

## Ontogeny of vocal signals in the little brown bat, *Myotis lucifugus*

CYNTHIA F. MOSS\*, DEBBY REDISH†, COLIN GOUNDEN\* &  
THOMAS H. KUNZ‡

\*Department of Psychology and Program in Neuroscience, Harvard University

†Department of Biology, Woods Hole Oceanographic Institution

‡Department of Biology, Boston University

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**Abstract.** This study reports developmental changes in the vocal signals produced by wild-caught pre-volant and volant *Myotis lucifugus*. Audio recordings were made from young animals (1–33 days old) and adults (over 1 year of age). The animals were removed from an attic maternity roost and studied individually in a room below. To stimulate flight-related behaviours, animals were released from a launching platform via a hinged floor, and their vocalizations were recorded as they approached a soft foam pad below. When the hinged floor opened, the youngest animals (1–4 days old) typically dropped onto the pad, but older animals either flapped their wings to achieve some horizontal displacement (>4 days) or sustained horizontal flight (>17 days). Vocalizations recorded under these conditions showed frequency modulation characteristic of adult echolocation sounds, even in animals as young as 4 days. Ontogenetic trends showed an increase in sound frequency, an increase in sound repetition rate and a decrease in sound duration as the animals matured. These data are discussed in the context of the development of echolocation behaviour in bats.

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Insectivorous bats use echolocation to orient in the environment and capture prey. The bat's vocal apparatus functions as a sonar transmitter of ultrasonic signals that reflect well off small objects, and the bat's auditory system functions as a sonar receiver that determines the angular position and distance of targets (Griffin 1958; Schnitzler & Henson 1980; Moss & Schnitzler 1995). Before young animals begin to hunt insects successfully during their first flights, they must be capable of producing high frequency sonar cries and of processing the spatial information contained in the sonar echoes. Thus, the vocal production system and the auditory system must develop and operate in concert for the bat to use its biological sonar.

Data on the vocalizations of young bats exist for several families, including Vespertilionidae

(e.g. *Antrozous pallidus*, Brown et al. 1978; *Eptesicus fuscus* and *Myotis lucifugus*, Gould 1971; *Nycticeius humeralis*, Scherrer & Wilkinson 1993; *Pipistrellus pipistrellus*, Jones et al. 1991), Molossididae (*Tadarida brasiliensis*, Gelfand & McCracken 1986), Noctilionidae (*Noctilio albiventris*, Brown et al. 1983), Phyllostomidae (*Phyllostomus discolor*, Esser & Schmidt 1989) Rhinolophidae (*Rhinolophus ferrumequinum*, Konstantinov 1973; *R. ferrumequinum nippon*, Matsumura 1979; *R. rouxi*, Rübsamen 1987) and Hipposideridae (*Hipposideros speoris*, Habersetzer & Marimuthu 1986). Shortly after birth, the vocal repertoire of an infant bat differs from that of an adult (Brown & Grinnell 1980), and during post-natal development there is a general trend for the vocalizations to rise in frequency, decrease in duration and become increasingly stereotyped (e.g. Gould 1971; Konstantinov 1973; Matsumura 1979; Brown et al. 1983; Habersetzer & Marimuthu 1986; Rübsamen 1987; Moss 1988; Jones et al. 1991).

The rise in vocalization frequency is accompanied by a developmental increase in auditory responses to high frequency sounds (e.g.

Correspondence: C. F. Moss, Department of Psychology, University of Maryland, College Park, MD 20742, USA (email: cmoss@bss3.umd.edu). D. Redish is at the Department of Biology, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, U.S.A. T. H. Kunz is at the Department of Biology, Boston University, Boston, MA 02215, U.S.A.

Konstantinov 1973; Brown et al. 1978; Rübsamen 1987; Rübsamen et al. 1989). Developmental data on changes in high frequency hearing in young bats come from neurophysiological measures, typically pure-tone evoked responses from the inferior colliculus in anaesthetized animals (Konstantinov 1973; Brown et al. 1978; Rübsamen 1987). These neurophysiological data show that the bat's auditory system develops to process the ultrasound frequencies present in the adult echolocation signal; however, they provide no ontogenetic index of echo information processing.

Direct behavioural measures of sonar function in young bats are difficult to obtain, because psychophysical procedures require lengthy training that would confound any observation of ontogenetic changes in echolocation performance. Field observations on the behaviour of young bats as they make the transition from maternal dependency to independent foraging provide indirect evidence for the emergence of echolocation. For example, little brown bats begin to fly out from the roost at 14–18 days of age, at which time they begin to forage on their own (Kunz & Anthony 1996). For approximately 1 week, young *M. lucifugus* consume both insects and mother's milk, and they become effective foragers shortly after their first evening flights (Buchler 1980; Kunz & Anthony 1996). *Myotis lucifugus* of less than 14 days of age do not forage, but they may take short practice flights in the confines of the maternity roost (Kunz & Anthony 1996). There are some published data on sounds produced by *M. lucifugus* during their first foraging flights (Buchler 1980); however, there are no comparable data on vocalizations of younger volant bats during their period of maternal dependency (Gould 1971). Vocalizations that accompany the flights of young bats inside the roost may serve an important functional role in the development of echolocation behaviour, because these vocal signals can guide early attempts at obstacle avoidance by sonar.

In the present study, we systematically characterized developmental changes in the vocal signals produced by pre-volant and volant *M. lucifugus*. We studied free-ranging bats, because captive-reared bats grow at different rates than those in the field (Buchler 1980; Kunz 1987). Vocalizations were recorded from bats ranging in age from 1 to 33 days under conditions that stimulated flight-related behaviours in young bats. Here we report

changes in vocal emission patterns that are consistent with those expected during the ontogeny of echolocation behaviour.

## METHODS

### Study Site and Animals

Bats were captured by hand in the attic of a large house in Canaan, New Hampshire, containing a maternity colony of approximately 850 adult and young *M. lucifugus* (Kunz & Anthony 1982; Powers et al. 1991). Bats were collected, measurements were taken, and vocalizations were recorded between about 2030 and 2330 hours from 19 June to 16 July 1989. In most cases, we removed young bats from dense clusters on attic beams or in crevices while the mothers were foraging. Young bats were captured soon after adults departed to feed and before they returned from their first nightly feeding. Once the young were fully volant, young and adult bats were captured prior to the nightly emergence. Upon capture, animals were temporarily housed in small groups of 4–5 (Kunz & Kurta 1988) to maintain conditions comparable to their natural roosts. Bats were weighed and sexed, and wing measurements were taken to estimate age (see below). After taking measurements and recording flight and vocal behaviour, we took care to return individuals to the location in the attic from which they were removed. Sound recordings were made from 83 young bats, ranging in age from 1 to 33 days, and two adults. Most bats were tested at only one age; however, 16 were recaptured and tested at two different ages and two were tested at three different ages ( $N=103$  test sessions).

### Ageing

We estimated the age of subjects based on equations derived from forearm length and from total epiphyseal gap length (Kunz & Anthony 1982). We measured forearm length to the nearest 0.1 mm with a dial caliper and used this to estimate age from birth to 12 days. The total epiphyseal gap was used to estimate age from 12 to 33 days. This was measured by extending the left wing, laying it flat on the stage of a dissecting microscope, and measuring the epiphyseal gap with a calibrated ocular micrometer (Kunz & Anthony 1982). A numbered plastic split-ring

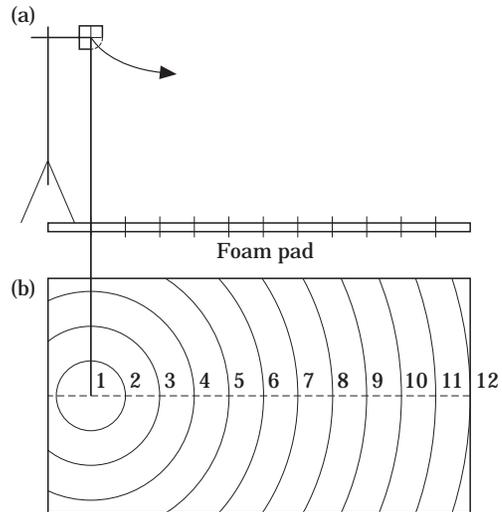
band (A. C. Hughes) was placed on the forearm of each bat for identification. Repeated measurements of selected recaptured individuals allowed us to cross-validate age estimates of infant and juvenile bats and to estimate the age of animals beyond 29 days. Additional data on wing morphology are presented elsewhere (Powers et al. 1991).

### Apparatus and Testing Procedures

Animals were studied individually in a room ( $4 \times 5$  m) on the floor below the attic roost. A custom-made flight launching apparatus was positioned towards the back of the room. The launching apparatus consisted of a small ( $6.3 \times 8.0 \times 2.5$  cm) transparent Lucite box with a hinged floor. The box was mounted at the end of a 0.5-m length of Lucite attached to a tripod that was adjusted to 1.5 m above the floor. The experimenter could open the hinged floor of the box by pulling a string to release a clip that held it closed. When the hinged floor opened, the bat dropped from the launching apparatus. A  $3.0 \times 2.3$ -m soft foam pad was located on the floor directly below the launching apparatus. Twelve circular divisions spaced at 20-cm intervals were drawn on the foam pad to score the distance covered by the bat once it was released from the platform (Fig. 1). Each bat was placed in the launching apparatus and released via the hinged floor at least three times in a given test session, and flight and vocal behaviour were recorded for each trial.

### Audio and Video Recordings

We used a Panasonic video camera (model AG160) to record the flight behaviour of each bat after it was released from the launching apparatus. The video camera was mounted on a tripod at the entrance to the room, 3 m from the launching apparatus. A QMC (200) ultrasound microphone was placed approximately 1.5 m from the launching apparatus at an elevation of 25 cm and  $45^\circ$  off axis from the video camera. Positioning of the microphone at this angle minimized interference with the bat's flight path and allowed adequate signal-to-noise ratio of the vocal signals after the hinged floor was opened and the animal was released into the room. The vocal signals were amplified ( $\times 5$ ) and recorded on reel-to-reel audio tape at 60 in/s with a Racal Store-4D recorder



**Figure 1.** (a) Schematic of the launching apparatus used to hold the bat and later release it for flight testing. Below the release platform is a soft foam pad. (b) Top view of the foam pad showing the 20-cm concentric divisions used to score horizontal displacement achieved during flight (Powers et al. 1991).

outside the test room. Audio and video recordings were made during all three trials for each bat tested.

### Flight Behaviour

The behaviour of the bat after its release from the launching apparatus was scored according to its wing-flapping response and its landing position on the foam pad (see Powers et al. 1991). Briefly, we designated group I (Flop) if the bat dropped directly onto the pad with no wing flapping. If the bat fluttered its wings but achieved no horizontal displacement, we assigned it to group II (Flutter). If the bat flapped its wings and landed between concentric rings 2 and 12, the horizontal displacement was recorded, and we assigned the bat to group III (Flap). If the bat cleared the foam pad and negotiated turns in the room, we assigned it to group IV (Fly).

### Sound Analysis

The sounds emitted by each bat were played back at 1/16 the original recording speed, digitized with 14 bit resolution at a sample rate of 19.2 kHz (Ariel PC 56D), producing an effective sample rate

of 307 kHz. Spectrograms were generated from 256 point FFTs and displayed using Sona-PC realtime sonagraph. Opening the hinged floor of the launching apparatus produced a distinct signal on the audio track, which was used to identify the sounds emitted by the bat after it was released into the room. Quantitative measures on the time-frequency structure were taken for the first three sounds produced by each bat after its release. These three sounds were recorded while the bat was well positioned with respect to the recording microphone, allowing good signal-to-noise ratio and minimal interference between the bat's direct vocalization and echoes from the launching apparatus and the floor. We measured the duration, bandwidth, starting frequency, ending frequency and sweep rate (frequency change per unit time) of these sounds and only included the first harmonic of the signal. The interval between the bat's sonar emissions was measured for up to 800 ms following its release from the launching platform. During this 800 ms, all bats reached the foam pad except for some older animals (>17 days) that cleared the floor and flew about the room.

An analysis of variance (ANOVA) was performed on the data set to determine whether the signal parameters of bandwidth, duration, upper/lower frequencies and sweep rate changed statistically with age. We also used ANOVA to examine whether the features of the signals reliably changed within the set of three sounds measured sequentially for each bat following release from the launching apparatus. Repeated measures taken from animals tested twice ( $N=16$ ) and those tested three times ( $N=2$ ) were omitted from the analysis.

## RESULTS

### Flight Behaviour

When released from the launching apparatus, the flight behaviour of all bats under 3 days of age placed them in the Flop category. By 3–4 days of age, 50% of the subjects fluttered their wings but achieved no horizontal displacement; the remaining 50% of this age group flopped to the foam pad below the launching apparatus. Between 14 and 20 days of age, 52% of the subjects tested flapped their wings to achieve some horizontal displacement along the foam pad. Flying around the room was first observed in individuals at about 17 days

of age. Additional details on the development of flight behaviour in young *M. lucifugus* are reported by Powers et al. (1991).

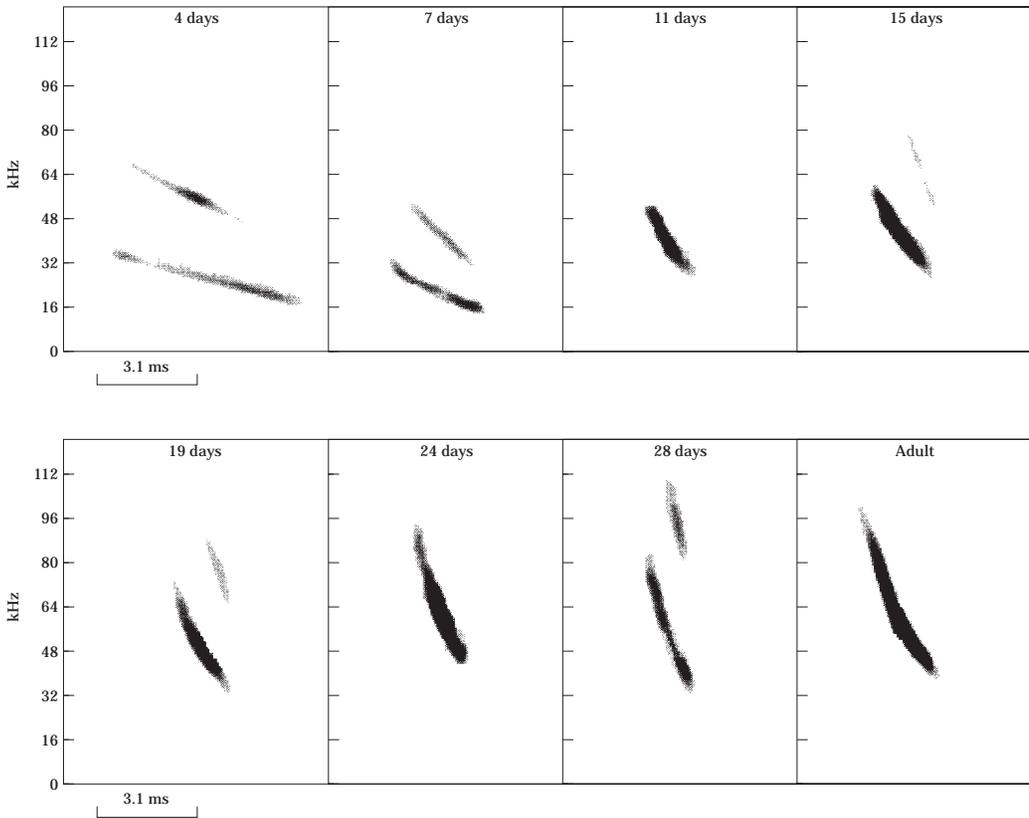
### Vocal Signals

The vocalizations of young bats released from the launching apparatus can be characterized as brief, frequency-modulated (FM) sounds. By 1 week of age, these sounds resembled adult echolocation signals (Fig. 2). Between 4 and 28 days of age, the sounds generally increased in starting frequency and increased in total bandwidth. This ontogenetic change resulted in an overall increase in sweep rate.

Quantitative data on signal bandwidth, starting and ending frequencies, duration and sweep rate were taken only from the first harmonic of the bat's vocalizations and plotted as a function of age (Fig. 3); higher harmonics were sometimes present but excluded from these quantitative measures. Each data point summarizes measurements of sound parameters for 6–17 bats, with the exception of the adult value which is based on sounds recorded from two individuals. Repeated measures from bats tested two ( $N=16$ ) and three ( $N=2$ ) times are included. The data points represent the mean values calculated for bats grouped by age in 3-day intervals (e.g. 1–3 days, 4–6 days, 7–9 days). Clustered about each age interval are three data points, each showing a mean value for the three sounds recorded from the bats following release from the launch apparatus. These sounds are referred to as pulse 1, pulse 2 and pulse 3.

Signal bandwidth significantly increased between 1 and 25 days of age ( $F_{1,82}=110.50$ ,  $P<0.001$ ; Fig. 3a). The increase in signal bandwidth as a function of age is due to both a rise in the starting (upper) and ending (lower) frequencies of the bat's sounds (Fig. 3b). The mean ending (lower) frequency of the sweep changed less with age, just below 20 kHz in the sounds produced by bats under 10 days of age and about 30 kHz in those produced by bats over 20 days of age. By contrast, the mean upper frequency of the sweep increased from about 30 kHz at 1–3 days of age to over 60 kHz by 21 days of age ( $F_{1,82}=138.1$ ,  $P<0.001$  and  $F_{1,82}=74.66$ ,  $P<0.001$ , respectively).

The duration of the bat's sounds decreased most dramatically during the first week, after which time the duration remained relatively



**Figure 2.** Sound spectrograms of FM sounds produced by *M. lucifugus* ranging in age from 4 to 28 days. Data for an adult is shown for comparison.

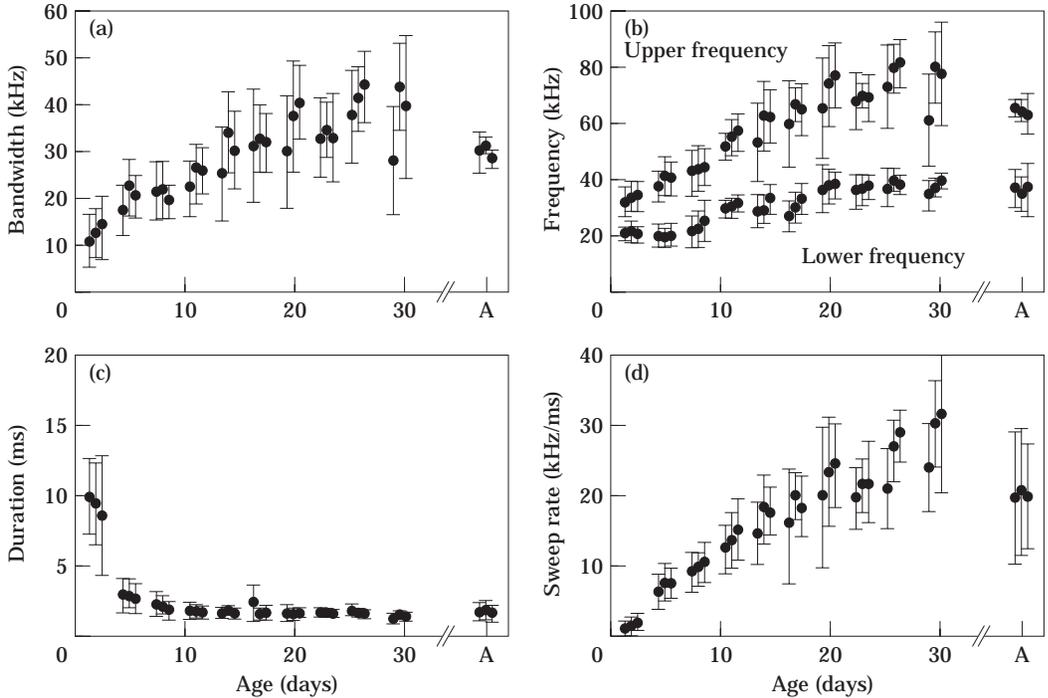
constant ( $F_{1,82}=186.8$ ,  $P<0.001$ ; Fig. 3c). During the first few days, the mean sound duration was about 10 ms, and by 4–6 days, the mean duration was less than 4 ms. The mean sound duration decreased further to about 2 ms by 9 days.

The sweep rate steadily increased over the first 30 days of age ( $F_{1,82}=176.0$ ,  $P<0.001$ ; Fig. 3d). Over the first 9 days, the increase in sweep rate can be attributed to a rise in the starting frequency of the FM sweep and a decrease in sound duration. Beyond 10 days of age, the rise in sweep rate stemmed from an overall increase in signal bandwidth with a relatively fixed duration.

For each of the sound parameters, we also examined whether differences between the measures taken for the three sounds were statistically reliable. Differences between the second and third sounds were not statistically significant for any of the sound parameters measured, and the

mean of pulses 2 and 3 was used for comparison with measures taken for pulse 1. There were reliable differences between pulse 1 and the mean of pulses 2 and 3 for upper frequency ( $F_{1,82}=4.58$ ,  $P<0.04$ ), lower frequency ( $F_{1,82}=4.22$ ,  $P<0.05$ ) and sweep rate ( $F_{1,82}=7.46$ ,  $P<0.01$ ). All other measures showed no significant differences between pulse 1 and the mean of pulses 2 and 3.

Given the statistically reliable differences between pulse 1 and the mean of pulses 2 and 3 for some of our sound measures, we examined whether this effect was stable across age. The effect of pulse number was greatest for the measure of sweep rate, kHz/ms (Fig. 4). The difference in sweep rate between pulses 1 and 2 increased over age, whereas the difference between pulses 2 and 3 fluctuated around zero for all ages tested (Fig. 4). We carried out two-tailed *t*-tests to compare the changes in sound measures taken for



**Figure 3.** The following parameters of vocal signals recorded from *M. lucifugus* are plotted as a function of age: (a) total signal bandwidth, (b) upper and lower frequencies, (c) sound duration and (d) sweep rate. Data points represent the mean values calculated for bats grouped by age in 3-day intervals and are based on measurements taken from the first harmonic of the bat vocalizations. Three successive sounds were analysed per animal, and the mean measures taken from each of the sounds (pulses 1, 2, 3) are plotted separately. Repeated measures from bats tested at two ( $N=16$ ) and three ( $N=2$ ) ages are included. Within each age interval, 6–17 bats were tested, with the exception of the adults ( $N=2$ ). Bars represent one standard deviation.

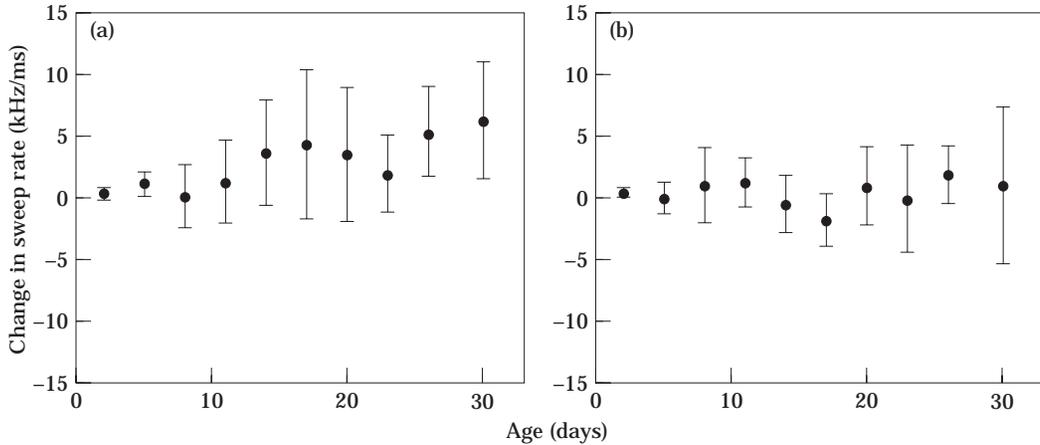
pulse 1 and the mean of pulses 2 and 3 in younger and older animals, and found that there were statistically significant age differences for upper frequency ( $t_{38}=2.50$ ,  $P<0.02$ ) and sweep rate ( $t_{36}=3.18$ ,  $P<0.005$ ), with a break between animals 1–13 days of age and those 14 days and older.

The number of sounds emitted by bats travelling to the foam pad increased with age, and the inter-pulse interval tended to decrease (i.e. sound repetition rate increased) with age (Fig. 5). By 12 days of age, 70% of the bats showed an increase in sound repetition rate following release through the trap door. Because we do not have precise records on the bat's position relative to the floor when each sound was produced, we cannot establish whether the sound repetition rate is what we would predict for a given distance to the foam pad below (Calhander et al. 1964). The overall

increase in sound repetition rate, however, is consistent with what would be predicted for a bat using echoes to guide its vocal emission pattern as it approached the floor.

The largest change in minimum inter-pulse interval occurred during the first 2 weeks of age (Fig. 6a). Bats between 1 and 3 days of age produced sounds at a minimum interval of over 100 ms (maximum repetition rate of less than 10/s). By 2 weeks of age, bats produced sounds at a maximum repetition rate of over 60/s.

The total number of sounds produced by the bats after being released from the launching apparatus also increased with age (Fig. 6b). Bats that ceased vocalizing within the first 300 ms ( $N=5$ ) were excluded from this summary. The number of sounds produced by the bats increased between approximately 1 and 3 weeks of age, after which it remained stable.



**Figure 4.** Difference in sweep rate between (a) pulse 1 and pulse 2 and (b) between pulse 2 and pulse 3 as a function of age in *M. lucifugus*. Each data point represents the mean difference measure taken from sounds produced by 6–17 bats at each age interval. Repeated measures from bats tested at two ( $N=16$ ) and three ( $N=2$ ) ages are included. Bars represent one standard deviation.

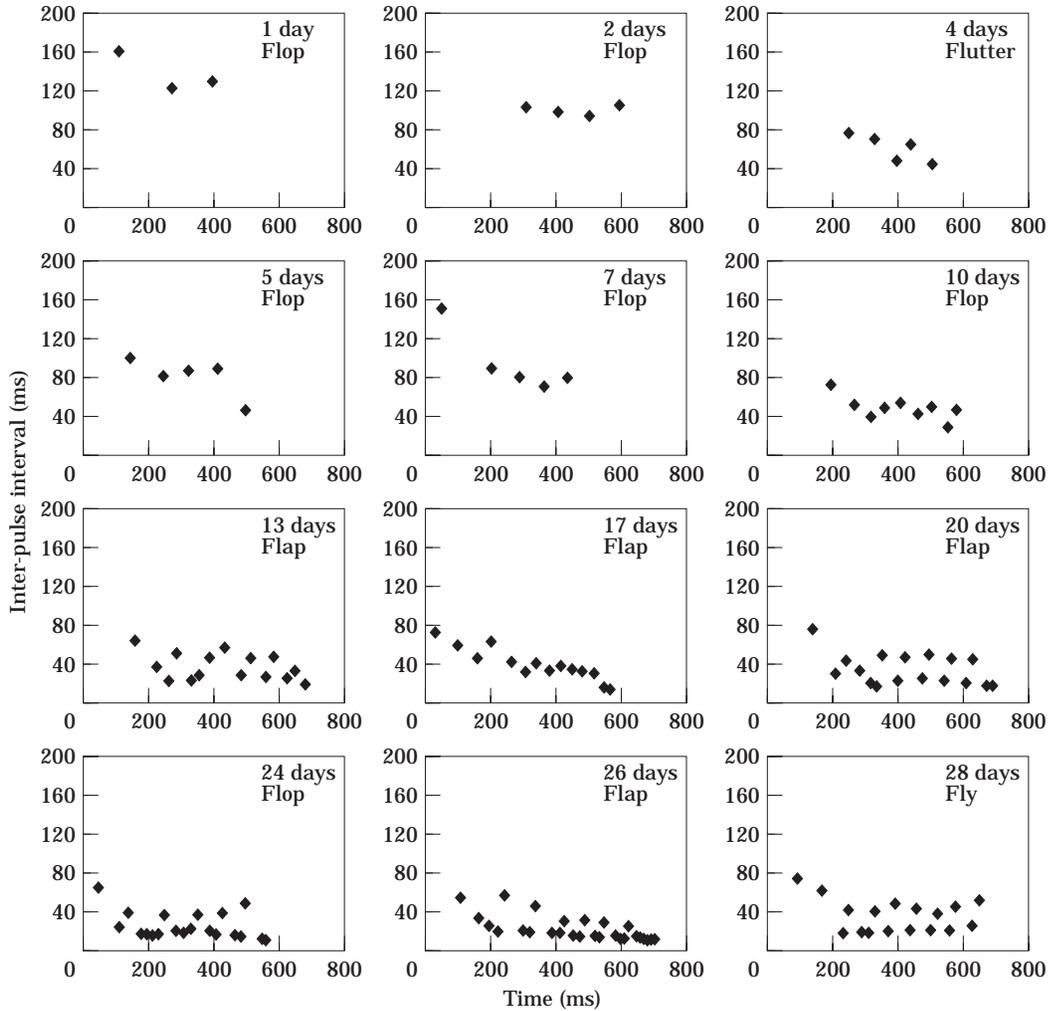
## DISCUSSION

Production of vocalizations is essential to the survival of an echolocating bat, and vocalizations during early postnatal development may lay the foundation for biosonar behaviour in the adult. The extent to which successful echolocation in an adult animal depends on early experience requires further study; however, work on sensorimotor development in other mammalian systems (e.g. Held & Hein 1963; Hein et al. 1979) suggests that coordinated vocalizations and echo processing may play a role in the ontogeny of biosonar behaviour.

Using laboratory-reared animals, Gould (1971) recorded vocalizations from individual *M. lucifugus* that he dropped from a height of approximately 2 m above a heavy cloth floor covering. He reported that bats younger than 12 days dropped to the floor, but older animals ‘pulled themselves out of a dive’. This finding contrasts with our data, which show that bats achieved some horizontal displacement as young as 1 week of age; this discrepancy may be because Gould’s bats were raised in the laboratory and ours were from the field. Buchler (1980) observed that the first foraging flights of captive-reared bats can be delayed by as much as 10 days over those living in the wild. Sound analyses from Gould’s recordings showed that bats under 2 weeks of age produced

vocalizations that were inconsistent in interval and duration; older bats used pulses that successively decreased in duration and in interval. These findings are in general agreement with those reported here. Gould (1971) presented no spectrographic data.

Spectrographic analysis of signals recorded from known-age bats as they were released from the launching apparatus reveals that bats as young as 4 days old emitted frequency-modulated (FM) sounds during early flights. Brief FM sounds of the type reported here have been described in *M. lucifugus* by Thomson et al. (1985) and referred to as short isolation calls. Gould (1971) also made note of ultrashort FM sounds and sonar calls recorded from captive-reared *M. lucifugus* under 5 days of age. Showing similar developmental patterns, captive-reared *E. fuscus* first produce brief FM sounds at about 6 days of age (Gould 1971; Moss 1988), and lab-reared *Noctilio albiventris* emit sounds that resemble adult echolocation sounds from the first few days of life (Brown et al. 1983). We exercise caution, however, in assigning a strict function to the FM sounds recorded in the present study. Sounds used primarily for echolocation could also serve a functional role in communication (Barclay et al. 1979). Conversely, sounds used primarily for communication could also serve a functional role in echolocation (see Möhres 1966; Moss 1988; Jones

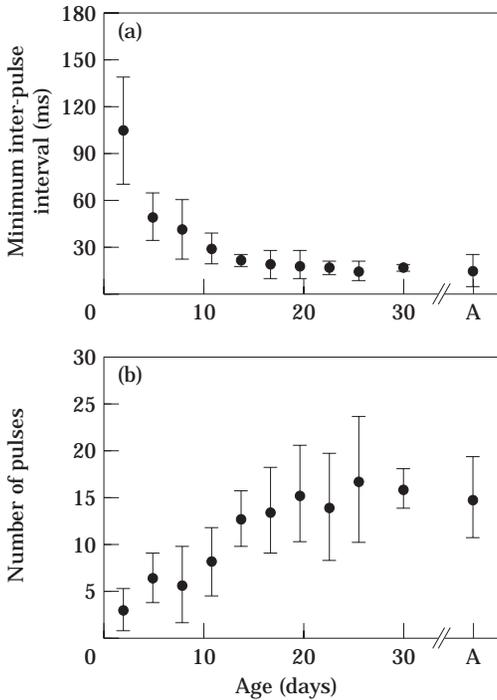


**Figure 5.** Inter-pulse interval of successive sounds produced by young *M. lucifugus* after release from the launching apparatus. Each panel summarizes data from an individual bat, whose age and flight behaviour score appear in the upper right. Data are shown for up to 800 ms following the opening of the trap door of the apparatus.

et al. 1991). The functional overlap of these two sound types may be important for young bats in particular.

In vespertilionid bats, the frequency and duration of vocalizations are controlled by contraction and relaxation of the cricothyroid muscles surrounding the larynx. Contraction of these muscles increases tension on the laryngeal membranes, and phonation occurs during relaxation. The frequency at which the laryngeal membranes vibrate depends upon the magnitude of cricothyroid muscle contraction. Gradual relaxation of

this muscle results in a downward FM sweep, and the rate at which the muscle relaxes determines the FM sweep rate (Novick & Griffin 1961; Suthers & Fattu 1973, 1982). The ontogenetic changes in starting frequency, bandwidth, sweep rate and duration of the FM sounds produced by *M. lucifugus* may reflect maturation of the larynx, its muscles and its innervation (Gould 1975). Maturation of the respiratory organs and their coordination with vocal organ musculature, along with the development of central motor circuits controlling vocalizations, are also important to the



**Figure 6.** Summary data on inter-pulse interval and total number of sounds produced by *M. lucifugus* after release from the launch apparatus. The data points represent the mean values calculated for bats grouped by age in 3-day intervals. Three observations were taken per animal; 6–13 bats were tested within each age interval, with the exception of the adults ( $N=2$ ). Bars represent 1 SD. (a) Mean minimum inter-pulse interval and (b) mean number of sounds produced during 300 ms after bats were released from the launching apparatus. Both plotted as a function of age.

ontogeny of sonar signal production in bats, although the relative contribution of each has not been studied developmentally. Development of the vocal apparatus giving rise to changes in vocal production coincides with rapid development of the flight musculature (Powers et al. 1991), which together permit integrated vocal and flight behaviour that are essential to successful foraging using echolocation.

One goal of this study was to obtain indirect measures of echolocation in young bats by examining the sounds they emitted after release from a launching apparatus. Adult *M. lucifugus* increase the repetition rate and decrease the duration of their sounds as they approach objects (Calhander

et al. 1964), adjusting vocal emission patterns with the changes in echo delay that accompany changes in target distance (e.g. Simmons & Kick 1984). Changes in vocalization features with target distance thus provide an index of active echolocation behaviour. In the present study, a decrease in inter-pulse interval (increase in repetition rate) after release from the launching apparatus was observed in bats as young 7–10 days of age, and it was present in 50% of the bats studied by 17 days of age. This change in sound repetition rate during descent to the foam pad suggests the bat's use of echo information to guide vocal behaviour and may serve as an index of active echolocation in these animals. Further evidence of how young *M. lucifugus* use echo information to guide vocal behaviour appears in changes in signal sweep rate from the first to the second pulse after release from the launching apparatus. Starting at about 12–14 days of age, bats showed an increase in upper frequency and signal sweep rate when beginning descent to the foam pad. The magnitude of these changes in sound parameters rose until about 3 weeks of age. Collectively, these findings suggest patterns in the development of biosonar behaviour in *M. lucifugus*, but more direct evidence is required to fully support the hypothesis that changes in vocal production in young bats reflect their use of echo information.

The ontogeny of echolocation requires the coordinated development of sonar signal production and hearing. In this study, we examined developmental changes in the vocal signals emitted by young bats, and our findings suggest that *M. lucifugus* begins at about 14–17 days of age to modify the features of its vocalizations (repetition rate of sound sequences and the sweep rate of individual sounds) in a manner consistent with adult bats using echoes to guide vocal production. No developmental data on auditory function are available for *M. lucifugus*, but auditory evoked responses from other species show that the onset of hearing generally occurs by the second postnatal week (e.g. Konstantinov 1973; Brown et al. 1978; Rübtsamen 1987). Since young *M. lucifugus* sometimes begin practice flights within the confines of their roost during the second postnatal week (Kunz & Anthony 1996), these bats may refine the use of biosonar before making their first attempts at insect capture. Further research in this area, perhaps using wire-avoidance experiments, may help to clarify changes in the bat's

echolocation performance at the ages encompassing the first flight manoeuvres inside the roost and early foraging in the field.

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