Vocal Repertoire Ontogeny in *Saccopteryx bilineata*

Evidence for Vocal Learning in a Bat

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Man is not the only animal that can make use of language to express what is passing in his mind, and can understand, more or less, what is so expressed by another. (…) The habitual use of articulate language is, however, peculiar to man. (…) That which distinguishes man from the lower animals is (…) not the mere articulation (…) nor is it the mere capacity of connecting definite sounds with definite ideas. (…) The lower animals differ from man solely in his almost infinitely larger power of associating together the most diversified sounds and ideas; and this obviously depends on the high development of his mental powers.

Charles Darwin

In: The Descent of Man and Selection in Relation to Sex.
Comparisons of the mental powers of man and the lower animals.
Pp. 84-86. 1871. John Murray, London.

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Summary

Vocal learning can impact both the usage and comprehension of signals and their production. Whereas evidence for contextual learning (*i.e.*, the context in which to use a signal or how to understand it is learned) is widespread in both birds and mammals, evidence for vocal production learning (*i.e.*, the learned acquisition or modification of a signal as a result of social influences) is remarkably scarce. Vocal production learning is an essential part of the faculty of language in humans but no other primate, not even our nearest relatives, the great apes, seems to be capable of it. Apart from humans, the only evidence for vocal production learning comes from birds (songbirds, parrots, and hummingbirds), cetaceans, seals, elephants, and bats. This patchy distribution suggests a multiple convergent evolution of vocal production learning which makes a comparative approach especially rewarding. Both the anatomical and neural specialisations necessary for vocal production learning and its functional significance can be compared across different taxa in order to understand the selective pressures on a complex vocal communication system and, ultimately, how and why language evolved in humans.

The vocal flexibility of bats exhibited during echolocation is considered to be a preadaptation for vocal production learning. However, up to now the sole evidence for vocal production learning was the social modification of signals in three different bat species. In the dissertation presented here, I describe the vocal repertoire ontogeny of the sac-winged bat, *Saccopteryx bilineata*. This species exhibits a rich vocal repertoire due to its complex social life in a harem-like resource-defence polygyny. I show that *S. bilineata* pups not only produce unusually complex isolation calls to communicate with their mothers but also engage in vocal babbling behaviour and exhibit both forms of vocal production learning, social modification and learned acquisition (vocal imitation *de novo*). Therefore, *S. bilineata* represents an ideal model organism for the study of vocal production learning in bats.

In contrast to other bat species, isolation calls of *S. bilineata* pups were multi-syllabic, with most of the vocal signature information encoded in the composite syllables at the end of calls. Playback experiments revealed that mothers were able to discriminate between their own pup and an alien young on the basis of isolation calls alone, which confirms the results of the statistical analysis on vocal signatures. Pups, on the other hand, indiscriminately vocalized in response to echolocation pulse trains from own and alien mothers, rendering the mother-pup recognition process unidirectional.

Pups also produced renditions of all known adult vocalization types and combined them together with isolation call syllables into long babbling bouts. These babbling bouts appeared to be independent of a distinct social context, but might have been used to reinforce maternal care. Babbling occurred in pups of both sexes, even though only adult males but not females utter all different vocalization types produced in infancy. This is the first evidence of babbling in a non-primate mammal and suggests that infant babbling may be necessary for the ontogeny of complex vocal repertoires.

Comparisons of isolation calls from different pups showed that in addition to an individual signature, isolation calls also exhibited a group signature that became more prominent during ontogeny. Genetic effects on individual or group signatures were not found. Isolation calls converged both towards the isolation calls of fellow pups and towards the territorial song of the respective harem male, two vocalizations that pups heard on a daily basis throughout ontogeny. Call convergence through social modification creates a 'social badge' that reliably associates individuals to their natal colony based on their isolation calls.

Pups of both sexes were capable of learning territorial song, a complex adult vocalization type, *de novo* through imitation, with simple precursor songs developing into genuine renditions. The resemblance of pup renditions to their acoustic model became more pronounced during ontogeny and was independent of the relatedness between pups and adults, suggesting that auditory input instead of physical maturation or genetic determination is essential for vocal development. This is the first evidence that complex vocal imitation occurs in bats.

Introduction

1 Why study vocal learning?

The importance of spoken language for our own species is undeniable, yet it is not clear how and why language has evolved (Hauser et al. 2002). The human ability to convey an unlimited range of meanings through sound appears to be unique in the animal kingdom. Only humans can communicate virtually any concept that they can think of, whereas other primates, even the great apes, are remarkably limited in their ability to encode meanings vocally (Snowdon 1990). Nevertheless, most primates appear to be fairly skilled at inferring complex meanings from vocal signals (Arnold & Zuberbühler 2006; Bergman et al. 2003; Seyfarth et al. 1980), which causes a remarkable asymmetry between perceptive and productive abilities in non-human primates. It is unclear why humans are the only primates capable of spoken language. At least three key innovations seem to have taken place during language evolution, namely speech, syntax, and semantics (Christiansen & Kirby 2003). Speech is the ability to produce distinct phonetic units acquired through vocal learning, syntax or 'grammar' allows the production of hierarchical structures, and semantics refers to the ability to intentionally encode and communicate definite meanings (Fitch 2005). Each of these innovations could have a diverse evolutionary history and hence require different explanatory principles. However, the capacity for speech, syntax, or semantics is impossible to derive from the fossil record. Studying vocal learning in extant animals is a useful alternative to shed light on its evolution in humans (Hauser et al. 2002).

This thesis is about vocal learning in a phylogenetically old mammalian lineage, the bats. It investigates the bats' capacity to encode meanings in different social signals. By providing new evidence for sophisticated vocal learning in bats, I hope to contribute to the understanding of vocal learning in general.

2 Different forms of vocal learning

Vocal learning can influence not only the way a signal is produced, but also in which context it is used and how it is comprehended. In an article about different forms of social learning in animal communication, Janik and Slater (2000) distinguished between production learning (how to produce or modify a signal) and contextual learning, which consists of usage learning (in which context to use a signal) and comprehension learning (how to interpret a signal).

Contextual learning, especially comprehension learning is well documented in many animals (Janik & Slater 1997, 2000). A classical example is the referential alarm call system found in vervet monkeys (*Cercopithecus aethiops*), in which different types of predators are associated with different alarm calls (Seyfarth et al. 1980). Both usage and comprehension of these alarm calls need to be learned by juvenile vervet monkeys (Seyfarth & Cheney 1980, 1986).

Production learning, on the other hand, is less widespread than contextual learning (Janik & Slater 1997, 2000). Song learning in oscine birds, in which nestlings are dependent on auditory input in order to learn the species-specific song properly, represents a well studied example (Doupe & Kuhl 1999). Vocal production learning can affect up to three different aspects of the vocal domain, namely the respiratory, the phonatory and the filter system (Janik & Slater 2000). Voluntary changes in the respiratory system are used to alter the duration and amplitude of a signal (*e.g.*, rhesus monkeys, *Macaca mulatta*, have somewhat conditional control over the duration and amplitude of their calls; Sutton et al. 1973). Voluntary changes in the phonatory system can modify the absolute frequency and modulation of a signal and voluntary changes in the filter system its relative energy distribution (*e.g.*, Hoover, a captive male harbour seal, *Phoca vitulina*, convincingly imitated not only his name but also English sentences, including the Maine accent of his caretaker; Ralls et al. 1985). Contextual learning and respiratory production learning are comparatively simple and therefore thought to have preceded the evolution of phonatory and filter production learning (Janik & Slater 2000). Production learning can occur either through the learned acquisition of new signals - vocal imitation - or through the social modification of existing signals (Boughman & Moss 2003).

3 Occurrence of vocal production learning in the animal kingdom

Vocal production learning is patchily distributed within the animal kingdom, which suggests a multiple convergent evolution of this ability (Fitch 2000; Hauser et al. 2002). Apart from humans, the sole evidence for vocal production learning comes from birds, cetaceans, seals, elephants, and bats. There is no conclusive evidence for vocal production learning in non-human primates (Snowdon 1990; but see Egnor & Hauser 2004). Vocal production learning is much more prevalent in birds than in mammals (for reviews see Janik & Slater 1997; Doupe & Kuhl 1999; Boughman & Moss 2003), despite its importance for language development in humans (Fitch 2000; Hauser et al. 2002). Vocal imitation in particular, in which some bird species excel, seems to be extremely rare in non-human mammals (Boughman & Moss 2003).

Vocal production learning occurs in three orders of birds (Passeriformes: Kroodsma 1982; Psittaciformes: Farabaugh & Dooling 1996; Trochilidae: Baptista & Schuchmann 1990) and is the norm in both oscine songbirds and parrots whereas only patchy examples exist in hummingbirds. Both vocal imitation and the social modification of existing signals occur in birds (Boughman & Moss 2003). Bird song is widely used as a model for understanding speech development in humans (Doupe & Kuhl 1999; Brainard & Doupe 2002; King et al. 2005), whereas bird calls have received less attention in the past (Baptista 1996; Sharp et al. 2005).

With regard to vocal production learning, cetaceans represent the best studied mammalian group. Dolphins and whales can not only modify vocalizations based on social influences (bottlenosed dolphins, *Tursiops truncatus*: Janik 2000; killer whales, *Orcinus orca*: Deeke et al. 2000; bowhead whales, *Balaena mysticetus*: Würsig & Clark 1993; humpback whales, *Megaptera novaeangliae*: Noad et al. 2000) but also imitate completely new sounds, even when they are artificial (bottlenosed dolphins, *Tursiops truncatus*: Richards et al. 1984, Reiss & McCowan 1993) or produced by different species (killer whales, *Orcinus orca*: Foote et al. 2006).

Pinnipeds are very vocal both under water and in air (Schusterman 2008). Walruses (Odobenidae) and earless seals (Phocidae) are capable of both the social modification of existing signals (Southern elephant seal, *Mirounga leonine*: Sanvito et al. 2007) and vocal imitation (Pacific walrus, *Odobenus rosmarus divergens*: Schusterman & Reichmuth 2007). A captive harbour seal, *Phoca vitulina,* has even been shown to imitate human speech (Ralls et al. 1985). Evidence for vocal production learning in eared seals (Otariidae) is still lacking (Janik & Slater 1997).

There is only a single example of vocal imitation in elephants so far (African savannah elephant, *Loxodonta africana*: Poole et al. 2005). Since studies on the vocal communication of elephants are forthcoming (Poole et al. 1988, Leong et al. 2003, Soltis et al. 2005a,b, Stoeger-Horwath et al. 2007), evidence for vocal learning in the two other species (African forest elephant, *Loxodonta cyclotis*; Asian elephant, *Elephas maximus*) is expected.

In bats, vocal production learning through social modification has been shown for signals used in individual recognition between mother and pup (echolocation pulses of the greater horseshoe bat, *Rhinolophus ferrumequinum*: Jones & Ransome 1993; isolation/directive calls of the lesser spear-nosed bat, *Phyllostomus discolor*: Esser 1994) and for signals used in the context of group cohesion between adults (screech calls of the greater spear-nosed bat, *Phyllostomus hastatus*: Boughman 1998). It has long been predicted that, in

addition to the social modification of already existing vocalizations, bats should also be capable of vocal imitation (Janik & Slater 1997) but so far it has not been demonstrated (Boughman & Moss 2003).

4 Functional significance of vocal production learning

The question of why vocal production learning arose in the first place is different from the question of why it persists in certain species. Hence, the selective pressures causing its evolutionary origin might be different from its current advantages for particular species. Nevertheless, searching for similarities between different species might aid in understanding the functional significance of vocal production learning and, ultimately, how and why it evolved multiple times within the animal kingdom.

What do all mammals exhibiting vocal production learning have in common? In addition to their relative longevity, all of them live in fairly complex social systems consisting either of fluid fission-fusion societies or stable social groups (*i.e.*, harems or matri-/patrilinear family groups). In these social systems, long-lived social bonds are based upon individual relationships and vocal communication is used for individual or group recognition. Most mammalian production learners live in high-background-noise environments (like the ocean or densely populated caves) and all of them are extremely mobile (mostly in a three-dimensional environment) and often visually separated from their conspecifics. Hence, these animals might be routinely out of range for any sensory modality except acoustic communication (Janik & Slater 1997).

The functional significance of vocal production learning in these groups probably consists of facilitated recognition on the individual, social group or population level (Kroodsma & Baylis 1982; Janik & Slater 1997; Boughman & Moss 2003). Evidently, recognition on these levels is not mutually exclusive (Hausberger 1997; McCowan & Reiss 1997; but see Boughman 1998). Recognition of individual, group or population identity might be beneficial for several reasons: maintenance of social relationships (individual level), inbreeding avoidance (individual level), deception of rivals (individual level), cooperation between group members (group level), identification and exclusion of strangers (group level), and maintenance of local adaptations (population level). Vocal production learning is likely shaped not only by natural selection (*e.g.*, cooperative hunting by group members) but also by both intersexual selection (*e.g.,* female preference for large male repertoires) and intrasexual selection (*e.g.,* song type sharing among rivalling neighbours). Obviously, these selective pressures need not be mutually exclusive (Janik & Slater 1997).

Learned individual signatures mainly occur in species with fission-fusion societies (elephants, *Loxodonta africana*: Poole et al. 2005; parakeets, *Aratinga canicularis*: Cortopassi & Bradbury 2006; dolphins, *Tursiops truncatus*: Janik et al. 2006) whereas learned signatures on the group/family level are mainly found in species with stable social groups (bats, *Phyllostomus hastatus*: Boughman 1998; birds, *Aegithalos caudatus*: Sharp et al. 2005; whales, *Orcinus orca*: Foote et al. 2006). Learned signatures on the population level (*i.e.*, local dialects) have only been demonstrated for birds with long territory tenure (Kroodsma 2005) and baleen whales (*Balaena mysticetus*: Würsig & Clark 1993; *Megaptera novaeangliae*: Noad et al. 2000).

5 Studying vocal production learning – why *Saccopteryx bilineata*?

Bats are a phylogenetically old mammalian lineage dating back to the Eocene (Novacek 1987; Simmons & Geisler 1998; Simmons 2000). The vocal flexibility exhibited during echolocation by bats might be a preadaptation for vocal production learning (Boughman & Moss 2003). Indeed, social signals seem to be processed by neurons also involved in echolocation processing (Esser et al. 1997; Ohlemiller et al. 1996) and auditory sensitivity is greatest for both echolocation pulses and social calls (Bohn et al. 2004, 2006).

Many bat species are less than ideal for behavioural and acoustic studies due to their well concealed day-roosts, light intolerance and relative inactiveness throughout the day. During the main activity period at night, synchronous behavioral observations and sound recordings are next to impossible, particularly during flight (Fenton 1985). The greater sac-winged bat, *Saccopteryx bilineata*, represents an exception from this pattern which makes this species ideal for studying vocal production learning in bats. The good accessibility of their well-illuminated day-roosts and the readiness with which they can be habituated to humans greatly facilitate simultaneous observations and sound recordings. *S. bilineata* has a particularly interesting social system with a correspondingly complex vocal repertoire and is one of the most thoroughly studied bat species (for a review see Voigt et al. 2008). It lives in a polygynous mating system in which territorial males defend harems containing up to nine females and their respective offspring. Day-roost colonies can consist of up to twelve harem territories belonging to different harem males (Bradbury & Emmons 1974; Bradbury & Vehrencamp 1976). Young males must either queue for harem access in their natal colony (Voigt & Streich 2003) or found a new colony elsewhere. Colonies have a patrilineal structure due to male natal philopatry (McCracken 1984; Nagy et al. 2007). On the contrary, females in a colony are unrelated because of female-biased natal dispersal (Nagy et al. 2007). Since

males are unable to sexually monopolize females, not all pups born in their harems are their descendants (Heckel et al. 1999; Heckel & von Helversen 2003). Female choice seems to play an important role and male-male competition is intense (Heckel & von Helversen 2002, 2003; Voigt et al. 2006, 2008). *S. bilineata* exhibits an unusually rich behavioral repertoire due that consists of elaborate visual, olfactory and acoustic displays (Voigt et al. 2008).

For most vocalization types, the distinct social context in which they are uttered is known (Behr & von Helversen 2004; Davidson & Wilkinson 2004; Knörnschild & von Helversen 2008). In particular, territorial songs represent a vocalization type whose function is well understood. Territorial songs are uttered by territorial males at dusk and dawn - but also during the day when disturbed - in order to announce their territory ownership and are also produced during aggressive male-male interactions (Bradbury & Emmons 1974; Bradbury & Vehrencamp 1976). They are complex multi-syllabic vocalizations that begin with variable syllables which gradually merge into stereotypic end syllables consisting of a noisy and a tonal part (Behr et al. 2004). Territorial songs are individually distinct (Behr et al. 2006). The peak frequency of territorial song end syllables is negatively correlated to both reproductive success (Behr et al. 2006) and the strength of the counter-song response (Behr et al. 2008), which makes them an indicator for male quality.

6 Contents and Aims

This thesis investigates several new aspects of the *S. bilineata* vocal repertoire, namely a report of vocalization types previously unknown, a description of the vocal repertoire ontogeny, and evidence for vocal production learning through both social modification and imitation. Results are presented in four chapters:

Chapter I Isolation Calls and Mother-Offspring Communication

The first chapter reports two new vocalization types and documents vocal mother-pup recognition through acoustic analyses and playback experiments.

- Which vocalization types are produced during mother-pup reunions?
- What is the acoustic structure of juvenile isolation calls and maternal directive calls?
- Does the acoustic analysis of juvenile isolation calls and maternal echolocation pulses reveal an individual signature?
- Is this vocal signature recognized by mothers and pups in playback experiments?

Chapter II Babbling Behaviour

The second chapter describes the ontogeny of the vocal repertoire, specifically a behaviour termed ‘vocal babbling’ which is exhibited by pups.

- Which vocalization types are uttered by pups throughout their development?
- Are vocalizations produced by babbling pups renditions of adult vocalizations?
- Are there sex-specific differences in babbling behaviour?
- What is the functional significance of vocal babbling?

Chapter III Social Modification of Isolation Calls

The third chapter analyses the development of juvenile isolation calls throughout ontogeny and examines social influences on isolation call production.

- Does the vocal signature of isolation calls change over time?
- Is there a group signature in addition to the individual signature?
- Is this group signature acquired through vocal production learning?
- What is the functional significance of a group signature that is shaped through social modification?

Chapter IV Vocal Imitation of Territorial Songs

The fourth chapter examines the development of territorial songs from simple juvenile precursor songs to genuine renditions of adult territorial songs.

- Are territorial songs innate or acquired through vocal production learning?
- Are harem males acoustic role models for pups?
- Are territorial songs acquired through vocal imitation?
- Are there sex-specific differences in the production of territorial songs by pups?

Chapter I

Isolation Calls and Mother-Offspring Communication

1 Abstract

We investigated the acoustical component of the recognition process leading to successful mother-pup reunions in the greater sac-winged bat, *Saccopteryx bilineata*, using both a statistical approach and playback experiments. Statistical evidence for individual distinctiveness was found in the isolation calls uttered by pups and, to a weaker degree, in the echolocation pulse trains emitted by mothers. In contrast to other bat species, isolation calls of *S. bilineata* pups were complex and multi-syllabic, with most of the vocal signature information encoded in the composite syllables at the end of calls. Playback experiments with free-living bats revealed that mothers were able to discriminate between their own pup and an alien young on the basis of isolation calls alone, which confirms the results of the acoustical analysis on vocal signatures in isolation calls. Pups, on the other hand, indiscriminately vocalized in response to echolocation pulse trains from own and alien mothers, rendering the mother-pup recognition process unidirectional. The one-sidedness of the vocal recognition process in *S. bilineata* as well as other bat species might be due to the lack of selective pressures shaping mutual vocal parent-offspring recognition in other species of mammals and birds. To our knowledge, this study is the first in which playbacks were used to experimentally elicit antiphonal calling behaviour between bat mothers and pups. We argue that vocal responses to playback stimuli are a more feasible and reliable response measure for conducting mother-pup recognition playbacks in bats than the phonotaxis behaviour used in the past.

2 Introduction

Evolutionary theory predicts that in gregariously breeding species it is vital for parents to discriminate between own and alien offspring in order to direct parental care to their own descendants (Hepper 1986; Beecher 1991). It may be advantageous for both parents and offspring if the recognition process is mutual instead of unidirectional. If offspring can recognize their parents as well as vice versa, parent-offspring reunions could be facilitated which, in turn, would have advantages for both sides: misdirected parental care would be less

likely, as well as aggressive reactions of adults to the solicitations from alien young (Beer 1970; Pierotti & Murphy 1987). Mutual parent-offspring recognition has been shown for several birds (*e.g.*, Falls 1982) and mammals (*e.g.*, Fischer 2004) but in general unidirectional recognition is more prevalent (Insley 2001). Parents should have a vital interest in avoiding confusion over reproductive investment (Halliday 1983) but for offspring it could be beneficial to exploit parental care and try to nurse indiscriminately if such a behavior is not punished severely (Trivers 1974; Porter 1987). Mutual recognition is likely to occur only when the recognition task is too complicated to be unidirectional (Insley 2001). Selective pressures driving mutual recognition include coloniality (Beecher 1990), offspring mobility (Insley et al. 2003), and time span of parental separation (Insley 1992). In the absence of these selective pressures unidirectionality prevails, resulting in a biased recognition task either towards the parents (e.g. Illmann et al. 2002) or the offspring (*e.g.*, Beer 1969).

In most bat species studied to date, mothers selectively nurse only their own offspring (Fenton 1985) though pups of some species attempt to suckle indiscriminately but with normally little success (Hughes et al. 1989; Gebhard 1997). The vocal component of mother-pup communication is well studied: Pups utter so-called isolation calls when communicating their wish to nurse or – when still not volant - to be retrieved from their current location. Mothers, in turn, produce either so called directive calls or emit echolocation pulses as a response to isolation calls (for an overview see Fenton 1985).To facilitate offspring recognition, isolation calls should contain enough individual variation to allow mothers to discriminate between own and alien young (Beecher 1989). The existence of such a 'vocal signature' in isolation calls has been shown for several bat species using a statistical approach (for overviews see Kunz & Hood 2000; Wilkinson 2003). However, studies verifying their statistical results about individual distinctiveness through playback experiments, in which mothers have to discriminate between recorded isolation calls of different pups, are still fairly scarce (Thomson et al. 1985; Rother & Schmidt 1985; DeFanis & Jones 1995, 1996; Balcombe 1990; Bohn et al. 2007). Vocal signatures in maternal directive calls (Esser & Schmidt 1989; Balcombe & McCracken 1992) as well as in echolocation pulses (DeFanis & Jones 1995; Masters et al. 1995; but see Siemers & Kerth 2006) have also been reported, but playback experiments with pups are even scarcer than with mothers. To our knowledge, the potential occurrence of reciprocal mother-pup recognition has only been studied in four bat species from three different families (Molossidae, Vespertilionidae, and Phyllostomidae) so far and the playback results are somewhat ambiguous: for two species, mutual recognition could not be shown (*T. brasiliensis*: Balcombe 1990; *P. pygmaeus*: DeFanis & Jones 1996),

whereas for two other species mutual recognition could be demonstrated but not statistically assured (*Plecotus auritus*: DeFanis & Jones 1995; *Phyllostomus discolor*: Esser 1998). Our study investigates a fifth species, the greater sac-winged bat *Saccopteryx bilineata* (family *Emballonuridae*), to gather more data on the potential occurrence of mutual mother-pup recognition in bats. Taxonomical broadness is important because only with data from enough species that differ sufficiently in their way of life (*e.g.*, in coloniality, roost fidelity, and amount of maternal separation) can we ultimately understand the influence of selective pressures shaping mother-offspring recognition in bats.

A *S. bilineata* mother hides her non-volant pup in varying night-roosts in the rainforest during the time she spends foraging (Tannenbaum 1975). In order to retrieve the pup later, spatial memory alone is likely to be insufficient for a successful mother-pup reunion because the pup might have crawled to a different location (to avoid predation) or fallen down. It should be beneficial if the calling behavior of pups was triggered by echolocation pulses of by-flying conspecifics because a constantly vocalizing pup would attract predators. It is uncertain whether pups call in response to all conspecifics echolocation pulses or whether they discriminate between own and alien mothers. Maternal echolocation pulses might contain enough individual variation to facilitate individual recognition (*e.g.*, by adult conspecifics), but whether this information is used by pups for discrimination depends on the exigency of such a behavior. Pups might only discriminate between own and alien mothers based on echolocation pulses if the predation risk is higher otherwise or if a unidirectional recognition process is insufficient in yielding successful mother-pup reunions.

The aim of this study was to investigate whether acoustically mediated mother-pup recognition takes place in *S. bilineata,* and if so, whether this recognition process is mutual or unidirectional. We studied the individual distinctiveness inherent in isolation calls uttered by pups and echolocation pulse trains produced by mothers, using both a statistical approach and playback experiments with free-living bats. We hypothesized that mothers are able to discriminate between own and alien offspring based on isolation calls alone and that the calling behavior of pups is triggered by conspecifics' echolocation pulses. We further tested whether pups could discriminate between own and alien mothers based on echolocation pulses. To our knowledge, this is the first bat study in which both mothers and pups were tested with the same experimental playback design that was applied to elicit vocal responses belonging to the correct social context instead of initiating phonotaxis behavior. This gave us the novel opportunity to experimentally elicit antiphonal calling behaviour between mothers and pups.

3 Methods

3.1 Study site and animals

Sound recordings and playback experiments were conducted during four field seasons (June-July 2004/2005, June-August 2006/2007) at the Biological Station La Selva (Organisation for Tropical Studies, OTS) in Costa Rica (10°25'N, 84° 0'W). The five study colonies of *S. bilineata* were located on the walls of buildings and contained one or two harems with several lactating females and their offspring each. Bats of all colonies were habituated to the presence of humans and sound recordings and behavioral observations in the day-roost could be made without causing noticeable disturbance. All adult bats in our study colonies were marked with plastic bands on their forearms, rendering them individually discernable from a distance. Bats were captured with mist-nets (Avinet, Inc., New York, USA) outside of the roost when they emerged at dusk or returned at dawn and banded with a unique combination of coloured and numbered plastic bands (A.C. Hughes Ltd., UK, size XCL). The banding procedure was already well established as part of a long term study since 1996 (see Heckel et al. 1999 for details) and there were no negative effects on the bats' behaviour or health we were aware of. Non-volant pups were first identified via their respective mothers and banded at a later stage. This is an accurate identification procedure since females bear only one pup per year and are aggressive towards alien pups. Vocalizations were analysed from nine pups in 2004 (when they were approximately 3-5 weeks old) and nine lactating females in 2005/2006. Playbacks were performed with nine lactating females in 2005 and nine pups in 2006/2007 (which were approximately 6 weeks old when being tested). The nine focal animals used in each data set came from at least three different colonies. We only used individuals for which we had high-quality sound recordings. Females were probably unrelated due to female-biased natal dispersal (Nagy et al. 2007) but pups from the same colony in the same year could be paternal half-siblings. When we conducted playback experiments, pups were already volant (but not weaned yet) and we were therefore able to catch a lactating female or her respective pup separately with a mist-net close to the day-roost and thus minimize disturbance in the colonies. Playbacks were conducted out of earshot of the focal bat's day-roost so that the respective pup or mother belonging to the focal bat being tested could remain undisturbed in its social group and did not have to be caught as well. Since pups were already volant and hence partly independent when we conducted playbacks, a short separation from their mothers did not pose a threat for their health nor had any other negative effects we were aware of. Immediately after the playbacks, focal bats were released close to their day-roost. In

all cases, focal mothers returned directly to their respective pups and vice versa. All field work complied with the current laws of Costa Rica.

3.2 Sound recording and playback equipment

Sound recordings were made to statistically analyse the potential individual distinctiveness of isolation calls from pups and echolocation pulse trains from mothers and to provide stimuli for our playback experiments. Isolation calls were recorded from pups actively pursuing their mothers in order to nurse and echolocation pulses were recorded from perched females responding to their respective pup's vocalizations. In addition, we gathered behavioral data on successful mother-pup reunions under natural circumstances in the day-roost. The vocalizations were digitally recorded with a high quality ultrasonic recording set-up (400 kHz sampling rate and 12 bit depth resolution) consisting of a ¼ inch Bruel & Kjaer microphone (type 4939; free field response ± 2dB from 4-100 kHz), a G.R.A.S. preamplifier (type 26 AB), a G.R.A.S. power module (type 12 AA; 20 dB amplification), a National Instruments A/D DAQCard 6062E, and a notebook computer running Avisoft-Recorder software (version 2.9, R. Specht, Berlin, Germany). The directional characteristic of the microphone was focussed by a 0.33 m diameter parabolic reflector mounted on a tripod with a dimmed laser-pointer attached to aim at focal animals. This set-up permitted individual recordings even if other bats were vocalizing in the vicinity.

Playback signals (300 kHz sampling rate) were fed into an ultrasonic amplifier (Avisoft Ultrasonic Power Amplifier; frequency response of ±1 dB from 0.1 to 100 kHz) and an ultrasonic speaker (Avisoft Ultrasonic Speaker ScanSpeak R2904-700000; frequency response of ±8 dB from 4 to 115 kHz). Amplitudes of playback stimuli where adjusted to 100 dB SPL at a distance of 0.1 m. Vocal responses to playbacks were recorded with a sampling rate of 100 kHz using the set-up described above.

3.3 Playback design

We used the same experimental design (Fig. 1) to investigate the vocal responses of both mothers and pups to the different playback situations. In a first set of playback experiments, lactating females were exposed to isolation calls of their own versus an alien pup; in a second set, pups were exposed to echolocation pulse trains of their own versus an alien mother. Vocal responses were defined as either isolation calls (from tested pups) or echolocation pulse trains (from tested mothers). No other vocalization types were ever recorded during playbacks. A playback started once the focal animal had habituated to the playback cage (15x25x15 cm,

consisting of a wire frame covered with soft mesh). The bat could freely move within the cage but normally perched on one vertical wall and appeared calm (e.g. started grooming) less than 10 minutes after it had been caught and transferred to the playback cage. Each playback trial had a total duration of nine minutes and consisted of a pre-observation period (two min), the first stimulus presentation period (two min), an observation period (one min), the second stimulus presentation period (two min), and a post-observation period (two min). Isolation calls or echolocation pulse trains in the stimulus presentation periods were either from the own pup (or mother) or from an alien one and the order in which they were broadcasted was pseudo-randomised. Vocalizations of focal animals were not only recorded in the stimulus presentation periods but also in the observation periods to control for changes in motivation throughout the playback experiment.

focal animal in playback	pre-observation 2 min	**stimulus presentation 1 2 min**	observation 1 min	**stimulus presentation 2 2 min**	post-observation 2 min
mothers		isolation calls of own/alien pup		isolation calls of alien/own pup	
pups		echolocation pulse trains of alien/own mother		echolocation pulse trains of own/alien mother	

Figure 1: Experimental design for playbacks used to test both mothers and pups. Observation periods alternated with stimulus presentation periods over the course of nine minutes. During the three observation periods, spontaneous vocalizations of the focal animal were recorded. During the two stimulus presentation periods, stimuli were presented and the elicited vocal response of the focal animal recorded. The order in which stimuli belonging to the own versus alien pup/mother were broadcast was pseudo-randomised between the two stimulus presentation periods.

3.4 Playback stimuli

To avoid pseudo-replication (McGregor et al. 1992), ten different isolation calls (or echolocation pulse trains) were chosen as stimuli from each pup (or mother). The stimuli were selected from different vocalization bouts each to minimize temporal dependence among vocalizations uttered in succession. The time interval between recordings of stimuli and playback experiments was less than a week in all cases. After filtering for background noise, the different stimuli were combined into in a single sound file interspaced with silent intervals of eight, ten, or twelve seconds. Every sound file started with five seconds of silence and was two minutes long. Sound files were generated using Cool Edit 2000 (Syntrillium, Phoenix,

USA). Every sound file was unique due to the random order of stimuli and silent interval lengths and used only once. If stimuli were used both as 'own stimuli' for the respective mother (or pup) and 'alien stimuli' for a different female (or pup), new sound files were generated. We used isolation calls and echolocation pulse trains from colony members as 'alien stimuli' in the playbacks because we wanted to test for individual recognition and not for an effect of familiarity (*i.e.*, colony member vs. non-colony member).

3.5 Acoustical analyses

Acoustic analysis of vocalizations was performed in Avisoft-SASLab Pro (version 4.1, R. Specht, Berlin, Germany). Measurements were taken from spectrograms generated using a 1024 point FFT and a Hamming window with 75 % overlap, which resulted in a frequency resolution of 390 Hz and a time resolution of 0.64 ms. To characterize echolocation pulses uttered by mothers, two temporal (duration; distance from start to maximum amplitude of the pulse) and six spectral parameters (peak frequency at start, middle, and end of the pulse; minimum, maximum, and peak frequency averaged over the entire pulse) were measured. Pups' isolation calls were multi-syllabic and consisted of simple syllables that gradually merged into composite syllables (Fig. 2a). Several different syllable types were categorized: simple, but variable syllables ('sv-syllables'; at the beginning of calls), composite syllables (at the end of calls, consisting of a noise-like beginning followed by a tonal part; 'nc-syllables and tc-syllables'), and simple, but stereotyped syllables ('ss-syllables'; immediately following the composite syllables). In order to characterize isolation calls, several different spectral parameters were measured according to the respective syllable type: peak frequency at start and end as well as number of frequency modulations for sv- and tc-syllables, bandwidth over the entire length for nc-syllables, and peak frequency at start and end for ss-syllables. Duration and number of syllables per call were measured for all syllable types. This resulted in a total of 17 spectral and temporal parameters used for characterizing isolation calls. To minimize temporal dependence among vocalizations uttered in succession, echolocation pulses and isolation calls were taken from different vocalization bouts on different days.

3.6 Statistical analyses

In order to test for individual distinctiveness of isolation calls and echolocation pulse trains, we performed discriminant function analyses (DFAs) that allowed us to optimally separate individuals in a multi-dimensional signal space defined by the acoustic parameters measured before. DFAs were calculated for isolation calls and echolocation pulse trains separately. All

acoustic parameters were included simultaneously into the respective DFAs. We used a subset-validation procedure to assign isolation calls and echolocation pulse trains to different individuals. This procedure randomly assigns calls to a 'training' set and a 'test' set (50% of all calls per set) and uses the training set to calculate discriminant functions with which the test set is then classified. The classification success depends on the number of individuals, vocalizations, and acoustic parameters measured per syllable. In general, the classification success decreases with increasing number of individuals and increases with increasing numbers of vocalizations per individual and acoustic parameters measured per syllable (Beecher 1989). After testing for normality, results from playback experiments were analysed using parametric tests (two-tailed; α=0.05). All statistical tests were conducted using SPSS version 11.5 (SPSS Inc., Chicago, IL, U.S.A.).

4 Results

4.1 Vocal mother-pup communication

During all mother-pup reunions in the day-roost, pups always uttered multi-syllabic isolation calls in which simple syllables gradually merged into composite syllables (see Fig. 2a). When pups approached their mothers, isolation calls were interspaced with silent intervals (mean: 8.53s, range: 1.5-36.1s; nine pups) that decreased in length towards the end of the solicitations (Wilcoxon signed-ranks test; matched pairs were the first and second half of successful solicitation periods: T=3, N=9, exact P=0.020). Mothers reacted with echolocation pulse trains (Fig. 2b), which were uttered while being perched in the roost. In addition, mothers produced so-called directive calls (Fig. 2c), barely audible vocalizations that resembled the sv-syllables of isolation calls. However, these directive calls were rarely uttered, mainly when pups were still very young and left their mother's teat for the first few times. As soon as pups were volant (but not weaned), we never recorded any more directive calls from their mothers. Therefore, they are not part of the analyses presented here.

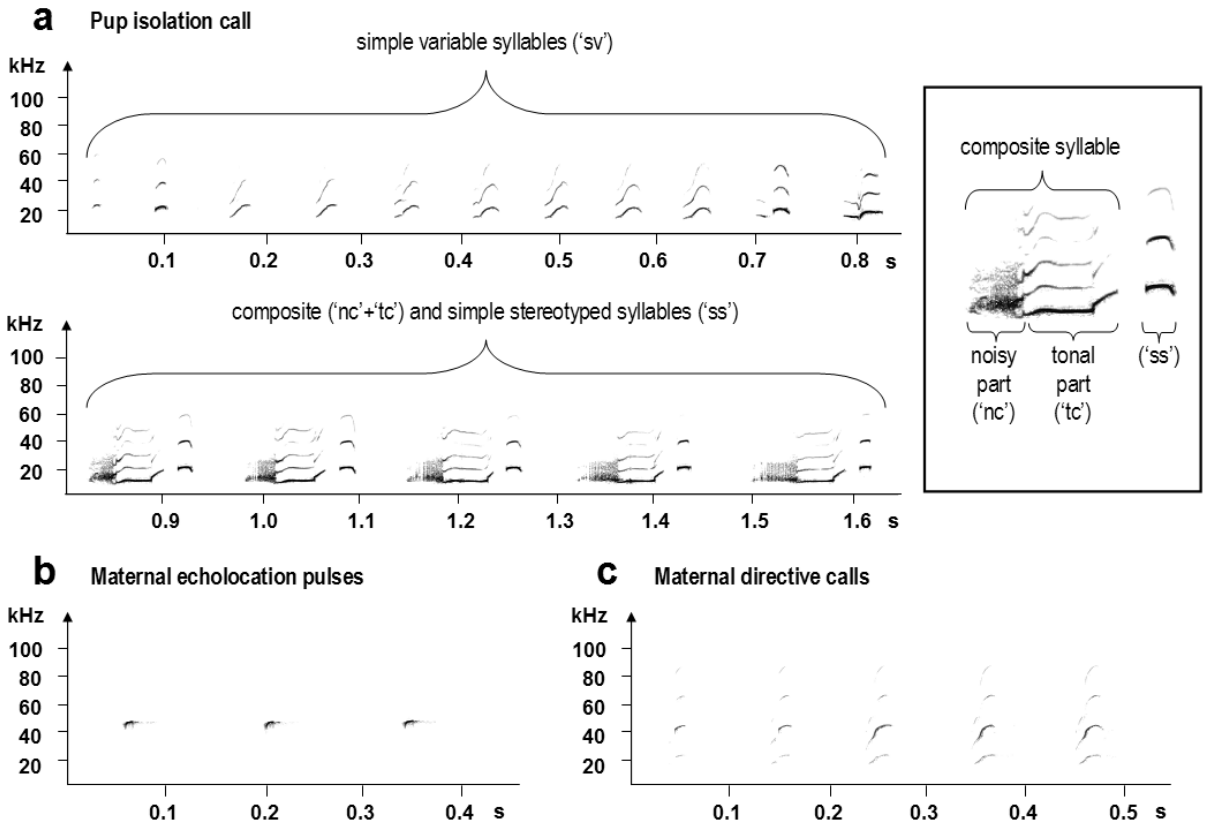


Figure 2: Spectrograms of a multi-syllabic isolation call from a 30 day old pup (**a**), three maternal echolocation pulses (**b**) and five maternal directive calls (**c**). Simple, but variable syllables (sv-syllables) in the beginning of the isolation call gradually merge into composite syllables consisting of a noisy (nc-syllables) and a tonal part (tc-syllables) which are followed by simple, but stereotyped syllables (ss-syllables). The spectrograms depict frequency as a function of time and were generated using a 1024 point fast Fourier transform and a Hamming window with 75 % overlap.

4.2 Statistical individual distinctiveness of isolation calls

All pups could be statistically distinguished based on the acoustical parameters extracted from isolation calls (Tab. 1). A DFA with 90 isolation calls of nine pups (ten calls each) classified 62 % of all calls to the correct individual, which was significantly higher than expected by chance alone (11.11 %; Wilcoxon signed-ranks test for matched pairs: $T=0$, $N=9$, exact $P=0.005$). The first three discriminant functions together accounted for 85.3 % of the observed variation. A DFA using only the parameters extracted from the composite syllables at the end of calls (nc- and tc-syllables) still assigned 53% of all calls to the correct pup. The obtained classification success was again significantly higher than expected in a random classification (11.11 %; Wilcoxon signed-ranks test for matched pairs: $T=1$, $N=9$, exact $P=0.01$), suggesting that most vocal signature information is encoded in the composite syllables.

4.3 Statistical individual distinctiveness of echolocation pulse trains

Mothers could be statistically distinguished based on the acoustical parameters of echolocation pulse trains (Tab. 1). A DFA with 90 echolocation pulse trains of nine mothers (ten trains each; mean of six pulses per train in the analysis) classified 40 % of all trains to the correct mother, which was significantly higher than expected by chance alone (11.11 %; Wilcoxon signed-ranks test for matched pairs: T=3, N=9, exact P=0.02) but considerably weaker than the result obtained for isolation calls, making it difficult to identify individuals reliably. The first three discriminant functions together accounted for 87.9 % of the observed variation.

Table 1. Statistical evidence for a vocal signature character in isolation calls and echolocation pulse trains.

Isolation calls (9 pups, 90 calls)				**Echolocation pulse trains (9 mothers, 90 trains)**		
acoustic parameters		**df 1**	**df 2**	**df 1**	**df 2**	**acoustic parameters**
sv-syllables	number	0.00	0.13	0.28	-0.42	duration
	duration	-0.04	0.05	-0.18	0.61	disttomax
	peak frequency (start)	0.12	0.02	0.07	0.09	peak frequency (start)
	peak frequency (end)	0.18	0.18	0.04	-0.20	peak frequency (middle)
	frequency modulations	0.05	0.16	0.02	-0.25	peak frequency (end)
tc-syllables	number	0.01	0.18	0.04	-0.19	peak frequency (entire pulse)
	duration	0.12	0.14	0.13	0.14	minimun frequency (entire pulse)
	peak frequency (start)	0.03	0.00	-0.15	-0.31	maximum frequency (entire pulse)
	peak frequency (end)	0.17	0.35			
	frequency modulations	0.26	0.07			
nc-syllables	number	-0.22	0.14			
	duration	-0.02	-0.24			
	bandwidth	-0.07	-0.19			
ss-syllables	number	0.08	0.13			
	duration	0.19	0.02			
	peak frequency (start)	0.05	0.10			
	peak frequency (end)	0.07	0.09			
Assessment of Model Fit						
eigenvalue		10.562	4.523	6.280	2.133	
proportion of variation [%]		50.9	21.8	58.5	19.9	
Wilks-Lambda		0.0001	0.005	0.007	0.053	
chi-square (all P<0.001)		238.093	162.212	174.620	104.146	

Correlations between the standardized canonical coefficients and the variables in the DFAs (subset validation) for the first two discriminant functions (*i.e.*, df 1 and df 2). The higher the correlation, the more important is the respective variable in shaping an axis. For an explanation of syllable-abbreviations and acoustic parameters see Methods section.

4.4 Playbacks with isolation calls

Mothers could clearly discriminate between own and alien offspring in our playbacks. Stimuli from the focal mother's own pup elicited significantly more often vocal responses than stimuli from an alien pup (Fig. 3a; paired t-test: t_8=-14.50, P<0.0001). Additionally, the response latency was significantly shorter for the 'own pup' stimuli than for the 'alien pup' stimuli (Fig. 3b; paired t-test: t_6=2.785, P=0.032). A one-factorial repeated measures ANOVA revealed a tendency towards significant differences between spontaneous calling behaviour in different observation periods ($F_{2,16}$=2.932, P=0.082, partial η^2=0.268) which was due to the fact that significantly more echolocation pulses were recorded during the preobservation than during the other two observation periods (pair-wise comparisons of estimated marginal means; mean difference=3.111, 95% confidence interval: 0.248-5.974, P=0.034; other mean differences were non-significant). The difference between spontaneous vocalizations before and during/after the playback (pre-observation: 1.4±0.5; observation: 0.8±0.7; post-observation: 0.8±0.7; means and standard deviations for the number of vocal responses from nine mothers) might be due to habituation but the short response latency (1.16 ± 0.66s for 'own' and 2.76±1.35s for 'alien' stimuli; means and standard deviations for nine mothers) showed that focal bats still readily responded to the playback stimuli.

4.5 Playbacks with echolocation pulse trains

In our playbacks, pups did not discriminate between own and alien mother on the basis of echolocation pulse trains. We found no significant difference in the percentage of stimuli eliciting vocal responses (Fig. 3a; paired t-test: t_8=0.667, P=0.524) or the response latency (Fig. 3b; paired t-test: t_7=0.847, P=0.425) between the two different stimulus types. No difference in spontaneous calling behavior between playback observation periods was found (repeated measures ANOVA: $F_{2,16}$=1.143, P=0.344), not even a trend towards habituation throughout the playback (pre-observation: 0.7±0.5; observation: 0.3±0.5; post-observation: 0.7±0.5; means and standard deviations for the number of vocal responses from nine pups). Despite the fact that our playbacks failed to demonstrate discrimination between own and alien mothers, we are certain that our playbacks were valid for two reasons: First, pups called significantly more often during stimulus presentation periods than during observation periods (paired t-test: t_8=5.679, P<0.0001; means of stimulus presentation (2.4±0.9 calls) and observation periods (0.6±0.3 calls) were used), suggesting that our stimuli indeed elicited calling behavior. Second, pups did not call randomly during stimulus presentation periods but

produced responses to the presented stimuli with only a short latency (1.77±0.56s after the beginning of the silent intervals between stimuli; mean and standard deviation for nine pups).

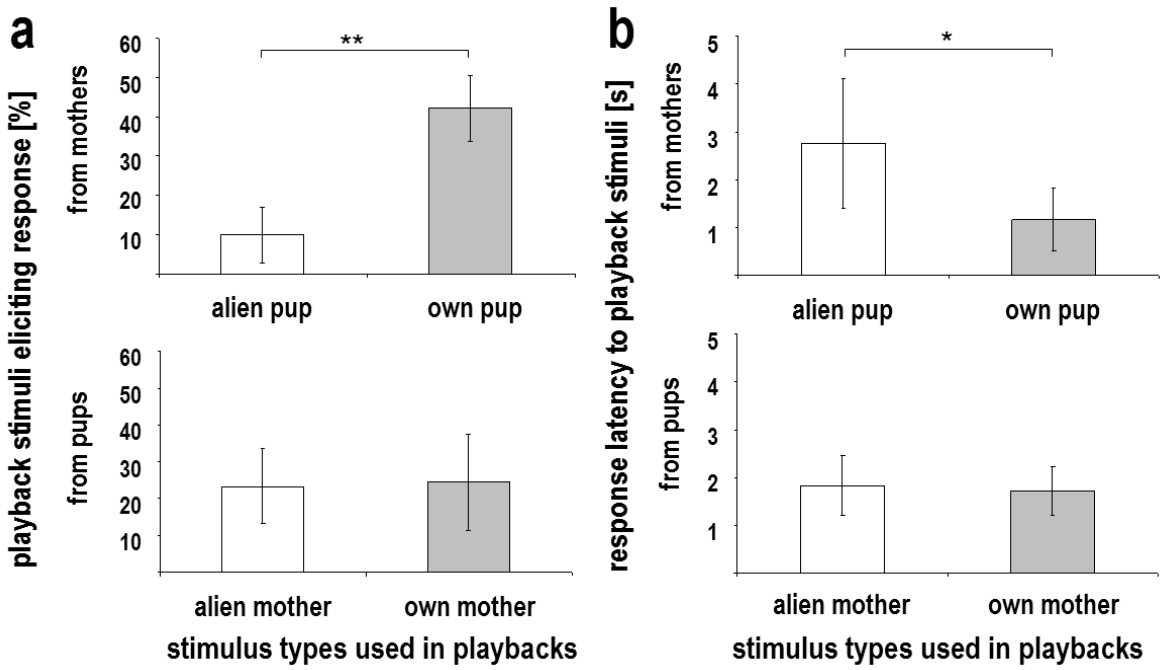


Figure 3: Percentage of playback stimuli eliciting vocal responses (**a**) or response latency to playback stimuli (**b**) from focal mothers (upper half) or pups (lower half) for the two different stimulus types used in the playbacks ('alien' and 'own'). Paired t-tests revealed that mothers responded significantly more often and with a shorter latency to stimuli coming from their own pup versus an alien one (** $P<0.0001$; * $P<0.05$), whereas pups responded indifferently to stimuli from their own and an alien mother. Means and standard deviations are shown.

5 Discussion

5.1 Statistical evidence for vocal signatures

Our results suggest that both isolation calls uttered by pups and echolocation pulse trains uttered by mothers contain enough individual variation to allow for statistical discrimination better than expected by chance alone. However, there are differences in the strength of the vocal signature character inherent in the two vocalization types. The vocal signature exhibited in pups' isolation calls seems to be rather strong, indicating that vocal offspring recognition by mothers is likely to occur. Since we could not control for the pups' precise age in our analysis as some other studies did (Jones et al. 1991; Scherrer & Wilkinson 1993; Knörnschild et al. 2007), age effects could have contributed to or masked differences between

pups in our study (Scherrer & Wilkinson 1993). Isolation calls of *S. bilineata* are among the most complex infant vocalizations reported for bats and most signature information is encoded in the composite end syllables of isolation calls. Maybe the function of the simple syllables at the beginning of calls, which contribute only very little to individual distinctiveness, lies in attracting the attention of a by-passing female in search of her pup, whereas the composite syllables are then used to communicate the identity of the vocalizing pup. The vocal signature inherent in maternal echolocation pulse trains was considerably weaker than the one in isolation calls, making it debateable whether echolocation pulses could be used by pups to identify their respective mothers. Several studies reported vocal signatures in echolocation pulses encoding group identity, age, sex, individual identity, or all of the above (Jones et al. 1992; Masters et al. 1995; Pearl & Fenton 1996; but see Siemers et al. 2005 and Siemers & Kerth 2006), and in most cases their obtained classification success was higher than ours.

5.2 Experimental evidence for vocal signatures

Mothers could clearly discriminate between own and alien offspring solely on the basis of isolation calls and responded more often and with shorter latency to their own young. Several other studies also verified vocal offspring recognition by mothers through playback experiments (*Phyllostomus discolor*: Rother & Schmidt 1985; T*adarida brasiliensis mexicana*: Balcombe 1990; *Pipistrellus pygmaeus*: DeFanis & Jones 1996; *Phyllostomus hastatus*: Bohn et al. 2007) but used phonotaxis behavior or, in psychoacoustic experiments, the Go/No-go procedure to evaluate the recognition abilities of the focal bats. To our knowledge, this study is the first to use vocal responses to playback stimuli as a measure of mother-offspring recognition in bats. We argue that vocalizations are a more feasible response measure than phonotaxis behaviour for conducting mother-pup recognition playbacks in bats. Phonotaxis through flight normally covers distances that are too large to be easily provided. Accordingly, most bird studies using phonotaxis as a response measure conducted playbacks with free-ranging animals or provided large flight cages (Searcy 1992). In spite of being more practicable, phonotaxis through crawling nevertheless demands an experimental set-up properly adjusted to normal bat behaviour. Crawling around in the roost can occur both along the vertical and horizontal axes but the only horizontal axis bats commonly craw along is the ceiling and not the floor. Therefore, we believe that forcing bats to exhibit phonotaxis behaviour while crawling *on* a horizontal surface (in contrast to *under* it) constitutes a highly unnatural situation. Especially for pups falling to the floor is a potential life-threatening

situation due to the increased risk of predation which they normally try to overcome by hectically crawling around until they find a vertical surface to gain elevation and even adult bats do not appear very comfortable on the floor. We doubt that such a situation would make them very responsive to a discrimination task. This is true for the majority of species even though there are exceptions like the vampire bat *Desmodus rotundus*, which normally crawls towards its sleeping prey and therefore performs well in a conventional Y-maze set-up (Gröger & Wiegrebe 2006). The described dilemma could be overcome by constructing Y-mazes or circular arenas which are either large enough to permit flight or in which the focal bats can crawl in a more natural way (*i.e.*, under a horizontal surface or along a vertical one). When testing temporarily captive bats under field conditions this might not be feasible whereas the use of vocalizations as a response measure constitutes a convenient alternative. In addition to the fact that phonotaxis in a conventional two-speaker design does not allow to distinguish between avoidance or preference of playback stimuli (Gerhardt 1992), vocalizations belonging to the correct social context (*i.e.*, mother-pup reunions) are easier to interpret as reactions to the playback stimuli than movements that could either be phonotaxis behaviour or escape attempts. This is true especially when negative results are obtained. Ideally, more than one response variable should be measured (McGregor 1992) and most playback studies performed on birds, anurans and insects do so. We argue that in cases where this is not feasible, vocal responses should be preferred over phonotaxis behaviour to assess acoustically mediated mother-pup recognition in bats.

Our playbacks demonstrated clearly that the production of pups' isolation calls was triggered by echolocation pulses from adult conspecifics. Under natural circumstances, this antiphonal calling behaviour is probably very useful to make the pup's current location known to any by-passing female that could be its mother. Apparently there is no adaptive advantage for *S. bilineata* pups to further discriminate between their own and alien mothers, which corresponds to the results of other studies (Balcombe 1990; DeFanis & Jones 1996; but see DeFanis & Jones 1995 and Esser 1998). This could be due to several reasons: First, the pups we tested might have been too young to perform a successful discrimination task (*e.g.*, because of incomplete hearing development, as suggested by Thompson et al. 1985). This seems unlikely in our case, since we used pups of approximately six weeks of age in our playbacks and hearing should be fully developed in volant pups due to the required orientation through echolocation. Second, there might be no strong selective pressures for mutual mother-pup recognition in this species.

5.3 Selective pressures influencing vocal parent-offspring recognition

Mutual parent-offspring recognition is well documented for several birds (penguins: Jouventin et al. 1999; alcids: Jones et al. 1987; Lefevre et al. 1998; Insley et al. 2003) and mammals, especially otariid pinnipeds (Trillmich 1981; Insley 2001; Charrier et al. 2003), dolphins (Sayigh et al. 1998), and ungulates (reindeer: Espmark 1971, 1974; domestic sheep: Searby & Jouventin 2003). In pinnipeds and penguins, mutual recognition might be essential to facilitate parent-offspring reunions because they breed in very large colonies and parents leave their young for long periods to forage, making the recognition task possibly too difficult to be unidirectional. In reindeer and sheep, neonates follow their mothers immediately after parturition and mutual vocal recognition should be beneficial to retain contact over a distance in a moving herd. Ungulates in which neonates hide between nursing periods, only exhibit unidirectional vocal recognition, either by the mother (goat: Terrazas et al. 2003; pig: Illmann et al. 2002) or the offspring (fallow deer: Torriani et al. 2006), suggesting that the species-specific differences in neonate mobility may have influenced the direction of vocal mother-offspring recognition. Accordingly, mutual vocal recognition in alcids is influenced by offspring mobility; in species with extended parental care at sea, unidirectional recognition might be insufficient to ensure successful parent-offspring reunions (Jones et al. 1987; Insley et al. 2003). Dolphins form long lasting social bonds and therefore a strong selection pressure on mutual vocal recognition is likely to exist, especially because they cannot use additional olfactory cues like pinnipeds and ungulates (Insley 2001; Searby & Jouventin 2003).

The fact that vocal mother-offspring recognition is unidirectional in all bat species studied to date (but see DeFanis & Jones 1995 and Esser 1998) might be due to a low selective pressure on mutual recognition, either because recognition errors are innocuous or because the discrimination task is simple enough to be unidirectional: long lasting mother-pup bonds are absent, pups are fairly immobile for their first few weeks after parturition, and other sensory modalities like olfaction and spatial memory can also be applied, especially when breeding aggregations are large.

Chapter II

Babbling Behaviour

1 Abstract

Infant babbling in humans and a few other primates plays an important role in allowing the young to practise the adult vocal repertoire during early behavioural development. Vocalizations uttered during babbling resemble to some degree the acoustic structure of adult vocalizations and are often produced in long bouts independently of any social context. Similar behaviour, 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 but not females utter all different vocalization types produced in infancy. To our knowledge, this is the first evidence of babbling in a non-primate mammal and suggests that infant babbling may be necessary for the ontogeny of complex vocal repertoires.

2 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 & 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 & Tees 1999; Doupe & Kuhl 1999). Infant babbling behaviour is also known from a few other primates (Elowson et al. 1998a,b; Omedes 1985; Winter & 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 & Tees 1999; Elowson et al. 1998a,b; Snowdon & Elowson 2001).

In support of this view, the vocalizations of young songbirds during the sensorimotor learning phase, namely subsong and plastic song (Doupe & Kuhl 1999; Goldstein et al. 2003),

have also been 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 & Peters 1982; Catchpole & Slater 1995; Marler & Slabbekorn 2004). Although babbling-like behaviour is widespread in songbirds, and infant babbling is known to occur in humans and a few non-human primates, it has to our knowledge never been reported for non-primate mammals.

While studying the vocal behaviour of sac-winged bats, *Saccopteryx bilineata*, we found strong evidence for infant babbling. The sac-winged bat is a neo-tropical species with harem-like social structures (Bradbury & Emmons 1974; Bradbury & Vehrencamp 1976). The mating system of *S. bilineata* can be described as a resource-defence polygyny (Emlen & Oring 1977). Males attempt to indirectly monopolize females in a harem by defending a 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 non-harem owners, competition among males for territories and access to females is high (Heckel et al. 1999) and female choice has a strong influence on male mating success (Heckel & von Helversen 2003).

Previous work has shown that *S. bilineata* has an unusually large vocal repertoire for a bat. Adult vocalizations depend on the social context and have been classified into 7 different vocalization types (Behr & von Helversen 2004). 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 context; 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 & 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 behaviour of *S. bilineata* pups have been scarce and anecdotal (Bradbury & Emmons 1974; Tannenbaum 1975). Here we describe vocalization bouts of *S. bilineata* pups in relation to the known vocal repertoire of adult conspecifics.

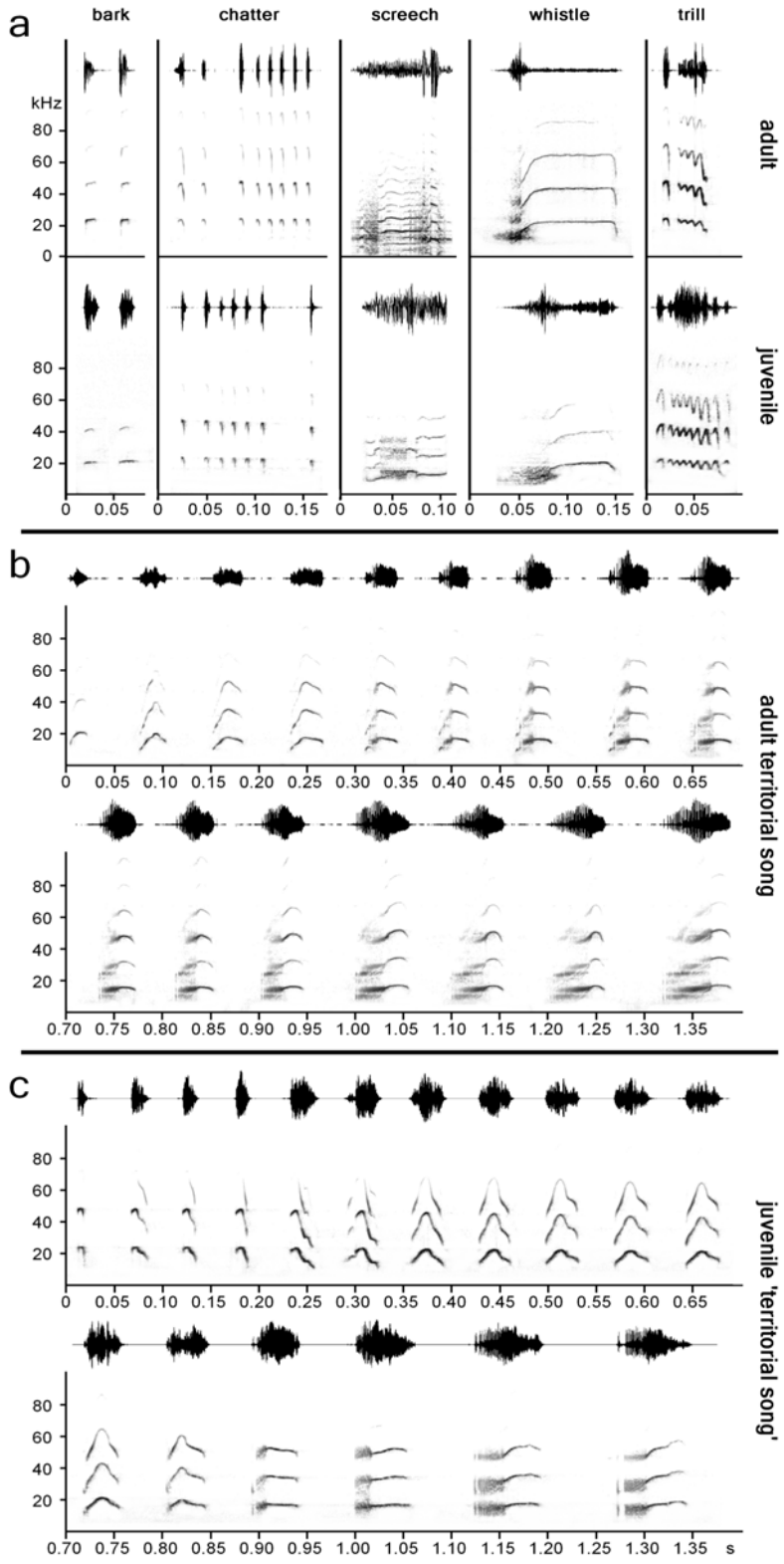


Figure 1: Amplitude envelopes and spectrograms illustrate vocalizations of adult and juvenile *S. bilineata*. Amplitude and spectral frequency are depicted as a function of time. (**a**) Adult vocalization types and the corresponding pup vocalizations: barks, chatter sequence, screech, whistle, and trill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

3 Methods

From December 2003 to March 2004 we studied a population of *S. bilineata* in Costa Rica (Organisation for Tropical Studies biological station La Selva; 10°20´N, 84°10´W). Our study population has been monitored continuously since 1994. Consequently, the bats in their daytime-roosts are habituated to human observers and can be approached to within a few meters. This allowed us to observe and record undisturbed individuals.

We recorded pup vocalizations and made behavioural observations of 11 vocalizing pups of both sexes (8 males and 3 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 (dB 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; 10° angular displacement). Recordings 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 infra-red pointer to the microphone that could be aimed at a recording subject; the infra-red 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 1024 point FFT 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 & von Helversen 2004).

4 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 but 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 together with isolation calls into long babbling bouts (Fig. 3). Pup renditions of adult vocalizations could not be correlated with a specific behavioural context and were normally neither elicited nor influenced by the vocalizations or behaviour of conspecifics. During babbling bouts, pups either solicited maternal care or hung motionless in the daytime-roost without interacting with colony members.

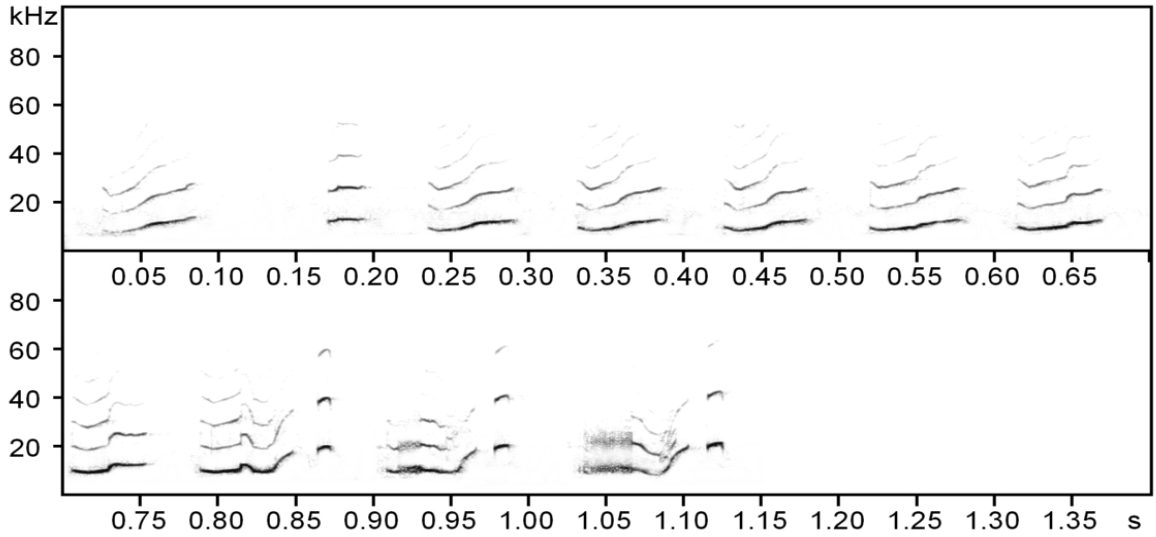


Figure 2: Spectrogram of a *S. bilineata* isolation call. Isolation calls were unique to pups and their most frequently produced vocalization. They were uttered by pups of both sexes.

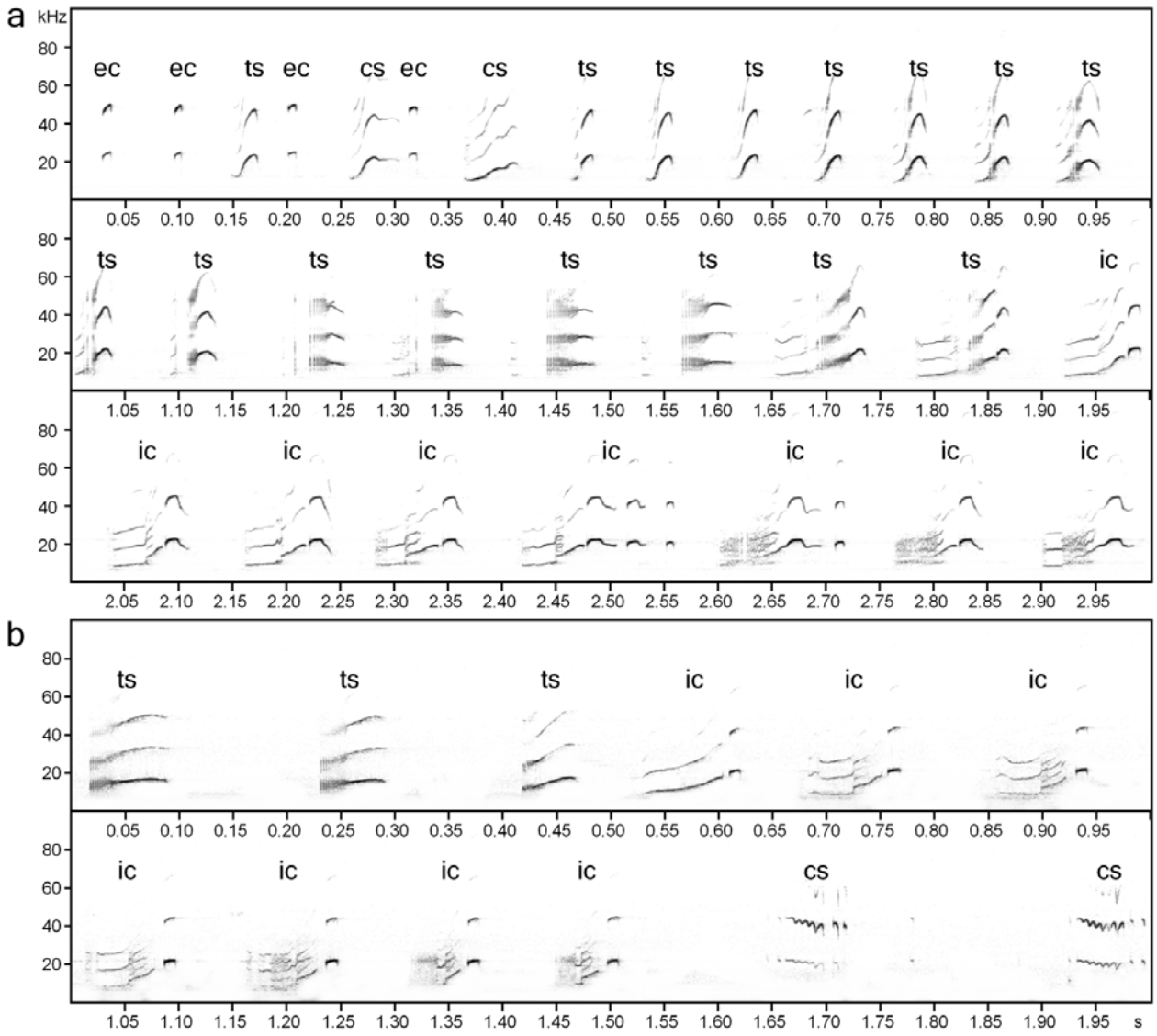


Fig. 3: Spectrograms of babbling bouts from two different individuals: (**a**) Echolocation pulses (ec), elements of territorial song (ts), courtship song (cs), and isolation calls (ic) in a single babbling bout. (**b**) Elements of territorial song (ts), courtship song (cs), and isolation calls (ic) in a single babbling bout.

5 Discussion

The novel aspect of this study is the documentation of babbling behaviour in a non-primate 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. In contrast to humans (Goldstein et al. 2003) and marmosets (Snowdon & Elowson 2001), there is a lack of responses from conspecifics to babbling in infant *S. bilineata*, which may be due to the fact that the social contact of a bat pup is mostly limited to mother-offspring interactions, with the pup's vocalizations

functioning as a 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 behaviour of humans (Doupe & 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 & Slater 1995; Marler & Slabbekorn 2004). Avian subsong and plastic song as the major non-human 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, *Cebuella pygmaea,* which represent a well studied system for mammalian babbling (Elowson et al. 1998a,b; Snowdon & Elowson 2001).

Occurrence of infant babbling and evidence for babbling-like vocalizations has been reported for few 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 behaviour 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.

Chapter III

Social Modification of Isolation Calls

1 Abstract

Vocal production learning can be defined as the learned acquisition or modification of a signal as a result of social influences. Despite the importance of vocal production learning in humans, evidence for it in other mammals is remarkably scarce. We studied vocal production learning in the bat *Saccopteryx bilineata*, which exhibits a rich vocal repertoire due to its complex social life in a harem-like resource-defence polygyny with patrilineal kin groups and female-biased natal dispersal. Comparisons of isolation calls from different pups showed that in addition to an individual signature, isolation calls also exhibited a group signature that became more prominent during ontogeny. Genetic effects on individual or group signatures were not found. Isolation calls converged towards both the territorial song of the respective harem male and towards the isolation calls of fellow pups. In *S. bilineata*, call convergence through social modification creates a 'social badge' that reliably associates individuals to their natal colony. We hypothesize that the potential benefits associated with this group signature are shaped by both intrasexual selection (resource defence) and intersexual selection (inbreeding avoidance). Our study provides the first evidence that learned group signatures occur in unrelated individuals of both sexes in a mammal with resource-defence polygyny.

2 Introduction

Human language is the most sophisticated form of communication in existence and the cornerstone of our cultural and technical achievements (Fitch 2000). Even though its importance for our own species is undeniable, it is not clear exactly how and why language has evolved (Hauser et al. 2002). One of the faculties essential for the acquisition of language is vocal imitation, *i.e.* speech in humans (Fitch 2000; Fitch 2004). Since the capacity for vocal imitation is impossible to derive from the fossil record, studying vocal imitation in extant animals is a useful alternative to shed light on its evolution in humans (Hauser et al. 2002). Specifically, the selective pressures shaping the need for a complex communication system (based on learning to imitate the sounds of conspecifics) can be compared across different taxa which, in turn, might ultimately help to understand how and why vocal learning evolved in humans.

Vocal learning can impact both the usage and comprehension of signals and their production. Whereas evidence for contextual learning (*e.g.*, the context in which to use a signal or how to understand it is learned) is widespread in both birds and mammals, production learning (vocal imitation) seems to be much rarer, especially in mammals. It has been demonstrated in three orders of birds (Passeriformes: Kroodsma 1982; Psittaciformes: Farabaugh & Dooling 1996; Trochilidae: Baptista & Schuchmann 1990) and is the norm in both oscine songbirds and parrots whereas only few patchy examples in four mammalian orders exist (for reviews see Janik & Slater 1997; Boughman & Moss 2003). Considering the importance of vocal production learning in humans (Locke & Snow 1997), the scarcity of evidence in other mammals seems remarkable. Examples come from groups not sharing a unique common ancestor such as cetaceans (Reiss & McCowan 1993; Noad et al. 2000; Foote et al. 2006), pinnipeds (Ralls et al. 1985; Schusterman & Reichmuth 2007), elephants (Poole et al. 2005) and bats (Jones & Ransome 1993; Esser 1994; Boughman 1998), suggesting that vocal learning has evolved independently in phylogenetically distinct groups.

Theoretically, vocal production learning can occur either through learned acquisition of new signals or through social modification of existing signals (Boughman & Moss 2003) but the latter seems to be more prevalent in mammals. Vocal production learning through social modification can affect both individual- and group-specific signals. Learned individual signatures often occur in species that live in fission-fusion societies and form long-lasting social bonds that are maintained vocally (Poole et al. 2005; Cortopassi & Bradbury 2006; Janik et al. 2006) whereas learned group signatures are mainly found in species with stable social groups (Boughman 1998; Sharp et al. 2005; Foote et al. 2006). However, individual and group signatures are not mutually exclusive (Hausberger 1997; McCowan & Reiss 1997; but see Boughman 1998).

Vocal learning of group signatures allows individuals to share vocalizations with a particular subset of conspecifics rather than with any conspecifics. Signals can either be shared with social rivals (*e.g.,* dialects or song type matching) or group mates (*e.g.,* duets or group-specific calls) and therefore the social interactions shaping signal convergence can be either aggressive or affiliative (Brown & Farabough 1997). Examples for learned signal convergence among rivals include many species of territorial songbirds (Kroodsma & Baylis 1982; Catchpole & Slater 1995; Marler & Slabbekorn 2004) but no mammals so far, whereas learned signal convergence among group mates has been found in both birds and mammals (for a review see Boughman & Moss 2003).

It is hypothesized that the vocal flexibility exhibited during echolocation by both dolphins and bats might be a preadaptation for vocal learning in these groups (Boughman &

Moss 2003). In bats, vocal learning through social modification has been shown for signals used in individual recognition (Jones & Ransome 1993; Esser 1994) and group cohesion during foraging (Boughman 1998) but, until now, not in male resource defence or female inbreeding avoidance. We investigated vocal production learning in the greater sac-winged bat, *Saccopteryx bilineata*. This species is common in the lowlands of Central America and well suited for such a study, partly because their vocal repertoire is documented (Behr & von Helversen 2004) and partly because tentative evidence for vocal production learning in this species already exists (geographic variation in male song: Davidson & Wilkinson 2002; babbling behavior of pups: Knörnschild et al. 2006). *S. bilineata* lives in a polygynous mating system in which territorial males defend harems containing up to nine females and their respective offspring. Day-roost colonies can contain up to twelve harem territories belonging to different harem males (Bradbury & Emmons 1974; Bradbury & Vehrencamp 1976). Young males must either queue for harem access in their natal colony (*i.e.,* 'peripheral males'; Voigt & Streich 2003) or found a new colony elsewhere. Colonies have a patrilineal structure and females in a colony are unrelated due to female-biased natal dispersal (Nagy et al. 2007). Since males are unable to sexually monopolize females, not all pups born in their harems might be their descendants (Heckel et al. 1999). Due to its complex social life, *S. bilineata* exhibits an unusually rich behavioral repertoire comprising visual, olfactory and acoustic displays (for a review see Voigt et al. 2008). For most vocalization types, the distinct social context in which they are uttered is known (Behr & von Helversen 2004; Davidson & Wilkinson 2004; Knörnschild & von Helversen 2008).

We studied the potential occurrence of production learning in isolation calls, the most common vocalization type produced by pre-weaned pups during ontogeny. In *S. bilineata*, isolation calls are uttered mainly by pups in order to elicit maternal care but we have anecdotic evidence that adult peripheral males still produce isolation calls during aggressive encounters with the current harem male or when courting females for the first time after a successful harem usurpation, suggesting their additional function as appeasement signals. Isolation calls of *S. bilineata* are the most complex bat isolation calls studied to date on account of their length (1-2 seconds) and multi-syllabic structure (up to 30 simple and composite syllables total). Isolation calls of different pups are statistically and experimentally distinguishable and the individual signature is located in the composite end syllables of calls (Knörnschild & von Helversen 2008). We compared isolation calls from 25 pups belonging to seven different social groups (*i.e.,* natal harems) throughout ontogeny and investigated both changes in the individual signature during ontogeny and influences of genetic effects (parental genes or gender) and social effects (maternal preference or social group) on isolation call

variation. We hypothesized that if vocal production learning occurred, social effects would influence isolation call variation to a greater extend than genetic effects.

3 Methods

3.1 Study site and animals

We conducted field work at the Biological Station La Selva (Organisation for Tropical Studies, OTS) in Costa Rica (10°25'N, 84° 0'W) during three consecutive summers (June-August 2005-2007). In total, seven different social groups of *S. bilineata* were monitored in their day-roosts. All our day-roosts contained only one social group each. Social groups (*i.e.*, 'harems') consisted of one harem male, several lactating females and their respective offspring. Since the social group composition changed within day-roosts during consecutive years (*i.e.,* the harem male and several adult females were different individuals than in the year before), we worked with different social groups in the same day-roost over the years (five of the seven social groups in our analyses were located in the same two day-roosts). One male held his territory for two consecutive years, but since the composition of adult females changed between years we considered his harems in 2006 and 2007 to be different social groups nevertheless. All bats were habituated to the presence of human observers in the day-roost and we were therefore able to conduct sound recordings and behavioral observations without causing noticeable disturbance. We individually identified adult bats by plastic bands on their forearms (A.C. Hughes Ltd., UK, size XCL). The banding procedure has been already well established as part of a long term study since 1996 (see Heckel et al. 1999 for details). Non-volant pups were first identified via their respective mothers and banded at a later stage, which is an accurate identification procedure because females are aggressive towards alien pups and bear only one pup per year.

3.2 Sound recordings

We used high-quality ultrasonic recording equipment (400 kHz sampling rate and 12 bit depth resolution) that permitted recordings of target individuals even if other bats were vocalizing in the vicinity (for details see Knörnschild & von Helversen 2008). In total, isolation calls of 25 pups belonging to seven different social groups (mean: 3.5, range: 2-5 pups per group) and territorial songs of the six respective harem males were recorded. Isolation calls were recorded from pups pursuing their mothers in order to nurse and behavioral observations verified the identity of the calling pups. Territorial songs were uttered by the respective harem

males at dusk and dawn. We analysed 20 isolation calls from each pup at two ontogenetic stages (non-volant and volant; 10 calls each) and five territorial songs from each harem male. To minimize temporal dependence among vocalizations, we chose only one isolation call or territorial song per recording day.

We are certain that the results we report here are not an artefact due to the recording situation or potential habitat matching. The different recording situations at every day-roost (*e.g.,* structure of roost site or distance to focal animals) could theoretically have led to acoustic similarities within groups. This was not the case in our study since different colonies using the same day-roost in different years did not cluster together in signal space (the seven social groups were located in only four different roost sites because two roosts were used repeatedly by new social groups over the years). Even though different habitats can have very different sound transmission characteristics (Marten et al. 1977), all of our study colonies were located in the same habitat with a maximum distance between colonies less than 1km, which makes habitat matching (*i.e.,* different social groups alter their signals together according to the different habitats they live in) very unlikely.

3.3 Acoustical analyses

Acoustic analysis of vocalizations was performed in Avisoft-SASLab Pro (version 4.1, R. Specht, Berlin, Germany). Measurements were taken from spectrograms generated using a 1024 point FFT and a Hamming window with 75 % overlap, which resulted in a frequency resolution of 390 Hz and a time resolution of 0.64 ms. Vocalizations were multiharmonic but we used only the first harmonic (fundamental frequency) for measurements because it normally contained most of the sound energy. Both isolation calls and territorial songs are multi-syllabic vocalizations (Fig. 1) and in order to characterize them properly, measurements were taken separately for each syllable type (for details on syllable types see Behr et al. 2006 and Knörnschild & von Helversen 2008). We distinguished four different syllable types in isolation calls (sv-, nc-, tc-, and ss-syllables; see Fig. 1a) and three different syllable types in territorial songs (sv, nc-, and tc-syllables; see Fig. 1b). For each syllable, we measured several temporal (duration, interval between syllables, distance from start to maximum amplitude of the syllable) and spectral parameters (number of frequency modulations of the entire syllable; peak frequency, minimum frequency, maximum frequency and bandwidth at a), five different locations that were distributed equally over the entire length of the syllable and b), averaged over the entire syllable). In addition, two measurements were taken from the waveform (root-mean-square and peak-to-peak-amplitude from the entire syllable). This resulted in a total of

38 acoustical parameters per syllable. Parameters of syllables belonging to the same syllable type were averaged for every isolation call and territorial song, adding up to 152 parameters per isolation call (four different syllable types) and 114 parameters per territorial song (three different syllable types).

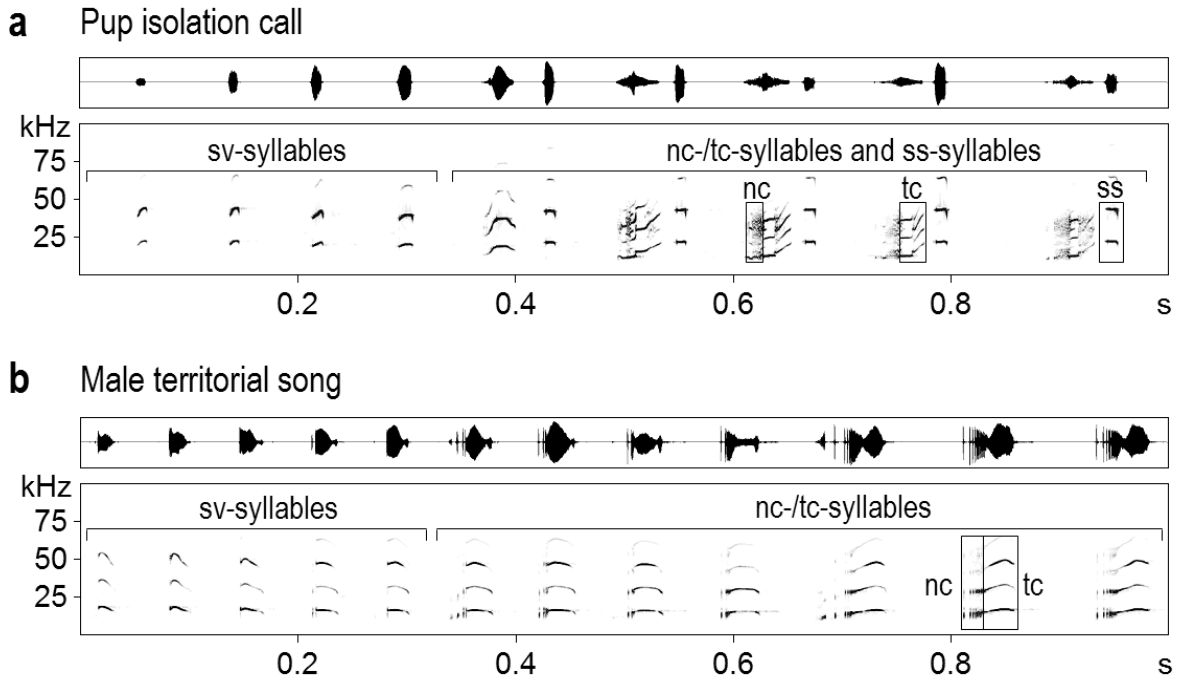


Figure 1: Oscillograms and sonograms of a pup isolation call (**a**) and a male territorial song (**b**). Isolation calls consist of four different syllable types (sv-, nc-, tc- and ss-syllables), territorial songs of three different syllable types (sv-, nc- and tc-syllables). Sonograms were created using a 1024 point FFT and a Hamming window with 75 % overlap.

3.4 Statistical analyses

Acoustical parameters were combined into principal components to obtain fewer and uncorrelated variables using a principal component analysis (PCA) with varimax rotation. We performed separate PCAs for isolation calls and territorial songs. For isolation calls, we obtained 20 principal components with eigenvalues greater than 1 (which explained 88% of the variation in our data). For territorial songs, only the first 12 principal components had eigenvalues greater than 1, but we extracted 20 principal components (which explained 98% of the variation in our data) nevertheless in order to make the different data sets comparable.

We performed discriminant function analyses (DFAs) that allowed us to optimally separate individuals in a multi-dimensional signal space defined by discriminant functions derived from the principal components. The mean canonical scores for every individual are

represented by so-called 'centroids'. All principal components were included simultaneously into the respective DFAs. In order to test for individual distinctiveness (*i.e.,* vocal signatures), DFAs were calculated for isolation calls and territorial songs separately. For the isolation calls, we used a subset-validation procedure which randomly assigns calls to a 'training' set and a 'test' set (50% of all calls per set) and uses the training set to calculate discriminant functions with which the test set is then classified. We repeated DFAs ten times, each time randomly choosing a different test and training set and then averaged the results. Due to the lower number of cases per group, this procedure was not possible for our territorial song data. Instead we used a cross-validation procedure which calculates the discriminant functions with all songs except the one being classified (n-1). The latter procedure is less conservative than the former, leading to a somewhat higher classification success. In general, classification success depends on the number of groups (*i.e.,* individuals), cases (*i.e.,* isolation calls or territorial songs), and variables describing the cases (*i.e.,* principal components); it decreases with increasing number of groups and increases with increasing numbers of cases per group and variables per case (Beecher 1989).

The distance between centroids (*i.e.,* the canonical mean of all isolation calls per pup) in signal space is a good indicator of similarity (Boughman 1998; Knörnschild et al. 2007), with similarly sounding individuals clustering together. We used the Euclidean distance between centroids of different individuals in a two-dimensional signal space as a measure for investigating whether maternal, gender, or social group effects influenced isolation call variation. We calculated the mean Euclidean distance between pups belonging to the same or different mother (over consecutive years), sex, or social group and compared the distances using Wilcoxon signed rank tests for matched-pairs (separately for maternal, gender, and social group effects).

We also utilized the Euclidean distance between centroids to compare the different ontogenetic stages (non-volant and volant) by calculating discriminant functions defining the signal space with the non-volant data and then using these discriminant functions to map the volant data into the same signal space. This enabled us to compare centroid distances for the two ontogenetic stages in the same signal space. We also applied this procedure to test whether isolation calls of pups converged towards the territorial songs of their respective harem males by plotting the territorial songs into the same signal space as the isolation call data for non-volant and volant pups.

Results were analysed using parametric tests (two-tailed, α=0.05), except when sample sizes were ten or less. In this case, the appropriate nonparametric tests were used, calculating exact instead of asymptotic *P* values (after Mundry & Fischer 1998). Means and one standard

deviation are given if not stated otherwise. All statistical tests were conducted using SPSS version 11.5 (SPSS Inc., Chicago, IL, U.S.A.).

3.5 Paternity analysis

We employed eleven highly polymorphic microsatellite loci for paternity analysis (Heckel et al. 1999; Heckel et al. 2000) and assigned parents as described in Heckel and von Helversen (2003). Paternity analysis was performed for 22 of 25 pups in the study. Additionally to the genotypes of the behaviourally assigned mothers (N=16, five mothers had pups in two years and one mother was not sampled genetically) and the genotypes of all adult males present in the study colonies in the summers of 2005, 2006 and 2007 (N=10) we also considered genotypes of adult males sampled in the study colonies and adjacent colonies in former years (N=207) for paternity analysis with Cervus 3.0 (Kalinowski et al. 2007). We obtained 99% of the genotypes at the eleven microsatellite loci and each animal was genotyped at least at ten loci. All behaviourally assigned mothers were also assigned genetically with 95% confidence and zero mismatches (N=20) or one mismatch at most (N=1). Paternity for the known mother-offspring pairs was assigned in 20 of 21 cases, with 95% confidence and zero mismatches (N=18) or at most one mismatch with one of the parents (N=2). The father/s of two pups remained undetermined, including the pup for whose mother we did not collect a DNA sample.

4 Results

4.1 Ontogeny of individual signatures in isolation calls

Pups produced complex multi-syllabic isolation calls (Fig. 1a). In both ontogenetic stages, most isolation calls could be correctly classified to the respective pup (non volant pups: 54.0±4.2%, volant pups: 52.6± 3.5%; data averaged over ten DFAs with subset validation each; 25 pups with ten calls each per ontogenetic stage). This classification success was better than expected in a random classification (4%; two-sample t-test for matched pairs; non-volant pups: t_{24}=10.849, P<0.0001; volant pups: t_{24}=13.081, P<0.0001). A comparison between both ontogenetic stages revealed that the classification success did not change during ontogeny (two-sample t-test for matched pairs: t_{24}=0.268, P=0.79), suggesting that the strength of the vocal signature remains unchanged as pups get older.

4.2 Maternal, gender and social group effects on isolation call variation

We used the Euclidean distance between centroids (*i.e.,* the canonical mean of all isolation calls per pup) in a two-dimensional signal space defined by the first two discriminant functions of a DFA (eigenvalues of discriminant functions: df1=3.439, df2=2.459; 25 pups with 20 calls each) to test for maternal, gender, and social group effects. The distance between centroids is a good indicator of similarity, since similarly sounding individuals cluster together in signal space.

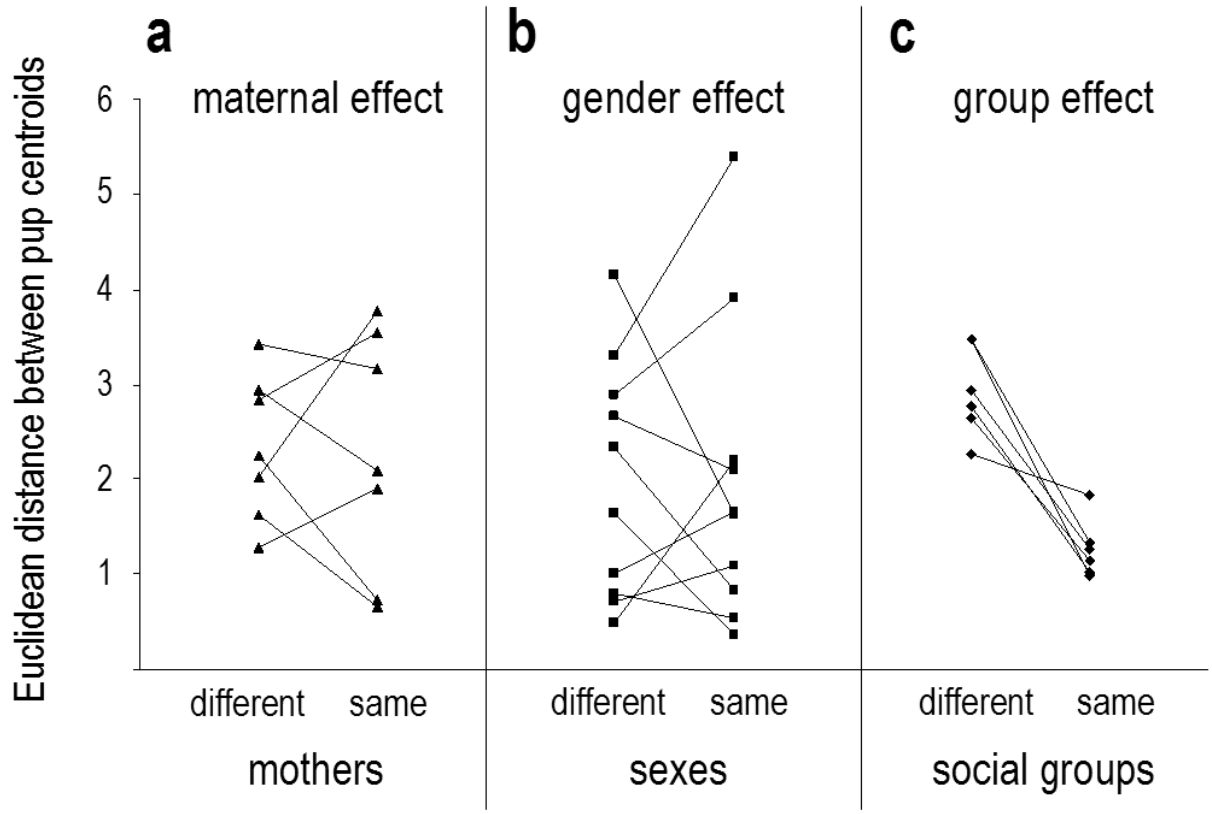


Figure 2: Euclidean distance between centroids of different pups in a two-dimensional signal space defined by the first 2 discriminant functions. Centroids belong to (**a**) pups from different versus the same mothers, **(b**) pups from different versus the same sex, and (**c**) pups from different versus the same social groups. Pups belonging to the same social group clustered together in signal space.

In our analysis, seven mothers had pups over two consecutive years. For these 14 pups, we compared the Euclidean distance between pups having the same mother ('same mother' distance) and between pups having different mothers ('different mother' distance). Our results show that pups with the same mothers did not cluster together in signal space (Wilcoxon signed rank test for matched pairs: N=7, exact P=0.578), suggesting that maternal effects (*i.e.,* maternal genes or maternal preference for certain isolation calls) did not influence isolation call variation (Fig. 2a).

We determined the sex for all but two pups in our data set (10 males, 13 females). For these 23 pups, we compared the Euclidean distance between pups of the same sex ('same sex' difference) or different sex ('different sex' difference). Pups of the same sex did not cluster together in signal space (Wilcoxon signed rank test for matched pairs: N=10, exact P=0.922), showing that gender did not effect isolation call variation (Fig. 2b).

The 25 pups in our data set came from seven different social groups. However, one group (group 6) had to be excluded from the analyses, because one pup from a different day-roost moved into this social group after it became volant, thus spending its non-volant time in a different social group than its volant time. We compared the Euclidean distance between pups from the same social group ('within group' distance) and different social groups ('between group' distance). The within group distance was significantly smaller than the between group distance (Wilcoxon signed rank test for matched pairs: N=6, exact P=0.031), showing that pups belonging to the same social group clustered together in signal space (Fig. 2c). This means that in addition to the individual signature, isolation calls also exhibit a group signature. Earlier work (Knörnschild & von Helversen 2008) located the individual signature in the composite end syllables of isolation calls and there the group signature can be best seen as well (Fig. 3).

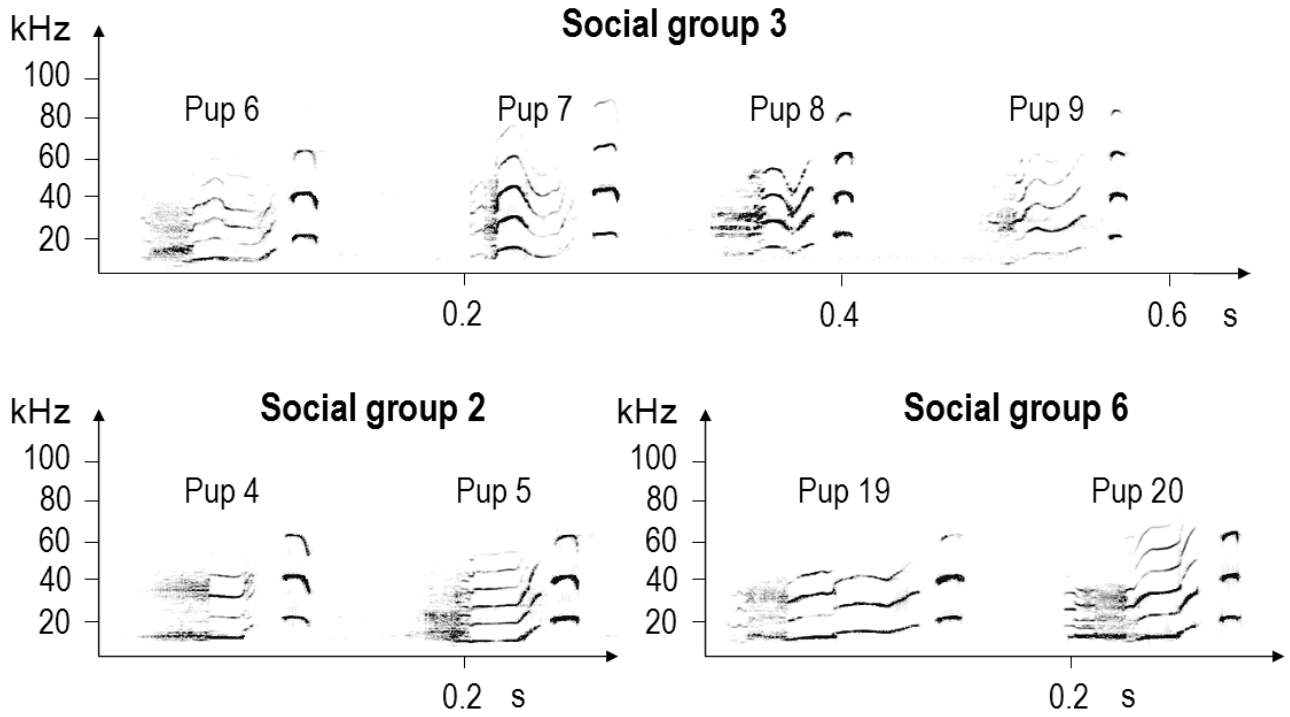


Figure 3: Individual and group signatures in end syllables of isolation calls from pups belonging to three different social groups. Note that even though end syllables are individually distinct, end syllables of pups from the same social group look more similar to each other than to end syllables of pups from other social groups.

4.3 Ontogeny of group signatures in isolation calls

When performing separate DFAs for the two ontogenetic stages (non-volant and volant; 25 pups with 10 calls per stage each) and comparing the Euclidean distance between pups from the same and different social groups, we had similar findings in both ontogenetic stages (Fig. 4). Within group distance was significantly smaller than between group distance for volant pups (Wilcoxon signed rank test for matched pairs: N=6, exact P=0.031) and there was a trend for non-volant pups as well (Wilcoxon signed rank test for matched pairs: N=6, exact P=0.063). To determine how the strength of the group signature changed during ontogeny, we compared the within group distances for both ontogenetic stages. Since Euclidean distances can only be compared within the same signal space, we calculated discriminant functions using the non-volant data and used them to plot both the non-volant and volant data into the same signal space. The within group distances decreased during ontogeny (Wilcoxon signed rank test for matched pairs: N=6, exact P=0.031), which suggests that the group signature becomes more prominent as pups mature.

The two pups belonging to social group 6 (which was excluded from our analyses) are a good example for the development of group signatures during ontogeny. Group 6 originally consisted of only one pup (#20) plus its mother and the harem male. Another pup (#19) from a near-by roost moved in this group once it became volant. This is a rather unusual behaviour for *S. bilineata* and it provided us with a 'natural' experiment – both pups were separated during their non-volant stage and we could monitor how their isolation calls changed when they were together during their volant stage. Figure 4 shows that isolation calls of both pups converged in signal space once they were in the same social group.

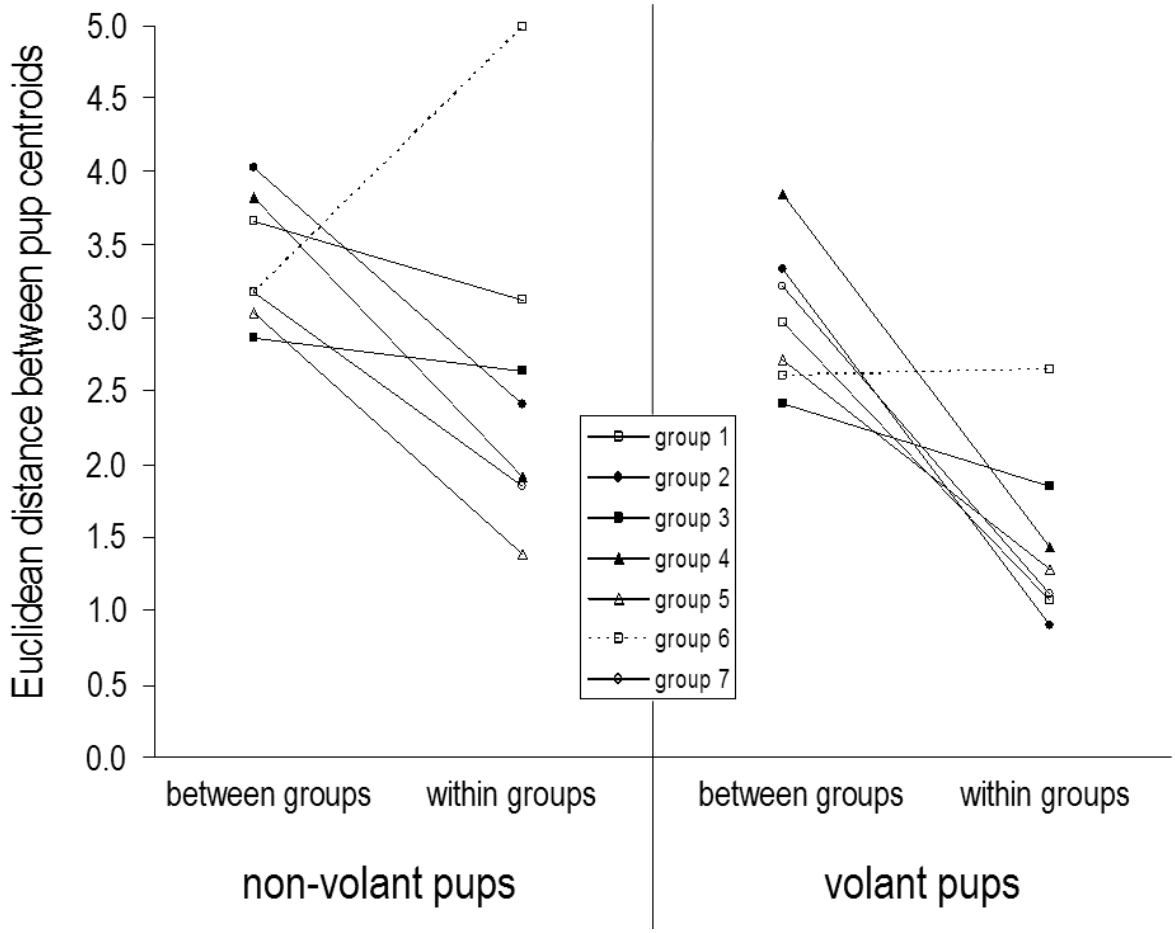


Figure 4: Mean Euclidean distances of pup centroids belonging to different or the same social groups in a two-dimensional signal space defined by the first two discriminant functions. In both ontogenetic stages, pups from the same social group clustered together in signal space. Note the special status of group 6 (see Results).

4.4 Influences of male territorial song on isolation calls

In order to investigate whether call convergence was influenced by more than just the isolation calls of fellow pups, we focused on another vocalization type that pups hear daily throughout ontogeny, the harem males' territorial song. For all social groups, we analysed recordings of territorial songs (Fig. 1b) from the respective harem males. A DFA with five territorial songs of six harem males (one male was the harem male of two different social groups) classified 50% of all songs to the correct individual, which was significantly higher than expected by chance alone (16.67%; Wilcoxon signed-ranks test for matched pairs: N=6, exact P=0.031) and corroborates the findings of an earlier study about individual distinctiveness of territorial songs (Behr et al. 2006).

To compare the distance in signal space between territorial songs of harem males and isolation calls of pups growing up in their respective harems, we used the discriminant functions calculated from the non-volant isolation call data to plot the volant isolation call

data and the territorial song data into the same signal space. Figure 5 shows that territorial songs of harem males are plotted in the vicinity of isolation calls from pups belonging to their harem.

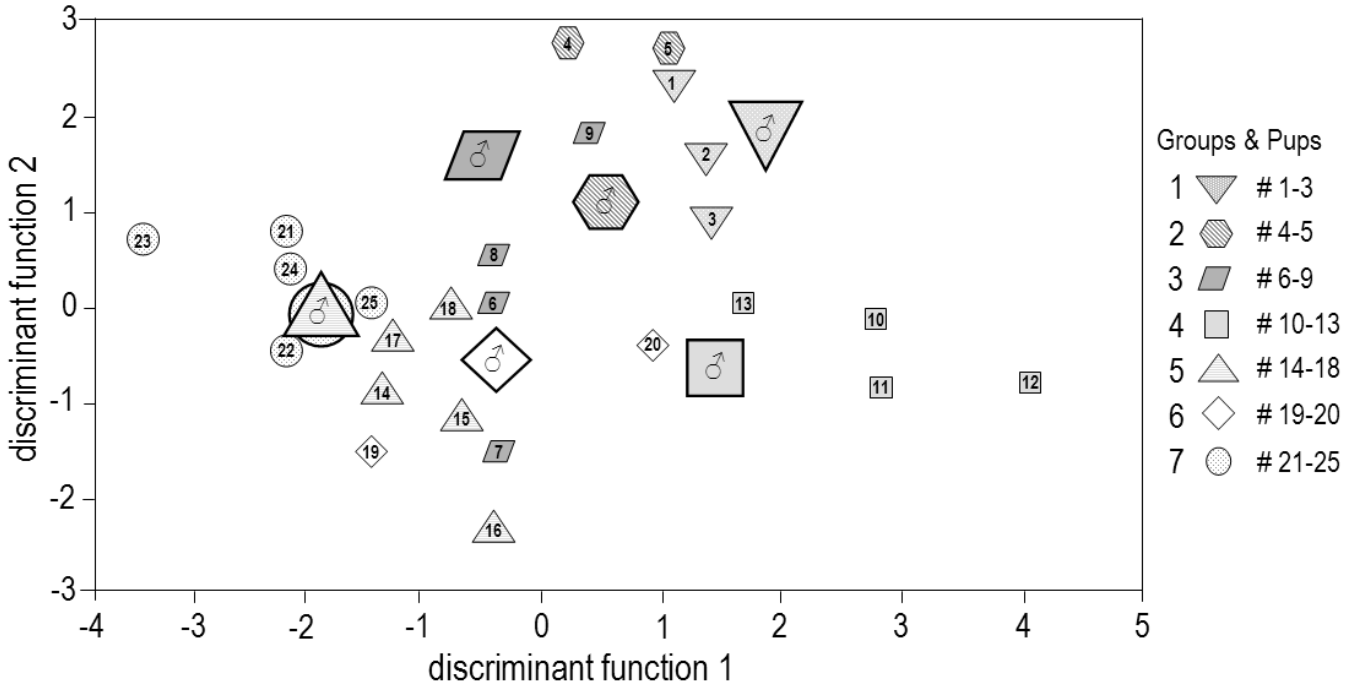


Figure 5: Centroids of isolation calls from volant pups and of territorial songs from their respective harem males plotted in the same two-dimensional signal space (defined by the first two discriminant functions that were calculated using the isolation call data). Harem males clustered in the vicinity of pups from their social group. Note that group 5 and 7 had the same harem male in two consecutive years.

We then compared the Euclidean distances between each pup and its harem male ('own male' distance) and all other males ('alien male' distance). Own male distance was significantly smaller than alien male distance for both ontogenetic stages (two-sample t-test for matched pairs; non-volant pups: t_{23}=-4.470, P<0.0001; volant pups: t_{23}=-7.742, P<0.0001; pup #19 excluded). The own male distance decreased significantly during ontogeny (two-sample t-test for matched pair: t_{23}=-2.364, P=0.027; pup #19 excluded), suggesting that isolation calls of pups not only converge in signal space towards each other but also towards the territorial song of their respective harem male (Fig. 6).

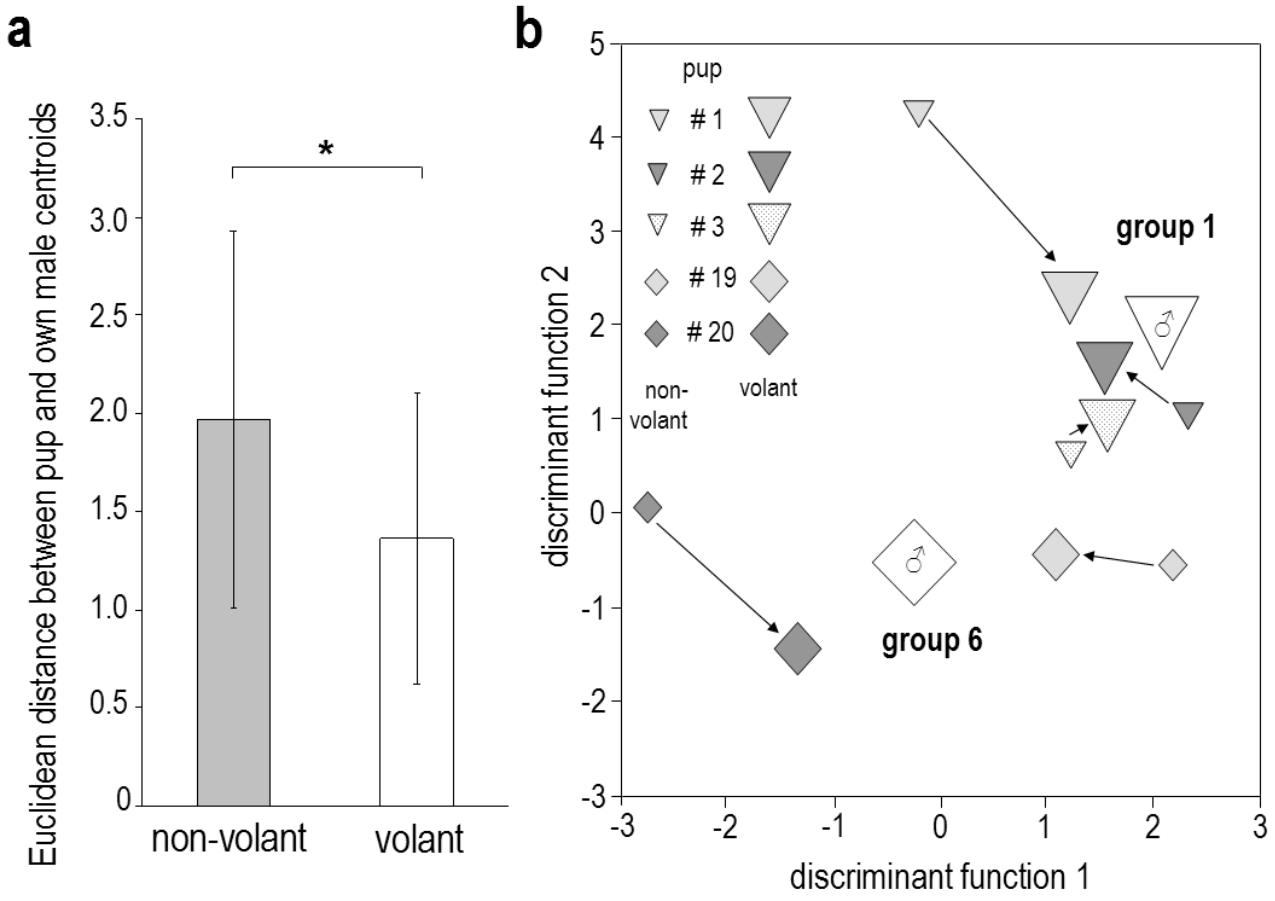


Figure 6: Euclidean distances between pup centroids and their own harem male centroids in a two-dimensional signal space defined by the first 2 discriminant functions (**a**). This distance becomes smaller during ontogeny, illustrating that isolation calls of pups converge not only towards each other but also towards the territorial songs of their respective harem males (**b**). Please note that pup #19 was excluded from the analyses (for reasons see Results).

In total, five pups grew up with a social father that was not their genetic one (pup #4-5 from group 2, pup #6 from group 3, pup #12 from group 4, and pup #25 from group 7). The former two were paternal half-siblings (but their sire was the harem male of group 3) whereas the latter three were completely unrelated to the other pups in their respective group. The isolation calls of these pups converged in signal space towards each other and towards the territorial song of their social father instead of their genetic one, suggesting that social influence instead of genetic determination is driving call convergence in *S. bilineata*.

5 Discussion

Convergence of isolation calls from pups belonging to the same social group occurred both among related and unrelated pups of both sexes. The resulting group signature of isolation

calls became more prominent during ontogeny and was likely influenced by two vocalization types that pups hear on a daily basis: the isolation calls of fellow pups and the territorial song of the respective social father. Our findings are strong evidence for vocal production learning through social modification (instead of *e.g.,* ontogenetic changes due to maturation or shared genes).

Interestingly, vocal convergence of group members occurred in isolation calls, a vocalization type that is under strong selective pressure for individual recognition (Beecher 1989; Kunz & Hood 2000; Wilkinson 2003). Our results indicate that the strength of the individual signature remained unchanged while the group signature became more prominent during ontogeny. This might reflect a balance between two different needs: maintaining individual identity and establishing a group-specific signal at the same time. This contrasts with the only other finding about group signatures in bats, where individual identity was not encoded in the call that conveyed group identity (Boughman 1997).

Of the few studies showing vocal learning through social modification in bats, two focused on signals used in individual recognition between mother and pup (*Rhinolophus ferrumequinum*: Jones & Ransome 1993; *Phyllostomus discolor*: Esser 1994) and one focused on signals used in the context of group cohesion between adults (*Phyllostomus hastatus*: Boughman 1998). Whereas the latter study found evidence for convergence of screech calls among unrelated adult females, we provide evidence for convergence of isolation calls among related and unrelated pre-weaned pups of both sexes. In contrast to other mammals, in which vocal learning of group signatures seems to have evolved in the context of feeding ground defence (Boughman 1998) or cooperative hunting (*Orcinus orca*: Ford 1991; Foote et al. 2006), call convergence of *S. bilineata* pups from the same social group seems to have a different function. Isolation calls seem to function as an acoustical 'social badge' which reliably associates individuals to their natal colony. This could be crucial for young peripheral males that are trying to queue for harem access in their natal colony (Voigt & Streich 2003). Isolation calls could function as a 'password' (*sensu* Feekes 1977) that harem holders utilize to recognize cheaters (*i.e.,* young males trying to queue for harem access in a non-natal colony). This should be beneficial to a harem holder even when pups that have been born in his harem but are not his descendants queue for harem access because these pups are likely to be sired by one of the other harem males in the colony (Heckel & von Helversen 2003). Since all harem males in a colony belong to only few patrilines (Nagy et al. 2007), the harem male might still obtain inclusive fitness benefits. Isolation calls functioning as a social badge might also provide important information for dispersing females which want to avoid mating with full- or half-siblings that have founded new colonies (for female inbreeding avoidance with

male descendants see Nagy et al. 2007). This is supported by our anecdotic evidence that isolation calls are used by adult peripheral males both to appease the harem male and during courtship attempts with females in a newly usurped harem.

Vocal learning can be expected to evolve if associated benefits are difficult to gain without learning. The possible functional significance of vocal learning can consist of individual signatures, social group signatures or population identity (*e.g.,* dialects), depending on the species involved (Kroodsma & Baylis 1982; Janik & Slater 1997; Boughman & Moss 2003). It has been argued by Janik & Slater (1997) that vocal learning can be shaped by both intersexual selection (*e.g.,* female birds prefer elaborate male song) and intrasexual selection (*e.g.,* territorial birds share song types with neighbors). Obviously, these selective pressures need not be mutually exclusive. The benefits associated with vocal learning of group signatures in *S. bilineata* might be shaped by both intrasexual and intersexual selection. Harem males should have a vital interest that only young males with whom they are related queue for harem access. Hence, intrasexual selection could drive call convergence, resulting in a 'password' function of isolation calls. Dispersing females joining an already existing harem should have a great interest in avoiding inbreeding (*e.g.,* joining harems of older siblings), especially because they disperse from their natal colony to avoid inbreeding in the first place (Nagy et al. 2007). Therefore, intersexual selection might drive call convergence as well.

Both intrasexual and intersexual selective pressures described above apply only to male pups, yet we found no difference in call convergence between the sexes. Call convergence among female pups might have evolved because they must learn something first in order to recognize it later (see also Knörnschild et al. 2006 for female participation in vocal babbling behavior). Analogous to birds (Marler and Peters 1982), female *S. bilineata* might have to create or, if mainly innate, reinforce an acoustic template of male vocalizations as a basis for future mate choice decisions. Acoustic isolation experiments are needed to determine whether the auditory template hypothesis (Marler 1976) that has been proposed for song learning in oscine birds might also apply to bats.

Chapter IV

Vocal Imitation of Territorial Songs

1 Abstract

Vocal imitation of complex signals is a rare ability in mammals even though it is prevalent in humans. Our study provides the first evidence that complex vocal imitation occurs in bats. We show that *Saccopteryx bilineata* pups of both sexes learn a complex adult vocalization type *de novo* through imitation, with simple precursor songs developing into genuine renditions. The resemblance of pup renditions to their acoustic model gets more pronounced during ontogeny and is independent of the relatedness between pups and adults, suggesting that auditory input instead of physical maturation or genetic determination is essential for vocal development.

2 Introduction

Vocal imitation is considered to be a key innovation in the evolution of speech (Fitch 2000) which, together with syntax and semantics, is an important component of language (Hauser et al. 2002). Current evidence for non-human vocal imitation is limited to birds, cetaceans, seals, and elephants (Fitch 2000; Hauser et al. 2002; Doupe & Kuhl 1999; Boughman & Moss 2003). It has long been predicted that bats should also be able to imitate complex acoustic signals *de novo* (Janik & Slater 1997) but it has never been demonstrated (Boughman & Moss 2003). Here we report that pups of the bat *Saccopteryx bilineata* learn to imitate a complex vocalization type of adult conspecifics. We recorded vocalizations of free-living pups from different social groups (consisting of one harem male and several females with one pup each) throughout ontogeny and territorial songs of their respective harem males. Territorial songs are complex multi-syllabic vocalizations used in the demarcation of harem territories (Behr & von Helversen 2004). During ontogeny, pups of both sexes first begin to produce precursor songs and later complete territorial songs (Knörnschild et al. 2006). We compared these pup versions with territorial songs of their harem males and tested whether they became more similar towards each other and whether gender or relatedness influenced vocal development.

3 Methods

S. bilineata exhibits an extremely rich vocal repertoire due to its complex social life in a harem-like resource-defence polygyny (Behr & von Helversen 2004; Voigt et al. 2008). We monitored day-roosts with one social group each (consisting of one harem male, one or several lactating females and their offspring) at the Biological Station La Selva in Costa Rica from 2005 to 2007. Individual bats were identified by plastic bands on their forearms (A.C. Hughes Ltd., UK).

We used high-quality ultrasonic recording equipment (400 kHz sampling rate, 12 bit depth resolution; for details see Knörnschild & von Helversen 2008). In total, we recorded 337 territorial songs/precursors of 17 pups belonging to seven different social groups and 57 territorial songs of the six respective harem males (one male was present and recorded during two seasons). We analysed 5-50 territorial songs/precursors from each pup at two ontogenetic stages (2-6 and 7-10 weeks old) and 5-13 territorial songs from each harem male.

Vocalizations were analysed in Avisoft-SASLab Pro (v4.1, R. Specht, Germany). Territorial songs/precursors are multi-syllabic; since all syllables other than the composite end syllables (consisting of a noisy and a tonal part) are variable and can also occur in other vocalizations (*e.g.,* isolation calls and babbling bouts; see Knörnschild et al. 2006), we focused on end syllables. Measurements of the first harmonic were taken from spectrograms. We measured several temporal (duration, interval between syllables, distance from start to maximum amplitude) and spectral parameters (peak, minimum, and maximum frequency and bandwidth at five locations equally distributed over the length of the syllable and averaged over the entire syllable). Parameters belonging to the same syllable part were averaged for every territorial song/precursor and combined into principal components. We performed discriminant function analyses (DFAs) with the obtained principal components. The distance between centroids (*i.e.,* the canonical mean of all vocalizations per individual) in signal space is a good indicator of similarity (Boughman 1998; Knörnschild et al. 2007), with similarly sounding individuals clustering together. We utilized the Euclidean distance between centroids to compare territorial songs of harem males with territorial songs/precursors uttered by pups during the two different ontogenetic stages. We calculated discriminant functions with the data from the first ontogeny stage and then mapped the remaining data into the same signal space. This enabled us to compare all centroids distances simultaneously. All statistical tests were conducted in SPSS (v11.5, SPSS Inc., Chicago, U.S.A.).

We employed eleven microsatellite loci for paternity analysis (Heckel et al. 2000) and assigned parents for 16 of 17 pups (Heckel & von Helversen 2003). Additionally to the

genotypes of the behaviourally assigned mothers (*N*=14; one was present in two seasons, one was not sampled genetically) and of all adult males present during this study (*N*=10) we also considered genotypes of adult males sampled in the study area in former years (*N*=207) for paternity analysis with Cervus 3.0 (Kalinowski et al. 2007). Genetical assignment of mothers (95% confidence, zero mismatches, *N*=15) concurred with the former behavioral assignment. Paternity for the known mother-offspring pairs was assigned in 14 of 15 cases with 95% confidence and zero mismatches (*N*=13) or at most one mismatch with one father (*N*=1). The fathers of two pups remained undetermined, including the pup for whose mother we did not obtain a DNA sample.

4 Results

During ontogeny, precursor songs gradually began to resemble adult territorial song (Fig. 1). Precursor songs were typically composed of territorial song end syllables (a stereotypic syllable consisting of a noisy and a tonal part) embedded in isolation calls and, later, in babbling bouts. During babbling, pups mix renditions of all adult vocalization types into long vocalization bouts, a behaviour probably supporting the acquisition of the species' complex vocal repertoire (Knörnschild et al. 2006).

The percentage of end syllables per vocalization increased significantly as pups matured (t-test for matched pairs: t_{16}=-3.290, *P*=0.005). Differences between pups and harem males were significant early in ontogeny (t-test: t_{22}=-3.219, *P*=0.004) but not later (t-test: t_{22}= -0.932, *P*=0.362), illustrating that precursor songs became more similar to their model.

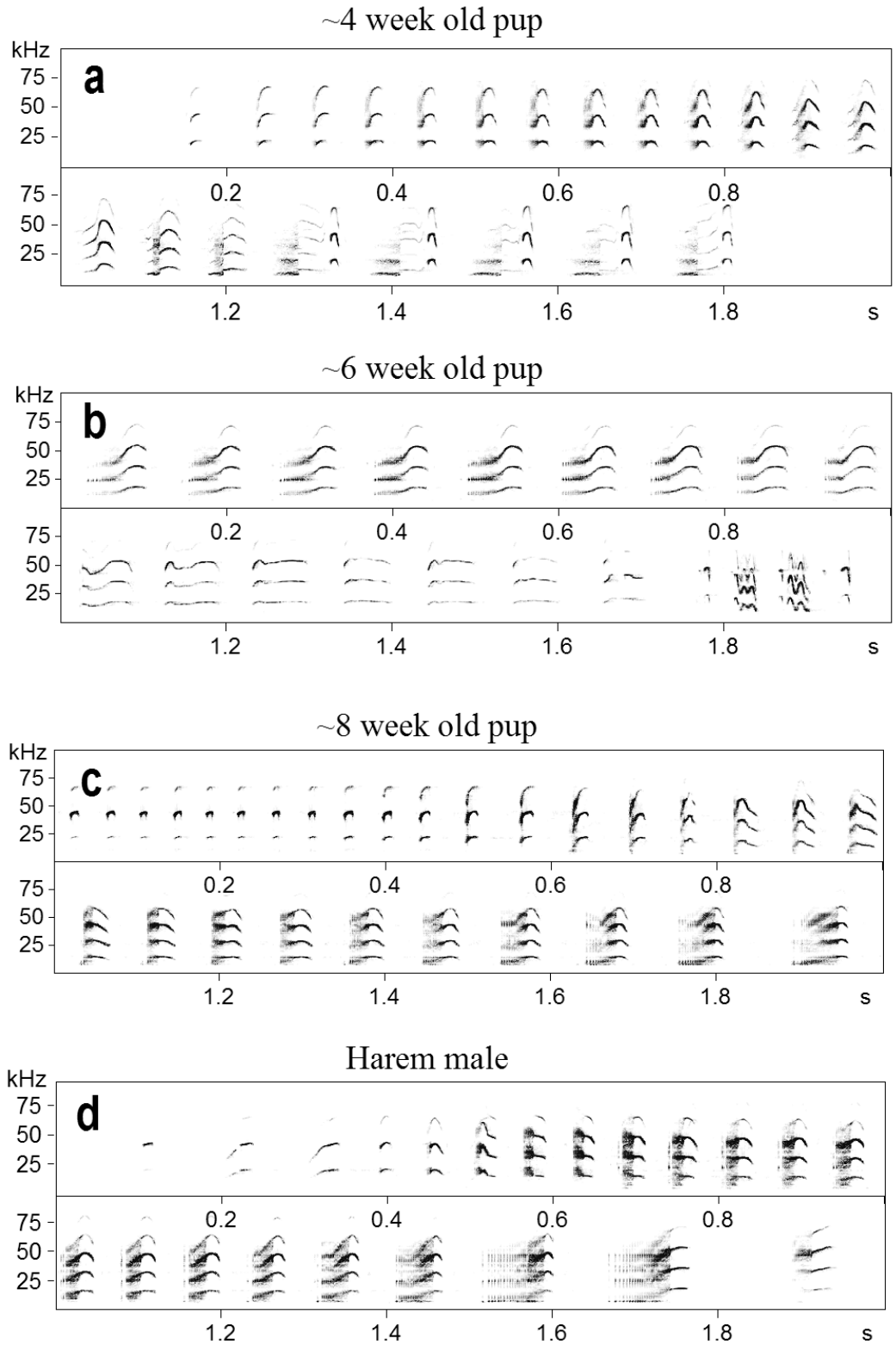


Figure 1: Sonograms of two precursor songs (**a**-**b**) and one complete territorial song (**c**) produced by one female pup at different ages and of a territorial song produced by the respective adult harem male (**d**). During ontogeny, territorial song end syllables were first produced within isolation calls (**a**, 0.35-0.85 s) and later during babbling bouts (**b**, 0.0-1.0 s). Shortly before weaning, pups produced complete territorial songs (**c**) which closely resembled adult territorial song (**d**). Sonograms were created using a 1024 point FFT and a Hamming window with 75 % overlap.

As an indicator of acoustical similarity between individuals we used the Euclidean distance between centroids (the canonical mean of all vocalizations per individual) in a signal space based on the acoustic parameters of end syllables. Similarly sounding individuals cluster together. We compared the Euclidean distances between each pup and its harem male and all other males. Pups always clustered significantly closer to their own harem male than to other males in the analysis (t-test for matched pairs; ontogeny stage 1: t_{16}=-2.963, P=0.009; ontogeny stage 2: t_{16}=-4.438, P<0.0001).

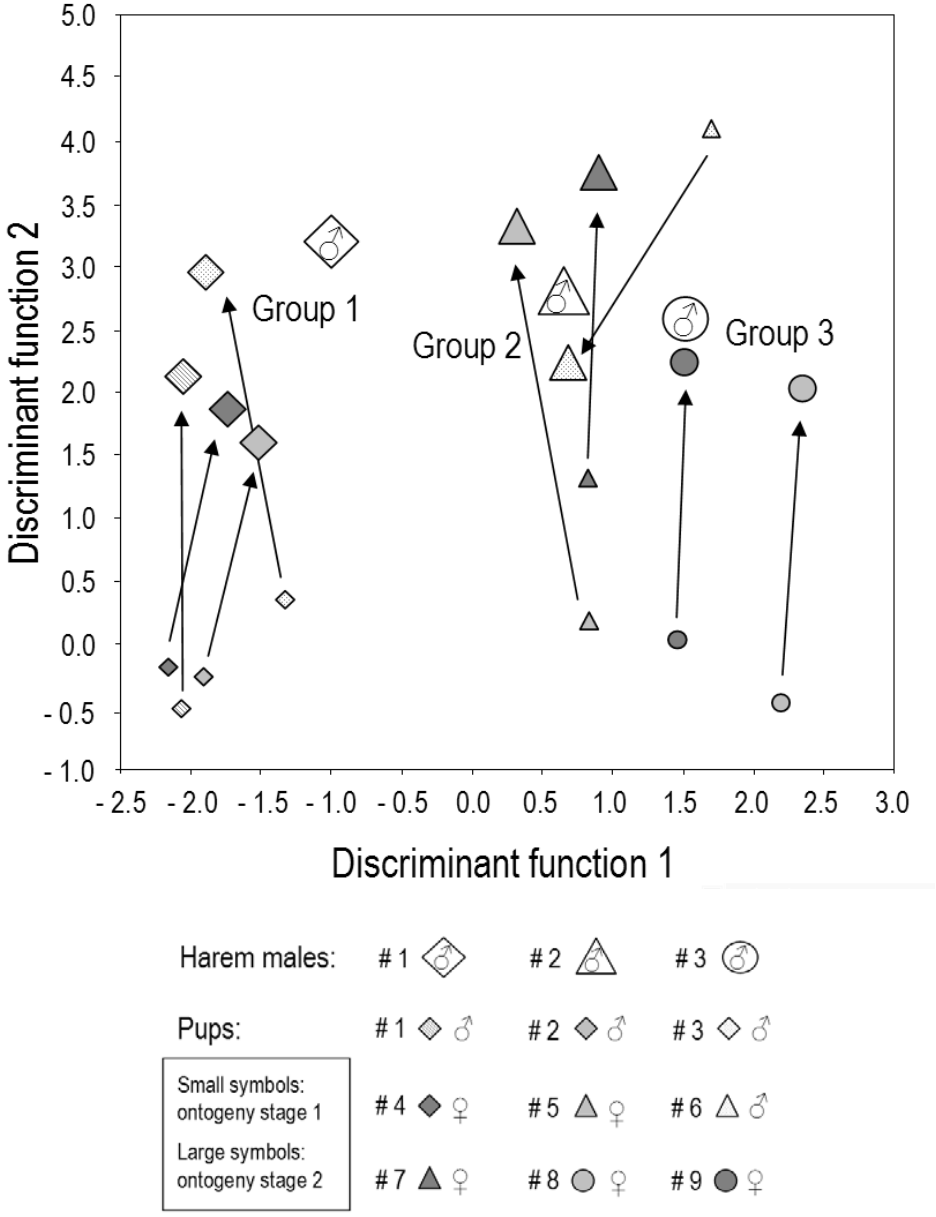


Figure 2: Centroids of territorial songs from pups at two different ontogenetic stages and from their respective harem males plotted in the same two-dimensional signal space. The Euclidean distance between pups and their respective harem males became significantly smaller during ontogeny, illustrating that the precursor/territorial songs of pups converged towards the territorial songs of their respective harem males. This convergence occurred independent of pup gender or relatedness towards the harem male. For clarity, only three of the seven social groups are shown.

The distance between pups and their harem males decreased significantly during ontogeny (t-test for matched pairs: t_{16}=4.304, P=0.001), showing that pup precursor/territorial songs converged towards the territorial song of their respective harem male (Fig. 2). This convergence occurred independently of pup gender (t-test: t_{14}=-0.048, P=0.962; 9 females, 7 males, 1 unsexed) or relatedness towards the harem male (t-test: t_{14}=0.875, P=0.397; 8 pups respectively sired or not sired by the harem male, 1 not sampled).

5 Discussion

Our data shows that pups of both sexes learn adult territorial songs *de novo* by traversing from simple precursor songs to genuine renditions. Pup renditions strongly resembled the territorial song of their harem males independent of the relatedness between pups and males and this resemblance became more pronounced during ontogeny, suggesting that auditory input instead of genetic determination or physical maturation is crucial for vocal development. Vocal imitative abilities in animals are typically more pronounced in males and often shaped by sexual selection (Fitch 2005). In *S. bilineata*, female pups imitate adult territorial songs as readily as male pups, even though only adult males utter territorial songs. Like some birds, female *S. bilineata* might have to create or reinforce an acoustic template of male vocalizations as a basis for future mate choice decisions (Doupe & Kuhl 1999). The unusual distribution pattern of vocal imitation across different taxa suggests a multiple convergent evolution in the animal kingdom (Fitch 2000; Hauser et al. 2002; Doupe & Kuhl 1999; Boughman & Moss 2003). Our finding that bats are capable of imitating complex acoustic signals will be beneficial for comparative studies on neural specializations or the functional significance of vocal imitation.

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Zusammenfassung

Durch vokales Lernen können sowohl Gebrauch und Verständnis eines Signals als auch die Struktur des Signals selbst verändert werden. Während das so genannte ‚vokale Kontextlernen' (d.h. die Bedeutung des Signals oder der Zusammenhang, in dem es benutzt wird, werden erlernt) bei Vögeln und Säugetieren weit verbreitet ist, ist das so genannte ‚vokale Produktionslernen' (d.h. das Neuerlernen eines Signals oder Modifizieren seiner Struktur) auffallend selten. Vokales Produktionslernen - also die Fähigkeit, Lautäußerungen nachzuahmen - ist ein essentieller Bestandteil der menschlichen Sprachfähigkeit, aber dennoch scheint keine andere Primatenart, nicht einmal die Menschenaffen, dazu fähig zu sein. Außer bei Menschen kommt vokales Produktionslernen nur bei einigen Vogelordnungen (Singvögel, Papageien und Kolibris), Walen, Delphinen, Robben, Elefanten und Fledermäusen vor. Das unregelmäßige Vorkommen von vokalem Produktionslernen innerhalb des Tierreichs lässt auf eine mehrfache konvergente Evolution dieser Fähigkeit schließen, was vergleichende Studien an verschiedenen Taxa besonders lohnenswert macht. Die anatomischen und neuronalen Anpassungen, welche vokales Produktionslernen möglich machen, können über verschiedene Tiergruppen hinweg verglichen werden, nicht nur um den Selektionsdruck auf komplexe akustische Kommunikationssysteme zu verstehen, sondern auch um zu begreifen, wie und warum menschliche Sprache evolviert ist.

Die vokale Flexibilität, die Fledermäuse bei der Echoortung zeigen, wird als eine Präadaptation für vokales Produktionslernen angesehen. Allerdings ist nur für drei Fledermausarten belegt, durch Lernen die akustische Struktur bereits existierender Signale zu modifizieren. In der vorliegenden Arbeit beschreibe ich die Ontogenie des Lautrepertoires der Sackflügelfledermaus *Saccopteryx bilineata*. Diese Fledermausart besitzt ein großes Repertoire von Soziallauten, was wahrscheinlich durch ihr komplexes Sozialsystem, einer haremähnlichen Ressourcen-Verteidigungs-Polygynie, bedingt wird. Ich zeige, dass *S. bilineata* Jungtiere nicht nur auffallend komplexe Isolationsrufe äußern, um mit ihren Müttern zu kommunizieren, sondern auch vokales Babbelverhalten zeigen und zum vokalen Produktionslernen durch Modifikation bereits existierender Signale und durch Imitation neuer Signale fähig sind. Daher stellt *S. bilineata* einen idealen Modellorganismus für die Untersuchung von vokalem Produktionslernen bei Fledermäusen dar.

Im Gegensatz zu anderen Fledermausarten waren die Isolationsrufe von *S. bilineata* Jungtieren mehrsilbig und ihre Endsilben trugen eine individuelle Signatur. Durch Playback-Experimente konnte gezeigt werden, dass Fledermausmütter ihre Jungtiere allein anhand der

Isolationsrufe identifizieren konnten, was die statistischen Hinweise auf eine individuelle Signatur bestätigt. Jungtiere hingegen unterschieden im Experiment nicht zwischen den Echoortungsrufen ihrer Mütter und der fremder Weibchen. Daher scheint die akustische Mutter-Kind-Erkennung allein von den Müttern geleistet zu werden.

Jungtiere produzierten auch mehr oder weniger korrekte Versionen aller bekannten adulten Lautäußerungen, die zusammen mit Silben aus Isolationsrufen in so genannte ‚Babbelphasen' gemischt wurden. Dieses Babbeln schien unabhängig von einem eindeutigen sozialen Kontext aufzutreten, könnte aber dazu dienen, mütterliche Zuwendung auszulösen. Jungtiere beiderlei Geschlechts wurden beim Babbeln beobachtet, obwohl nur adulte Männchen alle Lautäußerungen benutzten, die während des Babbelns produziert wurden. Dies ist der erste Beleg für Babbelverhalten in einem nicht zu den Primaten gehörenden Säugetier. Möglicherweise ist Babbelverhalten während der Ontogenie notwenig, damit sich Jungtiere das komplexe adulte Lautrepertoire aneignen können.

Vergleichende akustische Analysen der Isolationsrufe verschiedener Jungtiere zeigten, dass Isolationsrufe zusätzlich zu der individuellen Signatur auch eine Gruppensignatur trugen. Diese Gruppensignatur wurde während der Ontogenie der Jungtiere immer ausgeprägter. Genetische Effekte spielten für beide Signaturtypen keine Rolle. Im Verlauf der Ontogenie wurden Isolationsrufe zwei Lautäußerungen immer ähnlicher, welche die Jungtiere täglich hörten: zum einen den Isolationsrufen der anderen Jungtiere in der sozialen Gruppe, zum anderen den Territorialgesängen des jeweiligen Haremmännchens. Diese soziale Modifikation der Isolationsrufe ist ein Beleg für vokales Produktionslernen. Isolationsrufe fungieren als Erkennungszeichen, durch welches sich Individuen zuverlässig ihrer Geburtskolonie zuordnen lassen.

Jungtiere beiderlei Geschlechts lernten einen komplexen adulten Vokalisationstyp, den Territorialgesang, durch vokale Imitation, was einen weiteren Beleg für vokales Produktionslernen darstellt. Aus einfachen Vorläufergesängen entwickelte sich eine perfekte Wiedergabe des adulten Territorialgesangs. Die Ähnlichkeit der Jungtier-Gesangsversionen zu ihren akustischen Vorbildern wurde während der Ontogenie immer deutlicher und trat gleichermaßen zwischen verwandten und unverwandten Tieren auf. Dies deutet darauf hin, dass die Entwicklung von Lautäußerungen bei *S. bilineata* von auditorischen Reizen abhängt und nicht allein von körperlicher Reifung oder genetischer Determination. Dieses Ergebnis ist der erste Beweis, dass Fledermäuse komplexe akustische Signale durch Imitation erlernen können.

Lebenslauf

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Erklärung zur Dissertation

Hiermit erkläre ich, dass ich die vorliegende Dissertation "Vocal Repertoire Ontogeny in *Saccopteryx bilineata* – Evidence for Vocal Learning in a Bat" selbstständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.
Die Dissertation wurde nicht schon als Diplom- oder ähnliche Prüfungsarbeit verwendet.

Bayreuth, den 17.12.2008

Mirjam Knörnschild