# Postnatal growth, age estimation and development of foraging behaviour in the fulvous fruit bat *Rousettus leschenaulti*

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This study documents the postnatal growth, age estimation and development of the foraging behaviour of the fulvous fruit bat *Rousettus leschenaulti* under captive conditions. At birth, the young were naked and pink with closed eyes and folded pinnae. By day four of age, their eyes had opened and the pups began to move. The mean length of forearm in 5-day-old pups was 24·9 mm and body mass was 10·8 g, equivalent to 32·3% and 14·2% of the values from postpartum females. The length of forearm and body mass increased linearly until 45 and 50 days, respectively, and thereafter maintained an apparent stability. The epiphyseal gap of the fourth metacarpal-phalangeal joint increased until 15 days, then decreased linearly until 75 days and thereafter closed. Age was estimated quantitatively, based on linear changes observed in the length of the forearm and epiphyseal gap. Pups began to roost separately, but adjacent to their mothers when 30 days old and flew clumsily when they were about 40 days old. After attaining clumsy flight, the young bats made independent foraging attempts feebly by biting and licking small fruit pieces. Young bats were engaged in suckling as well as ingesting fruits when they were about 50 days old. Between 55 and 65 days, they flew well and fed on fruits. At the age of 75 days, the young bats were completely weaned and at two months, their foraging behaviour was similar to that of their mothers. There was no significant difference in the growth pattern of the young maintained in captivity compared with those under natural conditions.

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## 1. Introduction

Bats are represented by a taxonomically large and ecologically diverse order of mammals, and thus provide excellent opportunities for testing assumptions and predictions from life history theory. Data on growth rate are particularly useful in deriving equations, which are essential for behavioural, physiological and ecological studies in which accurate age determination is important (Kunz and Hood 2000). Morphometric variation has been used as an indicator in taxonomic and evolutionary studies including ecology, physiology, population biology, geographic variation and sexual dimorphism (Bookstein 1982; Findley and Wilson 1982; Willig 1986; Willig and Moulton 1989; Gannon *et al* 1992; Emmanuvel Rajan and Marimuthu 1999; Sterbing 2002). In ecological studies, it is often necessary to determine the exact age of an animal as otherwise, it is impossible to establish factors such as growth rates, development of various behavioural repertoires, sexual maturity, periodicity of reproduction or longevity. In vertebrates, postnatal growth rates may provide a valuable index of maternal investment, and milk energy output of females during lactation (Kunz and Stern 1995).

Growth and development of bats has been studied during prenatal and postnatal periods (Orr 1970; Tuttle and Stevenson 1982; Kunz and Hood 2000) under both natural (Kunz 1973, 1974; O'Farrell and Studier 1973; Buchler

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1980; Burnett and Kunz 1982; Kunz and Anthony 1982; Kunz and Robson 1995; Hoying and Kunz 1998; Stern and Kunz 1998; Baptista *et al* 2000) and captive conditions (Jones 1967; Kleiman 1969; Taft and Handley 1991; Hughes *et al* 1995; Emmanuvel Rajan and Marimuthu 1999; Swift 2001). Data on growth trajectories of bats also are valuable for estimating or predicting their ages. Such estimates have been used in studies on energy and mineral accretion (Studier and Kunz 1995; Papadimitriou *et al* 1996), milk composition (Kunz *et al* 1995), ontogeny of flight (Powers *et al* 1991; Kunz and Anthony 1996) and postnatal growth (Emmanuvel Rajan and Marimuthu 1999). Baptista *et al* (2000) studied the postnatal growth of free-ranging *Myotis lucifugus* using cross-sectional and longitudinal methods. They emphasized that the mark-recapture method (longitudinal sampling) is the most appropriate for deriving growth rates and to estimate age during the postnatal growth period.

Patterns of growth and development vary among species and families of bats (Tuttle and Stevenson 1982; Kunz and Hood 2000). A positive relationship between body masses of the young and their mothers occurs in the greater spear-nosed bat *Phyllostomus hastatus* (Stern and Kunz 1998). Most developmental studies have been conducted on microchiropteran bats. The present study was conducted to derive age predictive equations from the postnatal growth trajectories and to observe the development of foraging behaviour in juveniles of the fulvous fruit bat, *Rousettus leschenaulti*.

## 2. Materials and methods

This study was conducted at the Department of Animal Behaviour and Physiology, School of Biological Sciences, Madurai Kamaraj University, Madurai (9°58′N, 78°10′E) between November 1999 and August 2000. Pregnant females of *R. leschenaulti* were collected from their temple roosts (day roost) at Tiruparankundram, located at a distance of about 15 km south of the university campus. Bats were released into a free flight room (3·5 m long × 2·4 m wide × 3·5 m height) and maintained under a 12 : 12 h light and dark cycle. During the dark periods, pieces of fruits (guava, banana, papaya, sapota and manila tamarind) were placed in trays about 1·5 m above the floor level. Discarded fruits, faeces and rejecta were removed at 8 am on the following day. Five days after the onset of parturition, young bats were gently removed from their mothers and morphological measurements such as body mass, length of forearm and total epiphyseal gap of the fourth metacarpal-phalangeal joint were taken regularly at five day intervals between 5 and 130 days. The length of the forearm was measured with vernier calipers to the nearest 0·1 mm and body mass was measured to the nearest 0·1 g using a spring balance (Avinet). The length of the total epiphyseal gap in the fourth metacarpal-phalangeal joint was measured to the nearest 0·1 mm using a binocular microscope equipped with an ocular micrometer and substage illumination to view the transilluminated wing (Kunz and Anthony 1982). Observations were made using a night vision scope (FJW Optical Systems Inc) and dim red light. Upon completion of the study, all the bats were released after sunset at the site of capture. In addition to the captive study, wild young bats were collected from their temple roost and morphological measurements were taken to compare the growth patterns of both wild and captive grown bats after which they were immediately released.

Postnatal growth curves were constructed based on the growth of forearm, body mass and concurrent changes in the total epiphyseal gap of the fourth metacarpal-phalangeal joint. The linear increase in length of forearm (5 to 45 days) and linear decrease in length of total gap (20 to 75 days) were used to derive regressions and to derive age predictive equations. Ninety-five percent confidence intervals and prediction bands were plotted for the regression equations for lengths of forearm and total gap. Prediction intervals give the range of values within which the true age of a single *R. leschenaulti* will fall, whereas confidence intervals indicate the range within which the mean true age of bats of a given size will fall (Kunz and Anthony 1982). In order to determine the difference in the growth pattern of young that grew under captive and natural conditions (in temple roosts), the values of their body mass and epiphyseal gap relative to length of forearm were compared by performing a *t*-test. Since the age of the various sized free-ranging pups collected at temple roosts ($n = 37$) was unknown, the length of forearm was taken as an index in such comparison (Emmanuvel Rajan and Marimuthu 1999). Data are given as means ± SE. Visual observations aided by dim red light were made for 4 h from the time of placing the fruits. Intervals between the timing of placing the fruits on the trays and the initiation of their foraging were noted. In addition, intervals between the successive visits of known-age bats to the fruit trays were also noted.

## 3. Results

All the females roosted at the ceiling of the free flight room. The first parturition occurred six days after the bats were released into the room and the parturition period extended over 17 days. Each female produced a single offspring. Of the nine young born in captivity, three died at birth and one died at the age of nine days. The remaining five young (three males and two females) survived until the end of the study. At birth, young *R.*

*leschenaulti* were altricial and thus were naked and pink, with closed eyes and folded pinnae. The young bats positioned themselves firmly on the ventral side of their mothers and held one of her teats tenaciously in their mouths. Such positioning allowed them to hang upside down along with their mothers. By the fourth day of age, the eyes had opened and the pups began to move. The short, fine and soft hair of the pups was distinguishable between 6 and 10 days; and thereafter developed dark grey fur which was similar to that of the adults. The mothers enshrouded the young bats with their plagiopatagium for the first 25 to 30 days.

The length of forearm of the pups at 5 days ranged from 23·0 to 27·0 mm ($\overline{X}$ = 24·9 ± 0·7 mm, *n* = 5), body mass ranged from 10·0 to 12·0 g ($\overline{X}$ = 10·8 ± 0·4 g, *n* = 5) and length of total epiphyseal gap ranged from 5·1 to 5·7 mm ($\overline{X}$ = 5·4 ± 0·1 mm, *n* = 5). The mean length of forearm of 5-day-old pups was 32·3% and the body mass was 14·2% of postpartum females. Empirical growth curves were drawn for five captive *R. leschenaulti* based on body mass, lengths of the forearm, and epiphyseal gap of the fourth metacarpal-phalangeal joint (figure 1). Length of forearm increased linearly until 45 days with a mean growth rate of 0·6 ± 0·1 mm/day (figure 1a). The linear growth of forearm occurred until it reached 53·9 ± 0·5 mm (70% mother's forearm length) at the age of 45 days. Concurrently, body mass increased linearly until the age of 50 days to 23·5 ± 1·5 g, with a mean growth rate of 0·3 ± 0·1 g/day. Thereafter, body mass remained relatively constant (figure 1b). The length of the total epiphyseal gap of the fourth metacarpal-phalangeal joint showed a linear increase until 15 days and then decreased with increasing age until 75 days, indicating the formation of a secondary centre of ossification (figure 1c).

A linear regression equation predicts the age of young bats on the basis of forearm length from 24·9 ± 0·7 mm to 53·9 ± 0·5 mm (until 45 days) with 95% confidence intervals and prediction limits (figure 2). Another equation was derived to estimate the age from the length of the epiphyseal gap until 75 days, when the length of the total gap of the fourth metacarpal-phalangeal joint approached closer to zero (figure 3). At a mean length of forearm (40·9 mm), the width of the 95% confidence limit was ± 0·7 day. At the extreme lengths of forearm (24·9 mm and 53·9 mm) the widths were ± 1·4 days and ± 1·2 days, respectively. The age estimate from the length of epiphyseal gap with 95% confidence limits was ± 0·9 day at the mean length of total gap (3·3 mm). At the extremes (0·3 mm and 6·4 mm), the widths were ± 1·3 days and ± 1·2 days (figure 3). We compared the values of body mass and total epiphyseal gap with the length of forearm of the young bats that grew under captive and under natural conditions (figure 4). We found that there is no significant difference on the growth of these two parameters under both conditions (for body mass $t = 2{\cdot}0$, $df = 72$, $P > 0{\cdot}05$; for epiphyseal gap $t = 2{\cdot}0$, $df = 72$, $P > 0{\cdot}05$).

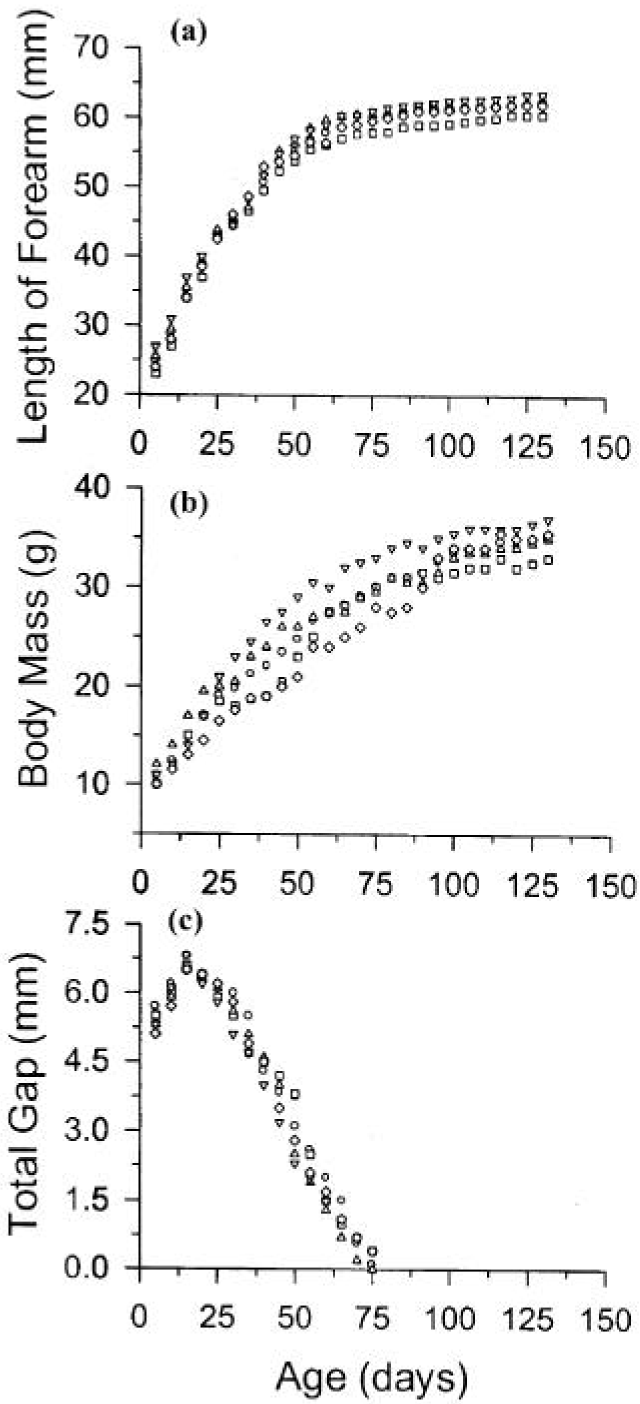


**Figure 1.** Empirical growth curves for (**a**) length of forearm (*N* = 130; from day 5 to 130), (**b**) body mass (*N* = 130; from day 5 to 130), (**c**) length of total gap of the fourth metacarpal-phalangeal joint (*N* = 75; from day 5 to 75) of captive young of *R. leschenaulti*. The values of five young bats are represented by five different symbols.

The percentage values of forearm length and body mass of the young bats in relation to the postpartum females are depicted in figure 5. During the early period (initial 25–30 days) of lactation the mothers always carried their pups even while flying up and down to collect pieces of fruits. About 5 min after placing the fruits the mothers began to fly around the room. After 8·0 ± 1·0 min (*n* = 25) they flew down towards the fruits, took a piece in their mouths, reached their roosts and started eating. The mothers repeated their visits every 23·0 ± 2·0 min (*n* = 25) to the trays to pick up pieces of fruits. The physical contacts between the mothers and pups decreased as the pups increased in age. At the age of 30 days, they began to roost separately, but adjacent to their mothers. The young bats flew clumsily when they were about 40 days old. After attaining such clumsy flights, they made feeble foraging attempts independently by biting and licking the fruit pieces, but did not carry them to their roosts. However, the mothers suckled their young till the latter were 45 to 55 days old (figure 5). Contacts between the mothers and young gradually decreased and suckling did not occur after 55 days. The young were completely weaned from their mothers by the age of 75 days. Their onset of flight synchronized with the offset of suckling (figure 5). Young bats flew well and began to feed on fruits when they were 55 to 65 days old. At this stage, they began to forage 24·0 ± 2·0 min (*n* = 25) after the fruits were made available. They repeated their visits to the fruit trays every 29·0 ± 3·0 min (*n* = 17). At 115 to 125 days the young bats began to forage 13·0 ± 1·0 min (*n* = 21) after the fruits were placed on trays. At these ages, the foraging timings of the young bats were similar to that of their mothers.

## 4. Discussion

Most of the studies carried out so far on postnatal growth and development of bats have been restricted mainly to microchiropteran bats; for example on Vespertilionidae (Tuttle and Stevenson 1982; Kunz 1987; De Fanis and Jones 1995; Hughes *et al* 1995; Isaac and Marimuthu

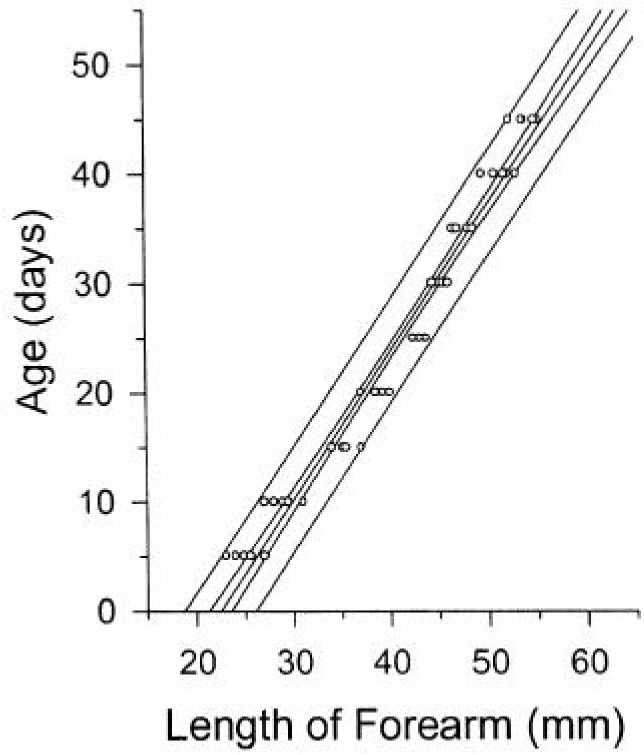


**Figure 2.** Regression line estimating the age of captive *R. leschenaulti* from the values of length of forearm from neonates to 45 days. The predictive equation is valid for length of forearm ranging from 24·9 ± 0·7 mm to 53·9 ± 0·5 mm. Narrow and wide bands indicate 95% confidence and prediction intervals respectively; $N = 45$, $r^2 = 0{\cdot}9$, $P < 0{\cdot}001$, age = – 30·4 + (1·4 × length of forearm).

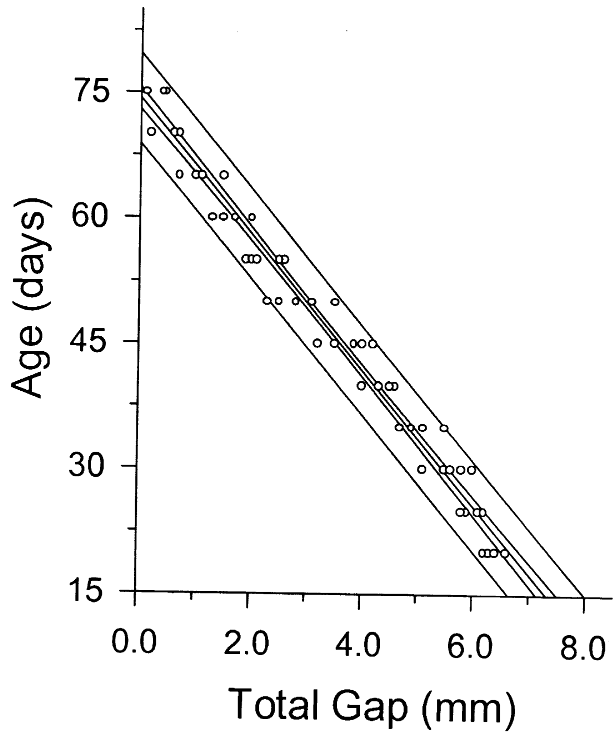


**Figure 3.** Linear regression line estimating the age of captive *R. leschenaulti* from the length of total gap of the fourth metacarpal-phalangeal joint between 20 and 50 days. The predictive equation is valid for the length of total gap ranging from 2·0 to 6·4 mm. Narrow and wide bands indicate 95% confidence and prediction intervals, respectively; $N = 65$, $r^2 = 0{\cdot}9$, $P < 0{\cdot}001$, age = 74·9 – (0·82 × total gap).

1996; Hoying and Kunz 1998), on Molossidae (Kunz *et al* 1995), on Phyllostomidae (Stern and Kunz 1998) and on Megadermatidae (Emmanuvel Rajan and Marimuthu 1999). Studies on growth aspects in megachiropterans are more limited (Kunz and Stern 1995; Kunz and Hood 2000). The present study covers the growth of a megachiropteran bat in detail.

The pattern of postnatal growth and development showed the basic trend of a linear growth of forearm and body mass during the preflight period. Juveniles of several

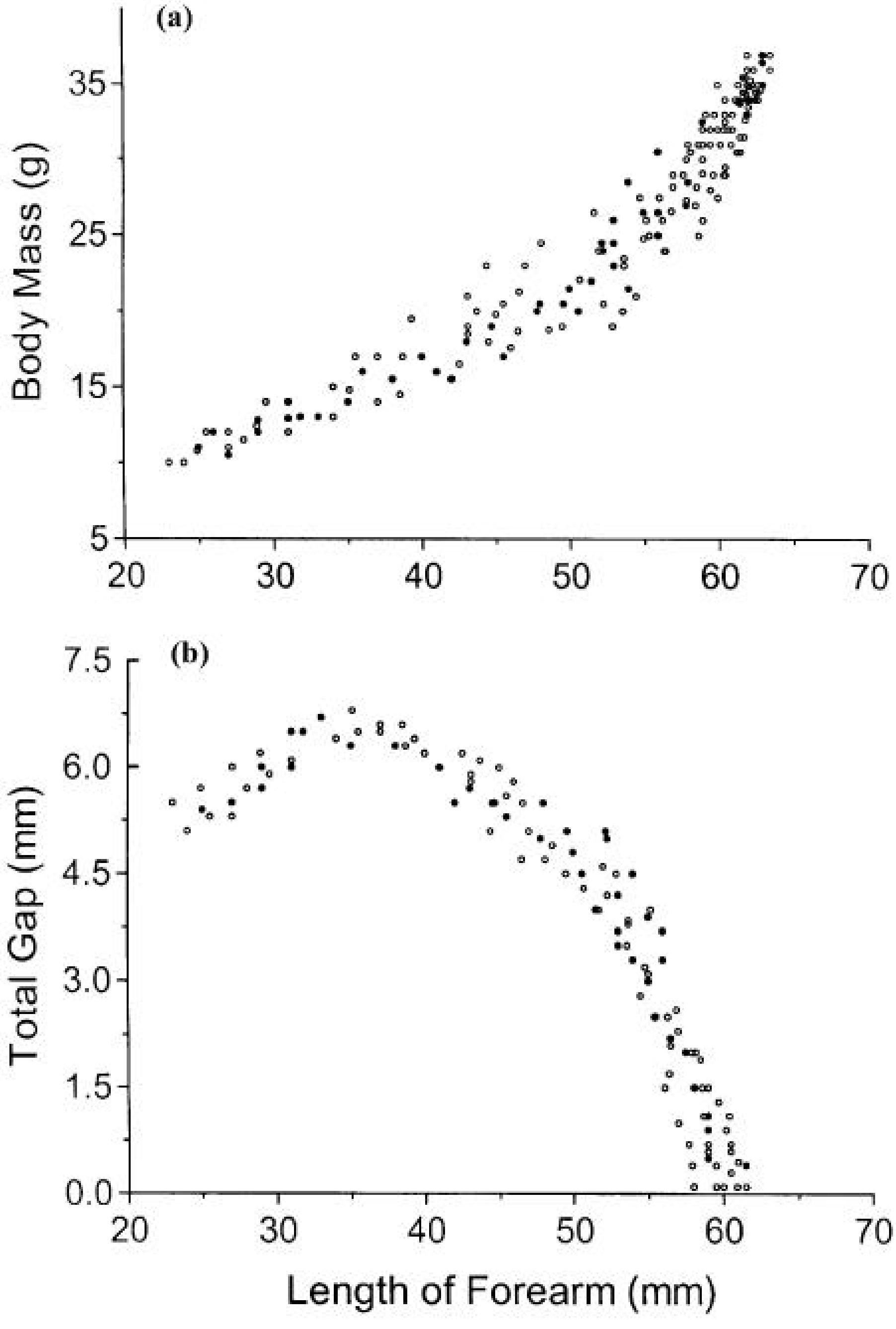


**Figure 4.** Comparisons of body mass (**a**) and the length of total gap of the fourth metacarpal-phalangeal joint (**b**) of young *R. leschenaulti* under captive (hollow circles) and wild (solid circles) conditions with their respective lengths of forearm; for body mass $N = 130$ (captive) and 41 (wild); for total gap length $N = 75$ (captive) and 41 (wild).

species of microchiropteran bats typically began to fly when they attained 70% of adult body mass and over 95% of adult skeletal size and wing dimension (Barclay 1995; Kunz and Stern 1995). However, young *R. leschenaulti* in the present study began to fly when they achieved even about 35% of adult body mass and nearly 75% of adult skeletal size. This observation substantiates the report of Orr (1970) who stated that megachiropterans are more advanced compared to microchiropterans during the course of development. We rule out the possibility of such advanced growth in captive conditions due to the overabundance of food, mainly based on the absence of significant changes in the growth pattern between captive and free-ranging bats. In theory, asymptotic body mass is achieved by bats when the postnatal growth rate becomes zero. The asymptotic mass of young bats is usually less than adult mass, because it does not include accretionary growth after the first year (Kunz and Stern 1995). The values of the lengths of forearm and epiphyseal gap during their linear phases of growth increased during the preflight period and decreased during the postflight period, and were reliable for deriving equations to estimate the age of young bats (e.g. Kunz and Robson 1995; Isaac and Marimuthu 1996; Hoying and Kunz 1998; Emmanuvel Rajan and Marimuthu 1999; Baptista *et al* 2000). Even though we found no significant difference in the postnatal growth pattern in *R. leschenaulti* between captive and free-ranging bats, a few reports state that there is a marked difference between these two conditions. For example, Buchler (1980) observed that *Myotis lucifugus* began to fly 10 days later in captivity than in the wild. Habersetzer and Marimuthu (1986) noted a slower growth rate in *Hipposideros speoris* maintained in an outdoor enclosure, compared with bats living in the natural caves. Orr (1954) observed that the young *Antrozous pallidus* began to fly a week earlier under natural conditions compared to the bats kept in captivity. However, in case of the Indian false vampire bat *Megaderma lyra* (Emmanuvel Rajan and Marimuthu 1999) the growth trajectories of body mass and total gap length in the fourth metacarpal-phalangeal joint, in relation to the growth in the length of forearm are apparently similar in both captive and natural conditions, akin to the present study. When Kunz and Stern (1995) removed the effect of body mass, they found no significant difference in growth conditions among 33 species of free-ranging and captive bats.

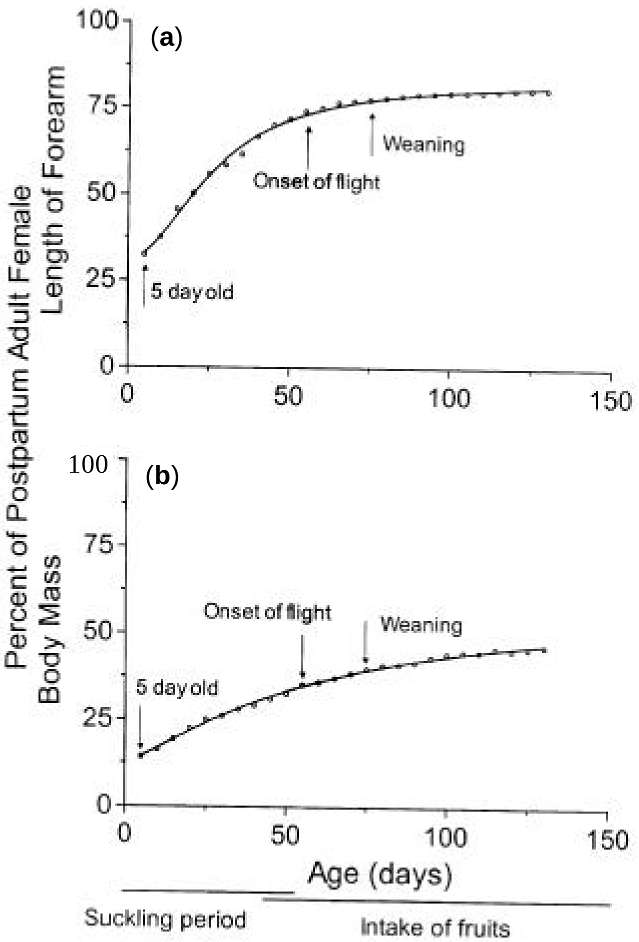


**Figure 5.** Relationships between growth of length of forearm (**a**) and body mass (**b**) at 5-day-old and at various stages such as onset of flight, weaning and period of suckling and intake of fruits. Values of young bats are expressed as percentage of mean values of postpartum females.

Baptista *et al* (2000) compared two sampling methods, longitudinal and cross-sectional, to predict the age of free-ranging bats. Their study suggests that the longitudinal method (based on mark-recapture sampling) is more reliable for age estimation when compared to the cross-sectional (grab sampling) method. Even though our bats were maintained in captivity, we employed the method equivalent to longitudinal sampling. Since there is no significant difference in the growth pattern between captive and free-ranging bats, our equations to predict the age of young *R. leschenaulti* may reliably be used in behavioural, physiological and ecological studies.

Attainment of flight and independence from maternal care are the two essential components for successful postnatal growth and development. The clumsy flights and foraging attempts of 40-day-old *R. leschenaulti* in the present study indicate that their neuromuscular system begins to establish the crucial circuitry for specialized tasks such as flight, navigation and feeding skills (Powers *et al* 1991; Stern *et al* 1997). Carrying a small load at this stage will increase wing loading, but will also decrease their manoeuvrability (Hayssen and Kunz 1996). This could be the possible reason why the young *R. leschenaulti*, at 40 days of age, do not carry fruit pieces to their roosts. Absence of synchronized foraging flights between mothers and the 45–55 day *R. leschenaulti* young bats suggests that they develop foraging skills independently. Young microchiropterans such as *Noctilio albiventris* (Brown *et al* 1983), *Eptesicus fuscus* (Brigham and Brigham 1989) and *Desmodus rotundus* (Wilkinson 1985) usually accompany their mothers which facilitate the young to learn foraging strategies. However, a few other microchiropterans such as *Myotis myotis* (Audet 1990), *M. lucifugus* (Buchler 1980; Adams 1996), *Pipistrellus pipistrellus* (Racey and Swift 1985) and *Rhinolophus ferrumequinum* (Jones *et al* 1995) began to forage independently. Paternal influence on the ontogeny of vocalizations (including echolocation in microchiropterans) and early flight and foraging of pups may be expected in monogamous species and polygynous species that form harems (Kunz and Hood 2000). Accordingly, in the monogamous microchiropteran bat *Lavia frons* when males and females forage together, their pups accompany them to a shared feeding site (Vaughan and Vaughan 1987). Similarly, in an another microchiropteran bat *Cardioderma cor*, mother-pup contact is maintained by calls emitted by the mothers at foraging areas (Vaughan 1976). Since the observations on *R. leschenaulti* in the present study were made under captive conditions where space for flight was restricted and fruits were routinely replenished, our conclusion that young bats began to forage by not accompanying their mothers must be considered preliminary. A detailed study on associations between mothers and infants of *R. leschenaulti* and other megachiropterans under natural conditions is warranted.

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