The vocal repertoire of two sympatric species of nectar-feeding bats (*Glossophaga soricina* and *G. commissarisi*)

MIRJAM KNÖRNSCHILD[1, 4], VOLKER GLÖCKNER[2], and OTTO VON HELVERSEN[3]

[1]*Institute of Experimental Ecology, University of Ulm, Albert-Einstein Allee 11, 89069 Ulm, Germany*
[2]*Institute of Zoology, University of Erlangen-Nuremberg, Staudtstr. 5, 91058 Erlangen, Germany*
[3]*Chair of Botany II, University of Wuerzburg, Julius-von-Sachs-Plaz 3, 97082 Wuerzburg, Germany*
[4]*Corresponding author: E-mail: mirjam.knoernschild@uni-ulm.de*

We recorded social vocalizations from two sympatric species of glossophagine bats, *Glossophaga soricina* and *G. commissarisi*, using habituated captive groups that were housed in separate flight cages. Whenever possible, the species-specific vocalization types were described in the light of the social context in which they were produced. Several vocalization types within each species' repertoire had remarkable similarities to vocalization types in the other species' repertoire. Out of these, four vocalization types with interspecific acoustic similarities (approach pulses, distress calls, aggressive trills, and alert calls) were used in similar behavioral contexts in both species. Approach pulses were produced whenever a bat was flying towards an already occupied roost. Distress calls were uttered whenever a bat was attacked by conspecifics or restrained by the observer, whereas aggressive trills were produced during aggressive encounters prior to physical contact. Alert calls were uttered when bats were disturbed or when several individuals were circling the same location. The interspecific similarity of both the social context and the acoustic structure of vocalization types suggest that the potential for interspecific communication is high in *G. soricina* and *G. commissarisi*.

Key words: acoustic similarity, distress calls, eavesdropping, interspecific communication, social calls, repertoire size

INTRODUCTION

Despite a growing interest in social vocalizations of bats (Fenton, 1985, 2003; Siemers, 2006), detailed descriptions of species-specific vocalizations other than echolocation pulses are still fairly scarce. While the vocal repertoire of some species has been described in impressive detail in its behavioural context (*Antrozous pallidus* — Brown, 1976; *Myotis lucifugus* — Barclay *et al.*, 1979; *Saccopteryx bilineata* — Davidson and Wilkinson, 2002; Behr and von Helversen, 2004; Knörnschild *et al.*, 2006; Knörnschild and von Helversen, 2008; *Tadarida brasiliensis* — Bohn *et al.*, 2008*a*, 2008*b*), other species have received far less attention, either because studies focussed specifically on selected vocalizations (isolation calls — Esser and Schmidt, 1989; Scherrer and Wilkinson, 1993; Bohn *et al.*, 2007; Knörnschild *et al.*, 2007; contact calls — Boughman, 1997; Carter *et al.*, 2008; Janßen and Schmidt, 2009; male displays — Barclay and Thomas, 1979; Zagmajster, 2003; Russ and Racey, 2007; Jahelková *et al.*, 2008; aggression calls — Bastian and Schmidt,

2008) or because the social context in which vocalizations were produced remained mostly unclear (Brown *et al.*, 1983; Kanwal *et al.*, 1994; Andrews *et al.*, 2006; Ma *et al.*, 2006). It is now well established that bats eavesdrop on the echolocation pulses or social calls of conspecifics (Fenton *et al.*, 1976; Barclay, 1982; Ryan *et al.*, 1985; Barlow and Jones, 1997; Russ *et al.*, 2005; Gillam, 2007) or other species (Barclay, 1982; Russ *et al.*, 2004). Eavesdropping may allow bats to better find rich patches of food (Barclay, 1982; Gillam, 2007), to maintain contact with group members (Wilkinson and Boughman, 1998) or to locate and prey on the calling bat (Fenton, 2003). Echolocation pulses are normally produced for the purpose of orientation, despite the fact that they often serve an additional communicative function (Wilkinson, 1995; Fenton, 2003). Social calls, however, are not mandatory for orientation and hence their utterance is likely to have some advantage for the vocalizing bat (Wilkinson, 1995), e.g., attracting other bats to repel a predator by mobbing (Russ *et al.*, 2004, 2005) or defending a food patch against conspecifics (Barlow and Jones, 1997).

Glossophagine bats are neotropical nectar-feeding bats within the family Phyllostomidae (Baker *et al.*, 1976). *Glossophaga commissarisi* and *G. soricina* are small bats (≈ 9 g) of similar size and appearance (Alvarez *et al.*, 1991; Webster and Knox-Jones, 1993). Even though both species are mainly nectarivorous for most of the year, they become predominantly frugivorous during periods of low nectar availability (Tschapka, 2004; Lopez and Vaughan, 2007) and may cover foraging distances of more than 60 km per night due to their dispersed diet (von Helversen and Reyer, 1984). Glossophagine bats occupy a wide variety of tropical habitats; *G. commissarisi* is distributed from South Mexico to North Colombia, with two separate subspecies populations in West Mexico and North Peru (Webster and Knox-Jones, 1993) whereas *G. soricina* is distributed from Northern Mexico to Northern Argentina (Alvarez *et al.*, 1991). Even though *G. commissarisi* is more abundant in humid areas and *G. soricina* in semi-arid areas (Howell, 1983), both species can also occur sympatrically in the same region (LaVal, 1970, Fleming *et al.*, 1972; Kelm *et al.*, 2008). Day roosts of both species are located in hollows of trees, caves, buildings or bridges (Fenton *et al.*, 2001) and are often shared with other bats species (Goodwin and Greenhall, 1961; Graham, 1988; Fenton *et al.*, 2001; Kelm *et al.*, 2008). In *G. soricina*, group size varies considerably from small (< 10) to fairly large (> 1,000) groups (Hall and Dalquest, 1963; Kelm *et al.*, 2008), with groups of 12–16 individuals of both sexes being the normal case (Goodwin and Greenhall, 1961). Group size estimates for *G. commissarisi* are scarce; the maximum group size reported so far is 49 individuals (Kelm *et al.*, 2008). Female glossophagine bats can reproduce once or twice per year and normally give birth to a single offspring per litter (Alvarez *et al.*, 1991; Webster and Knox-Jones, 1993). In general, the social behavior of both species is only poorly understood and crucial information is lacking, especially for *G. commissarisi*. Pink (1996) studied a captive group of *G. soricina* and reported that one adult male defended a group of females against the remaining other males and reproductively monopolized 'his' females. During the female post-partem oestrus, copulations were preceded by conspicuous male hover displays in front of females. Pups of both sexes dispersed from their natal roost after weaning (Pink, 1996). In the wild, both sexes of *G. soricina* may temporarily defend small feeding territories around concentrated food sources against other bat species (Tschapka, 2003) or conspecifics (Lemke, 1984). Females share feeding territories

with their immature offspring but other intruders are chased away aggressively. *G. soricina* vocalize while defending its feeding territory, but the social calls involved have not been described (Lemke, 1984).

Griffin (1958) called glossophagine bats 'whispering bats' due to the low intensity of their echolocation pulses. Both *G. commissarisi* and *G. soricina* emit short (1–2 ms) multi-harmonic downward modulated sweeps covering frequencies of 140–60 kHz (von Helversen and von Helversen, 2003; von Helversen, 2004; Simon *et al.*, 2006). Social calls of *G. commissarisi* or *G. soricina* have not been described so far, probably because the high frequency and low intensity of their vocalizations makes it very difficult to perform sound recordings, especially in the field. The aim of this study was to describe the vocal repertoire of *G. commissarisi* and *G. soricina* in its behavioral context using captive individuals.

Materials and Methods

Study Subjects

The captive breeding colonies of *G. soricina* (approximately 100 individuals) and *G. commissarisi* (18 individuals) have been housed separately in greenhouses at the University of Erlangen-Nuremberg since 1988 and 1990, respectively. For the duration of our study, six adult individuals (four females and two males) of each species were transferred from the breeding colonies into rooms suitable for sound recordings. Both species were housed separately in two similar rooms (3.8 m × 2.1 m × 2.5 m each) that contained a flight cage made of plastic film (2.5 m × 1.8 m × 2.1 m). We lined the flight cage with foam insulation (0.05 m thickness) to minimize acoustic echoes and background noise. Bats were kept at 25°C ambient temperature and 70% humidity. Individuals were banded with coloured split plastic rings (A.C. Hughes Ltd., UK, size XCS) on their forearm, rendering them individually discernible from a distance. Bats were provided ad libitum with a diet consisting of honey-water enriched with pollen, milk powder (Aletemil, Alete, Nestlé, Germany) or nectar (Nektar Plus, Nekton, Pforzheim, Germany). We maintained a reversed 12 h day and night cycle in the rooms in order to facilitate observations.

Sound Recordings

We made high-quality ultrasonic recordings (500 kHz sampling rate and 16 bit resolution) with a USG microphone (Avisoft UltraSoundGate mobile 116Hm; frequency response: 0.02–460 kHz) connected to a laptop computer (Toshiba Satellite 5200-701). Recordings were accompanied by direct observations while sitting on the floor of the flight cage. Low red light illumination was provided by a shaded lamp on the ground. Bats were habituated for a minimum of two weeks prior to recordings to minimize disturbance during observations. Our presence in the flight cage was the only way to observe the

corresponding social interactions; since glossophagine bats vocalize mostly during flight activity it was impossible to use an infrared video camera. Observations and recordings took place on 24 days from June–August and November–December of 2007. Observation sessions lasted for up to two hours per day. In total, we conducted 23.75 h of observation for *G. soricina* and 26 h for *G. commissarisi*. Both species were observed on each observation day.

Acoustical Analysis

Social calls were grouped together into preliminary vocalization types based on their visual similarity in sonograms. Calls were taken from different series within a recording session wherever possible to minimize temporal dependence among calls. The acoustic analysis of calls was performed in Avisoft-SASlab Pro (version 4.40, R. Specht, Berlin, Germany). In total, 246 social calls were measured (151 for *G. soricina* and 95 for *G. commissarisi*). Calls were detected visually in the sonograms and their startpoint and endpoint were determined by hand. Most calls were multi-harmonic in structure, but we only used the first harmonic (fundamental frequency) for measurements because it contained most of the sound energy. We measured two temporal (duration, distance to maximum amplitude) and 28 spectral parameters. Peak frequency (frequency of the maximum amplitude), minimum frequency, maximum frequency and bandwidth were measured at five different regions evenly distributed over the call and averaged over the entire call (mean: parameters derived from the average spectrum of the entire call; max: maximum amplitude of element). Table 1 shows an overview of selected acoustic parameters of all vocalization types in the study. Measurements were taken from sonograms which were generated using a 1,024-point fast Fourier transform, a frame size of 100% and a Hamming window with 87.5% overlap. This resulted in a bandwidth of 635 Hz, a frequency resolution of 488 Hz and a time resolution of 0.256 ms.

Statistical Analysis

Our preliminary visual classification of calls into vocalization types was confirmed by a cluster-analysis with the acoustic call parameters (median-clustering with square Euclidian distance as clearance between cluster-centroids). To avoid intercorrelations between variables and to reduce the number of original variables, we performed a principal component analysis (PCA) separately for each species and for both species combined. Principal components with an eigenvalue larger than one were then used in subsequent analyses. To assess the variation within the call repertoire of one species and to compare it between both species we performed discriminant function analyses (DFAs) using the principal components obtained from the PCAs (separately for each and for both species combined). DFAs generate canonical discriminant functions representing the linear combinations of principal components which optimally separate calls into vocalization types in a multidimensional signal space. All principal components were included simultaneously into the DFAs. We used the method of cross-validating, in which all cases other than the testing case are used to create the discriminant functions. The mean values of the discriminant functions for every group are represented by group centroids, which can be depicted in a multidimensional scatter plot defined by the discriminant functions. In order to evaluate whether *G. soricina* and *G. commissarisi* might be able to communicate

with each other, we assessed the potential similarity of selected vocalization types from both species. We used the Euclidian distance between the centroids of the respective vocalization types as a measure of similarity (Boughman, 1998; Knörnschild *et al.*, 2007, 2009). The Euclidian distance in an *n*-dimensional space is described by the formula:

$$d(x,y) = \sqrt{\sum_{i=1}^{n} (x_i - y_i)^2}$$

The higher the similarity of two vocalization types to each other, the smaller is the numerical value describing the distance between the centroids. Statistical test were conducted using SPSS version 14.0 (SPSS Inc., Chicago, IL, U.S.A.).

RESULTS

We obtained four principal components from the *G. soricina* data and seven from the *G. commissarisi* data which explained 89% and 91% of the variation, respectively. A DFA performed on the obtained principal components confirmed our previous visual categorization of vocalisations into 15 different vocalisation types for *G. soricina* (98.7% of all vocalisations were classified correctly — Table 2 and Fig. 1A) and into eight different vocalization types for *G. commisarisi* (95.8% of all vocalizations were classified correctly — Table 2 and Fig. 1B).

In the vocal repertoires of both species (Fig. 2), most social calls were monosyllabic and uttered either singly (GS2–4, GS8–9, GS15; GC1–4, GC8) or repeatedly in sequence (GS1, GS5–7, GS10, GS12–14, GC5–7). Only one vocalization type in the *G. soricina* repertoire was multisyllabic (GS11). Bats of both species produced characteristic approach pulses (GS5, GC5) that occurred in clusters of five or more. These vocalization types were observed when a bat approached the roost, shortly before landing. We think that bats in the roost produce the approach pulses since the approaching bat always turned its back towards the microphone and any vocalizations from this bat should have therefore been too faint to record. Approach pulses were among the most frequently produced vocalization types in both species. Distress calls were produced by both species (GS11, GC7) when a bat was attacked by conspecifics and was somehow trapped so that it could not get away immediately (e.g., in the confined space of the dayroost) or manually restrained by the observer. The distress call of *G. commissarisi* was monosyllabic and repeated in series, whereas the distress call of *G. soricina* was multisyllabic. It consisted of three different syllables (S1–S3), of which S1 was always the first syllable; the others (S2–S3) were combined variably within

TABLE 1. Selected acoustical parameters ($\bar{x} \pm$ SD) of social calls from *G. soricina* and *G. commissarisi*. Distomax — distance from start to maximum amplitude; Peak frequency — peak frequency at start, centre and end of the call; Mean peak frequency — peak frequency averaged over entire call. Combined measurements of all syllable types are shown for GS11

Social call	Behavioral context	n	Duration (ms)	Distomax (ms)	Peak frequency			Mean peak Frequency (kHz)
					Start (kHz)	Centre (kHz)	End (kHz)	
GS1	Unknown	10	7.19 ± 1.0	4.8 ± 0.6	58.0 ± 31.6	80.9 ± 1.3	50.7 ± 0.7	80.6 ± 7.2
GS2	Alert call	10	30.4 ± 1.1	19.8 ± 2.1	68.3 ± 7.0	37.7 ± 2.3	24.5 ± 3.6	25.4 ± 2.7
GS3	Tandem/ chases	7	7.3 ± 1.5	4.2 ± 1.2	65.5 ± 4.9	39.0 ± 2.9	25.1 ± 4.1	37.2 ± 4.1
GS4	Alert call	20	26.0 ± 2.3	7.1 ± 5.5	65.9 ± 4.6	15.9 ± 6.0	12.0 ± 1.6	17.4 ± 7.3
GS5	Approach pulses	10	1.2 ± 0.2	0.6 ± 0.1	55.5 ± 5.7	49.9 ± 5.0	44.9 ± 4.7	50.0 ± 5.0
GS6	Aggresive trills	9	17.2 ± 1.7	9.6 ± 5.8	43.1 ± 3.2	40.5 ± 9.0	10.2 ± 1.2	25.9 ± 8.5
GS7	Contact call	10	2.6 ± 0.3	1.7 ± 0.2	70.5 ± 5.1	56.6 ± 1.6	49.3 ± 1.0	54.1 ± 1.7
GS8	Unknown	10	22.0 ± 0.5	16.7 ± 1.2	58.8 ± 6.7	29.0 ± 7.3	11.9 ± 1.5	29.3 ± 4.2
GS9	Unknown	10	11.9 ± 3.3	5.0 ± 1.9	49.5 ± 4.5	40.1 ± 3.5	35.5 ± 6.6	40.1 ± 3.5
GS10	Unknown	6	5.4 ± 0.2	1.6 ± 0.9	46.1 ± 5.5	70.9 ± 2.9	42.3 ± 1.3	46.6 ± 4.0
GS11	Distress call	9	4.5 ± 0.6	2.8 ± 0.5	57.9 ± 2.7	37.4 ± 2.5	32.4 ± 2.5	36.7 ± 2.4
GS12	Unknown	10	8.9 ± 1.1	7.1 ± 1.3	60.6 ± 5.1	83.3 ± 6.2	41.0 ± 6.8	57.7 ± 8.7
GS13	Unknown	10	20.2 ± 2.6	12.7 ± 6.4	22.4 ± 6.4	61.6 ± 1.7	33.0 ± 9.0	50.7 ± 8.9
GS14	Unknown	10	2.4 ± 0.2	1.3 ± 0.4	48.0 ± 2.2	41.6 ± 2.5	35.6 ± 2.7	41.8 ± 4.1
GS15	Unknown	10	24.0 ± 5.4	18.3 ± 4.7	11.9 ± 1.7	10.4 ± 0.9	10.0 ± 0.5	10.4 ± 0.7
GC1	Tandem/ chases	10	14.5 ± 1.1	12.8 ± 1.3	86.1 ± 2.6	90.9 ± 6.6	27.6 ± 3.9	40.5 ± 2.7
GC2	Tandem/ chases	30	10.3 ± 1.9	8.3 ± 2.0	89.3 ± 6.1	57.1 ± 5.6	22.7 ± 5.9	35.2 ± 3.9
GC3	Alert call	10	19.8 ± 0.8	11.7 ± 0.8	86.7 ± 2.4	39.9 ± 5.1	9.50 ± 0.4	23.2 ± 8.9
GC4	Tandem/ chases	10	9.8 ± 1.0	6.0 ± 3.8	31.0 ± 1.3	79.7 ± 11.9	28.5 ± 8.4	34.4 ± 3.2
GC5	Approach pulses	9	1.5 ± 0.4	0.8 ± 0.2	55.5 ± 4.0	47.8 ± 4.0	42.1 ± 5.1	47.7 ± 4.1
GC6	Aggresive trills	8	27.1 ± 4.1	17.9 ± 9.9	58.3 ± 20.9	30.3 ± 26.5	10.1 ± 1.8	20.7 ± 6.8
GC7	Distress call	10	22.8 ± 5.1	15.1 ± 5.7	63.1 ± 7.7	58.5 ± 9.1	37.6 ± 2.5	40.1 ± 7.3
GC8	Unknown	8	33.9 ± 2.2	25.1 ± 1.4	67.6 ± 7.0	68.8 ± 2.6	11.0 ± 1.3	23.2 ± 10.8

the call. Aggressive trills (GS6, GC6) were uttered by bats of both species in an aggressive context prior to physical contact. They were loud vocalizations that were relatively low in frequency when compared to the rest of the vocal repertoire. Bats of both species produced alert calls (GS2/4, GC3) when behaving warily and vigilantly, for example when disturbed by the observer or when several individuals were circling around the same location (i.e., roost or nectar source). In *G. soricina*, males produced contact calls (GS7) during tandem flights with females. We never recorded this vocalization type in another context. However, we cannot be sure whether these calls are part of male courtship. In both species, various social calls (GS3, GC1–2, GC4) were uttered during tandem-flights and chases. We do not know, however, which of the involved bats uttered the

respective vocalization types and whether they were used in an aggressive or affiliative context. For the remaining vocalization types, we were unable to describe the distinct social context they occurred in (GS1, GS8–10, GS12–15; GC8). We described all observed social behaviors and assigned them with distinct vocalization types whenever possible (Table 3).

In order to compare the vocal repertoires of both species within the same signal space, we performed a principal component analysis on both data sets combined and obtained six principal components which explained 88% of the variation. A DFA calculated with the principal components confirmed our previous visual classification of vocalizations into 23 different vocalisation types (93.9% of all vocalizations classified correctly — Table 2). In order to estimate the potential similarity of vocalization

TABLE 2. Assessment of model fit for DFAs on the social calls of *G. soricina*, *G. commissarisi* and both species together, showing only values for the first two discriminant functions

Assessment of model fit	G. soricina		G. commissarisi		Both species	
	d.f. 1	d.f. 2	d.f. 1	d.f. 2	d.f. 1	d.f. 2
Eigenvalue	52.13	24.19	21.26	14.99	25.50	24.44
Proportion of variation (%)	52.7	24.4	46.8	33.0	34.6	33.2
Wilks-Lambda	0.0001	0.0001	0.0001	0.001	0.0001	0.0001
χ^2 (all $P < 0.001$)	1,698.1	1,139.9	878.9	610.6	3,050.2	2,294.8

types across different species, we calculated the Euclidian distance between centroids of selected vocalization types from *G. soricina* and *G. commissarisi*. Based on visually assessed resemblance (Fig. 2), we selected approach pulses (GS5 and GC5), distress calls (GS11 and GC7), aggressive trills (GS6 and GC6), alert calls (GS2/4 and GC3) and two other vocalization types (GS13 and GC4) for comparisons. We compared the distance of each selected pair of vocalizations to the mean distance between each pair member and all other vocalization types from the same species (Fig. 3). Our results
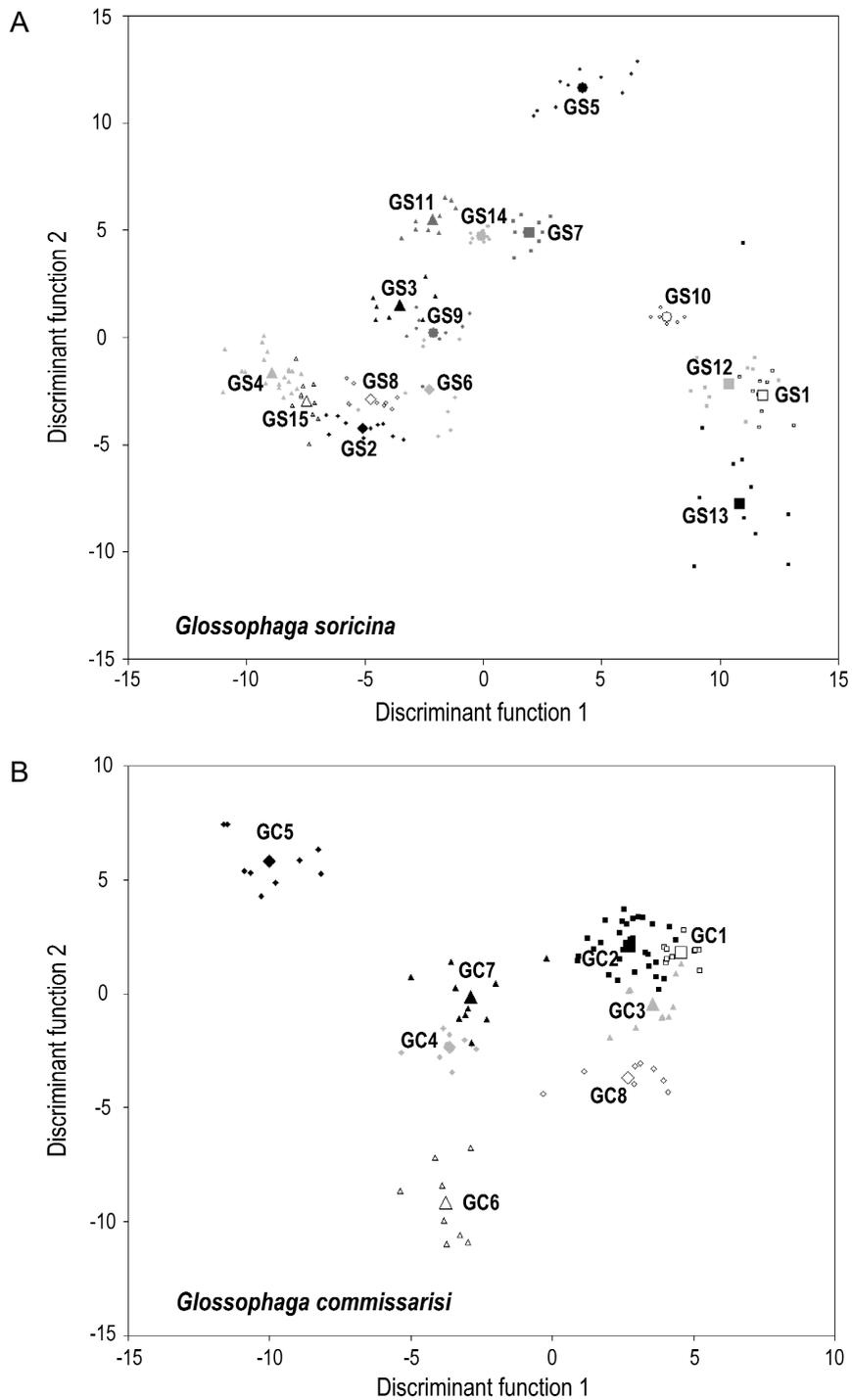
FIG. 1. The spacing of different vocalization types of *G. soricina* (A) and *G. commissarisi* (B) in a two-dimensional signal space defined by the first 2 discriminant functions. Small symbols represent individual social calls whereas large symbols represent centroids (i.e., the canonical mean of all calls per vocalization type)
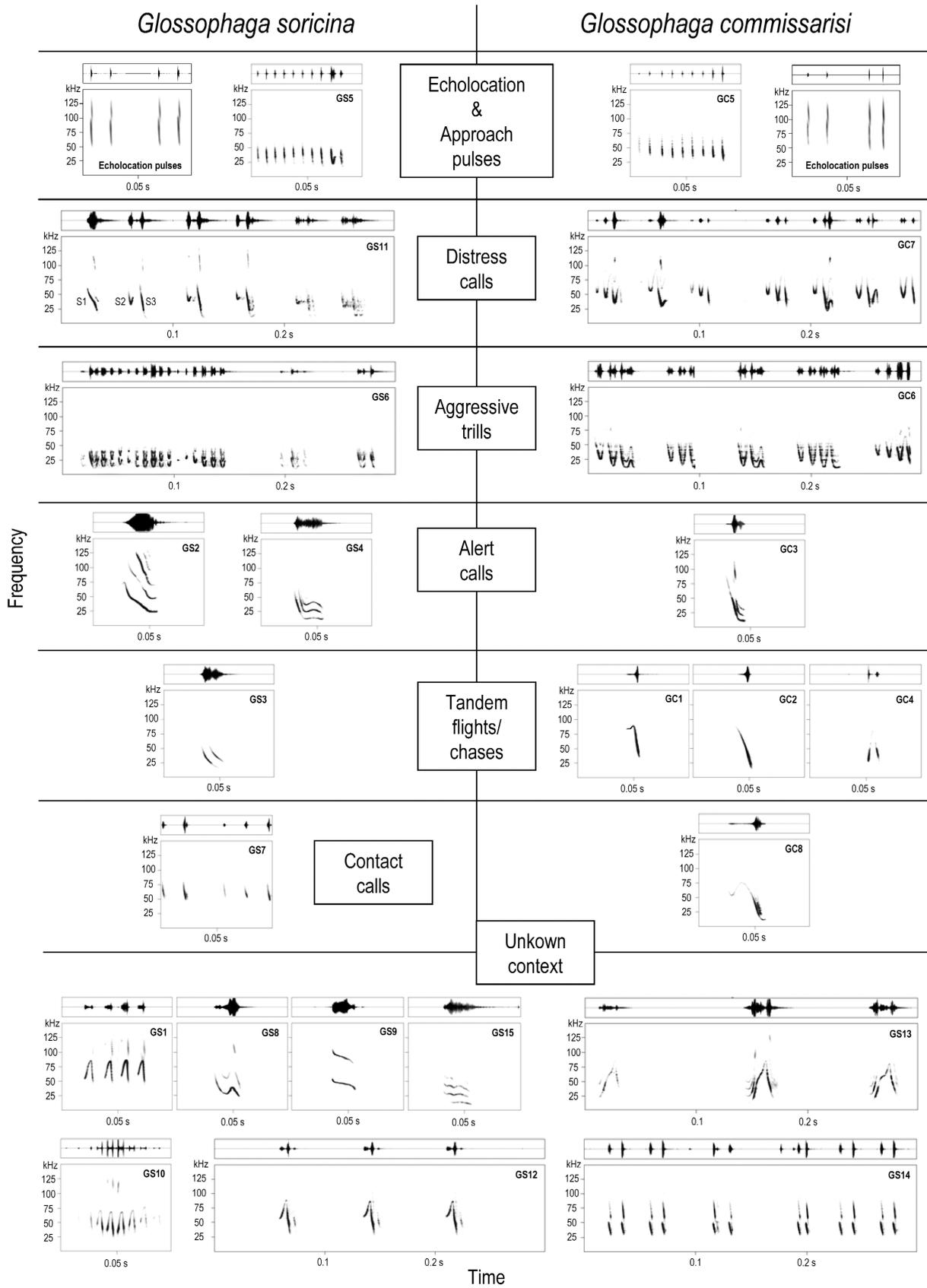
FIG. 2. Oscillograms and sonograms depicting echolocation pulses and social calls of *G. soricina* and *G. commissarisi*. Sonograms were created using a 1,024 point FFT and a Hamming window with 87.5% overlap. The social context in which each vocalization type occurred is stated whenever it is known. Echolocation pulses are shown for comparative reasons

TABLE 3. Ethogram describing frequent behaviors exhibited by *G. soricina* and *G. commissarisi* and the social vocalizations recorded in the respective behavioral contexts

Behavior	Description	Vocalization types	
		G. soricina	*G. commissarisi*
Resting	No movement, no scanning	No vocalizations	No vocalizations
Scanning	Lifting the head by bending the neck backwards while rotating around one outstretched leg; often accompanied by open mouth and twitching ears	Echolocation	Echolocation
Grooming	Cleaning of coat and wings with tongue and hind feet	No vocalizations	No vocalizations
Hovering	Hovering in midair in front of conspecifics or feeder	Echolocation	Echolocation
Alert flying	Vigilant flying behavior after a disturbance or the sudden presence of a conspecific	Alert calls (GS2 and GS4)	Alert calls (GC3)
Tandem flight	One bat following another bat in flight without aggressive intentions; often fixed inter-individual distance during flight	Contact calls (GS7) and GS3	GC1, GC2, GC4
Aerial chase	One bat pursuing another bat in flight in an aggressive context; inter-individual distance often becomes shorter during the chase	GS3	GC1, GC2, GC4
Aerial collision	Two bats colliding in midair and hitting each other with their wings; often the outcome of an aerial chase	Aggressive trills (GS6) and distress calls (GS11)	Aggressive trills (GC6) and distress calls (GC7)
Landing on roosting conspecific	One bat landing on the back of a conspecific roosting on the wall; often followed by aggression or avoidance	Aggressive trills (GS6) and distress calls (GS11)	Aggressive trills (GC6) and distress calls (GC7)
Aggression	Biting or hitting conspecifics with folded wing	Aggressive trills (GS6)	Aggressive trills (GC6)
Avoidance	Crawling or flying away to avoid aggressive interaction; when trapped defense behavior	Distress calls (GS11)	Distress calls (GC7)
Approaching roost	Approaching the roost by repeatedly flying up close or even landing briefly	Approach pulses (GS5)	Approach pulses (GC5)
Wing stretch	One or both wings fully stretched out	Echolocation or no vocalizations	Echolocation or no vocalizations
Yawn	Wide open mouth with both rows of teeth and gum exposed	No vocalizations	No vocalizations
Tongue stretching	Complete extension of the tongue, often repeated several times in a row	No vocalizations	No vocalizations

suggest that all pairs of vocalization types were significantly more similarly to each other than to the other vocalization types (Friedman test, $\chi^2 = 8.4$, exact $P = 0.008$, $d.f. = 2$, $n = 5$; n corresponds to the five selected pairs of vocalizations — Fig. 4). Pairwise post-hoc comparisons showed a significant difference between Euclidean distance within pairs types and Euclidean distance within each pair member and all other species-specific vocalization types (Friedman post hoc test, $Q > 12$, $P < 0.05$, $n = 5$).

DISCUSSION

The vocal repertoire we described for *G. soricina* and *G. commissarisi* is obviously not complete because we did not document any mother-pup interactions or obvious male courtship. Nevertheless, the vocalization types described here probably represent the majority of vocalizations uttered outside of the mating and breeding season. Even though the total observation time was slightly higher for *G. commissarisi* than for *G. soricina*, the latter produced almost twice as many different vocalization types. This finding could represent a true difference in repertoire size. Alternatively, it could potentially be caused by *G. commissarisi* being more timid and hence less vocal during observations.

The vocalization types of *G. soricina* and *G. commissarisi* fit well into general types of bat calls that were assigned in an earlier study. Pfalzer and Kusch (2003) recorded vocalizations from 16 different European bat species and grouped them independently of species into four different general types of calls. These general call types seem to have similar functions across different bat species, namely aggression, distress, contact and mate attraction

(for details see Pfalzer and Kusch, 2003). One general call type that is long, of low frequency and noisy (type A in Pfalzer and Kusch, 2003) was not found in the vocal repertoire of either *G. soricina* or *G. commissarisi.* This might be due to the fact that both glossophagine species have much higher frequency ranges (up to 140 kHz) than the bats recorded by Pfalzer and Kusch (2003); maybe glossophagines are unable to produce such low and noisy calls. Instead, they conveyed aggression by producing low frequency trills with a high repetition rate.

Alert calls are the most common vocalizations in the field that are audible to the human ear. They are frequently heard when bats are scared out of their day-roost or when they congregate at flowers (M. Knörnschild, personal observation). It is unknown whether alert calls have a territorial function as well (Lemke, 1984; Tschapka, 2003). Few of the other vocalizations are within the human hearing range (aggressive trills, GS15, GS8, GC8), which, together with the generally low intensity of glossophagine vocalizations (Griffin, 1958) makes it extremely hard to conduct sound recordings and behavioral observations with free-living glossophagines.

The interspecific acoustic similarity of approach pulses, aggressive trills, alert calls and distress calls could indicate their potential for interspecific communication, especially because these vocalizations are uttered in the same social context in both species. It is unclear whether the remaining two vocalization types that have a structural similarity between species (GS13 and GC4) fit into this scheme as well, because we do not know the social context in which they were produced. Bradbury and Vehrencamp (1998) defined distress calls as vocalizations that cause dispersed individuals to move towards an isolated caller. In this respect, distress calls differ from 'alarm calls', because the latter term is applied to signals produced by individuals that have detected a predator, but have not been attacked by it
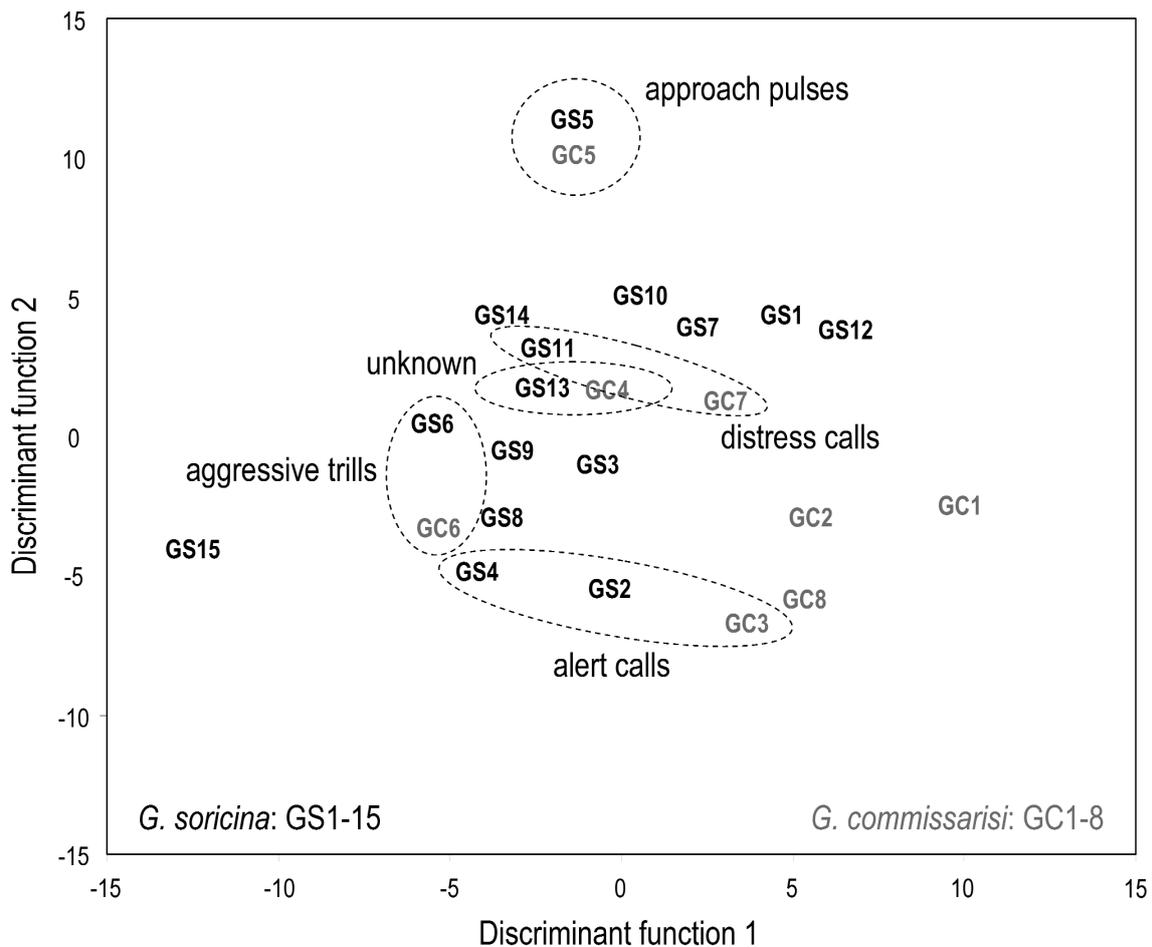

FIG. 3. All vocalization types described for both *G. soricina* and *G. commissarisi* depicted in the same two-dimensional signal space. Several vocalization types showed interspecific acoustic similarity and were located in the vicinity of each other in signal space (approach pulses: GS5 and GC5; distress calls: GS11 and GC7; aggressive trills: GS6 and GC6; alert calls: GS2/4 and GC3; unknown context: GS13 and GC4)
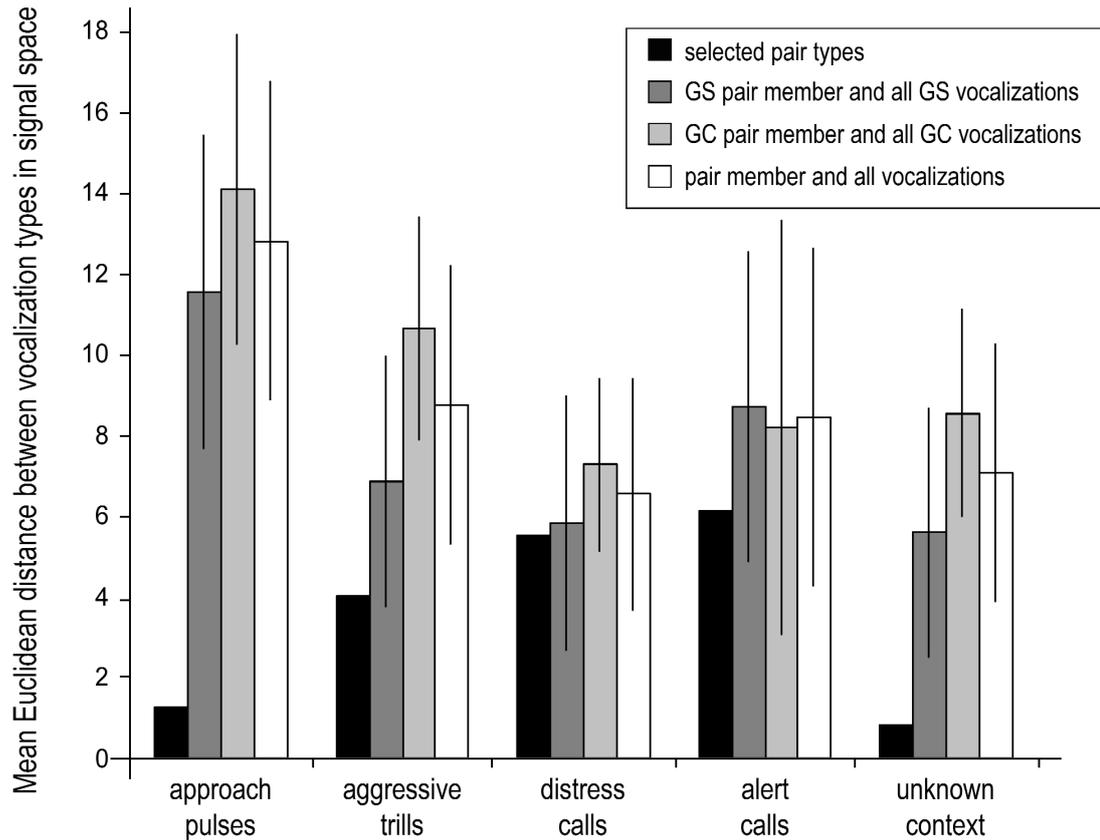
FIG. 4. Mean Euclidean distance between selected pairs of vocalization types (black columns) and between each pair member and all species-specific vocalization types (dark and light grey columns) as an indicator of acoustic similarity. For comparison, the mean Euclidean distance between each pair member and all vocalization types from both species is shown as well (white columns). Note that the difference in Euclidean distance is least pronounced for distress calls. Error bars show one standard deviation of the mean

(Seyfarth and Cheney, 1990; Magrath *et al.*, 2009). Distress calls should be easy to localize and optimized for long-distance communication, e.g. by presenting highly repetitive amplitude and frequency modulations (Wiley and Richards 1982; see Fig. 2). Distress calls can elicit responses from both conspecifics (bats — Ryan *et al.*, 1985; Russ *et al.*, 2005; birds — Jurisevic and Sanderson, 1998) and heterospecifics (bats — Barclay, 1982; Russ *et al.*, 2004; birds — Stefanski and Falls, 1972; Chu, 2001). Similar to findings in birds (Aubin, 1991), the distress calls of *G. soricina* and *G. commissarisi* contain noticeable acoustic similarities that could facilitate interspecific responses to the distress calls of the sympatric species.

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