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Postnatal Growth and Vocalization Development in the Long-fingered Bat, *Myotis capaccinii* (Chiroptera, Vespertilionidae)

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Robab Mehdizadeh, Hojjat Eghbali, and Mozafar Sharifi (2018) We simultaneously monitored postnatal growth and vocalization development in a free living population of the long-fingered bat, *Myotis capaccinii*, in a maternity colony in the Mahidasht cave, western Iran. Length of forearm and body mass of 1-day-old neonates averaged 19.59 ± 1.23 mm and 3.59 ± 0.23 g and followed linear pattern of growth at mean growth rates of 0.74 mm/day and 0.15 g/day until 28 days of age, after which is increased slowly. A similar nonlinear growth pattern was found for ten wing characteristics (wingspan, wing area, handwing length, handwing area, armwing length, armwing area, aspect ratio, wing loading, tip length ratio, and tip area ratio). However, postnatal growth followed a two phase linear pattern of increase-decrease for the epiphyseal-phalangeal gap and decrease-increase for wing loading. At birth, infant bats produced low, short frequency sonar and oral calls in isolation before they could open their eyes. Isolation calls obtained at age 1-4 days old from *M. capaccinii* pups were frequency modulated shallow calls with longer duration (7.54 ± 1.83 ms) and lower peak frequency (20.07 ± 0.89 kHz) compared to adult female isolation calls (2.35 ± 0.75 ms and 54.02 ± 4.34 kHz). During days 12-16, calls began to resemble adult echolocation calls. Duration of calls increased slightly before 7 days old and then gradually decreased. The peak, start and end frequencies of spontaneous calls increased with age. When the juvenile bats started foraging outside the cave, they only omitted nasal FM calls with 1-2 harmonics. Comparing postnatal changes in body and wing characteristics with those of vocalization, we found that the most positive correlation was between body (forearm length and body mass) and wing features (wing area, wingspan, handwing area, armwing area and aspect

ratio) and call parameters (peak, start and end frequency), while wing loading had a significant negative correlation with the call parameters.

Key words: Isolation calls, Body features, Wing development, Ontogeny, Peak frequency.

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BACKGROUND

Postnatal development in various body and vocal features are crucial processes in which variation in external and internal environment can cause a lifelong effect on different fitness-related traits such as survival, growth, reproduction, various life history traits, and competitive strength (Rödel et al. 2009). Hoying and Kunz (1998) reviewed these parameters for mammals and broadly classified them as intrinsic and environmental factors. These authors provided evidence indicating that factors such as hormonal condition of the mother, quantity and quality of her milk, clutch size, temperature, weather condition and parasite load impact the postnatal growth of mammals. It has also been shown that development in the early postnatal period is also strongly affected by maternal care and behavior (Weaver et al. 2004). Most bats recognize and distinguish their own infants using spatial memory, acoustic, olfactory and visual stimuli and the isolation calls emitted by infant bat are the most important signals for mother-infant interaction and identification (Kunz and Hood 2000; Bohn et al. 2007). Before neonatal bats begin to fly successfully, they must be able to produce high frequency sonar signals familiar to their parents. They should also be capable of intercepting the environmental information contained in the sonar calls.

Echolocation and flight are key components of adaptive traits for survival of the bats. As a result, wing morphology and echolocation features should have a synchronized growth toward attaining low wing loading and aspect ratio. At the same time, echolocation calls gradually develop to sustain stereotype calls with short duration, low intensity and high frequency able to distinguish prey (Arita and Fenton 1997). The postnatal period is an important life stage for bats to develop wings and flight ability, because the flight membrane and wing bones mainly develop during this time (Elangovan et al. 2004, 2007; Hermanson and Wilkins 2008). On the other hand, the complexity of acoustic communication behaviors between mothers and pups appears to be the most important factor in the

early postnatal period because the process of identifying infant bats initiates parental investment to genetic relatedness (Fanis and Jones 1995; Liu et al. 2007).

The ontogeny of echolocation in the Chiroptera is poorly studied. Few species of bats have been studied for postnatal variation in body, wing and echolocation features simultaneously. Data on echolocation ontogeny in bats may only exist for a few species, including *Pipistrellus pipistrellus* (Jones et al. 1991), *Carollia perspicillata* (Sterbing et al. 2002), *Pteronotus parnellii* (Vater et al. 2003), *Tylonycteris pachypus* and *T. robustula* (Zhang et al. 2005), *Rhinolophus ferrumequinum* (Liu et al. 2007), *Rhinolophus cornutus* (Funakoshi et al. 2010), *Vespertilio sinensis* (Jin et al. 2012), *Miniopterus fuliginosus* (Funakoshi et al. 2013), *Myotis macrodactylus* (Wang et al. 2014), *Eptesicus fuscus* (Monroy et al. 2011; Mayberry and Faure 2015), *Glossophaga soricina* (Engler et al. 2017) and *Saccopteryx bilineata* (Fernandez and Knörnschild 2017). Generally, results obtained from these investigations revealed that young bats are very sensitive to any kind of stress such as cold or touching and displacement from the roost, which can cause them to produce loud vocal sounds through the mouth (isolation call) (Liu et al. 2007; Zhang et al. 2005). Adult bats can discriminate between calls from different pups in their colony or in different social group (e.g., *Phyllostomus hastatus*, Bohn et al. 2007; *Carollia perspicillata*, Knörnschild et al. 2013; *Hipposideros pomona*, Jin et al. 2015). Young bats can also recognize their parents' calls (Balcombe and McCracken 1992). Overall, during the ontogeny of vocalizations there is a general trend in which vocalizations rise in frequency, decrease in duration and becoming increasingly stereotyped as bats grow (Jones et al. 1991; Zhang et al. 2005; Liu et al. 2007).

Age estimation and postnatal growth have been surveyed for several species of bats in western Iran. These include Mehely's horseshoe bat (*Rhinolophus mehelyi*) (Sharifi 2004a), the lesser mouse-eared bat (*Myotis blythii*) (Sharifi 2004b; Sharifi and Akmal 2006), Kuhl's Pipistrelle bat (*Pipistrellus kuhlii*) (Sharifi et al. 2012), the long-fingered bat (*Miniopterus pallidus*) (Sharifi and Vaissi 2013) and the Mediterranean horseshoe bat (*Rhinolophus euryale*) (Eghbali et al. 2018). In the present study, we aimed to survey the typical postnatal growth in body, wing and echolocation characteristics in a free living population of *Myotis capaccinii*. We hypothesized that changes in sonar calls are in synchrony positively (or negatively) with simultaneous modification in body and wing characteristics during the postnatal period. Therefore, we aimed to measure the associations between various body and wing changes with those of echolocation calls.

MATERIALS AND METHODS

The present study was conducted in the Mahidasht cave (33°23'N, 47°30'E; 1615 m a.s.l.) from May 18 to July 25 in 2017. The cave located in the mid-Zagros Range, Kermanshah Province, Iran. The cave has three large inter-connected corridors and its entrance is approximately 2 m high and 2.5 m wide. A mixed colony of around 50 *Rhinolophus mehelyi*, 70 *Miniopterus pallidus*, 80 *Myotis capaccinii* and 300 *Myotis blythii* roosted in this cave. Relative humidity and average temperature in the cave during the study period were 76% and 20°C, respectively. The long-fingered bat, *M. capaccinii*, have large feet, inhabit places close to aquatic habitats of the Mediterranean areas of the Levant, Europe and the Maghreb to coastal Asia Minor and also Mesopotamia from Turkey to Iran (DeBlase 1980; Benda et al. 2012). Records of *M. capaccinii* in Iran are restricted to the basins of larger rivers and near the rivers of areas adjacent to the western and south-western slopes of the Zagros Mts. and eastern extension of the Mesopotamian lowland (Benda et al. 2012; Sharifi and Akmal 2006). The conservation status of *M. capaccinii* is assessed as 'vulnerable' (A4bce ver 3.1) by the IUCN (Paunović 2016). *Myotis capaccinii* is also considered a rare species in Iran according to a conservation evaluation system consisting of common, rare, very rare and extremely rare (Sharifi et al. 2000).

We hand-captured neonates with great care immediately after the nightly emergence of female bats. Surgical gloves were used to handle the pups in order to maintain their bodies' odor so that their mothers do not reject them. Pups with an attached umbilical cord and sometimes placenta were assumed to be 1-day old (Kunz and Robson 1995). Upon capture, we placed the pups individually in white cloth bags and, following sex determination, newborn pups were tagged with numbered aluminum band rings (Porzana, Co. Ltd. Norfolk, UK) on forearms. Lengths of the forearm and total epiphyseal gap of the 4th metacarpal-phalangeal joint were measured with a digital caliper to the nearest 0.01 mm. Infants were then weighed with an electronic balance to the nearest 0.01 g. We subtract the tag weight (0.05 g) from the weight of the bat in each measurement. The gap was measured while the bat's wing was spread over a transparent solid plastic sheet above a strong torch in order to make the gap visible (Sharifi 2004a). All data on weights and lengths are presented as the mean and one standard deviation.

In order to measure wing characteristics (wing area, wingspan, handwing area, armwing area, aspect ratio, wing loading, handwing length, armwing length, tip length ratio and tip area ratio), we placed each infant bat on its ventral side over a sheet of graph paper, extended the right wing with the leading edge perpendicular to the body axis, and traced the outer margin of the wing (Kunz et al. 2009;

Sharifi et al. 2012; Eghbali et al. 2018). The tracings were scanned and converted to pictures in JPG format on a computer, then analyzed with Digimizer software version 4.1.1.0 and AutoCAD software version 2013, and the wing parameters were measured to the nearest 0.01 mm or 0.01 mm². Wingspan was measured as 2 times the distance from the body axis to the wing tip. Aspect ratio was calculated by dividing the square of the wingspan by wing area. We calculated wing loading (Nm⁻²) by multiplying body mass by the value of acceleration due to gravity (9.8) and dividing the product by the wing area. 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, body and legs).

The acoustic calls were recorded by a Pettersson D240X Bat Detector (Pettersson Elektronik AB, Uppsala, Sweden; frequency response 10 to 120 kHz) with time expanded (10×). The bat detector was located at 7-10 cm away from pups and a sound recorder was connected to a transportable laptop computer. Every 4 days, we placed each infant in a white bag individually and, after gently touching, the bat isolation calls (and short calls) were recorded. Isolation calls were emitted with mouth open, whereas short calls were emitted with mouth closed. In order to avoid disturbing the infants and their mothers at the roost place, we limited our sampling for infant-mother communication calls to one pair. We captured neonates after the female bats' nightly emergence and captured a few pairs of infant-pups at the time of reunion with their mothers when they returned to the roost. After recording, the infants were brought back to the cave where we captured them. Multiple calls per individual were processed using the software BatSound v1 (Pettersson Elektronik AB, Uppsala) with spectrogram condition (512 points, Hanning window). We recoded a total of 363 i-calls of 51 *M. capaccinii* pups during the 28 days of the postnatal growth period. Isolation calls were multiharmonic and we used only the fundamental frequency (first harmonic) because it contained most of the sound energy. The following four parameters were measured from each pup's call: start frequency (SF), end frequency (EF), peak frequency of the call which contained most energy (PF) and call duration (CD). CD in millisecond (ms) was measured from oscillograms, SF and EF in kilohertz (kHz) were measured from a spectrogram, and PF (kHz) from power spectrum.

We expressed postnatal changes in body mass, forearm length and epiphyseal gap length together with ten wing features and four echolocation variables in four different time frames characterized by Funakoshi et al. (2010) by the following life traits: 1) newborn stage with flapping pups able to form colonies, 2) colony-forming stage capable of moving by fluttering of wings, 3) flyers pups, able to keep

balance during flight inside the cave and 4) foraging juveniles able to forage and capture prey. At least 8 calls from each individual were chosen and a mean value for the calls was calculated in each stage and considered for the analysis. Preliminary data exploration by normality tests showed that call variables distribution within the whole sample of juveniles are normal, and comparisons between sex and age classes were performed by parametric tests. To investigate whether there were sex-specific differences in isolation call parameters, we used independent sample t-tests. A Spearman's rank coefficient was used to explore the correlation between echolocation variables with body and wing features. Analyses were carried out with commercial statistics software (SPSS 20.0 and Excel 2013). All field and experimental procedures were in accordance with institutional guidelines of Razi University implemented by the University Etic Committee issued on 2017/05/25, number 396-2-019.

RESULTS

Newborn stage

We found the first *Myotis capaccinii* pup with attached umbilical cord on May 18 and last one on May 25. At birth, newborn pups were altricial and naked with red brownish back, pink ventral part, closed eyes and folded pinnae. The pups positioned themselves firmly on the ventral side of their mothers for 6-8 days after birth. Eyes opened and the pinnae unfolded at the age of 6-8 days. The pups began to move at the age of 5-7 days, but they did not show any free wing-flapping behavior. The short and soft hairs of pups were distinguishable at about 5-8 days after birth; thereafter they developed grey fur, which appeared similar to that of adults. For newborns with umbilical cords, no significant difference was found in forearm length between males and females ($t = 0.40$, $df = 4$, $P = 0.70$). Similarly, body mass of males and females did not differ significantly ($t = 1.56$, $df = 4$, $P = 0.19$). The mean values of forearm length and body mass of newborns with umbilical cords were 19.59 ± 1.23 mm (mean \pm SD) and 3.59 ± 0.23 g, and they were about 47% (ca. 41.90 mm) and 40% (ca. 8.97 g) of that of adult females, respectively. The mean values of infants' wing area and wingspan were 2800.50 ± 174 and 116.00 ± 5.22 mm² and they were 23% and 42% of that of adult females, respectively. The life history characteristics and measurements of body and wing features for one-day old pups and subsequently on other sampling occasions of the postnatal period (until 36 day) are given in table 1.

Pups of *M. capaccinii* produced a range of vocalizations at birth and during the first two weeks they were audible (long call or isolation call), but some were brief and short. The short calls produced by neonates have similarities with the echolocation calls emitted by the parent. The neonate short calls at early developmental stages in the first week after birth have one harmonic and are lower in frequency compared with those of adult females (Fig. 1, Table 2). Newborn pups with attached umbilical cord produced vocalizations that have a lower start and end frequency and low peak frequency compared with those of adult females (Fig. 1). However, call duration in the neonate is longer than in adults. Short calls have the same average fundamental frequency as that of isolation calls but significant differences are found in the call duration between the two call types, as indicated in table 3.

We found no evidence for a sex-specific differences in isolation call. None of the 4 analyzed acoustic parameters showed significant differences between male and female pups ($P > 0.05$ in all cases) ,suggesting that isolation call bouts do not encode information on pups' sex. During the first 3-4 days, infants emitted loud and noisy sounds (isolation call) by mouth. These calls contained 3 to 4 harmonics, the first of which contained most energy with the average fundamental frequency of 20.07 ± 0.89 kHz (mean \pm SD) (Fig. 2, Table 4). The higher harmonics contained progressively less energy and the maximum frequencies of the first harmonic increased as the bat grew during the next stages. They emitted calls as shown in figure.2 with peak frequency as high as 37% of the parental calls. During 4-8 days of age, neonates produced calls that were similar to the first 3-4 days, but pulse duration increased slightly until 7-days old, when calls became shorter in duration. The vocalizations produced during these days may be for the purpose of forming mother-infant interaction and recognition.

Table 1. Changes in body mass, forearm length, epiphyseal-phalangeal gap and ten wing characteristics measured on ten occasions in the free ranging *Myotis capaccinii* in a nursery colony in the Mahidasht cave

Body and wing features	Age									
	1	4	8	12	16	20	24	28	32	36
Weight (g)	3.59 ± 0.23	4.49 ± 0.17	5.15 ± 0.15	5.70 ± 0.23	6.16 ± 0.29	6.65 ± 0.24	6.94 ± 0.31	7.41 ± 0.40	7.59 ± 0.37	8.39 ± 0.34
Forearm length (mm)	19.59 ± 1.23	23.15 ± 1.27	26.12 ± 1.37	29.39 ± 1.11	31.66 ± 1.63	33.90 ± 1.02	35.56 ± 1.10	37.84 ± 1.22	38.87 ± 0.78	40.90 ± 0.78
Epiphyseal gap	3.35 ± 0.16	3.94 ± 0.15	4.33 ± 0.18	4.86 ± 0.15	4.33 ± 0.16	4.02 ± 0.13	3.60 ± 0.23	2.72 ± 0.25	2.13 ± 0.21	1.64 ± 3.03
Handwing length (mm)	25.18 ± 2.08	29.92 ± 1.14	34.73 ± 2.62	38.08 ± 2.08	42.90 ± 2.43	45.92 ± 2.32	48.91 ± 2.26	53.76 ± 2.24	58.57 ± 2.69	62.97 ± 2.66
Armwing length (mm)	29.39 ± 1.38	33.15 ± 1.55	36.88 ± 2.42	40.85 ± 3.32	45.17 ± 3.40	45.95 ± 2.48	49.42 ± 2.89	49.83 ± 2.86	51.99 ± 2.72	54.67 ± 2.08
Wingspan (mm)	116.00 ± 5.22	137.85 ± 4.74	153.33 ± 4.74	170.88 ± 6.64	189.83 ± 5.65	208.00 ± 8.46	224.00 ± 8.46	237.71 ± 8.40	250.33 ± 8.1	261.71 ± 4.38
Handwing area (mm ²)	328.50 ± 36	438.92 ± 54	622.57 ± 42	720.75 ± 110	871.18 ± 52	980.44 ± 110	1155.33 ± 45	1289.61 ± 58	1542.06 ± 88	1648.78 ± 101
Armwing area (mm ²)	667.11 ± 71	853.09 ± 95	1069.60 ± 60	1435.31 ± 112	1567.60 ± 115	1811.26 ± 128	1944.38 ± 98	2124.76 ± 138	2387.85 ± 97	2619.62 ± 61
Wing area (mm ²)	2800.50 ± 174	3640.85 ± 294	4644.60 ± 234	5666.17 ± 421	6413.30 ± 380	7320.21 ± 339	8222.70 ± 362	9428.76 ± 397	10428.00 ± 388	11088.79 ± 256
Tip length ratio	0.85 ± 0.03	0.90 ± 0.05	0.94 ± 0.06	0.93 ± 0.07	0.95 ± 0.06	1.00 ± 0.05	1.00 ± 0.08	1.08 ± 0.05	1.13 ± 0.10	1.15 ± 0.07
Tip area ratio	0.49 ± 0.04	0.51 ± 0.05	0.55 ± 0.06	0.56 ± 0.05	0.58 ± 0.03	0.58 ± 0.02	0.59 ± 0.01	0.60 ± 0.04	0.61 ± 0.03	0.62 ± 0.03
Aspect ratio	4.81 ± 0.27	5.01 ± 0.60	5.08 ± 0.38	5.18 ± 0.52	5.63 ± 0.37	5.92 ± 0.38	6.11 ± 0.28	6.13 ± 0.41	6.16 ± 0.30	6.18 ± 0.23
Wing loading (Nm ⁻²)	12.94 ± 0.59	12.42 ± 1.15	11.10 ± 0.56	10.11 ± 0.83	9.62 ± 0.36	9.10 ± 0.53	8.45 ± 0.44	7.87 ± 0.50	7.28 ± 0.29	7.56 ± 0.024

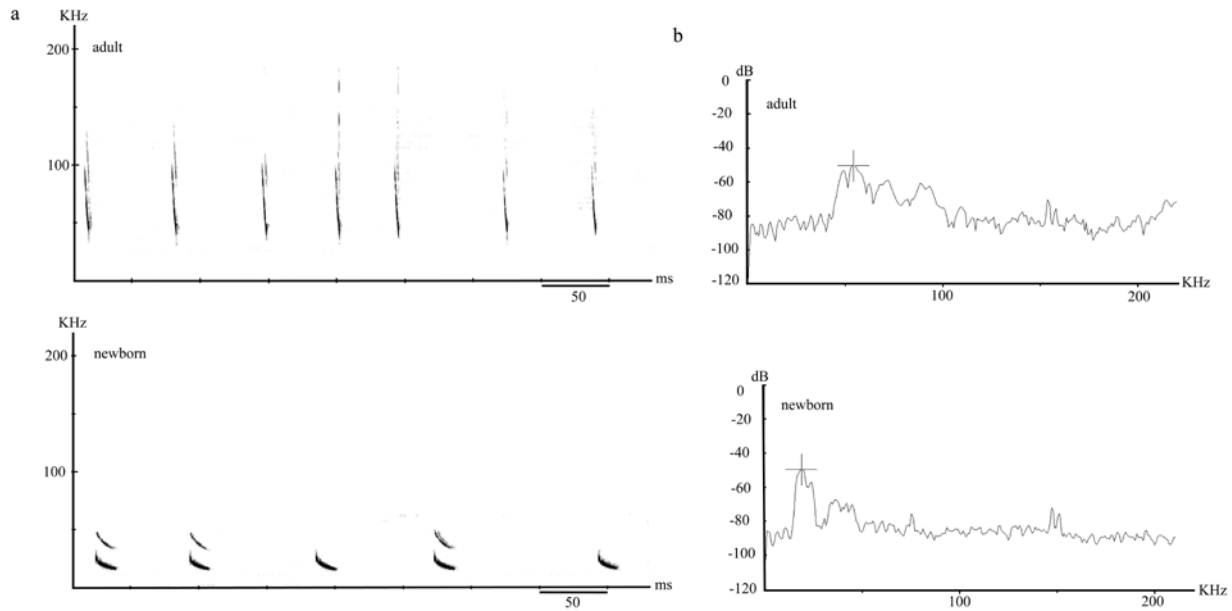


Fig. 1. A comparison between echolocation calls of an adult and newborn long-fingered bat, *Myotis capaccinii*. (a) Sonogram, showing calls composed of a frequency modulation (FM) component with a variable range of frequencies. (b) Power spectrogram, showing the dominant frequency of the call.

Table 2. Comparing echolocation features, including start frequency (SF), end frequency (EF), peak frequency (PF) and call duration (CD), between newborn and adult female *Myotis capaccinii*

Call feature	n	(1-4)-day-old Pups	n	Adult female	p-value
SF (kHz)	6	26.48 ± 3.27	4	72.50 ± 8.80	< 0.05
EF(kHz)	6	16.29 ± 1.535	4	39.55 ± 2.72	< 0.05
PF(kHz)	6	20.07 ± 0.89	4	54.02 ± 4.34	<0.05
CD (ms)	6	7.54 ± 1.83	4	2.35 ± 0.75	< 0.05

Table 3. Comparing long and short calls in the recognition stage with mean ± SD

		SF (kHz)	EF (kHz)	PF (kHz)	CD (ms)
calls	I-call (14)	26.75 ± 2.12	15.86 ± 1.10	20.00 ± 0.82	10.76 ± 2.42
	Short call (16)	26.12 ± 2.31	16.62 ± 1.15	20.14 ± 1.06	6.07 ± 1.28
P-value		> 0.05	> 0.05	> 0.05	< 0.05

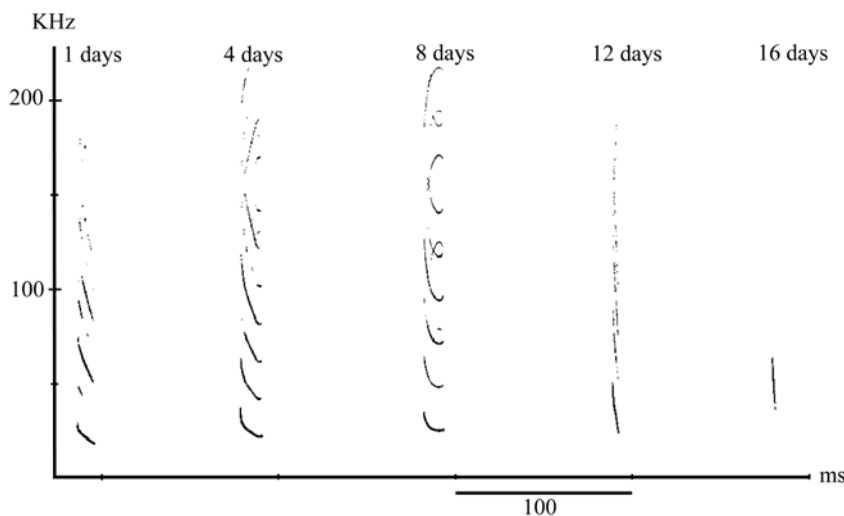


Fig. 2. Changes in the calls emitted by *Myotis capaccinii* infants during postnatal growth from day 1 - 16.

Table 4. Developmental changes in the isolation call in starting frequency (SF), end frequency (EF), peak frequency (PF), call duration (CD) and forearm length (FAL) with mean \pm SD and range

Vocal eatures	Age							
	1 week old		2 weeks old		3 weeks old		4 weeks old	
	1day (n = 6)	4days (n = 6)	8 days (n = 6)	12days (n = 6)	16days (n = 6)	20days (n = 5)	24 days (n = 6)	28 days (n = 7)
SF (kHz)	26.48 \pm 3.27	31.81 \pm 1.35	36.25 \pm 3.80	49.14 \pm 7.28	66.02 \pm 4.51	70.98 \pm 0.84	70.11 \pm 0.99	70.21 \pm 1.02
	22.83-31.89	29.38-33.25	32.07-44.88	39.92-60.50	58.89-69.88	70.17-72.24	68.77-71.20	68.77-71.49
EF (kHz)	16.29 \pm 1.535	20.27 \pm 1.66	21.41 \pm 1.98	28.30 \pm 3.75	37.80 \pm 1.98	39.92 \pm 0.80	39.73 \pm 0.62	40.27 \pm 0.91
	14.50-18.44	17.94-22.00	19.00-24.31	21.75-33.43	34.78-40.54	39.46-41.33	38.77-40.67	38.76-41.12
PF (kHz)	20.07 \pm 0.89	24.12 \pm 1.22	27.98 \pm 3.22	39.72 \pm 5.33	52.41 \pm 1.45	53.94 \pm 1.49	53.06 \pm 1.55	54.90 \pm 1.85
	18.75-21.22	22.15-25.78	23.85-34.59	32.52-45.69	50.56-54.13	51.80-55.70	51.50-55.45	52.60-57.10
CD (ms)	7.54 \pm 1.83	10.66 \pm 1.76	7.42 \pm 2.22	3.47 \pm 0.98	2.70 \pm 0.64	2.91 \pm 0.82	2.59 \pm 0.48	2.50 \pm 0.52
	4.59-9.62	8.98-14.03	4.75-10.34	2.63-5.66	2.14-3.84	2.31-4.12	2.08-3.20	1.90-3.00

Flapping stage

The bat colony increased in size at this stage as a result of more parturition of other sympatric species. The young were fully furred with brownish gray in hair color and their eyes had opened. The young were unable to fly inside the cave. Ten day-old pups could flutter about 20 cm and, at day 16, they could flutter longer distances up to 150 cm. By the end of the first week, average body mass and forearm length were 5.15 ± 0.15 g and 26.12 ± 1.37 mm, respectively, which were equivalent to 57% and 62% of the values of adult females, respectively. At day 16, forearm length and body mass of the young had increased linearly up to 75% and 69% of adult size, respectively. The average wing area and wingspan of the young in this stage were 4644.60 ± 234 to 6413.30 ± 380 mm² and 153.33 ± 4.74 to 189.83 ± 5.65 mm² indicating an increase of 38% and 24%, respectively. Wing loading decreased from 11.10 ± 0.56 to 9.62 ± 0.36 Nm⁻², showing a 13% decrease. However, the aspect ratio increased 11% from 5.08 ± 0.38 to 5.63 ± 0.37 .

Infants gradually became capable of producing short and well-timed pulses at the end of this period (Fig. 2). However, the dominant, start and end frequency of i-calls all increased with growing age, as shown in figure 2, and these calls are used in echolocation and communication. At this stage, the young bats are able to show wing flapping movements, which are due to the maturation of muscular and bones. Laryngeal musculature and vocal apparatus were developing. Sonogram and power spectrogram of calls emitted by young *M. capaccinii* bats still had higher energy, about half of adult bats'.

Flyers inside the cave

At this stage, young bats are very active inside the cave and were difficult to capture by hand. However, at the beginning of this period some young were able to keep their balance during flight and could flutter and glide when they were released by hand. They frequently flew around the cave and changed their roosting site. At the end of this stage the cohort of the nursing colony, comprising four species, began to disintegrate into several smaller colonies. Mean forearm length and body mass of 24-day-old pups were 35.56 ± 1.10 mm and 6.94 ± 0.31 g, respectively. After 16 days, neonate-adult wing span and wing area ratios were 68% and 52%, and reached to 80% and 66% of adult females at 24 days after birth, respectively. Wing loading continued to decrease to 8.45 ± 0.44 approximately 65% of the

1-day-old neonates'. At this stage, the aspect ratio of young increased to 6.11 ± 0.28 and the young (16-day-old) emitted linear FM pulses only through the nose at an average dominant frequency of 54 kHz, which is more like the modulate frequency (FM) echolocation calls emitted by adults. Figure 2 shows that the neonate bats acquired the typical stereotype call at about 16 days of age, before many of body and wing features became well developed.

Foraging juveniles

The young bats displayed flapping flights inside the cave at the age of 24-32 days. At 30-35 days, the young *M. capaccinii* began their first foraging flights. At this age the bat could only be captured by mist net. The average forearm length and body mass of the young were 38.87 ± 0.78 mm and 7.59 ± 0.37 g (93% and 85% of adult females), respectively, and wingspan and total wing area averaged 250.33 ± 8.1 mm² and 10428.00 ± 388 mm² (89% and 84% of adult females), respectively (Table 1). Wing loading decreased from 8.45 ± 0.44 to 7.28 ± 0.29 Nm⁻², a 14% decrease. However, the aspect ratio increased from 6.11 ± 0.28 to 6.16 ± 0.30 . A continuous sequence of calls produced during vocalization development are shown in figure 2. During the early postnatal period, calls began long in duration (4.59-9.62 ms) and became progressively more like the brief frequency modulated (FM) echolocation calls emitted by the mother (Table 4). About two weeks before the pups could fly, they emitted calls that were very similar to the echolocation calls of adults. However, during this time the pups emitted mainly short calls, and only a few i-calls. When the juvenile bats started foraging outside the cave, they only emitted nasal FM calls with 1-2 harmonics.

Association between postnatal development of acoustic and morphological features

Based on a correlation matrix between four echolocation parameters (starting frequency (SF), end frequency (EF), peak frequency (PF) and call duration (CD)) and 8 body and wing characteristics (body mass (BM), forearm length (FAL), wing area (WA), wing span (WS), hand-wing area (HWA), arm-wing area (AWA), wing loading (WL) and aspect ratio (AR)), we found significant positive and negative relationships between body features (FAL and BM) and call parameters (PF, SF, EF). However, the duration call had a significant negative correlation with forearm length (Figs. 3, 4; Table 5). Likewise, we found significant positive correlations between call parameters (PF, SF, EF) and most wing features (WA, WS, HWA, AWA and AR). WL showed a significant negative correlation with

call parameters (PF, SF, EF) (Table 5, Fig. 3, 4). Also, the call duration call had a significant negative correlation with all wing features except the WL. Generally, the range of variations in the call parameters was faster than body and wing characteristics.

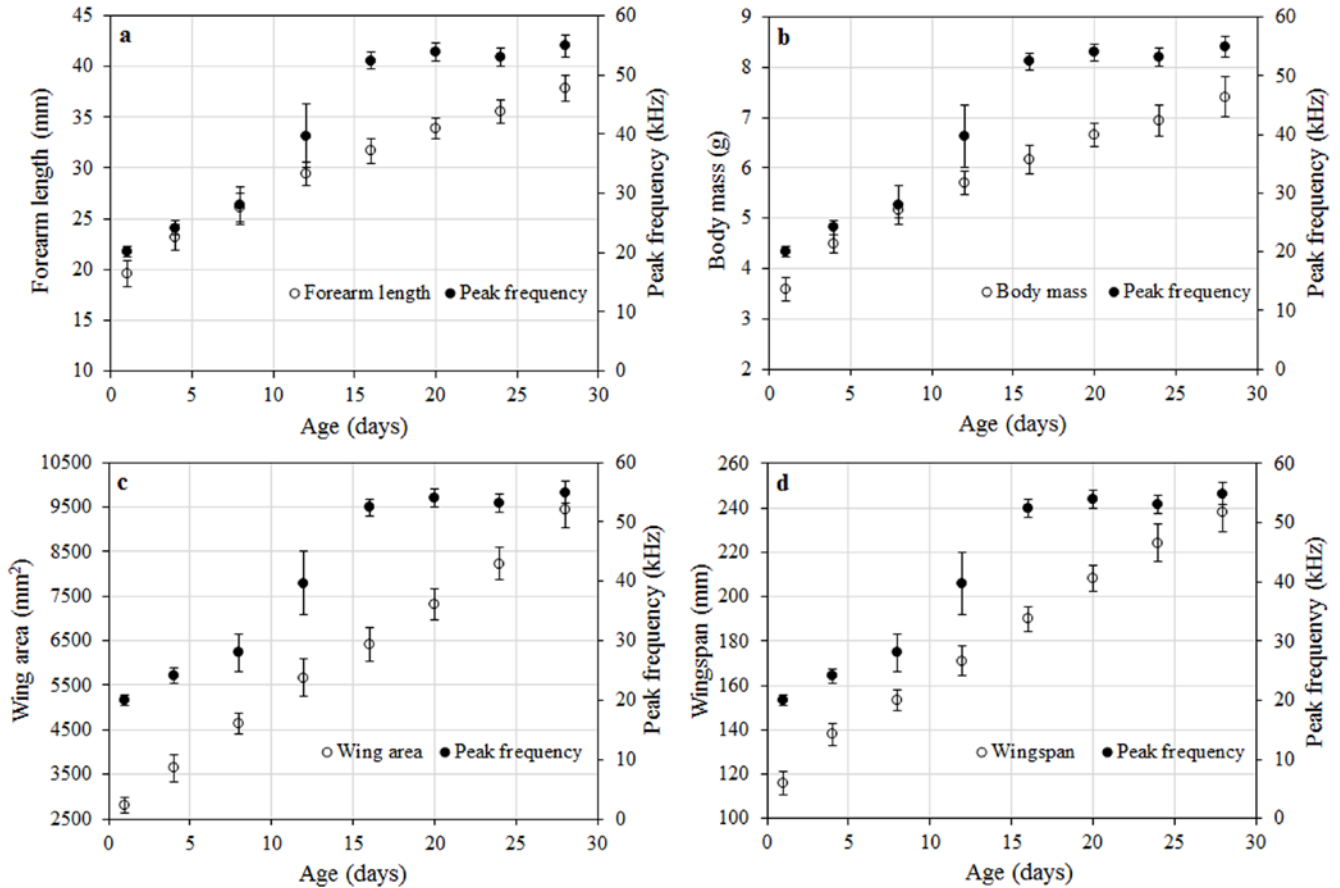


Fig. 3. Positive associations between changes of the peak frequency of calls emitted by *Myotis capaccinii* infants with a) forearm length, b) body mass, c) wing area and d) wingspan from day 1- 28.

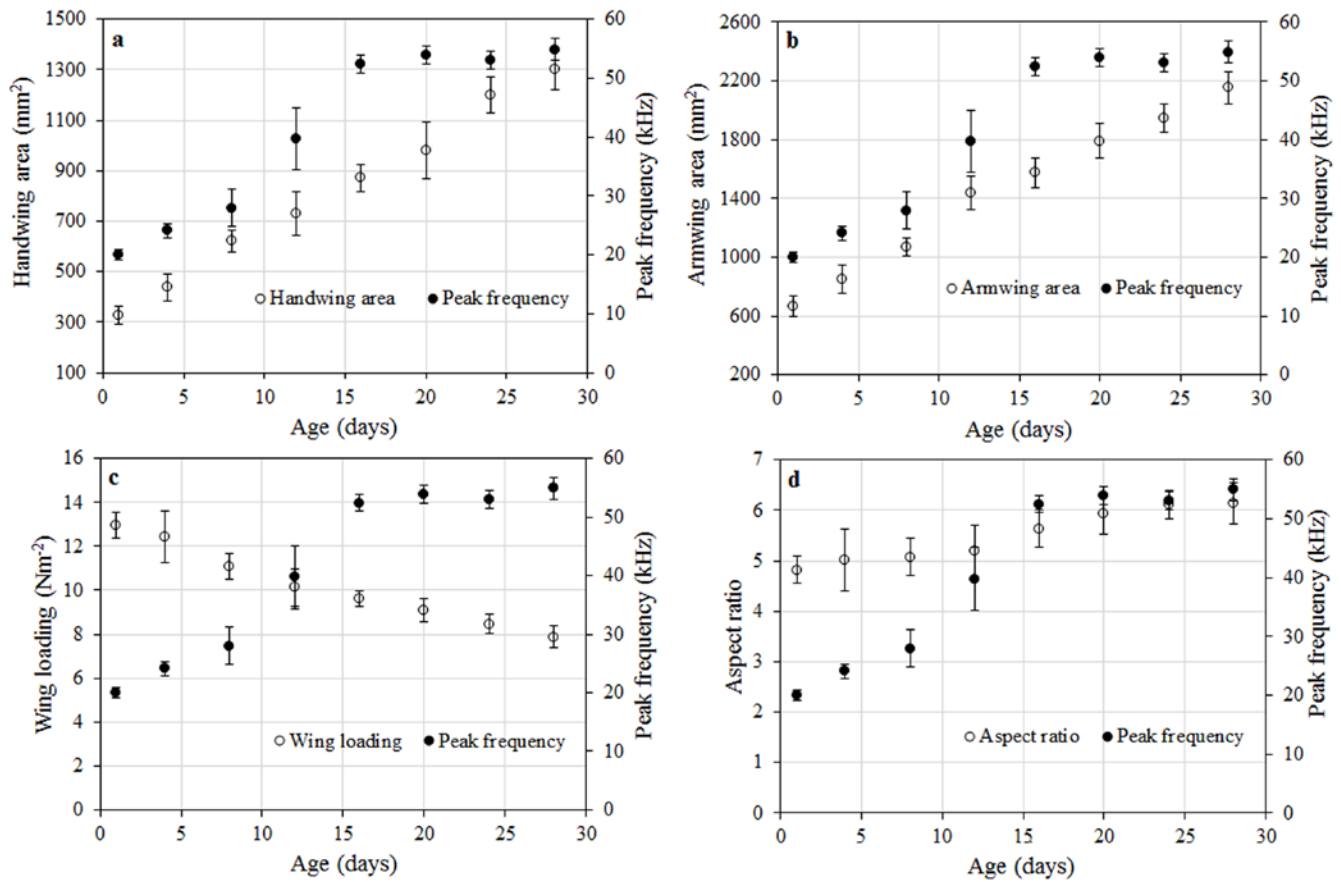


Fig. 4. Positive associations between changes in the peak frequency and handwing area, armwing area and aspect ratio. Negative associations are illustrated between changes in the peak frequency and wing loading.

Table 5. Pearson’s correlation coefficient values between the call parameters for frequencies (starting frequency (SF), end frequency (EF), peak frequency (PF) and call duration (CD)), body mass (BM), forearm length (FAL) and wing features (wing area (WA), wing span (WS), hand-wing area (HWA), arm-wing area (AWA), wing loading (WL) and aspect ratio (AR)) during the postnatal period

Call parameters	Body features		Wing features					
	FAL	BM	WA	WS	HWA	AWA	WL	AR
PF (kHz)	0.92	0.90	0.91	0.93	0.90	0.94	-0.88	0.71
SF (kHz)	0.92	0.89	0.91	0.93	0.90	0.93	-0.87	0.72
EF (kHz)	0.93	0.90	0.91	0.93	0.90	0.93	-0.87	0.71
CD (ms)	-0.76	-0.73	-0.74	-0.74	-0.73	-0.78	0.73	-0.53

Communication calls between mothers and infants

We only recorded the isolation calls emitted in the recognition stage from one mother-infant pair. The infant bat produced long oral sounds (isolation calls) with higher energy and frequency when separated from its mother (Table 6, Fig. 5). The pup, before and after separation from the mother, emitted calls that were almost similar to the calls produced in the absence of the mother (Fig. 5). Mother bats used similar directive calls during social interactions, regardless of whether it was in the presence or absence of its pup. When a pup emitting i-calls was introduced to a stranger mother, the pup would be rejected. The mother did not reject its own pup when it emitted i-calls. In other words, the mother can recognize its own infant through long, begging sounds, indicating that the isolation calls emitted by infant bats might play a role in drawing attention as the mother showed taking back position.

Table 6. Change in emitted calls by pup while separating from its mother and before and after separation from its mother

Recording modes	PF (kHz)	SF (kHz)	EF (kHz)	CD (ms)
Calls before separating	22.29 ± 0.59	29.43 ± 2.07	20.43 ± 1.13	11.01 ± 1.38
Calls separating	31.47 ± 1.37	43.75 ± 2.63	23.50 ± 0.58	21.32 ± 2.63
Calls after separating	23.25 ± 1.08	26.87 ± 0.83	20.87 ± 0.35	10.58 ± 1.83

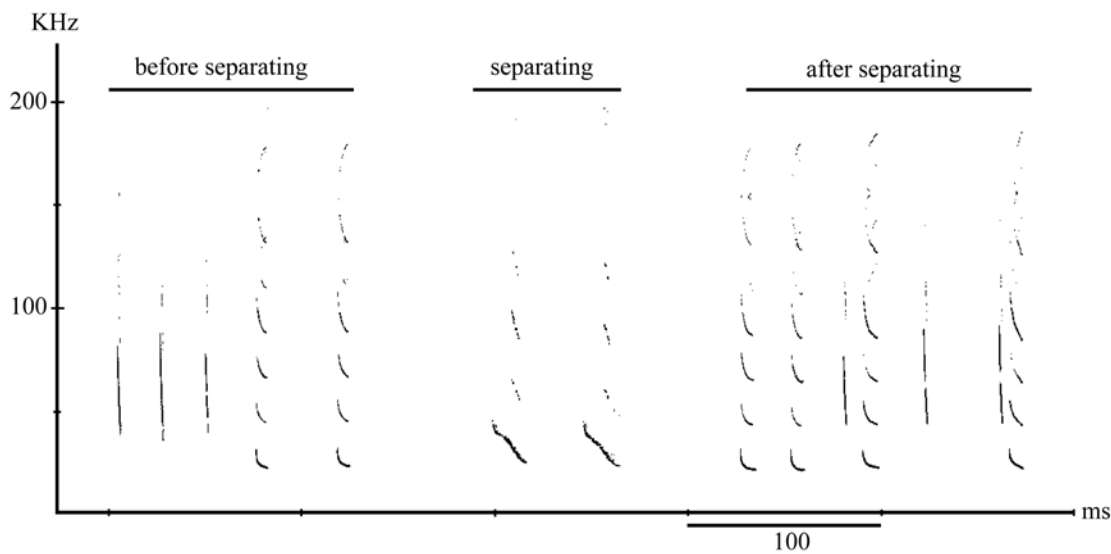


Fig. 5. Recording calls by a mother-infant pair when the infant bat is separating from its mother and modes before and after separation from its mother. One to two harmonic calls with high-frequency in the before and after separation step belong to the mother and multi-harmonic calls with low-frequency belong to the pup.

DISCUSSION

Development of body and wing features

The average percentage of pup's body mass to that of mother's postpartum mass obtained in the present study (40%) was larger than the average ratio for most bat species (ca. 28.3%) reported by Kunz and Hood (2000). Neonate-adult forearm-length ratio was 0.46 at birth. Previous studies have reported that forearm length, wingspan, total wing area and other wing characteristics grow quickly at early stages of life until the first flight, after which the growth rates decreases (Reiter 2004; Jin et al. 2010; Lin et al. 2010, 2011; Sharifi and Vaissi 2013). For newborn *Myotis capaccinii*, length of forearm and wing area increased rapidly - with little deviation - through a linear increase from birth until the age of about 28 days. During the first two weeks after birth, wing area increased faster than body mass, resulting in a decrease in wing loading, whereas during the later period the wing loading fell steadily until after the age of sustained flight. Such a high wing loading at an early stage of life increases the cost of flight. Hughes et al. (1995) and Funakoshi et al. (2010) suggested that having a smaller body size and larger skeleton size at the onset of flight results in a lower wing loading and, in turn, contributes to increased maneuverability and decreased cost of flight, which is important for the survival of young bat. Obtaining such features could allow adult-sized young to develop wings that support a lower force per unit area during flight, indicating substantially lower wing loading than adults. The resulting lower pressure could reduce energy loss and thus facilitate maneuverability, which is particularly important when the young bats begin to learn to fly and monitor and catch prey (Chen et al. 2016).

Most young in the suborder Microchiroptera cannot fly until their wing dimension approaches 90% of adult size (Barclay 1995). In the present study, young *M. capaccinii* first took flight at an age of 4 weeks, when forearm length and body mass had 90.31% and 82.60% of adult size at the onset of flight, respectively. Several microbats exhibit unequal growth rates of body mass and forearm length toward the asymptote of their adult size (Sharifi 2004a; Chaverri and Kunz 2006; Chen et al. 2016). In this study, relatively higher body mass as a percentage of maternal mass at postpartum (40%) could enhance wing loading and might have a detrimental effect on the flight learning and foraging capabilities of the bat as well as survival when the neonate bat become self-forager (Norberg and Rayner 1987; Sharifi et al. 2012).

Vocalization development

Vocal production and echolocation ability are very important elements to the survival of an echolocating bat, and vocalizations development during the early postnatal period may enhance innate biosonar behavior in the adult (Zhang et al. 2005). In this study, we also focused on the development of vocalizations in *M. capaccinii* during the postnatal growth period. The findings indicate that *M. capaccinii* pups are capable of vocalization when they are still blind. There were three stages in the development of i-calls. When taken from their colony during the initial postnatal days 1-8, newborn bats could emit both short calls with heads, ears shaking or nasal and also long sequences of loud isolation calls through the mouth. Individual i-calls with umbilical cords were long (~8 ms), harmonically structured, and contain energy in frequency bands that were audible to the human ear (Fig. 2, Table 4). Short calls emitted by one week old infants were similar to isolation calls but shorter in duration call (Fig. 1, Table 3). Zhang et al. (2005) considered the short calls produced by pups of *Tylonycteris pachypus* or *T. robustula* to be precursors of echolocation calls. This result is parallel to earlier findings. Jones et al. (1991), Knörnschild et al. (2007) and Jin et al. (2012) suggested that early echolocation in studied species do not originate from isolation calls but are innate and indicating that bat brainstem areas differentially control echolocation and isolation pulses (Fenzl and Schuller 2007; Jin et al. 2012).

In this study, we found no significant difference in postnatal growth rate of body and wing characteristics between male and female pups. Moreover, we did not detect a gender difference in isolation calls in early vocalization development between male and female neonates, which corroborates findings on other bat species (e.g., *Glossophaga soricina*, Engler et al. 2017; *Saccopteryx bilineata*, Knörnschild et al. 2012; *Carollia perspicillata*, Knörnschild et al. 2013). In *M. capaccinii*, during recognition part of the first stage, the duration of i-calls increased slightly in pups that were up to 7-day old and then decreased when a close relationship developed between the mothers and pups. This phenomenon has also been reported for the ontogeny of vocal development in several other species (*Tylonycteris pachypus* and *T. robustula*, Zhang et al. 2005; *Vespertilio sinensis*, Jin et al. 2012). However, the duration of i-calls increased in some species during development (Nelson 1964; Vater et al. 2003; Liu et al. 2007), while i-calls decreased with age in others (Habersetzer and Marimuthu 1986; Moss 1988; Bohn et al. 2007; Knörnschild et al. 2007; Mayberry and Faure 2015). Zhang et al. (2005) suggested that the longer duration of both the mothers' and infants' calls may

facilitate reunion, and the lower frequency of the female directive calls may be more easily heard by the infant because its i-calls also contain lower frequencies.

During postnatal development in the second stage (8-16 days after birth), the young bats gradually displayed pulses with a higher frequency range and lower duration, and in the end of this stage produced calls similar to that of adult echolocation signals. This finding is consistent with reports of other bat species emitting echolocation signals during the second week of their postnatal period (e.g., *Myotis lucifugus*, Moss et al. 1997; *Myotis macrodactylus*, Wang et al. 2014). From the flapping to flying stages in *M. capaccinii*, peak frequency of the calls shifted gradually from 52.41 ± 1.45 to 54.90 ± 1.85 kHz, while pulse duration shortened slightly from 2.70 ± 0.64 to 2.50 ± 0.52 ms (Table 4). These values were similar to those of their mothers (54.02 ± 4.34 kHz and 2.35 ± 0.75 ms, respectively). Thus, it is conceivable that the development of the echolocation system in these young bats is essentially completed by the end of these stages. In general, in the third stage, long calls became closer to the brief frequency modulated (FM) calls emitted by the mother and may serve mainly for infant-mother communication functions. Finally, our findings correspond to other studies on the vocalization development suggest that echolocation calls develop by showing a reduction in duration and an increase in frequency during postnatal growth as reported by Jones et al. (1991), Sterbing et al. (2002), Zhang et al. (2005), Liu et al. (2007) and Monroy et al. (2011).

CONCLUSIONS

The changes in body features and wing and sonar characteristics in *Myotis capaccinii* reported in this study are basically similar to previous studies. Forearm length increased linearly until 28 days after birth and both began to fly and echolocate similar to their parents. During the postnatal period, vocal growth and development changed in parallel with maturation and behavioral changes. However, we observed a gradual growth pattern in which vocalization development proceeded more rapidly than body and wing characteristics. In this species, from the flapping to flying stages, the young bats emitted pure tone sounds with intense first harmonic components similar to those of their mothers. Nevertheless, we found consistent correlations between vocal parameters and body and wing characteristics. The present study shows that changes in acoustic structure correlate with various morphological characteristics that are associated with bat flying foraging, and feeding abilities.

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Authors' contributions: RM and HE performed the field work and collected data. RM carried out vocalization studies. HE analyzed body and wing growth. All authors participated in revising the manuscript. MSH organized the study and finalized the manuscript. RM and HE contribute equally to this work.

Competing interests: The authors declare that they have no competing interests.

Availability of data and materials: We have all data that is included in this study.

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