

INTRASPECIFIC VARIATION IN POSTNATAL GROWTH IN THE GREATER SPEAR-NOSED BAT

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Intraspecific variation in size at birth, postnatal growth, and survivorship of young mammals may reflect genetic variation, differential investment of mothers, gender of offspring, and environmental factors. We quantified size at birth and postnatal growth in free-ranging *Phyllostomus hastatus* (Chiroptera: Phyllostomidae) to develop age-predictive equations and examine effects of maternal size and age on size at birth and survivorship of young. There was a positive relationship between body mass of mothers and young; however, we found no relationship between maternal length of forearm or age on size of young at birth or survivorship. Males weighed more than females at birth and gained mass at a faster rate, although we found no significant gender differences at birth in length of forearm or length of total epiphyseal gap. High variation in size at birth and maturity suggests that there may be few environmental or life-history constraints on body size and postnatal growth in *P. hastatus*.

Key words: *Phyllostomus hastatus*, greater spear-nosed bat, sexual dimorphism, postnatal growth, intraspecific variation

While interspecific variation in vertebrate growth has been examined with respect to adult body size, basal metabolic rate, diet, and mortality (Case, 1978; Kunz and Stern, 1995; Lack, 1968; Ricklefs, 1973), causes and consequences of intraspecific variation have received less attention. Observed variation in postnatal growth within a species presumably reflects compromises and constraints imposed by opposing selection pressures. Captive studies on postnatal growth have established the maximum rate of growth under controlled environmental conditions (ad lib. food and constant temperature). In contrast, studies of postnatal growth in free-ranging populations, in which individuals often experience highly variable food supplies and environmental conditions, may identify factors that influence patterns of growth. Intraspecific variation in postnatal growth may reflect environmental factors such as temperature, availability of food, and litter size, as well as biological factors such as size at birth, metabolic rate, and foraging success (Kunz and Stern, 1995; Tuttle and Stevenson, 1982).

In mammals, pre-weaning rates of growth may be influenced by the ability of the mother to provision young. A large litter may decrease rates of growth by reducing the amount of food available to each individual. In cotton rats (*Sigmodon hispidus*), individuals from small litters grow faster than those from large litters (Rogowitz and McClure, 1995). Similarly, in pallid bats (*Antrozous pallidus*), single young grow faster than twins (Bassett, 1984). Season and climate potentially can affect growth. Moreover, under conditions of food shortage, young mammals may experience stunted growth but undergo compensatory growth after food becomes abundant (Hoying and Kunz, in press). In a study of free-ranging gray bats (*Myotis grisescens*), Tuttle (1975) found that pre-weaning rates of growth were greatest in the warmest and largest colonies, suggesting that the largest colonies were more effective at warming intrinsically cool caves. Thus, postnatal rates of growth may be indicators of nutritional status or physiological condition. Lit-

ters raised at different times of year may be exposed to different environmental temperatures and availability of food, which in turn may affect rates of growth (McWilliam, 1987). In highly gregarious species, large colony size may offer thermal advantages, but increased numbers of individuals may be detrimental, especially if newly weaned young must compete with experienced adults for food (Tuttle, 1975, 1976).

Studies of postnatal growth also may help explain how and when individuals of sexually dimorphic species, generally males, attain greater body size. Differences in pre-weaning growth may indicate different strategies of investment by females in their offspring, whereas post-weaning differences may reflect individual variation in behavior, foraging efficiency, environmental quality, or genetic variation (Tuttle, 1975, 1976).

Factors that may be important in choice of a species for studies of postnatal growth include fidelity to a particular site, accessibility of mother-young pairs, ease of capture and recapture, and susceptibility of individuals to repeated disturbance (Kunz, 1987). We studied the greater spear-nosed bat, *Phyllostomus hastatus*, because females roost in discrete groups, give birth synchronously within a period lasting 2–3 weeks, show high site fidelity while rearing young, and appear to tolerate repeated captures (McCracken and Bradbury, 1981). Young are left mostly unattended at night while females forage and thus can be handled with minimal disturbance to the colony. These criteria make *P. hastatus* an excellent model for testing hypotheses about effects of gender and maternal size and age on postnatal growth. Because the cave environment where *P. hastatus* typically roosts is relatively warm and stable (Kunz et al., in press), effects of variation in the environment of the roost on postnatal growth should be minimal.

The mating system of *P. hastatus* is based on a system of resource-defense po-

lygyny in which dominant males may sire ≥ 50 offspring and other males may never mate (McCracken and Bradbury, 1981). Males have a body mass ca. 15% greater than females (McCracken and Bradbury, 1981), which suggests that males either grow faster than females or continue to grow after growth of females ceases. In this study, we asked the following questions. How and when does sexual dimorphism develop? How much variation exists in size at birth, size at weaning, and in the adult population? Is size at birth or postnatal growth related to survivorship, and finally, how do maternal influences, such as age and size, relate to growth and survival of young?

MATERIALS AND METHODS

Our study was conducted at Guanapo Cave in the Northern Range of Trinidad, West Indies (McCracken and Bradbury, 1981). The small size and low ceiling of the cave enabled us to locate and capture both mothers and young in their roosts with relative ease. From April to July 1993, we quantified rates of growth in known-age young. Additional data on day-old young and size of mothers were collected during the parturition period in April 1994. Most young in Guanapo Cave were born within a 3-week period in April, facilitating banding of day-old young (identified by presence of an umbilicus—Kunz, 1973). Mother-offspring pairs were captured during the day and banded on the forearm (males on the right, females on the left) using numbered butt-end bands made of stainless-steel (National Band and Tag Co., Newport, KY). Other newborns were banded after females departed to feed at night. Known-age young were given a second band covered with reflective tape (Scotchlite, 3M Corp., Minneapolis, MN) to facilitate recapture.

Changes in the length of the epiphyseal cartilages provide a method for determination of age. A dissecting microscope, fitted with an ocular micrometer, was used to view the transilluminated wing and measure length of the total epiphyseal cartilage (gap) of the fourth metacarpal-phalangeal joint (Kunz and Anthony, 1982). After formation of a secondary center of ossification at ca. 3 weeks of age, distal and proximal gaps were measured. Length of forearm was

measured with dial calipers, and body mass was measured to the nearest 0.05 g using a portable electronic balance (Ohaus CT-200, Florham Park, NJ). Young were held in clusters in cloth bags to simulate roosting conditions and were returned to the roost within 2 h of capture. Known-age young were recaptured and measured at 5-day intervals. Data from 35 known-age young were used to construct postnatal growth curves. Curves were fitted using three nonlinear techniques: Gompertz, von Bertalanffy, and logistic (Kunz and Robson, 1995; Ricklefs, 1979; Zullinger et al., 1984), using the Marquardt-Levenberg algorithm (SigmaPlot for Macintosh, version 3.1—Jandel Scientific, Inc., 1991). The sum of squares for each curve was used to indicate goodness of fit for each equation. Because repeated handling may have affected rates of growth, we compared linear growth (test for coincidence of slopes and intercepts—Kleinbaum et al., 1988) of young captured every 5 days with those captured every 10 days (as part of a broader study on energetics). Linear rates of growth of males and females were compared using the same statistical tests. Forearm, body mass, and total epiphyseal gap of males and females at birth were compared with analysis of covariance with year as a covariate for forearm and body mass. Data are presented as $\bar{X} \pm SD$ unless otherwise noted.

Relative age of adults was scored using an index of toothwear similar to that designated by Twente (1955) but on a scale of one to five, with sharply-pointed canines and molars scored as one and completely worn teeth scored as five (G. S. Wilkinson, pers. comm.). Because body mass of adults changes with season, reproductive condition, and stomach contents, we included in our analysis only adult animals that were post-absorptive and captured from mid-April through mid-July, when body mass of adults was relatively stable (Stern et al., 1997). Effects of length of maternal forearm, body mass, and toothwear on size of offspring were tested using one-way analysis of variance. Year was included as a covariate in analyses involving body mass of young because neonates weighed more the first year of the study. Because data on survival of young were categorical, the relationship of size at birth, maternal size, and maternal age to survival was tested using a logistic regression.

Rates of mortality were recorded for a cohort of 40 young, banded at birth in 1993 with re-

flective bands. The small size of Guanapo Cave, combined with high visibility of the reflective bands, allowed location and capture of banded young with nearly 100% success inside the cave. When an individual was not captured after two successive attempts, we assumed that the bat died shortly after it was last captured. It was not possible to distinguish between mortality and dispersal after bats become volant; thus, our estimate of rate of mortality is a maximum.

RESULTS

Growth and development.—Size at birth in *P. hastatus* was highly variable (Table 1, Figs. 1 and 2). For 1-day-old young (both years combined), length of forearm ranged from 29.5 to 39.6 mm ($\bar{X} = 34.1 \pm 2.1$ mm, $n = 80$), length of total epiphyseal gap ranged from 4.0 to 5.0 mm ($\bar{X} = 4.5 \pm 0.21$ mm, $n = 35$), and body mass ranged from 10.8 to 22.5 g ($\bar{X} = 15.8 \pm 1.8$ g, $n = 74$). Variability in body size also was evident in lactating females, whose forearms ranged from 75.4 to 85.8 mm. Mean length of forearm at birth was 42% of adult size. Body mass of newborn bats was 20.7% of adult mass, close to the average of 22.3% for bats (Kurta and Kunz, 1987). We used values of 76.1 ± 5.16 g ($n = 56$ post-partum females) and 81.9 ± 1.8 mm ($n = 148$ lactating females) as estimates of adult body mass and forearm, respectively. We found no relationship between maternal and neonatal length of forearm ($F = 0.46$; $d.f. = 1, 57$; $P = 0.50$), but there was a positive relationship between maternal and neonatal body mass ($F = 5.75$; $d.f. = 1, 50$; $P = 0.02$). There was no relationship between age of mother, as indicated by toothwear, and body mass of neonates ($F = 0.38$, $d.f. = 1, 43$; $P = 0.54$). Age of mother was related to length of forearm at birth ($F = 4.13$, $d.f. = 1, 48$; $P = 0.048$), but when a Bonferroni correction was applied that significance disappeared. Young born in 1994 were significantly heavier than bats born the previous year (Table 1), but no climatic or environmental factors were readily discernible that might explain this difference. Males weighed more at birth and continued

TABLE 1.—Measurements of neonatal *Phyllostomus hastatus* by gender and year. Statistical values represent comparisons of pooled data (both years) for males versus females. Forearm and body mass were compared with an analysis of covariance with year as a covariate; epiphyseal gap was compared using an analysis of variance.

| | Female | | | | | | Male | | | | | | | |
|-------------------------------------|-----------|-------|----|-----------|------|----|-----------|------|----|-----------|------|----|-------|--------|
| | 1993 | | | 1994 | | | 1993 | | | 1994 | | | | |
| | \bar{X} | SD | n | \bar{X} | SD | n | \bar{X} | SD | n | \bar{X} | SD | n | F | P |
| Length of total epiphyseal gap (mm) | 4.46 | 0.23 | 16 | 4.47 | 0.19 | 19 | | | | | | | 0.03 | 0.87 |
| Length of forearm (mm) | 34.6 | 12.16 | 17 | 34.22 | 2.20 | 20 | 34.08 | 1.39 | 21 | 34.08 | 1.39 | 21 | 0.76 | 0.39 |
| Body mass (g) | 15.69 | 1.17 | 16 | 16.98 | 1.90 | 17 | 16.02 | 1.50 | 21 | 16.02 | 1.50 | 21 | 14.49 | 0.0003 |

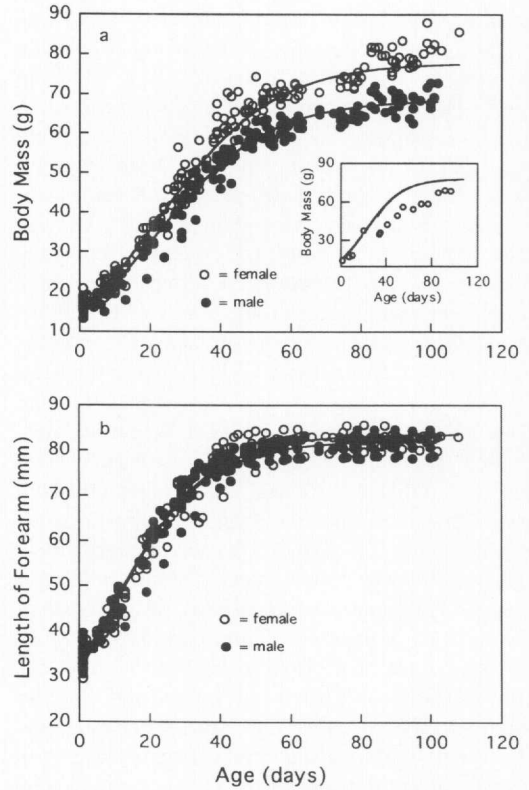


FIG. 1.—Postnatal growth curves for a) body mass and b) length of forearm in free-living *Phyllostomus hastatus*. Inset compares average growth curve with that of a single young male that was atypically small for its age; it achieved volancy and was still alive when the study ended.

to grow after female mass had reached asymptotic size (Fig. 1), but we found no significant difference in length of the total epiphyseal gap or length of forearm at birth (Table 1). A comparison of rates of growth during the linear part of the growth period indicated that slopes for males were greater (forearm: $t = -6.34$, body mass: $t = -4.39$; $d.f. = 161$; both $P = 0.001$) than for females. Variation in growth rates between individuals was apparent. One young male was noticeably smaller than its peers (Fig. 1), yet appeared healthy, achieved volancy, and was still present in the cave when the study ended.

Three equations currently in use attempt

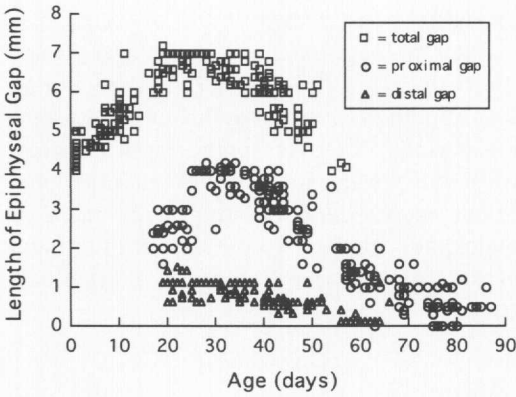


FIG. 2.—Postnatal changes in lengths of epiphyseal gaps in free-ranging *Phyllostomus hastatus*. Although length of the total epiphyseal gap could be used for prediction of age from birth, length of forearm was a better predictor. The linear decrease in length of the proximal gap was used for predicting age from day 35.

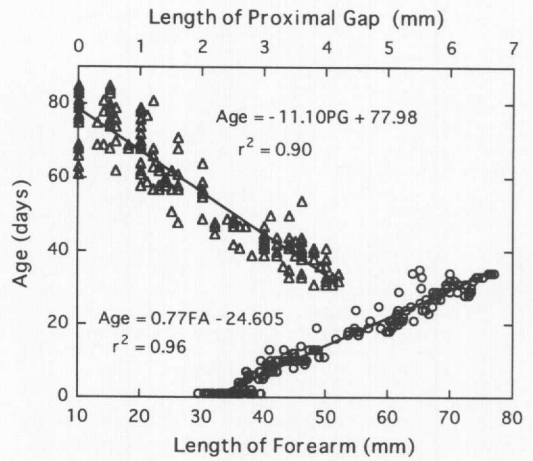


FIG. 3.—Age-predictive equations for *Phyllostomus hastatus* young based on length of forearm (FA) and length of proximal epiphyseal gap (PG); the independent variable (age) was placed on the Y axis to facilitate prediction of age.

to describe growth by fitting a sigmoidal curve to growth data. When fit to the data, each equation yields a value for asymptote (A), growth constant (K), and inflection point (I). Of the three growth models tested, the best fit (determined by the smallest coefficient of variation for A, K, and I and smallest sum of squares) was provided by the logistic growth equation, $M(t) = A\{e^{K(t-I)} + 1\}^{-1}$, for both length of forearm and body mass. A high coefficient of variation indicated that a parameter added little to the model's predictive ability. The logistic equation tended to yield the lowest asymptotic value and the greatest growth constant and inflection point. Both the Gompertz and von Bertalanffy equations occasionally yielded negative values for the inflection point.

Length of forearm increased linearly until the fifth week, and bats attained adult dimensions by the eighth week (Fig. 2). Length of total gap increased linearly to the age of 16–18 days, when secondary centers of ossification appeared, making measurement of the lengths of the proximal and distal gaps possible (Kunz and Anthony, 1982). Bats initiated flight between 6–7

weeks of age (Stern et al., 1997). The post-weaning body mass of young was below that of post-lactating females. Yearlings captured during a 2-week period in February in the following year averaged 7.8% (females, $t = 5.04$, $d.f. = 101$, $P = 0.0001$) and 7.7% (males, $t = 2.99$, $d.f. = 34$, $P = 0.005$) lighter than their adult counterparts caught in the same period. Yearling females also were distinguishable from adults in the summer after their birth by having small, unpigmented nipples.

Prediction of age.—Length of forearm was initially a better predictor of age than length of the total epiphyseal gap (Fig. 3), because the greater magnitude of change reduced the error in estimating age. Length of epiphyseal gaps continued to change after length of forearm reached an asymptote, allowing prediction past 35 days. Age-predictive equations until day 35 were based on measurements of the length of forearm, but measurements of the proximal gap allowed age prediction to day 64 (Fig. 4). There was no difference in linear growth of bats captured once every 5 days and bats captured at 10-day intervals or greater (forearm, $t =$

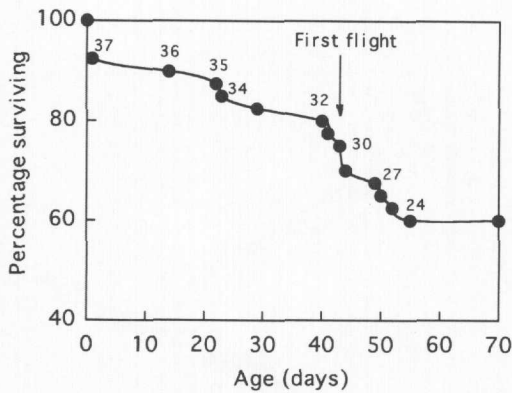


FIG. 4.—Survivorship of 40 *Phyllostomus hastatus*; mortality is highest as bats achieve volancy and begin to forage independently (numbers above data points indicate sample size).

-0.26 , $d.f. = 186$; body mass, $t = -0.08$, $d.f. = 181$; both $P < 0.05$). Measurements collected in 1994 produced a curve visually indistinguishable from that in 1993, suggesting that the predictive ability was robust to annual variation in *P. hastatus*.

Mortality.—We found no significant relationship between size at birth (body mass, length of forearm) and mortality. Moreover, we found no correlation between mortality of young and maternal body mass, forearm, or age using logistic regression (all $P > 0.18$). Mortality was highest immediately after birth (5 of 40) and during weaning (9 of 40). Overall mortality through day 60 was 16 of 40, or 40% (Fig. 4). Because that value included five bats never recaptured after initial banding, it represented a maximum estimate of mortality. It was not possible to distinguish between dispersal and mortality after bats began to fly. We never found young other than at their natal caves, although we visited several other nearby caves with substantial populations of *P. hastatus*.

Newly volant bats were initially inept fliers. On several occasions while working at night, we heard crashing sounds in the vegetation near the opening of the cave and upon investigation, found a young bat clinging awkwardly to a branch. Risk of

mortality was certainly high as young first learned to negotiate, navigate, and forage (Stern et al., 1997). Of 27 marked young that remained in the cave through the weaning period, 15 (seven males, eight females) were still present in the cave 7 months later. Males were found roosting with bachelor males, but females were either in their natal harem or roosting with females in other harems.

DISCUSSION

The pattern of postnatal growth in *P. hastatus* is similar to that of many species of bats (Kunz and Stern, 1995). Length of forearm and body mass increased linearly before reaching asymptotic values. Males achieve their greater size through a combination of greater mass at birth, faster linear rates of growth, and continued growth after weaning, but the larger length of forearm results solely from a longer period of growth. The pattern of faster mass gain in males during the suckling period has been noted in other sexually dimorphic mammals (Lee and Moss, 1986; Soderquist, 1995). Sexual dimorphism in body mass and length of forearm in this species is evident before weaning, suggesting differential maternal investment.

Growth rates vary with geographic distribution, diet, body size, taxonomic affinity, and environmental factors (Kunz and Stern, 1995). Species-specific growth constants in bats can vary 15-fold over a range of body mass of <20 g (Kunz and Stern, 1995). Rates of growth of bats also vary with latitude. Tropical bats grow more slowly than temperate species, possibly due to relaxed constraints of moderate seasonality (Kunz and Stern, 1995). Given that many factors affect growth, rates of growth for *P. hastatus* appear to be consistent for its size and geographic distribution, although no information is available on the effect of an omnivorous diet on rates of growth in bats. Case (1978:246) described postnatal rates of growth of bats as “moderate,” in the same category as rodents,

prosimians, and fissiped carnivores, but he considered only the linear part of growth, which extends until young have reached 30–50% of adult size. Rodents typically are weaned by this time (Millar, 1977), but bats remain nutritionally dependent until ca. 70% of adult mass (Barclay, 1994). A more universal approach may be to compare growth parameters derived from sigmoidal equations, which include all parts of growth until achievement of asymptotic size (Zullinger et al., 1984). Further, growth constants from nonlinear equations are independent of body size and period of growth (Kunz and Robson, 1995), facilitating comparisons between species and across broad taxonomic groups. Although such data are limited for bats, Zullinger et al. (1984) found that growth constants of bats and rodents were similar.

Mortality and dispersal.—Disappearance of banded young from Guanapo Cave could be attributed to several factors. Five neonates that were never recaptured after their initial banding could have disappeared due to relocation by the mother to another roost, loss of the band, or mortality within a few days following birth. Extensive surveys of the area have yielded no nearby alternate roosts and transport of young by adult females incurs both increased risk of predation and high energetic costs, making relocation to a new cave unlikely. Relocation within the cave did occur frequently. Loss of bands also could produce false estimates of mortality. We captured two young (one each year) whose bands had slipped over the wrist and were lodged on the phalanges. Those bands slid off completely when pulled gently, and it was likely that some of the initial disappearance of banded young was due to loss of bands. Predation also may have contributed to mortality of young. In April 1993, coincident with the onset of parturition, we observed an adult opossum (*Didelphis marsupialis*) with several young inside the cave in a crevice ca. 1 m from the ceiling. During weekly visits to the cave from February to April 1994,

an opossum was sighted only once, again in April as bats were being born. Young bats frequently fell, and videotapes made during a concurrent study of behavior showed an opossum making nightly visits to the cave during the birthing season (G. S. Wilkinson, pers. comm.). Although most harems at Guanapo cave are located 2–3 m above the floor, population increases in recent years have resulted in bats aggregating where an opossum could conceivably prey on unattended young. Post-weaning disappearance could be due to either mortality or dispersal. Little is known about dispersal patterns in *P. hastatus*, but some young may remain in their natal roosts for periods of ≥ 1 year after birth (Kunz et al., in press), and many remain for years after leaving their natal harem (G. S. Wilkinson, pers. comm.).

Intraspecific variability.—One of the most intriguing aspects of our study was the high degree of variability observed in nearly every parameter we measured, both in young and adults. Body mass of the largest 1-day-old bats was twice that of the smallest young, and length of the proximal epiphyseal gap of some bats closed 10 days earlier than others. This variation may provide one explanation for differential mortality at weaning. With as much as an 8-g difference in body mass between individuals at weaning, some individuals may have sequestered more body stores for the transition between maternal provisioning and independent foraging. Length of lactation in adults also was variable (Stern, 1996), and greater supplementation of milk by some mothers after young began to forage may have increased rates of survival. However, survival of a male that was significantly smaller than others of its age group (Fig. 1a), and the lack of correlation between size at birth and mortality, indicates that the relationship between size and mortality functions within relatively broad constraints.

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