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Postnatal Growth and Age Estimation in Horsfield's Leaf-Nosed Bat *Hipposideros larvatus*

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Ai-Qing Lin, Long-Ru Jin, Ying Liu, Ke-Ping Sun, and Jiang Feng (2010) Postnatal growth and age estimation in Horsfield's leaf-nosed bat *Hipposideros larvatus*. *Zoological Studies* **49**(6): 789-796. Patterns of postnatal growth and development in the length of the forearm, body mass, and length of the total gap of the 4th metacarpal-phalangeal joint of *Hipposideros larvatus* were studied under natural conditions in southwestern China. Based on these data, we developed empirical growth curves, derived growth rates, and established age-predictive equations and 3 nonlinear growth models. The length of the forearm and body mass followed linear patterns of growth until day 16 with respective growth rates of 1.66 mm/d and 0.40 g/d, and subsequently decreased to a stable level. The length of the total epiphyseal gap increased up to 12 d and then linearly decreased. Some young bats could take flight with 89.32% of the forearm length and only 62.13% of the body mass of adults by day 20. Two linear regression equations for age estimation were derived from the forearm length and the length of the total epiphyseal gap for 1-32 d. Growth patterns of the forearm length and body mass were both best described by logistic nonlinear growth models. The growth rate of *Hipposideros larvatus* was greater than that of many tropical bat species. http://zoolstud.sinica.edu.tw/Journals/49.6/789.pdf

Key words: Postnatal growth, *Hipposideros larvatus*, Age estimation, Body mass.

The postnatal growth period is a time that young mammals develop appropriate sensory and locomotor skills necessary to become independent of the mother (Baptista et al. 2000, Sharifi 2004a). Postnatal growth studies are important for understanding how life-history traits are influenced by extrinsic and intrinsic factors, e.g., local and regional climates, food supply, latitude, seasonal variations, roosting environments, colony and litter sizes, maternal conditions, gender, and birth timing (Kunz et al. 2009). In addition, accurate age determination is important to determine growth rates and to establish the timing of sexual maturity, the periodicity of reproduction, and the longevity and development of various behavioral repertoires (Elangovan et al. 2002, Chen et al. 2007). Data on growth trajectories of bats are particularly significant in deriving equations to predict age (Brunet-Rossinni and Wilkinson 2009).

Numerous studies on the postnatal growth of bats have been conducted under both natural (O'Farrrell and Studier 1973, Koehler and Barclay 2000, Chaverri and Kunz 2006, Liu et al. 2009, Jin et al. 2010) and captive conditions (Jones 1967, Boyd and Myhill 1987, Rajan and Marimuthu 1999, Elangovan et al. 2002). Bats under captive conditions are often fed an unnatural diet, or are not provided appropriate roosting environments and adequate flight space for exercise (Gould 1971, Buchler 1980, Mclean and Speakman 2000).

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Studies from captive conditions do not reflect the compromises and constraints imposed on animals in the wild (Kunz and Robson 1995). Investigations under natural conditions normally provide the most ecologically meaningful data. Under natural conditions, the 2 most common methods to assess postnatal growth are based on mark-recapture (longitudinal) sampling (Kunz and Anthony 1982, Isaac and Marimuthu 1996, Shen and Lee 2000, Reiter 2004, Dietz et al. 2007, Jin et al. 2010) and grab (cross-sectional) sampling (Baptista et al. 2000, Sharifi 2004a, Welbergen 2010). Compared to the cross-sectional method, the longitudinal method is more reliable for deriving growth rates and estimating ages during the postnatal growth period in free-ranging bats (Baptista et al. 2000).

Forearm length, body mass, and the length of the total epiphyseal gap were shown to be important variables for assessing postnatal growth rates and predicting the age of young bats at different growth stages (Kunz and Anthony 1982, Isaac and Marimuthu 1996). The length of the forearm and total epiphyseal gap remain the best variables for evaluating age-related changes during the postnatal period (Kunz and Robson 1995, Brunet-Rossinni and Wilkinson 2009). Body mass was also proven to be an important variable for assessing postnatal growth rates in bats (Kunz and Stern 1995). Kunz and Hood (2000) found a significant negative correlation between the postnatal growth rate and asymptotic body mass among bats. Moreover, 3 nonlinear models are generally used to describe the pattern of postnatal growth in bats (Mclean and Speakman 2000, Elangovan et al. 2003, Sharifi 2004a, Liu et al. 2009).

Most studies on postnatal growth in bats were conducted on vespertilionids (Jones 1967, O'Farrell and Studier 1973, Isaac and Marimuthu 1996, Hoying and Kunz 1998, Baptista et al. 2000, Koehler and Barclay 2000, Sharifi 2004b, Hermanson and Wilkins 2007, Liu et al. 2009). Only a few focused on the Hipposideridae (Gould 1979, Habersetzer and Marimuthu 1986, Cheng and Lee 2002, Jin et al. 2010), a family which is widespread in the Old World tropics and subtropics. Being a widespread and abundant species, ranging from northeastern South Asia into Southeast Asia (Simmons 2005), *Hipposideros larvatus* Horsfield plays an ecologically and economically important role in tropical and subtropical Old World localities. This species is listed as a species of least concern by the IUCN (Bates et al. 2008). However, nothing about the external characters at birth or postnatal growth has been reported, and little information is known concerning the life history of *H. larvatus*. Accordingly, the present study, based on our field work in southwestern China, was conducted to provide background data on patterns of postnatal growth and a quantitative method for aging immature individuals of this species.

MATERIALS AND METHODS

The study was conducted in 2 caves (22°36'N, 103°51'E and 22°36'N, 103°49'E) in Hekou Country, Yunnan Province, southwestern China in Apr.-June 2009. The caves had similar physical characteristics (ca. 100 m in total length × 2 m wide × 2.2 m high), and were located in the tropics surrounded by dense forest of mostly rubber trees (*Hevea brasiliensis* Müll. Arg.). One housed a mixed colony of around 50 *Hipposideros larvatus*, 150 *H. pomona* Andersen, and 200 *H. cineraceus* Blyth, and the other around 100 *H. larvatus* and 200 *H. pomona*.

From our previous work, we know that *H. larvatus* gives birth in mid-May. We checked the caves daily about 15 d before parturition. We gently hand-captured neonates, and those with an attached umbilical cord and sometimes a placenta were assumed to be 1 d old (Kunz 1973, Kunz and Robson 1995, Kunz et al. 2009). Forty-three neonates with umbilical cords were marked with a uniquely numbered, plastic, split-ring band on the right forearm (Table 1).

Body mass was measured with an electronic balance (LC-50 ProScale, Northglenn, CO, USA) to the nearest 0.01 g. Lengths of the forearm and total gap of the 4th metacarpal-phalangeal joint were measured with electronic vernier calipers (IP67, TESA-CAL, Renens, Switzerland) to the nearest 0.01 mm. The length of the total epiphyseal gap was measured while the wing of the bat was spread over a transparent solid

Table 1. Numbers of newborn *Hipposideros larvatus* captured on day 1 and subsequently recaptured on other sampling occasions

Parameter	Day of sampling								
	1	4	8	12	16	20	24	28	32
Number of recaptured bats	43	39	36	31	29	22	21	20	18
Marked bats recaptured (%)	-	91	84	72	67	51	49	47	42

plastic sheet lighted from below with a flashlight in order to make the gap visible (Sharifi 2004b). To minimize the error of using vernier calipers, the mean of 3 repeated measurements for each individual was used for the analysis. Pups were returned to the site of capture after observations and measurements were obtained. We visited the caves twice in the 1st wk following parturition and then every 4 d timed after the nightly emergence of adults. The study continued to when the young began to make foraging trips, after which it was difficult to capture them.

No significant difference was found in the forearm length (25.32 ± 0.53 vs. 25.35 ± 0.58 mm; $t = -0.09$, $d.f. = 41$, $p = 0.93$) or body mass (5.1 ± 0.27 vs. 5.11 ± 0.26 g; $t = -0.05$, $d.f. = 41$, $p = 0.96$) of bats at birth in the 2 caves. There was also no significant difference between growth rates of forearm length of bats during the period of a linear increase in the variable (1-16 d; 1.65 ± 0.08 vs. 1.66 ± 0.11 mm/d; $t = -0.76$, $d.f. = 27$, $p = 0.45$) in the 2 caves. Therefore, the morphological data of young bats in the 2 caves were pooled together for subsequent analyses.

We used a linear regression analysis, with age as the dependent variable, to derive age-predictive equations based on the pooled data of linear changes of forearm length and length of the total gap of the 4th metacarpal-phalangeal joint. Ninety-five percent confidence intervals and prediction limits were plotted for the regression equations of the length of the forearm and total epiphyseal gap. Growth data of the forearm and body mass of young bats were fitted to the following 3 models using the Marquardt-Levenberg algorithm: the logistic equation, the Gompertz equation, and the von Bertalanffy equation (Zullinger et al. 1984). The equations are as follows:

Logistic: $W = A (1 + \exp(-K (t - I)))^{-1}$,
Gompertz: $W = A \exp (-\exp(-K (t - I)))$, and
Von Bertalanffy: $W = A (1 - (1/3) \exp(-K (t - I)))^3$;

where A is the asymptotic value (g), W is the body mass (g) at age (t), K is the growth rate constant (1/d), and I is the age at the inflection point (d). Parameters A and K in each model were estimated for the growth of mass in the neonate population. Similar equations were used for the length of the forearm. Results from the 3 different models were compared by the goodness of fit, which was inversely related to the sum of squares of the models after checking systematic deviations (Zullinger et al. 1984, Swift 2001, Elangovan et al. 2003). All statistical analyses were performed using SPSS vers. 16.0 (SPSS, Chicago, IL, USA)

RESULTS

The 1st newborn *H. larvatus* with an attached umbilical cord was found on 14 May and the last one on 25 May 2009. All females with young had a single offspring. Young of *H. larvatus* at birth were naked with gray dorsal and pink ventral areas. Their eyes were closed, ears were folded, and teeth were deciduous. Eye slits opened at ca. 12 d of birth. Some young were able to make a straight-line flight at 20 d and flew freely inside the cave at 24 d of age. The young bats left the cave for their 1st foraging flights at about 1 mo old, when the epiphyseal gap in the metacarpal-phalangeal joint was still visible.

Neonates were born with a forearm length averaging around 42.87% of the length of adult females, and around 23.64% of the body mass of adult females. During the 1st 16 d, both forearm length and body mass increased in linear fashions, with respective growth rates of 1.66 mm/d and 0.40 g/d (Figs. 1A, B). Subsequently, the rate of increase in these 2 characters slowed. On the contrary, the length of the total epiphyseal gap linearly increased until 12 d, and then linearly declined (Fig. 1C). Young bats could fly for a short distance with 62.13% of the body mass and 89.32% of the forearm length of adults by day 20. The young had reached 61.49% of the body mass and 92.44% of the forearm length of adults on day 24 when they could freely fly in the cave. Most young bats experienced a loss of body mass (Fig. 1B) after the 1st flights in the 4th wk when they initially mastered flying skills. At the age of 32 d, the young approached 72.07% of the body mass and 96.13% of the forearm length of adults.

Age was estimated quantitatively, based on linear changes observed in the length of the forearm (1-16 d) and the length of the total epiphyseal gap (12-32 d). A linear regression equation allowed age estimates according to forearm length values ranging 25.32-49.81 mm (Fig. 2A). High values of the correlation coefficient ($r^2 = 0.99$, $p < 0.001$) indicated that the length of the forearm was a reliable character for estimating the age of young *H. larvatus* in the 1st 16 d. A similar equation, based on the length of the total epiphyseal gap, was derived to predict the age from 12 d after birth when it ranged

5.41-2.76 mm (Fig. 2B). Forearm length and body mass were both fitted to the 3 non-linear models. The predicted values for the forearm length of the 3 non-linear growth models had correlation coefficients of > 0.99. Nevertheless, based on the model sum of squares, the logistic model appeared to be the best-fitting growth model for forearm length (Table 2). The predicted values for body mass of the 3 non-linear growth models had correlation coefficients of > 0.97. We chose the logistic equation as the best-fitting growth model to express the postnatal change in body mass utilizing the same statistical criteria. Forearm length and body mass respectively indicated an asymptotic maximum value of 57.99 mm with a growth rate of 0.13 mm/d and an asymptotic maximum value of 13.91 g with a growth rate of 0.12 g/d for young bats.

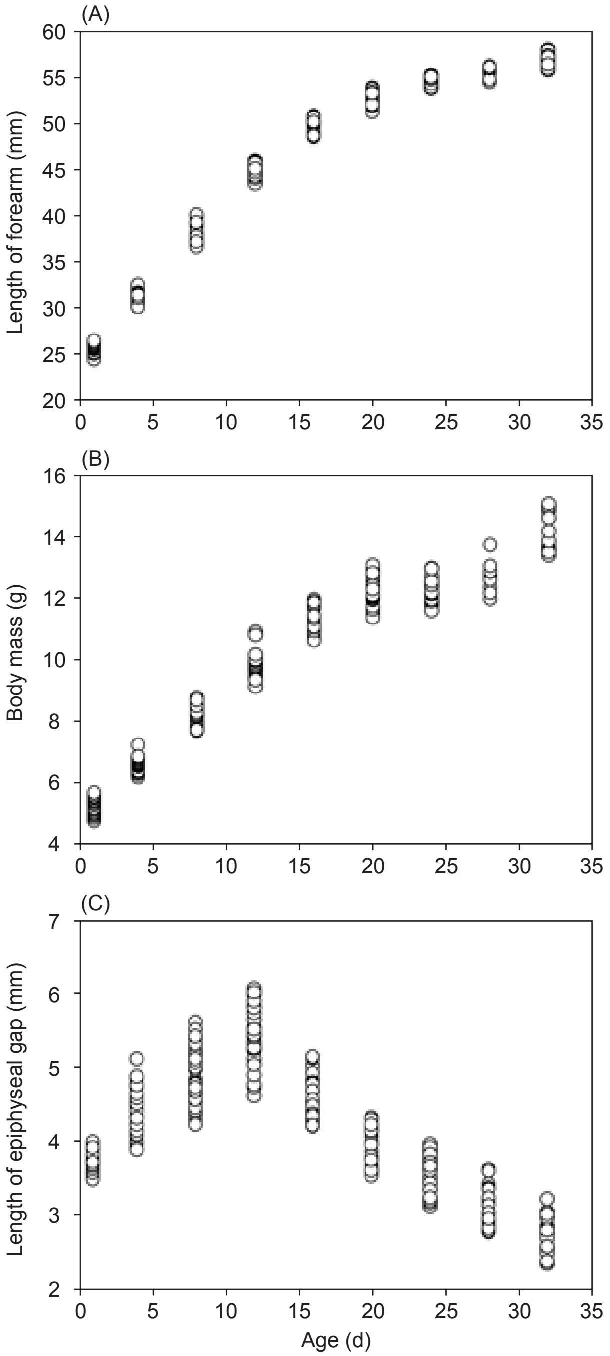

Fig. 1. Empirical growth curves for (A) the length of the forearm, (B) body mass, (C) the length of the total gap of the 4th metacarpal-phalangeal joint of young *Hipposideros larvatus* from days 1 to 32. Forty-three neonates were marked. Some points represent more than 1 observation.

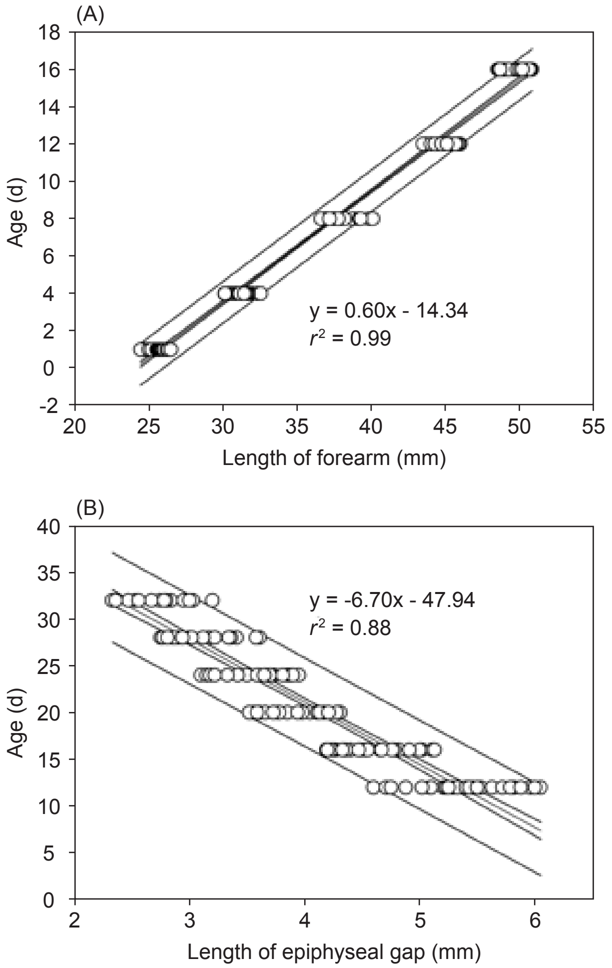

Fig. 2. Regression line estimating the age of *Hipposideros larvatus*, including 95% confidence intervals (narrow band) and prediction intervals (wide band), for values of forearm length (A) for the 1st 16 d; and from the length of the total gap of the 4th metacarpal-phalangeal joint (B) for days 12-32. Some points represent more than 1 observation.

DISCUSSION

Among bats, the young average around 22.3% (12%-43%) of their mother's body mass at birth (Kurta and Kunz 1987). Neonates of *H. larvatus* weighed around 23.64% of the mother at birth, which is similar to vespertilionids. Like other bat species, e.g., *Myotis lucifugus* (Kunz and Anthony 1982, Baptista et al. 2000), *Artibeus watsoni* (Chaverri and Kunz 2006), and *M. septentrionalis* (Krochmal and Sparks 2007), forearm length and body mass of *H. larvatus* linearly increased during the early postnatal period, and then the rates of growth decreased. The length of the total gap of the 4th metacarpal-phalangeal joint showed an increase, and then linearly declined in the later period.

Most microbats cannot fly before they attain 70% of the adult body mass and over 90% of the adult wing dimensions (Barclay 1994, Kunz and Stern 1995). However, on day 20 when they could fly a short distance, young *H. larvatus* had only achieved 89.32% of the forearm length and 62.13% of the body mass of adults. Even at the age of 32 d when the young took their 1st foraging flights, they had attained only 72.07% of the body mass of adults. Climate and food may be the most important factors influencing postnatal growth in bats (Tuttle and Stevenson 1982, Kunz and Stern 1995, Dietz et al. 2007). Generally, the activity of flying insects may be altered by climatic factors such as abnormal temperatures (Hoying and Kunz 1998, Fenoglio et al. 2008). Growth rates of young bats should be lower if lactating females are subjected to lower levels of nutrition (Hoying and Kunz 1998, Dietz et al. 2007). Hoying and Kunz (1998) found that the postnatal growth in body mass of *Pipistrellus subflavus* in eastern Massachusetts, USA was lower in 1982 than in 1981. They mainly attributed this difference to contrasting temperatures and insect abundances during the 2 yr of study. However, climate and food resources were probably not the reasons for the low level of body mass of *H. larvatus* in our tropical study area. Wing loading is highly correlated with body mass and wing dimensions (Norberg and Rayner 1987). Changes in body mass can dramatically affect the flight capability of bats. A smaller body mass causes a lower wing loading in the young, which in turn increases maneuverability and decreases the cost of flight at a time when young bats are learning how to fly, and detect and forage for flying insects (Hughes et al. 1995). A low body mass was probably the reason for the rapid development of flight in young *H. larvatus*. Similar disproportional developments of wing dimensions and body mass were reported for other bats, e.g., *P. subflavus* (Hoying and Kunz 1998) and *Rhinolophus mehelyi* (Sharifi 2004a). However, the low body mass of young *H. larvatus* is rare in microbats. The mechanism of postnatal growth of the body mass in *H. larvatus* should be further studied.

Table 2. Parameters derived from the logistic, Gompertz, and von Bertalanffy growth models of forearm length and body mass ($\overline{X}$ ± S.E.) data of 43 young *Hipposideros larvatuss*

Model	Parameter	Forearm length	Body mass
Logistic	A	57.99 ± 0.154	13.91 ± 0.129
	K	0.13 ± 0.001	0.12 ± 0.004
	I	3.00 ± 0.052	5.24 ± 0.191
	MSS	144.04	67.19
Gompertz	A	59.47 ± 0.22	14.56 ± 0.181
	K	0.10 ± 0.001	0.09 ± 0.003
	I	-0.40 ± 0.054	1.55 ± 0.154
	MSS	186.09	67.68
Von Bertalanffy	A	60.18 ± 0.263	14.90 ± 0.213
	K	0.09 ± 0.001	0.07 ± 0.003
	I	-13.10 ± 0.228	-13.84 ± 0.563
	MSS	208.82	68.71

A, asymptotic size of forearm length (mm) or body mass (g); K, growth rate constant; I, age at the inflection point (d); MSS, model sum of squares.

Young *H. larvatus* experienced a loss of body mass in the 4th wk during the early flight period, which was also reported in other bats, e.g., *P. subflavus* (Hoying and Kunz 1998), *Plecotus auritus* (Mclean and Speakman 2000), *R. mehelyi* (Sharifi 2004a), and *M. macrodactylus* (Liu et al. 2009). Such a temporary loss in body mass possibly reflects the poor foraging ability to provide food when they are weaned and/or a shift by young animals from a diet of milk to one composed of insects (Kunz 1987). However, Hughes et al. (1995) compared the trajectories of the body mass of 3 groups of young *P. pipistrellus*. There were different growth regimes and very disparate body masses in the early growth period among these 3 groups. Nevertheless, all groups experienced a mass recession and converged to precisely the same body mass at the same time. Hamilton and Barclay (1998) showed that juveniles of *Eptesicus fuscus* maintained a low body mass even under conditions that permitted adults to accumulate greater fat deposits. Therefore, a loss of body mass might be related to a reduction in flight costs and the risk of predation at a time when flight and foraging skills are still developing (Hamilton and Barclay 1998).

In the present study, the length of the forearm and the total gap of the 4th metacarpal-phalangeal joint were identified as the best variables for evaluating age-related changes during the postnatal period in *H. larvatus*. Similar results were also found in other species, e.g., *M. lucifugus* (Baptista et al. 2000), *H. terasensis* (Cheng and Lee 2002), and *M. blythii* (Sharifi 2004b). Due to the 2 linear regression equations, we can estimate the age of young *H. larvatus* at 1-32 d.

The forearm length and body mass in *H. larvatus* were both fitted to the 3 non-linear models (logistic, Gompertz, and von Bertalanffy). The logistic model was judged to provide the most appropriate description of growth rates in *H. larvatus* because the overall sum of squares from the model was the smallest, and the model was computationally simple but with biological relevance (Kunz and Robson 1995, Krochmal and Sparks 2007). Body mass in the logistic model indicated an asymptotic maximum value of 13.91 g for young bats, which approached 71.04% of the weight of adults (19.58 g). The asymptotic mass of young bats is usually less than the adult mass, because it does not include accretionary growth after the 1st yr, nor does it include the deposition of fat in autumn (Kunz and Stern 1995). We were unable to quantify changes in young bats beyond an age of 32 d because it was difficult to recapture young flying bats. Nevertheless, we predict that the body mass of young *H. larvatus* would gradually increase to the range of adults because of their mature foraging ability.

By means of the logistic growth equation, Kunz and Hood (2000) found a significant negative correlation between the postnatal growth rate and asymptotic body mass. After the effect of body mass was removed, latitude was the only extrinsic variable that affected postnatal growth rates. However, when tropical species were examined, no significant relationship between asymptotic body mass and postnatal growth was observed. They mainly attributed this result to the small sample size. Based on reviews by Kunz and Hood (2000) and Kunz and Stern (1995), growth constants of body mass of all tropical bats (K = 0.01 to 0.10, n =19) that were larger in asymptotic mass were lower than that of *H. larvatus* (K = 0.123) in our study. The other tropical species (*Molossus molossus*, K = 0.08; *P. mimus*, K = 0.11) that had a smaller asymptotic mass also had a lower growth constant. Moreover, we studied the postnatal growth of *H. cineraceus* (with an asymptotic maximum value of body mass of 3.53 g, Jin et al. 2010) in the present study area during a corresponding period. Young of *H. cineraceus* were much smaller in size and had a slightly lower growth constant of body mass (K = 0.12) than those of *H. larvatus*. Our limited comparison is consistent with Kunz and Hood's (2000) result about the relationship between asymptotic body mass and postnatal growth rate in tropical bat species. Postnatal growth rates are likely influenced by climate, seasonal conditions, food supply, habitat, latitude, social environment, maternal factors, gender, and litter and colony sizes (Bernard and Cumming 1997, Hoying and Kunz 1998, Kunz and Hood 2000, Dietz et al. 2007, Kunz et al. 2009). Additionally, even if studies under natural conditions are preferred over those of captive animals, there are some drawbacks. For instance, it is not always clear what factors influence growth rates, because all of them are very seldom measured or measurable (Kunz et al. 2009). Therefore, integrated data on various factors collected utilizing appropriate methods are important for interspecific and intraspecific comparisons.

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