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Development of wing morphology in the Indian pygmy bat *Pipistrellus mimus*

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Abstract. The growth and development of the wing parameters of the Indian pygmy bat *Pipistrellus mimus* was studied under natural conditions. Newborn young were marked with nontoxic coloured paint and were later marked with split rings. The wingspan and wing area showed linear growth until the age of five weeks, after which the rate of growth decreased. The observations on flight showed that at the age of 19 days the young were able to flutter their wings, at the age of 22 days they flew for a short distance and at the age of 29 days they exhibited sustained flight. The development of wing loading and aspect ratio are also presented. The decrease in wing loading as the bat grows is discussed as an advantage to sustain flight. The aspect ratio showed a high degree of scatter at early stages of life which decreased at the later period of growth. In general the development of wing morphology of *P. mimus* is similar to that of other vespertilionid bats.

Keywords. Aspect ratio; flight; *Pipistrellus mimus*; wing area; wing loadⁱng; wingspan.

1. Introduction

Among vertebrates, birds (Dhawan 1991) and bats (Norberg and Rayner 1987; Fenton 1990) are empowered with flight to utilize a variety of foraging niches which are inaccessible to other animals. The development of flight is one of the characteri-stic aspects of the growth and development of bats. The young bats must learn to fly and to capture prey on the wing, before becoming independent of maternal care. This requires a sufficient development in wing structure, flight musculature and vocal and auditory (echolocation) characteristics before the onset of flight (Kunz 1987). Juveniles of several species of bats typically start to fly when they attained about 70% of adult body mass and over 95% of adult skeletal size (Barclay 1995). Development of wing morphology and flight behaviour during the postnatal growth has been studied in a few species of bats such as *Rhinolophus ferrumequinum* (Hughes *et al* 1989), *Artibeus jamaicensis* (Taft and Handley 1991), *Myotis lucifugus* (Powers *et al* 1991) and *Pipistrellus pipistrellus* (Hughes *et al* 1995). The present study describes the development of morphological changes in the wings studied under natural conditions in the Indian pygmy bat *Pipistrellus mimus,* the smallest bat in India. Adult body mass is about 4g, and the forearm length is about 28 mm. It occupies crevices in rocks, buildings, and trees. The study involves measurement of the morphological parameters of the wing membranes of infant and adult bats and derivation of aerodynamic aspects.

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2. Materials and methods

The study was conducted on a colony of *P. mimus* consisting of about 20 adult bats (16 males, 4 females). The colony was located in an unused tunnel (24·0 m long by 0·9 m wide by 1·3 m high), which formed a part of the southern side of a building housing the Department of Animal Behaviour at the Madurai Kamaraj University, Madurai (9° 58' N; 78° 10' E). Females roosted in small groups with their infants, and adult males roosted singly inside crevices along the length of the tunnel. Visits to the tunnel were made at least twice weekly. Typically mothers left young in the tunnel while they foraged, which facilitated collection of young for marking and recapture. Because newborn young were tiny and delicate, and marking them with bands caused injuries, a nontoxic coloured paint was applied

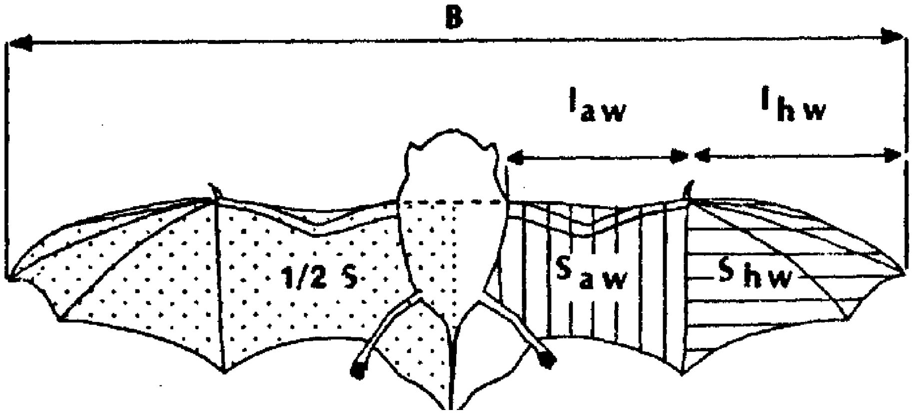

Figure 1. Diagrammatic representation of a bat showing the various wing parameters. The wingspan (B) is measured from tip to tip of the extended wings. Armwing and handwing lengths are shown by l_{aw} and l_{hw} respectively. The dotted area represents 1/2 wing area (1/2 S). Vertical lines indicate armwing area (S_{aw}) and horizontal lines indicate handwing area (S_{hw}).

Table 1. Aerodynamic aspects of wing parameters of young bats of *P. mimus* at diferent ages expressed in percentage to mean values of the adult.

	Age (days)						
	1	10	18	22	28	36	Adult mean value
Body mass (g)	16·60	54·30	70·86	74·60	80·00	—	3·50
Wingspan (cm)	30·90	52·97	76·35	81·93	87·41	92·01	19·54
Armwing length (cm)	36·80	61·33	84·00	86·90	92·00	93·33	3·75
Handwing length (cm)	23·90	43·67	68·36	75·10	83·67	90·81	4·90
Armwing area (cm^2)	11·80	30·91	61·43	67·94	71·36	87·39	12·29
Handwing area (cm^2)	03·93	17·85	49·13	53·93	64·01	80·80	10·42
Tip length ratio	64·90	70·99	81·68	86·26	90·83	96·94	1·31
Tip area ratio	34·12	56·47	80·00	—	89·41	91·76	0·85
Wing area (cm^2)	09·33	25·92	55·60	63·03	65·85	80·35	57·02

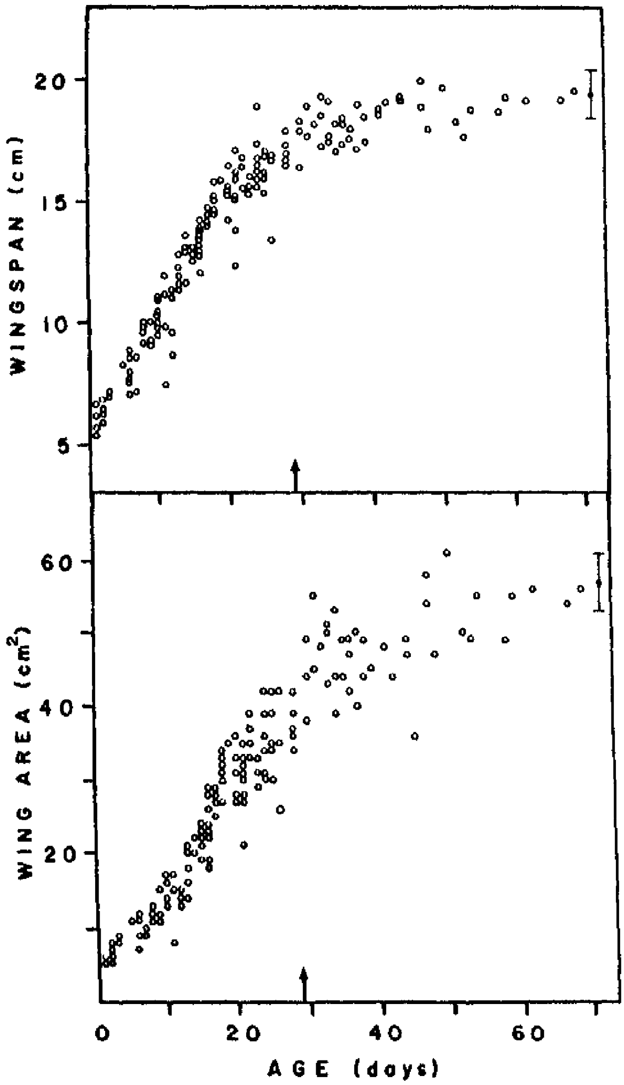

Figure 2. Age related changes in wingspan (top) and wing area (bottom) during postnatal growth. Adult mean values (± SD; *n* = 15 for wingspan and 14 for wing area) are shown as vertical bars. The arrows denote the age of sustained flight.

Wingspan=5· 15 + 0 · 6 × age – (0 · 0064 × age^2).

Wingarea=0 ·117 + 1·78 × age – (0·014 × age^2).

on the claws of a foot or thumb. The paint lasted for about 5 days, making it necessary to recoat the marking frequently. When the pups were 2 weeks old they were marked with numbered and coloured-plastic split rings, with males on the left and females on the right forearm. Body mass was recorded to the nearest 0·1 g using an Avinet spring balance.

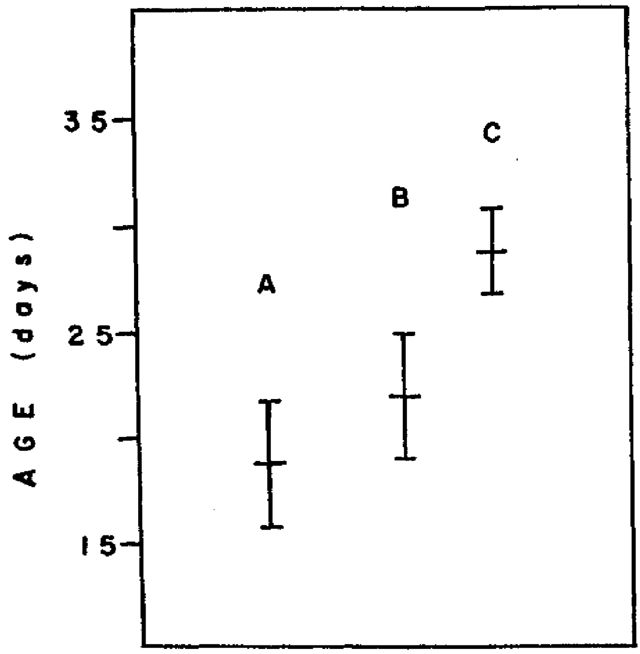

Figure 3. The mean (± SD) ages of flight performance are indicated by A, fluttering (n = 29); B, first flight (n = 17); C, sustained flight (n = 15).

Young of known age (Isaac and Marimuthu 1996) were collected from the crevices after their mothers left for foraging during the early night hours. By following the method of Norberg and Rayner (1987) the wing parameters for a total of 175 infants of both sexes at various age levels were measured. Each individual was placed on a graph sheet and the outer margin of the extended wings including the tail membrane was drawn. The wingspan (cm) and wing area (cm^2) were measured directly from the tracings. We used Polynomial regression test to analyse the growth pattern of wing parameters. Figure 1 shows all the morphological parameters of the wing. The aerodynamic characters were calculated by using the following method:

Wingspan (cm) = distance between the wingtips of a bat with the wing extended so that the leading edge is straight.

Wing area (cm^2) = all appropriate surfaces used in the production of lift including the areas of the wings, the tail membrane and the body between the wings excluding the head

Tip length ratio = handwing length/ armwing length.

Tip area ratio = handwing area/ armwing area.

$$\text{Aspect ratio} = \frac{\text{wing span}^2}{\text{wing area}}$$

$$\text{Wingloading } (Nm^{-2}) = \frac{\text{body mass} \times \text{acceleration due to gravity (i.e. 9·8)}}{\text{wing area}}$$

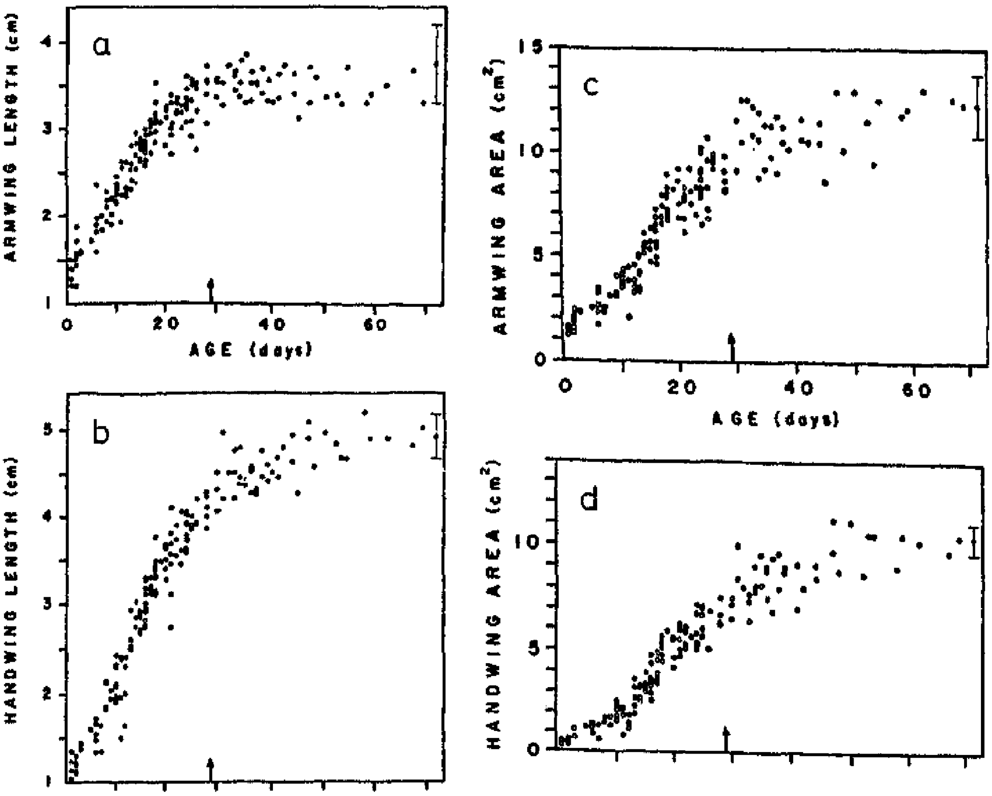

Figure 4. Growth of armwing length (a), handwing length (b), armwing area (c) and handwing area **(d)** in relation to age. Adult mean values (± SD, n = 15 for each) are shown as vertical bars. The arrows denote the age of sustained flight.
Armwing length = 1·37 + 0·1 × age – (0·00123 × age^2).
Handwing length = 0·84 + 0·15 × age – (0·0015 × age^2).
Armwing area = 0·43 + 0·41 × age – (0·0037 × age^2).
Handwing area = 0·88 + 0·34 × age – (0·0026 × age^2).

3. Results

Table 1 shows adult values for wing measurements and the percentage of these values attained by the juveniles since birth. The mean wing area at birth was 5·32 ± 0·22 cm^2 and showed a linear increase of 1·3 cm^2 per day until five weeks after which the rate of growth decreased (figure 2 bottom; d.f. = 174, P < 0 001). The wing area of adults was 57·1 + 4·6 cm^2. The mean wingspan at birth was 6·04 ± 0·45 cm and showed similar linear increase of 0·4 mm per day until five weeks and then the growth attained an apparent stability (figure 2 top; d.f. = 171, P < 0·001). The wingspan of adults was 19·5 ± 1·0 cm. The linear growth of the wingspan and wing area facilitated the young bats to flap their wing membrane. They fluttered their wings at the age of about 19 days, flew for a short distance at 22 days, negotiated turns and showed a sustained flight at 29 days (figure 3).

While the growth of the armwing length (d.f. = 175, P <0·001) and armwing area (d.f. = 173, P < 0·001) increased linearly and began to decrease at the stage of sustained flight, the handwing length (d.f. = 174, P < 0· 001) and handwing area (d.f. = 170, P < 0·001) continued to grow for a few more days (figure 4). Thus the tip length ratio (d.f. = 173,

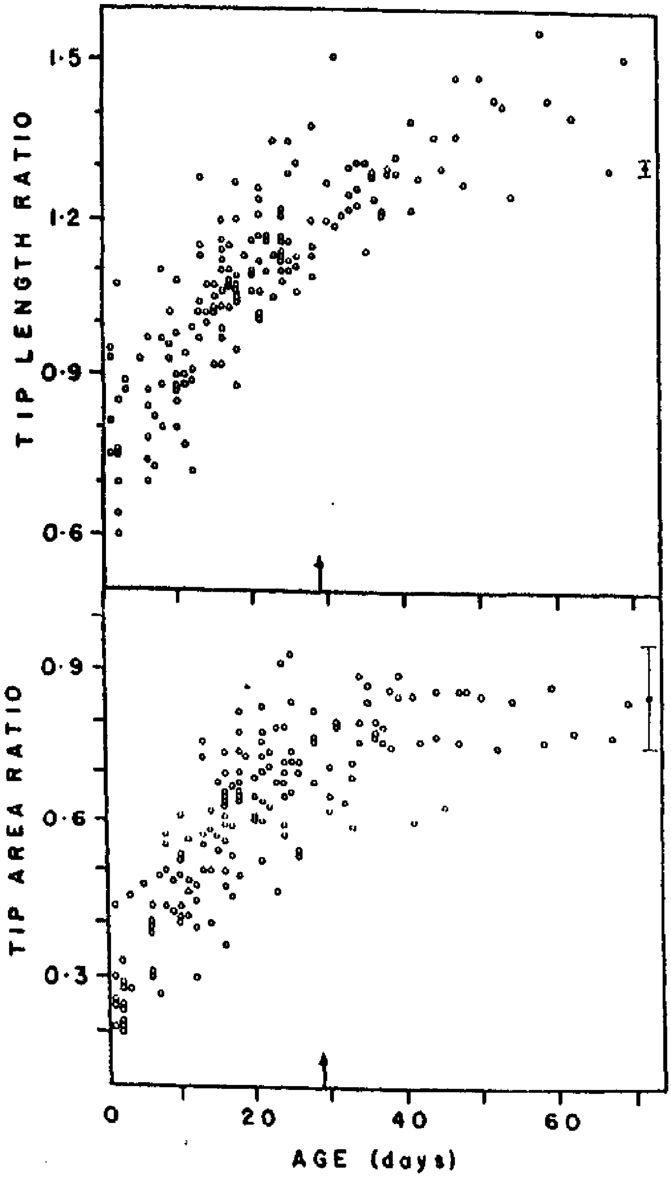

Figure 5. Development of tip length ratio (top) and tip area ratio (bottom) during the postnatal period. Other details as in figure 4.
Tip length ratio = 0·76 + 0·019 × age – (0·00015 × age^2)
Tip area ratio = 0·267 + 0·023 × age – (0·00025 × age^2)

$P < 0{\cdot}001$) and tip area ratio (d.f. = 173, $P < 0{\cdot}001$) increased steadily with age and slowed down after the stage of sustained flight (figure 5). The tip length ratio at birth was 0·85 ± 0·07 and for the adults it was 1·3 ± 0·1. The tip area ratio at birth was 0·29 ± 0·08. At the time of sustained flights it reached the value of adults, which was 0·86 ± 0·09.

Neonates had a high wing loading of 10·3 ± 0·9 Nm^{-2}. Initially it increased during the first week, then decreased with increasing age and approached the adult value of

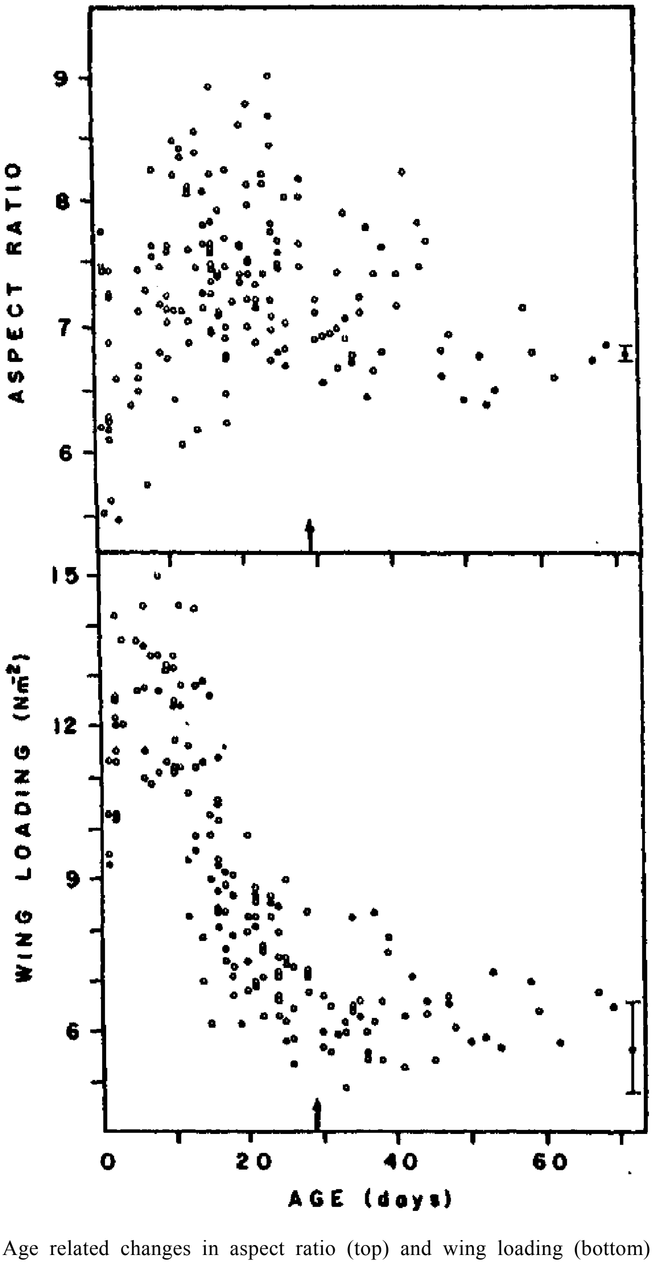

Figure 6. Age related changes in aspect ratio (top) and wing loading (bottom) during the postnatal period. Other details as in figure 4.

5·7±0·9 Nm^{-2} at the age of about 30 days (figure 6 bottom; d.f. = 173, $P < 0{\cdot}001$). The aspect ratio showed a complex development. At early stages there was a high degree of scatter which decreased with age and reached the adult value of 6·8 ± 0·6 after the stage of sustained flights (figure 6 top; d.f. = 172, p<0·001). The wing tracings, which were not used to calculate the wing area, made on a single individual male at different ages are superimposed to show the growth of the wing membrane (figure 7).

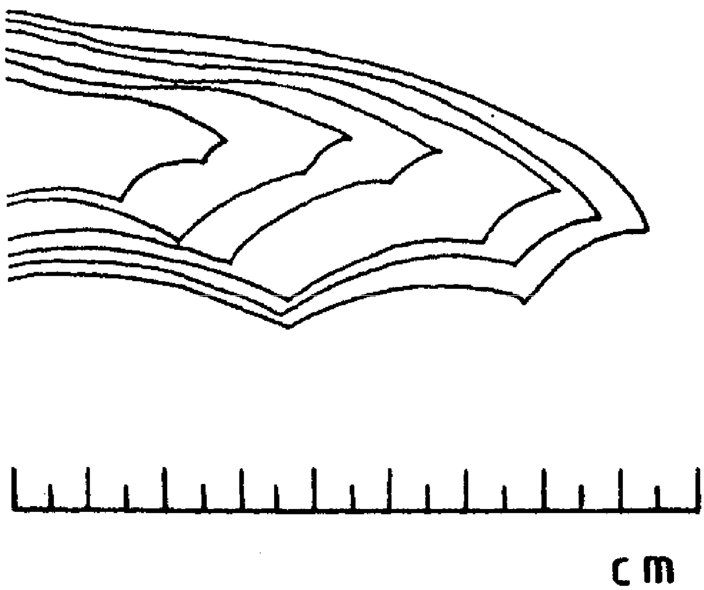

Figure 7. A series of wing tracings of a single male *P. mimus* at the ages of 3,10,16,33 and 52 days. The outermost tracing is of an adult male bat.

4. Discussion

Since the flight of a bat starts only a few weeks after birth the wings are relatively underdeveloped in neonates. The young of *P. mimus* became volant at the age of three weeks implying that the wing membranes at this stage have developed sufficiently to allow sustained flight. The hand wing of *P. mimus* is not completely formed compared to the fully developed armwing at birth similar to other bat species (Hughes *et al* 1989; Taft and Handley 1991; Powers *et al* 1991). However the handwing grows more rapidly than the armwing during postnatal development. Subsequently the handwing is longer than armwing and the tip length ratio becomes greater than unity. Since the handwing is used to produce the bulk of the thrust generated during the downstroke, its growth at the time of initiation of flight is important (Norberg 1976; Rayner 1986; Norberg and Rayner 1987).

In *P. mimus* wing area increased rapidly and linearly, with little scatter, until the age of about 35 days. During the first week after birth, body mass increased faster than wing area, resulting in an increase of wing loading, whereas during the later period the wing area grew faster, causing wing loading to fall steadily until after the age of sustained flight. Cost of flight is related to wing loading and at this energetically expensive time, while the young becomes less dependent on maternal care, a low wing loading will be highly advantageous to sustain their flight and to forage on their own (Norberg and Rayner 1987; Hughes *et al* 1989; Powers *et al* 1991).

Wingspan is an important factor influencing wing loading and aspect ratio. Wingspan directly influences the cost of flight, and increased steadily until around 35 days. There may be a strong need to achieve a large wingspan and wing area in a short period, and hence their linear increase represent fast and steady growth rates.

Aspect ratio can be considered a measure of the efficiency of a wing (Norberg and Rayner 1987; Norberg 1990), so its value is probably unconstrained before the animal flies. Hence a wide range of values for aspect ratio at early stages is probably unimportant. It converged slowly following the onset of flight during which mechanical and ecological pressures operate on the fledgling bats, leading to changes in the wing parameters followed by the conformation of the values of adults. Usually, aspect ratio is much closer to adult range when the young bats exhibit their practice flights (O'Farrell and Studier 1973; Yokoyama *et al* 1975; Hughes *et al* 1989; Powers *et al* 1991). Generally the pattern of development of wing morphology of P. *mimus* is in agreement with those observed in other bats like *Nycticeius humeralis* (Jones 1967), *Nyctalus noctula* (Mohr 1932), *Myotis daubentonii* (Kratky 1981), *Rhinolophus ferrumequinum* (Hughes *et al* 1989), *Pipistrellus pipistrellus* (Hughes *et al* 1995) and *Plecotus auritus* (de Fanis and Jones 1995).

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References

Barclay R M R 1995 Does energy or calcium availability constrain reproduction by bats?; *Symp. Zool. Soc. London* **67** 245–258

de Fanis E and Jones G 1995 Post-natal growth, mother-infant interactions and development of vocalizations in the vespertilionid bat *Plecotus auritus; J. Zool. London* **235** 85–97

Dhawan S 1991 Bird flight; *Sadhana* **16** 275–352

Fenton M B 1990 The foraging behavior and ecology of animal-eating bats; *Can. J. Zool* **68** 411–422

Hughes P M, Ransome R D and Jones G 1989 Aerodynamic constraints on flight ontogeny in free-living greater horse-shoe bats, *Rhinolophus ferrumequinum;* in *European bat research 1987* (eds) V Hanak, I Horacek and J Gaisler (Praha: Charles Univ. Press) pp 255–262

Hughes P M, Rayner J M V and Jones G 1995 Ontogeny of 'true' flight and other aspects of growth in the bat *Pipistrellus pipistrellus; J. Zool. London* **235** 291–318

Isaac S S and Marimuthu G 1996 Postnatal growth and age estimation in the Indian pygmy bat *Pipistrellus mimus; J. Mammal.* **77** 199–204

Jones C 1967 Growth, development and wing loading in the evening bat, *Nyticeius humeralis* (Rafinesque); *J. Mammal.* **48** 1–14

Kratky J 1981 Postnatale Entwicklung der Wasserfledermaus, *Myotis daubentoni* Kuhl, und bisherige Kenntnis dieser Problematik im Rahmender Unterordnung Microchiroptera (Mammalia: Chiroptera); *Fol. Mus. Ref. Natur. Bohem. Occid. Pizen. Zool.* **16** 3–34

Kunz T H 1987 Post–natal growth and energetics of suckling bats; in *Recent advances in the study of bats* (eds) M B Fenton, P A Racey and J M V Rayner (Cambridge: Cambridge University Press) pp 395–420

Mohr E1932 Haltung und Aufzucht des Abendseglers (*Nyctalus noctula* Schreb.); *Zool. Gart. Lpz.* **5** 106–120

Norberg U M 1976 Aerodynamics, kinematics and energetics of horizontal flapping flight in the long-eared bat *Plecotus auritus; J. Exp. Biol.* **65** 179–212

Norberg UM 1990 *Vertebrate flight: mechanics, physiology, morphology, ecology, and evolution* (Berlin, Heidelberg: Springer)

Norberg U M and Rayner J M V 1987 Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation; *Phil. Trans. R. Soc.* **B316** 335–427

O'Farrell M J and Studier E H 1973 Reproduction, growth and development in *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae); *Ecology* **54** 18–30

Powers L V, Kandarian S C and Kunz T H 1991 Ontogeny of flight in the little brown bat, *Myotis lucifugus:* behavior, morphology and muscle histochemistry; *J. Comp. Physiol.* **A168** 675–685

Rayner J M V 1986 Vertebrate flapping flight mechanics and aerodynamics and the evolution of flight in bats; in *Biona Report no. 5, Bat flight-Fledermausflug* (ed.) W Nachtigall (Stuttgart: Gustav Fischer) pp 27–74

Taft L K and Handley C O Jr 1991 Reproduction in a captive colony; in *Demography and natural history of the common fruit bat, Artibeus jamaicensis on Barro Colorado Island, Panama* (eds) C O Handley Jr, D E Wilson and A L Gardner (Washington: Smithsonian Institution Press) pp 19–42

Yokoyama K, Uchida T A and Shiraishi S 1975 Functional morphology of the wings from the standpoint of adaptation for flight in Chiroptera. I. Relative growth and ossification in forelimb, wing loading and aspect ratio; *Zool. Mag. Tokyo* **84** 233–247

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