Flying heavy: the effect of variation in body mass on flight performance in bats

Ph.D. Dissertation proposal

INTRODUCTION

Most mammals, including chiropterans, experience daily and seasonal variations in body mass. Seasonal variations are related to seasonal changes in the environment and/or due to reproductive periods. Bats respond to changes in biotic (e.g., food abundance) and abiotic factors (e.g., temperature, light) by modifying their body mass. Numerous species have been documented to hibernate during winter periods. Preparation for hibernation involves the accumulation of fat reserves during autumn, prior to the onset of food shortage, which is believed to provide the almost exclusive source of energy during the extended winter fast (Kunz et al., 1998). Besides sustaining hibernation, some accumulated fat must sustain mating activities during autumn and winter, and in females, support ovulation at the end of hibernation (Buchanan, 1987; Kunz et al., 1998). Indirect evidence suggests that the amount of fat stored during autumn affects annual survival and fecundity, requiring a minimum value to successfully undergo hibernation (see references in Kunz et al., 1998). In some bats, the increment in body mass prior to hibernation, in both males and females, can be greater than the body mass of pregnant females (Barclay and Harder, 2003). For example, in *Myotis lucifugus*, males and females increase their body mass approximately 30% in preparation for hibernation.

During reproductive periods, bats considerably increase their body mass as well. Bats generally produce large individual neonates compared to most terrestrial mammals of similar size, typically 20-30% of post-partum mother’s body mass (Kurta and Kunz, 1987), and they have relatively long gestation periods (from 40 days to 5-6 months; (Altringham, 1996; Kurta and Kunz, 1987; Racey, 1973). Therefore, large increases in body mass are often associated with pregnancy in bats. After parturition, bats reduce their body mass significantly, but females during lactation may surpass the body mass that at the start of pregnancy as well (Speakman and Racey, 1987).

Body mass and flight performance

It has been widely assumed that changes in body mass affect flight performance, but actual studies supporting such a statement are rather limited. Some theoretical models predict how differences in body mass and size could affect flight performance. These models are derived from conventional aerodynamic theory assuming that flying animals are similar to fixed-wing aircrafts. They have provided a starting point for animal flight studies, but the morphological, physiological and behavioral complexity of actual biological systems requires a more sophisticated treatment.

Early models tried to evaluate how changes in size would affect different aspects of flight (Andersson and Norberg, 1981; Pennycuick, 1989). Later developments included analyses of consequences of fuel accumulation in birds (e.g., body mass increase due to fat accumulation without changes in wing morphology) could change flight performance (Hedenström, 1992). Based on these studies, increments in body mass such as those observed in bats would reduce maneuverability, increasing the minimum turning radius and reducing the maximum acceleration in the roll plane. Also, changes in body mass should reduce maximum forward velocity, acceleration, and therefore the ability to outclimb predators (Hedenström, 1992).

Some empirical studies have tried to test predictions derived from these models, particularly take-off parameters in birds, but no clear pattern has emerged. A number of studies have shown that some aspects of flight thought to be critical to escape from predators may be impaired by an increase in body mass (Kullberg et al., 1996; Kullberg et al., 2002; Lee et al., 1996; Marden, 1987; Metcalfe and Ure, 1995; Witter et al., 1994), while others have failed to find a mass-dependent effect on performance (Kullberg, 1998; Van der Veen and Lindström, 2000; Veasey et al., 1998). These contradictory findings seem to indicate that “flying animals are more than just physics”, and that behavioral modifications could be important (Van der Veen and Lindström, 2000). Most of these studies evaluate the effect of change in body mass on escape performance assuming that animals are functioning at their maximum capacity. Thus, any increment in body mass would impose an increased cost on the required mechanical output and consequently a reduction in escape performance. There is no evidence, however, for the assumption of maximum-performance. On the contrary, it has been observed in some organisms the use of sub-maximal speeds during escapes, which has been explained as a mechanism to keep an ‘extra’ locomotor capacity for rare, power-consuming activities (e.g., jumpings, maneuvers) (Irschick and Jayne, 1999). This excess capacity could be used when body mass is increased in order to maintain a constant performance. Mechanical power required for hovering, for example, remains constant in hummingbirds living at different altitudes, contrary to predictions of aerodynamic theory. This is achieved by modifications of their wingbeat frequency and amplitude. Excess mechanical power, however, is reduced at higher altitudes and probably limiting costly activities as vertical ascend or maneuverability (Altshuler et al., 2004).

Far more information exists about how body mass affects flight performance for birds than for bats. Usually the information gathered in avian studies has been applied to bats uncritically. Only a single study has evaluated the effect of differences in body mass on flight performance (Hughes and Rayner, 1991). Bats with naturally or artificially increased body mass of up to 46% flew more slowly, in contrast to expectations derived from aerodynamic theory, and employed higher wingbeat frequencies during short straight flights. As wingbeat frequency and flight speed are negatively correlated (Bullen and McKenzie, 2002), the observed changes in wing kinematics could be simply a product of a slower flight. It is possible that birds and bats respond in similar ways because of the physical constraints of flight. However, flight in these two groups differs in several respects. Birds maintain relatively stiff wings when flying, but bats have very structurally complex and flexible wings, that can be actively modulated during flight (Swartz et al., 2003). Whether or not bats are affected by changes in body mass in the same way as birds is not known. However, testing ideas derived from bird experimentation can be heuristically useful to start to understand how flight works in bats, how different factors affect performance, and how these changes can affect the ecology of bats.

OBJECTIVES

The specific purpose of the present thesis is to evaluate from a biomechanical perspective how variations in body mass affect flight performance in bats and how these variations might reflect in several aspects of bat ecology, like foraging behavior or habitat use. Flight performance will be used in a broad sense that includes characteristics of steady (e.g., forward velocity) and unsteady flight (e.g., turning), although most of the work will be focused on the turning capabilities of bats. Thus, three main questions will be addressed in this thesis: 1. what are the behavioral compensations, if any, to changes in body mass during forward flight, 2. what is the effect of increased body mass on turning behavior, and 3. what is the mechanics of turning flight and how this relates to changes in body mass.

EXPERIMENTS

1. Body mass effect on forward flight kinematics

For an animal flying steadily, any increment of body mass implies an increased generation of lift to counteract the added weight. This extra lift must be produced by behavioral modification of wing shape and/or through changes in wing kinematics. Little information on how wing function is modulated to cope with changes in body mass exists, but the available data does not indicate a clear pattern. On one hand, kestrels trained to fly carrying lead masses attached to their feet, of up to 30% of their body mass, fly at slower velocities and with higher wing beat frequencies and amplitudes (Videler et al., 1988). Some bats tend to show similar patterns. When carrying natural and artificial loads of up to 46% body mass, *Plecotus auritus* also reduces its flight forward velocity and increases wing beat frequency (Hughes and Rayner, 1991). Under certain experimental conditions, however, some nectar-feeding bats increase their flight speed with gains of body mass (Winter, 1999). Cockatiels, on the other hand, tend to respond differently depending of the amount of body mass increment, with decreased flight speed at intermediate loads and normal speed and high wing beat frequency at the highest load (20% body mass) (Hambly et al., 2004). As flying speed is also modified, any change in wing kinematics cannot be unequivocally assumed to be a kinematic response to changes in body mass. It has been shown for numerous mega- and microchiropterans that wingbeat frequency decreases and amplitude increases with flight speed (Bullen and McKenzie, 2002). Wingbeat frequency remains almost constant at high flight speeds but increases sharply as speed decreases. If this pattern is true for other species, an increased wingbeat frequency could be explained by the reduction in flight speed, but cannot be resolved if there is any change produced by changes in body mass.

Methodology

I will perform kinematic analyses of bats flying in a wind tunnel to control for flight speed. Bats will be flown under at least two body mass conditions: control (normal body mass) and increased body mass. Increased body mass can be achieved artificially, with external ‘backpack’, and naturally, by overfeeding the animals. Each method has its strengths and weakness. By overfeeding the animals, the added weight is distributed in a natural way throughout the body. If any change on the center of mass occurs, it can be assumed that the mass distribution is similar to what is found in wild bats after a meal. A problem with this method is that the amount of food ingested cannot be controlled. With artificial loads, it is easy to control the amount of increment of weight that is applied to the bat, but we risk modifying the bat’s center of mass and its normal performance. In addition, bats can be non-cooperative with artificial loads added onto them and try to remove them. Another alternative to ‘backpacks’ is injecting individuals with an intraperitoneal saline solution to the desired mass. It is not expected that this methodology will affect the distribution of mass of the bats in any unnatural way, since the density of water and food is similar. Thus, an artificially ‘inflated’ abdomen should not be very different from an abdomen of a recently fed bat. Intraperitoneal injections have been used in birds (Witter et al., 1994) and rodents (unpublished results) without notorious manifestations of discomfort. Moreover, resting metabolic rate was measured in experimental rodents, before and after the injection. Elevated resting metabolic rates are used as indicators of discomfort and stress in animals, but experimental animals did not show changes in resting metabolic rate with the injection (unpublished results). This methodology allows immediate and precise increase of body mass. In rodents, the added mass remains constant for about four hours and the experimental subject returns to its original body mass within 24 hours. These times would be probably lower in bats considering their high rates of food processing.

To choose at what speeds the bats will be flown in the wind tunnel, the same bats will be also trained to fly in a corridor under the same body mass treatments (normal and loaded). This will allow to determine the preferred speed for each treatment. Thus, these speeds will be used in the wind tunnel experiments so that a particular bat will fly in four conditions in a factorial experiment: loaded/unloaded, preferred speed loaded/preferred speed unloaded.

2. Body mass effects on turning behavior

Aerodynamic theory predicts that turning radius increases with increments in body mass. As previously indicated, bats suffer important daily and seasonal changes in mass. The effect of these changes on maneuverability for bats that live in spatially complex environments could be very important for their flying and foraging behavior. Studies have shown a weak, but significant, relationship between microhabitat use (open vs cluttered), maneuverability and wing loading (Aldridge and Rautenbach, 1987; Kalcounis and Brigham, 1995; but see Stockwell, 2001). Although indirect, this might be considered evidence of a relationship between body mass and turning abilities. No study has examined how individual variation in mass affects maneuverability in bats.

Methodology

To evaluate how body weight affects flight abilities in bats I propose a series of experiments using natural and artificial modifications of mass. Flight performance[1] is going to be measured pre- and post-feeding event. This would allow me to compare the effect of an increment of body mass on wing kinematic parameters. Initially, the experiments are designed to be carried out with the nectar-feeding bat *Glossophaga soricina* (Glossophaginae: Phyllostomidae), a 10-g bat that hovers to obtain the nectar from flowers. This particular bat is very suitable for this kind of experiments as *G.*

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[1] The particular performance will be dependent of the species of bat finally used. See below for discussion.

soricina is able to consume up to 150% of its body mass in nectar during the night (Winter and Von Helversen, 1998). Although nectar is processed quickly there is a gradual increase of at least 10-15% in body mass and up to 30% throughout the night (Winter, 1999; Winter and Von Helversen, 1998). Also, there is relatively large amount of information about ecology, physiology and behavior (Voigt, 2003; Voigt and Winter, 1999; Winter, 1998; Winter, 1999; Winter et al., 1998; Winter and Von Helversen, 1998) that enables to put biomechanical and aerodynamical findings in context.

Performance will be measured as the ability of the bat to catch a prey in air. *G. soricina*, in the field, obtains most of its protein from arthropods, implying that this bat has to actively pursue prey (Herrera et al., 2001). It is theoretically possible to train this bat to catch flying insects to get its dose of protein. An experimental individual could be placed in a closed acrylic container (or other material) with a standard amount of fruit flies. The subject would have to fly and chase the flies, an event that could be filmed. At least 2 high-speed cameras would be placed in lateral and dorsal view to reconstruct the 3D flight trajectory. If animals cannot be trained to catch flies ‘on command’, normal cameras could be potentially used if the body velocities are not too high. This protocol has been used for hummingbirds needing to supplement their nectar-based alimentation with protein obtained from flies catch on air (López-Calleja et al., 2003). Although these experiments were used to determined time budgets, the same kind of protocol could be co-opted for my experiments.

In case that this experiment cannot be carried out with *G. soricina*, *Eptesicus fuscus* could be used alternatively. *E. fuscus* can be trained to capture mealworms hanging from a thin filament. To be able to estimate flight performance in this case, a device would be built to generate a pseudo-random movement of the mealworm. A rotating disk is an alternative that could be used to increase the difficulty of catching the mealworm. Another option is to increase the spatial complexity around the mealworm so the bat has to sort the obstacles to get to it. Due to the reduced ability to control the bat's path in this kind of experiment, a camcorder would be used instead of high-speed cameras. Camcorders have the advantage of allowing more filming time, although sacrificing temporal resolution, with a maximum speed of 60 fps. Because of that, only whole-body kinematics are planned to be obtained (i.e., flying speed, turning radius, angular velocities depending of the quality of the videos).

3. Mechanics of turning flight

Many bats inhabit and forage in cluttered environments, and many bats actively pursue prey. This is the case for numerous insectivorous species, where the agile and unpredictable movements of their prey likely impose strong selection on the ability to alter direction and speed of flight. Successful foraging, in particular in cluttered environments, is not solely dependent on flying abilities. Vision and echolocation in mega- and microchiropterans respectively, also influence performance during hunting or traveling in cluttered environments. The relative importance of these factors for the ecology of bats is unknown, but it is reasonable to assume that flight abilities play an important role in survivorship.

Maneuverability is generally understood as the ability to change flight direction. Norberg and Rayner (1987) distinguish between *maneuverability* and *agility*, a distinction that has mechanical implications for the measurement of performance. *Meneuverability* is defined as the ability to alter the flight path while keeping a constant flying speed, measuring the amount of space required to turn effectively. *Agility* is defined as the maximum roll acceleration during the initiation of a turn, measuring the rapidity with which the flight path can be altered (Norberg and Rayner, 1987).

Studies of bird and bat maneuvering have been restricted to analyses using steady-state (i.e., fixed-wing) aerodynamics (Aldridge, 1987; Norberg and Rayner, 1987; Norberg, 2002). By equating the centripetal force needed to produce the curved path with the lift force, maneuverability (or its analogous, turning radius, *r*) is defined solely by wing loading ($M_\mathrm{b}S^{-1}$)

$$M_b V_b^2 r^{-1} = \frac{1}{2} V_w^2 S \rho C_L \sin\theta$$

$$r = \frac{2M_b}{\sin\theta S \rho C_L}$$

$$r \propto M_b S^{-1}$$

where θ is the bank angle, ρ is the density of air, C_L is the dimensionless coefficient of lift, S is the area of the wing, M_b is the body mass of the organism, V_w is the incident velocity of the air over the wings and V_b is the velocity of the organism's center of mass. This equation represents the turning radius of a fixed-wing model (e.g., an airplane) assuming that V_w and V_b are equal. This equation is useful to analyze turning maneuvers of gliding organisms, but most flying animals perform using highly non-steady dynamics and usually violate the assumptions of steady-state equations. The consequences of assuming steady-state conditions in performance analyses have not been established.

Regardless, predictions derived from steady-state models have been applied extensively in the bird and bat research communities, particularly when looking for morphological correlates of turning performance and their ecological implications (Aldridge, 1986; Bullen and McKenzie, 2001; Kalcounis and Brigham, 1995; Norberg and Rayner, 1987).

Recent information on maneuvering flight of birds (Warrick et al., 2002; Warrick and Dial, 1998; Warrick et al., 1998) and insects (Fry et al., 2003) has expanded the discussion beyond wing shape, indicating the importance of temporal sequences of wing movements that must be analyzed to understand the mechanical basis of turning behavior. The fundamental mechanism to initiate a turn and maneuver is to introduce an aerodynamic force asymmetry along the wingspan. This asymmetry can be achieved by at least four ways; this list is by no means exhaustive, but represents the most widely cited explanations of the mechanics of turning flight:

i) differential flexion of the shoulder and/or elbow joint. This produces a difference in the surface area projected parallel to the airflow, therefore varying the amount of lift generated by the left and right airfoils.

ii) differential pronation/supination of part of the wings. This creates a difference in the angle of attack between the wings and hence the coefficients of lift. An extreme case would be one wing at a negative angle of attack while the other is at a positive angle of attack.

iii) stalling one wing. Extreme supination/pronation would bring the wing beyond the critical angle of attack, producing a large increase in drag and loss of lift for that wing.

iv) increasing the camber on the outside wing. This will produce a difference in lift, as in i) and ii).

To create a banked turn, a gliding animal must produce at least one force asymmetry event to produce the bank and a second to stop it. In flapping flight, however, force production is temporally discontinuous, and it is believed that aerodynamic force is produced mostly during downstroke, at least during slow flight, so other mechanisms could operate. Flying through an obstacle course, pigeons produce several muscular force asymmetries in each wingbeat cycle (Warrick et al., 1998). Kinematically, a rolling moment is produced by higher downstroke velocity in the outer wing at the beginning of the wingbeat cycle, and this moment is arrested by higher downstroke velocity of the inner wing later in the wingbeat cycle (Warrick and Dial, 1998). Most of the time, the banking moment and the arresting force asymmetry were produce during the same downstroke, but asymmetries in upstroke velocities were also observed. Thus, the asymmetry in force production is discontinuous during slow turning maneuvering, with discrete changes in directions throughout the turn (one change per wing beat) (Warrick and Dial, 1998).

There is little information about the kinematics and aerodynamics of turning behavior in bats. Aldridge (1987) studied the turning behavior of several species of microchiropterans of different sizes. Coefficients of lift were estimated during turns from basic kinematic measurements suggesting that turns in these species were glided, without flapping support, except for the biggest species studied. Aldridge (1987), however, does not give any direct information about kinematics of turning flight.

The aim of this study is to describe the wingbeat kinematics of slow turning maneuvering in a species of bat while making a 90-degree turn to evaluate the aerodynamical basis of maneuverability in bats.

PRELIMINARY DATA

Material and Methods

Three female lesser short-nosed bats, *Cynopterus brachiotis*, were trained to fly in an L-shaped flight corridor making a 90-degree turn midway in each flight. The total flight distance was approximately 5 meters. Reflective markers were placed on both wings (wingtip, thumb, and tip of the 5th distal phalanx) and on the body (hip, right and left chest) and were recorded with three synchronized high-speed video cameras to reconstruct the three-dimensional kinematics of the wing. Bats were allowed to make either a right or a left turn.

Results and discussion

So far, data from two individuals have been analyzed. The wingtip kinematics is highly repeatable among trials and among individuals. Turning in bats is discontinuous, where the flight path is straight with sudden changes of direction associated with wingbeat events. Analysis of the wingtip kinematics shows a complicated wingbeat with an asymmetry in the timing of the downstroke and upstroke between the wings. Both wings are synchronized at the beginning of the downstroke, but the inner wing starts the upstroke earlier than the outer wing. At the end of the upstroke, both wings synchronize again (Figure 1a). This asynchrony is the result of the rolling of the body during the wingbeat sequence; the rolling angle increases during the first part of downstroke and decreases during the second part of downstroke and the initial part of upstroke (Figure 2). When the coordinate system is switched to a dynamic system centered on the hip of the bat, with the horizontal plane defined by the three body markers, the kinematic pattern of the wingtips becomes symmetrical (Figure 1b). The yaw of the body, measured by the heading angle, changes primarily during the synchronous upstroke (Figure 3a), but the actual displacement of the center of mass is temporally delayed compared to the change in heading angle (Figure 3b). This can be understood as the inertial resistance of the body to change direction, i.e., the body changes its angle but continues to move in the same direction momentarily. This suggests that bats redirect the position of the body first and therefore the force vectors are positioned to make the turn.

To evaluate possible mechanistic causes of change in direction, multiple regression analyses were performed between several parameters characterizing the difference in wing position between left and right wing and the change in heading angle. Results varied for upstroke and for downstroke. For downstroke, differences in wing down and forward velocities, measured as angular velocities, account for ca. 95% of variation in heading angle. On the other hand, during upstroke differences in folding of the wing and vertical positioning explained between 85 and 99% of variation in heading angle. These values were obtained for one individual and more trials and 3 more individuals remain to be analyzed. New parameters are also going to be analyzed.

A strong correlation was found between the change in heading angle and the change in pitching angle (r = -0.94 to -0.98). When the body of the bat pitched up, it also turned to the side (Figure 4). A possible explanation could be that the increment in pitching results in a decrease in rotational inertia of the body, which allows the bat to turn more easily.

Future directions

Body and wing kinematics for the same bats with increased body mass. As bats are allowed to choose their preferred flight speed, these changes in body mass will allow to evaluate overall changes in turning behavior (e.g., flight speed, turning radio). But also bats can be motivated to flight at higher speeds allowing to analyze specific changes in body and wing kinematics to produce enough lift and thrust in loaded conditions.

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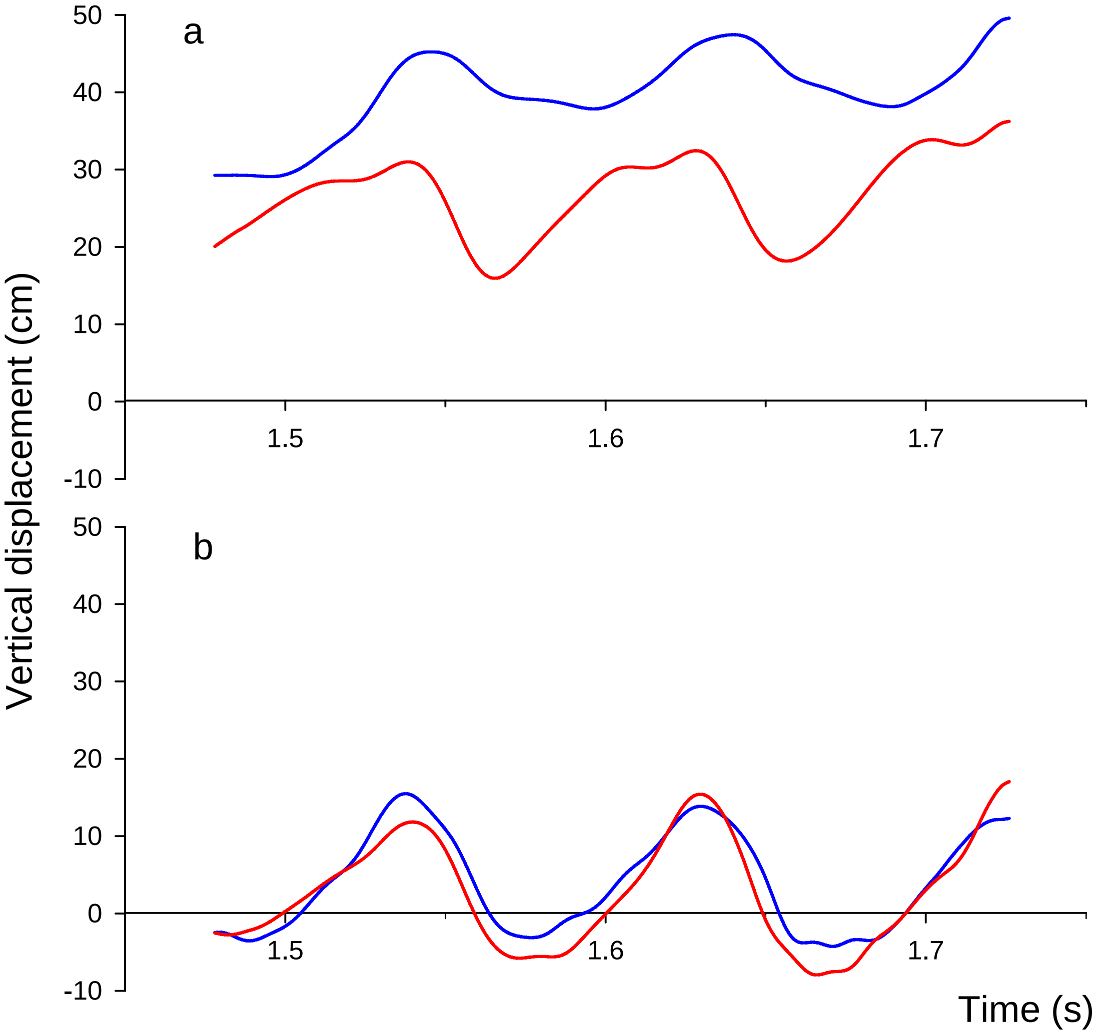
Figure 1. Vertical displacement of the wingtip, from a) a fixed global coordinate system and from b) a dynamic coordinate system with origin at the hip of the bat. Red line corresponds to the inner wing and the blue line, the outer wing.



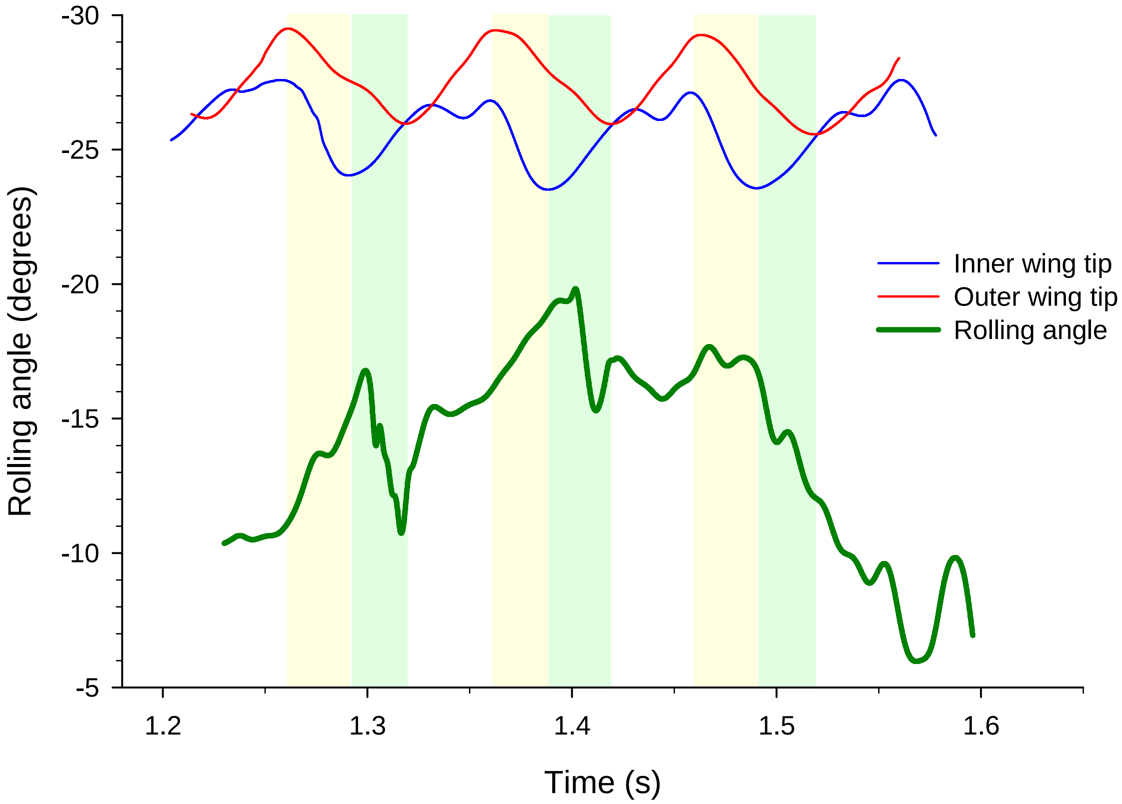


Figure 2. Rolling angle (angle between the horizontal plane and the plane of the body) for a representative trial. The blue and red line represent the vertical displacement of the wing tips to indicate the different parts of the wingbeat. The yellow shadow correspond when to both wing in downstroke; the green shadow, when the inner wing is in downstroke and the outer wing is still in downstroke; and the white shadow, when both wing are in upstroke.

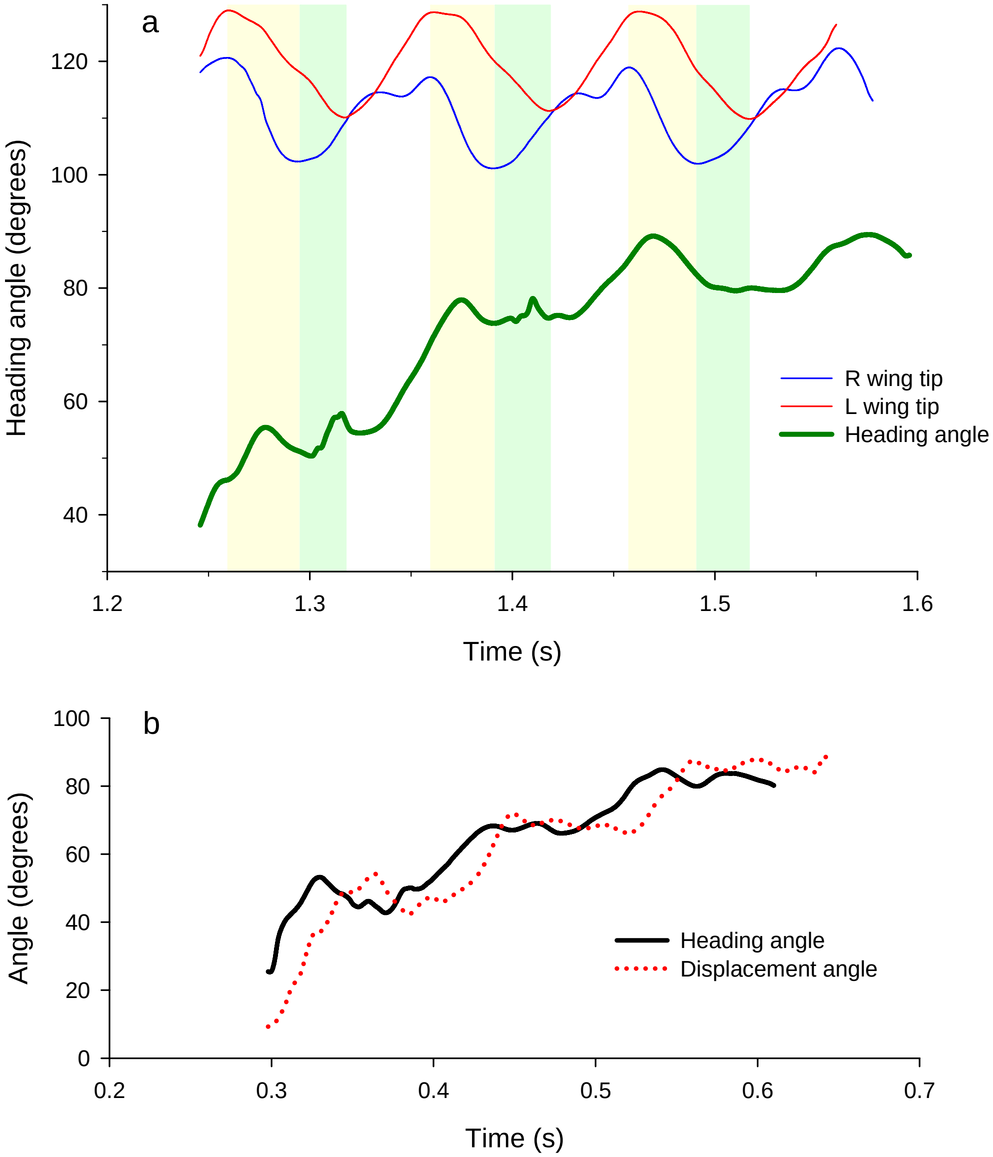


Figure 3. (a) Heading angle for a representative trial. Lines and areas as in Figure 2. (b) Heading angle and displacement angle for a representative trial.

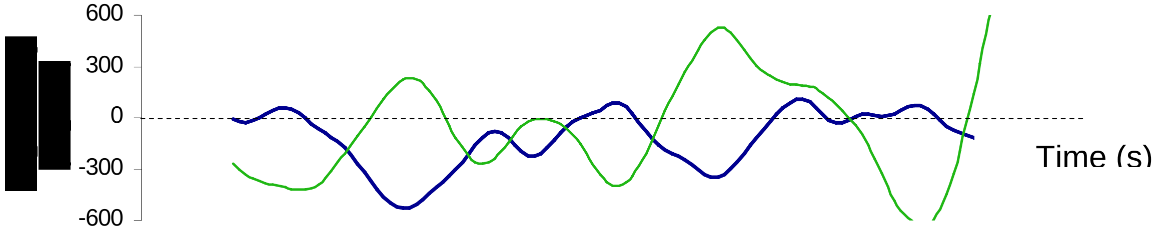

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Figure 4. Change in heading and pitch angle (measured as angular velocities). Green line corresponds to the change in pitching angle and the blue line, the change in heading angle.