

Wing morphology and flight development in the short-nosed fruit bat *Cynopterus sphinx*

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Received 3 July 2006; received in revised form 4 February 2007; accepted 6 February 2007

Abstract

Postnatal changes in wing morphology, flight development and aerodynamics were studied in captive free-flying short-nosed fruit bats, *Cynopterus sphinx*. Pups were reluctant to move until 25 days of age and started fluttering at the mean age of 40 days. The wingspan and wing area increased linearly until 45 days of age by which time the young bats exhibited clumsy flight with gentle turns. At birth, *C. sphinx* had less-developed handwings compared to armwings; however, the handwing developed faster than the armwing during the postnatal period. Young bats achieved sustained flight at 55 days of age. Wing loading decreased linearly until 35 days of age and thereafter increased to a maximum of 12.82 N m^{-2} at 125 days of age. The logistic equation fitted the postnatal changes in wingspan and wing area better than the Gompertz and von Bertalanffy equations. The predicted minimum power speed (V_{mp}) and maximum range speed (V_{mr}) decreased until the onset of flight and thereafter the V_{mp} and V_{mr} increased linearly and approached 96.2% and 96.4%, respectively, of the speed of postpartum females at the age of 125 days. The requirement of minimum flight power (P_{mp}) and maximum range power (P_{mr}) increased until 85 days of age and thereafter stabilised. The minimum theoretical radius of banked turn (r_{min}) decreased until 35 days of age and thereafter increased linearly and attained 86.5% of the r_{min} of postpartum females at the age of 125 days.

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Keywords: Flight performance; Wing loading; Growth curves; Logistic equation; Pteropodid bats

Introduction

Morphological parameters of bats constrain the use of different habitats. Wing morphology of flying animals and habitat use are interrelated (Aldridge and

Rautenbach, 1987; Norberg and Rayner, 1987; Block et al., 1991; Landmann and Winding, 1993; Bogdanowicz et al., 1999; Rhodes, 2002; Jennings et al., 2004). The association between wing morphology of bats and their habitat use has been inferred using aerodynamic theory (Norberg, 1985; Fullard et al., 1991), and habitat use of bats has been correlated with wing morphology without examining flight performance (McKenzie and Rolfe, 1986; Crome and Richards, 1988). In microchiropteran bats, the ontogeny of flight is associated with the development of echolocation (Buchler, 1980; Brown

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et al., 1983; Rother and Schmidt, 1985; RübSamen, 1987). The development of vocal sound and the mother–infant relationship is also related to the development of flight (Barclay et al., 1979; Brown et al., 1983; Gelfaud and McCracken, 1986; Habersetzer and Marimuthu, 1986; Jones et al., 1991).

Wing morphology and flight behaviour during post-natal growth have been studied in several species of microchiropteran bats such as *Myotis lucifugus* (Buchler, 1980), *Artibeus jamaicensis* (Taft and Handley, 1991), *Pipistrellus pipistrellus* (Hughes et al., 1995), *Phoniscus papuensis* (Rhodes, 1995), *Phyllostomus hastatus* (Stern et al., 1997) and *P. mimus* (Isaac and Marimuthu, 1997). Few studies simultaneously investigated flight behaviour, wing morphology, muscle biochemistry and flight physiology of bats (Carpenter, 1985; Powers et al., 1991). Wing loading is highly correlated with body mass and wing dimensions are used to predict foraging habits (Norberg and Rayner, 1987; Norberg, 1990) and habitats (Kalcounis and Brigham, 1995). Changes in body mass may dramatically affect the flight capability of bats. Increase in body mass, and thus wing loading, results in decreased flight manoeuvrability (Aldridge, 1987; Norberg and Rayner, 1987; Aldridge and Brigham, 1988) and an increase in energy costs (Hughes and Rayner, 1991). Several studies have been carried out on the relationship among aerodynamics, wing shape and flight mode (e.g. Penny-cuick, 1975, 1989; Norberg and Rayner, 1987; Rayner, 1988; Norberg, 1990).

The growth patterns of bats have been evaluated using different growth models on a few species of bats such as *Tadarida brasiliensis* (Kunz and Robson, 1995), *Plecotus auritus* (McLean and Speakman, 2000) and *M. nattereri* (Swift, 2001). The non-linear growth equations give the best fit for the postnatal growth data. Most of the studies mentioned above have been conducted on neotropical bats, while a detailed report on wing morphology, flight development and growth patterns of paleotropical bats, particularly Indian fruit bats, is scarce (Elangovan et al., 2004). The aim of this study was to describe the relation between wing morphology and flight development in the free-flying short-nosed fruit bat *Cynopterus sphinx*. In addition, we used aerodynamic flight models to predict the effects of wing morphology on theoretical flight performance, and the growth patterns of wingspan and wing area were compared using three non-linear equations.

Materials and methods

The study was conducted at the Department of Animal Behaviour and Physiology, School of Biological Sciences, Madurai Kamaraj University, Madurai, India

(09°58'N, 78°10'E) between February and August 2002. A group of five pregnant *C. sphinx* was collected from their foraging area on the university campus. Bats were released into a free-flight room (3.5 m long × 2.4 m wide × 3.5 m high) and maintained under 12:12 h light and dark cycles. Bats were fed with their natural diet such as fruits of *Annona squamosa*, *Psidium guajava*, *Mangifera indica*, *Carica papaya* and *Achras sapota* and leaves of *Coccinia indica* and *Cassia fistula* during the dark period. No minerals and vitamin supplements were added with the diet. Discarded fruits, faeces and bolus were removed at 0600 h of the following morning. Bats were marked with thin aluminium neck collars (laboratory-made) for individual recognition. The bats did not show any adverse reaction to tagging.

Five days after the onset of parturition, the pups were gently removed from their mothers and morphological parameters including body mass, wingspan and wing area were measured from 5 to 125 days of age at 5-day intervals. Simultaneously, bats were observed twice a day to study their behaviour. Wing area (cm²) was measured by placing the young bat on its ventral side over a black sheet, extending the right wing with the leading edge perpendicular to the body axis and tracing the outline. The traced area was carefully cut out and used to calculate wing area using a leaf area meter (Area Meter AM100, Analytical Development Company Ltd, Herts, UK). Wingspan was calculated as two times the distance from the body axis to the wing tip. Tip length ratio was calculated by dividing handwing length (distance from the wrist to the wing tip) by armwing length (distance from the shoulder joint to the wrist). Tip area ratio was calculated by dividing handwing area (area of membrane spanned by the second–fifth digit) by armwing area (area of wing between the fifth digit, the body and the legs). Aspect ratio was calculated as wingspan squared divided by wing area. Wing loading (Nm⁻²) was calculated by multiplying individual body mass by 9.8 (acceleration due to gravity) and dividing the result by the wing area. Body mass was measured to the nearest 0.1 g using a spring balance (Avinet, Dryden, New York).

Flight tests were carried out once every 5 days from 20 to 65 days of age to test the stages of flight development. A foam pad (3 cm thick, 1.85 m wide, 2 m long) was placed on the floor of the flight test chamber (1.85 m width, 14 m length, 3.5 m height) to cushion the fall of young bats. Young bats were brought to the flight chamber and suspended by their hind feet on the flight-launching apparatus (1.5 m height). The distance travelled by the bat in the flight chamber was measured. Each bat was tested at least three times and the best performance of each individual was recorded. The flight ability of pups was rated by following the method of Powers et al. (1991) as follows: Group I (Floppy): bat dropped to the floor exhibiting no flapping behaviour

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