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A dual function of echolocation: bats use echolocation calls to identify familiar and unfamiliar individuals

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Bats use echolocation for orientation during foraging and navigation. However, it has been suggested that echolocation calls may also have a communicative function, for instance between roost members. In principle, this seems possible because echolocation calls are species specific and known to differ between the sexes, and between colonies and individuals for some species. We performed playback experiments with lesser bulldog bats, *Noctilio albiventris*, to which we presented calls of familiar/unfamiliar conspecifics, cohabitant/noncohabitant heterospecifics and ultrasonic white noise as a control. Bats reacted with a complex repertoire of social behaviours and the intensity of their response differed significantly between stimulus categories. Stronger reactions were shown towards echolocation calls of unfamiliar conspecifics than towards heterospecifics and white noise. To our knowledge, this is the first time that bats have been found to react to echolocation calls with a suite of social behaviours. Our results also provide the first experimental evidence for acoustical differentiation by bats between familiar and unfamiliar conspecifics, and of heterospecifics. Analysis of echolocation calls confirmed significant individual differences between echolocation calls. In addition, we found a nonsignificant trend towards group signatures in echolocation calls of *N. albiventris*. We suggest that echolocation calls used during orientation may also communicate species identity, group affiliation and individual identity. Our study highlights the communicative potential of sonar signals that have previously been categorized as cues in animal social systems.

The recognition of other individuals is a crucial component of social interactions, which are most often mediated via visual, olfactory or acoustical cues (reviewed in Bee 2006). Vocalizations in particular have been described as an important modality to signal and perceive individual identity, for example in anurans (e.g. Bee & Gerhardt 2002), birds (reviewed in Falls 1982) and mammals (e.g. Rendall et al. 1996). Similarly, acoustical discrimination between familiar and unfamiliar individuals, also known as ‘neighbour–stranger’ discrimination, is well described for a variety of animal species, most notably birds (reviewed in Temeles 1994).

Bats, as the most gregarious mammalian order, often form large colonies and commonly share roosts with other bat species (Kunz 1982). The role of acoustic communication in social interactions among conspecifics and heterospecifics sharing roosts remains largely unclear. Bats are a special case in acoustic communication as they possess two different call types: social calls, exclusively used in social interactions, and echolocation calls, emitted for orientation and foraging. In contrast to ultrasonic echolocation calls, social calls are often lower than 20 kHz in frequency and thereby in principle audible to humans, and usually of multiharmonic structure (Fenton 2003). Social calls have been shown to be individually distinct (Carter et al. 2008), to mediate group foraging (Wilkinson & Boughman 1998), and to be used also in agonistic (Racey & Swift 1985) and territorial interactions (Behr et al. 2006) as well as in courtship displays (Behr & von Helversen 2004). By contrast, echolocation has for a long time only been viewed as an acoustical tool that enables bats to orient in darkness, a prerequisite for the location of prey and navigation at night (e.g. Griffin 1958; Schnitzler et al. 2003). Although the unique echolocation abilities of bats have received much scientific attention, research efforts have mainly focused either on the extraordinarily precise spatial discrimination

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achieved with echolocation (e.g. Simmons et al. 1983; Grunwald et al. 2004) or on neural processing of echolocation calls in the auditory cortex (e.g. Suga & O'Neill 1979; Firzlaff et al. 2006). Some basic insights on how echolocation calls can influence bat behaviour have been obtained in field studies. For instance, bats may eavesdrop on conspecifics' feeding buzzes, echolocation calls emitted shortly before a prey capture attempt (Balcombe & Fenton 1988; Gillam 2007; Dechmann et al. 2009). Several studies have shown that bats adjust frequency and pressure levels of their echolocation calls according to the presence of conspecifics (e.g. Obrist 1995; Ratcliffe et al. 2004), noisy environments (Schaub et al. 2008) or habitat types (e.g. Obrist 1995; Gillam & McCracken 2007). We are aware though of only three laboratory studies that have investigated the potential of echolocation for communication and social recognition. Kazial & Masters (2004) found that female *Eptesicus fuscus* reduce their average call repetition rate in response to echolocation calls emitted by other females, but not in response to those emitted by males. In a habituation–discrimination experiment, Kazial et al. (2008) demonstrated that *Myotis lucifugus* can recognize individuals based on echolocation calls. Similarly, Yovel et al. (2009) showed that trained *Myotis myotis* are able to distinguish between two individuals in forced-choice experiments. Independently, numerous studies have statistically confirmed that echolocation calls code for age (Jones & Ransome 1993; Jones & Kokurewicz 1994; Masters et al. 1995), family affiliation (Masters et al. 1995), sex (Neuweiler et al. 1987; Jones & Kokurewicz 1994), colony membership (Masters et al. 1995; Pearl & Fenton 1996) and individuality (Fenton et al. 2004), which suggests a large communication potential of echolocation calls that remains thus far unexplored. Here, we used the lesser bulldog bat, *Noctilio albiventris*, to test experimentally whether echolocation is used for communication and, if so, what messages might be communicated via echolocation among roost members.

Noctilio albiventris has a circumtropical distribution in the New World (Hood & Pitocchelli 1983). They roost in large colonies of up to 700 individuals in hollow trees and houses (Brown et al. 1983; Hood & Pitocchelli 1983). Brooke (1997) reported that *Noctilio leporinus*, the only other species of this genus, forms long-term female associations of three to nine individuals. Our own observations suggest that, most likely, *N. albiventris* also forms small and stable female groups within their colony roost. Individuals caught together when emerging from their roost also foraged together over the water (Dechmann et al. 2009). Means to discriminate between group members and nongroup members are probably important to maintain such social bonds. Olfactory recognition seems an unlikely mechanism to serve this function during flight. However, acoustic recognition via echolocation calls might play a crucial role, as bats have to echolocate continuously while foraging. Accordingly, we hypothesized that either individual and/or group signatures in echolocation calls may function as a social recognition system.

Noctilio albiventris uses constant frequency and frequency-modulated signals while foraging, the proportion of the two components changing with the animals' flight behaviour and information requirements (Kalko et al. 1998). Brown et al. (1983) described variation among individual echolocation calls, with fundamental frequencies of 65–75 kHz. They assumed that echolocation calls in *N. albiventris* might serve a dual function, as they frequently observed bats calling antiphonally as well as mothers and juvenile bats duetting on the juveniles' first foraging flights.

In addition to living in social groups with conspecifics, this species often shares roosts with another common neotropical bat species, the Pallas's mastiff bat, *Molossus molossus* (Bloedel 1955; Dolan & Carter 1979; personal observation). In general, bats frequently share roosts with other species and roost interactions between cohabitant species have been anecdotally described in a number of species (e.g. Graham 1988).

We hypothesized that echolocation calls have a dual function. We argue that echolocation as a tool for navigation at night may also communicate social information, for example species identity, group membership or familiarity. Thus, either playback of calls carrying different social information should elicit different sets of behaviours, or subject bats should adjust the intensity of their reaction to the playback's information content. To address this question, we quantified the bats' responses to five stimulus categories in a playback experiment. Stimulus categories were calls from (1) familiar conspecific individuals, (2) unfamiliar conspecific individuals, (3) cohabitant heterospecifics (*M. molossus*), (4) noncohabitant heterospecifics (*Uroderma bilobatum*) and (5) ultrasonic white noise within the frequency range of *N. albiventris* echolocation calls. We used ultrasonic white noise as a control to test whether bats distinguish between noise in their own frequency range from conspecific and heterospecific calls.

We predicted that *N. albiventris* can distinguish between all stimuli and that they would respond differently to the stimulus categories. Furthermore, we analysed the echolocation calls of all individuals used in our experiment to test for individual and/or group signatures in echolocation calls of *N. albiventris*. We predicted that echolocation call parameters would differ between individuals and between social groups.

METHODS

Study Site and Bats

We conducted field work in Gamboa, Panama (09° 07′N, 79° 41′W) from March to May 2008. All bats used in this study (*N. albiventris*, Noctilionidae; *M. molossus*, Molossidae; *U. bilobatum*, Phyllostomidae) were caught with mist nets (Ecotone, Warszawa, Poland) or a hand-made harp trap (adapted from Tuttle 1974). In total, we caught four social groups of *N. albiventris*. The first three groups were caught during evening emergence from daytime roosts in buildings in Gamboa. The first group consisting of three males and two females was only used for stimulus acquisition and was released immediately after recordings had been obtained. The other social groups were used in the playback experiment (see below). The second group consisted of four females and three males and the third of six females and two males. The fourth group consisting of four males and one female was caught while foraging over the water in the surroundings of Barro Colorado Island (BCI), Panama (09° 10′N, 79° 51′W).

Upon capture we determined sex, age and reproductive status of each bat, and only adult nonlactating individuals were kept for experiments or recordings. We measured body mass (with a handheld Pesola balance; accuracy ± 0.5 g) and forearm length (with callipers, accuracy ± 0.5 mm) of each bat and marked all *N. albiventris* individually by injecting passive integrated transponders (PIT tag, Euro ID, Weilerswist, Germany) under the dorsal skin. In previous studies, transponders have successfully been used to mark wild bats and to observe their behaviour with no record of adverse effects on the animals (e.g. *Myotis bechsteinii*: Kerth & König 1996; *Trachops cirrhosus*: Page & Ryan 2006; *Lophostoma silvicolum*: Dechmann et al. 2007; *Nyctalus lasiopterus*: Popa-Lisseanu et al. 2008). In our study we routinely checked the animals' health status carefully during recaptures. We noted only a single case where a transponder had harmlessly moved to the side of the bat's body. All other transponders remained in their original position parallel to the spine on the upper back and in all cases the sites of transponder insertion healed within a few days after marking.

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Animals were kept in their social groups in a shaded room in small mosquito tents (36 × 15 cm and 38 cm high, PeaPod, KidCo, Libertyville, IL, U.S.A.) at ambient temperature and humidity (on average 26 °C and 65%). Holding tents were located in separate rooms to avoid familiarization between the groups via sound, vision or odour. We fed bats an ad libitum diet of mealworms (larval stages of *Tenebrio molitor*) and water, and weighed them on a regular basis to monitor their wellbeing.

After the experiments all bats were released at the site of capture. All experimental procedures were carried out under permits from the Autoridad National del Ambiente (ANAM) of Panama and STRI IACUC protocols.

Stimulus Acquisition

We used five playback stimulus categories. These were calls from (1) familiar conspecifics (group members, $N = 15$ individuals from three social groups), (2) unfamiliar conspecifics (nongroup members, $N = 5$), (3) cohabitant heterospecifics (*M. molossus*, $N = 5$), (4) noncohabitant heterospecifics (*U. bilobatum*, $N = 5$) and (4) white noise in the frequency range of a typical frequency-modulated *N. albiventris* call (35–75 kHz). Apart from white noise, for each stimulus category we created five files from five individual recordings (see below).

To make the playback files, we recorded echolocation calls from individual bats. Recordings of *N. albiventris* and *U. bilobatum* were made when bats rested on the interior walls of an outdoor flight cage (6 × 2 m and 5 m high). Recordings from *M. molossus*, which are unable to fly in a flight cage because of their morphology, were obtained when hand releasing the bats close to their daytime roost. We held a single bat in our hands until it started to echolocate. To make the recordings comparable with those of the other species, we only used calls that were emitted shortly before the bat started to fly. *Uroderma bilobatum* and *M. molossus* were released immediately after the recordings. All *N. albiventris*, except the five individuals used to obtain the unfamiliar conspecific stimulus, were kept in captivity (as described above) for playback experiments.

We made all recordings with an Avisoft condenser ultrasound microphone (CM16/CMPA) and the software Recorder USGH version 3.4 (Avisoft Bioacoustics, Berlin, Germany). Recordings were done with a 16 bit resolution and a 250 kHz sampling rate. We only chose recordings with a good signal to noise ratio for playback stimuli and treated the sequences with a high-pass filter above 30 kHz to eliminate background noise. We attempted to use calling bouts 8 s long for stimulus construction. If this was not possible, we repeated individual recordings until the sequences were 8 s long. All playback files were of the same duration. We did not, however, standardize playback files in respect to calling rate and amplitude. The reason was that, like spectral parameters, such call characteristics might be used by bats for decoding. We used SASLab Pro 4.40 (Avisoft Bioacoustics) to construct playback sequences.

Experimental Procedure

Experiments were conducted with 20 experimentally naïve bats belonging to the three social groups. As *N. albiventris* that leave the roost together usually forage as a group (Dechmann et al. 2009), we assumed that individuals caught in the same bout emerging from the roost or flying together belonged to the same social group or were at least familiar with each other. However, to ensure this, we kept bats that we had caught simultaneously together in cages for at least 5 days before we started experiments.

For playback experiments, we transferred single bats into the flight cage and placed them in an open plastic box (l37 × 52 cm and 14 cm high). The test box was covered with a see-through mosquito screen on its open side to enable video recording and inside to provide a substrate for the bats to cling on. The box was horizontally positioned with the mosquito screen facing a Sony NightShot handy-cam to record the physical responses of bats. Experiments were conducted between 1800 and 0300 hours. For the playback we placed an Ultrasonic Dynamic Speaker (Scan Speak, Avisoft Bioacoustics) 65 cm from the left corner of the test box. We illuminated the flight cage with a 25 W red light bulb and additionally placed a red light bulb directly above the test box to facilitate filming. Additionally, we recorded the acoustic response of bats with the microphone and settings described above. The microphone was positioned 75 cm from the right corner of the test box.

We allowed the bats to get used to the experimental situation for at least 30 min before the start of experiments. Prior to each trial, we played back a so-called feeding buzz, a call emitted by bats shortly before a feeding event. From previous experiments we knew that this is a very strong stimulus for *N. albiventris* (Dechmann et al. 2009), and this allowed us to check whether bats were alert and motivated to participate in the experiment. Each bat was tested in five trials. We presented each stimulus category in random order during these five trial sessions. We conducted only one trial per day with each bat to avoid habituation.

One playback trial consisted of three phases: a preplayback phase (2 min), a playback phase (8 s) and a postplayback phase (5 min). The preplayback phase started when bats had been hanging motionless and silent for at least 2 min. For analysis we recorded the behavioural and acoustical responses of the bat during the 5 min postplayback phase.

Analysis of Postplayback Responses

We analysed videos using the software Interact (Mangold, Arnstorf, Germany). We defined six behavioural variables that we had observed as behavioural responses to the test stimuli: crawling, nodding, wing stretching, yawning, grooming and urinating (see below). We also commonly observed these behaviours in other experiments, where either two familiar or unfamiliar bats were confronted with each other. Most of these behaviours have also been described in other bat species within a social context (see in detail below).

We recorded the duration of crawling (s) and frequencies (N/5 min) for all other behaviours included in this study. Based on acoustic recordings, we counted the echolocation calls (Kalko et al. 1998) and calls that resembled the honk calls described by Suthers (1965) for *N. leporinus*, in spectrograms using 512 FFT size, an overlap of 50% and Hamming window in SASlab Pro. All videos and audio files were coded blindly by a single person.

Behavioural Responses

(1) Crawling. The baseline of our experiment required that bats were hanging still. In addition, bats were previously allowed to habituate to the experimental situation. Therefore we can exclude the possibility that the increase in locomotor activity of test animals stems from the artificial situation they encountered. Instead, we assume that crawling probably indicates arousal and general increased activity of animals during the experiment.

(2) Nodding. This behaviour was characterized by a movement of the head to the chin. It was the most frequent response behaviour in our experiments. We are not aware of the use of nodding in a social context from other taxa, and we can only speculate that this behaviour might be connected with olfactory cues from gular glands that these bats possess. In the sac-winged bat, *Saccopteryx bilineata*, Caspers et al. (2009) demonstrated that mandibular

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glands are used for territorial scent marking. Additionally, this behaviour could also be an indicator of emotional arousal in *N. albiventris*. In the holding tent, this behaviour was often shown by bats shortly after awakening when they were about to receive their food (personal observation).

(3) Wing stretching. We assume that wing stretching is part of an olfactory display intended to signal individuality in the roost, since *N. albiventris* possess glands in the subaxillary region underneath their wings that produce an oily and very strong-smelling secretion. Such behaviour has also been observed in *N. leporinus* (Brooke & Decker 1996), where individuals sniffed the subaxillary glandular area of a conspecific during dyadic interactions, and secretions of this area differed significantly between the sexes in their chemical composition. Wing displays are also known to be part of the social behaviour in other bat species (Tyrell 1990; Singaravelan & Marimuthu 2008).

(4) Grooming. This behaviour was characterized by the bats mostly scratching but also licking themselves. Grooming has been described as part of displacement or 'transition' behaviour in several other animal species (e.g. Tinbergen 1940; Fentress 1988).

(5) Yawning. This behaviour was characterized by the bats slowly opening their mouths so that their teeth were visible. Yawning has also been observed in other bats. Gebhard (1997), for example, suggested that the intense scent in *Nyctalus* roosts originates from the buccal glands which are exposed when males yawn during social interactions. Voigt & von Helversen (1999) observed male *S. bilineata* to frequently yawn prior to or after agonistic interactions.

(6) Urinating. Urinating could also be related to olfactory signalling in *N. albiventris*. Male Mexican free-tailed bats, *Tadarida brasiliensis*, for example, urinate or defecate when presented with a cotton swab bearing another male's scent (Gustin & McCracken 1987). Brooke (1997) reported that roosting sites of male *N. leporinus* were marked by a clearly defined urine stain.

Acoustical Responses

Noctilio albiventris emitted two types of calls as an acoustical response to our experiments: 'normal' echolocation calls similar to the calls of bats orienting in the flight cage, and another type of call, very similar to normal echolocation calls, but with a lower terminal frequency and containing additional harmonics (Fig. 1). For a lack of a better term, we refer to them as 'honk' calls as they resembled the honk calls described by Suthers (1965) for *N. leporinus*.

Statistical Analysis of Responses

For each of the 20 bats, we averaged the behavioural responses in a given stimulus category over the five trials. For all responses except honk calls, we performed either repeated measures ANOVAs or Friedman tests, followed by Bonferroni or Dunn's multiple comparison post hoc tests, depending on the distribution of data. In the post hoc tests we tested whether the reaction of bats differed between the treatment familiar conspecific compared to all other stimuli, unfamiliar conspecific compared to all other stimuli, and between the stimuli cohabitant and noncohabitant heterospecific.

Only 12 of the 20 bats responded with honk calls to playbacks. Thus the power of testing with multiple comparisons would have been insufficient. For this variable we decided to perform a pairwise comparison with a Wilcoxon signed-ranks test only between the categories familiar conspecific and unfamiliar conspecific. Statistical analyses were performed using GraphPad Instat version 3.0 (GraphPad Software, Inc., La Jolla, CA, U.S.A.).

Analysis of Individual and Group-specific Calls

We analysed echolocation call parameters from all 20 *N. albiventris* to test for statistical differences between the calls of the four social groups. We extracted four separate spectral parameters (fundamental frequency at start and maximum of a call, and maximum frequency at start and maximum of a call), for 20 randomly chosen calls of each individual. We then performed an analysis of similarity (ANOSIM) with 999 permutations to test for statistical evidence for individual or group signatures in *N. albiventris* echolocation calls. Statistical tests were performed with Primer 6 (PRIMER-E Ltd, Plymouth, U.K.).

All tests were two tailed and the significance level was set to 0.05. We tested the normal distribution of data using Kolmogorov–Smirnov tests.

RESULTS

Behavioural Responses

The 20 test animals reacted with a complex repertoire of social behaviours to all stimulus categories in most trials, but adjusted the intensity of their response to the stimulus presented (Table 1). When a stimulus was played back, bats became active and started crawling around in the box, while frequently displaying wing

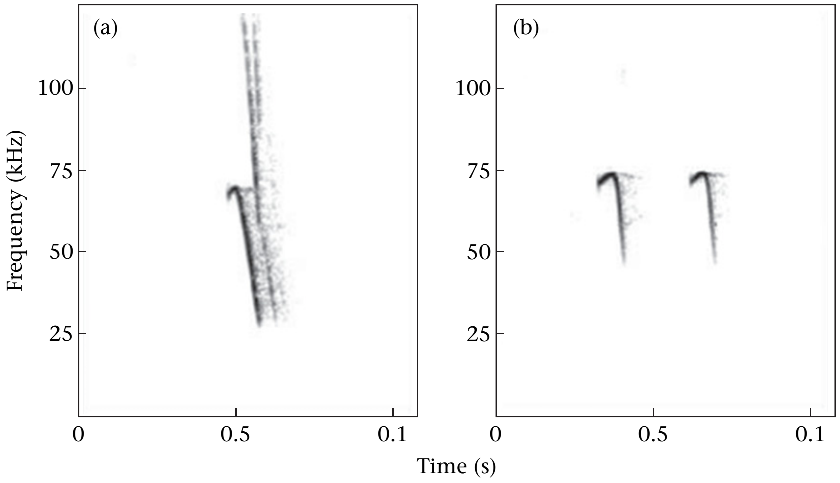

Figure 1. Spectrogram of (a) a honk call and (b) typical orientation calls of *Noctilio albiventris* emitted as a response to playback experiments.

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Table 1
Behavioural responses of 20 bats to familiar conspecifics (FC), unfamiliar conspecifics (UC), cohabitant heterospecifics (CH), noncohabitant heterospecifics (NCH) and white noise (WN) in the 5 min postplayback period

Behaviour	Stimulus category				
	FC	UC	CH	NCH	WN
Crawling	49 (9–168)	66 (4–153)	19 (0–122)	30 (0–70)	41 (0–168)
Nodding	7.2 (0.5–17.0)	8.2 (1.5–29.6)	2.9 (0.0–10.0)	4.1 (0.0–14.0)	4.5 (0.0–17.0)
Wing stretching	2.2 (0.0–5.4)	2.5 (0.0–12.2)	1.4 (0.0–4.8)	1.1 (0.0–3.6)	1.0 (0.0–3.8)
Grooming	1.7 (0.2–10.8)	3.0 (0.6–7.0)	1.4 (0.0–7.6)	1.5 (0.0–4.6)	2.0 (0.0–4.2)
Yawning	0.3 (0.0–1.2)	0.5 (0.0–1.0)	0.3 (0.0–1.0)	0.3 (0.0–1.0)	0.4 (0.0–1.0)
Urinating	0.1 (0.0–0.6)	0.0 (0.0–0.6)	0.0 (0.0–0.6)	0.0 (0.0–0.8)	0.1 (0.0–0.6)
Echolocation	503 (0–1635)	367 (0–1624)	153 (0–3124)	177 (0–1275)	340 (0–1095)
Honk calls	0.5 (0.0–111.0)	0.0 (0.0–107.0)	0.0 (0.0–7.0)	0.0 (0.0–24.0)	0.0 (0.0–16.0)

Responses are given as median and range in parentheses. Crawling is given as a duration (s); all other behaviours are presented as frequencies (*N*/5 min).

stretching, nodding and yawning interrupted by grooming, which included scratching and occasionally licking.

Stimulus-specific Responses

Bats differed in the time they spent crawling as a response to the five treatments (Table 2, Fig. 2a). Post hoc tests showed that bats crawled significantly less after playbacks of cohabitant heterospecifics (CH) and noncohabitant heterospecifics (NCH) than after hearing playbacks of familiar conspecifics (FC). Bats spent less time crawling after hearing calls of CH, NCH and white noise (WN) compared to unfamiliar conspecifics (UC).

The frequencies of nodding, wing stretching and grooming also differed significantly between the five treatments (Table 2, Fig. 2b, c, d). Bats nodded less frequently after playbacks of CH, NCH and WN than after playback of UC. They showed wing stretching significantly more often to playbacks of UC than to playbacks of FC, and more frequently to those of UC than to those of CH, NCH and WN. They also groomed themselves significantly more often after hearing playbacks of UC than after playbacks of CH, NCH and WN. The frequencies of yawning and urinating did not differ significantly between the five treatments (Table 2).

The Friedman test showed significant differences for the response behaviour echolocation, but post hoc tests revealed no significant differences for any of the pairwise comparisons (Table 2).

The pairwise comparison between the categories FC and UC revealed a significant difference (Wilcoxon signed-ranks test: $W = 69$, $T+ = 80$, $T- = -11$, $P = 0.013$; Table 2). Bats produced more honk calls after hearing playbacks of UC than FC.

Individual and Group-specific Calls

Echolocation calls differed significantly between individuals (global $R_{19} = 0.677$, $P = 0.01$; Fig. 3). We found a nearly significant trend for group signatures for the four groups used as stimuli (one UC, three FC), but no significant effect of group affiliation on the echolocation call features analysed (global $R_3 = 0.69$, $P = 0.08$).

DISCUSSION

We investigated whether echolocation calls used for foraging and orientation can also play a role in the social communication of bats. We were able to show that bats respond with a set of social behaviours to the playback of echolocation calls and ultrasonic white noise. To our knowledge, this is the first demonstration that playback of echolocation calls may elicit social behaviours in bats. In accordance with our predictions, *N. albiventris* adjusted their responses to stimulus categories, showing the highest frequencies in all response behaviours towards echolocation calls of unfamiliar conspecifics and the lowest frequencies towards playbacks of other species and white noise.

Behavioural responses to ultrasonic white noise and calls of other species were not different from those towards playbacks of familiar conspecifics, with the exception of crawling. All these sounds share the common property of being of relatively little social relevance to the bats, which might be the reason why they evoked similar responses. Alternatively, these results might indicate that ultrasonic sounds in their own frequency range may be perceived as calls of a familiar conspecific. However, free-ranging, foraging *N. albiventris* never reacted to white noise (Dechmann et al. 2009), suggesting that auditory cues are interpreted and/or perceived differently by bats under varying conditions and depending on the social context.

We conclude that *N. albiventris* can indeed distinguish between calls of conspecifics and heterospecifics, and between calls of familiar and unfamiliar conspecifics. In contrast, we found no difference in their reaction to cohabitant heterospecifics and noncohabitant heterospecifics. Our results demonstrate that

Table 2
Comparisons of response behaviours of *Noctilio albiventris*, calculated with repeated measures (RM) ANOVAs or Friedman tests followed by Bonferroni or Dunn's multiple comparison post hoc tests

Response behaviour	Test	Test value	*P*	Post hoc	FC–UC	UC–CH	UC–NCH	UC–WN	FC–CH	FC–NCH	FC–WN	CH–NCH
Crawling	RM ANOVA	10.171 (*df*=4,15)	**<0.0001**	Bonferroni	NS	**<0.001**	**<0.001**	**<0.05**	**<0.05**	**<0.01**	NS	NS
Nodding	Friedman	23.949 (*m*=5, *N*=20)	**<0.0001**	Dunn's	NS	**<0.001**	**<0.01**	**<0.05**	NS	NS	NS	NS
Wing stretching	RM ANOVA	8.250 (*df*=4,15)	**<0.0001**	Bonferroni	**<0.05**	**<0.001**	**<0.001**	**<0.001**	NS	NS	NS	NS
Grooming	Friedman	21.086 (*m*=5, *N*=20)	**0.0003**	Dunn's	NS	**<0.001**	**<0.01**	**<0.01**	NS	NS	NS	NS
Yawning	Friedman	3.941 (*m*=5, *N*=20)	0.414	x	x	x	x	x	x	x	x	x
Urinating	Friedman	6.161 (*m*=5, *N*=20)	0.188	x	x	x	x	x	x	x	x	x
Echolocation	Friedman	13.664 (*m*=5, *N*=20)	**0.036**	Dunn's	NS	NS	NS	NS	NS	NS	NS	NS
Honk calls	Wilcoxon	*W*=69 (*N*=20 pairs)	**0.013**[*]	x	x	x	x	x	x	x	x	x

Statistically significant results are highlighted in bold. Post hoc comparisons were performed between FC and UC, CH, NCH, WN; UC and CH, NCH, WN; and CH and NCH. Honk calls were compared with a Wilcoxon signed-ranks test between the categories familiar conspecific and unfamiliar conspecific. CH: cohabitant heterospecific; FC: familiar conspecific; NCH: noncohabitant heterospecific; UC: unfamiliar conspecific; WN: white noise. An 'x' indicates that no post hoc comparison was made.

[*] Significance of comparison of FC–UC with a Wilcoxon signed-ranks test.

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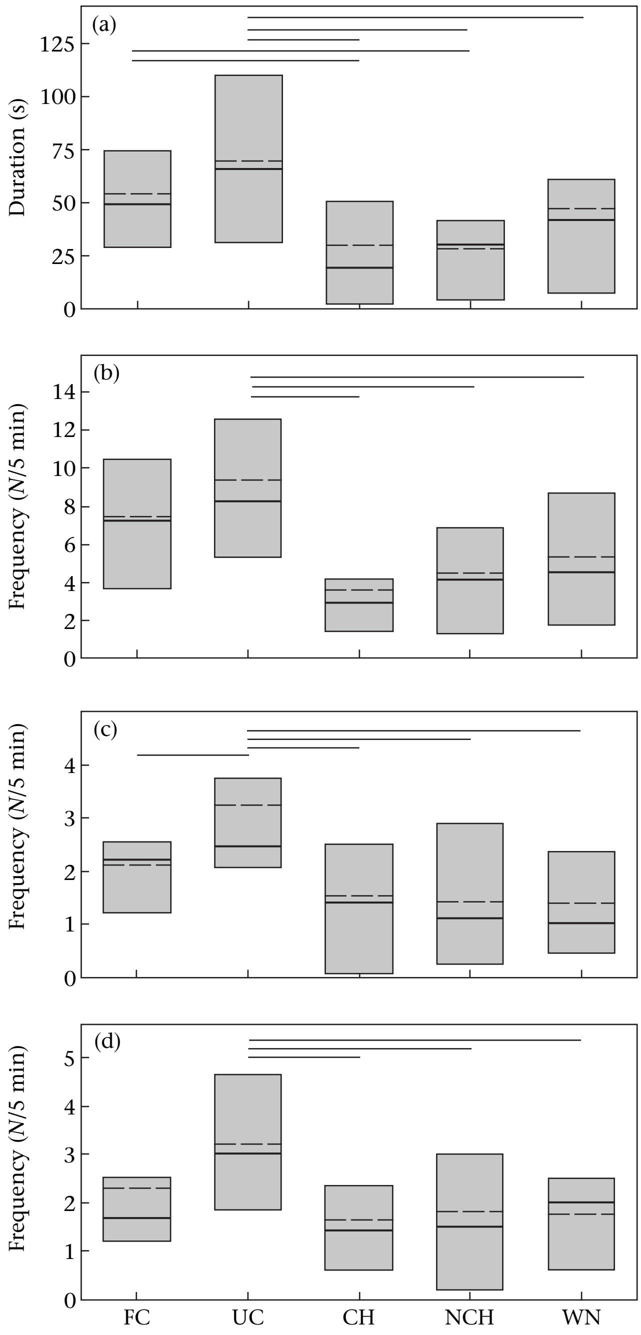

Figure 2. Duration of (a) crawling and frequencies of (b) nodding, (c) wing stretching and (d) grooming of 20 *Noctilio albiventris* in response to playbacks of calls of familiar conspecifics (FC), unfamiliar conspecifics (UC), cohabitant heterospecifics (CH), noncohabitant heterospecifics (NCH) and white noise (WN) within a 5 min postplayback phase. The median is represented by a solid black line and the mean by a dashed black line within a box. The borders of boxes are 25 and 75 percentiles. Significant differences between two stimulus categories are indicated by bars above box plots. Respective *P* values are given in Table 2.

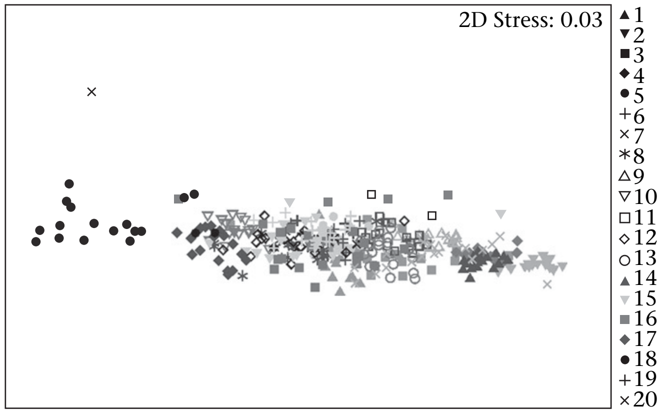

Figure 3. Two-dimensional plot calculated after multidimensional scaling analyses. The graph is based on Bray–Curtis similarities of log($x + 1$) transformed acoustical features of 20 calls of each of 20 individual *Noctilio albiventris* bats, belonging to four social groups. Each symbol represents one individual.

echolocation is not necessarily and not only ‘autocommunication’ (sensu Bradbury & Vehrencamp 1998) implying that echolocation is only perceived and processed by the individual producing the sound. Instead, other individuals may also obtain information about species identity and group affiliation by listening to echolocation calls. We therefore support the idea that echolocation has a dual function and is used for orientation and foraging as well as acoustic communication in bats. The characteristics that might have served test bats to distinguish between different echolocation call types include spectral, temporal and amplitudinal information. The roles of these call characteristics for discrimination purposes will need to be clarified in future studies.

Why did bats generally respond more frequently with social behaviours to unfamiliar conspecifics than to heterospecifics, and significantly more often with wing stretching and honk calls to unfamiliar than to familiar conspecifics? As any behaviour imposes costs, animals should carefully allocate their efforts. For this reason, we suppose that *N. albiventris* might reduce costs of repeated social interactions with familiar conspecifics and socially less important other species, and thus in comparison would respond more strongly to unfamiliar conspecifics. This is similar to a pattern found in various, mostly territorial animal species that tend to be less aggressive towards familiar neighbours, more aggressive towards strangers, and often show no aggression at all towards other species (reviewed in Temeles 1994).

Acoustical Response Behaviour

The number of echolocation calls emitted during experiments did not differ between playback categories, but bats did respond more often with honk calls to playbacks of unfamiliar than familiar conspecifics. The observed honk calls of *N. albiventris* resemble those of *N. leporinus*, anecdotally described by Suthers (1965). Flying *N. leporinus* are thought to use ‘honks’ to avoid collision with conspecifics. Alternatively, honk calls could also be a call coding for individual identity, similar to the signature whistle calls found in dolphins (Tyack 1986; Smolker et al. 1993; Sayigh et al. 1999), chirp contact calls of white-nosed coatis, *Nasua narica* (Maurello et al. 2000) or phee calls of the common marmoset, *Callithrix jacchus* (Jones et al. 1993).

Echolocation and the Social System of N. albiventris

Noctilio albiventris forage in small social units of up to five individuals that emerge from larger colonies (Dechmann et al. 2009), but have been reported to live in colonies comprising up to 700 individuals (Brown et al. 1983). Thus, we assume that individuals foraging together also roost close to each other, a pattern similar to that observed in *Phyllostomus hastatus*. This bat species lives in large colonies with smaller stable subunits and uses group-specific social

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calls to coordinate foraging activities (Wilkinson & Boughman 1998). As individual recognition is an essential condition for maintaining stable social groups (Beecher 1989), and we almost never found *N. albiventris* to emit social calls while foraging (Dechmann et al. 2009; personal observation), it seems likely they may use acoustical signatures in their echolocation calls to mediate group foraging. Furthermore, our results suggest that the same may hold true for the maintenance of social groups within the roost. This is supported by significant call differences between individuals and a trend towards group signatures in their echolocation calls. Recognition of group affiliation may be important, since the efficiency of group foraging in *N. albiventris* probably depends on an optimal group size (Beauchamp & Fernández-Juricic 2005). Radiotracking data support the hypothesis that foraging social groups are stable over time in *N. albiventris* (Dechmann et al. 2009) and *N. leporinus* (Brooke 1997). Individual signatures in echolocation calls and the bats' ability to differentiate between them may be a prerequisite for the complex social systems of both *Noctilio* species.

Individual and Species Recognition in Bats

Social recognition systems differ between species, depending on an animal's perceptual abilities and degree of sociality. In bat species studied to date, scent plays a key role in species recognition (*S. bilineata*; Caspers et al. 2009), recognition of colony members (De Fanis & Jones 1995; Bouchard 2001; Safi & Kerth 2003), kin (Gustin & McCracken 1987) and individuals (Caspers et al. 2008). However, even if social recognition via scent may be optimal at close range, that is, mainly in the roost, it is unlikely to function in long-range communication. For that purpose, echolocation calls seem an ideal modality for social recognition and communication as, irrespective of the context, bats invariably have to produce them at high rates (several calls/s) for orientation, either in the roost or during foraging.

It is generally assumed that echolocation has evolved from ancestral social calls that gradually developed according to the bats' foraging requirements during the night (e.g. Fenton 1983). Echolocation call design thus reflects the strong selection pressures faced by bats when foraging. Consequently, even distantly related bat species share similar features in call design when facing similar ecological conditions (Schnitzler et al. 2003). For this reason, echolocation call design has been used as a textbook example of convergent evolution (e.g. Dawkins 1996). However, echolocation calls may have also evolved partly in the context of social systems. The possibility of an ultrasound-based mechanism of species recognition was first addressed by Heller & von Helversen (1989), who argued that rhinolophid bats partition the acoustical communication channel by using species-specific echolocation calls (but see Kingston et al. 2000). This would facilitate the recognition of species-specific calls. Further evidence for this hypothesis was reported by Russo et al. (2007), who found island rhinolophids had diverging echolocation calls from mainland species. They suggested that species recognition and facilitation of intraspecific communication are the most likely factors explaining the observed phenomenon.

One fundamental condition for a signal to be useful for social communication is to be species specific, but also to differ between the sexes, social groups or, most importantly, individuals. Bats may benefit from recognizing individual signatures in echolocation calls, as they might enhance social bonds between group members and optimize the efficiency of group foraging. In fact, echolocation calls can be used by conspecifics to obtain information about the quality of feeding grounds (for *N. albiventris*: Dechmann et al. 2009, for other bats: Barclay 1982; Gillam 2007). Similarly, inexperienced juvenile *M. lucifugus* are guided to hibernacula by echolocation calls of swarming bats (Thomas et al. 1979) and several bat species locate roosts faster when eavesdropping on conspecific echolocation calls (e.g. Ruczynski et al. 2007, 2009). In a mating context, echolocation calls could be used by bats as indicators of state and quality of mates, territories, mating grounds or swarming sites. Female *E. fuscus*, for example, adjust their calling rate after having heard an echolocation playback stimulus depending on the sex of the call producer (Kazial & Masters 2004). Grilliot et al. (2009) found that male and female *E. fuscus* differed in echolocation call features in a roosting situation, but not while flying. Generally, the use of echolocation calls within the roost is difficult to study because of the nocturnal and cryptic lifestyle of bats. Our experiment, however, provides crucial evidence that echolocation indeed plays a role in social recognition within the roost, and that it may be used by bats to obtain essential social information from echolocating individuals.

A Dual Function of Echolocation

Communication in the ultrasonic range, although unusual and seemingly not practical because of the strong attenuation of high frequencies, is nevertheless used by species of several different taxa, such as mating calls in frogs (Feng et al. 2006), alarm calls in squirrels (Wilson & Hare 2004) and calls produced in social contexts by dolphins (Lammers et al. 2003). However, these are all examples of animals intentionally producing vocalizations for communication. In contrast, bat echolocation has a dual role: it is used by bats for orientation and foraging, but can also communicate species identity (this study), individual identity (Kazial et al. 2008; Yovel et al. 2009), sex (Kazial & Masters 2004) and group affiliation (this study). We are not aware of any other taxon in which a ubiquitous behaviour exhibited by an animal explicitly for a nonsocial purpose, such as orientation, additionally serves a function as a signal for its conspecifics. This makes bats a unique model for studying the coexistence of two functions in one signal, and may shed light on so far unexplored but important aspects of the evolution of communication.

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