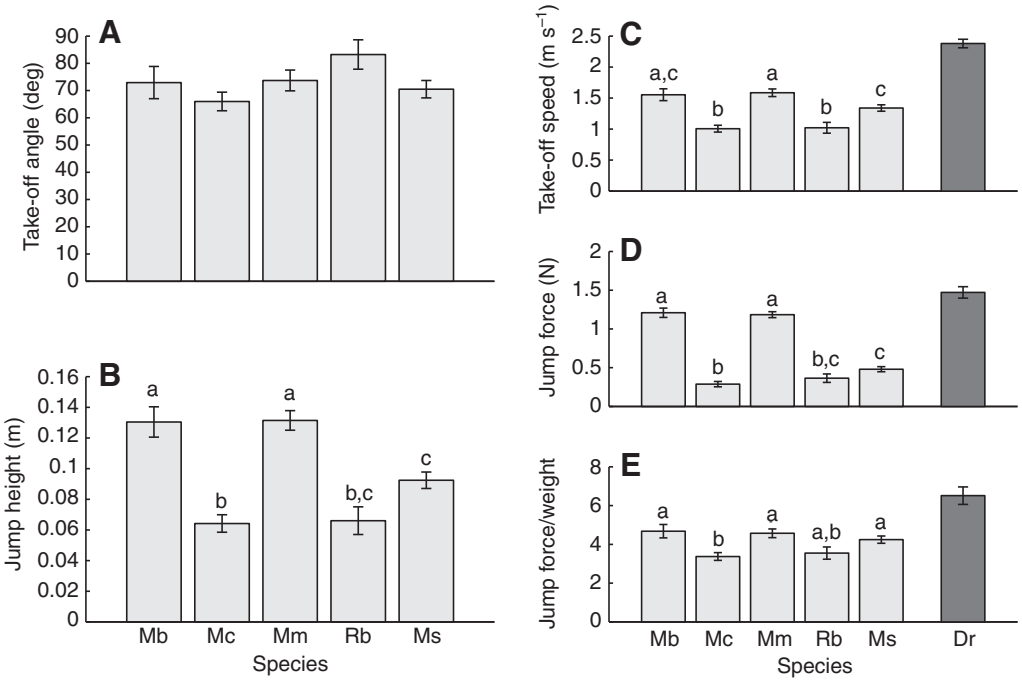

Fig. 3. Kinematic variables for jumping bat species. *Myotis blythii* (Mb, *N*=5), *Myotis capaccinii* (Mc, *N*=15) *Myotis myotis* (Mm, *N*=12), *Rhinolophus blasii* (Rb, *N*=6) and *Miniopterus schrebersi* (Ms, *N*=17). Data for *Desmodus rotundus* (Dr) are included for comparative purposes (Schutt et al., 1997). (A) Take-off angle. (B) Jump height. (C) Take-off speed. (D) Jump force. (E) Jump force/weight. Letters above the bars indicate significant differences ($P<0.05$) determined from the Tukey *post hoc* analyses. Bars with the same letters are not significantly different from each other and all data are shown with standard error bars.

associated with video digitisation here, a test piece of footage was digitised five times and the standard deviations of the kinematic variable means were calculated. The standard deviations due to the digitisation process were 0.3 mm (0.33% of the mean) for jump height position, 0.027 m s^{-1} (2.01% of the mean) for take-off speed and 2.07 m s^{-2} (4.87% of the mean) for peak acceleration. These errors are unlikely to be systematic and therefore should not cause bias between species comparisons. The jump forces calculated here, however, should be regarded as estimates rather than direct measurements, such as those derived from a force plate.

Differences in the kinematic variables for each species were tested using one-way ANOVA and Tukey *post hoc* tests. The scaling relationships of the forearm length, jump height, take-off speed and jump force were also tested using least-squares regression. Least-squares regression was chosen over reduced major axis (RMA) as RMA can artificially inflate the slopes if the r^2 is low.

The scaling exponents (slopes) from the regression analyses were then tested against exponents predicted from the literature. A summary of the scaling predictions based on two distinct geometric models, the first being the classic Hill (Hill, 1950) model and the second a newer model from Richard and Wainwright (Richard and Wainwright, 1995), is given in table 1 of Toro et al. (Toro et al., 2003). The experimental scaling exponents from our study were tested against the predictions from both models. The models differ in their predictions of the relationship between velocity and increasing size. Hill's model predicts that velocity does not increase with increasing body size (Hill, 1950), whereas Richard and Wainwright's model predicts that velocity will increase 1:1 with increasing length (Richard and Wainwright, 1995).

Published data (Schutt et al., 1997) for the vampire bat *D. rotundus* were plotted on the figures for comparative purposes. The data for *D. rotundus*, however, were not included in the statistical analyses as they were collected using a different methodology.

RESULTS

All the bats in the study followed a similar pattern during a take-off jump (Fig. 1). First, a small amount of counter-movement was observed in the footage, signalling the start of a jump. This was followed by a rapid jump using the wing musculature to propel the bat off its wrists. The bat's feet tended to leave the ground before the wrists. Once the wrist left the ground (end of the jump) the wings were quickly brought upwards and the first downstroke started, which tended to have a smaller amplitude than subsequent downstrokes. The bats then typically flew off at an angle shallower than the angle of the initial jump.

There was no detectable difference in the take-off angle used by the bats (Fig. 3A, Table 1), with all bats typically jumping at an angle between 70 and 80 deg from horizontal. The jump height achieved

Table 1. Summary of means (±s.e.) and ANOVA results for the jump kinematic variables of five species of insectivorous bat

	Species						
Variable	*Myotis blythii* (*N*=5)	*Myotis capaccinii* (*N*=15)	*Myotis myotis* (*N*=12)	*Rhinolophus blasii* (*N*=6)	*Miniopterus schrebersii* (*N*=17)	$F_{4,54}$	*P*
Mass (g)	26.3±0.7	8.7±0.4	26.4±0.5	10.5±0.7	11.5±0.4	296.84	<0.001
Forearm length (mm)	59.9±0.6	42.0±0.4	63.3±0.4	46.0±0.6	45.4±0.3	532.48	<0.001
Take-off angle (deg)	72.9±5.9	66.0±3.4	73.7±3.8	83.2±5.4	70.5±3.2	1.95	0.116
Jump height (m)	0.130±0.010	0.064±0.006	0.131±0.006	0.066±0.009	0.092±0.005	21.21	<0.001
Take-off speed (m s^{-1})	1.55±0.10	1.01±0.06	1.59±0.06	1.02±0.09	1.34±0.05	16.92	<0.001
Jump force (N)	1.21±0.06	0.29±0.03	1.18±0.04	0.36±0.05	0.48±0.03	110.66	<0.001
Jump force/weight	4.68±0.35	3.37±0.20	4.57±0.22	3.55±0.32	4.24±0.18	5.94	<0.001

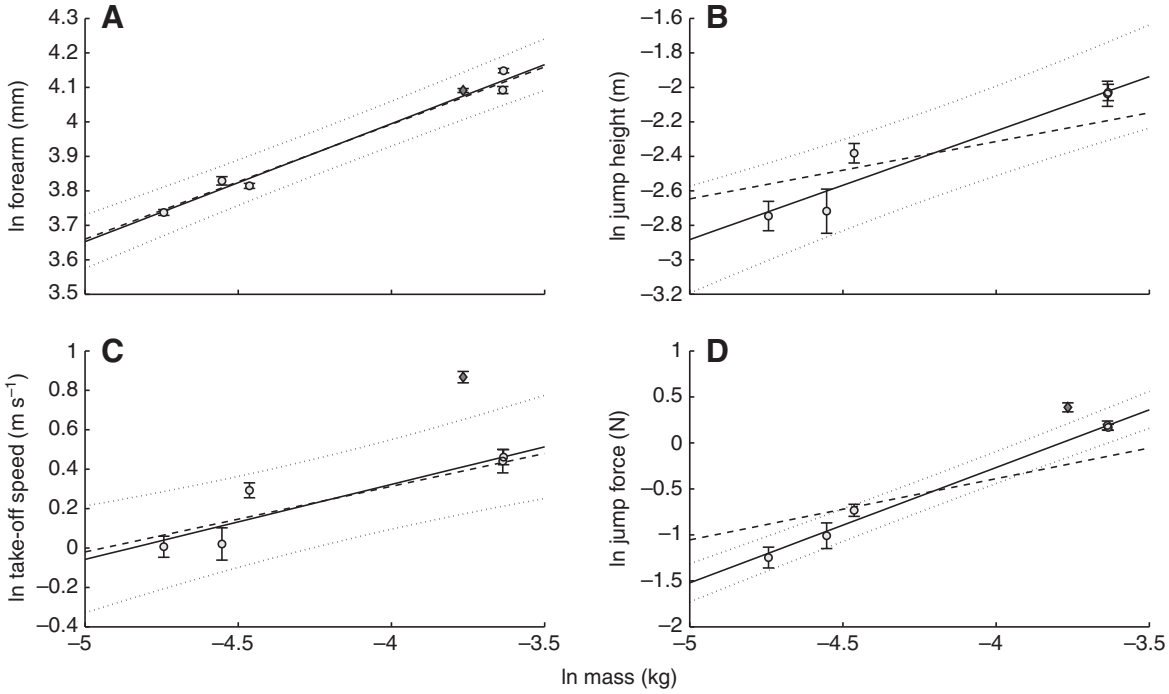

Fig. 4. Least-squares regression of bat jump variables against body mass for the five species of insectivorous bat (circles). Data from *Desmodus rotundus* (Schutt et al., 1997) (diamonds) are included for comparative purposes and are not used in the calculation of the regression lines. (A) Forearm length. (B) Jump height. (C) Take-off speed. (D) Jump force. All data are shown with standard error bars. Solid lines are the calculated regression slopes and dashed lines are the slopes from the predicted scaling exponents (Table 2). Dotted lines represent 95% confidence limits.

at the onset of the first downstroke varied considerably amongst species (Fig. 3B, Table 1), with the larger bats (*M. blythii* and *M. myotis*) jumping twice the height of the smaller *M. capaccinii* and *R. blasii*. *Miniopterus schreibersii* jumped higher than *M. capaccinii*, but not significantly higher than *R. blasii*. Take-off speed (Fig. 3C, Table 1) and jump force (Fig. 3D, Table 1) produced similar results to jump height, with the larger bats generally outperforming the smaller species. When jump force was corrected for body weight (N) (Fig. 3E, Table 1), however, the differences between the bats in the study were much smaller, with all species producing a force of between 3.5 and 4.5 times their body weight. Only the force to weight ratio produced by *M. capaccinii* was significantly lower than that of any of the other bats. The comparative data for *D. rotundus* suggest that it is likely to outperform all the bat species in this study in terms of take-off speed, jump force and the ratio of jump force to body weight (Fig. 3). Indeed, although the absolute jump force produced by *D. rotundus* is not much larger than that of *M. blythii* and *M. myotis*, when compared with its body weight the difference is striking. *Desmodus rotundus* is able to produce a force over 6 times larger than its body weight whilst jumping (Schutt et al., 1997).

The scaling relationships investigated were all significantly different from zero (Fig. 4, Table 2). The scaling exponents from the regression of the bats' forearm length, jump height and take-off speed against M_b, however, were not significantly different from the predicted exponents from Richard and Wainwright's model (Richard and Wainwright, 1995) (Fig. 4, Table 2). In contrast, the calculated scaling exponents were different from those expected using Hill's model (Hill, 1950), which predicts no relationship between jump height or speed and M_b. Both the scaling models predict that jump force should scale as $M_b^{0.66}$. The calculated exponents, however, showed positive allometry (Fig. 4D, Table 2), with larger bats generating higher forces than expected by the models. The comparative data of *D. rotundus* show that whilst it clearly falls within the 95% confidence limits for the scaling of forearm length (geometrically similar to the other bat species), it produces a greater than expected take-off speed and jump force.

Table 2. Summary of regression statistics used to calculate the scaling exponent for selected bat jump variables, which was then *t*-tested against theoretically expected exponents from two theoretical scaling models

	Predicted theoretical scaling exponents		Least squares regression				*t*-test of the experimental against the theoretical exponents	
Variable	Hill	Richard and Wainwright	Experimental scaling exponent	r^2	t_3	*P*	t_3	*P*
Forearm (mm)	0.333	0.333	0.342±0.028	0.981	12.42	0.001	0.34	0.756
Jump height (m)	0	0.333	0.631±0.110	0.916	5.72	0.011	2.70	0.074
Take-off speed (m s^{-1})	0	0.333	0.381±0.096	0.839	3.95	0.029	0.50	0.655
Jump force (N)	0.666	0.666	1.255±0.074	0.990	17.01	<0.001	7.99	0.004

Hill: Hill, 1950. Richard and Wainwright: Richard and Wainwright, 1995.

DISCUSSION

Contrary to what was originally hypothesised, the jumping ability of the study bats appears to be driven more by their body size than by their foraging strategy, with the strongly selected-for and highly developed flight musculature providing a secondary ability of propelling the bat into the air from the ground. A potential exception to the lack of an obvious ecological trend in jump performance is perhaps *D. rotundus*, which has an extraordinary jumping ability possibly due to its highly unique sanguivorous foraging strategy.

The jumping technique used by the study bats for initiating flight (Fig. 1) is consistent with the technique previously described for *D. rotundus* (Altenbach, 1979; Schutt et al., 1997). The jump force is produced by the forearms and directed onto the ground through the wrist joint, with the hindlimbs leaving the ground first. This jump technique is completely different from the take-off of birds. Birds generate a large proportion of their take-off speed with their hindlegs, and the wings are used to continue the initial movement (Earls, 2000). In our study of bats, a small amount of counter-movement was typically observed before the start of each jump. Larger jumping animals often use counter-movement before jumping to stretch tendons, storing energy and improving the overall jump performance (Alexander, 2003). The bats may have been able to make some use of this technique, even though they are not specialist jumpers, given humans (also non-specialists at jumping) have been shown to improve jump performance through pre-jump tendon stretching (James et al., 2007).

The bats in the present study that typically feed near the ground or vegetation (gleaners) were expected to have a better jumping performance (i.e. higher jumps and faster take-off speeds) than the bats that feed in open areas (hawkers). The results, however, do not support this hypothesis, with the larger bats tending to outperform the smaller bats in absolute terms, with no clear ecological trend apparent (Fig. 3, Table 1). *Rhinolophus blasii* (a ground gleaner) was predicted to outperform both *M. schreibersii* (a fast-flying hawker) and *M. capaccinii* (a trawler) as it spends a significantly larger portion of time foraging on the ground. The three bats, however, had similar jump abilities, with the performance of *R. blasii* and *M. capaccinii* being indistinguishable. Indeed, *M. schreibersii* actually had a faster take-off speed than *R. blasii* (Fig. 3C, Table 1). *Myotis capaccinii* did not show a particularly reduced jumping performance despite possessing exceptionally large feet; extra weight at the extremities tends to reduce jumping performance (Alexander, 1995). The results support earlier evidence from a study of three Rhinolophid species, which also found no ecological trend in jump performance (Siemers and Ivanova, 2004).

The scaling exponent of forearm length against M_b was not significantly different from that expected for geometric similarity (0.33), a fundamental assumption of both scaling models tested here (Hill, 1950; Richard and Wainwright, 1995) (Fig. 4, Table 2). Furthermore, as there is generally an isometric scaling of muscle mass with M_b for mammals (Alexander et al., 1981; Schmidt-Nielsen, 1984), the percentage of the muscle mass available to the bats for jumping should be the same for all species. The scaling of both jump height and take-off speed with M_b supports the geometric model of Richard and Wainwright (Richard and Wainwright, 1995), rather than Hill's model (Hill, 1950). This suggests that the muscles involved in bat jumping behave so that any increase in length causes a 1:1 increase in contraction velocity. This predicted 1:1 relationship is based on the assumption that sarcomere length is constant within muscles during ontogeny (Richard and Wainwright, 1995). The scaling relationships determined here, however, are interspecific, which implies that sarcomere length must be relatively constant across the bat species studied. Both models (Hill, 1950; Richard and Wainwright, 1995) fail to predict the scaling of jump force, as larger bats were able to produce relatively more force ($F \propto M_b^{1.255\pm0.074}$) than the models predicted ($F \propto M_b^{0.66}$). These results differ from a study of 12 *Anolis* lizard species (Toro et al., 2003), which found that peak force did scale as predicted by the models. Lizard jump speed, however, was not predicted by either model, which also contrasts with the bat results, as the scaling of bat take-off speed was not significantly different from the predictions of Richard and Wainwright's model (Richard and Wainwright, 1995). These inconsistencies highlight the fact that the scaling of muscle performance and how it relates to animal kinematics are likely to vary across taxa.

An exception to the lack of an ecological influence on take-off performance is perhaps *D. rotundus*, which seems to outperform the bats in this study (Fig. 3). The jump force and take-off speed of *D. rotundus* are clearly greater than would be expected based on the scaling relationships for the other five species of bat, as they fall far outside the 95% confidence limits (Fig. 4). Vampire bats frequently take on 50% of their body mass in blood during feeding; thus, their extraordinary jumping ability may have evolved to cope with this increase in body mass, ensuring they can still get airborne (Altenbach, 1979). Indeed, Harris and Steudel found that fat mass relative to lean body mass explained most of the variation in the jump velocity of cats (Harris and Steudel, 2002). *Desmodus rotundus* falls well within the confidence intervals for the scaling of forearm length against M_b (Fig. 4), whereas other specialist jumpers have elongated limbs to improve jumping (James et al., 2007), suggesting that the improved performance of *D. rotundus* is not related to limb morphology but perhaps to muscle physiology. Schutt and colleagues propose that during a *D. rotundus* jump different muscle fibre types are sequentially recruited, which may help maximise jump performance (Schutt et al., 1997). Whether this suggested sequential recruitment of muscle fibres occurs in all bats or perhaps only *D. rotundus* remains unknown. Another explanation for the exceptional jump performance of *D. rotundus* compared with the bats in this study, however, may relate to differences in methodology. The data in the study of Schutt and colleagues (Schutt et al., 1997) were collected using a force plate, whereas this study utilised high-speed video footage. Nevertheless, the two techniques are known to produce comparable results (Arampatzis et al., 2000; Saini et al., 1998; Thirunarayan et al., 1996). Therefore, the difference in the jump performance of *D. rotundus* is likely to be due to ecological pressures and not methodological differences.

The data presented here show that, contrary to expectations, there is no obvious ecological trend to the jumping performance of the study bats. Rather, the bats' jump performance seems to correlate with their body mass, with the strongly selected-for wing musculature providing the necessary force for take-off from the ground. It is likely that selection for flight performance is dominant in shaping the forelimbs and associated musculature of bats, with the relationship between the two tightly constrained to provide an aerodynamic optimum and, hence, similar levers and motors for jumping with. Comparisons of the bat data with scaling models are supportive of the model of Richard and Wainwright (Richard and Wainwright, 1995), except when considering force production. This failure of existing models to predict the scaling of jump force and the apparent differences between taxa indicate that further investigations of bat jumping, and vertebrate muscle performance in general, are required.

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General Discussion

The study of vertebrate flight has a long and colourful history. The earliest attempts of gentlemen scientists began by building gliders based on the flapping of bird wings; today cutting edge particle image velocimetry (PIV) and computer fluid dynamics (CFD) give us insight in to the finer details of animal aerodynamics. Over the years, however, the study of vertebrate flight has tended to focus on birds, with bat flight generally receiving less attention. In focusing on the relationship between the morphology, ecology and locomotor performance of gleaning bats, however, this thesis has demonstrated that the study of the form and function of the morphology of bats and their locomotion can help illuminate not only bat ecology, but indicate how a suite of ecologic and physiological pressures shape a basic mammalian blueprint into a variety of unique solutions.

The morphology of bats is tightly constrained by flight. Within these constraints, however, there is significant variation in both the morphology of bat wings (Fenton, 1972, Norberg & Rayner, 1987, Baagøe, 1987) and ancillary structures such as the ears (Vaughan, 1966, Bullen & McKenzie, 2001), and the tail membrane (Lawlor, 1973, Norberg, 1990). Indeed, one of the most striking adaptations of some bats is the size of their ears, which can be almost as long as their forearms (Altringham, 2003). Bats with large ears tend to forage using a technique called gleaning that involves capturing prey from vegetation or the ground (Swift, 1998). The large ears are used to passively listen (i.e. not echolocate) for prey-generated sounds (Anderson & Racey, 1991). Large ears, however, could clearly have significant energetic and aerodynamics implications,

because of their potential to produce additional drag. Chapter 2 of this thesis provided insight into the morphological trade-offs that are made between a bat's foraging success and its aerodynamics efficiency. Chapter 2 presents the first study of the aerodynamics of the large ears of *Plecotus auritus* using a simple wind-tunnel model. The primary conclusions that can be drawn from this chapter, published as Gardiner *et al.* (2008), are:

1. The large ears of the brown long-eared bat *P. auritus* produce additional lift and drag forces, which are comparable to the body weight of the bat.
2. The energetic cost of large ears may be minimised by appropriate positioning and angling of the ears relative to the incoming air.
3. Large ears of bats don't appear to have any flight control function.

From these conclusions it appears necessary that the functional morphology of the ears of many species of gleaning bat (i.e. not just *P. auritus*) should be considered from an aerodynamic as well as an auditory perspective. Indeed the findings in this study emphasise the value of testing physical models in the wind tunnel, since they allow the direct measurement of aerodynamic forces. At the same time it needs to be remembered that these results are based on a model and not on data from living bats and therefore further research is required to confirm and elucidate these initial findings. One study that supports the conclusions of Chapter 2 is Canals *et al*. (2005), which argued that bats with large ears tend to have relatively larger hearts due to the additional drag the ears produce. Chapter 2 showed the energetic cost of large ears may be minimised

through appropriate positioning. Bats, therefore, would be predicted to adjust their ear angle to match their flight speed. This hypothesis could be further tested by capturing some long-eared bats and flying them either in a wind-tunnel or a flight cage, at a variety of speeds and recording the angle at which the ears are held in flight. Further to this, typical foraging ranges of long-eared bats could be compared to species with smaller ears, through the use of radio tags (see for example O'Donnell, 2001), to investigate whether differences are detectable in the size of their foraging ranges. Studies of the foraging range of a similarly longed eared bat, the spotted bat (*Euderma Maculatum*) of North America, indicated that typical foraging ranges were under 10km (Wai-Ping & Fenton, 1989). One study, however, found that a female *E. maculatum* would consistently travel over 30km between day roost and her foraging site (Rabe *et al.*, 1998). These studies highlight that there is still a lot to learn about the relationship between the foraging ecology, morphology and physiology of long-eared gleaning bats. Additional data from further range studies of long-eared bats would put us in a better position to understand these trade-offs and also potentially, therefore, aid bat conservation efforts. The research presented in Chapter 2 also highlights that even features not typically associated with animal aerodynamics such as ears can play important roles in not only energetics but the whole ecology of a species.

The conclusions of Chapter 2 and also previous research have clearly shown that the external morphology of bats has profound implications for their locomotor performance and specifically their aerodynamics. Chapter 2 makes it clear that not only must wing morphology be considered in the flight

performance of bats, but also other external morphological features. Many of these external features are already known to correlate with other aspects of bat ecology, such as the ears and tail membrane (Fenton, 1972, Lawlor, 1973, Norberg & Rayner, 1987, Bullen & McKenzie, 2001). Which features, however, are most prevalent in distinguishing between foraging strategies, and how variation in those features influence flight energetics, was unclear. Chapter 3, therefore, was designed to identify key features of bat morphology that are correlated with foraging behaviour and flight style. Using anatomical data collected from museum skins and modelling of aerodynamic power curves led to the conclusions of the paper Gardiner *et al.* (2011a), presented in Chapter 3, that:

1. The length of ears and tail membranes is well correlated with bat foraging strategies.
    a. Gleaning bats have the longest ears.
    b. Commuting bats have the shortest tails.
2. Tail membranes are likely to be an important feature for flight control. The energetic consequences, however, are hard to quantify, but the length of the membrane is likely to be a trade-off between flight/foraging performance and energetic cost.
3. Large ears are an additional flight cost for bats at higher speeds. At lower speeds the cost is much smaller and the ears are likely to provide an improved foraging performance for gleaners.

Chapter 3 demonstrates that the relationship between a bat's morphology, their locomotion and their energetic cost is complicated and highlights some of

the failings in current models of the energetics of vertebrate flight. Although Pennycuick's model (1968) has been used in many studies to help provide explanations for the flights speeds and behaviours observed in the field, it struggles to deal with the finer intricacies of aerodynamics and therefore can only be used to clarify broad hypotheses and questions. For example, Pennycuick's model (1968) was helpful in Chapter 3 for providing ecological hypotheses based on the findings that both ear length and tail length are highly variable between bat foraging groups. Nevertheless, it is hard to derive concrete conclusions based on the model. Field-work and further modelling, therefore, is required to elucidate the findings presented. In particular there is difficulty in identifying the costs associated with tail membranes due to differences in the two forms of the induced power equation (see Chapter 3, equations 1a and 1b). A study of tail streamers in hummingbirds (Clark & Dudley, 2009) showed that the long tail streamers (which are sexually selected for) increase the metabolic cost of flight in these birds. Interestingly, however, removing the tail feathers also slightly increased flight cost, possibly because a normal tail can decrease body drag (Clark & Dudley, 2009). A similar study in bats would be difficult since skin is a living tissue, whereas feathers are dead beyond their base. A modelling approach does not suffer this problem and can help clarify some of the details of bat tail membrane aerodynamics.

The tail membrane of bats has been highlighted in Chapter 3 as a morphological feature that is highly variable between species and potentially important for flight control. Several other studies have suggested that the tail membrane may have an aerodynamic function (Vaughan, 1970, Lawlor, 1973,

Norberg, 1990, Bullen & McKenzie, 2001). It should, therefore, come as no surprise that the tail membrane of bats may be important for flight, particularly since the aerodynamic function of bird tails has frequently been researched and hotly debated (Thomas, 1993, Norberg, 1994, Thomas, 1996, Evans & Thomas, 1997, Maybury & Rayner, 2001, Maybury *et al.*, 2001, Evans *et al.*, 2002, Evans, 2003). Somewhat surprisingly similar studies into the aerodynamics of tail membranes had not been undertaken. Chapter 4, therefore, attempted to address this gap in our understanding of bat flight using a physical wind tunnel model similar to that used in the study described in Chapter 2. The model was designed so that adjustments in the leg position moved not only the tail membrane but also changed the camber of the inner surface of the wing, since the tail membrane is in effect a continuation of the wing surface and not a separate aerodynamic surface. The main conclusions of the paper Gardiner *et al.* (2011b) presented in Chapter 4 were:

1. The tail membrane is useful for controlling the pitching moment generated by the bat model, via adjustments of leg position.
2. The tail membrane doesn't appear to be important for lift generation.
3. Adjustments in leg position also increase the camber of the inner wing surface, which in turn increases lift production.
4. Tail membranes may decrease the drag produced by the bat's body.

This demonstrates that the tail membrane is potentially critical to the flight performance of bats. The model in Chapter 4 (and Chapter 2) was based on the

gleaning bat *P. aurit*us in forward flight. Studies of *P. auritus* in forward flight show that the tail membrane tends to move in phase with the wings of the bat (Norberg, 1976a), suggesting that the tail is an active aerodynamic surface. This hypothesis is further supported when the tail synchrony of *P. auritus* in forward flight is compared to the synchrony in hovering flight. In hovering flight in contrast to forward flight the tail flaps out of phase with the wings (Norberg, 1976b) suggesting perhaps a change in function for the tail membrane between forward flight and hovering. Video and PIV studies of bats with large tail membranes in forward flight and hovering, would allow any distinctions in the aerodynamics and therefore function to be found.

A key question in the evolution of the tail membrane of bats is whether its primary function it to aid flight or to aid the capture of insects, by being used as a capturing pouch in flight (Webster & Griffin, 1962). In Chapter 4 it was shown that bat tail membranes are likely to be important for flight control. Why some species lack tail membranes is difficult to interpret and without further studies on both the aerodynamics and ecological importance of the bat tail, possible answers to this question are speculative. For example, it was suggested that some species lack tail membranes because of roosting habits (Vaughan, 1970). From an evolutionary perspective a key way of assessing which function may have developed first is to consider a step-by-step transition. Indeed, if one asks what benefit a gradual increase in tail membrane size would be for both insect capture and flight, the answer would tend to come out in favour of flight. A small tail membrane would not form a sufficiently sized pouch to aid insect capture but would nevertheless still form an active aerodynamic surface. Indeed, bats which

do not feed on insects and would have no use for the tail membrane to capture insects, often stiff have a tail membrane, albeit typically reduced in size. Even the large old world fruit bats (commonly called the megabats) often have thin flaps of skin behind the legs and body possibly to help reduce drag. Further modelling of bat tails in the wind tunnel would potentially help to clear up this evolutionary question, since the aerodynamic function of a gradual increase in the size of a tail membrane could be investigated.

Leg position plays a critical role in the positioning of the tail membrane and the level of camber on the inner wing surface, both of which potentially strongly influence the aerodynamics of bat flight as shown by the model in Chapter 4. It would, therefore, be extremely valuable to study whether bats actually manipulate their leg position during flight, as the wind tunnel model results suggest this would be aerodynamically beneficial. Studies of bats in flight show that they constantly move their legs in synchrony with the wings (Norberg, 1976a) . It is not clear, however, whether these leg movements are passive due to the legs being connected to the arm via the wing membrane or active and controlling the tension, and camber of the wing membrane. Electromyography (EMG) implants in the leg muscles of a large bat species would provide data on muscle activity and could be recorded in synchrony with flight footage to help understand whether bats are using their legs muscles in flight. Furthermore, if the leg muscles are active in flight, the data would illuminate which part of the wing-stroke each leg muscle is synchronised with and provided valuable data to advance our understanding of bat aerodynamics. A similar method was used by Swartz *et al.* (1992) to record the strain on bat arm bones in flight.

It is obvious that a huge amount of bat morphology is influenced by their requirement to fly. Bats, however, don't only fly but also crawl, climb and jump, but little research has investigated this aspect of bat locomotion. Many bat species have been recorded as being able to jump off the ground to get back into the air. Indeed, a few species have been documented as being extremely proficient at terrestrial locomotion, such as *Desmodus rotundus* (Altenbach, 1979, Schutt *et al.*, 1997). Terrestrial and aerial locomotion, however, place a bat's body under very different evolutionary pressures and therefore trade-offs between the morphological requirements for the two forms of locomotion are bound to exist. For example the hind legs have been shown in Chapter 4 to be potentially important for controlling bat aerodynamics, but legs are also clearly essential for terrestrial locomotion and jumping. Little research, however, has investigated terrestrial locomotion and jumping in bats. In general research into the terrestrial locomotion of animals is well established. In particular the research of jumping behaviour has received a lot of attention (see for example Alexander (2003) for an overview), since a jump is a single discrete event, which is more easily measured and comparisons across species and ontogeny are simpler to make. The study in Chapter 5 was, therefore, designed to further our understanding of the jumping performance of bats and how this related to their foraging strategies. Video footage of several bat species jumping for a illuminated platform back into flight was digitised and analysed. The analysis led to the key findings of chapter 5, which were published in Gardiner & Nudds (2011), that:

1. No ecological trend can be found in the jump performance of the bats studied (i.e. no correlation of foraging strategy with the jump performance parameters could be identified).
2. Larger bats outperform smaller bats in absolute terms (i.e. jump height, take-off speed etc).
3. Flight so dominates bat locomotor morphology that secondary locomotor behaviour, such as jumping, tend to be derivative.

The results presented in Chapter 5 support the broad conclusion that flight is so strongly selected for in bats, that other forms of locomotion tend to be derivative (i.e. bats ability to crawl and jump is limited by the extreme demands that flight places on their morphology). Jumping behaviour in bats relies on the powerful flight musculature and long forearms to propel them into the air. Any selection pressures on wing morphology related to the gleaning bat foraging style, which involves spending substantial time on the ground, tend to be overshadowed by the enormous requirements that flight places on the bats. In a few very unique cases, like the vampire bat *Desmodus rotundus*, a frequent and unusual ground foraging behaviour has resulted in better terrestrial performance than other similarly sized bats (Altenbach, 1979, Schutt *et al.*, 1997). In the majority of bats, however, the selection pressures for a ground take-off are not large enough to produce quantifiable differences between bats. Indeed, due to the amazing plasticity in bat foraging behaviour, both generalist diets and generalist morphology seem to prevail. The statistical analysis in Chapter 3 supports this conclusion since large areas of overlap are seen between the foraging groups.

This highlights the fact that placing individual bat species into ecological, morphological or locomotor groups is a difficult task, since they are remarkably versatile and opportunistic mammals.

This thesis has examined the question "How does the morphology of gleaning bats constrain their locomotor performance?". Although the work has provided information on the form and function of a number of aspects of gleaning bat morphology, it has generated many more questions and areas for future research. Trade-offs are evident between the morphology of gleaning bats and their locomotion. Chapters 2, 3 and 4 demonstrate that the ears and tail membranes of bats are clearly linked to their foraging strategy and aerodynamic performance. Furthermore, whilst both large ears and a large tail membrane are likely to boost foraging success through improved low frequency sound detection and improved flight manoeuvrability, they also impose additional energetic costs on the bats. Ears are an additional drag cost and potentially limit the bats flight speed and foraging range. Tails are likely to be a hindrance in other forms of locomotion such as arboreal climbing or terrestrial walking. The effect of tails on flight costs is much harder to clarify than ears and requires further work before a clearer picture emerges. Finally, Chapter 5 investigated whether a key feature of gleaning bat behaviour (more time spent foraging on or near the ground compared to other bat groups) affected their locomotor performance (in this case jumping back into flight). It was clear from Chapter 5, however, that all the bats studied had comparable jump performance regardless of foraging preference and no ecological/foraging bias could be detected. Flight so dominates bat shoulder and forearm morphology, and musculature in bats that other forms of locomotion

(i.e. jumping) appear to be derivative. In other words, whilst some trade-offs between the morphology of gleaning bats and their locomotor performance can be detected (i.e. the costs of benefits of larges ears and tail membranes), in other areas flight is so strongly selected for that other ecological pressures on morphology are difficult to detect.

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