Acta Chiropterologica, 5(1): 107–116, 2003
PL ISSN 1508-1109 © Museum and Institute of Zoology PAS

Postnatal development in the Indian short-nosed fruit bat *Cynopterus sphinx*: growth rate and age estimation

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We studied the patterns of postnatal growth and changes in length of forearm, body mass and total epiphyseal gap in the captive free-flying short-nosed fruit bat *Cynopterus sphinx*. At birth young were altricial. By day five, their eyes had opened, and the pinnae become unfolded between sixth and ninth day of age. At the age of three days, the mean forearm length and body mass were equivalent to 42.2% and 18.2%, respectively of the values of postpartum females. The length of forearm increased linearly until 36 days and attained 94.1% of mean forearm length of postpartum females at the age of 219 days. Body mass of pups increased linearly until 60 days and attained 72.7% of mean mass of postpartum females at the age of 219 days. The length of total epiphyseal gap of fourth metacarpal-phalangeal joint increased until 15 days of age and subsequently decreased linearly, and closed at about 60 days of age. The age predicting equation based on the length of forearm is valid when its dimensions are between 29.4 mm and 52.4 mm (3–36 days of age). Similar equation but based on the length of total epiphyseal gap is valid when its dimensions range from 47.0 μm to 6.0 μm (15–60 days of age). Growth patterns of forearm length and body mass were best described by the logistic and Gompertz nonlinear growth models, respectively. There was no significant difference in the growth patterns of body mass and length of total epiphyseal gap with reference to lengths of forearm of captive and wild-grown pups.

Key words: *Cynopterus sphinx*, age estimation, growth curve, growth rate, postnatal development

INTRODUCTION

Bats exhibit both precocial (Kurta and Kunz, 1987) and altricial (Powers *et al*., 1991; Hughes *et al*., 1995) characteristics at birth. At the time of birth many species of bats are altricial and thus unable to fly and forage independently until they are weaned. The important features of postnatal growth and development in bats are the attainment of flight and independence from parental care. Studies on postnatal development and growth rate are particularly important in deriving equations to predict age, which is useful in behavioural, physiological and ecological studies (Kunz and Hood, 2000). In ecological studies it is often necessary to determine the exact age of an animal. Without knowing an animal's age it is impossible to establish certain factors, such as growth rates, sexual maturity, development of various behavioural repertoire, periodicity of reproduction or longevity of an animal.

Growth and development of bats have been studied during prenatal and postnatal periods (Orr, 1970; Tuttle and Stevenson, 1982; Kunz and Hood, 2000) under both natural (e.g., Kunz, 1973; O'Farrell and Studier, 1973; Buchler, 1980; Kunz and Robson, 1995; Hoying and Kunz, 1998; Stern and Kunz, 1998; Baptista *et al*., 2000) and captive (e.g., Jones, 1967; Kleiman, 1969; Taft and Handley, 1991; Hughes *et al*., 1995; Rajan and Marimuthu, 1999; Swift, 2001) conditions. Postnatal growth data have been used in studies of 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 ontogeny of echolocation sounds (Habersetzer and Marimuthu, 1986; Moss *et al.*, 1997). Baptista *et al*. (2000) studied the postnatal growth in 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.

Body mass, length of forearm and length of total epiphyseal gap have been proved as important variables for assessing postnatal growth rates in bats (Kunz and Stern, 1995; Kunz, 1987; Kunz and Anthony, 1982). The growth rates and patterns of bats have been evaluated using different growth models on very few species of bats such as *Tadarida brasiliensis* (Kunz and Robson, 1995), *Plecotus auritus* (McLean and Speakman, 2000) and *Myotis nattereri* (Swift, 2001). Most of the above studies have been conducted on microchiropteran bats. The present study is conducted to derive age predictive equations and to quantify growth rates of short-nosed fruit bat *Cynopterus sphinx*. We have also compared the growth of body mass and length of total epiphyseal gap with respect to the growth of forearm length of captive and wild populations.

MATERIALS AND METHODS

Study was conducted at the Department of Animal Behaviour and Physiology, School of Biological Sciences, Madurai Kamaraj University, India (09°58'N, 78°10'E) between January 1999 and August 2000. Advanced stage pregnant females of *C. sphinx* were collected from their foraging area, in the botanical garden, at the university campus between 18:30 and 23:00 h. Bats were released into a free flight room (3.5 m long × 2.4 m wide × 3.5 m height) and maintained under 12:12 h light-dark cycles. During dark periods, pieces of any one kind of fruits (guava, banana, papaya, sapota, grape and manila tamarind) were placed on trays about 1.5 m above the floor level. Discarded fruits, faeces and bolus were removed at 08:00 h of the following mornings. Newborn young were soft and fragile and their separations from mothers caused high mortality (Priya, 2000). Hence young bats were gently removed with great care from their mothers and morphological measurements such as body mass, length of forearm and length of total epiphyseal gap of the fourth metacarpal-phalangeal joint were made between three and 219 days at an interval of three to five days. Mothers and pups were tagged with different colour beads for individual recognition. Each tag was prepared with a thin, flexible aluminum wire loaded with plastic beads (3 mm). In order to resist pressure the wires were inserted into soft, flexible, transparent plastic tubes with the beads were well exposed. The tags were then placed round the necks of mothers and pups and the two ends of the wire were tightened gently and sufficiently. The bats did not show any adverse reaction on such tagging. Length of 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). Length of the total epiphyseal gap in the fourth metacarpal-phalangeal joint was measured to the nearest 1.0 μ 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 under captive condition. On completion of the study the tags were removed and all bats were released during dark hours at the site of capture.

We used linear regression analysis, with age as the dependent variable to derive age predictive equations and to estimate the linear changes in the lengths of forearm and total epiphyseal gap. We divided the growth patterns of the lengths of forearm into linear and nonlinear periods and the linear changes were used to derive age predictive equation. In the lengths of total epiphyseal gap, the phase of linear decrease was taken for age estimation. The best-fit postnatal growth models of the length of forearm and body mass were fitted using three standard nonlinear growth models (Simply Growth, Version 1.7, PISCES Conservation Ltd. 2002). These models (Logistic, Gompertz and von Bertalanffy) were fitted using mean values across the individuals for length of forearm and body mass, and the growth patterns were compared among the three models. Goodness of fit was taken inversely related to the sum of squares of the models after checking systematic deviations (Zullinger *et al*., 1984; Boyd and Myhill, 1987; Hughes *et al*., 1995; Kunz and Robson, 1995; McLean and Speakman, 2000; Swift, 2001).

In addition to captive study, wild grown pups were collected with their mothers by erecting mist nets adjacent to their day roosts (palm trees) in the botanical garden at the time of emergence. A total of 69 mother-pup pairs were captured at five-day intervals during July and August 2000. Upon capture, their morphometric measures such as length of forearm, body mass and length of total epiphyseal gap were taken and then released after attaching them with their mothers. Since the ages of various sized free-ranging pups were unknown, we considered the length of forearm of captive and wild pups as an index to correlate the postnatal changes in their body masses and lengths of total epiphyseal gap by comparing the slopes of linear regression. Linear regression analyses were performed using SigmaStat for Windows Version 2.03 (SPSS Inc., 1995), and in age predicting equations 95% prediction and confidence limits were plotted using SigmaPlot Version 2.0 (Jandel Corporation, 1994). Means are expressed with ± SD throughout the text.

RESULTS

First parturition occurred seven days after the bats were released into the free flight room and the parturition period extended over 27 days. Each female gave birth to a single pup. A total of 12 young had born in captivity, one died at birth and two died at the age of three days. The remaining nine young (3 ♂♂ and 6 ♀♀) survived till the end of the study. Newborn pups were altricial and thus they were naked, pink with closed eyes and folded pinnae. The pups positioned themselves firmly on the ventral side of their mothers. Eyes had opened and the pups began to move at the age of 5.0 ± 0.87 days. The pinnae were unfolded at the age of 7.3 ± 1.22 days. The short, fine, soft hairs of pups were distinguishable at about ninth day and thereafter, developed grey fur, which appeared similar to that of subadults. The mothers enshrouded their young with their plagiopatagium for the first 24 days. During such period the mothers foraged with their attached young. Pups started to roost separately adjacent to their mothers at the age of 30 days and to fly clumsily when they were about 45 days old. After the attainment of clumsy flight, the pups made foraging attempts by biting and licking fruit pieces. Between the age of 45 and 55 days, the young bats engaged in both suckling and feeding upon fruits. After 55 days, the young stopped suckling totally and engaged in independent foraging. They were completely weaned from their mothers at about 65 days of age, when the length of total epiphyseal gap became invisible.

The forearm length of pups at 3-day-old ranged from 27.0 to 31.0 mm ($\bar{x}$ = 29.4 ± 1.63 mm), body mass ranged from 7.7 to 8.7 g ($\bar{x}$ = 8.2 ± 0.45 g) and dimension of total epiphyseal gap varied from 35 to 42 µm ($\bar{x}$ = 38.0 ± 3.01 µm). The mean values of the length of forearm and body mass of 3-day-old pups were 42.2% and 18.2% of postpartum females, respectively. Even though body mass increased throughout the study period, growth was rapid and linear until 60 days of age and thereafter it became curvilinear (Fig. 1A). A considerable amount of deviation occurred in body mass during later period of growth. Pups obtained 40% of mean mass of postpartum females at seventh week of age and exhibited their first flight. At the age of 219 days the young bats attained 32.9 ± 1.80 g of body mass, which

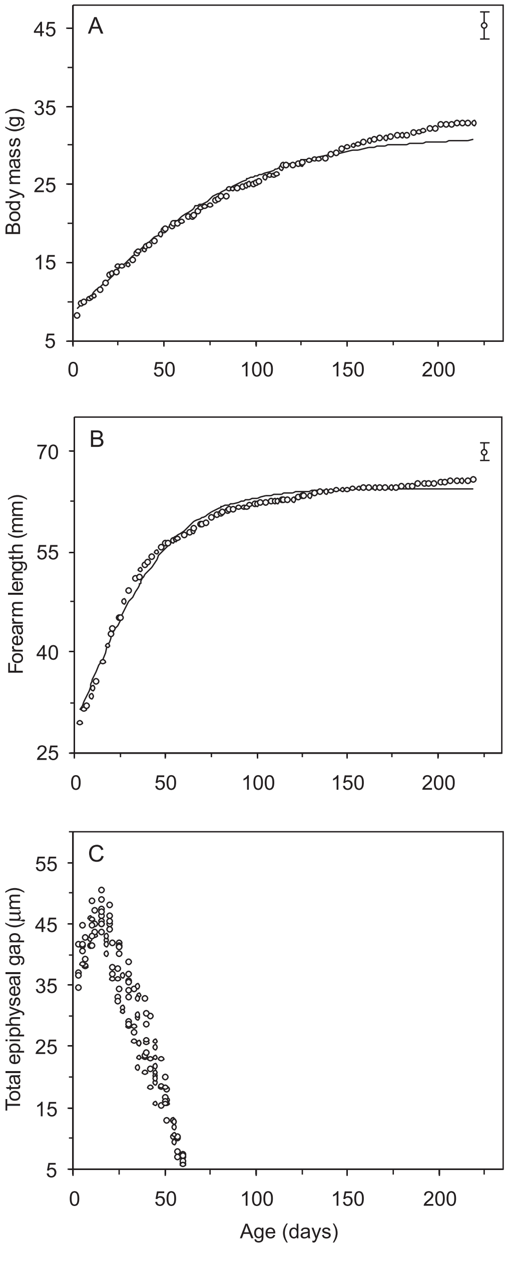

FIG. 1. Empirical growth curves for (A) body mass from 3 to 219 days (*n* = 90), (B) length of forearm from 3 to 219 days (*n* = 90), (C) length of total epiphyseal gap of the fourth metacarpal-phalangeal joint from 3 to 60 days (*n* = 138) of captive young *C. sphinx*. The open circles in A and B represent the mean observed values of nine captive *C. sphinx*. The uninterrupted lines show the nonlinear growth of Gompertz (for body mass) and logistic (for forearm length) models. Vertical bars indicate the values of postpartum females (*n* = 9)

was 72.7% of mean mass of postpartum females. The length of forearm increased linearly until 36 days (up to 52.4 ± 1.13 mm) and thereafter it became nonlinear (Fig. 1B). By the time of first flight (ca. 45 days) the pups attained mean forearm length of 54.9 ± 1.58 mm which was 79% of forearm length of postpartum females. At the age of 219 days the pups attained 94.1% of forearm length of postpartum females. The length of total epiphyseal gap of fourth metacarpal-phalangeal joint showed a linear increase for the first 15 days and then decreased with increasing age until 60 days, indicating the formation of secondary centre of ossification (Fig. 1C).

A linear regression equation allowed to predict age of young *C. sphinx* on the basis of length of forearm from 29.4 ± 1.63 mm to 52.4 ± 1.13 mm (3–36 days) with 95% confidence and prediction limits (Fig. 2A). Another equation was derived to estimate the age from the length of total epiphyseal gap between 15 and 60 days of age when the dimensions decreased linearly from 47.0 ± 2.1 µm to 6.0 ± 1.7 µm (Fig. 2B). At a mean length of forearm (41.5 mm), the extent of deviation from the estimated value at 95% confidence limit was ± 1.0 day. At the extreme lengths of forearm (29.4 mm and 52.4 mm) the extent of deviations were ± 1.55 days and ± 1.67 days, respectively. At the mean length of total epiphyseal gap (26.0 ± 13.0 µm), the estimation of age with 95% confidence limit was ± 1.43 days. At its extremes (6 µm and 50 µm) the extent of deviations were ± 2.53 days and ± 2.55 days, respectively. Analysis of coefficients of determination for the relationships between length of forearm and age, and between length of total epiphyseal gap and age revealed that the length of forearm can be used reliably to estimate the age of young *C. sphinx* up to 36 days old, thus until the length of forearm ≤ 52.4 mm

(Fig. 2A), whereas the age predicting equation based on length of total epiphyseal gap is valid for young ranging from 15 to 60 days, when the forearm exceeds 52.4 mm.

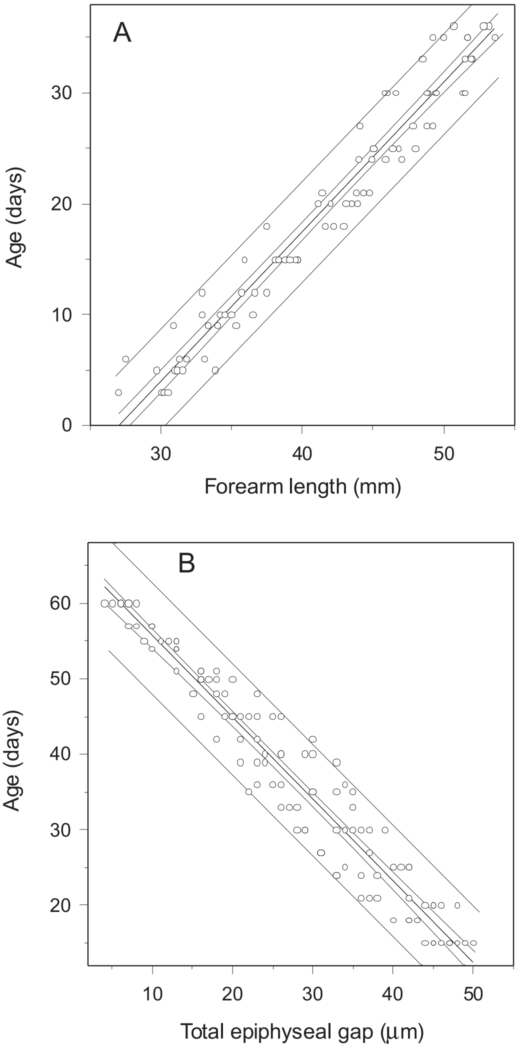

FIG. 2. Regression line estimating the age of *C. sphinx* from the values of (A) length of forearm and (B) length of total epiphyseal gap. Based on the length of forearm age predictive equation is valid for the dimensions ranging from 29.4 ± 1.63 mm to 52.4 ± 1.13 mm; age = -36.3 + (1.34 × forearm length); $r^2 = 0.95$, *d.f.* = 82, $P < 0.001$. The age predictive equation based on the length of total epiphyseal gap is valid when the dimensions range from 47 ± 2.1 µm to 6 ± 1.7 µm; age = 66.5 - (1.1 × total gap); $r^2 = 0.93$, *d.f.* = 112, $P < 0.001$. Narrow and wide bands indicate 95% confidence and prediction limits, respectively

Curves derived from the three models for body mass were similar in shape, since the correlation coefficient of the predicted values for each model was ≥ 0.99. Nevertheless, the Gompertz equation appeared to be the most appropriate model on the basis of statistical criteria describing postnatal changes in body mass of *C. sphinx* (Fig. 1A; see also Table 1):

$$\text{Body mass}_{(t)} = 31.31e^{-e^{-0.0196(t-13.62)}}$$

where ‘e’ is 2.718 and ‘t’ is time in days.

The predicted values for the length of forearm of three nonlinear growth models had correlation coefficients ≥ 0.99. Because of these high correlations in the lengths of forearm, it was difficult to graphically distinguish among the three models. However, after deriving an equation based on each model we chose the logistic equation as best-fit growth model to express the postnatal changes in the length of forearm of *C. sphinx* (Fig. 1B; Table 1):

$$\text{Forearm length}_{(t)} = 64.32[e^{-0.04(t-4.28)} + 1]^{-1}$$

The negative value (-4.12) of an inflection point in the equation describing the length of the forearm argues against the suitability of Gompertz model for postnatal growth rates in *C. sphinx*. Coefficients of variation for the estimates of growth parameters were consistently lesser when derived from the logistic growth model (0.342), compared to the von Bertalanffy (0.394) model.

We compared the values of body mass (Fig. 3A) and total epiphyseal gap (Fig. 3B) with the respective lengths of forearm of the young that were grown under captive and natural conditions. We found null significant changes and the slopes did not differ significantly from unity in the growth of body mass ($r^2 = 0.897$, *d.f.* = 128, $P < 0.05$) and total epiphyseal gap (r^2 =

TABLE 1. Growth parameters of *Cynopterus sphinx*, derived from the logistic, Gompertz and von Bertalanffy nonlinear growth models. A = asymptotic size of length of forearm (mm) or body mass (g); K = growth rate constant; I = inflection point; T_0 = time when length of forearm or body mass is 0; CV = coefficient of variation

Growth model	Parameter	Forearm length versus age				Body mass versus age			
		Estimate	SE	CV (%)	Sum of squares model	Estimate	SE	CV (%)	Sum of squares model
Logistic	A	64.32	0.22	0.342	7331.4	31.48	0.389	1.235	6744.19
	K	0.04	0.001	3.56		0.025	0.001	3.000	
	I	4.28	0.848	19.82		34.63	1.236	3.568	
Gompertz	A	64.39	0.223	0.346	7516.26	31.31	0.334	1.067	3745.44
	K	0.036	0.063	175.28		0.02	0.013	66.24	
	I	-4.12	34.83	845.04		13.62	17.26	126.67	
von Bertalanffy	A	64.87	0.256	0.39	7473.61	36.34	0.867	2.38	4225.77
	K	0.028	0.0011	3.7		0.01	0.0006	5.72	
	T_0	-17.91				-26.32			

0.851, *d.f.* = 118, $P < 0.05$) under both conditions.

DISCUSSION

Most of the studies carried out so far on postnatal development and age estimation have been restricted mainly to microchiropterans; for example on Vespertilionidae (e.g., Krátký, 1981; De Fanis and Jones, 1995; Hughes *et al.*, 1995; Isaac and Marimuthu, 1996; Hoying and Kunz, 1998; Swift, 2001), Molossidae (Kunz *et al.*, 1995), Phyllostomidae (Stern and Kunz, 1998), Megadermatidae (Rajan and Marimuthu, 1999) and Hipposideridae (Cheng and Lee, 2002). Studies on growth aspects in megachiropterans are much limited (Kunz and Stern, 1995; Kunz and Hood, 2000). This is the first report in detail concerning the growth rate of a megachiropteran bat.

Although at the age of three days, *C. sphinx* weighs 18.2% of mean mass of postpartum females, which is slightly lesser than most of microchiropterans, the forearm length was 42.2% of postpartum females as in microchiropterans (Kurta and Kunz, 1987). 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 species of microchiropteran bats typically began to fly when they have attained 70% of adult body mass and over 95% of adult skeletal size and wing dimension (Maeda, 1972; Barclay, 1995; Kunz and Stern, 1995). Swift (2001) has also argued that no juvenile bats of any species yet been shown to exhibit flight before they attain at least 90% of adult skeletal size. However, we provide the first record in the present study that young *C. sphinx* began to fly when they achieved about 40% of adult body mass and nearly 79% of adult skeletal size. Such occurrence

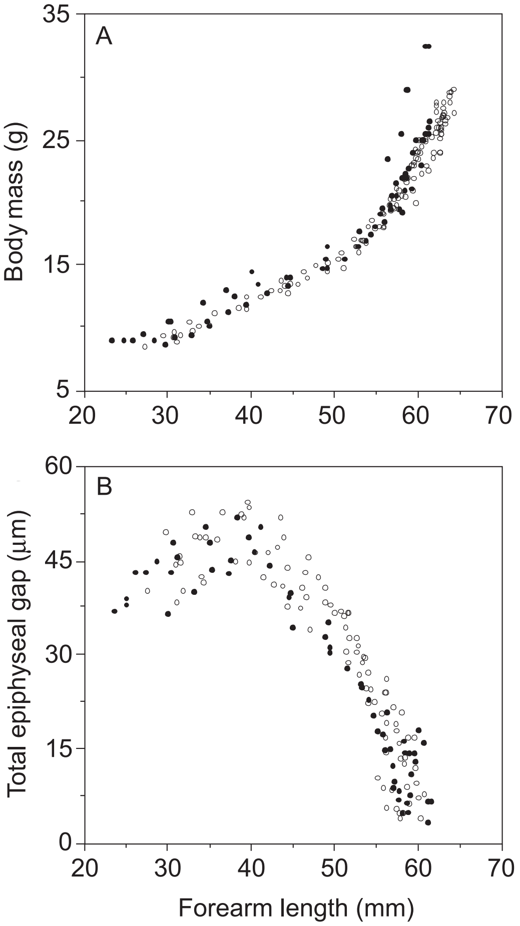

FIG. 3. Comparisons of (A) body mass and (B) the length of total epiphyseal gap of the fourth metacarpal-phalangeal joint of young *C. sphinx* under captive (open circles) and wild (solid circles) conditions with their respective forearm lengths; *n* = 225 (captive) and 69 (wild) for body mass, and *n* = 126 (captive) and 69 (wild) for the length of total epiphyseal gap

of early flight suggests that megachiropterans presumably do not need to manoeuvre so accurately during their foraging sallies as microchiropterans do. Kunz and Stern (1995) found that growth rates in body mass were negatively correlated with asymptotic body size, thus the smaller species growing faster than larger ones. Theoretically, asymptotic body mass is achieved by bats when growth becomes zero. However, 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). We rule out the possibility of advanced growth in captive condition due to the overabundance of food, mainly based on the absence of significant changes in the growth pattern between captive and free-ranging bats. Length of forearm should be an appropriate choice to predict age until its growth pattern becomes nonlinear. In addition, the length of total epiphyseal gap can be used as soon as the secondary centre of ossification formed and the epiphyseal gap begins to decrease linearly (after 15 days in *C. sphinx*). The values of linear increase in the forearm length and linear decrease in the total epiphyseal gap are used to derive equations for estimating the age of young bats in several studies (e.g., Kunz and Anthony, 1982; De Paz, 1986; Kunz and Robson, 1995; Isaac and Marimuthu, 1996; Rajan and Marimuthu, 1999; Baptista *et al.*, 2000; Cheng and Lee, 2002).

Our analysis of postnatal growth based on three models showed that the logistic and Gompertz models best described the growth patterns of length of forearm and body mass of *C. sphinx*, respectively. The logistic growth model best fitted to the growth rates of forearm length as well as body mass of *T. brasiliensis* (Kunz and Robson (1995), *Pipistrellus pipistrellus* (Boyd and Myhill, 1987) and *Plecotus auritus* (De Fanis and Jones, 1995). Similarly, McLean and Speakman (2000) reported that growth of forearm in *Plecotus auritus* best described by the logistic equation, and this model reflects a rapid growth and attainment of asymptote than von Bertalanffy equation. Nevertheless, Kunz and Robson (1995) pointed out that the logistic model might not be appropriate in all growth studies. Hughes *et al.* (1995) found that growth patterns of body mass and forearm length of *P. pipistrellus* sensu lato were best fitted by the logistic and Gompertz functions, respectively. Even though these nonlinear models are useful to compare between different species, such studies should be based on the same models (Zullinger *et al.*, 1984).

A few reports presented a marked difference in the postnatal growth pattern between free-ranging and captive bats. 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 maintained in captivity. However, similar to the present study, the growth trajectories of body mass and length of total epiphyseal gap in the fourth metacarpal-phalangeal joint in relation to the growth in the length of forearm of the Indian false vampire bat *Megaderma lyra* (Rajan and Marimuthu, 1999) are apparently similar in both captive and natural conditions. Since it is difficult to mimic the diet and foraging environment of insectivorous bats in captivity, such species usually show slower growth in captivity. On the other hand, it is relatively easy to provide and replenish regularly an acceptable diet to carnivorous and frugivorous bats. 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.

Baptista *et al*. (2000) compared two sampling methods, longitudinal and cross-sectional, to predict the age of free-ranging bats. Their study suggests that longitudinal method (mark-recapture sampling) is more reliable for age estimation compared to 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 *C. sphinx* based on the postnatal changes in the length of forearm and total epiphyseal gap may reliably be used in their behavioural, physiological and ecological studies.

ACKNOWLEDGEMENTS

We thank the two unknown referees for providing suggestions on an earlier version of the manuscript. The work was supported by a DST ‘Fast Track Scheme for Young Scientists’ to VE and a CSIR research project to GM.

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Received 16 October 2002, accepted 26 January 2003