



universität  
wien

# DIPLOMARBEIT

Titel der Diplomarbeit

**A dual function of echolocation:**

**Do bats use echolocation calls to identify familiar and unfamiliar individuals of their own and other species?**

angestrebter akademischer Grad

Magister der Naturwissenschaften (Mag. rer.nat.)

Verfasserin:

Silke Luise Heucke

Matrikel-Nummer:

0305968

Studienrichtung (lt. Studienblatt):

Zoologie

Betreuerin / Betreuer:

Prof. Dr. Michael Taborsky

Wien, im

Mai 2009

## Table of Contents

1. <b>Abstract</b> .....	2
2. <b>Zusammenfassung</b> .....	3
3. <b>Introduction</b> .....	4
4. <b>Methods</b> .....	7
4.1. Study Site and Bats.....	7
4.2. Stimulus Acquisition.....	7
4.3. Experimental Procedure.....	8
4.4. Physical and Acoustical Analysis of Responses .....	9
4.5. Statistical Analysis of Responses.....	10
4.6. Individual and Group-specific Echolocation Calls: Analysis of Similarity.....	10
5. <b>Results</b> .....	11
5.1. Physical Response Behaviour of <i>Noctilio albiventris</i> in Playback Experiments.....	11
5.2. Acoustical Response Behaviour of <i>Noctilio albiventris</i> in Playback Experiments....	11
5.3. Stimulus-specific Responses.....	12
5.4. Individual and Group-specific Calls: Analysis of Similarity .....	15
6. <b>Discussion</b> .....	16
6.1. Physical Response Behaviour of <i>Noctilio albiventris</i> in Playback Experiments.....	17
6.2. Acoustical Response Behaviour of <i>Noctilio albiventris</i> in Playback Experiments....	19
6.3. The Importance of Echolocation in the Social System of <i>Noctilio albiventris</i> .....	19
6.4. Individual and Species Recognition in Bats.....	20
6.5. Echolocation: Signal or Cue in Chiropteran Communication? .....	22
6.6. A Dual Function of Echolocation: Bats as a unique Model in Animal Communication.....	23
7. <b>References</b> .....	24
8. <b>Acknowledgements</b> .....	31
9. <b>Curriculum Vitae</b> .....	32

## Abstract

Bats use echolocation for orientation during foraging and navigation. However, it remained unclear whether echolocation calls may also have a communicative function, for instance between members of the same roost site. In principle, this seemed possible because echolocation calls are species-specific and known to differ between sexes, and among colonies and individuals. We performed playback experiments with lesser bulldog bats, *Noctilio albiventris*, to which we presented calls of familiar/unfamiliar conspecifics, cohabitant/non-cohabitant heterospecifics and ultrasonic white noise. Bats reacted with a complex repertoire of social behaviours and the intensity of their response differed significantly between stimulus categories. Overall, the strongest reactions were shown toward echolocation calls of unfamiliar conspecifics than toward heterospecifics and white noise. Bats responded with two behaviours more frequently to unfamiliar than to familiar conspecifics. To our knowledge, this is the first time that bats were found to react to echolocation calls with a suite of social behaviours. Our data also provide the first evidence for acoustical differentiation of bats between familiar and unfamiliar conspecifics, and heterospecifics. Analysis of echolocation calls confirmed significant differences between the echolocation calls of individuals. We found a trend towards group signatures in echolocation calls of *N. albiventris*. Consequently, we suggest that echolocation calls used during orientation may also communicate species identity, group-affiliation and individual identity in the completely different context of social situations. Our study highlights the communicative potential of ubiquitous signals that have previously been categorized as cues in animal social systems. Hence, by improving our understanding of the multiple functions of such signals, we may gain further important insight into the evolution of communication in animals.

## Zusammenfassung

Fledermäuse nutzen Echoortung bei der nächtlichen Jagd und zur Orientierung. Es ist jedoch noch nicht bekannt, ob Echoortsrufe zusätzlich eine kommunikative Funktion besitzen, beispielsweise in der sozialen Interaktion zwischen Mitgliedern des gleichen Tagesquartiers. Prinzipiell scheint dies möglich, da Echoortungsrufe sich auf der Ebene der Art, der Geschlechter, der Kolonien und der Individuen unterscheiden können. Wir untersuchten das Antwortverhalten der Kleinen Hasenmaulfledermaus (*Noctilio albiventris*) auf Echoortungsrufe bekannter und unbekannter Individuen der eigenen Art sowie auf Echoortungsrufe einer Fledermausart, die die gleichen Quartiere bewohnt, und einer Art, die gänzlich andere Quartiere bewohnt. Die Fledermäuse reagierten mit einem komplexen sozialen Verhaltensrepertoire auf die präsentierten Ortungsrufe und sie unterschieden sich signifikant in der Intensität des Antwortverhaltens gegenüber den verschiedenen Stimuluskategorien. Die Tiere reagierten insgesamt am stärksten auf Echoortungsrufe unbekannter Individuen der eigenen Art im Vergleich zu solchen von Tieren einer anderen Art und weißem Rauschen. Die Tiere reagierten mit zwei Verhaltensweisen häufiger auf unbekannte als auf bekannte Individuen der eigenen Art. Soweit uns bekannt ist, ist dies das erste Mal, dass bei Fledermäusen soziales Verhalten als Antwort auf Echoortungsrufe gezeigt werden konnte. Unsere Daten liefern zudem erste Hinweise auf eine akustische Differenzierung der Fledermäuse zwischen bekannten und unbekanntem Tieren der eigenen Art und anderen Arten. Akustische Analysen der Echoortungsrufe bestätigten, dass signifikante Unterschiede zwischen Rufen einzelner Individuen bestehen. Zudem fanden wir Hinweise auf Gruppensignaturen in den Echoortungsrufen von *N. albiventris*. Unsere Ergebnisse weisen darauf hin, dass Fledermäusen Echoortungsrufe zusätzlich dazu nutzt, um Art- und Gruppenzugehörigkeit sowie Individualität zu kommunizieren. Unsere Untersuchung weist auf das kommunikative Potential allgegenwärtiger Signale im Tierreich hin, die bisher als ‚Cues‘ bewertet wurden. Wir vermuten deshalb, dass durch ein besseres Verständnis der multiplen Funktionen solcher Signale, weitere wichtige Einsichten über die Evolution der Kommunikation im Tierreich gewonnen werden können.

## Introduction

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 and Gerhardt 2002), birds (reviewed in Falls 1982) and mammals (e.g. Rendall et al. 1996). Likewise, the 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, so-called heterospecifics (Kunz 1982). The role of acoustic communication in social interactions among conspecifics and different species sharing roosts however, is 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, audible to many humans and usually of multi-harmonic structure (Fenton 2003). Social calls have been shown to be individually distinct (Carter et al. 2008), to mediate group foraging (Boughman and Wilkinson 1998; Wilkinson and Boughman 1998), and they are also used in agonistic (Racey and Swift 1985) and territorial interactions (Behr et al. 2006) as well as in courtship display (Behr and Helversen 2004). By contrast, echolocation has for a long time only been viewed as an acoustical tool that enables bats to orientate in darkness; a prerequisite for location of prey and navigation in space and time at night (e.g. Griffin 1958; Schnitzler et al. 2003). Although the unique echolocation abilities of bats have received great scientific attention, so far research efforts have mainly focused either on the extraordinarily precise spatial discrimination bats can achieve with echolocation (e.g. Simmons et al. 1983; Moss and Surlykke 2001; Grunwald et al. 2004) or on neural processing of echolocation calls in the auditory cortex (e.g. Grinnell 1973; Suga and 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 example, bats may eavesdrop on conspecifics' feeding buzzes, echolocation calls shortly emitted before a prey capture attempt (Balcombe and Fenton 1988; Gillam 2007; Dechmann et al. in press). Several studies have also shown that bats adjust frequency and pressure levels of their echolocation calls according to the presence of conspecifics (Obrist

1995; Ibáñez et al. 2004; Ratcliffe et al. 2004; King 2005; Gillam et al. 2007; Bates et al. 2008), noisy environments (Schaub et al. 2008) or habitat types (Obrist 1995; Ibáñez et al. 2004; Gillam and McCracken 2007). We are aware though of only two laboratory studies that investigated the potential of echolocation for communication and social recognition. Kazial and 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* recognizes individuals based on echolocation calls. Independently, numerous studies have statistically confirmed that echolocation calls code for age (Jones and Ransome 1993; Jones and Kokurewicz 1994; Masters et al. 1995), family affiliation (Masters et al. 1995), sex (Neuweiler et al. 1987; Jones and Kokurewicz 1994), colony membership (Masters et al. 1995; Pearl and Fenton 1996) and individuality (Fenton et al. 2003), which suggests a great communication potential of echolocation calls that remained thus far mostly unexplored. Here, we used the lesser bulldog bat, *Noctilio albiventris*, to experimentally test whether echolocation is used for communication among roost members and if so, what messages might be communicated via echolocation.

*Noctilio albiventris* has a circum-tropical distribution in the New World (Hood and Pitocchelli 1983). They roost in large colonies of up to 700 individuals in hollow trees and houses (Brown et al. 1983; Hood and Pitocchelli 1983). Brooke (1997) reported that *Noctilio leporinus*, the larger sibling species, forms long-term female associations ranging from 3 to 9 individuals. 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. in press). Means to discriminate between group-members and non-group-members are probably important to maintain such social bonds. Olfactory recognition seems an unlikely mechanism to serve this function during flight. Acoustic recognition via echolocation calls however, could possibly play a crucial role as bats anyways have to echolocate continuously while foraging. Accordingly, we hypothesised that either individual or group signatures in echolocation calls, may function as an acoustically mediated social recognition system. *Noctilio albiventris* employ constant frequency and frequency modulated signals while foraging, the proportion of the two components changing with the animals' behaviour and information requirements (Kalko et al. 1998). Their echolocation calls are highly plastic and are adjusted to foraging context, flying mode and social context (Brown et al. 1983; Kalko et al. 1998). Brown and co-authors (1983) already described variations among individual echolocation calls, with fundamental frequencies

ranging from 65 to 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, this species often shares roosts with another common neotropical bat species, the Pallas's mastiff bat, *Molossus molossus* (personal observation; records for *Molossus sp.* sharing roost with *Noctilio albiventris*: Bloedel 1955; Dolan & Carter 1979). In general, bats frequently share roosts with other species and roost interactions between cohabitant species have been anecdotally described in a number of species (Kunz 1982; Swift and Racey 1983; Graham 1988; Wohlgenant 1994; Rodríguez-Durán 1998).

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, e.g. species-identity, group-membership or familiarity. Thus, playback of calls carrying different social information should elicit either different sets of behaviour, or targeted bats should adjust the intensity of their reaction to the playback's information content. To address this question, we quantified the response behaviours to five stimulus categories in a playback experiment. Stimulus categories were calls from (1) familiar conspecific individuals, (2) unfamiliar conspecific individuals, (3) cohabitant heterospecifics (*Molossus molossus*), (4) non-cohabitant 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 calls.

We expected that *N. albiventris* can distinguish between all stimuli and that they would adjust their response differently to 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 should differ among 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 (*Noctilio albiventris*, Noctilionidae; *Molossus molossus*, Molossidae; *Uroderma bilobatum*, Phyllostomidae) were caught with mistnets (Ecotone, Warzwawa, Poland) or a hand made harp trap (Tuttle 1974) when emerging from their daytime roosts. In total, we caught four social groups of *N. albiventris*. The first group was only used for stimulus acquisition and was released immediately after recordings were obtained. The other three social groups were later on used in the playback experiment (see below). Two of these groups were caught during evening emergence from different day-time roosts in buildings. The first group consisted of four females and three males, the second of six females and two males. The third group consisting of four males and one female was caught while foraging over the water in the surrounding 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 non-lactating individuals were kept for experiments or recordings. We measured body mass (handheld balance, Pesola, Switzerland; accuracy  $\pm 0.5$  g) and forearm length (calipers, Bahr-Digimess, Germany, accuracy  $\pm 0.5$  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 (Kerth and König 1996).

### *Stimulus Acquisition*

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

To make the playback files, we caught the above mentioned bat species when they emerged from their day-roost. We then 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 x 2 x 5 m). Recordings from *M. molossus*, who are unable to fly in a flight cage due to 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 (holding conditions described below) 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). Sampling rate was always 250 kHz and the bit rate was 16. 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. As recordings were usually of short duration (a few ms), we repeated them until the sequences were eight seconds long. We used SASLab Pro 4.40 (Avisoft Bioacoustics, Berlin, Germany) to construct playback sequences.

### ***Experimental Procedure***

Experiments were conducted with twenty experimentally naïve bats belonging to three social groups. *Noctilio albiventris* that leave the roost together usually forage as a group (Dechmann et al. in press). Therefore 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 five days before we started experiments. Cages were located in separate rooms, to avoid familiarization between the groups via sound, vision or odour. Animals were kept in a shaded room in small mosquito tents (14 x 6 x 15 inches, Pea pod, KidCo, USA) at ambient temperature and humidity. Bats were maintained on an ad libitum diet of mealworms (larval stages of *Tenebrio molitor*) and water, and were weighed on a regular basis to monitor the well-being of the animals.

For playback experiments, we transferred single bats into a flight cage and placed them in a plastic box (137 x 52 x 14 cm) covered with mosquito screen. Experiments were conducted between 1800 and 0300 hours. For the playback we placed an Ultrasonic Dynamic Speaker (Scan Speak, Avisoft Bioacoustics, Berlin) at a 65 cm distance to the left corner of the test box. We illuminated the flight cage with two 25 W red light bulbs to facilitate filming

and used a SONY NightShot handy-cam (Sony, Tokyo, Japan) to record the physical responses of bats. Additionally, we recorded the acoustic response of bats with the microphone and settings described above. The microphone was positioned at a 75 cm distance from the right corner of the test box.

Bats were allowed to get used to the experimental situation for at least 30 min before the start of experiments. Prior to each playback 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. in press) 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 pre-playback phase (2 min), a playback phase (8 s) and a post-playback phase (5 min). The condition for a pre-playback phase was that bats had to be hanging motionless and silent for at least two minutes. If this condition was fulfilled, we started the playback phase of eight seconds by presented the respective stimulus. For analysis we recorded the physical and acoustical responses of the bat during the five minute post-playback phase.

### ***Physical and Acoustical Analysis of Responses in the Post-playback Period***

We analyzed videos using the software Interact (Mangold, Arnstorf, Germany). We defined six behavioural variables that we had observed as physical responses to the test stimuli: crawling, nodding, wing-stretching, yawning, grooming and urine marking. We also commonly observed these behaviours in other experiments, where either two familiar or unfamiliar bats were confronted with each other (Dechmann et al. in prep). Most of these behaviours have also been described in other bat species within a social context (wing-displays: Tyrell 1990; Singaravelan and Marimuthu 2008; yawning displays: Gebhard 1997; Voigt and von Helversen 1999; urine marking: Gustin and McCracken 1987; Brooke 1997)

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 number of echolocation calls (Kalko et al. 1998) and calls that resembled the honk calls described by Suthers (1965) for *Noctilio leporinus*, in spectrograms using 512 FFT size, an overlap of 50% and Hamming window in SASlab Pro. All videos and audio files were coded blind by a single person.

### ***Statistical Analysis of Responses***

We averaged every behavioural reaction of each of the twenty bats to the same stimulus category over the five trials. For statistical analysis of physical responses and the number of echolocation calls, we performed either repeated measures ANOVAs or Friedman tests, depending on the distribution of data. When performing repeated measures ANOVAs we used Bonferroni Multiple Comparisons for post-hoc tests. After Friedman tests, we used Dunn's Multiple Comparisons as post-hoc tests. In 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 non-cohabitant heterospecific.

Only twelve out of twenty bats responded with honk calls to playbacks. Thus the power of testing with multiple comparisons would have been insufficient. We decided for this variable to perform a pairwise comparison with Wilcoxon matched-pairs signed-ranks test only between the categories familiar conspecific and unfamiliar conspecific, because similar honk calls were found to be involved during intra-specific communication in *N. leporinus* (Suthers 1965). Statistics were performed using GraphPad InStat version 3.0 (GraphPad Software, Inc., La Jolla, U.S.A.).

### ***Individual and Group-specific Echolocation Calls: Analysis of Similarity (ANOSIM)***

To test for statistical differences between the calls of the three experimental groups (familiar conspecific stimuli) and the group whose calls were presented as the unfamiliar conspecific stimulus, we analyzed echolocation call parameters from all twenty *N. albiventris*, whose calls we used in our experiments. We extracted four separate spectral parameters (fundamental frequency (at start and maximum of a call), maximum frequency (at start and maximum of a call), for twenty randomly chosen calls of each individual. We then performed an analysis of similarity (ANOSIM: see Clarke and Warwick 1994) 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 values are presented as means  $\pm$  one standard deviation (SD). 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

### *Physical Response Behaviours of Noctilio albiventris in Playback Experiments*

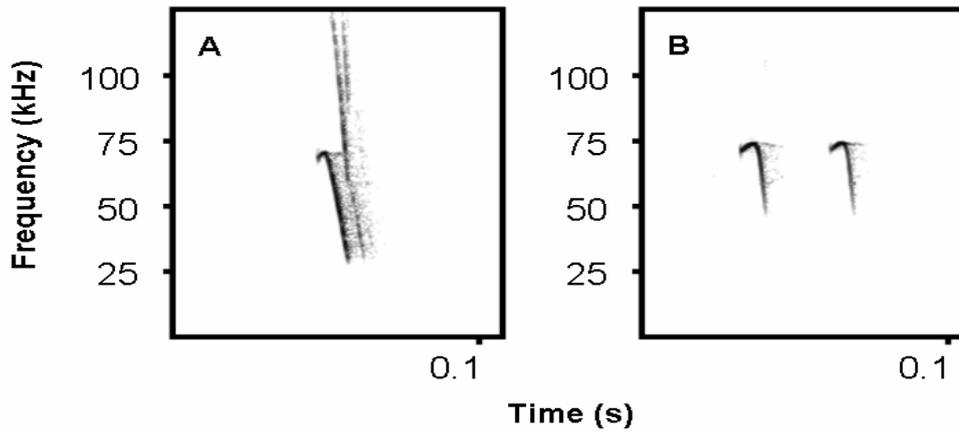
The twenty test animals reacted with a complex repertoire of social behaviours to all stimulus categories in most trials, but adjusted the intensity of their response to the stimulus presented (Table 1). When a stimulus was played back, bats became active and started crawling around in the box, while frequently displaying wing-stretching, nodding, and yawning interrupted by grooming, which included scratching and occasionally licking.

**Table 1.** Behavioural responses of twenty bats to familiar conspecifics (FC), unfamiliar conspecifics (UC), cohabitant heterospecifics (CH), non-cohabitant heterospecifics (NCH) and white noise (WN) in the five minute post-playback period. Responses are given as median and numbers in brackets depict minimum and maximum values; parameter crawling in seconds of duration, all other behaviours are presented as frequencies (n / 5 min).

Behaviour	Stimulus Category				
	FC	UC	CH	NCH	WN
Crawling	49 (9-168)	66 (4-153)	19 (0-122)	30 (0-70)	41 (0-168)
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)
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)
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)
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)
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)
Echolocation Calls	503 (0-1635)	367 (0-1624)	153 (0-3124)	177 (0-1275)	340 (0-1095)
Honk Calls	0.5 (0.0-111)	0.0 (0.0-107.0)	0.0 (0.0-7.0)	0.0 (0.0-24.0)	0 (0.0-16.0)

### *Acoustical Response Behaviour: Echolocation and Honk Calls*

*Noctilio albiventris* emitted two types of calls in the ultrasonic range as acoustical response to our experiments: ‘normal’ echolocation calls similar to the calls of bats orientating 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 (Figure 1). For a lack of a better definition, we classified them as ‘honk’ calls as they resembled the honk calls described by Suthers (1965) for *Noctilio leporinus*.



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

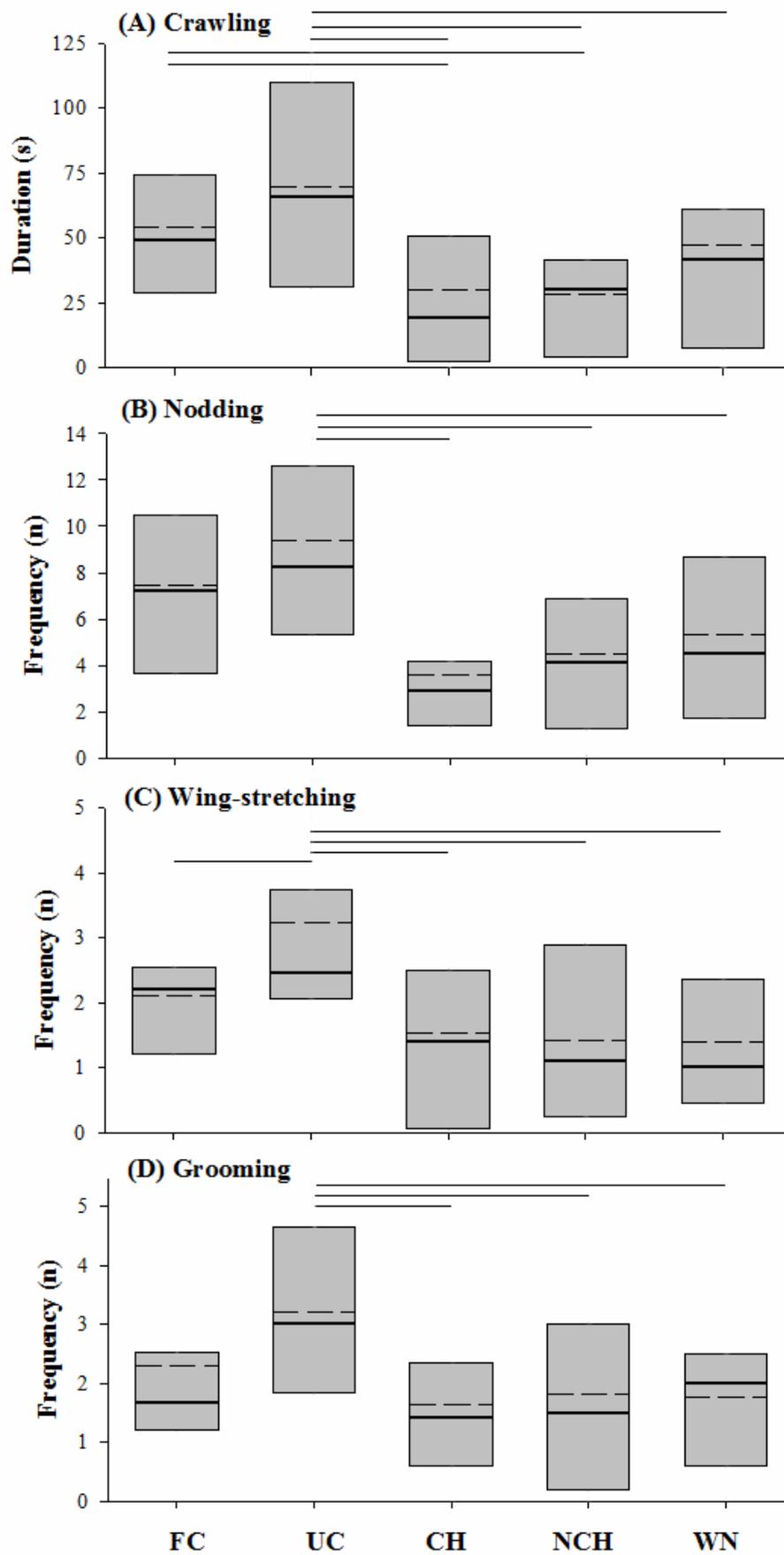
### ***Stimulus-specific Response***

The frequency of yawning and urinating were not found to differ significantly between the five playback categories (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). Bats differed in the time they spent crawling as a response to the five stimuli (Table 2; Figure 2 A). Post-hoc tests showed that bats crawled significantly less after playbacks of cohabitant heterospecifics (CH) and non-cohabitant heterospecifics (NCH) compared to their response 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 frequency of self-grooming differed significantly among the playback categories (Table 2; Figure 2 D). Post-hoc tests showed that bats groomed themselves significantly more often after hearing playbacks of unfamiliar conspecifics compared to their reaction toward playbacks of CH, NCH and WN. We also found the response behaviour nodding to differ significantly among the five treatments (Table 2; Figure 2 B). Bats nodded less frequently after playbacks of CH, NCH and WN when compared to their reaction to playback of UC. Moreover, the frequency of wing-stretching differed significantly among the five playback treatments (Table 2; Figure 2 C). Here, bats showed the behaviour wing-stretching significantly more often to playbacks of unfamiliar than to playbacks of familiar conspecifics, and more frequently toward those of UC than to CH, NCH and WN. For the response behaviour honk calls, we found pairwise comparison between the categories FC and UC to be significant (Wilcoxon matched-pairs signed rank test,  $W = 69$ ,  $T_+ = 80$ ,  $T_- = -11$ ,  $p = 0.0134$ ; Table 2).

**Table 2:** Comparisons of response behaviours in playback experiment with twenty *Noctilio albiventris*. Comparisons were calculated with repeated measures ANOVAs (RM-ANOVA) and with Friedman tests depending on the distribution of data. For post-hoc tests we choose Bonferroni Multiple Comparisons for parametric testing and Dunn’s Multiple Comparisons for non-parametric testing. Post-hoc comparisons were performed between FC and UC, CH, NCH, WN; UC and CH, NCH, WN; and CH and NCH. For the response behaviour honk calls, we performed a pairwise comparison with Wilcoxon matched-pairs signed-ranks test between the categories familiar conspecific and unfamiliar conspecific. Abbreviations are: CH = cohabitant heterospecific, d.f. = degrees of freedom, FC = familiar conspecific, n.s. = not significant, NCH = non-cohabitant heterospecifics, UC = unfamiliar conspecific, WN = white noise.

Response Behaviours	Test	Test-value	P-value	Post-hoc	FC-UC	UC-CH	UC-NCH	UC-WN	FC-CH	FC-NCH	FC-WN	CH-NCH
<b>Crawling</b>	RM-ANOVA	10.171 (d.f.= 4,15)	<b>&lt;0.0001</b>	Bonferroni	n.s.	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.05</b>	<b>&lt;0.05</b>	<b>&lt;0.01</b>	n.s.	n.s.
Yawning	Friedman	3.941 (m = 5, n = 20)	0.4141	Dunn’s	x	x	x	x	x	x	x	x
<b>Grooming</b>	Friedman	21.086 (m = 5, n = 20)	<b>0.0003</b>	Dunn’s	n.s.	<b>&lt;0.001</b>	<b>&lt;0.01</b>	<b>&lt;0.01</b>	n.s.	n.s.	n.s.	n.s.
<b>Nodding</b>	Friedman	23.949 (m = 5, n = 20)	<b>&lt;0.0001</b>	Dunn’s	n.s.	<b>&lt;0.001</b>	<b>&lt;0.01</b>	<b>&lt;0.05</b>	n.s.	n.s.	n.s.	n.s.
Urinating	Friedman	6.161 (m = 5, n = 20)	0.1875	Dunn’s	x	x	x	x	x	x	x	x
<b>Wing-Stretching</b>	RM-ANOVA	8.250 (d.f. = 4,15)	<b>&lt;0.0001</b>	Bonferroni	<b>&lt;0.05</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	n.s.	n.s.	n.s.	n.s.
Echolocation Calls	Friedman	13.664 (m = 5, n = 20)	<b>0.0356</b>	Dunn’s	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
<b>Honk Calls</b>	Wilcoxon	W = 69 (n = 20 pairs)	<b>0.013</b>	x	<b>0.013<sup>a</sup></b>	x	x	x	x	x	x	x

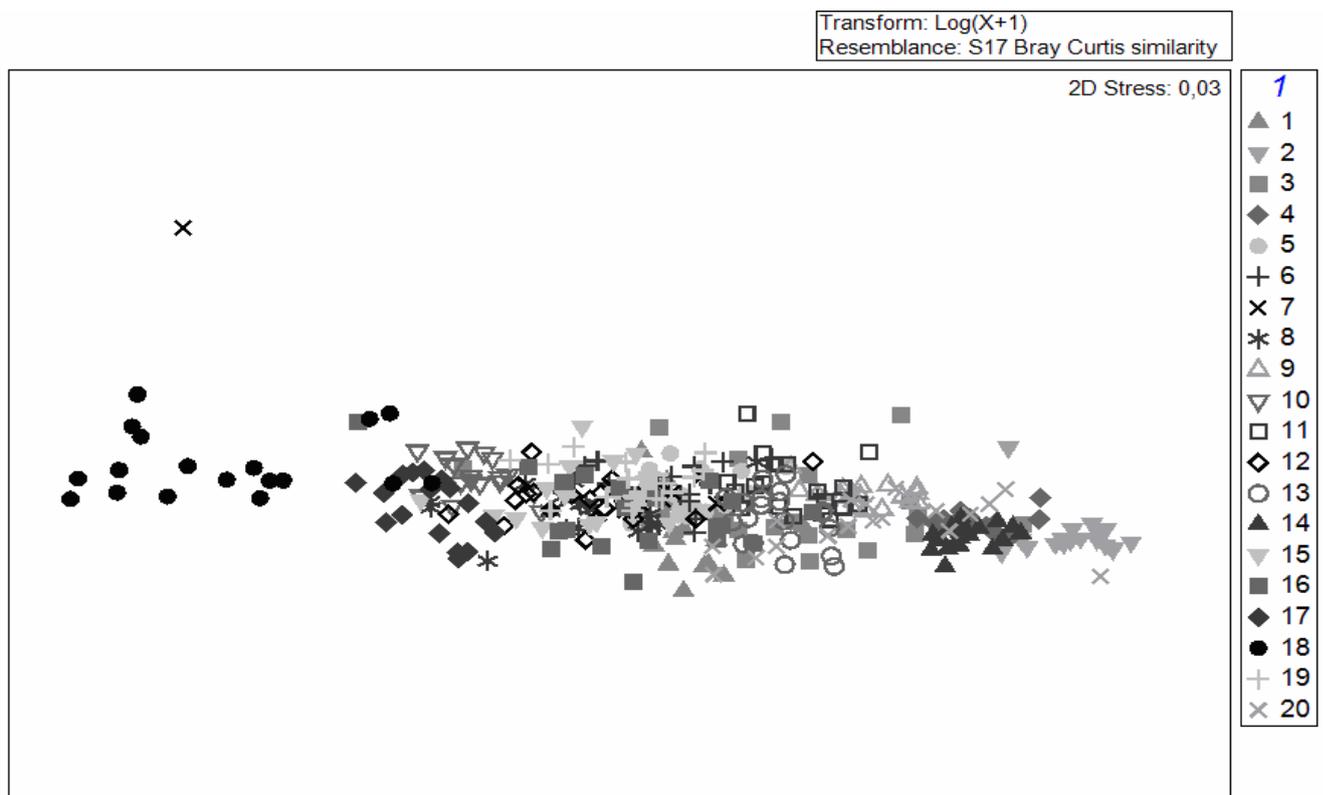
<sup>a</sup> indicates significance of comparison of FC-UC with Wilcoxon matched-pairs signed-ranks test.



**Figure 2.** Duration of crawling (A) and frequencies of nodding (B), wing-stretching (C) and grooming (D) of twenty *Noctilio albiventris* in response to playbacks of calls of familiar conspecifics (FC), unfamiliar conspecifics (UC), cohabitant heterospecifics (CH), non-cohabitant heterospecific (NCH), and white noise (WN) within a five minute post-playback phase. The median is represented by a solid black line, the mean by a dashed black line within a box. The borders of boxes are 25 and 75 percentiles. Significances between two stimulus categories are indicated by bars above box-plots. P-values are given in table 2.

***Individual and Group-specific Echolocation Calls:***

Echolocation calls of twenty *N. albiventris* differed significantly among individuals (ANOSIM, Global R = 0.677, df = 19, p = 0.01; Figure 3). We found a trend for group-signatures, but no significant effect of group-affiliation on analysed echolocation call features (ANOSIM; Global R=0.69, df = 3, p = 0.08).



**Figure 3.** Two-dimensional plot calculated after Multi-Dimensional-Scaling (MDS) analyses. The graph is based on Bray-Curtis similarities of log(x+1) transformed acoustical features of twenty calls of each of the twenty individual *N. albiventris* bats, belonging to four social groups. Each symbol represents one individual.

## Discussion

In this study, we showed that bats responded with a set of social behaviours to the playback of echolocation calls and ultrasonic white noise. To our best knowledge, we are the first to demonstrate that playback of echolocation calls may elicit social behaviours in bats. In accordance with our predictions, *Noctilio albiventris* adjusted their responses according to stimulus categories; generally showing the highest frequencies in all response behaviours toward echolocation calls of unfamiliar conspecifics and the lowest frequencies toward playbacks of other species and white noise.

Bats showed the highest frequencies of crawling, grooming, nodding and wing-stretching after listening to calls of unfamiliar conspecifics compared to their reaction to other bat species and white noise. Moreover, they reacted more often with wing-stretching and honk-calls to unfamiliar conspecifics than to familiar individuals of their own social group. With the exception of the behaviour crawling, bats never differed in their behavioural responses to ultrasonic white noise and other species compared to their reaction toward playbacks of familiar conspecifics. This indicates that ultrasonic sound in their own frequency range may be perceived as calls of a potential conspecific. This seems plausible as this specific frequency range and thus, this communication channel is only used by *N. albiventris*. However, free-ranging, foraging *N. albiventris* never reacted to white noise (Dechmann et al. in press), suggesting that echolocation calls are interpreted and/or perceived differently by bats under varying conditions and depending on the social context. Interestingly, bats reacted in a similar way to familiar conspecifics, other species and white noise in their own frequency range.

We conclude that *N. albiventris* indeed may distinguish between calls of conspecifics and heterospecifics, and between calls of familiar and unfamiliar conspecifics. We found however no effect of familiarity on the bats' response when comparing their reaction to cohabitant heterospecifics and non-cohabitant heterospecifics. Our results demonstrate that echolocation is not necessarily and not only 'auto-communication' (sensu Bradbury and Vehrencamp 1998), which implies that echolocation is only perceived and processed by the individual producing the sound. Other bats may as well obtain information about species identity and group-affiliation by listening to echolocation calls. We therefore propose that echolocation has a dual function and is used for both orientation and acoustic communication in bats.

Why did bats generally respond more frequently with social behaviours to unfamiliar conspecifics than to heterospecifics, and responded significantly more often with wing-stretching and honk calls to unfamiliar than to familiar conspecifics? As any behaviour imposes some costs, animals should carefully allocate their efforts. For this reason, we suppose that *N. albiventris* might reduce costs of repeated social interactions with anyhow familiar conspecifics and socially less important other species and thus, is more likely to respond to an unfamiliar conspecific. This is a pattern similar to what is found in various, mostly territorial animal species that tend to exhibit lower levels of aggression toward familiar neighbours and higher levels of aggression towards stranger, and often no aggression at all toward other species (reviewed in Temeles 1994).

We presume however, that all recorded behaviours in this experiment are not of aggressive nature, but rather suggest that some of them (particularly the behaviour wing-stretching and honk-calls) represent a form of greeting behaviour in which bats signal individuality to con- and heterospecifics. Greeting behaviours have already been reported from a variety of animals (Baboons: Smuts and Watanabe 1990; Colobus: Kutsukake et al. 2006; Hyenas: East et al. 1993; Pipefish: Sogabe and Yanagisawa 2007, Bechstein bats: Kerth et al. 2003). However, we can only speculate about the true function of all observed behaviours. In the following two paragraphs, we therefore try to assess the potential specific function of every physical and acoustical behaviour that we observed as response in our playback experiment.

### ***Physical Response Behaviours of *Noctilio albiventris* in Playback Experiments***

Bats spent more time crawling around in the test box after hearing playbacks of unfamiliar conspecifics compared to their reaction to playbacks of other bat species' echolocation calls and white noise. They also spent more time crawling in response to calls of familiar conspecifics in comparison to cohabitant and non-cohabitant heterospecifics. As the base-line of our experiment required still hanging bats, and bats were previously allowed to habituate to the experimental situation, we can exclude that the increased activity of test animals stems from the artificial situation they found themselves in. Instead, we assume that crawling most likely indicates arousal and general increased activity of animals during the experiment due to interest in the presented playback stimuli.

*Noctilio albiventris* yawned regularly after receiving playback stimuli. 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 and von Helversen (1999) observed male *Saccopteryx bilineata* to frequently yawn prior to or after agonistic interactions. They suggested yawning to represent a combined olfactory and visual signal towards other males when defending their territory. As *N. albiventris* performed this behaviour at night, we assume that the function of yawning is more of olfactory than of visual nature, intentioned to signal individuality via scent.

Both yawning and self-grooming have been described as part of displacement or 'self-directed' behaviours in several other animal species (e.g. Tinbergen 1940; Tinbergen 1947; Castles and Whiten 1998). Accordingly, self-grooming which was exhibited more frequently by bats after hearing echolocation calls of unfamiliar conspecific in comparison to the stimuli cohabitant heterospecific, non-cohabitant heterospecific and white noise, could be also interpreted as displacement behaviour. In rodents, grooming has often also been described in the context of displacement or as transition-behaviour between to socially relevant actions (Fentress 1988). Scratching, the most commonly displayed grooming behaviour of *N. albiventris*, has also been reported as displacement behaviour in baboons (Easley et al. 1987).

Nodding was the most frequently exhibited response behaviour in our experiments. Bats nodded more frequently after listening to playbacks of unfamiliar conspecifics compared to their reaction to other species and also white noise. As we are not aware of similar observations from other taxa including bats, we can only speculate what this behaviour might indicate. *Noctilio albiventris* has small elevations of cuticular tissue underneath the chin which could potentially be a gland. By nodding their heads and thus pressing their chin on their breast, they could possibly set off glandular secretions. Facial glands such as gular or mandibular glands are common in bats (e.g. Dalquest and Werner 1954; Safi and Kerth 2003; Caspers et al. 2009). In the sac-winged bat, Caspers et al (2009) demonstrated that mandibular glands are used for territorial scent marking. However, we never observed any secretions from this region.

We found bats to respond more frequently with wing-stretching to unfamiliar conspecifics than to familiar conspecifics. Moreover, bats showed this behaviour more often in response to unfamiliar conspecifics compared to their reaction toward other species and white noise. 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 sub-axillary region underneath their wings, which produce an oily and very strong smelling secretion. By flipping the wing, bats could fan volatiles from secretions of these glands towards conspecifics. Such behaviour has also been observed in *Noctilio leporinus*, the larger sibling species of *N.*

*albiventris* (Brooke and Decker 1996). The authors reported that individuals sniffed the sub-axillary glandular area of a conspecific during dyadic interactions and secretions of this area differed significantly in chemical composition between sexes. Wing-displays are also known to be part of the social behaviour in other bat species (Tyrell 1990; Singaravelan and Marimuthu 2008). The context and function of wing displays are however unknown in these bat species.

Urinating could also be related to olfactory signalling in *N. albiventris*. Male Mexican Free-tailed bats (*Tadarida brasiliensis*) for example, urinated or defecated when faced with a cotton swab bearing another male's scent (Gustin and McCracken 1987). Brooke (1997) reported that roosting sites of male *N. leporinus* were marked by a clearly defined urine stain. Alternatively, urinating could also be interpreted as a sign of tension or fear. In general, bats often tend to urinate when facing stressful situation such as after being caught in a net (personal observation).

#### ***Acoustical Response Behaviour of Noctilio albiventris in Playback Experiments***

The number of echolocation emitted during experiments did not differ between playback categories. We found however that bats responded more often with honk calls to playback of unfamiliar than to familiar conspecifics. The observed honk calls of *N. albiventris* resemble the honk calls of *N. leporinus* anecdotally described by Suthers (1965). Flying *N. leporinus* 'honk' at conspecifics on collision courses by lowering the terminal frequency of their echolocation calls. Possibly honk calls of *N. albiventris* also have a spacing function, as sounds of lower frequency carry further, a prerequisite for an efficient territorial display. Alternatively, honk calls could also possibly be a call coding for individual identity, similar to the signature whistle calls found in dolphin (Tyack 1986; Smolker et al. 1993; Sayigh et al. 1999), chirp contact calls of white-nosed coatis (Maurello et al. 2000) or phee calls of the common marmoset (Jones et al. 1993).

#### ***The Importance of Echolocation in the Social System of Noctilio albiventris***

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

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, it seems likely they use acoustical signatures in their echolocation calls to mediate group-foraging. Furthermore, our data suggest that the same may hold true for the maintenance of social groups within the roost. This is supported by our analysis of acoustical features potentially coding for individuality and/or group-membership. Our data shows that echolocation calls differed significantly among individuals, and that there is a trend towards differences among echolocation calls of social groups. A larger sample size perhaps might have revealed significant differences. Recognition of group affiliation may be important, since the efficiency of group foraging in *N. albiventris* most likely depends on an optimal group size. Radio-tracking data support that foraging social groups are stable over time in *N. albiventris* (Dechmann et al. in press) 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 system of both *Noctilio* species.

### ***Individual and Species Recognition in Bats***

To understand animal social interactions, it is important to know how, whether and if so, on which level (i.e. inter-specific or intra-specific) recognition is achieved (Bee 2006). Social recognition systems differ among species, depending on an animal's perceptual abilities and most likely on its degree of sociality. Thus, modalities used for social recognition may be of visual (e.g. lizards: Macedonia and Stamps 1994), tactile (e.g. spiders: Barth 1993), olfactory (e.g. hamsters: Johnston et al. 1993) or acoustical (e.g. birds: Elmen 1972) nature. In several mammalian species, olfaction seems to be the major signal used for social recognition. In bats, recognition by scent plays a key role in species recognition (Caspers et al. 2009), recognition of colony-members (De Faniis and Jones 1995; Bouchard 2001; Safi and Kerth 2003), kin (Gustin and McCracken 1987) and individual recognition (Caspers et al. 2008). Social recognition via scent may be optimal in close-range communication, thus only in the roost, but is unlikely to function for long-range communication. Intuitively, echolocation seems an ideal modality for social recognition and communication as, irrespective of the context, bats invariably have to call at high rates (several calls/m) to orientate, 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. Echolocation call design thus reflects the strong selective pressures bats face when foraging

for food. Consequently, bats share similar features in call designs when facing similar ecological conditions (Schnitzler et al. 2003). Even distantly related species that forage in similar habitats or prey on similar insects have often evolved a similar echolocation call design. 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 response to natural selection in the context of social systems. The possibility of an ultrasound-based mechanism of species recognition has first been addressed by Heller and 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 and colleagues (2007), who found island rhinolophids to have diverging echolocation calls from mainland species. They suggested that species recognition and facilitation of intra-specific communication are the most likely factors explaining the observed phenomenon.

One fundamental condition for the use of a signal to work for social communication is to be species-specific, but also to differ between sexes, among social groups or most importantly individuals. Individual signatures in bat echolocation calls have already been demonstrated in several other studies: either statistically (Brigham and Cebek 1989; Obrist 1995; Fenton et al. 2003; but see Siemers and Kerth 2006) or experimentally (Kazial et al. 2008). Bats may benefit from recognizing individual signatures in echolocation calls as they might enhance social bonds between group-members and optimise the efficiency of group foraging. In a foraging context, it has previously been demonstrated that echolocation calls can be used by conspecifics to obtain information about the quality of feeding grounds (for *N. albiventris*: Dechmann et al. in press, for other bats: Barclay 1982; Gillam 2007). Likewise, inexperienced juvenile *M. lucifugus* are guided to hibernacula by echolocation calls of swarming bats (Thomas et al. 1979). Similarly, *Nyctalus noctula* locate roosts faster when being able to eavesdrop on conspecific echolocation calls (Ruczynski et al. 2007; Ruczynski and Bogdanowicz 2008). The same holds true for 3 other bat species (Ruczynski et al. 2009). In a mating context, echolocation calls potentially could be used by bats as indicators of territories, mating grounds or swarming sites. Female *Eptesicus fuscus*, for example, adjusted their calling rate after having heard an echolocation playback stimulus depending on the sex of the call producer (Kazial and Masters 2004). And Grilliot and co-authors (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 due

to the nocturnal and cryptic lifestyle of bats. Our experiment however, provides crucial hints that echolocation indeed does play a role in social recognition within the roost and is used by bats to obtain essential social information from echolocation individuals on species-identity and group-affiliation.

### ***Echolocation: Signal or Cue in Chiropteran Communication?***

Maynard-Smith and Harper (2003) defined a signal as ‘any act which alters the behaviour of other organisms, that has evolved because of that fact, and which is effective because of the receiver’s response that has also evolved’. The requirement that a signal evolved due to its effect on other organisms tears signals apart from cues. According to a definition proposed by Hasson (1997) cues are any feature used by an animal as a guide to future actions, such as feeding noises produced while eating prey items. Following these definitions, echolocation calls emitted during foraging and orientation are not true signals in animal communication, but instead cues that other bats may use to obtain information about the sender. Thus, the term ‘echolocation signal’ that is regularly used to describe a single call, can be misleading. However, the picture is different when looking at echolocation calls produced by stationary bats, for example in the roost. In our experiment, we found the number of echolocation calls produced by bats to be related to the stimulus presented beforehand. Hearing calls of conspecifics lead to a higher, although not significant, echolocation rate than the presentation of heterospecific calls. Kazial and Masters (2004) found female *E. fuscus* to echolocate at significantly higher rates after hearing a female’s echolocation calls than after a male calling. Here, echolocation could be interpreted as an acoustic response, an intentionally produced vocalization with the goal to directly alter the behaviour of the (simulated) caller or to indicate individual identity and/or group membership. Consequently, in this situation the definition of a signal proposed by Maynard Smith & Harper (2003) would fit. We therefore advocate that depending on the context, echolocation calls may either be viewed as cues produced by foraging conspecifics, i.e. eavesdropping on feeding buzzes, or may be viewed as intentionally produced dual signals, i.e. for orientation in the roost while simultaneously promoting social recognition.

### ***A dual Function of Echolocation: Bats as a unique Model in Animal Communication***

Communication in the ultrasonic range, although unusual and seemingly not practical due to the strong attenuation of high frequencies, is nevertheless used by species of several different taxa, such as calls in frogs (Feng et al. 2006), alarm calls in squirrels (Wilson and Hare 2004),

and calls produced in social contexts by dolphins (Lammers et al. 2003). However, these are all examples of animals producing vocalizations intentioned for communication. In bats, echolocation potentially has a dual role: it is used by bats for orientation and to communicate species identity (this study), individual identity (Kazial et al. 2008) and, most likely depending on the social system, also sex (Kazial & Masters 2004) and group-affiliation (this study). We are not aware of any other species in which a ubiquitous behaviour exhibited by an animal explicitly for a non-social purpose, such as orientation, additionally serves a function as signal for its conspecifics. This makes bats a unique model for studying the co-existence of two functions in one signal, and may shed light on so far unexplored but important aspects in the evolution of communication.

## References

- Balcombe, J.P. and M.B.Fenton (1988). "Eavesdropping by bats: the influence of echolocation call design and foraging strategy." Ethology **79**(2): 158-166.
- Barclay, R.M. R. (1982). "Interindividual use of echolocation calls: eavesdropping by bats." Behavioral Ecology and Sociobiology **10**(4): 271-275.
- Barth, F.G. (1994). "Sensory guidance in spider pre-copulatory behaviour: Sensory guidance in arthropod behaviour" Comparative biochemistry and physiology. A. Comparative physiology **104**(4): 717-733
- Bates, M.E., S.A. Stamper and J.A. Simmins (2008). "Jamming avoidance response of big brown bats in target detection." Journal of Experimental Biology **211**(1): 106.
- Bee, M.A. and H. C. Gerhardt (2002). "Individual voice recognition in a territorial frog (*Rana catesbeiana*)." Proceedings: Biological Sciences: 1443-1448.
- Bee, M.A. (2006). "Animal communication: Individual recognition in animal species." In: The Encyclopedia of Language and Linguistics: Volume 2, Elsevier Science
- Beecher, M. D. (1989). "Signalling systems for individual recognition: an information theory approach." Animal behaviour **38**: 248-261
- Behr, O. and O. Helversen (2004). "Bat serenades—complex courtship songs of the sac-winged bat (*Saccopteryx bilineata*)." Behavioral Ecology and Sociobiology **56**(2): 106-115.
- Behr, O., O. Von Helversen, G. Heckel, M. Nagy, C.C. Voigt and F. Mayer (2006). "Territorial songs indicate male quality in the sac-winged bat *Saccopteryx bilineata* (Chiroptera, Emballonuridae)." Behavioral Ecology **17**(5): 810.
- Bloedel, P. (1955). "Observations on the life histories of Panama bats." Journal of Mammalogy: 232-235.
- Bouchard, S. (2001). "Sex discrimination and roostmate recognition by olfactory cues in the African bats *Mops condylurus* and *Chaerephon pumilus*." Journal of Zoology **254**:109–117
- Boughman, J.W. and G.S. Wilkinson (1998). "Greater spear-nosed bats discriminate group mates by vocalizations." Animal Behaviour **55**(6): 1717-1732.
- Bradbury, J.W. and S.L. Vehrencamp (1998). Principles of animal communication, Sinauer Associates Sunderland, Massachusetts.
- Brigham, R.M. and J.E. Cebek (1989). "Intraspecific variation in the echolocation calls of two species of insectivorous bats." Journal of Mammalogy: 426-428.
- Brooke, A.P. (1997). "Social organization and foraging behaviour of the fishing bat, *Noctilio leporinus* (Chiroptera: Noctilionidae)." Ethology **103**(5): 421-436.

- Brooke, A.P. and D.M. Decker (1996). "Lipid compounds in secretions of fishing bat, *Noctilio leporinus* (Chiroptera: Noctilionidae)." Journal of Chemical Ecology **22**(8): 1411-1428.
- Brown, P.E., T. W. Brown and A.D. Grinnell (1983). "Echolocation, development, and vocal communication in the lesser bulldog bat, *Noctilio albiventris*." Behavioral Ecology and Sociobiology **13**(4): 287-298.
- Carter, G.G., M.D. Skowronski, P.A. Faureand, B. Fenton (2008). "Antiphonal calling allows individual discrimination in white-winged vampire bats." Animal Behaviour **76**(4): 1343-1355.
- Caspers, B., S. Franke and C.C. Voigt (2008). "The wing sac odour of male greater sac-winged bats (*Saccopteryx bilineata*) as a composite trait: seasonal and individual differences." In: Hurst JL, Beynon RJ, Roberts SC and Wyatt TD (eds) *Chemical signals in vertebrates XI*. Springer, New York,
- Caspers, B., G. Wibbelt and C.C. Voigt (2009). "Histological examinations of facial glands in *Saccopteryx bilineata* (Chiroptera, Emballonuridae), and their potential use in territorial marking." Zoomorphology **128**(1): 37-43.
- Castles, D. L. and A. Whiten (1998). "Post-conflict behaviour of wild olive baboons. II. Stress and self-directed behaviour." Ethology **104**(2): 148-160.
- Clarke, K.R. and R.M. Warwick (1994). "Change in marine communities: an approach to statistical analysis and interpretation." Plymouth Marine Laboratory.
- Dalquest, W. W. and H.J. Werner (1954). "Histological aspects of the faces of North American bats." Journal of Mammalogy: 147-160
- Dawkins, R. (1996). "The blind watchmaker: Why the evidence of evolution reveals a universe without design " Longman, Harlow, Essex.
- Dechmann, D., S.L. Heucke, L. Giuggioli, K. Safi, C.C. Voigt and M. Wikelski (in press). "Experimental evidence for group hunting via eavesdropping in echolocating bats." Proceedings of the Royal Society B
- De Fanis, E. and Jones G. (1995). "The role of odour in discrimination of conspecifics by pipstrelle bats." Animal Behaviour **49**:835–839
- Dolan, P.G. and D.C. Carter (1979). "Distributional notes and records for Middle American Chiroptera." Journal of Mammalogy: 644-649.
- Easley, S.P., A.M. Coelho and L.L. Taylor (1987). "Scratching, dominance, tension, and displacement in male baboons." American Journal of Primatology **13**(4)
- East, M. L., H. Hofer and W. Wickler (1993). "The erect 'penis' is a flag of submission in a female-dominated society: greetings in Serengeti spotted hyenas." Behavioral Ecology and Sociobiology **33**(6): 355-370.

- Elmen S.T. (1972). "An Experimental Analysis of the Parameters of Bird Song Eliciting Species Recognition." Behaviour **41**(1-2):130-171
- Falls, J.B. (1982). "Individual recognition by sounds in birds." In: Kroodsma, D.E. & E.H. Miller (eds.) *Acoustic communication in birds*. New York: Academic Press.
- Feng, A.S., P.M. Narins, Chun-He X., Wen-Yu L., Zu-Li Y., Qiang Qiu, Zhi-Min X. and Jun-Xian S. (2006). "Ultrasonic communication in frogs." Nature **440**: 333-336.
- Fenton, M. B. (2003). "Eavesdropping on the echolocation and social calls of bats." Mammalian Review **33**(3-4): 193-204.
- Fenton, M.B., D.D. Jacobs, E.J. Richardson, P.J. Taylor and W.White (2004). "Individual signatures in the frequency-modulated sweep calls of African large-eared, free-tailed bats *Otomops martiensseni* (Chiroptera: Molossidae)." Journal of Zoology **262** (01): 11-19.
- Fentress, J.C. (1988). "Expressive Contexts, Fine Structure, and Central Mediation of Rodent Grooming." Annals of the New York Academy of Sciences **525** (1): 18-26
- Firzlaff, U., S. Schornich, S. Hoffmann, G. Schuller and L. Wiegrebe (2006). "A neural correlate of stochastic echo imaging." Journal of Neuroscience **26**(3): 785-791.
- Gebhard, J. (1997). "Fledermäuse", Birkhäuser Verlag, Berlin
- Gillam, E.H. (2007). "Eavesdropping by bats on the feeding buzzes of conspecifics." Canadian Journal of Zoology **85**(7): 795-801.
- Gillam, E.H. and G.F. McCracken (2007). "Variability in the echolocation of *Tadarida brasiliensis*: effects of geography and local acoustic environment." Animal Behaviour **74**(2): 277-286.
- Gillam, E.H., N. Ulanovsky and G.F. McCracken (2007). "Rapid jamming avoidance in biosonar." Proceedings of the Royal Society B: Biological Sciences **274**(1610): 651-660.
- Graham, G.L. (1988). "Interspecific associations among Peruvian bats at diurnal roosts and roost sites." Journal of Mammalogy: 711-720.
- Griffin, D.R. (1958). "Listening in the dark." Yale University Press, New Haven, Connecticut
- Grilliot, M.E., S.C. Burnett And M.T. Mendonça (2009). "Sexual Dimorphism in Big Brown Bat (*Eptesicus fuscus*) Ultrasonic Vocalizations is Context Dependent." Journal of Mammalogy **90**(1): 203-209.
- Grinnell, A.D. (1973). "Neural processing mechanisms in echolocating bats, correlated with differences in emitted sounds." The Journal of the Acoustical Society of America **54**: 147.
- Grunwald, J.E., S. Schornich and L. Wiegrebe (2004). "Classification of natural textures in echolocation." Proceedings of the National Academy of Sciences **101**(15): 5670-5674.
- Gustin, M.K. and G.F. McCracken (1987). "Scent recognition between females and pups in the bat *Tadarida brasiliensis mexicana*." Animal Behaviour **35**(1): 13-19.

Kerth, G., B. Almasi, N. Riebi, D. Thiel and S. Lüpold (2003). "Social interactions among wild female Bechstein's bats (*Myotis bechsteinii*) living in a maternity colony." Acta ethologica **5**(2): 107-114.

Kutsukake, N., N. Suetsugu and T. Hasegawa (2006). "Pattern, distribution, and function of greeting behavior among black-and-white colobus." International Journal of Primatology **27**(5): 1271-1291.

Hasson, O. (1997). "Towards a general theory of biological signaling." Journal of Theoretical Biology **185**(2): 139-156.

Heller, K.G. and O. Helversen (1989). "Resource partitioning of sonar frequency bands in rhinolophoid bats." Oecologia **80**(2): 178-186.

Hood, C.S. and J. Pitocchelli (1983). "*Noctilio albiventris*." Mammalian Species: 1-5.

Ibáñez, C., J. Juste, R. López-Wilchis, and A. Núñez-Garduño (2004). "Habitat variation and jamming avoidance in echolocation calls of the sac-winged bat (*Balantiopteryx plicata*)." Journal of Mammalogy **85**(1): 38-42.

Johnston, R.E., A. Derzie, G. Chiang, P. Jernigan and H-C. Lee (1993). "Individual scent signatures in golden hamsters: evidence for specialization of function." Animal Behaviour **45**:1061-1070

Jones, B. S., D.H.R. Harris & C.K. Catchpole (1993). "The stability of the vocal signature in phee calls of the common marmoset, *Callithrix jacchus*." American Journal of Primatology **31**(1):67-75

Jones, G. and T. Kokurewicz (1994). "Sex and age variation in echolocation calls and flight morphology of Daubenton's bats *Myotis daubentonii*." Mammalia **58**(1): 41-50.

Jones, G. and R.D. Ransome (1993). "Echolocation calls of bats are influenced by maternal effects and change over a lifetime." Proceedings of the Royal Society B: Biological Sciences **252**(1334): 125-128.

Kalko, E.K.V., H.U. Schnitzler, I. Kaipf and A.D. Grinnell (1998). "Echolocation and foraging behavior of the lesser bulldog bat, *Noctilio albiventris*: preadaptations for piscivory?" Behavioral Ecology and Sociobiology **42**(5): 305-319.

Kazial, K.A., T.L. Kenny and S.C. Burnett (2008). "Little brown bats (*Myotis lucifugus*) recognize individual identity of conspecifics using sonar calls." Ethology **114**(5): 469-478.

Kazial, K.A. and W.M. Masters (2004). "Female big brown bats, *Eptesicus fuscus*, recognize sex from a caller's echolocation signals." Animal Behaviour **67**(5): 855-863.

Kerth, G. and B. König (1996). "Transponder and an infrared-videocamera as methods in a fieldstudy on the social behaviour of Bechstein's bats (*Myotis bechsteini*)." Myotis **34**: 27-34.

King, B. (2005). "Changes in echolocation calls of *Eptesicus fuscus* when flying with conspecifics in a laboratory setting." Scienes Honors Thesis, Department of Animal Sciences, The Ohio State University.

- Kingston, T., G. Jones, A. Zubaid, T.H. Kunz (2002). "Resource partitioning in rhinolophoid bats revisited". Oecologia **124**:332–342
- Kunz, T.H. (1982). "Roosting ecology of bats." In *Bat Ecology*, T.H. Kunz and M.B. Fenton (ed), The University of Chicago Press, Chicago
- Lammers, M.O., W.W.L. Au and D.L. Herzing (2003). "The broadband social acoustic signaling behavior of spinner and spotted dolphins." The Journal of the Acoustical Society of America **114**: 1629.
- Macedonia, J.M. and J.A. Stamps (1994). "Species recognition in *Anolis grabami* (Sauria, Iguanidae): evidence from responses to video playbacks of conspecific and heterospecific displays". Ethology **98**(3-4):246-264.
- Masters, W.M., K.A.S. Raver and K.A. Kazial (1995). "Sonar signals of big brown bats, *Eptesicus fuscus*, contain information about individual identity, age and family affiliation." Animal Behaviour **50**(5): 1243-1260.
- Maurello, M.A., J.A. Clarke & R.S. Ackley (2000). "Signature characteristics in contact calls of the white-nosed coati." Journal of Mammalogy **81**(2): 415-421.
- Maynard-Smith, J. and D. Harper (2003). "Animal signals." Oxford series in ecology and evolution (OSEE), Oxford University Press, Oxford.
- Moss, C.F. and A. Surlykke (2001). "Auditory scene analysis by echolocation in bats." The Journal of the Acoustical Society of America **110**: 2207.
- Neuweiler, G., W. Metzner, U. Heilmann, R. Rübesamen, M. Eckrich and H.H. Costa (1987). "Foraging behaviour and echolocation in the rufous horseshoe bat (*Rhinolophus rouxi*) of Sri Lanka." Behavioral Ecology and Sociobiology **20**(1): 53-67.
- Obrist, M.K. (1995). "Flexible bat echolocation: the influence of individual, habitat and conspecifics on sonar signal design." Behavioral Ecology and Sociobiology **36**(3): 207-219.
- Pearl, D.L. and M.B. Fenton (1996). "Can echolocation calls provide information about group identity in the little brown bat (*Myotis lucifugus*)?" Canadian Journal of Zoology **74**(12): 2184-2192.
- Racey, P.A. and S.M. Swift (1985). "Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour." The Journal of Animal Ecology: 205-215.
- Ratcliffe, J.M., H. M. ter Hofstede, R. Avila-Flores, M.B. Fenton, G.F. McCracken, S. Biscardi, J. Blasko, E. Gilliam, J. Orpecio and G. Spanjier (2004). "Conspecifics influence call design in the Brazilian free-tailed bat, *Tadarida brasiliensis*." Canadian Journal of Zoology **82**(6): 966-971.
- Rendall, D., P.S. Rodman and R.E. Emond (1996). "Vocal recognition of individuals and kin in free-ranging rhesus monkeys." Animal Behaviour **51**(5): 1007-1015.

- Rodríguez-Durán, A. (1998). "Nonrandom aggregations and distribution of cave-dwelling bats in Puerto Rico." Journal of Mammalogy: 141-146.
- Ruczynski, I. and W. Bogdanowicz (2008). "Summer Roost Selection by Tree-dwelling Bats *Nyctalus noctula* and *N. leisleri*: A Multiscale Analysis." Journal of Mammalogy **89**(4): 942-951.
- Ruczynski, I., E.K.V. Kalko and B.M. Siemers (2007). "The sensory basis of roost finding in a forest bat, *Nyctalus noctula*." Journal of Experimental Biology **210**(20): 3607.
- Ruczynski, I., E.K.V. Kalko and B.M. Siemers (2009). "Calls in the Forest: A Comparative Approach to How Bats Find Tree Cavities." Ethology **115**(2): 167-177.
- Russo, D., M. Mucedda, M. Bello, S. Biscardi, E. Pidincheda and G. Jones (2007). "Divergent echolocation call frequencies in insular rhinolophids (Chiroptera): a case of character displacement?" Journal of Biogeography **34**(12): 2129-2138.
- Safi, K. and G. Kerth (2003). "Secretions of the interaural gland contain information about individuality and colony membership in the Bechstein's bat." Animal Behaviour **65**(2): 363-369.
- Sayigh, L.S., P.L. Tyack, R.S. Wells, A.S. Solow, M.S. Scott and A.B. Irvine (1999). "Individual recognition in wild bottlenose dolphins: a field test using playback experiments." Animal Behaviour **57**(1): 41-50.
- Schaub, A., J. Ostwald and B.B. Siemers (2008). "Foraging bats avoid noise." Journal of Experimental Biology **211**(19): 3174.
- Schnitzler, H.U., C.F. Moss and A. Denzinger (2003). "From spatial orientation to food acquisition in echolocating bats." Trends in Ecology & Evolution **18**(8): 386-394.
- Siemers, B.M. and G. Kerth (2006). "Do echolocation calls of wild colony-living Bechstein's bats (*Myotis bechsteinii*) provide individual-specific signatures?" Behavioral Ecology and Sociobiology **59**(3): 443-454.
- Simmons, J.A., S.A. Kick, B.D. Lawrence, C. Hale, C. Bard and B. Escudíe (1983). "Acuity of horizontal angle discrimination by the echolocating bat, *Eptesicus fuscus*." Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology **153**(3): 321-330.
- Singaravelan, N. and G. Marimuthu (2008). "In situ feeding tactics of short-nosed fruit bat (*Cynopterus sphinx*) on mango fruits: evidence of extractive foraging in a flying mammal." Journal of Ethology **26**(1): 1-7.
- Smolker, R.A., J. Mann and B.B. Smuts (1993). "Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants." Behavioral Ecology and Sociobiology **33**(6): 393-402.
- Smuts, B. B. and J. M. Watanabe (1990). "Social relationships and ritualized greetings in adult male baboons (*Papio cynocephalus anubis*)." International Journal of Primatology **11**(2): 147-172.

- Sogabe, A. and Y. Yanagisawa (2007). "The function of daily greetings in a monogamous pipefish *Corythoichthys haematopterus*." Journal of Fish Biology **71**(2): 585-595.
- Suga, N. and W.E. O'Neill (1979). "Neural axis representing target range in the auditory cortex of the mustached bat." Science **206**(4416): 351-353.
- Suthers, R.A. (1965). "Acoustic orientation by fish-catching bats." Journal of Experimental Zoology **158**(3).
- Swift, S.M. and P.A. Racey (1983). "Resource partitioning in two species of vespertilionid bats (Chiroptera) occupying the same roost." Journal of Zoology **200**(2): 249-259.
- Temeles, E.J. (1994). "The role of neighbours in territorial systems: when are they'dear enemies'?" Animal Behaviour **47**(2): 339-350.
- Thomas, D.W., M. Brock Fenton and R.M.R. Barclay (1979). "Social behavior of the little brown bat, *Myotis lucifugus*." Behavioral Ecology and Sociobiology **6**(2): 129-136.
- Tinbergen, N. (1940). "Die Übersprungbewegung." Zeitschrift für Tierpsychologie **4**: 1-40.
- Tinbergen, N. (1947). "Displacement Reactions in the Three-Spined Stickleback." Behaviour: 56-63.
- Tuttle, M.D. (1974). "An improved trap for bats." Journal of Mammalogy: 475-477.
- Tyack, P. (1986). "Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: mimicry of signature whistles?" Behavioral Ecology and Sociobiology **18**(4): 251-257
- Tyrell, K. (1990). The Ethology of the Malayan False Vampire Bat (*Megaderma spasma*): With Special Emphasis on Auditory Cues Used in Foraging, University of Illinois at Urbana-Champaign, USA.
- Voigt, C.C. and O. von Helversen (1999). "Storage and display of odour by male *Saccopteryx bilineata* (Chiroptera, Emballonuridae)." Behavioral Ecology and Sociobiology: 29-40.
- Wilkinson, G.S. and J.W. Boughman (1998). "Social calls coordinate foraging in greater spear-nosed bats." Animal Behaviour **55**(2): 337-350.
- Wilson, D.R. and J.F. Hare (2004). "Animal communication: Ground squirrel uses ultrasonic alarms." Nature **430**: 523.
- Wohlgenant, T.J. (1994). "Roost interactions between the common vampire bat (*Desmodus rotundus*) and two frugivorous bats (*Phyllostomus discolor* and *Sturnira lilium*) in Guanacaste, Costa Rica." Biotropica: 344-348.

## **Acknowledgements**

First of all, I would like to express my special gratitude to my external supervisor Dr. Dina Dechmann for the freedom to develop my own ideas within the 'Noctilio'-project, and to Prof. Michael Taborsky who kindly accepted to advise me throughout my diploma thesis.

I am deeply indebted to my caring and loving parents, who always gave me the opportunity to live my dreams and supported me in any aspect of my life.

I would like to thank all my friends in Vienna, who made my time there unforgettable and beautiful. Special thanks to my former flat-mates Daniela and Sandra and the whole Handelskai-Crew for countless bright and cheerful moments around the kitchen table.

Many thanks also to everyone at the Department for Behavioural Biology at the Free University, Berlin, especially to the whole nightingale group, for providing my working space, discussing ideas and providing the humour background during sometimes tedious times of video coding and data analysis.

The research project was partly funded by the German Science Foundation (VO 890/11-1). Many thanks to Kamran Safi and Björn Siemers for letting us use their playback equipment. The research presented in this thesis would not have been possible without the practical help of Stefanie Ohler, Felix Fornoff and in particular Antje Kretschmar.

Finally, I have to thank my dear partner for his continuous encouragement during the ups and downs of my life.

## Curriculum Vitae

### Silke L. Heucke

Siegfried-Berger-Straße 46, 12557 Berlin, Germany

E-mail: silke.heucke@googlemail.com

### Personal Details

---

**Name:** Silke Luise Heucke  
**Birth:** 9. April 1982 in Hamburg, Germany  
**Nationality:** German

### Education

---

08/89 – 07/92	Primary School in Friedrichsdorf, Germany
08/92 – 05/01	Kaiserin-Friedrich-Schule, Bad Homburg, Germany
Since 10/03	<b>University of Vienna</b> , Austria, studying biology
10/07 – 07/08	<b>Humboldt University Berlin</b> , Erasmus program
Since 02/08	<b>Diploma Thesis:</b> “ <i>Dual function of echolocation: Do bats identify unfamiliar and familiar individuals of their own and other species?</i> ” at the Leibniz Institute for Zoo and Wildlife Research (IZW), Berlin, Germany, under the supervision of <b>Dr. Dina Dechmann &amp; Prof. Michael Taborsky</b>

### Work experience

---

09/01 - 04/02	<b>Field assistant</b> for Dr. Christa Weise, at the Smithsonian Tropical Research Institute, Panamá
05/02 – 07/02	<b>Field assistant</b> for Dr. Kamran Safi, Zoological Institute University of Zürich
09/05	<b>Field assistant</b> for PD Dr. Christian Voigt, IZW, at La Selva, Biological Station, Costa Rica
02/06	<b>Student assistant:</b> for PD Dr. Christian Voigt, IZW

08/07-08/07      **Field assistant** for Dr. Dina Dechmann, IZW, in  
Gamboa, Panama

11/07              **Field course** with the Tropical Biology  
Association (TBA) in Kirindy Forest,  
Madagascar

## **Grants**

---

British Ecological Society, travel grant for TBA course, **320 €**

University of Vienna, “*Brief research travels abroad*” grant, **1650 €**

## **Publications**

---

Dechmann DKN, **Heucke SL**, Guggioli L, Safi K, Voigt CC, Wikelski M (in press).  
Experimental evidence for group hunting via eavesdropping in echolocating bats.  
Proceedings of the Royal Society: Biological Sciences

Range F, **Heucke SL**, Gruber C, Konz A, Huber L, Virányi Z (accepted).  
The effect of ostensive cues on dogs’ performance in a manipulative social learning task.  
Applied Animal Behaviour Science