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Postnatal growth and age estimation in the broad-tailed bat (*Nyctinomops laticaudatus*)

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Postnatal growth in bats has been studied in various species, but its documentation often depends on access to roosts, the ability to handle pups, and reliable marking systems for recapture. We examined the postnatal growth and development of the Broad-eared Free-tailed Bat (*Nyctinomops laticaudatus*) in a colony at the Governor's Palace, Uxmal Archaeological Zone, Yucatán, Mexico. Marked pups were measured from birth until the onset of flight for forearm length, body mass, and fourth digit length. Growth curves were generated, from which growth rates and age-prediction equations were derived. At birth, forearm length, fourth digit length, and body mass were 45%, 29%, and 31% of postpartum female values, respectively. These traits grew linearly up to 40 days, with average rates of 0.44 mm/day (forearm), 0.54 mm/day (fourth digit), and 0.14 g/day (body mass). Growth rates slowed after the onset of flight. Forearm length provided a reliable predictor of age for pups between 1 and 40 days old when measurements were ≥37 mm. Flight trials indicated that pups began flapping and short horizontal movements at 15 days and achieved sustained flight by day 40. The growth rates observed in *N. laticaudatus* exceeded those reported for many other tropical insectivorous bats. Documenting postnatal development in molossids enhances our understanding of this critical stage in bat life history, and comparative studies across tropical species will provide valuable insights into the evolution of bat growth strategies.

Key words: age-estimation, development, Molossidae, *Nyctinomops laticaudatus*, postnatal growth.

El crecimiento postnatal en murciélagos se ha estudiado en varias especies, pero su documentación a menudo depende del acceso a los refugios, la posibilidad de manipular a las crías y la disponibilidad de sistemas de marcaje confiables para su recaptura. Examinamos el crecimiento y desarrollo postnatal del murciélago de cola suelta ancha (*Nyctinomops laticaudatus*) en una colonia ubicada en el Palacio del Gobernador, Zona Arqueológica de Uxmal, Yucatán, México. Las crías marcadas fueron medidas desde el nacimiento hasta el inicio del vuelo en longitud del antebrazo, masa corporal y longitud del cuarto dedo. Se generaron curvas de crecimiento, a partir de las cuales se derivaron tasas de crecimiento y ecuaciones para la predicción de la edad. Al nacer, la longitud del antebrazo, la longitud del cuarto dedo y la masa corporal correspondían al 45%, 29% y 31% de los valores registrados en hembras posparto, respectivamente. Estos rasgos crecieron de manera lineal hasta los 40 días, con tasas promedio de 0.44 mm/día (antebrazo), 0.54 mm/día (cuarto dedo) y 0.14 g/día (masa corporal). Las tasas de crecimiento disminuyeron después del inicio del vuelo. La longitud del antebrazo resultó un predictor confiable de la edad para crías de entre 1 y 40 días, cuando las mediciones fueron ≥37 mm. Las pruebas de vuelo indicaron que las crías comenzaron a aletear y realizar movimientos horizontales cortos a los 15 días, y alcanzaron el vuelo sostenido alrededor del día 40. Las tasas de crecimiento observadas en *N. laticaudatus* superaron las reportadas para muchos otros murciélagos insectívoros tropicales. Documentar el desarrollo postnatal en molósidos amplía nuestra comprensión de esta etapa crítica en la historia de vida de los murciélagos, y los estudios comparativos entre especies tropicales proporcionarán información valiosa sobre la evolución de las estrategias de crecimiento en estos mamíferos.

Palabras clave: crecimiento postnatal, desarrollo, estimación de edad, Molossidae, *Nyctinomops laticaudatus*.

An organism's life history comprises those events or traits in its life cycle that influence its fitness. In this context, life history theory explains variations in survival and reproductive success—both of which play a fundamental role, as they allow inferences about evolutionary processes and help assess population viability (Steams 1992). The main characteristics that comprise an organism's life history are gestation length, birth size, postnatal growth, growth rate, age and size at maturity, offspring size and number, senescence related to longevity, and mortality rates (Stearns 2000; Roff *et al.* 2006; Fabian and Flatt 2012).

The postnatal growth period is a time when young mammals develop appropriate sensorial and locomotor skills, necessary to become independent of the mother (Baptista *et al.* 2000). Many researchers have studied this period with respect to changes in behavior, physiology, and ecology to investigate life history traits (Kunz *et al.* 2009; Eastick *et al.* 2022). Postnatal growth studies are essential 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, litter sizes, maternal conditions, gender, birth timing; Kunz *et al.* 2009; Eghbali and Sharifi 2023).

Growth and development of bats were studied during the postnatal period (Orr 1970; Tuttle and Stevenson 1982), under both natural (Stern and Kunz 1998) and captive conditions (Hughes *et al.* 1995). Studies from captive conditions do not reflect the compromises and constraints imposed on animals in the wild, as these conditions did not reflect their natural environments (Kunz and Robson 1995; Mclean and Speakman 2000). Studies conducted in the field, based on pups marked at birth and recaptured

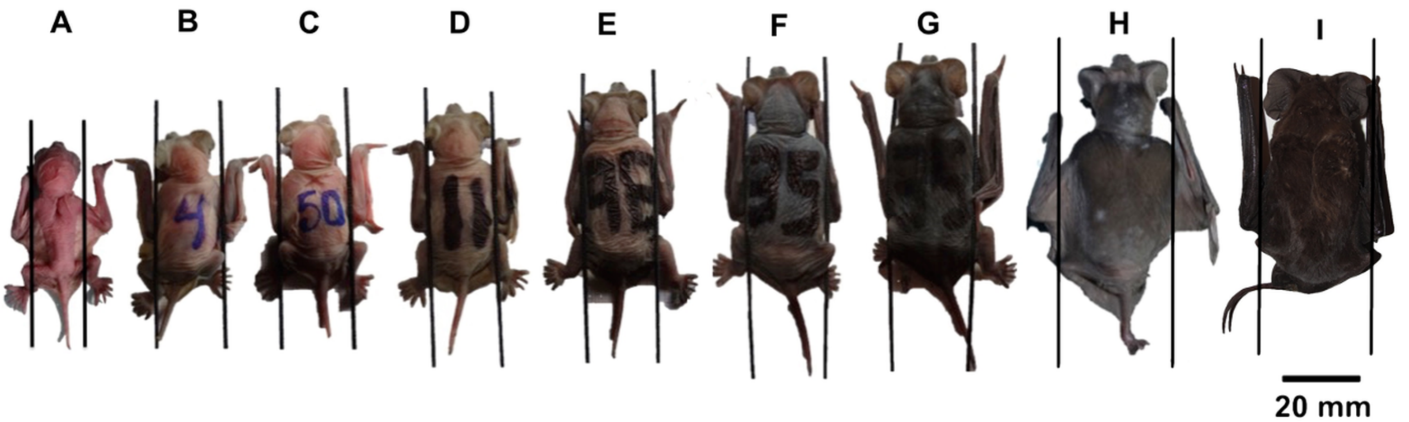

Figure 1. Development of *N. laticaudatus*: A.- Newborn (1 day); B.- juvenile five days old; C.- Juvenile 10 days old; D.- Juvenile 15 days old; E.- Juvenile18 days old; F.- Juvenile 21 days old; G.- Juvenile 27 days old; H. Juvenile 35 days old; I.- Adult (45 days).

at regular intervals, should yield the most ecologically meaningful results on postnatal growth in bats. Previous studies have shown that measurements of the length of the forearm, the length of the fourth finger, and body mass are helpful to estimate the age of bats during the early postnatal period (Kunz and Anthony 1982; Kunz and Robson 1995; Stern and Kunz 1998). Forearm length is the most accurate and reliable character for estimating age during the early linear growth period of bats.

Most studies on postnatal growth in bats were conduct 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); with only a few efforts on the Molossidae (Short 1961; Pagels and Jones 1974; Kunz and Robson 1995; Allen *et al.* 2010); which is widespread in the tropics and subtropics of the world.

The Broad-eared Free-tailed Bat *Nyctinomops laticaudatus* (Chiroptera: Molossidae) is rare or uncommon throughout most of its geographic range, as confirmed by the few records from several countries (Barquez *et al.* 1999). However, it is relatively common in some areas, especially within the Yucatan Peninsula (Jones *et al.* 1973; Bowles *et al.* 1990). This species is listed as a least concern by the IUCN (Barquez *et al.* 2015). However, nothing about the external characters at birth or postnatal growth has been reported, and little information is known concerning the life history of *N. laticaudatus* (Avila-Flores *et al.* 2002). This paper aimed to provide such background data on the pattern of postnatal growth for *N. laticaudatus* from México and to derive age-specific growth equations based on a quantitative analysis of forearm, fourth finger. and body mass.

Materials and Methods

Study area and collecting data. The study was conducted between June and August 2015 in Governor's Palace at the Archeological Zone of Uxmal, Yucatán, México (20° 21´N, 89° 46´W). This Mayan ruin housed a colony of approximately 5,000 *N. laticaudatus* (Málaga and Villa 1956; Ortega *et al.* 2010). The Governor's Palace was constructed on a platform 12 meters high and 100 meters long and is composed of three independent blocks, with nine interior chambers and 11 exteriors. There are cavities in the corner of every chamber with particular dimensions of approximately 30 X 30 centimeters, and an average depth of 70 centimeters. The nursery roost of this species is located inside the cavities of the chambers (Ortega *et al.* 2010).

Marking and recapture. Prior investigation indicated that the females of *N. laticaudatus* in this area give birth from late June to early July (Ortega *et al.* 2010). Therefore, we checked the cave daily from about 10 days before birthing. When newborn pups were observed, we began collecting them by hand. Once neonates were found, we would gently hand-capture them during the morning (usually at 09:00 h). Young bats were immediately placed in warm cloth bags and taken into a temporary laboratory near the roost. Neonates with an attached umbilical cord were assumed to be one day old (Kunz and Robson 1995). Following determination of the sex of pups, a unique number was placed on the body (temporal marker, *Sharpie*®) of each bat for individual identification (Figure 1). Forearm length and fourth finger were measured to the nearest 0.01 mm with a digital caliper (Digimatic Cd-6 B 500-133, *Mitutoyo*®). Body mass was recorded to the nearest 0.01 g using an electronic balance (Electronic balance # 501A-*LG*®). To minimize errors in using calipers, individual measurements were repeated three times, and the means were used in the analysis.

To limit disturbance and possible abandonment, the bats were returned to the sites of capture after observations and measurements had been obtained. We visited the roost every day for one month, and bats were collected and recorded daily. Fieldwork procedures followed the guidelines approved by the American Society of Mammalogists (Sikes *et al.* 2011). All permits needed for the capture and handling of bats were obtained from Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT—SGPA/DGVS/12598/15) and Instituto Nacional de Antropología e Historia (INAH).

Statistical analysis. A chi-square with Yate's correction test was applied to evaluate whether sex ratio at birth was different from chamber (Sokal and Rohlf 1979). We used a multivariate analysis of variance (*Manova*) test to compare length of forearm, length fourth finger and body mass of males and females at birth. The proportions of size to the birth of the pups with regard to that of adult mothers was obtain across the comparison of the variables, with 20 nursing females gathered during the period of study (Kunz and Robson 1995). The growth rates (mm/day or g/day) were calculated using the equation of McOwat and Andrews (1995): where "R" is the growth rate of postnatal growth, "L1" and "L2" are the length or mass for the captures one and two, and "t1" and "t2" is the time in the captures one and two. By using the rates of growth of the recaptured newborn, the precision of the equation will be improved. We used a linear regression analysis, with age as the dependent variable, to derive age predictive equations based on the data of linear changes of the forearm length, length of the fourth finger, and body mass.

Results

We sampled 31 crevices from the nursery roost from June to August 2015. Inside cavity, neonates with umbilical cords were captured and marked as *N. laticaudatus*, of which 48 were females (49%) and 50 males (51%). The sex ratio (1.04♂: 0.96♀) did not differ significantly from unity (X2 Yates= 0.01, d.f.= 1, P= 0.92034). No significant difference was found between the length of the forearm, fourth finger, and body mass of male and female pups at birth (Manova: λ-Wilk: 0.9741, F= 0.8636, P= 0.4787; Table 1).

Table 1. Descriptive statistics of the variables used to evidence sexual dimorphism in pups of *N. laticaudatus* in Uxmal, Yucatán. n= number of marked bats; SD= standard deviation; CV= coefficient of variation.

	Forearm (mm)		
Sex	mean ± SD	min-max	CV (%)
Male (n= 50)	19.4824 ± 1.0892	15.84 - 22.23	5.59
Female (n= 48)	19.2250 ± 1.0608	17.04 - 22.64	5.51
	Forth finger (mm)		
Sex	mean ± SD	min - max	CV (%)
Male (n= 50)	16.6762 ± 0.8021	14.92 - 18.65	4.81
Female (n= 48)	16.6441 ± 0.9156	14.44 - 19.59	5.50
	Body mass (g)		
Sex	mean ± SD	min - max	CV (%)
Male (n= 50)	3.642 ± 0.5140	2.04 - 6.08	14.11
Female (n= 48)	3.559 ± 0.4221	2.77 - 4.79	11.86

The size of the pups at birth in relation to the adult (20 nursing females) presented the following proportions: 45% of the forearm, 29% of the fourth finger, and 31% of the body mass (Table 2).

The results obtained by the equation McOwat and Andrews (1995), from 385 recaptures, indicated that the average growth rate of the forearm (mean ± SD) is 0.44010 ± 0.1391 mm/day, the fourth finger is 0.5389 ± 0.2003 mm/day, and body mass is 0.093 ± 0.1415 g/day. These rates remained constant during the pre-flight young.

Table 2. Size at birth of *N. laticaudatus* and its proportion with regard to the size of the adult, SD= standard deviation.

	Pups at birth (n= 98) mean ± SD	Adult (n= 20♀) mean ± SD	% of the adult
Forearm	19.35 ± 1.07 mm	43.05 ± 1.62 mm	45%
Fourth finger	16.66 ± 0.85 mm	58.34 ± 2.08 mm	29%
Body mass	3.60 ± 0.47 g	11.52 ± 0.62 gr	31%

The linear regression analysis of the variables of growth with respect to age showed high determination coefficients for the variables: forearm (R2= 0.8807; Figure 2a), fourth finger (R2= 0.875; Figure 2b), and body mass (R2= 0.8446; Figure. 2c), which indicates a high degree of relationship between age and growth variables. The coefficient of determination for the variables no forearm (1-R2= 0.1193; 11.9%), fourth finger (1-R2= 0.1250; 12.5%) and weight (1-R2= 0.1554; 15.5%) lower privileges, as among 11.9% and 15.5% of the variation in the variables was not explained by the regression model with respect to age.

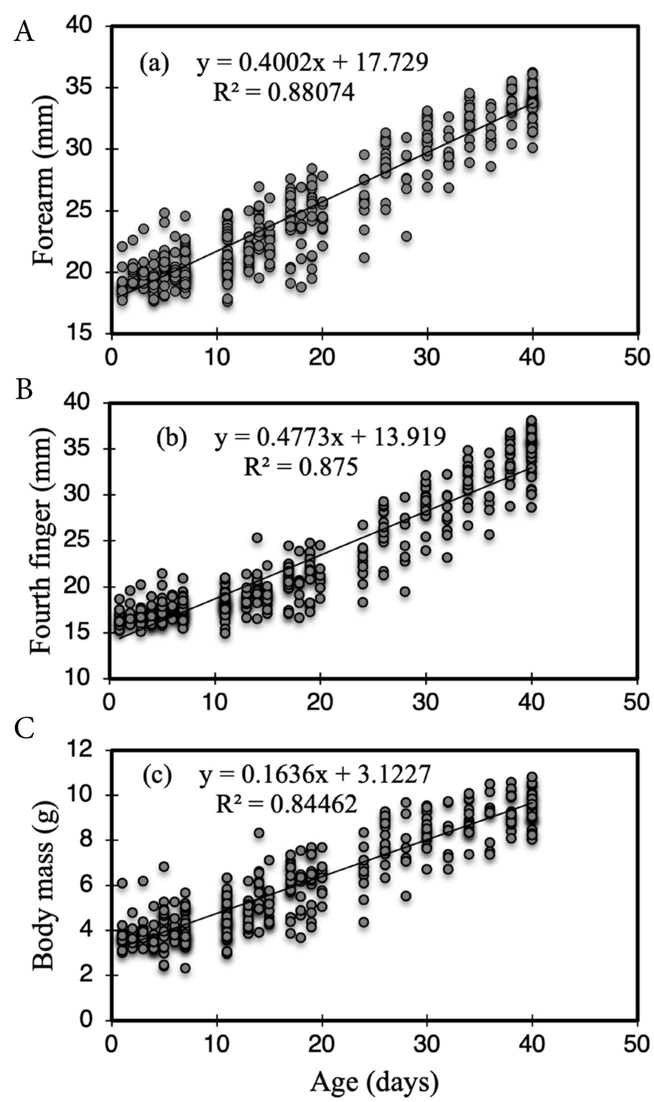

Figure 2. Age-related changes in (a) forearm, (b) fourth finger, (c) body mass during the postnatal growth of *N. laticaudatus*. Growth trajectories were fit using unary linear regression equations.

Age was estimated quantitatively based on linear changes observed in the length of the forearm (1 - 40 days). A linear regression equation allowed age estimates according to forearm length values ranging from 17.64 to 36.12 mm. High values of the correlation coefficient (R2= 0.880) indicated that the length of the forearm was a reliable character for estimating the age of young *N. laticaudatus* in the first 40 days of age (Figure 3).

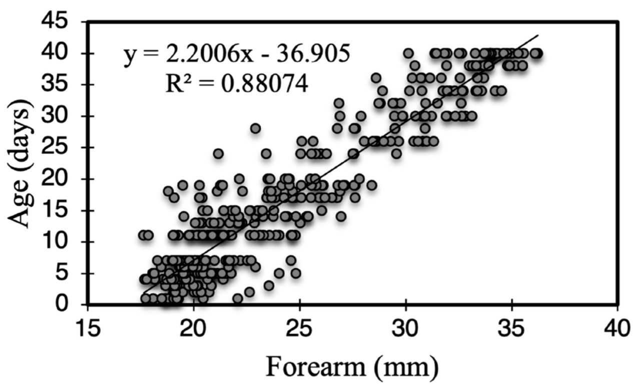

Figure 3. Age-predictive equations for *N. laticaudatus* young based on length of forearm; the independent variable (age) was placed on the Y axis to facilitate prediction of age.

All females collected with young had single offspring with closed eyes at birth. The eyes of the pups opened during the second day after birth. The ears are folded toward the head at birth and take their stand normal to second day. Fur was visible predominantly on the back and ventral side of the body from the third week. However, the development of adult fur is visible up to 43 days. The young were able to flutter and glide when dropped from their hands at 20 days of age. At 30 days, pups were able to fly freely inside the cave. At 45 days, it was not possible to catch young of *N. laticaudatus* at the nursery site.

Discussion

The sex ratio in pups was 1: 1 (1.04♂: 0.96♀; *P*= 0.92034) in the area, likewise this ratio remained constant to the stage preflight. For this species in Uxmal, two previous records in 2006 and 2013 (Ortega *et al.* 2010) and in this study showed no sex ratio deviations in pups. Also, in previous studies, the sex ratio 1: 1 have been report for other of insectivorous bats: *Myotis austroriparius* (Rice 1957), *M. lucifugus* (Smith 1957), *Eptesicus fuscus* (Mills *et al.* 1975), *Myotis yumanensis* (Milligan and Brigham 1993), *Tadarida brasiliensis* (Kunz and Robson 1995), *Pipistrellus subflavus* (Hoying and Kunz 1998), *Myotis velifer* (Loucks and Caire 2007), and *Hipposideros terasensis* (Cheng and Lee 2002).

The size of newborns, as well as their growth and development, are affected by factors such as sex, litter size, geographical location of the population, the temperature and relative humidity of the shelter. The influence of sex is remarkable in species where there is sexual dimorphism, since the rate of growth is faster in the sex of larger size, such as in the males of *Phyllostomus hastatus*, or females *Lasiurus cinereus* (Stern and Kunz 1998; Koehler and Barclay 2000).

Neonates are large compared with those of other small mammals; they come to represent between 12 and 43 % of postpartum maternal weight (Kunz *et al.* 2009). The size of the forearm of *N. laticaudatus* pups at birth is 45% relative to the size of the forearm of the mother, the fourth finger is 29 % the size of the mother's, and their weight is 31% of the mother's. Comparing these proportions with other tropical bats, it shows that the size of the forearm corresponds to half the size of the mother's forearm, similar in all species (Kunz *et al.* 2009). The exception is *Phyllostomus hastatus*, probably because this species is considerably larger than the other phyllostomids, where there is an inverse relationship between the size of the adult and litter size at birth (Tuttle and Stevenson 1982). The mass of pups observed was within the range, but they were slightly heavier than most insectivorous pups (Kunz *et al.* 2009).

The average growth rates of the forearm (0.44 ± 0.13 mm/day) and weight (0.14 ± 0.09 g/day) were low compared to those reported for the family Vespertilionidae (1.2 ± 0.6 mm/day, and 0.9 ± 0.4 g/day), Phyllostomidae (0.9 ± 0.8 mm/day and 0.3 ± 0.09 g/day) and sister species of family Molossidae (0.8 ± 0.2 mm/day and 0.4 ± 0.2 g/day; Short 1961; Pagels and Jones 1974; Kunz and Robson 1995; Allen *et al.* 2010). It is known that changes in temperature and humidity influence growth rates of bats, so that a decrease in the temperature of the shelter retards the rate of growth and development of the fetus or the cost of thermoregulation increases (Tuttle and Stevenson 1982). However, the temperature increase accelerates the metabolism and consequently the growth rate (Hoying and Kunz 1998). Therefore, it is possible that the constant ambient conditions (temperature and humidity) in the Palace of Governor during the present study do not directly influence an increase or decrease in growth rates; instead, this species may be seeking a thermostable site condition for the hanger nursery. Although in this study we could not compare two colonies of *N. laticaudatus*, for two roosting sites of *Tadarida brasiliensis* found significant differences in growth rates associated with changes in the temperature (Allen *et al.* 2010). These results contrast with a report for *Phyllostomus hastatus* (Stern and Kunz 1998), where the authors could not link any variable to differences in the size of infants from different years. It is possible that this variation is a result of not evaluated intrinsic factors such as sex, food availability, maternal care and some social factors (Klima and Gaisler 1968; Gould 1975; Tuttle and Stevenson 1982; Hoying and Kunz 1998; Porter and Wilkinson 2001).

The analysis of growth models allows comparison of the parameters derived with other studies regardless of the size and analyzed growth period body (Kunz and Robson 1995). The adjustment of variables forearm, fourth finger, and body mass of *N. laticaudatus* were higher for the linear model for the pre-flight, contrary to other bat species where the logistic model is the most common or the only one is tested (*Tadariada brasiliensis*, *Noctilio albiventris*, and most species of Vespertilionidae and Phyllostomidae family (Kunz *et al.* 2009).

It is challenging to compare growth parameters in these studies and that most of them do not realize the division as a turning point in the stages of pre-flight and post-flight during the development of the young, because several authors agree that growth models should be tested in two stages and each of these have physiological, ecological and behavioral characteristics different from each other (Lin *et al.* 2011). There are some articles where high coefficients of determination for the linear model for the pre-flight phase are reported, as in the case of *Myotis myotis* (Paz 1986), *M. lucifugus* (Baptista *et al.* 2000), *M. emarginatus* (Eghbali and Sharifi 2018), *M. capaccinii* (Mehdizadeh *et al.* 2018), *Tadarida brasiliensis* (Allen *et al.* 2010), *Hipposideros pomona* (Lin *et al.* 2011), *Pteropus giganteus* (Sudhakaran *et al.* 2013), *Natalus mexicanus* (Martínez-Coronel *et al.* 2021), and *Leptonycteris yerbabuenae* (Martínez-Coronel *et al.* 2014).

Nyctinomops laticaudatus pups are altricial, as they are born hairless and with their eyes closed. Their tendency to cluster into nursery groups suggests that they have poor thermoregulatory abilities, are incapable of self-feeding, and possess an underdeveloped echolocation system, as well as immature wing muscles and bones.

The results of this study provide valuable insight into the postnatal growth patterns of *Nyctinomops laticaudatus*, revealing an initial phase of linear growth in key morphological traits, followed by a slowdown as the flight stage approaches. These findings not only enhance our understanding of ontogenetic development in this species but also allow for the establishment of functional parameters for age estimation in pups—an essential tool for studies on population dynamics, management, and conservation.

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