

Postnatal Growth and Wing Development in Kuhl's Pipistrelle *Pipistrellus kuhlii* (Chiroptera: Vespertilionidae) in Captivity

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Mozafar Sharifi, Somaye Vaissi, Hossein Javanbakht, and Vahid Akmali (2012) Postnatal growth and wing development in Kuhl's pipistrelle *Pipistrellus kuhlii* (Chiroptera: Vespertilionidae) in captivity. *Zoological Studies* 51(8): 1235-1247. Postnatal growth of the body mass, forearm, and epiphyseal phalangeal gap, and changes in wing morphology including the wingspan, wing area, handwing length, armwing length, armwing area, aspect ratio, and wing loading were studied in 12 Kuhl's pipistrelles, *Pipistrellus kuhlii*, which were born and reared in a flight cage. The pups at birth had a mean \pm S.E. of 1.04 ± 0.08 g of body mass and forearm length of 11.48 ± 0.45 mm. At 60 d, the mean body mass had reached 87.56% of the adult postpartum mass (5.47 ± 0.07 g), and the mean forearm length was 89.46% of the adult length (35.97 ± 0.86 mm). Rates of body mass gain and forearm growth during the 1st 23 d were 0.10 ± 0.10 g/d and 0.64 ± 0.61 mm/d, respectively. The wingspan and wing area increased linearly until 33 d of age, at which time, young bats exhibited clumsy flight with gentle turns. Analysis of changes occurring in the wing morphology indicated that 7 wing characteristics exhibited rapid growth rates in the "pre-flight" period and secondary slower growth rates in the "post-flight" period. Wingspan, handwing length and area, armwing length and area, and total wing area increased linearly until the age of the 1st flight, after which growth rates significantly declined (all $p < 0.000$). Wing loading decreased linearly (-0.80 N/m²/d) until 41 d of age and thereafter increased to a maximum of 25 N/m² at 88 d of age. The aspect ratio showed a high degree of scatter in the early stages of life, which decreased in the latter period of growth. Additionally, linear regression equations, confidence intervals, and prediction intervals were used for age estimations based on data available for the forearm, body mass, total gap of the 4th metacarpal-phalangeal joint, armwing length, handwing length, and wingspan. <http://zoolstud.sinica.edu.tw/Journals/51.8/1235.pdf>

Key words: Postnatal growth, *Pipistrellus kuhlii*, Wing development, Age estimation.

Postnatal growth studies are important for understanding how life-history traits are influenced by extrinsic and intrinsic factors (Kunz et al. 2009). In addition, data collected in postnatal studies can be used to determine growth rates and establish the timing of sexual maturity, the periodicity of reproduction, and longevity. Data on growth trajectories of bats are particularly significant in deriving equations to predict age (Brunet-Rossinni and Wilkinson 2009). Several studies on the postnatal growth of bats were conducted under both natural (Chaverri and Kunz 2006, Liu et al. 2009, Jin et al. 2010, Tang et al. 2012) and

captive conditions (Elangovan et al. 2002, Sharifi and Akmali 2006, Elangovan et al. 2007). In a typical postnatal study, the forearm length, body mass, length of the total epiphyseal gap and wing characteristics are important variables for assessing postnatal growth rates and predicting the age of young bats at different growth stages. However, the length of the forearm and total epiphyseal gap remain the best variables for evaluating age-related changes during the postnatal period (Brunet-Rossinni and Wilkinson 2009). Body mass was also found to be an important variable for assessing postnatal growth rates in

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bats (Liu et al. 2009). Moreover, several nonlinear models are generally used to describe the pattern of postnatal growth in bats (McLean and Speakman 2000, Elangovan et al. 2003, Sharifi 2004a).

The development of flight is a distinguishing aspect of the postnatal growth of bats. Young bats must learn to fly and capture prey on the wing, before becoming independent of maternal care. This requires sufficient development of the wing structure, flight musculature, and vocal and auditory abilities before the onset of flight. Juveniles of several species of bats typically begin flying when they attain about 70% of the adult body mass and over 95% of the adult skeletal size (Barclay 1995). Associations between the wing morphology of bats and their habitat use were inferred using aerodynamic theory (Norberg 1985, Fullard et al. 1991). Habitat use by bats was also well correlated with wing morphology (Bogdanowicz et al. 1999). Wing morphology and flight behavior during postnatal growth were studied in several species of bats such as *Myotis lucifugus* (Powers et al. 1991), *Rhinolophus ferrumequinum* (Hughes et al. 1989), *Artibeus jamaicensis* (Taft and Handley 1991), *Pipistrellus pipistrellus* (Hughes et al. 1995), *Phoniscus papuensis* (Rhodes 1995), *Pip. mimus* (Isaac and Marimuthu 1997), *Phyllostomus hastatus* (Stern et al. 1997), *Plecotus auritus* (McLean and Speakman 2000), *Rousettus leschenaultia* (Elangovan et al. 2004), *Cynopterus sphinx* (Elangovan et al. 2007), and *Hipposideros pomona* (Lin et al. 2011).

In studying postnatal changes in bats, growth patterns of bats have been evaluated using different growth models in several species of bats such as *Tadarida brasiliensis* (Kunz and Robson 1995), *Ple. auritus* (McLean and Speakman 2000), *M. nattereri* (Swift 2001), *Rhi. mehelyi* (Sharifi 2004a), *M. blythii* (Sharifi 2004b), and *Hip. larvatus* (Lin et al. 2010). While most of the above-mentioned studies used non-linear growth equations to provide the best fit for the postnatal growth data, Lin et al. (2011) used an analysis of covariance of 7 wing characteristics during “pre-flight” and “post-volancy” periods to support the hypothesis that postnatal growth in *Hip. pomona* had 2 growth trajectories. In this paper, we describe the postnatal growth and derive quantitative estimates of age and development of morphological changes in wings of young *Pip. kuhlii* under captive conditions.

MATERIALS AND METHODS

Kuhl's pipistrelle *Pipistrellus kuhlii* (Kuhl, 1817) used in this study were mist-netted on the Razi Univ. Campus (34°23'459"N, 47°07'117"E) in Kermanshah, Iran in June 2011. This study was conducted in a flight cage at Razi Univ. A wooden cage (8 m long × 2 m wide × 2 m high) with a black PVC lattice and covered on the outside with sheets of cardboard to isolate the bats from excess light and noise. The cage was maintained under a natural light regime. The cage was located in an isolated animal room on the university campus and was accessible only to those working on the bats (the 2nd and 3rd authors). Bats had unlimited access to fresh water in shallow dishes and to mealworms in plates placed on the floor of the cage and also on a desk about 1 m above the ground. The food was supplemented at weekly intervals by mixing the mealworms in multivitamin syrup (Multivitamin, Oral Drops, Hakim, Tehran, Iran). Initially, all captured bats were fed by hand, but at 2-5 d after capture, they began feeding themselves.

Seven pregnant females were kept in the large flight cage. Pregnant females were kept under a permit issued by the regional office of the environment. All young born in captivity and their mothers were released after the experiment was completed in Sept. 2011. Pregnant females gave birth to 2 sets of twins and 8 singles. The 12 pups were ringed at the age of 4 d. Young bats were gently removed from their mothers, and the body mass was measured to the nearest 0.01 g with an electronic balance. The forearm was measured with electronic Vernier calipers to the nearest 0.01 mm. The length of the total epiphyseal gap in the 4th metacarpal phalangeal joint was measured to the nearest 0.1 mm using a binocular microscope equipped with an ocular micrometer and sub-stage illumination to view the transilluminated wing (Kunz and Anthony 1982). Measurements were carried out at early stages of postnatal growth at 3-d intervals (4 times), 4-d intervals (twice), 7-d intervals (twice), and 10-d intervals (5 times) until day 88 when the experiment was finished. Regression equations were derived to predict the age on the basis of values of forearm length, body mass, and the gap in the phalangeal joint. Using age as the dependent variable, age-estimating equations were derived using a linear regression analysis.

To study wing development, pups were gently removed from their mothers, and morphological

parameters, including armwing length, handwing length, wing area, armwing area, handwing area, and tip to tip of the extended wings, were measured. We placed each individual on its ventral side on a piece of graph paper, extended the right wing with the leading edge perpendicular to the body axis, and traced the outer margin of the wing (Norberg and Rayner 1987, Kunz et al. 2009, Lin et al. 2011). Tracings were scanned and converted to pictures in JPG format on a computer, which were then analyzed with AUTOCAD software 2009 (downloaded free from the Internet) to measure the wingspan, handwing length, armwing length, handwing area, armwing area, and total wing area to the nearest 0.01 mm or 0.01 mm². These morphological parameters were also used to calculate the aspect ratio, wing loading, tip length ratio, and tip area ratio using equations described by Norberg and Rayner (1987). Data were recorded as the mean \pm standard error (S.E.). Wing loading (N/m²) was calculated by multiplying an individual's body mass by 9.8 (acceleration due to gravity) and dividing the result by the wing area. The aspect ratio was calculated as the wingspan squared divided by the wing area. The distance from the body axis to the wing tip multiplied by 2 was defined as the wingspan, while the tip length ratio was calculated by dividing the handwing length (distance from the wrist to the wing tip) by the armwing length (distance from the shoulder joint to the wrist). The tip area ratio was calculated by dividing the handwing area (area of the membrane spanned by the 2nd-5th digits) by the armwing area (area of the wing between the 5th digit, the body, and legs).

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 in the body mass, forearm length, and length of the total gap of the 4th metacarpal-phalangeal joint. Ninety-five percent confidence intervals (CIs) and prediction limits were plotted for the regression equations of body mass, length of the forearm, total epiphyseal gap, handwing and armwing lengths, and wingspan. Growth data of the forearm and body mass of young bats were fitted to logistic and Gompertz equations as follows:

Logistic equation $W = A (1 + \exp(-K(t - I)))^{-1}$
and

Gompertz equation $W = A \exp(-\exp(-K(t - I)))$;

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 growth data in the neonate population. All statistical analyses were performed using SPSS vers. 16.0 (SPSS, Chicago, IL, USA).

Following the test of goodness of the fit of the logistic and Gompertz equations to the data, we drew growth curves (dX/dt) for 11 variables (body mass, forearm length, wing area, wingspan, armwing length, armwing area, handwing area, handwing length, tip length ratio, and tip area ratio). In order to define changes in growth patterns and trajectories, we adopted an early differential equation used by Krebs (1972) as a description of logistic growth as follows:

$$dX/dt = rX(K - X) / K;$$

where X is the variable size at birth, t is the time, r is the early exponential growth rate for the variable in the pre-flight period, and K is the upper asymptote or maximal value of the variable X.

The early exponential growth rate (r) was determined as the slope of a line fitted to the variable data in a graph in which the y-coordinate was $\ln((K - X)/K)$, and the x-coordinate was time (Krebs 1972). For variables including the gap of the 4th metacarpal-phalangeal, rates of growth of wing loading and the aspect ratio, which did not follow the logistic pattern of increase, were measured using linear regression equations separately fitted to postnatal values during pre-flight and post-flight periods (Lin et al. 2011).

RESULTS

The 1st newborn *Pipistrellus kuhlii* with an attached umbilical cord was found on 19 June and the last one on 30 June 2011. Within 11 d, 7 females had given birth to 2 sets of twins and 8 singles. Table 1 shows the life history characteristics and early measurements of the body and wings of these neonates. Young bats were attached to their mother's nipples every time they were examined during their 1st 2-3 d. By the end of the 1st wk, the ears were erect, and a few sparse hairs had grown on their bodies. In the 1st wk, the eyes opened, and pups began to move. The short, soft fur of the pups was distinguishable at 6-10 d. The dark gray color of the fur changed to light gray which was similar to that of adults. At the age of 30 d, they began to roost separately

but close to their mothers. Young bats' ability to fly improved when they were about 30 d old. At this time, they began to independently bite and lick the mealworms. Young bats flew well and began to feed on mealworm when they were 41-45 d old. Young bats were able to make a straight-line flight about 40 d old and flew freely inside the cage. Neonates were born with a forearm length averaging around 31.92% of the length and around 19.01% of the body mass of adult females. Similar respective values for armwing length, handwing length, and wingspan were 30.55%, 16.63%, and

22.79%.

During the 1st 2 wk, both forearm length and body mass increased in linear fashions, with respective growth rates of 0.64 ± 0.61 mm/d and 0.10 ± 0.1 g/d (Figs. 1A, 2A). The pattern of the growth rate (dFa/dt) in forearm length (Fig. 1B) demonstrated an early linear increase followed by a rapid decrease in the post-volancy period. The shape of the growth rate (dW/dt) in body mass (Fig. 2B) illustrated a bimodal pattern of growth because of loss of body mass in the 5th week. Subsequently, rates of increase in these 2

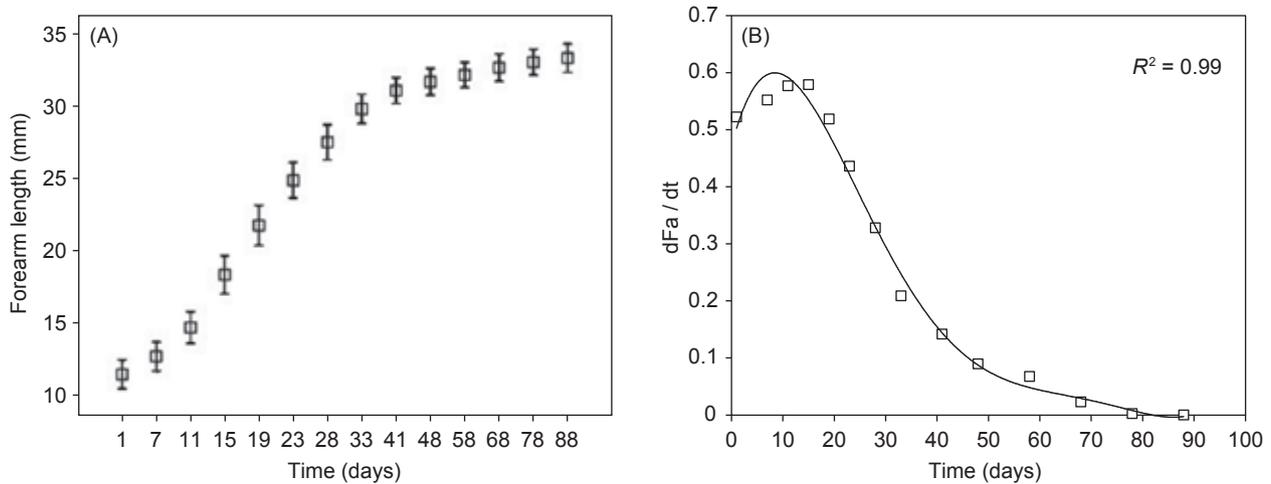


Fig. 1. Average and one standard error of the length of forearm (A) and the pattern of growth rate (B) for forearm (dFa/dt) fitted to the growth values during postnatal period in *P. kuhlii* reared in a flight cage.

Table 1. Life history characteristics and early measurements of the body and wings of 12 neonates of *P. kuhlii*

Life history and body characteristics	
Parturition dates	19-30 June
Number of pups born	12
Sex ratio (male: female)	6: 6
Birth weight \pm S.E. (g)	1.04 ± 0.08
Forearm length at birth \pm S.E. (mm)	11.48 ± 0.45
Handwing length at birth \pm S.E. (mm)	10.36 ± 0.53
Armwing length at birth \pm S.E. (mm)	14.28 ± 0.94
Wingspan at birth \pm S.E. (mm ²)	55 ± 2.08
Handwing area at birth \pm S.E. (mm ²)	55.38 ± 13.52
Armwing area at birth \pm S.E. (mm ²)	204.42 ± 23.04
Wing area at birth \pm S.E. (mm ²)	248 ± 24.86
Tip length ratio at birth \pm S.E.	0.76 ± 0.07
Tip area ratio at birth \pm S.E.	0.35 ± 0.10
Aspect ratio at birth \pm S.E.	14.46 ± 2.02
Wing loading at birth \pm S.E. (N/m ²)	38.83 ± 4.82

S.E., standard error.

characters slowed and approached an asymptotic level.

Neonates of *Pip. kuhlii* showed no flight behavior and remained attached to their mothers until 14 d of age. At an age of 15-20 d, juveniles were able to flutter if released by hand. At the age of 25-30 d, they flew reasonably well and could make a rapid turn at the end of the cage (2 m). At the age of 41 d, they were capable of sustained flight in the flight cage and roosted away from their mothers. At that time, they were able to forage and roost on their own inside the cage. The mean wing area (Fig. 3A) at birth was $248 \pm 24.86 \text{ mm}^2$ and showed a polynomial growth (dW_a/dt) pattern with a peak at day 30 of over $200 \text{ mm}^2/d$ during the preflight period (Fig. 3B). The average wing

area of adults was $2456.1 \pm 16 \text{ mm}^2$. The rate of increase in the wing area was fairly linear and constant during the 2 mo of postnatal growth.

The mean wingspan at birth was $55 \pm 2.08 \text{ mm}$ and showed a similar linear increase during the 1st 33 days, and then the growth attained apparent stability (Fig. 4A). The wingspan of adults reached $230.59 \pm 4.31 \text{ mm}$ at the end of the postnatal period. Similar to wing area, the rate of increase in wingspan during the 1st 5 weeks of the postnatal period was high up to 24 mm/day and then decreased to 0 at the end of the postnatal growth period (Fig. 4B). The rapid growth of the wingspan and wing area facilitated the young bats swiftly flapping their wing membranes. The average armwing length in *Pip. kuhlii* at birth was

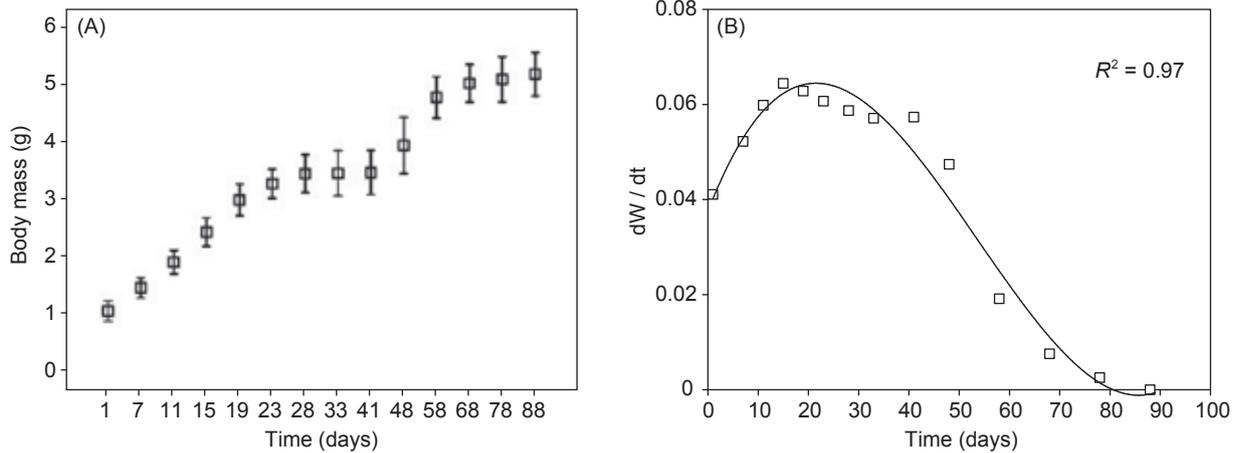


Fig. 2. Average and one standard error of the body mass (A) and the pattern of growth (B) of body mass (dW/dt) fitted to the growth values in *P. kuhlii* reared in a flight cage.

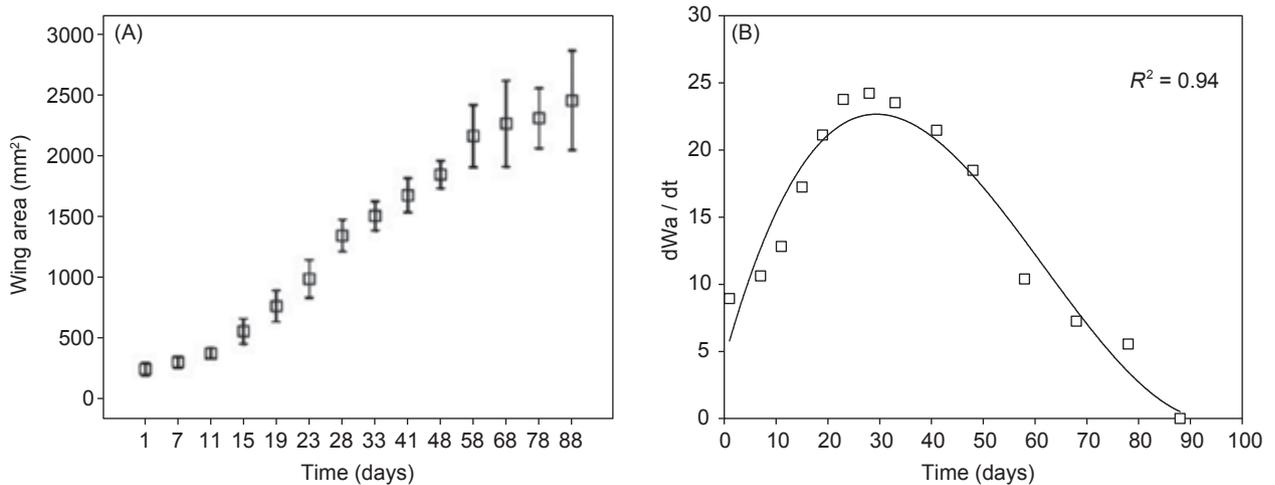


Fig. 3. Average and one standard error of the wing area (A) and the pattern of growth rate (B) (dW_a/dt) fitted to the growth values during postnatal period in *P. kuhlii*.

14.28 ± 0.94 mm. The early increase in armwing length was linear until day 33 but the rate of increase in armwing length gradually decreased afterward and reached an asymptotic value of 0 at the end of the postnatal period (Fig. 5A, B). The rate of increase in armwing length in early rapid growth during the pre-flight period was 0.89 mm/d.

Postnatal growth of the armwing area is illustrated in figure 6A. This pattern of increase in armwing area also followed a logistic model and indicated an early rapid increase from 204.42 mm² up to > 1194.4 mm² (Fig. 6A). The growth rate for armwing area during the pre-flight period was 33.87 mm²/d. This rate drastically dropped when

the bat approached and passed the post-volancy period (Fig. 6B). While growth of the armwing length and area increased rapidly in the early postnatal period and began to decrease at the stage of sustained flight, the handwing length and area continued to grow for a few more days (Figs. 7, 8). Thus, the tip length ratio and tip area ratio steadily increased with age and slowed down after the stage of sustained flight (Figs. 9, 10). The tip length ratio at birth was 0.76 ± 0.07, while for the adults, it was 1.3 ± 0.01. The tip area ratio at birth was 0.35 ± 0.1. At the time of sustained flight, it had reached the value of adults of 0.93 ± 0.06.

Figure 7A demonstrates the average and

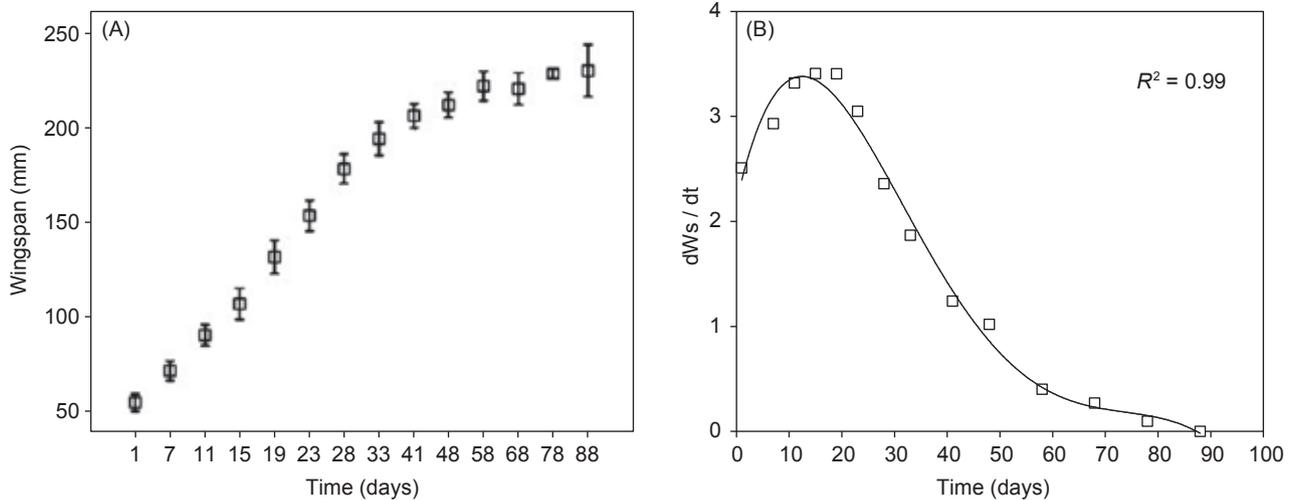


Fig. 4. Average and one standard error of the wingspan during postnatal growth from 1 to 88 days (A) and the pattern of growth rate (B) (dWs/dt) fitted to the growth values in *P. kuhlii*.

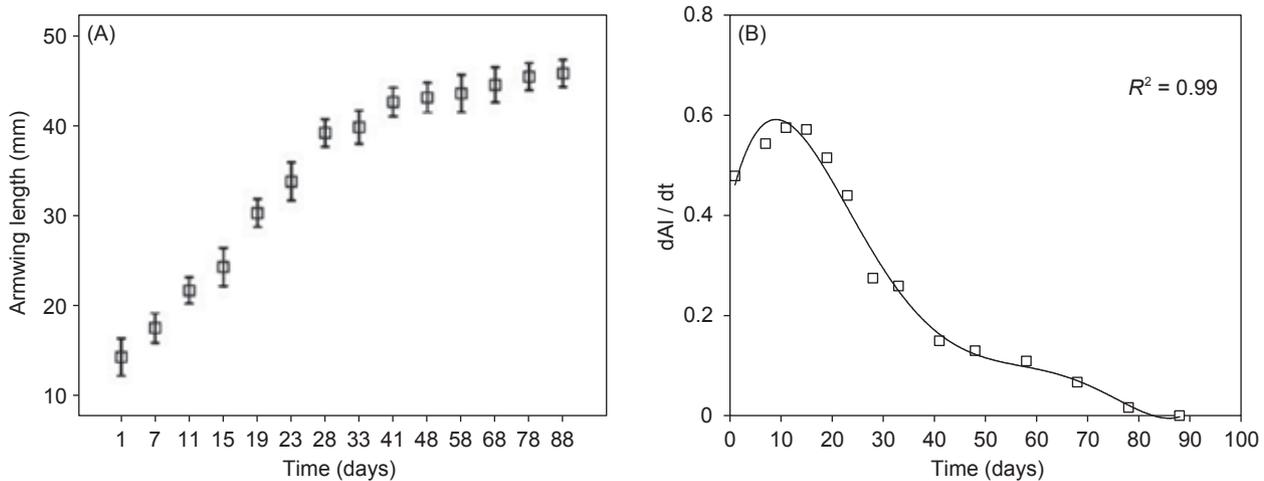


Fig. 5. Average and one standard error of the armwing length during postnatal growth from 1 to 88 days (A) and the pattern of growth rate (B) (dAl/dt) fitted to the growth values for 12 *P. kuhlii* reared in a flight cage.

1 S.E. of the handwing area during postnatal growth at 1-88 d. The handwing area at birth was approximately $55.38 \pm 13.52 \text{ mm}^2$ and had reached $1467.4 \pm 1.18 \text{ mm}^2$ by the end of the postnatal period. The growth rate pattern (Fig. 7B) for the handwing area was very rapid during the 1st 4 wk but decreased rapidly at the end of the postnatal period. The average and 1 S.E. of the handwing length are shown in figure 8. The handwing length at birth was $10.36 \pm 0.53 \text{ mm}$ and reached a maximum of $59.54 \pm 0.77 \text{ mm}$ at maturity. The growth rate followed a typical logistic model with an early rapid increase followed by a decrease in growth at the end of the postnatal period.

The average and 1 S.E. of the tip length ratio

during postnatal growth are shown in figure 9A. The growth ($d\text{Tlr}/dt$) pattern for the tip length ratio for the same period is shown in figure 9B. The tip length ratio value at birth was 0.76 ± 0.07 , which was approximately 58.46% of the adult value. Similar values for the average and 1 S.E. of the tip area ratio during postnatal growth at 1-88 d and the pattern of the growth rate ($d\text{Tar}/dt$) in *Pip. kuhlii* are shown in figure 10A and 10B.

On the contrary, the length of the total epiphyseal gap increased linearly until day 23, and then linearly declined (Fig. 11). Young had reached 63.43% of the body mass and 86.49% of the forearm length of postpartum adults by day 41 when they could freely fly in the cage. Most young

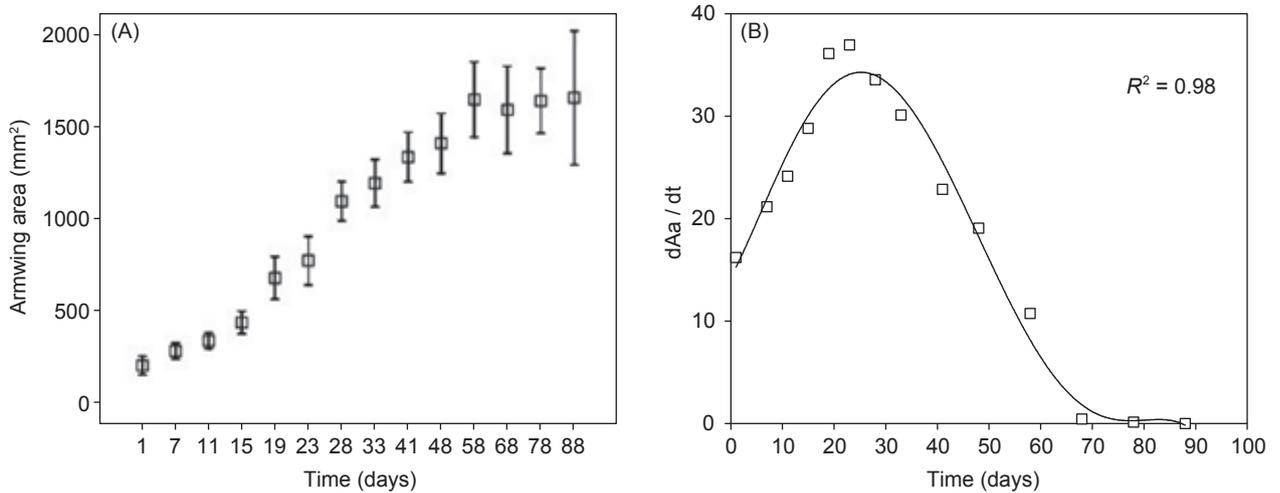


Fig. 6. Average and one standard error of the armwing area (A) and the pattern of growth (B) rate (dAa/dt) fitted to the growth values during postnatal period in 12 *P. kuhlii* reared in a flight cage.

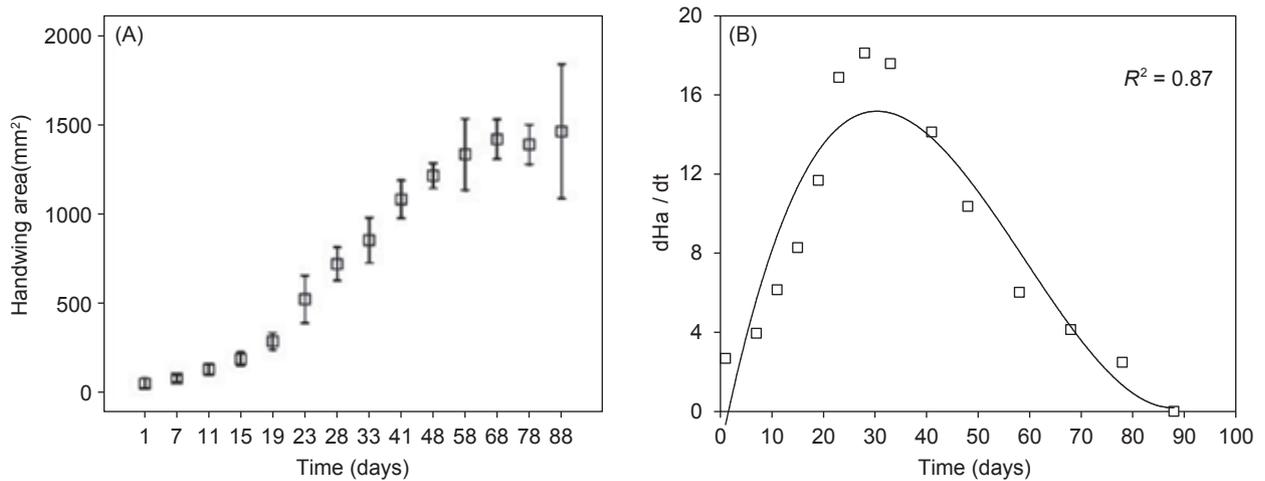


Fig. 7. Average and one standard error of the handwing area during postnatal growth from 1 to 88 days (A) and the pattern of growth (B) rate (dHa/dt) fitted to the growth values in *P. kuhlii*.

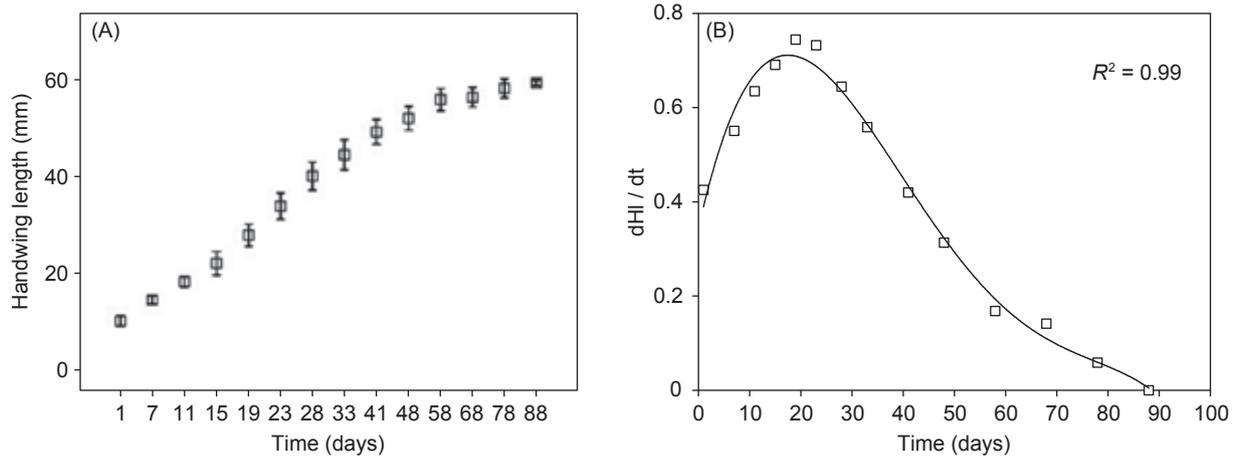


Fig. 8. Average and one standard error of the handwing length during postnatal growth (A) and the pattern of growth (B) rate (dHI/dt) fitted to the growth values in *P. kuhlii*.

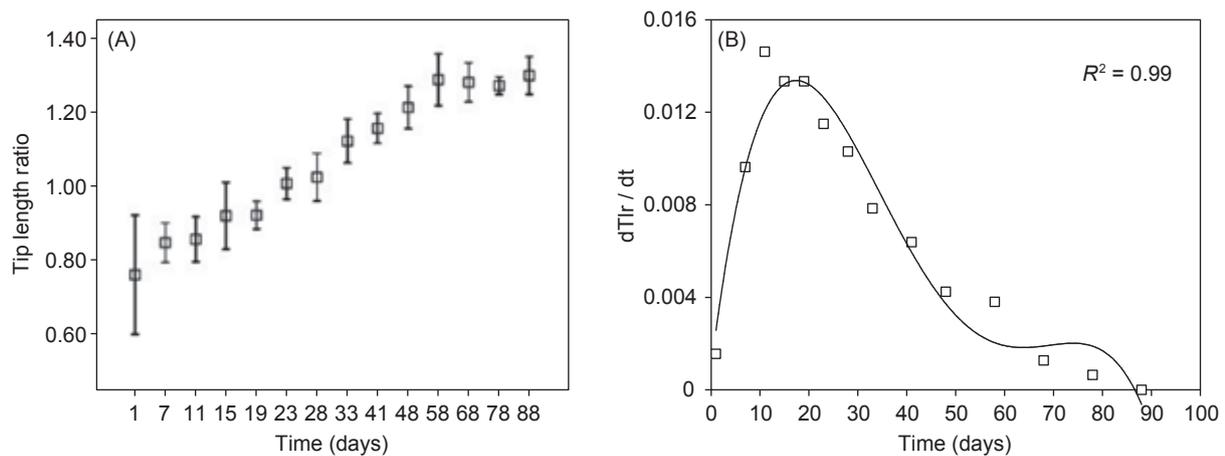


Fig. 9. Average and one standard error of the tip length ratio during postnatal growth (A) and the pattern of growth (B) rate (dTlr/dt) fitted to the growth values in *P. kuhlii*.

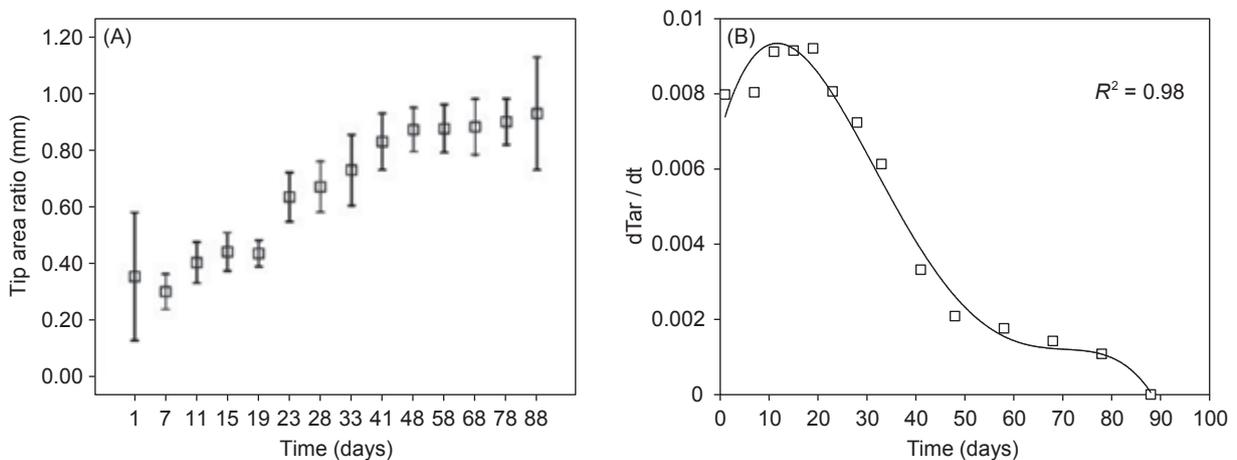


Fig. 10. Average and one standard error of the tip area ratio during postnatal growth (A) and the pattern of growth (B) rate (dTAr/dt) fitted to the growth values in *P. kuhlii*.

bats experienced a loss of body mass (Fig. 2) after the 1st flights in the 5th week when they initially mastered flying skills.

The newborn *Pip. kuhlii* had an average aspect ratio of 14.46 ± 2.02 . The aspect ratio increased linearly during the 1st 3 wk of age and stabilized thereafter (Fig. 12). In the early stages, there was a high degree of scatter which decreased with age and reached the adult value of 25.93 ± 2.24 after the stage of sustained flight. *Pip. kuhlii* at birth had an average wing loading of $38.83 \pm 4.82 \text{ N/m}^2$, which was equivalent to 3.69%

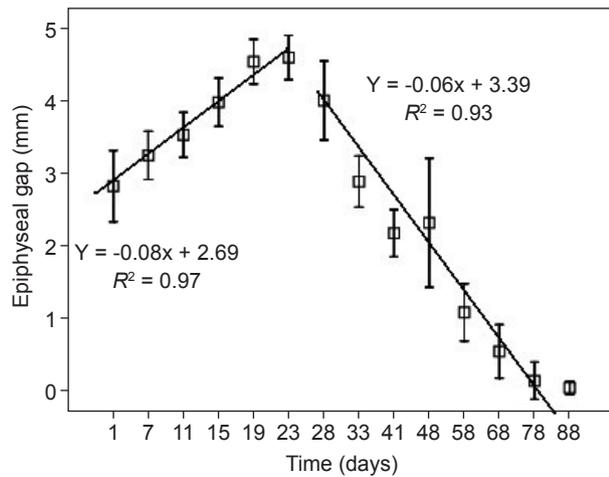


Fig. 11. Average and one standard error of the total epiphyseal gap. Pattern of growth of the gap per day fitted to the growth values in pre-flight (days 1-23) and post-flight period (days 23-88) in *P. kuhlii* reared in a flight cage.

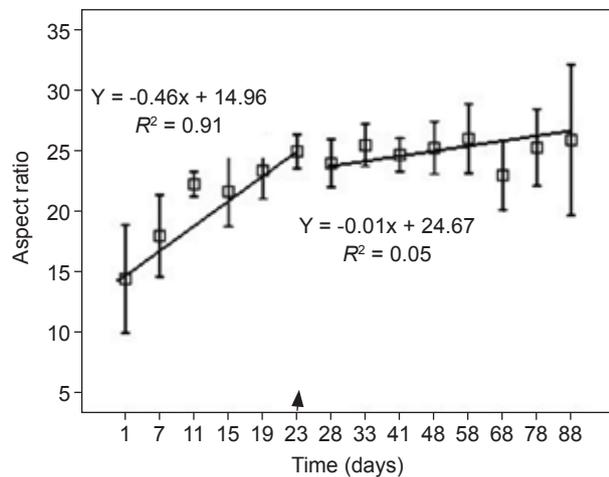


Fig. 12. Average and one standard error of the aspect ratio during postnatal growth from 1 to 88 days. Pattern of growth of is shown by fitted the regression lines to the growth values in pre-flight (days 1-23) and post-flight period (days 23-88) in *P. kuhlii* reared in a flight cage.

of that of adults. After 1 wk, the wing loading increased to its highest value of 51.5 ± 6.05 and then decreased to its lowest value (19.7 ± 1.00) at the age of 41 d. With increasing age, the wing loading smoothly approached the adult value ($25 \pm 2.08 \text{ N/m}^2$) (Fig. 13).

Both the forearm length and body mass of *Pip. kuhlii* fit the 2 non-linear models (logistic and Gompertz). The logistic model was judged to provide the most appropriate description of forearm growth rates (Table 2) in *Pip. kuhlii*, because the overall sum of squares from the model was the smallest, and the model was computationally simple but biologically relevant (Krochmal and Sparks 2007). The Gompertz model had the most suitable fit to the body mass growth curve because the correlation (0.864) was slightly larger than that of the logistic model (0.854). Predicted values for wing characteristics of the 2 non-linear growth models (logistic and Gompertz) had correlation coefficients of > 0.95 . Nevertheless, based on values obtained for the correlation coefficients, the logistic model appeared to be the best-fitting growth model (Table 2). We therefore chose the Gompertz equation as the best-fitting growth model to express the postnatal change in body mass utilizing the same statistical criteria. However, the logistic equation appeared to be the most appropriate model on the basis of the coefficients of variation obtained for the forearm, wingspan, handwing length, and armwing length (Table 2). A summary of growth parameters derived from the 2

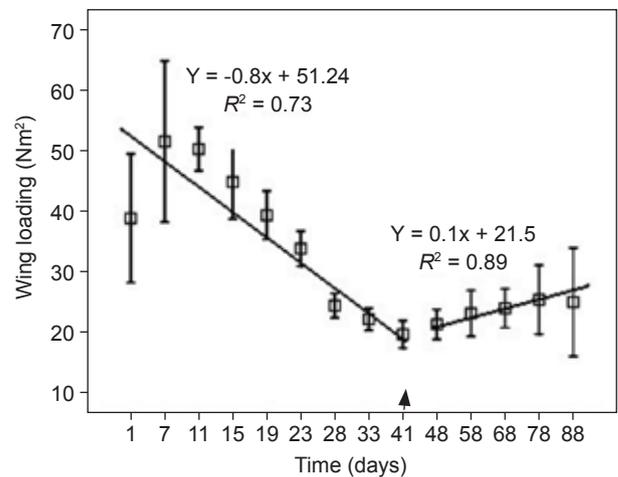


Fig. 13. Average and one standard error of the wing loading during postnatal growth from 1 to 88 days. Patterns of growth rate fitted to the growth values in pre-flight and post-flight periods in *P. kuhlii*.

non-linear growth models fitted to various growth parameters is given in table 2.

Age was quantitatively estimated, based on linear changes observed in the forearm (days 1-23), body mass (days 1-23), total gap of the 4th metacarpal-phalangeal joint (days 28-88), armwing length (days 1-33), handwing length (days 1-33), and wingspan (days 1-33). In all of

these estimations, the linear regression equations allowed age estimates according to values and the dates the values were obtained. Narrow and wide bands respectively indicate 95% CIs and prediction intervals. Some points on this graph may represent more than 1 observation. Relatively higher correlation coefficients for wingspan and handwing indicated that the lengths of these 2

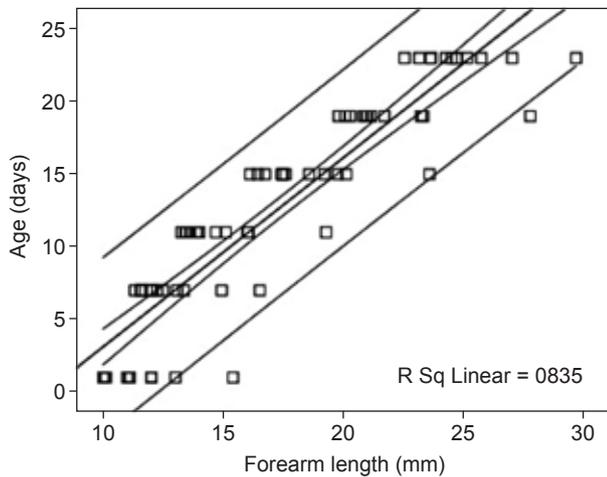


Fig. 14. Regression line estimating the age of *P. kuhlii*, including 95% confidence intervals (narrow band) and prediction intervals (wide band), for values of the length of forearm for days 1-23.

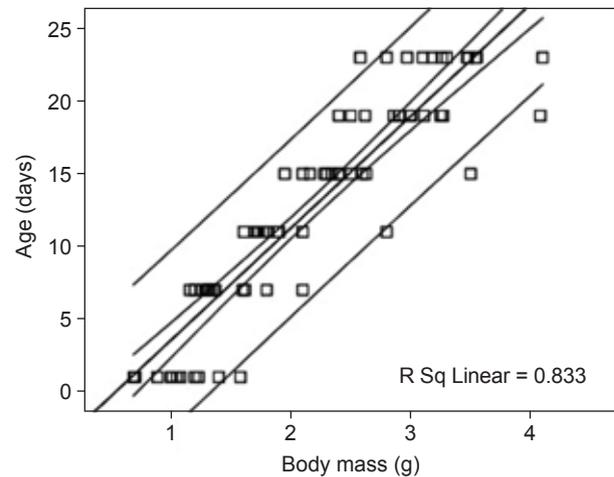


Fig. 15. Regression line estimating the age of *P. kuhlii*, with 95% confidence intervals (narrow band) and prediction intervals (wide band), for values of body mass for days 1-23.

Table 2. Parameters obtained from fitted growth curves to the forearm, body mass, wingspan, handwing length, and armwing length data of 6 male and 6 female *P. kuhlii* reared in a flight cage

Equation	Parameter	Body mass (mean ± S.E.)	Forearm (mean ± S.E.)
Logistic Gompertz	K	0.59 ± 0.005	0.088 ± 0.004
	A	5.14 ± 0.13	33.32 ± 0.31
	R ²	0.854	0.950
	K	0.042 ± 0.004	0.063 ± 0.003
	A	5.30 ± 0.16	33.97 ± 0.39
	R ²	0.864	0.941
Equation	Wingspan (mean ± S.E.)	Handwing length (mean ± S.E.)	Armwing length (mean ± S.E.)
Logistic Gompertz	0.093 ± 0.003	0.087 ± 0.003	0.065 ± 0.004
	226.93 ± 2.16	57.93 ± 0.72	46.25 ± 0.65
	0.968	0.963	0.939
	4.40 ± 2.73	0.056 ± 0.003	0.092 ± 0.004
	160.83 ± 5.53	60.39 ± 0.95	45.25 ± 0.53
	0.249	0.960	0.931

A, asymptotic mass (g) or length (mm); K, growth rate constant (d); R², correlation coefficient. *p* < 0.000 for all data. S.E., standard error.

parameters were more reliable characters for estimating the age of young *Pip. kuhlii* in the 1st 35 d of life. The length of the total epiphyseal gap was derived to predict the age at 28-88 d after birth. Figure 16 illustrates the regression line estimating the age of *Pip. kuhlii*, including 95% CIs and prediction intervals, for values of the length of the total gap of the 4th metacarpal-phalangeal joint for days 28-88. Similar regression lines estimating the age of *Pip. kuhlii*, and 95% CIs and prediction intervals for values of armwing length and handwing length in days, and wingspan for days 1-33 are illustrated in figures 17-19.

DISCUSSION

Patterns of postnatal growth and development obtained from *Pipistrellus kuhlii* are similar to those of other species which showed linear growth of forearm length and body mass during the preflight period (Racey 1982, Kunz 1987). Juveniles of several species of microchiropteran bats typically began to fly when 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 40 when they could fly, young *Pip. kuhlii* had only achieved 86.49% of the forearm length

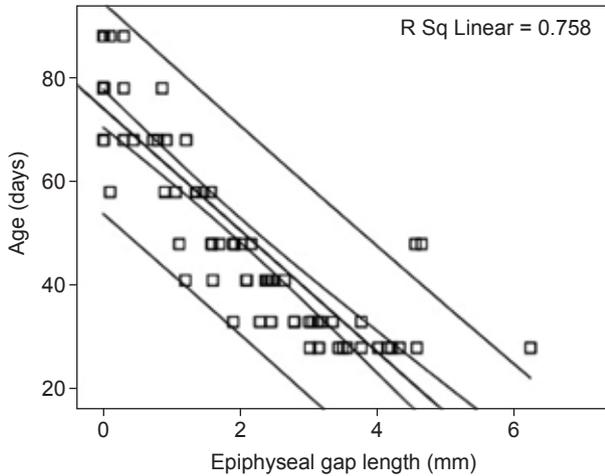


Fig. 16. Regression line estimating the age of *P. kuhlii*, including 95% confidence intervals (narrow band) and prediction intervals (wide band), for values of the length of the total gap of the 4th metacarpal-phalangeal joint for days 28-88.

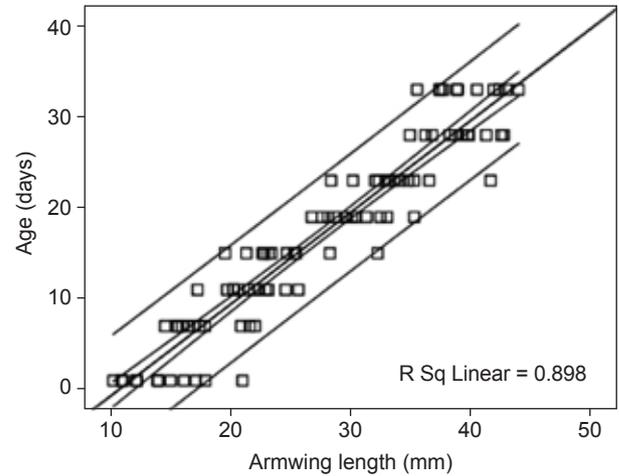


Fig. 17. Regression line estimating the age of *P. kuhlii*, and 95% confidence intervals (narrow band) and prediction intervals (wide band), for values of the armwing length days 1-33.

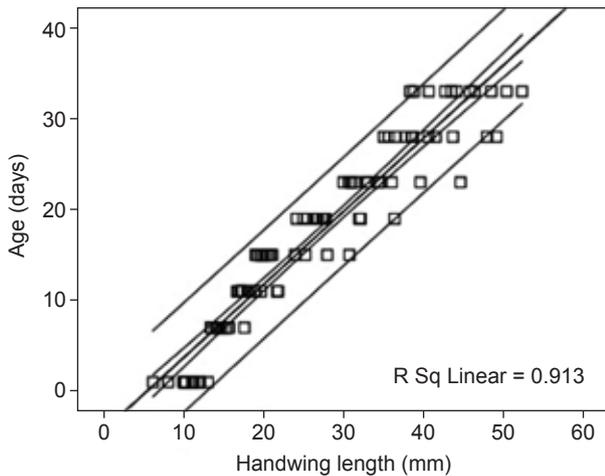


Fig. 18. Regression line estimating the age of *P. kuhlii*, and 95% confidence intervals (narrow band) and prediction intervals (wide band), for values of the handwing length days 1-33.

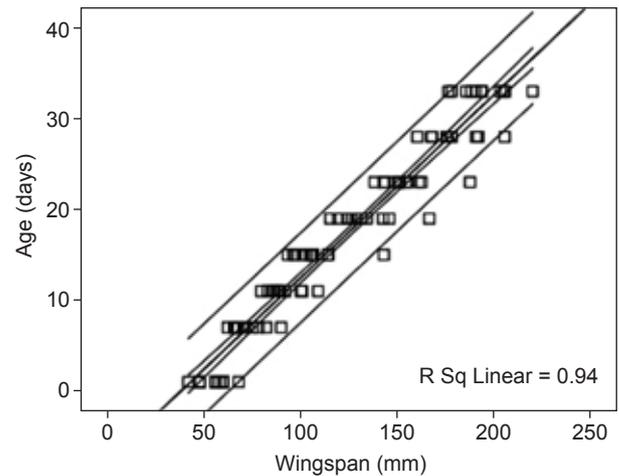


Fig. 19. Regression line estimating the age of *P. kuhlii*, and 95% confidence intervals (narrow band) and prediction intervals (wide band), for values of the wingspan days 1-33.

and 63.43% of the body mass of adults. At the end of the 2nd month after parturition when young bats began flying freely in the flight cage, the length of the forearm was 89.46% of the adult length while the mean body mass was 87.56% of the adult mass. In several other studies on the postnatal growth of bats, it was documented that at the onset of flight, wing dimensions approach adult proportions at an earlier time compared to body mass (Kunz and Stern 1995). Such differences in development of wing length and body mass may provide increased maneuverability and decrease the cost of flight at a time when young bats are learning how to fly and detect and capture insects.

Since the flight of a bat begins only a few weeks after birth, the wings compared to the body mass or forearm are relatively underdeveloped at birth (Fig. 13). Young of *Pip. kuhlii* became volant at the age of 3 wk, implying that the wing membranes at this stage had sufficiently developed to allow early flight. However, at the age of 3 wk, the handwing of *Pip. kuhlii* had not fully formed (Fig. 7). Also, as is shown in figure 8, the handwing grew slightly less rapidly than the armwing during postnatal development. Subsequently as is shown in figures 5 and 8, the handwing became longer than the armwing and the tip length ratio became greater than unity. Since the role of the handwing in flight is to produce the bulk of the thrust generated during the downstroke, its growth and development is important at the time of initiation of flight.

As indicated in figures 2 and 14 in *Pip. kuhlii* during the 1st wk after birth, the body mass increased faster than the wing area, resulting in an increase of wing loading, whereas during the latter period, the wing area grew faster, and causing wing loading to fall steadily until after the age of sustained flight. Similar patterns of an early decrease and subsequent increase were also reported for *Pip. mimus* (Isaac and Marimuthu 1997). The cost of flight is related to wing loading, and at an early stage of postnatal growth when the young become independent of maternal care, a low wing loading will be highly advantageous to allow sustained flight and foraging on their own (Norberg and Rayner 1987). The wingspan directly influences the cost of flight, and increased steadily until around 33 d. There may be a strong need to achieve a large wingspan and wing area in a short period, and hence their linear increases represent rapid and steady growth rates. The aspect ratio influences the efficiency and speed of flight, so its value is probably not significant before

the animal finishes its postnatal growth. The value of the aspect ratio of *Pip. kuhlii* was nearly constant during the postnatal period (Fig. 12). In other species of bats, values for the aspect ratio slowly converge following the onset of flight. As a result, the aspect ratio is much closer to the adult range when the young bats begin to practice flights (Hughes et al. 1989, Powers et al. 1991).

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