

Babbling behavior in the sac-winged bat (*Saccopteryx bilineata*)

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Abstract Infant babbling in humans and a few other primates plays an important role in allowing the young to practice the adult vocal repertoire during early behavioral development. Vocalizations uttered during babbling resemble, to some degree, the acoustic structure of adult vocalizations and are often produced in long bouts independent of any social context. Similar behavior, termed subsong or plastic song, is known from a variety of songbirds. Here, we show that pups of the sac-winged bat (*Saccopteryx bilineata*), a species with an unusually large vocal repertoire, produce renditions of all known adult vocalization types during bouts of vocalizations, which appear to be independent of a distinct social context. Babbling occurs in pups of both sexes, even though only adult males, not females, utter all different vocalization types produced in infancy. To our knowledge, this is the first evidence of babbling in a nonprimate mammal and suggests that infant babbling may be necessary for the ontogeny of complex vocal repertoires.

Introduction

Infant babbling in humans is considered to be an important step in early language acquisition. In infants, the ability to produce speech is limited by the immaturity of the vocal tract and the related musculature (Werker and Tees 1999), and babbling may provide vocal practice. Across all cultures, human infants will start to produce this form of speech at about 7 months of age, whereas the first words

are usually uttered at about 14 months of age (Werker and Tees 1999; Doupe and Kuhl 1999). Infant babbling behavior is also known from a few other primates (Elowson et al. 1998a, b; Omedes 1985; Winter and Rothe 1979). In the well-studied pygmy marmoset (*Cebuella pygmaea*), for example, infants produce long repetitions of mixed call types that are similar to the vocalizations of adult conspecifics and resemble the babbling bouts produced by human infants (Elowson et al. 1998a, b). In general, babbling is believed to play a role in the acquisition of the adult vocal repertoire (Werker and Tees 1999; Elowson et al. 1998a, b; Snowdon and Elowson 2001).

In support of this view, the vocalizations of young songbirds during the sensorimotor learning phase, namely, subsong and plastic song (Doupe and Kuhl 1999; Goldstein et al. 2003), were also compared to the babbling of human infants. Subsong is the first type of song young songbirds produce and is described as soft rambling vocalizations with no species-specific character. The more mature and species-specific plastic song is thought to be a rehearsal of learned material that eventually develops into the crystallized song of adults (Marler and Peters 1982; Catchpole and Slater 1995; Hultsch and Todt 2004). Although babbling-like behavior is widespread in songbirds, and infant babbling is known to occur in humans and a few nonhuman primates, it has to our knowledge, never been reported for nonprimate mammals.

While studying the vocal behavior of sac-winged bats (*Saccopteryx bilineata*), we found strong evidence for infant babbling. The sac-winged bat is a neotropical species with harem-like social structures (Bradbury and Emmons 1974; Bradbury and Vehrencamp 1976). The mating system of *S. bilineata* can be described as a resource-defense polygyny (Emlen and Oring 1977). Males attempt to indirectly monopolize females in a harem by defending a

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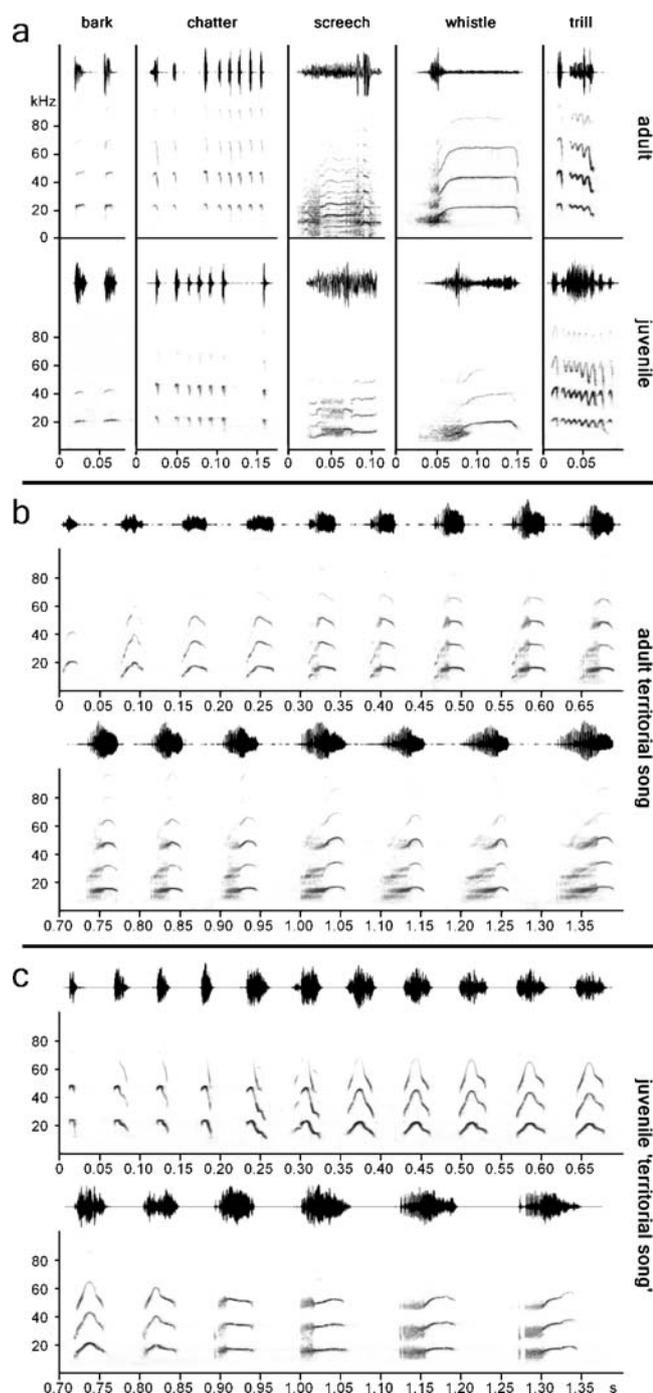


Fig. 1 Amplitude envelopes and spectrograms illustrate vocalizations of adult and juvenile *S. bilineata*. Amplitude and spectral frequency are depicted as a function of time. **a** Adult vocalization types and the corresponding pup vocalizations: barks, chatter sequence, screech, whistle, and trill (element of male courtship song). **b** Territorial song of an adult male and **c** a juvenile rendition of ‘territorial song’

long-term territory in their daytime roost in which females can choose to roost all year round (Tannenbaum 1975). Because harem owners have higher reproductive success than nonharem owners, competition among males for territory and access to females is high (Heckel et al. 1999)

and female choice has a strong influence on male mating success (Heckel and von Helversen 2003).

Previous work showed that *S. bilineata* has an unusually large vocal repertoire for a bat (Behr and von Helversen 2004). Adult vocalizations depend on social context and can be classified into seven different vocalization types. Territorial males vocalize far more than females. In addition to echolocation pulses, the vocal repertoire of both sexes consists of barks, chatters, and screeches (Fig. 1), which are used in a number of different social contexts; territorial males also utter whistles and courtship songs to court females, and territorial songs to repel male intruders from their territories (Fig. 1).

Females can give birth to one pup per year. Birth is highly synchronized within harems and is timed to the onset of the rainy season when food abundance is highest (Tannenbaum 1975; Bradbury and Vehrencamp 1976). Pups are able to fly at 2–3 weeks of age but are nursed for another 8 weeks. After weaning, female pups disperse while male pups often remain in their birth colonies or close by. Descriptions of the vocal behavior of *S. bilineata* pups were scarce and anecdotal (Bradbury and Emmons 1974; Tannenbaum 1975). Here, we describe vocalization bouts of *S. bilineata* pups in relation to the known vocal repertoire of adult conspecifics.

Materials and methods

From June to July 2004, we studied a population of *S. bilineata* in Costa Rica (Organization for Tropical Studies biological station, La Selva; 10°20'N, 84°10'W). Our study population was continually monitored since 1994. Consequently, the bats in their daytime roosts are habituated to human observers and can be approached within a few meters. This allowed us to observe and record undisturbed individuals.

We recorded pup vocalizations and made behavioral observations of 11 vocalizing pups of both sexes (eight males and three females). The pups were 4–8 weeks old and able to fly, but they were still nursing. Digital recordings were made in daytime-roosts using a microphone capsule BT 1759 (Knowles) and a microphone amplifier OP 37 attached to a parabolic reflector (diameter 30 cm). The microphone set-up was highly directional (decibel loss at 10° angular displacement from center for off-center sound sources was 10 and 16 dB in the vertical and horizontal planes, respectively) and had a free field response of ± 10 dB from 0.5 to 32 kHz and of ± 18 dB from 0.5 to 90 kHz. The distance between the focal bat and the microphone ranged between 1 and 7 m. The diameter of the focal field of the microphone increased with increasing distance to the focal animal and had a maximum of 2.5 m (7 m distance and 10° angular displacement). Recordings

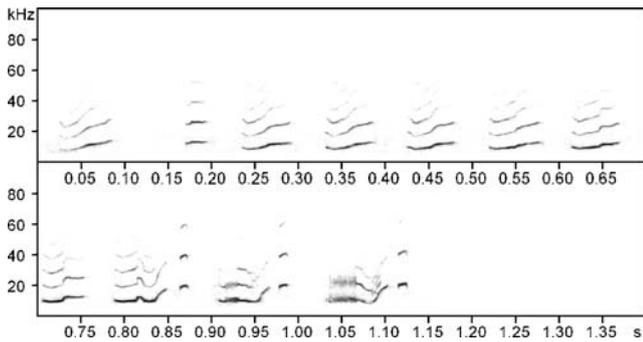


Fig. 2 Spectrogram of a *S. bilineata* isolation call series depicting spectral frequency as a function of time. Isolation calls unique to pups were their most frequently produced vocalization and were uttered by pups of both sexes. The production of isolation calls was also shown for a variety of other bat species (for an overview, see Wilkinson 2003)

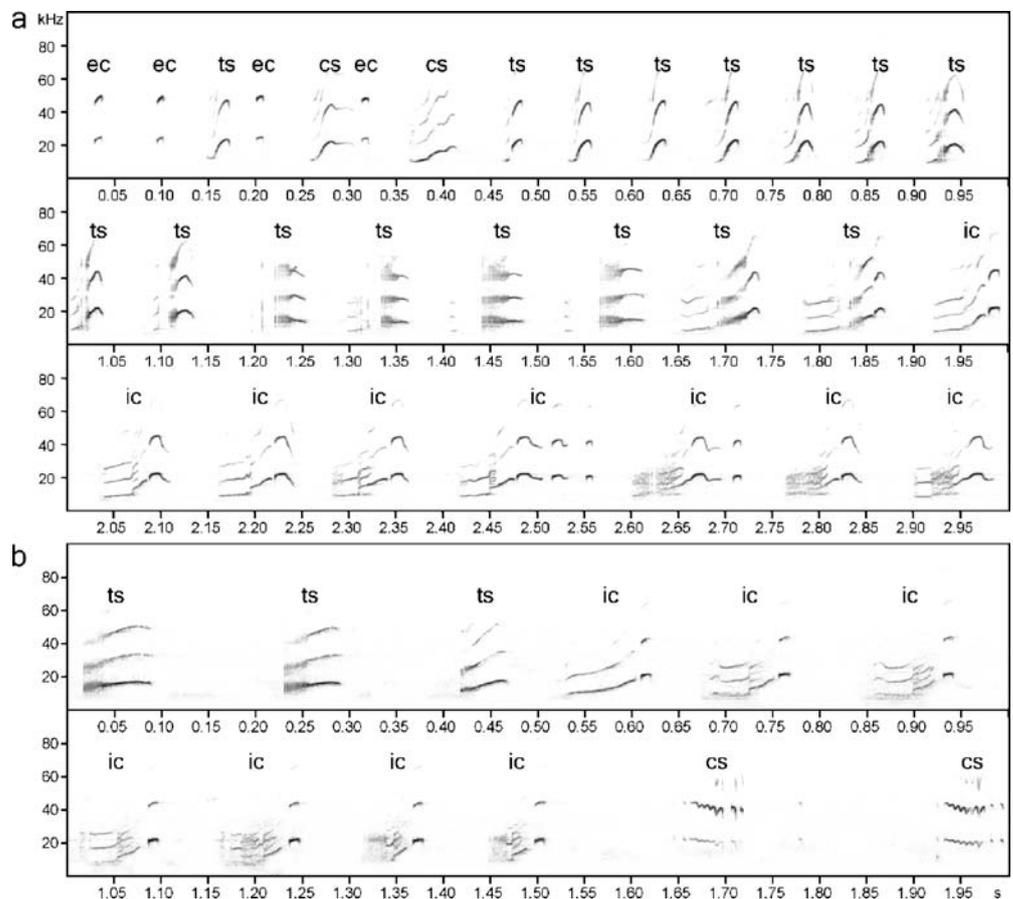
were digitized at a sampling rate of 387 kHz and 16 bit resolution using Avisoft-RECORDER (v2.9) software running on a notebook computer (Toshiba Satellite 5200-701) equipped with an A/D sound card (National Instruments DAQ-Card 6062E). To ensure that the microphone was pointed directly at the focal bat, we mounted a dimmed infrared pointer to the microphone that could be aimed at a recording subject; the infrared spot could then be located

with a night vision device (Litton Monocular M911). This set-up permitted recordings of single individuals without disturbing the bats by using flashlights for localization. Spectrograms were generated in Avisoft-SASLab Pro (v4.1) using a 1,024-point fast Fourier transform and a Hamming window with 75% overlap. Pup vocalizations were then compared to a large data set of adult vocalizations previously recorded in the same population (Behr and von Helversen 2004).

Results

Apart from uttering isolation calls (Fig. 2) when separated from their mothers, all observed *S. bilineata* pups also produced elements that strongly resembled all other known vocalization types of the adult repertoire. In addition to echolocation pulses, pups of both sexes frequently uttered barks, chatters, and screeches, which are produced by both adult males and females (Fig. 1). Furthermore, pups of both sexes uttered vocalizations that are produced only by adult males, not females. These vocalizations consisted of whistles, elements of courtship songs (trills), and territorial songs (Fig. 1). In contrast to adults, pups combined the various vocalization types that adults use in distinctly different social contexts into single vocalization bouts

Fig. 3 Spectrograms of babbling bouts from two different individuals depicting spectral frequency as a function of time: **a** echolocation pulses (*ec*), different elements of territorial song (*ts*), courtship song (*cs*), and isolation calls (*ic*) in a single babbling bout; **b** elements of territorial song (*ts*), courtship song (*cs*), and isolation calls (*ic*) in a single babbling bout



together with isolation calls (Fig. 3). Pup renditions of adult vocalizations could not be correlated with a specific behavioral context and were neither elicited nor influenced by the vocalizations or behavior of other nearby bats. During bouts of vocalizations, pups never performed activities like grooming, feeding, or flying but hung in the daytime roost without interactions with their mothers or other colony members.

Discussion

The novel aspect of this study is the documentation of babbling behavior in a nonprimate mammal, the sac-winged bat. The absence of any clear social context in which babbling bouts were produced suggests that *S. bilineata* pups vocalize for training rather than for communication with conspecifics. The lack of social responses to babbling in infant *S. bilineata* in contrast to humans (Goldstein et al. 2003) and marmosets (Snowdon and Elowson 2001) may be due to the fact that the social contact of a bat pup is mostly limited to mother–offspring interactions in which the pup’s isolation calls function as a vocal signal to get attention. In humans and marmosets, not only mothers but also other members of the respective social group assist in infant care and infant babbling is associated with increased social interactions with group members.

With the repetition and juxtaposition of different adult vocalization types, pup vocalizations resemble infant babbling behavior of humans (Doupe and Kuhl 1999) and some other primates (Elowson et al. 1998a, b), and they also bear resemblance to the subsong and plastic song of young songbirds (Catchpole and Slater 1995; Hultsch and Todt 2004). Avian subsong and plastic song as the major nonhuman models for infant babbling have the limitation of being male biased, occurring at puberty and covering only part of the adult vocal repertoire, whereas babbling in *S. bilineata* pups occurs in both sexes at infancy and covers the whole adult vocal repertoire. This is also the case for infant pygmy marmosets, *C. pygmaea*, which represent a well-studied system for mammalian babbling (Elowson et al. 1998a, b; Snowdon and Elowson 2001).

Occurrence of infant babbling and evidence for babbling-like vocalizations was reported for a number of primate species (see Elowson et al. 1998b). Our study documents infant babbling in sac-winged bat pups. This suggests that the occurrence of infant babbling behavior has evolved in species in which juveniles have to acquire complex vocal repertoires. Babbling may be a common mechanism necessary for infants to develop fully functional adult vocalizations.

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References

- Behr O, von Helversen O (2004) Bat serenades—complex courtship songs in the sac-winged bat (*Saccopteryx bilineata*). *Behav Ecol Sociobiol* 56:106–115
- Bradbury JW, Emmons L (1974) Social organization of some Trinidad bats. I. *Emballonuridae*. *Z Tierpsychol* 36:137–183
- Bradbury JW, Vehrencamp SL (1976) Social organization and foraging in Emballonurid bats. I. Field studies. *Behav Ecol Sociobiol* 1:337–381
- Catchpole CK, Slater PJB (1995) *Birdsong: biological themes and variations*. Cambridge University Press, Cambridge, UK
- Doupe AJ, Kuhl PK (1999) *Birdsong and human speech: common themes and mechanisms*. *Annu Rev Neurosci* 22:567–631
- Elowson AM, Snowdon CT, Lazaro-Perea C (1998a) Babbling and social context in infant monkeys: parallels to human infants. *Trends Cogn Sci* 2:31–37
- Elowson AM, Snowdon CT, Lazaro-Perea C (1998b) Infant ‘babbling’ in a nonhuman primate: complex vocal sequences with repeated call types. *Behaviour* 135:643–664
- Emlen ST, Oring LW (1977) Ecology, sexual selection and the evolution of mating systems. *Science* 197:215–223
- Goldstein MH, King AP, West MJ (2003) Social interaction shapes babbling: testing parallels between birdsong and speech. *Proc Nat Acad Sci USA* 100(13):8030–8035
- Heckel G, von Helversen O (2003) Genetic mating systems and the significance of harem associations in the bat *Saccopteryx bilineata*. *Mol Ecol* 12:219–227
- Heckel G, Voigt CC, Mayer F, von Helversen O (1999) Extraharem paternity in the white-lined bat *Saccopteryx bilineata* (*Emballonuridae*). *Behaviour* 136:1173–1185
- Hultsch H, Todt D (2004) Learning to sing. In: Marler P, Slabbekorn H (eds) *Nature’s music: the Science of birdsong*. Elsevier Academic, London, pp 80–107
- Marler P, Peters S (1982) Subsong and plastic song: their role in the vocal learning process. In: Kroodsma DE, Miller EH (eds) *Acoustic communication in birds, vol. 2: song learning and its consequences*. Elsevier Academic, London, p 25–50
- Omedes A (1985) Infantile calls of the silvery marmosets (*Callithrix argentata melanura*) during the first 10 weeks. *Misc Zool* 9:412–418
- Snowdon CT, Elowson AM (2001) Babbling in pygmy marmosets: development after infancy. *Behaviour* 138:1235–1248
- Tannenbaum BR (1975) *Reproductive strategies in the white-lined bat*. Ph.D. thesis, Cornell University
- Werker JF, Tees RC (1999) Influences on infant speech processing: toward a new synthesis. *Annu Rev Psychol* 50:509–535
- Wilkinson GS (2003) Social and vocal complexity in bats. In: de Waal FBM, Tyack PL (eds) *Animal social complexity*. Harvard University Press, Cambridge, MA, p 322–341
- Winter M, Rothe H (1979) Darstellung des Lautrepertoires handaufgezogener Weissbüscheläffchen (*Callithrix j. jacchus*) unter besonderer Berücksichtigung der fließenden Übergänge zwischen den einzelnen Lautgruppen. *Primates* 20:259–276