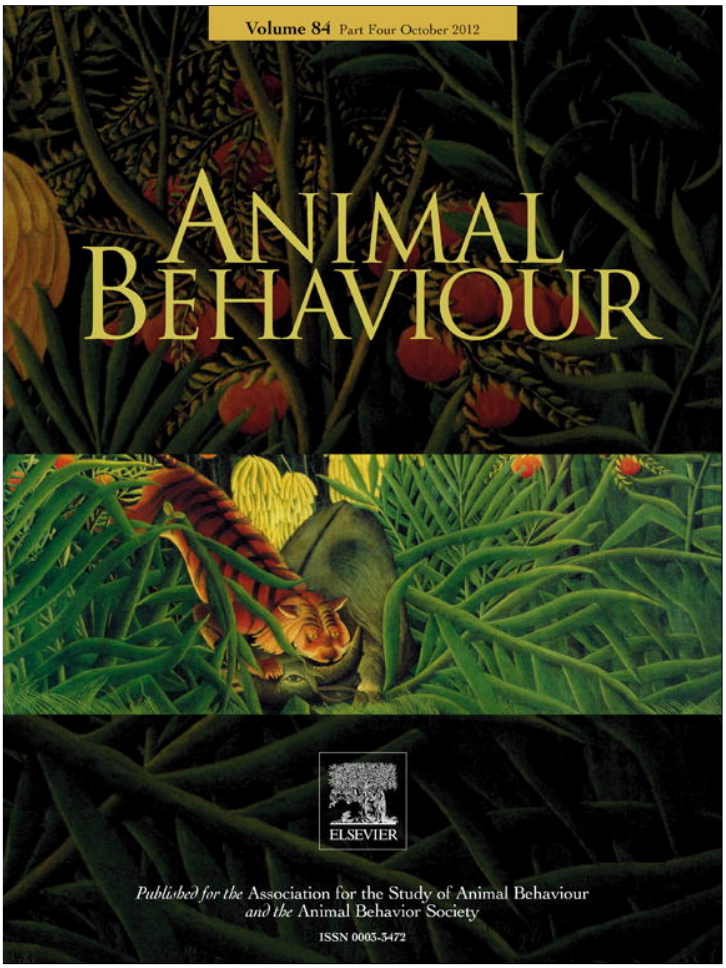

Animal Behaviour 84 (2012) 761–769

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Learned vocal group signatures in the polygynous bat *Saccopteryx bilineata*

Mirjam Knörnschild [a,*], Martina Nagy [b], Markus Metz [a], Frieder Mayer [b], Otto von Helversen [c]

[a] *Institute for Experimental Ecology, University of Ulm, Ulm, Germany*
[b] *Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany*
[c] *Institute for Zoology, University of Erlangen-Nuremberg, Erlangen, Germany*

ARTICLE INFO

Article history:
Received 21 March 2012
Initial acceptance 13 April 2012
Final acceptance 18 June 2012
Available online 2 August 2012
MS. number: 12-00230R

Keywords:
call convergence
greater sac-winged bat
horizontal learning
peer influence
Saccopteryx bilineata
vocal learning

Vocal group signatures facilitate group cohesion or the exclusion of nongroup members and thus greatly affect the social system of any given species. This is especially significant for highly mobile animals such as bats. The greater sac-winged bat, *Saccopteryx bilineata*, lives in a harem-based resource defence polygyny with patrilineal kin groups and female-biased natal dispersal. Pups of both sexes produce isolation calls to elicit maternal care. We analysed isolation calls from 25 pups born in seven different social groups in search of vocal signatures. In addition to a constant individual signature, isolation calls exhibited a group signature that became more prominent during ontogeny. Call convergence of fellow pups was independent of relatedness among pups and not driven by maturation effects, showing that the group signature was acquired through social modification, a form of vocal production learning. Behavioural observations of free-living bats indicated that isolation calls were used by adult males to appease more dominant males and to court unfamiliar females. The learned group signature in isolation calls may function as a 'password' that reliably associates individuals with their natal colony. This, in turn, could facilitate male harem acquisition and female inbreeding avoidance in the polygynous *S. bilineata*. The flexibility inherent in the vocal-learning process guarantees that crucial information can be promoted even under shifting social circumstances.

Group-living animals often negotiate social interactions with accompanying vocalizations that may encode information on individual identity or social group affiliation (Bradbury & Vehrencamp 1998). Vocal signatures are either innate or acquired through vocal production learning (Janik & Slater 1997). Vocal production learning is defined as the imitation of new signals or the social modification of existing signals; the latter seems to be more prevalent in mammals (Janik & Slater 1997, 2000; Boughman & Moss 2003). Vocal production learning 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 (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).

Learned group signatures normally originate from social modification (sensu Boughman & Moss 2003), that is, existing vocalizations of different individuals converge because they are modified in response to social interactions with one another. Signal convergence leads to increased acoustic similarity between signallers (Boughman & Moss 2003). Vocal group signatures can be shared with either 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 aggressive or affiliative. Examples of learned signal convergence among rivals include many species of territorial songbirds (Kroodsma & Baylis 1982) but no mammals so far, whereas learned signal convergence among group members has been found in both birds and mammals (Boughman & Moss 2003; Tyack 2008) and is sometimes termed horizontal learning (Bertin et al. 2007).

Call convergence among group members may have multiple implications ranging from group cohesion under highly mobile circumstances (Ford 1991; Boughman 1998; Hile & Striedter 2000) and affiliative interactions with social partners (Vehrencamp et al. 2003) to the exclusion of nongroup members. In the latter scenario, a vocal group signature functions as a badge or password (summarized in Tyack 2008) that allows access to limited resources shared among group members. In contrast to innate vocal group signatures, learned ones offer more flexibility, which is especially important when individuals disperse to a new social group (Wright & Wilkinson 2001), form only temporary associations (Janik & Slater 1998) or when the vocal signature not only encodes the social origin but also the current social affiliations of an individual (Sewall 2009). Generally

* Correspondence: M. Knörnschild, Institute for Experimental Ecology, University of Ulm, Albert-Einstein-Allee 11, 89081 Ulm, Germany.
E-mail address: mirjam.knoernschild@uni-ulm.de (M. Knörnschild).

0003-3472/$38.00
http://dx.doi.org/10.1016/j.anbehav.2012.06.029

speaking, learned vocal group signatures have an adaptive value, whereas innate group signatures may be adaptive or simply a by-product of genetic similarities among group members that is not used for discrimination (Townsend et al. 2010).

In bats, one species is known to use learned vocal group signatures to mediate group cohesion during foraging (Boughman 1998), but the screech call encoding group identity in the bat *Phyllostomus hastatus* does not additionally encode individual identity. Individual and group signatures are not mutually exclusive per se (Nousek et al. 2006); yet, to our knowledge, no study on joint individual and group signatures in vocal-learning bats exists so far. Even though bats are the second largest mammalian order, fewer than 10 species have been shown to be capable of vocal production learning (Janik & Slater 1997; Boughman & Moss 2003; Wilkinson 2003). Vocal production learning is probably much more widespread in bats than currently thought; however, their elusive nocturnal life makes it difficult to work with most wild bats and only a small fraction of all species do well in captivity. In this study, we worked with a free-living Neotropical bat species capable of vocal production learning (Knörnschild et al. 2010) to investigate the development and acquisition mechanisms of individual and group signatures in bats.

The insectivorous greater sac-winged bat, *Saccopteryx bilineata*, lives in a polygynous mating system in which territorial males defend harems containing up to eight females and their respective offspring. Day-roost colonies can contain up to 12 harem territories belonging to different harem males (reviewed in Voigt et al. 2008). Young males (i.e. nonharem males) normally queue for harem access in their natal colony (Voigt & Streich 2003) or may establish a new colony elsewhere. Colonies have a patrilineal structure and females in a colony are unrelated owing to female-biased natal dispersal (Nagy et al. 2007). Since males are unable to monopolize females sexually, not all pups born in their harems must be their descendants (Heckel et al. 1999). *Saccopteryx bilineata* exhibits an unusually rich behavioural repertoire comprising visual, olfactory and acoustic displays (reviewed in Voigt et al. 2008). For most vocalization types, the distinct behavioural context in which they are uttered is known (Behr & von Helversen 2004; Knörnschild & von Helversen 2008).

We studied the development and acquisition of vocal signatures in isolation calls, a common vocalization type produced by bat pups during ontogeny. In *S. bilineata*, isolation calls are uttered primarily by pups to elicit maternal care (Knörnschild & von Helversen 2008) but we had anecdotal evidence that adult males produce isolation calls under certain conditions as well. Isolation calls of *S. bilineata* are the most complex bat isolation calls studied to date on account of their length (1–2 s) and multisyllabic structure (up to 30 simple and composite syllables in total). Isolation calls of different pups are individually distinct and most signature information is encoded in the composite end syllables (Knörnschild & von Helversen 2008).

In this study, we investigated the ontogeny of the individual signature in isolation calls of *S. bilineata* pups. Moreover, we tested whether a vocal signature encoding social group affiliation was present in isolation calls. We hypothesized that the group signature was acquired by vocal production learning and tested this by determining whether social effects influenced the vocal group signature to a greater extent than genetic or maturation effects.

METHODS

Study Site and Animals

We conducted sound recordings at the Biological Station La Selva in Costa Rica (10°25′N, 84°0′W) during three consecutive summers (June–August in 2005–2007). In total, seven different social groups of *S. bilineata* were monitored and recorded in their day-roosts. Each of our day-roosts contained only one social group (i.e. harem) that consisted of one harem male, several lactating females and their respective offspring (Appendix Table A1). All bats were habituated to the presence of human observers in the day-roost, enabling us to conduct sound recordings and behavioural observations without noticeable disturbance. We individually identified adult bats by plastic bands on their forearms (A.C. Hughes Ltd., U.K., size XCL). Nonvolant 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. The banding procedure is well established and seems to have no negative effects on the bats; banded bats behave normally and do not show signs of physical constraint (Heckel et al. 1999). Bats were captured with mist nets (Avinet Inc., Dryden, NY, U.S.A.), separately kept in homemade cylindrical soft mesh cages (diameter: 20 cm; height: 30 cm; fabric: polyester) and processed at the capture site. Bats were sexed and banded. For genetic analysis, we used a biopsy punch to take a tissue sample 4 mm in diameter from the bats' wing membrane (plagiopatagium). The resulting hole in the plagiopatagium does not impede flight and heals completely within 4 weeks. Each bat was kept for a maximum of 30 min and released at the capture site. Additional behavioural observations with simultaneous sound recordings were made at La Selva Biological Station, Santa Rosa National Park (10°50′N, 85°37′W) and Curú Wildlife Sanctuary (09°47′N, 85°04′W) in Costa Rica (July–August 2007–2008, January–February 2009, February–April and September 2010) to investigate the use of isolation calls by adult male *S. bilineata*. All field work was approved by the Costa Rican Ministerio del Ambiente y Energía (MINAE).

Paternity Analysis

We employed 11 highly polymorphic microsatellite loci for paternity analysis (Heckel et al. 1999, 2000) and assigned parents as described in Heckel & von Helversen (2003). Paternity analysis was performed for 23 of 25 pups in the study. Additionally to the genotypes of the behaviourally assigned mothers ($N = 16$; five mothers each had one pup in 2 consecutive years, one mother had one pup in 3 consecutive years) 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 11 microsatellite loci and each animal was genotyped at least at 10 loci. All behaviourally assigned mothers were also assigned genetically with 95% confidence and zero mismatches ($N = 21$) or one mismatch at most ($N = 2$). Paternity for the known mother–offspring pairs was assigned in 22 of 23 cases, with 95% confidence and zero mismatches ($N = 19$) or at most one mismatch with one of the parents ($N = 3$). The father of one pup remained undetermined.

Sound Recordings and Analysis

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 were recorded (Appendix Table A1) throughout ontogeny. Behavioural observations verified the identity of the calling pups. We analysed 20 isolation calls from each pup at two ontogenetic stages (nonvolant and volant; 10 calls each). To minimize temporal dependence among vocalizations, we analysed only one isolation call per pup and recording day.

We used Avisoft-SASLab Pro v4.1 (R. Specht, Berlin, Germany) for acoustic analysis. 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. Isolation calls were multiharmonic but we used only the first harmonic (fundamental frequency) for measurements because it normally contained most of the sound energy. Since isolation calls are multisyllabic vocalizations, measurements were taken separately for each syllable type/part (sensu Knörnschild & von Helversen 2008). We visually distinguished four different syllable types/parts in isolation calls (Fig. 1). Isolation calls began with variable syllables (vs) that gradually merged into composite end syllables that were each followed by short stereotypic syllables (ss). The composite end syllables consisted of a noisy and a tonal part (nc and tc part). Each syllable type/part was composed of syllables similar in shape. For each syllable type/part, 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 (1) five different locations that were distributed equally over the entire length of the syllable and (2) 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 acoustic parameters per syllable. Acoustic parameters of syllables belonging to the same syllable type/part were averaged for every isolation call. Since we had four different syllable types/parts, we used a total of 152 acoustic parameters to describe each isolation call.

We combined the acoustic parameters into principal components using a principal component analysis (PCA) with varimax rotation. We performed separate PCAs for different syllable types/parts to fulfil KMO and Bartlett's test criteria. In total, we obtained 21 principal components with eigenvalues greater than one (vs: five PC explaining 87.6% of variance; nc: four PC explaining 83.2% of variance, tc: seven PC explaining 85.7% of variance; ss: five PC explaining 89.4% of variance). The principal components were used in discriminant function analyses (DFAs) that allowed us to separate individuals optimally in a multidimensional signal space. The principal components included in the DFAs came from four different PCAs (one for each syllable type/part) and were included simultaneously. We used both a subset-validation and a 'leave-one-out-cross-validation' procedure. The subset validation procedure randomly assigned calls to a 'training' set and a 'test' set (50% of all calls per set) and used the training set to calculate discriminant functions with which the test set was then classified. The leave-one-out-cross-validation procedure classified each call based on discriminant functions established with all calls except the call being classified. The latter procedure led to a higher classification success because more calls were available for establishing the discriminant functions. We calculated separate DFAs for both ontogenetic stages to test for an individual signature in isolation calls. We estimated the significance of the classification success by using two-tailed binomial tests (following Mundry & Sommer 2007). Additionally, we used a paired *t* test to compare the classification success for each pup between ontogenetic stages.

The distance between centroids (i.e. mean canonical score for every individual) in signal space is a good indicator of acoustic similarity (Boughman 1998; Knörnschild et al. 2007, 2010), with similarly sounding individuals clustering together. We used all isolation call data (pooled over both ontogenetic stages) to calculate the squared Mahalanobis distance between centroids of 25 pups in a 21-dimensional signal space defined by the discriminant functions to investigate whether sex, genetic relatedness (shared maternal or paternal genes) or social group affiliation influenced isolation call variation. For each pup, we calculated distances between itself and (1) individuals of the same or opposite sex, (2) maternal/paternal half-siblings or unrelated pups, (3) pups from the same or different social groups. We compared these distances using paired *t* tests. Subsequent sequential Bonferroni corrections were applied (following Holm 1979). Additionally, we performed a permutated DFA (1000 permutations, level of test factor: 7 [social groups]; level of control factor: 25 [pups]; for details see Mundy & Sommer 2007) on all isolation call data (pooled over both ontogenetic stages) to test whether there was a vocal group signature in isolation calls. The permutated DFA (pDFA) enabled us to calculate the influence of social group affiliation on isolation call variation while controlling for the fact that each pup was represented by more than one isolation call in our analysis (Mundry & Sommer 2007).

We also used the squared Mahalanobis distance between centroids to compare the pups' vocal development during both ontogenetic stages (nonvolant and volant pups). We calculated discriminant functions defining the signal space with the nonvolant data and then used 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 (Boughman 1998; Knörnschild et al. 2010) and to monitor how the vocal group signature developed as the pups matured. We also applied this procedure to test whether isolation calls of pups converged because of maturation effects towards a 'species mean' (i.e. the centroid of all isolation calls in the analysis) by plotting the species mean into the same signal space as the isolation call data for nonvolant and volant pups (Knörnschild et al. 2010). Additionally, we performed a MANOVA to test whether pups' sex and relatedness (shared maternal or paternal genes) influenced the distance between fellow pups in both ontogenetic stages and the observed call convergence during ontogeny. Call convergence was estimated

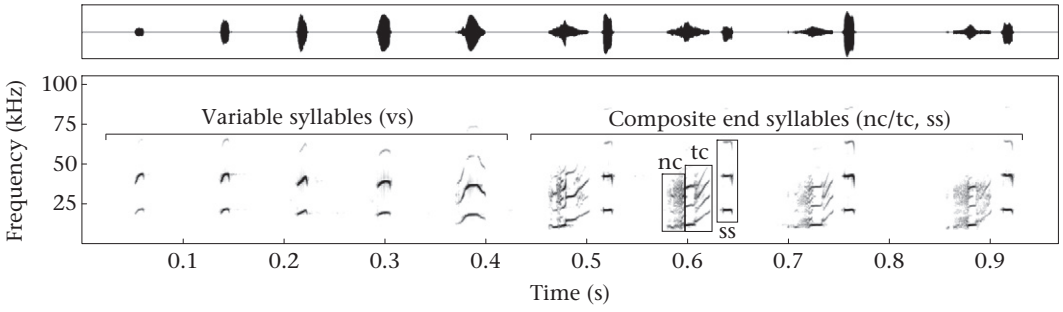

Figure 1. Oscillogram and sonogram of an isolation call from a female pup (ID 1). Isolation calls began with variable syllables (vs) that gradually merged into composite end syllables followed by short stereotypic syllables (ss). In total, four different syllable types or parts were distinguished (vs syllables, nc and tc parts of composite end syllables and ss syllables). Sonograms were created using a 1024-point FFT and a Hamming window with 75% overlap.

by calculating the difference between two distances for each pup: the mean distance between a pup and its fellow pups or the distance between a pup and the species mean in ontogeny phase 1 (= 'distance 1') and in ontogeny phase 2 (= 'distance 2'). Thus, 'distance 1' minus 'distance 2' equalled the ontogenetic call convergence towards fellow pups or towards the species mean.

Behavioural observations with simultaneous sound recordings enabled us to investigate isolation call production in adult male *S. bilineata*. We monitored adult males during courtship displays and during aggressive encounters with rival males and determined whether and in which situation isolation calls were produced. We observed adult harem males ($N = 10$) that courted both familiar females and newly dispersed, that is, unfamiliar, females. We also observed adult nonharem males ($N = 8$) that had two different types of aggressive encounters with resident harem males: encounters were either resolved without a fight or they escalated. Conducting sound recordings during these behavioural observations enabled us to identify the social context in which isolation calls were used by adult males. Ad libitum focal animal sampling (sensu Altmann 1974) was applied until we obtained at least one clearly identified behavioural interaction of each focal male courting (1) a familiar female and (2) an unfamiliar female, and engaging in agonistic interactions with a rival male that (3) ceased its aggression in one situation and (4) escalated its aggression in another. Two behavioural situations (1, 3) were very common and we were able to document them more than 20 times for each focal male. However, the other two behavioural situations (2, 4) were much rarer and we were able to document them only once or twice for each focal male. Each documented occurrence of the above-mentioned behavioural categories (1–4) was checked for isolation call production by the focal male. Data were collected as count data (female: familiar/unfamiliar; male rival: aggression ceased/escalated; isolation calls of focal male: present/absent). Since repeated observations per focal male yielded identical results within each respective behavioural category, the count data were averaged per focal male and behavioural category. We used exact Fisher's tests to analyse the count data on the behavioural context in which adult males produced isolation calls.

All statistical tests were conducted using SPSS v17.0 (SPSS Inc., Chicago, IL, U.S.A.), STATISTICA v10 (Statsoft, Tulsa, OK, U.S.A.) and R v2.10.0 (R Development Core Team 2008). We used parametric, two-tailed statistical tests. The pDFA followed an R script provided by R. Mundry (Mundry & Sommer 2007).

RESULTS

Individual Signature

In both ontogenetic stages, many isolation calls could be correctly classified to the respective pup (subset validation: 56.8% [nonvolant], 53.6% [volant]; leave-one-out-cross-validation: 84.8% [nonvolant], 79.6% [volant]), indicating a moderately strong individual signature. The classification success was significantly better than expected in a random classification (binomial test: nonvolant: $P < 0.001$; volant: $P < 0.001$; random classification success: 4%). A comparison between ontogenetic stages revealed that the classification success did not change during ontogeny (paired t test: $t_{24} = 0.406$, $P = 0.689$), suggesting that the strength of the individual signature remained unchanged as pups matured.

Group Signature

We used the squared Mahalanobis distance between pup centroids to test for sex, genetic and social group effects on isolation call variation. We determined the sex for all but two pups in our data set (10 males, 13 females). Pups of the same sex did not cluster together in signal space (paired t test: $t_{22} = 1.465$, $P = 0.157$, corrected $\alpha = 0.025$), showing that pups' sex did not affect isolation call variation (Fig. 2a). In our analysis, 13 pups were maternal half-siblings belonging to six different mothers (Appendix Table A1). Pups from the same mothers did not cluster together in signal space when compared with unrelated pups (paired t test: $t_{12} = -0.100$, $P = 0.922$, corrected $\alpha = 0.05$), suggesting that maternal effects (i.e. maternal genes or maternal preference for certain isolation calls) did not influence isolation call variation (Fig. 2b). Twenty-three pups in our data set were fathered by seven different males (Appendix Table A1). Paternal half-siblings clustered significantly closer together than unrelated pups (paired t test: $t_{20} = -3.667$, $P = 0.002$, corrected $\alpha = 0.0167$); however, social group affiliation and shared paternal genes are confounding effects here since fellow pups were normally sired by the same male. Therefore, we used a subset of pups that were paternal half-siblings but grew up in different social groups and repeated the analysis. Our results show that pups clustered significantly closer to their fellow pups than to paternal half-siblings from another social group (paired t test: $t_{12} = -5.022$, $P < 0.0001$, corrected $\alpha = 0.0125$), suggesting that the effect of social group affiliation overrides the effect of shared parental genes (Fig. 2c). Correspondingly, related and unrelated pups belonging to the same social group clustered significantly closer together than pups from different social groups (paired t test: $t_{24} = -8.826$, $P < 0.0001$, corrected $\alpha = 0.01$), suggesting that isolation calls encode a group signature (Fig. 2d) in addition to the individual signature. Comparable results were obtained by a pDFA that classified 77.2% of isolation calls to the correct social group they were produced in (cross-validation; $P = 0.001$). Earlier work (Knörnschild & von Helversen 2008) located the individual signature in the composite end syllables of isolation calls and there the group signature was clearly visible in the sonograms as well (Fig. 3).

Ontogeny of Group Signature

To determine how the strength of the vocal group signature changed during ontogeny, we compared the squared Mahalanobis distances between fellow pups (i.e. within group distances) in both ontogenetic stages. The within-group distances decreased significantly during ontogeny (paired t test: $t_{24} = 2.292$, $P = 0.031$; nonvolant pups = 22.86 ± 1.78, volant pups = 15.87 ± 0.85; mean $\pm$ SE of Mahalanobis distance), suggesting that the group signature became more prominent as pups matured (Fig. 4).

We investigated whether the observed call convergence was caused by physical maturation effects by comparing the movement of pups in signal space (i.e. the difference between ontogeny stages) towards their fellow group members and towards the species mean. The pups' convergence towards fellow pups was significantly greater than towards the species mean (paired t test: $t_{24} = 2.166$, $P = 0.040$; convergence to fellow pups = 4.47 ± 1.97, convergence to species mean = -1.04 ± 1.35; mean $\pm$ SE of Mahalanobis distance), indicating that isolation call convergence was not primarily caused by physical maturation but by the auditory input from fellow pups. The negative convergence values illustrate that pup calls were actually diverging from the species' mean. Neither the within-group distance in both ontogeny stages nor the call convergence during ontogeny was influenced by the pups' sex or relatedness towards fellow pups (MANOVA with sex, mothers and fathers as fixed factors; sex: $F_{2,2} = 0.131$, $P = 0.884$; mothers: $F_{24,6} = 0.785$, $P = 0.694$; fathers: $F_{4,6} = 1.151$, $P = 0.417$), showing that the group signature developed through the modification of isolation calls based on vocal influences from fellow pups.

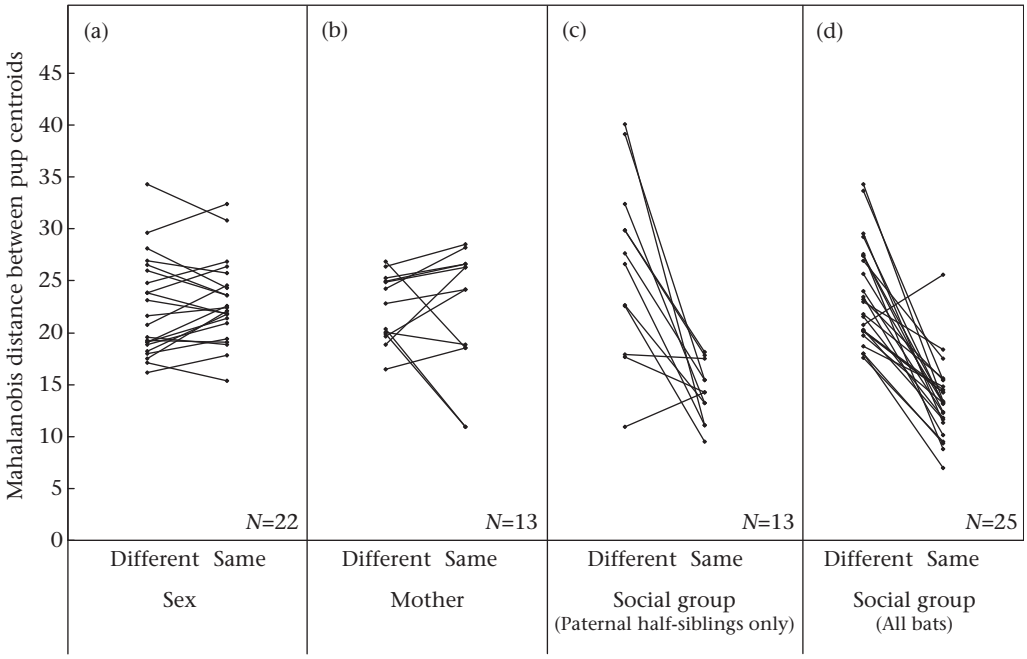

Figure 2. Squared Mahalanobis distance between centroids of different pups in a 21-dimensional signal space defined by the discriminant functions. Centroids belong to (a) pups from different versus the same sex, (b) pups from different versus the same mothers, (c) paternal half-siblings from different versus the same social groups, and (d) all pups from different versus the same social groups.

Isolation Call Production by Adult Males

Isolation calls were uttered not only by pups of both sexes to elicit maternal care but also by adult males during two distinctly different behavioural situations: to appease more dominant males (Fig. 5; Appendix Table A2) and to court unfamiliar females (Appendix Table A3). Synchronous behavioural observations and sound recordings of eight pairs of harem and nonharem males indicated that the production of isolation calls by nonharem males significantly influenced the outcome of the agonistic interaction (2×2 Fisher's exact test on paired data: $P < 0.0001$). When a nonharem male threatened by a harem male produced isolation calls, the harem male was appeased and further aggression was prevented in all observed interactions. When the nonharem male failed to produce isolation calls, however, the dominant harem male continued to threaten the nonharem male or even attacked it. Seven of the eight nonharem males were philopatric and thus able to learn the respective 'correct' group signature during ontogeny; the philopatric status of one male was unknown (Appendix Table A2). Behavioural observations with synchronous sound recordings of 10 harem males during courtship showed that the level of familiarity with the courted female significantly influenced the production of isolation call end syllables (2×2 Fisher's exact test with paired data: $P < 0.0001$). In all observed interactions, each male produced isolation call end syllables during courtship song when the courted female was a nonresident female that had newly visited his harem (dispersing young females may sample several harems before they settle in one). When the courted female was a resident harem female, however, the same 10 harem males never produced isolation call end syllables during courtship songs.

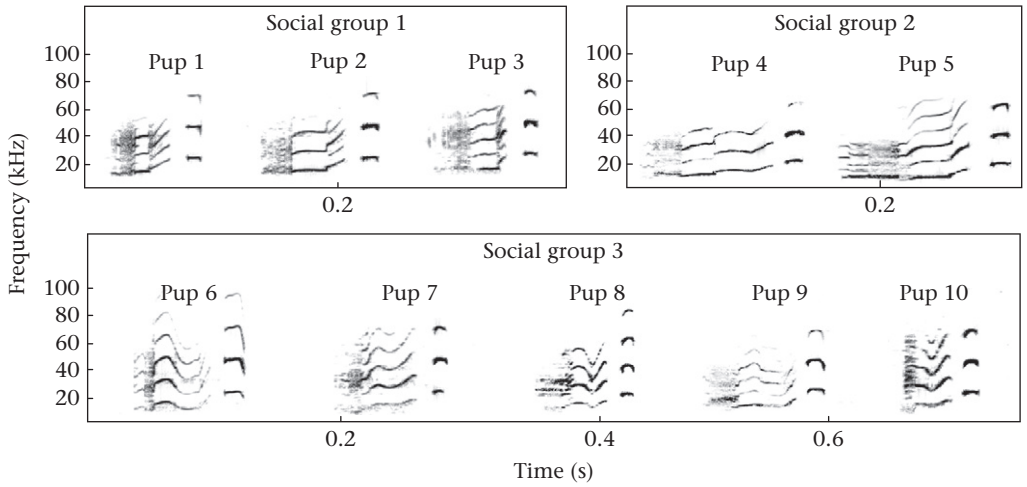

Figure 3. Individual and group signatures in composite end syllables of isolation calls from 10 pups (ID 1–10) belonging to three different social groups. Signatures are best visualized in the modulations of the tonal part. Sonograms were created using a 1024-point FFT and a Hamming window with 75% overlap.

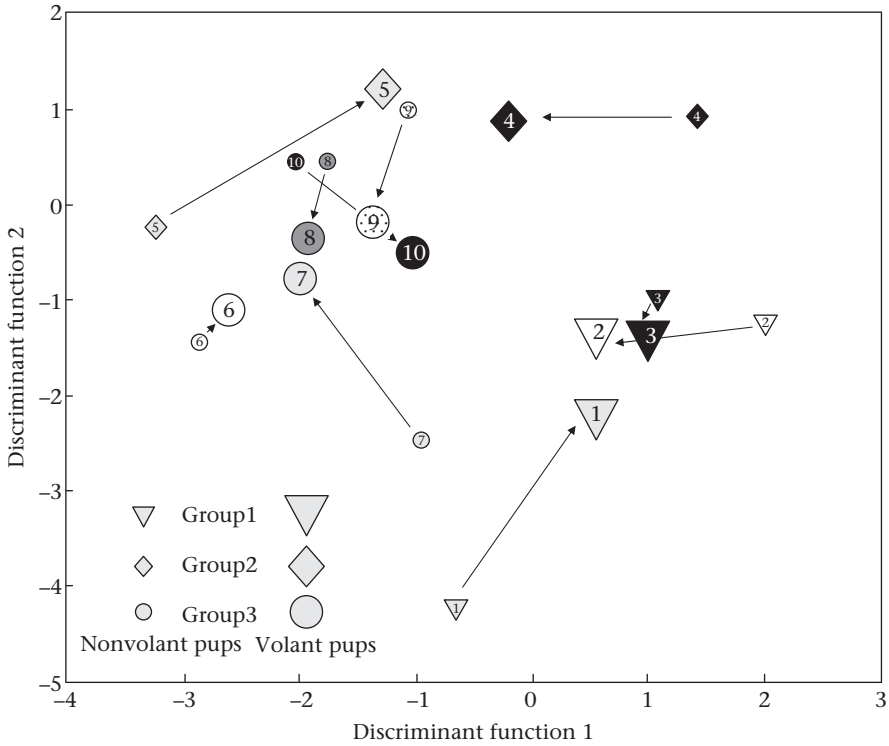

Figure 4. Centroids of nonvolant and volant pups in a two-dimensional signal space (defined by the first two discriminant functions that were calculated using the nonvolant pup data). For clarity, only 10 of 25 pups are depicted. Note that in this subset of the data, one pup (ID 10) was not related to his fellow pups (ID 6–9).

DISCUSSION

Call convergence of fellow group members occurred among both related and unrelated pups. The resulting group signature in isolation calls became more prominent during ontogeny and was not influenced by the pups' sex or relatedness. The influence of maturation effects on group signature development was negligible. We therefore conclude that the group signature in isolation calls was caused by the vocal input of fellow pups whose isolation calls were heard on a daily basis. Our findings are strong evidence for vocal production learning through social modification (sensu Boughman & Moss 2003). We are certain that the results we report here are not an artefact of the recording situation or potential habitat matching. The different recording situations at every day-roost could theoretically have led to acoustic similarities within groups. This was not the case in our study since different social groups using the same day-roost in different years did not cluster together in signal space (e.g. group 1 and 3 in Fig. 3). Different habitats can have very different sound transmission characteristics (Marten et al. 1977); however, all of our study colonies were located in the same habitat (i.e. the same patch of lowland tropical rainforest) with a maximum distance between colonies of less than 1 km, which makes habitat matching very unlikely.

Vocal convergence of group members occurred in isolation calls, a vocalization type that is under strong selection pressure for individual recognition (Kunz & Hood 2000). Both individuality and group membership are probably encoded in a combination of mainly spectral parameters that define the modulated tonal part of the composite end syllables of isolation calls (see Knörnschild & von Helversen 2008 for the location of the individual signature in isolation calls). 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 learned group signatures in bats, where individual identity was not encoded in the call that conveyed group identity (in *P. hastatus*; Boughman 1997).

In contrast to other mammals, in which learned group signatures seem to have evolved in the context of feeding ground defence (Boughman 1998), social provisioning or cooperative hunting (reviewed in Tyack 2008), call convergence of *S. bilineata* group members probably has a different function. Our behavioural data on isolation call production in adult males showed that isolation calls were used to appease more dominant males and to court nonresident females. Therefore, isolation calls apparently function as a submissive or placating signal in adults. At present, it is unclear whether any isolation calls would suffice in these situations or whether only the ones carrying a specific group signature would do so. The group signature in isolation calls reliably associates individuals with their natal colony. Assuming that receivers use this information, the group signature could be important for young males that are queuing for harem access (Voigt & Streich 2003). The vocal group signature could potentially function as a 'password' (sensu Feekes 1977) that harem holders use to determine whether queuing young males originate from their colony. Young males are normally unable to immigrate into a colony they were not born in, probably because they are excluded by the resident males who may cooperate on colony defence (Nagy et al. 2012). Thus, harem males seem to obtain direct fitness benefits from tolerating male kin because their tenure as harem males and, in turn, their reproductive success increases with the number of resident males in the colony (Nagy et al. 2012). Since all males in a colony belong to only a few patrilines (Nagy et al. 2007), harem males also obtain inclusive fitness benefits by tolerating young related males (Nagy et al. 2012).

The group signature in isolation calls could also provide important information for females. Dispersing females joining an already existing harem should have great interest in inbreeding

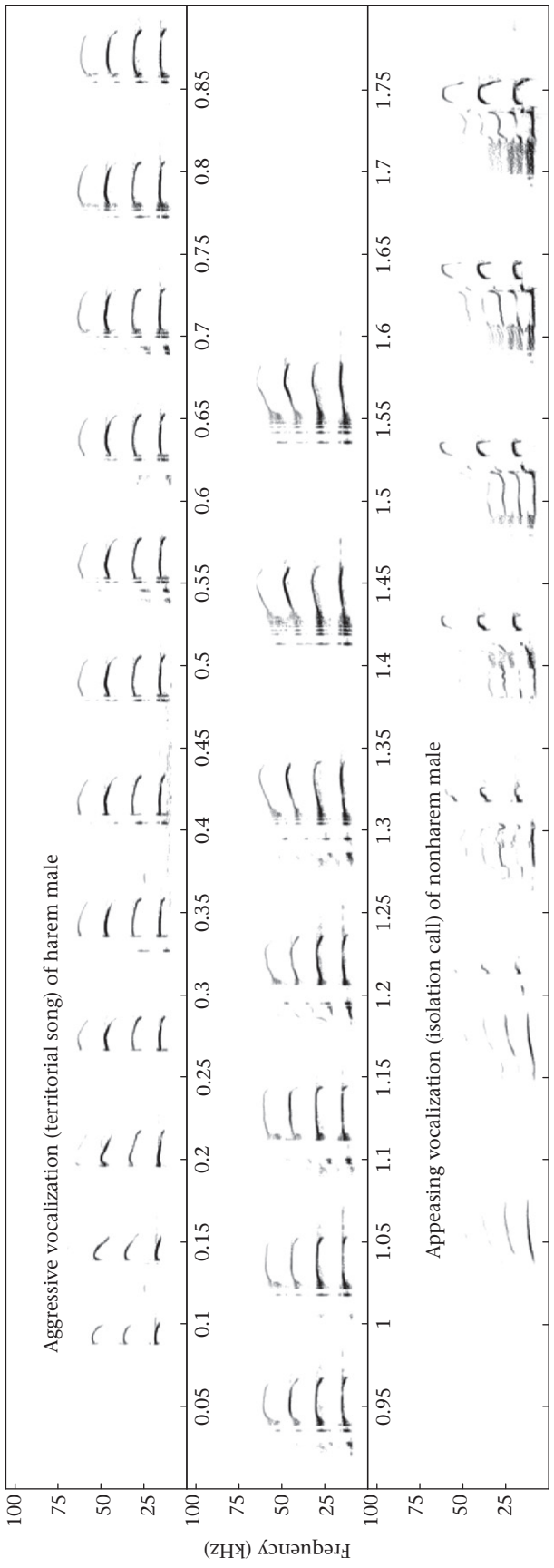

Figure 5. Sonogram depicting a behavioural interaction between a dominant harem male and a subordinate nonharem male. An aggressive vocalization (territorial song) of the harem male was immediately followed by an isolation call of the nonharem male. Thereafter, the harem male ceased his aggressive behaviour.

avoidance (i.e. not joining harems of older siblings); they disperse from their natal colony to avoid inbreeding in the first place and, later in life, engage in extraharem copulations if one of their male descendants takes over the harem they roost in (Nagy et al. 2007). Surprisingly, we found no difference in call convergence between the sexes even though our hypothesis about the password function of vocal group signatures would be beneficial for male pups only. Call convergence among female pups might have evolved because females must learn a pattern first to recognize it later (see Knörnschild et al. 2006 for female participation in vocal babbling behaviour). Analogous to birds (Marler & 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 (Marler 1976). Subsequent playback experiments are needed to investigate whether *S. bilineata* actually use the vocal group signature for kin recognition.

A learned vocal group signature may represent an effective mechanism to identify related and unrelated individuals. More importantly, learned kin recognition cues also allow individuals to react flexibly to shifting social circumstances (Boughman 1998), for instance when an impregnated female switches between colonies. In this scenario, pups could adapt to the changed situation by learning the group signature of the respective colony they grow up in. This would not be possible if the group recognition cue was genetically determined. However, we cannot exclude the possibility that unlearned, genetic components such as odour components also play a role in kin recognition in *S. bilineata*.

Theory predicts that evolutionarily stable group signatures should be costly, that is, time consuming or risky, for nongroup members to copy (Grafen 1990). The vocal differences between groups are substantial, presumably making copying difficult to achieve in a short period of time. Moreover, it is probably risky to settle within earshot of a colony and eavesdrop on their vocal group signature. Isolation calls are low-amplitude vocalizations that cannot be heard from a safe distance, which means that the aggression of resident males would have to be endured before copying was possible. These costs make it unlikely that the copying of vocal group signatures from non-natal colonies would occur in adults (see also Boughman 1998).

To conclude, our study provides strong evidence for a learned group signature in bat social vocalizations and indicates that the vocal group signature could facilitate the recognition of related and unrelated group members in the polygynous bat *S. bilineata*. Our results are in line with other studies on learned vocal group signatures in nonhuman mammals (bats: Boughman 1998; cetaceans: Tyack & Sayigh 1997; Watwood et al. 2004; Nousek et al. 2006; primates: Elowson & Snowdon 1994; Crockford et al. 2004; Snowdon 2009; ungulates: Briefer & McElligott 2012), thus adding to the growing body of evidence that social influences play an important role in the ontogeny of mammalian vocalizations.

Acknowledgments

We thank R. Mundry and K. Gerow for statistical advice and La Selva Biological Station, especially M. Lang, for technical support. Valuable comments by M. Beecher, B. Fenton, E. Briefer and two anonymous referees substantially improved the manuscript. This work was supported by grants from the German Merit Foundation (M.K.), the Deutsche Forschungsgemeinschaft (F.M.) and the National Geographic Society (O.v.H.).

References

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**, 227–267.

Behr, O. & von Helversen, O. 2004. Bat serenades: complex courtship songs of the sac-winged bat *Saccopteryx bilineata*. *Behavioral Ecology and Sociobiology*, **56**, 106–115.

Bertin, A., Hausberger, M., Henry, L. & Richard-Yris, M.-A. 2007. Adult and peer influences on starling song development. *Developmental Psychology*, **49**, 362–374.

Boughman, J. 1997. Greater spear-nosed bats give group-distinctive calls. *Behavioral Ecology and Sociobiology*, **40**, 61–70.

Boughman, J. 1998. Vocal learning by greater spear-nosed bats. *Proceedings of the Royal Society B*, **265**, 227–233.

Boughman, J. & Moss, C. F. 2003. Vocal learning and development of mammal and bird calls. In: *Acoustic Communication. Springer Handbook of Auditory Research* (Ed. by A. M. Simmons, A. N. Popper & R. R. Fay), pp. 138–213. Berlin: Springer Press.

Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of Animal Communication*. Cambridge, Massachusetts: Sinauer Press.

Briefer, E. & McElligott, A. G. 2012. Social effects on vocal ontogeny in an ungulate, the goat (*Capra hircus*). *Animal Behaviour*, **83**, 991–1000.

Cortopassi, K. A. & Bradbury, J. W. 2006. Contact call diversity in wild orange-fronted parakeet pairs, *Aratinga canicularis*. *Animal Behaviour*, **71**, 1141–1154.

Crockford, C., Herbinger, I., Vigilant, L. & Boesch, C. 2004. Wild chimpanzees produce group-specific calls: a case for vocal learning? *Ethology*, **110**, 221–243.

Elowson, A. M. & Snowdon, C. T. 1994. Pygmy marmosets, *Cebuella pygmaea*, modify vocal structure in response to changed social environment. *Animal Behaviour*, **47**, 1267–1277.

Feekes, F. 1977. Colony specific song in *Cacicus cela* (Icteridae, Aves): the password hypothesis. *Ardea*, **65**, 197–202.

Ford, J. K. B. 1991. Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Canadian Journal of Zoology*, **69**, 1454–1483.

Grafen, A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology*, **144**, 517–546.

Heckel, G. & von Helversen, O. 2003. Genetic mating system and the significance of harem associations in the bat *Saccopteryx bilineata*. *Molecular Ecology*, **12**, 219–227.

Heckel, G., Voigt, C. C., Mayer, F. & von Helversen, O. 1999. Extra-harem paternity in the white-lined bat *Saccopteryx bilineata*. *Behaviour*, **136**, 1173–1185.

Heckel, G., Achmann, R. & Mayer, F. 2000. Highly polymorphic microsatellite markers in the white-lined bat (*Saccopteryx bilineata*). *Molecular Ecology*, **9**, 242–244.

Hile, A. G. & Striedter, G. F. 2000. Call convergence within groups of female budgerigars (*Melopsittacus undulatus*). *Ethology*, **106**, 1105–1114.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, **6**, 65–70.

Janik, V. M. & Slater, P. J. B. 1997. Vocal learning in mammals. *Advances in the Study of Behaviour*, **26**, 59–99.

Janik, V. M. & Slater, P. J. B. 1998. Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Animal Behaviour*, **56**, 829–838.

Janik, V. M. & Slater, P. J. B. 2000. The different roles of social learning in vocal communication. *Animal Behaviour*, **60**, 1–11.

Janik, V. M., Sayigh, L. S. & Wells, R. S. 2006. Signature whistle shape conveys identity information to bottlenose dolphins. *Proceedings of the National Academy of Sciences, U.S.A.*, **103**, 8293–8297.

Kalinowski, S. T., Taper, M. L. & Marshall, T. C. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology*, **16**, 1099–1106.

Knörnschild, M. & von Helversen, O. 2008. Nonmutual vocal mother-pup recognition in the greater sac-winged bat. *Animal Behaviour*, **76**, 1001–1009.

Knörnschild, M., Behr, O. & von Helversen, O. 2006. Babbling behavior in the sac-winged bat (*Saccopteryx bilineata*). *Naturwissenschaften*, **93**, 451–454.

Knörnschild, M., von Helversen, O. & Mayer, F. 2007. Twin siblings sound alike: individual variation in the noctule bat, *Nyctalus noctula*. *Animal Behaviour*, **74**, 1055–1063.

Knörnschild, M., Nagy, M., Metz, M., Mayer, F. & von Helversen, O. 2010. Complex vocal imitation during ontogeny in a bat. *Biology Letters*, **6**, 156–159.

Kroodsma, D. E. & Baylis, J. R. 1982. A world survey of evidence for vocal learning in birds. In: *Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 311–337. New York: Academic Press.

Kunz, T. H. & Hood, W. R. 2000. Parental care and postnatal growth in the Chiroptera. In: *Reproductive Biology of Bats* (Ed. by E. G. Crichton & P. H. Krutzsch), pp. 415–468. London: Academic Press.

Marler, P. & Peters, S. 1982. Subsong and plastic song: their role in the vocal learning process. In: *Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 25–50. New York: Academic Press.

Marler, P. 1976. Sensory templates in species-specific behavior. In: *Simpler Networks and Behavior* (Ed. by J. Fentrees), pp. 314–329. Sunderland, Massachusetts: Sinauer Associates.

Marten, K., Quine, D. & Marler, P. 1977. Sound transmission and its significance for animal communication. II: Tropical forest habitats. *Behavioral Ecology and Sociobiology*, **2**, 291–302.

Mundry, R. & Sommer, C. 2007. Discriminant function analysis with nonindependent data: consequences and an alternative. *Animal Behaviour*, **74**, 965–976.

Nagy, M., Heckel, G., Voigt, C. C. & Mayer, F. 2007. Female-biased dispersal and patrilocal kin groups in a mammal with resource-defence polygyny. *Proceedings of the Royal Society B*, **274**, 3019–3025.

Nagy, M., Knörnschild, M., Voigt, C. C. & Mayer, F. 2012. Male greater sac-winged bats gain direct fitness benefits when roosting in multimale colonies. *Behavioral Ecology*, **23**, 597–606.

Nousek, A. E., Slater, P. J. B., Wang, C. & Miller, P. J. O. 2006. The influence of social affiliation on individual vocal signatures of northern resident killer whales (*Orcinus orca*). *Biology Letters*, **2**, 481–484.

R Development Core Team 2008. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. http://www.R-project.org.

Sewall, K. B. 2009. Limited adult vocal learning maintains call dialects but permits pair-distinctive calls in red crossbills. *Animal Behaviour*, **77**, 1303–1311.

Sharp, S. P., McGowan, A., Wood, M. J. & Hatchwell, B. J. 2005. Learned kin recognition cues in a social bird. *Nature*, **434**, 1127–1129.

Snowdon, C. T. 2009. Plasticity of communication in nonhuman primates. *Advances in the Study of Behaviour*, **40**, 239–276.

Townsend, S. W., Hollen, L. I. & Manser, M. B. 2010. Meerkat close calls encode group-specific signatures but receivers fail to discriminate. *Animal Behaviour*, **80**, 133–138.

Tyack, P. L. 2008. Convergence of calls as animals form social bonds, active compensation for noisy communication channels, and the evolution of vocal learning in mammals. *Journal of Comparative Psychology*, **122**, 319–331.

Tyack, P. L. & Sayigh, L. S. 1997. Vocal learning in cetaceans. In: *Social Influences on Vocal Development* (Ed. by C. Snowdon & M. Hausberger), pp. 208–233. Cambridge: Cambridge University Press.

Vehrencamp, S. L., Ritter, A. R., Keever, M. & Bradbury, J. W. 2003. Responses to playback of local versus distant contact calls in the orange-fronted conure, *Aratinga canicularis*. *Ethology*, **109**, 37–54.

Voigt, C. C. & Streich, W. J. 2003. Queuing for harem access in colonies of the sac-winged bat. *Animal Behaviour*, **65**, 149–156.

Voigt, C. C., Behr, O., Caspers, B., von Helversen, O., Knörnschild, M., Mayer, F. & Nagy, M. 2008. Songs, scents, and senses: sexual selection in the greater sac-winged bat, *Saccopteryx bilineata*. *Journal of Mammalogy*, **89**, 1401–1410.

Watwood, S. L., Tyack, P. L. & Wells, R. S. 2004. Whistle sharing in paired male bottlenose dolphins, *Tursiops truncatus*. *Behavioral Ecology and Sociobiology*, **55**, 531–543.

Wilkinson, G. S. 2003. Social and vocal complexity in bats. In: *Animal Social Complexity: Intelligence, Culture, and Individualized Societies* (Ed. by F. B. M. de Waal & P. L. Tyack), pp. 322–341. Cambridge, Massachusetts: Harvard University Press.

Wright, T. & Wilkinson, G. S. 2001. Population genetic structure and vocal dialects in Amazon parrots. *Proceedings of the Royal Society B*, **268**, 609–616.

Appendix

Table A1
Saccopteryx bilineata pups included in the study

Social group	Day-roost	Pup ID in analyses	Pup sex	Pup genetic ID	Maternal genetic ID	Paternal genetic ID	Harem male genetic ID
1	BH	1	Female	IN 1364	IN 922	IN 1332	IN 1332
1	BH	2	Male	IN 1346	IN 1168	IN 1332	IN 1332
1	BH	3	Female	IN 1347	IN 1339	IN 1332	IN 1332
2	C2	4	Female	IN 1407	IN 939	IN 1223	IN 1425
2	C2	5	Female	IN 1423	IN 1100	IN 1223	IN 1425
3	BH	6	Female	IN 1504	IN 922	IN 1428	IN 1428
3	BH	7	Male	IN 1494	IN 627	IN 1428	IN 1428
3	BH	8	Male	IN 1503	IN 1388	IN 1428	IN 1428
3	BH	9	Male	IN 1493	IN 1437	IN 1428	IN 1428
3	BH	10	Male	IN 1492	IN 1452	IN 1447	IN 1428
4	BoH	11	Female	IN 1365	IN 1152	IN 1224	IN 1236
4	BoH	12	Female	IN 1376	IN 939	IN 1224	IN 1236
5	C2	13	Female	IN 1351	IN 1100	IN 1223	IN 1224
5	C2	14	Male	IN 1350	IN 1337	IN 1224	IN 1224
5	C2	15	Female	IN 1352	IN 1338	IN 1224	IN 1224
5	C2	16	Unknown		IN 1248		IN 1224
6	RS	17	Male	IN 1368	IN 1189	IN 1330	IN 1330
6	RS	18	Male	IN 1363	IN 1181	IN 1330	IN 1330
6	RS	19	Female	IN 1362	IN 1043	not found	IN 1330
6	RS	20	Male	IN 1401	IN 1272	IN 1330	IN 1330
7	BH	21	Unknown		IN 922		IN 1428
7	BH	22	Male	IN 1429	IN 1339	IN 1332	IN 1428
7	BH	23	Female	IN 1427	IN 627	IN 1332	IN 1428
7	BH	24	Female	IN 1470	IN 1388	IN 1332	IN 1428
7	BH	25	Female	IN 1430	IN 1349	IN 1332	IN 1428

Two pups (16, 21) were never caught; therefore, their sex and genetic ID remained unknown. The paternal genetic ID for one pup (19) could not be found because it was sired by a male not included in our genetic database. One harem male (IN 1428) held his territory over 2 consecutive years, but since the composition of adult females changed between years we considered his respective harems to be different social groups.

Table A2
Isolation call use in adult male *Saccopteryx bilineata*: appeasement of harem males

No.	Year	Colony/ site	HM	NHM	NHM vocalizations	HM behaviour
1	2007	RH/LS	IN 1343	IN 1421	Isolation calls	Aggression ceased
					No social calls	Threatening continued
2	2008	STR/LS	IN 1519	IN 1483	Isolation calls	Aggression ceased
					No social calls	Threatening continued
3	2009	CA/SR	IN 71	IN 72	Isolation calls	Aggression ceased
					No social calls	Attacking
4	2009	DJH/SR	IN 65	IN 77	Isolation calls	Aggression ceased
					No social calls	Threatening continued
5	2009	CR/SR	IN 15	IN 57	Isolation calls	Aggression ceased
					No social calls	Attacking
6	2009	CR/SR	IN 51	IN 55	Isolation calls	Aggression ceased
					No social calls	Threatening continued
7	2010	CA/SR	IN 85	IN 94	Isolation calls	Aggression ceased
					No social calls	Threatening continued
8	2010	RH/LS	IN 1419	IN 1608	Isolation calls	Aggression ceased
					No social calls	Threatening continued

HM = harem male, NHM = nonharem male. Study sites: LS = Biological Station La Selva, SR = National Park Santa Rosa. Each line in the table summarizes data on 1–20 behavioural interactions between two individuals. All NHM except one were born in the colony in which they were recorded. The philopatric status of one NHM (IN 94) was unknown but he was probably born in the colony in which he was recorded (not all pups from this colony were banded in the summer of 2008 and IN 94 was caught there as a young adult early in 2009).

Table A3
Isolation call use in adult male *Saccopteryx bilineata*: courting unfamiliar females

No.	Year	Colony/ site	HM	Females	Vocalizations of HM	Residency of female
1	2007	RH/LS	IN 1342	IN 1211	CS	Colony resident
				IN 1504	CS with IC end syllables	Newly dispersed to colony
2	2007	BH/LS	IN 1428	IN 1339	CS	Colony resident
				Unbanded	CS with IC end syllables	Newly dispersed to colony
3	2008	CR/SR	IN 15	IN 23	CS	Colony resident
				Unbanded	CS with IC end syllables	Newly dispersed to colony
4	2008	CR/SR	IN 52	ID 19	CS	Colony resident
				Unbanded	CS with IC end syllables	Newly dispersed to colony
5	2008	CR/SR	IN 58	ID 16	CS	Colony resident
				Unbanded	CS with ic end syllables	Newly dispersed to colony
6	2010	RH/LS	IN 1644	IN 1643	CS	Colony resident
				Unbanded	CS with IC end syllables	Newly dispersed to colony
7	2010	RH/LS	IN 1419	IN 1626	CS	Colony resident
				Unbanded	CS with IC end syllables	Newly dispersed to colony
8	2010	RH/LS	IN 1572	IN 1515	CS	Colony resident
				Unbanded	CS with IC end syllables	Newly dispersed to colony
9	2010	CG/LS	IN 1628	IN 1648	CS	Colony resident
				Unbanded	CS with IC end syllables	Newly dispersed to colony
10	2010	LT/C	IN 215	IN 340	CS	Colony resident
				IN 344	CS with IC end syllables	Newly dispersed to colony

HM = harem male. Vocalizations: CS = courtship song; IC = isolation call. Study sites: LS = Biological Station La Selva, SR = National Park Santa Rosa, C = Curú. Each line in the table summarizes data on 1–20 behavioural interactions between two individuals.