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POSTNATAL GROWTH, AGE ESTIMATION, AND SEXUAL MATURITY IN THE FORMOSAN LEAF-NOSED BAT (*HIPPOSIDEROS TERASENSIS*)

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Changes in body mass, length of forearm, and length of total epiphyseal gaps of young Formosan leaf-nosed bats (*Hipposideros terasensis*) were monitored by marking and recapturing at a maternity colony in central Taiwan. Length of forearm and body mass of 1-day-old neonates averaged 43.3 mm ± 2.7 *SD* and 15.9 g ± 3.3 *SD*, respectively. Increase in forearm length and body mass was fastest in the 1st week after birth, but rate of increase decreased thereafter. Length of total epiphyseal gap increased to its maximum size at about 10 days after birth and subsequently decreased linearly. Growth constants derived from the logistic growth model were 0.096 and 0.114 for the increase in length of forearm and body mass, respectively. Age of *H. terasensis* between 1 and 44 days can be estimated either by length of forearm when forearm length is ≤91 mm or by length of total epiphyseal gap when forearm length is >91 mm. Subsequent monitoring suggested that males of *H. terasensis* are capable of reaching sexual maturity in their 1st year and females in their 2nd year. When compared with other bats, growth rate of *H. terasensis* was faster than that of many tropical species but slower than that of most temperate species.

Key words: body mass, growth constant, Hipposideridae, length of forearm, subtropical insectivorous bat, total epiphyseal gap

Studies on sizes of animals at birth and on subsequent postnatal growth are important for understanding the aspects of their life history (Kunz and Robson 1995) and for understanding a wide range of ecological, behavioral, and developmental patterns (Habersetzer and Marimuthu 1986; Powers et al. 1991; Studier and Kunz 1995). Many studies on postnatal growth and development of bats have been conducted under natural conditions (Baptista et al. 2000; Hoying and Kunz 1998; Isaac and Marimuthu 1996; Koehler and Barclay 2000; Kunz and Anthony 1982; Kunz and Robson 1995) because such studies provide the most ecologically meaningful data. Tuttle and Stevenson (1982) reported that 14 of the 19 chiropteran families lack data on postnatal growth, and ≤3% of known bat species have been investigated regarding their growth and development. Eighty percent of studies on postnatal growth are restricted to the family Vespertilionidae, particularly bats of the temperate zone. Our study on *Hipposideros terasensis* is the 1st to report postnatal growth of a subtropical insectivorous member of the family Hipposideridae.

Members of the family Hipposideridae, or the Old World leaf-nosed bats, inhabit tropical and subtropical regions of Africa, Asia, and Australia (Nowak 1994). The Formosan leaf-nosed bat (*H. terasensis*) is the largest insectivorous bat endemic to Taiwan. Average body mass of an adult is about 60 g. *H. terasensis* generally roosts in caves, abandoned tunnels, and buildings

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at elevations of ≤1,000 m, and individuals assemble at a distance of about 5–10 cm from each other. Pregnant females usually give birth to a single young each year between May and early June (Chen 1995; Cheng 1999; Lin et al. 1997). *H. terasensis* was once regarded as a subspecies of *H. armiger* (Kishida 1924; Nowak 1994). However, some scholars consider *H. terasensis* as a separate species on the basis of its distinct morphological characteristics (Bogdanowicz and Owen 1998; Yoshiyuki 1991).

Postnatal growth period, which is defined as the time from birth until the epiphyses of long bones become visibly closed (Kunz 1987; Kunz and Anthony 1982), may extend from several weeks up to several months in bats. The period can be operationally divided into 3 distinct stages: preflight, early flight and weaning, and postflight (Kunz 1987). Body mass, length of forearm, and length of total epiphyseal gap have been shown to be important variables for estimating age of young at different growth stages on the basis of mark–recapture data of known-age young (Baptista et al. 2000; Isaac and Marimuthu 1996; Kunz and Anthony 1982; Kunz and Robson 1995; Rajan and Marimuthu 1999). Reliable equations for estimating age of young bats can be derived by combining mean changes in length of forearm during the preflight period with changes in the 4th metacarpal–phalangeal epiphyseal gap during the early flight and weaning period. Body mass is not a good character for estimating age because of its sensitivity to nutritional input, energy expenditure, and water flux (Kunz 1987), but it is ideal for interspecific comparison of growth rates throughout the postnatal growth period among species from different regions (Kunz and Stern 1995). Kunz and Hood (2000) reviewed and compared growth rates of postnatal body mass in 41 species of bats, including 31 microchiropterans from temperate and tropical regions. They found that growth rates of young bats decreased linearly with increasing asymptotic body mass. When the effect of body mass was removed, latitude (tropical or temperate) became the only variable that had a significant effect on postnatal growth rates, with temperate species growing faster than tropical species.

In this study we measured the size of *H. terasensis* at birth. We describe the pattern of their postnatal growth under natural conditions from birth to the postflight period and derive equations for estimating their ages. We also describe the trend in changes in body mass and length of forearm for young *H. terasensis* using recapture data in subsequent months until the subjects migrated to winter hibernacula. In addition, we monitor changes in the percentage of sexually mature individuals in a cohort in subsequent years to determine age of sexual maturity of both males and females. Finally, we compare the growth constant and age of sexual maturity of *H. terasensis* with that of other bats described by Kunz and Hood (2000), Kunz and Stern (1995), and Tuttle and Stevenson (1982). Because *H. terasensis* is a large microchiropteran species inhabiting subtropical regions, we predict that postnatal growth rate of *H. terasensis* will be slower than that of most temperate bats but faster than that of most tropical species and that age of sexual maturity of *H. terasensis* will be later than that of most temperate bats but earlier than that of most tropical species.

Materials and Methods

Our study was conducted at a roost of *H. terasensis* inside an abandoned tunnel at Chungliao, Nantou County, in central Taiwan (120°44′E, 23°54′N). The tunnel, which has 2 entrances facing east and west, is 300 m long, 3.7 m wide, and 4 m high and is surrounded by betel nut (*Areca catechu* L.) plantations and orchards. A stream flows adjacent to the south side of the tunnel. Approximately 300 individuals roosted in this tunnel during the breeding season from 1997 to 1999. Bats usually arrive in late February or early March and depart in late November or December each year.

In mid-May to early July 1997, we hand-captured young *H. terasensis* by plucking them off the wall inside the tunnel immediately after the nightly emergence of adults at 2- to 9-day intervals. Infants with an attached umbilical cord were assumed to be 1 day old (Hoying and Kunz 1998; Isaac and Marimuthu 1996; Kunz and Anthony 1982; Kunz and Robson 1995). We placed the young in cloth-holding bags after they were caught and processed them as follows. We weighed individuals to the nearest 0.05 g using a portable electronic balance (Acculab, Huntingdon Valley, Pennsylvania) and measured the length of forearm and total epiphyseal gap of the 4th metacarpal–phalangeal joint to the nearest 0.05 mm using dial calipers (Mitutoyo, Japan; Kunz and Anthony 1982; Kunz and Robson 1995). When measuring the length of epiphyseal gap, we placed a lamp under the wing of the subject so that the cartilaginous band would show up clearly. We marked each young by fitting a uniquely numbered aluminum band (5.2 by 5.5 mm; Lambournes Ltd., Birmingham, United Kingdom) to the right arm of females and to the left arm of males. Then, we returned the young by hand to the site of capture inside the tunnel. We completed the whole task within 1 h to minimize disturbance. Lactating females generally return to the roost about 1 h after they emerge. Within the hour, we captured and measured as many young as possible (usually 10–15 pups each time).

We continued to recapture young until they approached adult size and could fly independently. We estimated age of sexual maturity of the 1997 cohort by recapturing and examining their reproductive characteristics every month from August 1997 to May 1999, except in winter. Females were considered mature if they were pregnant or showed signs of parturition or nursing, i.e., swollen and elongated nipples or pubic nipples (or both), which are a special tissue situated in the pubic region in species of *Hipposideros* and which can be observed easily on nursing females (Racey 1988). Males were considered mature if they had enlarged testes or epididymides (or both), indicating active spermatogenesis. During the period of active spermatogenesis, which generally begins in April, peaks in June, and ceases in September (Chen 1998), the sizes of testes may increase from 12.1–24.2 mm^3 in the nonspermatogenesic stage to 38.4–96.1 mm^3 and can be easily diagnosed from the outside. We mist-netted postpartum females at tunnel entrances and measured their body mass and length of forearm in late May of 1997 to provide a measurement of the sizes of standard adults.

We used a linear regression model to derive equations of age estimation for young *H. terasensis* on the basis of changes in length of forearms and epiphyseal gaps (Kunz and Anthony 1982; Kunz and Robson 1995). We used data only from those young that were captured more than once during the analysis of growth and age estimation. We used an unpaired *t*-test to compare length of forearm and body mass of males and females at birth and chi-square test to evaluate whether sex ratio at birth was different from unity. The logistic model was applied to derive growth curves and growth constants of young (Kunz and Robson 1995; Stern and Kunz 1998). We also compared growth rate of *H. terasensis* with that of other microchiropteran bats, described by Kunz and Hood (2000), by comparing growth constants of these bats.

RESULTS

Ten young *H. terasensis* were captured and marked on the 1st night of this study on 20 May 1997. Length of forearm of the largest young without an attached umbilicus was 57.5 mm, and body mass was 24.5 g. According to the age-estimation equation given subsequently, this young bat was about 6–7 days old. During this study the last young with an attached umbilicus was captured on 27 May 1997. In June we did not capture any young with attached umbilici. These results reveal that *H. terasensis* in this roost gave birth from mid- to late May in 1997, which coincides with the beginning of warm and wet season in the Nantou area (Fig. 1).

A total of 63 young (33 females and 30 males) were captured and measured between 20 May and 2 July, during the preflight stage. The sex ratio (1 female : 0.91 males) did not differ significantly from unity ($\chi^2 = 0.14$, $d.f. = 1$, $P > 0.05$). Only 9 of these young had an attached umbilicus. Length of forearm of these 1-day-old young ranged from 40.0 to 47.1 mm ($\bar{X} = 43.3 \pm 2.7$), and their body mass ranged from 11.2

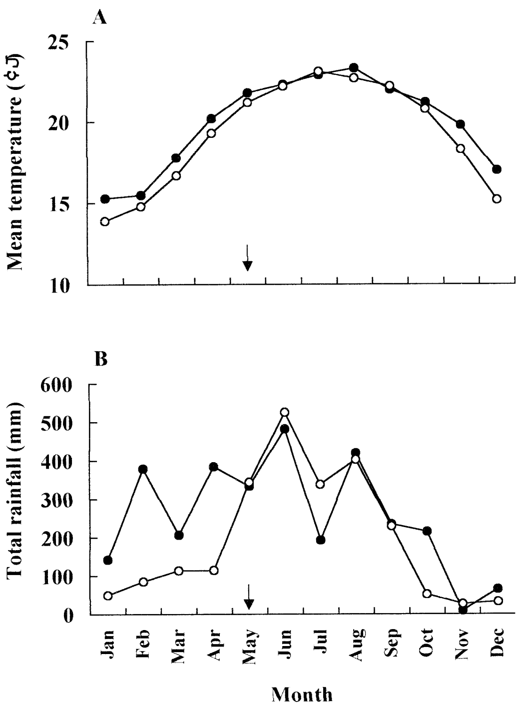

FIG. 1.—Climatic conditions throughout the year at study site in Nantou, central Taiwan. A) Mean daily temperature and B) total rainfall in the Nantou area in 1961–1990 (open symbols) and 1997 (closed symbols). Data from Sun Moon Lake weather station. Arrow indicates beginning of parturition of *Hipposideros terasensis*.

to 20.2 g ($\bar{X}$ = 15.9 ± 3.3). No significant difference was found between length of forearm of male ($\bar{X}$ = 47.0 ± 0.1, n = 2) and female ($\bar{X}$ = 42.2 ± 2.3, n = 7; t = 0.03, *d.f.* = 6, $P > 0.05$) young, although average length of forearm of males is longer. Similarly, body masses of male ($\bar{X}$ = 18.5 ± 2.4, n = 2) and female ($\bar{X}$ = 15.3 ± 3.0, n = 7) young were not significantly different (t = 0.21, *d.f.* = 6, $P > 0.05$).

Newborns are naked with a gray dorsal part and a pink ventral part. Their eyes are closed, and ears are folded. Eye slits appear within 1 week after birth, and eyes are completely open after 2 weeks. Ears become erect at about 1 week of age. When roosting inside tunnel, young often firmly attach to 1 of the 2 pubic nipples on the ventral side of their mothers, in a head-up position. After mothers emerge to forage, the young that are left behind generally hang on the wall in a loose group. They can fly a short distance inside the tunnel when 3–4 weeks old. Some mothers carry their young to forage even when the young are already fairly large in size (41–43 g). On 7 July 1997 a mother–young pair was captured, and the young was estimated to be about 6 weeks old. When young are about 1 month old, their fur is similar to that of adults but darker in color, which makes them easily distinguishable from their mothers' brown-colored fur. The young could fly independently at about 7 weeks old, but most of those caught in early August still had a visible epiphyseal gap on the metacarpal–phalangeal joint.

Of the 63 young captured during this study, 7 were recaptured once, 9 were recaptured twice, 3 were recaptured thrice, and 5 were recaptured 4 times, for a total of 54 recaptures before they could fly independently. Therefore, only 24 young (38.1%) were recaptured 1 or more times during the growth period. The recapture intervals of these young ranged from 2 to 28 days. To increase sample size for deriving postnatal growth curve, those young with a forearm length <47.1 mm, but without an attached umbilicus, were regarded as 2 days old.

By examining recaptured young, we found that rate of increase in body mass was highest in the 1st week (2.06 g/day), after which growth rate decreased (Fig. 2a). The rate of increase was reduced to 0.62 g/day in the 2nd week and then to 0.38, 0.27, 0.21, and 0.17 g/day in subsequent weeks. Average body mass of neonates is about 23% of that of their mother (60.33 ± 3.21 g, n = 3) and approaches 70% of their mother's mass when they are 6 weeks of age.

Length of forearm also increased continuously during the 6-week period of postnatal growth (Fig. 2b). During the 1st week, rate of increase in length of forearm was

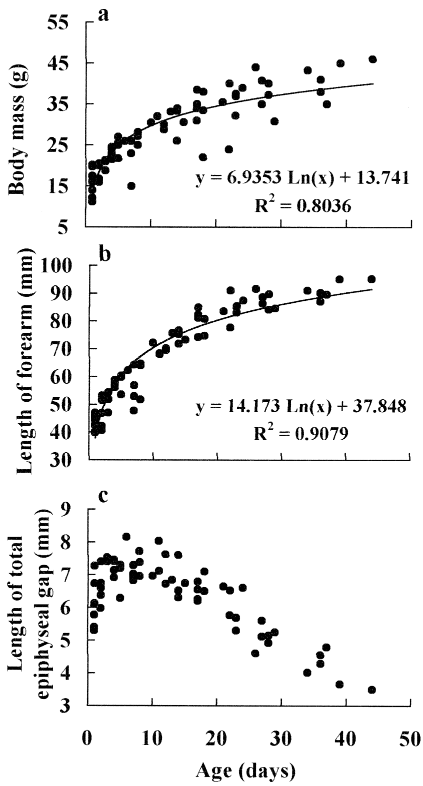

FIG. 2.—Postnatal growth patterns of young *Hipposideros terasensis* based on measurement of a) body mass, b) length of forearm, and c) length of total epiphyseal gap of 4th metacarpal–phalangeal joint.

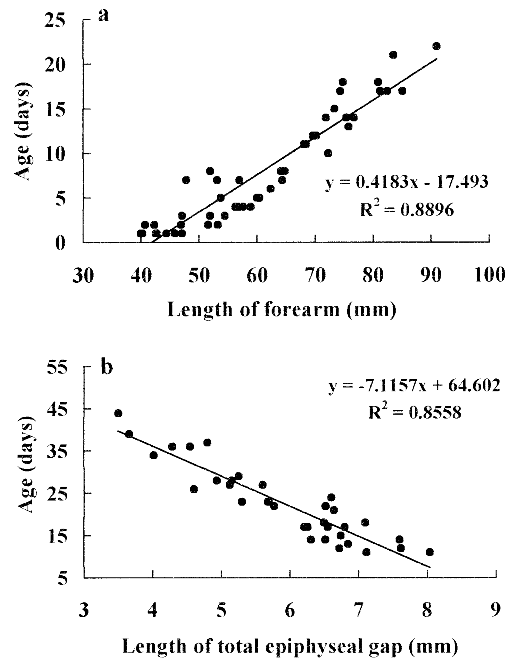

FIG. 3.—Age-predictive relationships between a) length of forearm and age (1–22 days) and b) length of total epiphyseal gap and age (14–44 days) in *Hipposideros terasensis*. The age-predictive equation in a) is valid when length of forearm $\leq$ 91 mm and the age-predictive equation in b) is valid when length of forearm $>$ 91 mm.

highest (4.21 mm/day), with length of forearm nearly doubling in the 1st week. Thereafter, rate of increase reduced to 1.27 mm/day in the 2nd week and then to 0.77, 0.56, 0.44, and 0.36 mm/day in subsequent weeks. Length of forearm of newborn *H. terasensis* was about 40% of that of an adult female (93.6 $\pm$ 0.17 mm, $n = 3$). By 14 days of age, length of forearm averaged about 80% of the adult size. By 44 days, length of forearm was almost the same as that of an adult female. Length of total epiphyseal gap increased linearly for about 10 days and then decreased linearly from 10 to 44 days (Fig. 2c).

We derived logistic equations to describe postnatal growth patterns of young *H. terasensis* by fitting a sigmoidal curve to growth data (see Kunz and Robson 1995; Stern and Kunz 1998). Equations are as follows: forearm length $= 93.91[e^{-0.096(t-1.51)} - 1]^{-1}$ and body mass $= 40.7[e^{-0.114(t-3.33)} - 1]^{-1}$, where t is age in days, and 0.096 and 0.114 are growth constants.

To derive regression equations for predicting age on the basis of length of forearms and total epiphyseal gaps, we divided the postnatal growth period into 2 stages over which linear regressions could be computed. Regression analysis indicates that length of forearm can be used to reliably estimate age of young *H. terasensis* up to 21 days. The equation for estimating age on the basis of length of forearm is valid if this dimension is $\leq$91 mm (Fig. 3a), i.e., age (days) = 0.42 (forearm length) − 17.49 ($r^2 = 0.89$, *d.f.* = 48, $P < 0.05$). To estimate

TABLE 1.—Sexual maturation of male and female *Hipposideros terasensis* as shown by recapture of bats from the newborn cohort of 1997 in 1997, 1998, and 1999.

	Year					
	1997		1998		1999	
	Female	Male	Female	Male	Female	Male
Number recaptured	42	42	15	16	14	4
Number sexually mature	0	0	0	10	8	4
Percent sexually mature	0	0	0	62.5	57.1	100

age of young when length of forearm is >91 mm, length of total epiphyseal gap was used (Fig. 3b). By reversing the axes of regression analysis for age versus length of epiphyseal gaps (see Kunz and Anthony 1982), the equation for age estimation on the basis of length of total epiphyseal gap was derived, i.e., age (days) = -0.71 (total epiphyseal gap) + 64.60 ($r^2 = 0.86$, $d.f. = 33$, $P < 0.05$). Age estimation by this equation is valid for young that are 22–44 days old when length of forearm is >91 mm. Together, these 2 equations allow us to predict the age of young *H. terasensis* from 1 to 44 days after birth.

From May to November 1997, a total of 84 young bats (42 females and 42 males) were captured. Of these, 31 bats (15 females and 16 males) were recaptured in 1998 and 18 (14 females and 4 males) in 1999. In 1997 none of the recaptured females or males had reached sexual maturity (Table 1). In 1998 none of the recaptured females had the status of pregnancy, parturition, or nursing, but 62.5 % of the recaptured males had enlarged testes or epididymides (or both); these males were regarded as sexually mature. We found the 1st young male with enlarged testes on 21 April 1998. This finding showed that young males could reach sexual maturity within 12 months of birth. In 1999, 57.1% of the recaptured females had elongated pubic nipples, which are signs of sexual maturity. All the recaptured males showed evidence of spermatogenesis. Results indicated that some male *H. terasensis* are capable of reaching sexual maturity in their 1st year, whereas females do not become sexually mature until their 2nd year or later.

DISCUSSION

Altringham (1996) showed that megachiropterans can fly at an age of 9–12 weeks, with weaning at 15–20 weeks, whereas in microchiropterans these traits occur at 2–6 weeks and 5–10 weeks, respectively. Young vespertilionid bats become volant at ages between 2 weeks and 2 months, mostly at 3–4 weeks, and weaning occurs between 5 and 8 weeks (Tuttle and Stevenson 1982). Young *H. terasensis* born in mid- to late May begin to fly at ages of 3–4 weeks and emerge to feed independently at about 7 weeks of age. This coincides with the time of weaning, when their diet consists mainly of insects (Chiu 2000). However, most of the young caught in early August still had a visible epiphyseal gap on the metacarpal–phalangeal joint. According to the definition of Kunz and Anthony (1982), postnatal growth period of *H. terasensis* might extend to 2.5 months before their metacarpal–phalangeal joints consolidate. Habersetzer and Marimuthu (1986) found that young *H. speoris* became volant when 25–30 days old. Weaning is initiated at about 2 months of age, and young are able to fend for themselves at 3 months of age. *H. commersoni* is weaned at an age of 20 weeks (Brosset 1969). *H. speoris* and *H. commersoni* are both tropical species from India. The time at which young *H. terasensis* become volant does not seem to be much different from that of tropical Hipposideridae and Vespertilionidae, but their weaning time is earlier than that of some tropical species of *Hipposideros*. The phenomenon of early weaning time in young *H. terasensis* is similar to that of some temperate species (hibernating bats), such as *Lasiurus cinereus* and *Rhinolophus ferrumequinum nippon*. Young of these species are weaned when they are 4 and 7 weeks old (Koehler and Barclay 2000; Sano 2000). One of the reasons *H. terasensis* has an earlier weaning time may be related to the survival strategy for their 1st winter. To deposit enough energy (fat) to be used throughout hibernation, an earlier weaning time and long postflight period may be necessary for young hibernating bats in the subtropics, as it is for the temperate species (Hoying and Kunz 1998; Kunz and Hood 2000; Kunz and Stern 1995) but not for nonhibernating tropical species.

The young of most microchiropterans weigh around 20–30%, mostly about 25%, of their mother's weight at birth (Altringham 1996; Kurta and Kunz 1987). From the perspective of relative body mass at birth, bats are clearly precocial because they are generally heavier than the young of other mammals having comparable litter size (Kurta and Kunz 1987), which average only 5–10% of adult weight (Altringham 1996). However, bats are highly altricial with respect to development of forelimb and locomotive function (Powers et al. 1991). Most microchiropteran bats cannot fly before they attain 90% of adult wing dimensions (Barclay 1995). In our study, average length of forearm of *H. terasensis* at birth was 43.3 mm and about 40% of the mean value of postpartum females, and average body mass at birth was 15.9 g and about 23% of the size of adult females. They could fly for a short distance at 3–4 weeks of age when their length of forearm was about 89% of that of an adult female, but they rarely emerged from their roost independently before they were 6 weeks old. In *R. ferrumequinum* (a larger member of Rhinolophidae in the temperate region, with an adult body mass of 23.6 g), body mass at birth is 5.8 g (Ransome et al., in litt., cited in Kunz and Hood 2000), which is much less than that of *H. terasensis*. Length of forearm of neonates averages 25.2 mm, which increases rapidly to reach 90.4% of adult size in just 16–18 days, when they start to fly (Sano 2000). In *H. speoris* (a smaller tropical *Hipposideros*) average length of forearm and body mass of newborn are 16 mm and 2.3 g, which are about 31% and 21% of that of their mother, respectively (Habersetzer and Marimuthu 1986). Young of *H. speoris* are also much smaller than those of *H. terasensis*, and they cannot fly for a short distance before they are 5–6 weeks old, when their length of forearm is only about 70% of that of the mother. These results indicate that, although *H. terasensis* is a much larger insectivorous bat, its growth rate is still greater than that of its smaller tropical counterpart and less than that of temperate species.

Kunz and Hood (2000) reviewed and compared postnatal growth rates of body mass of 41 species of bats, including 31 microchiropterans from temperate and tropical regions, by means of the logistic growth equation. They found a significant negative correlation between postnatal growth rate and asymptotic body mass. After the effect of body mass was removed, latitude (tropical or temperate) was the only extrinsic variable that affected postnatal growth rates, i.e., temperate species grow faster than tropical species. On the basis of reviews by Kunz and Hood (2000) and Kunz and Stern (1995), growth constants of body mass of all megachiropterans ($K = 0.01$ to 0.04, $n = 10$) and tropical microchiropterans ($K = 0.04$ to 0.11, $n = 11$) are lower than that of *H. terasensis* ($K = 0.114$). In contrast, most temperate microchiropteran species have a higher growth constant ($K = 0.12$ to 0.25, $n = 13$), and only 4 species have a lower growth constant ($K = 0.04$ to 0.10) than that of *H. terasensis*. This demonstrates, again, that postnatal growth of *H. terasensis* (a subtropical microchiropteran) is faster than that of tropical bats but slower than that of most temperate bats. The fact that young of *H. terasensis*, which are larger in size at birth, grow faster than smaller bats in the tropics and slower than bats in the temperate regions suggests that latitude is a stronger factor than body size in affecting postnatal growth rate of young bats.

Ages of sexual maturity are highly variable among taxa, between males and females of a single species, and sometimes even between individuals of the same sex (Tuttle and Stevenson 1982). In both microbats and megabats, sexual maturity is normally reached within 1–2 years (Altringham 1996). In some species, females may be sexually mature within a few months, for instance 5–6 months for *Hypsignathus monstrosus* and *Rousettus leschenaulti* in megachiropterans and 3 months for *R. hipposideros* in microchiropterans (Tuttle and Stevenson 1982). Churchill (1995) compared 8 tropical species of Hipposideridae and found that both males and females generally reach sexual maturity at 16–24 months, except for females of *H. speoris*, *H. ater*, and *Rhinonycteris aurantius*, which mature at 6–8 months. Male and female *H. terasensis* become sexually mature in their 1st and 2nd years after birth (mostly <12 months), which was earlier than in the case of most tropical species of *Hipposideros* reported by Churchill (1995). The result seems to agree with the conclusion of Kunz and Stern (1995), that climate (latitude) is also important in affecting age of sexual maturity and that temperate species mature earlier than subtropical species, which mature earlier than tropical species.

Few species of bats have been studied regarding the relationship between postnatal growth rate and age of sexual maturity. By comparing results of our study with the available information in Kunz and Stern (1995) and Tuttle and Stevenson (1982), it appeared that species with a higher postnatal growth rate tend to mature earlier than those that have a lower postnatal growth rate, especially in females. However, *Pipistrellus mimus*, a tropical species from India that undergoes parturition 3 times a year and gives birth to 2 young per litter has a slower growth rate than most other vespertilionids have; but these females reach sexual maturity at only 4 months after birth (Isaac and Marimuthu 1996). Therefore, more information on various species is needed to examine the relationship between postnatal growth rate and age of sexual maturity in bats.

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