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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.