



Antiphonal calling allows individual discrimination in white-winged vampire bats

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Mother bats use pup contact calls ('isolation calls') to find and recognize their young. In white-winged vampire bats, *Diaemus youngi*, adults produce social calls that are structurally similar to the pup isolation calls of many other bat species. In addition, *D. youngi* seem to exchange these calls in a duet-like fashion. To determine whether calls elicit precise antiphonal responses, we simultaneously recorded social calls from groups of four captive bats vocally interacting. To examine call function, we conducted isolation experiments, permuted discriminant function analyses (pDFA) of individual variation in call structure, and a habituation–discrimination playback experiment. We found that adult *D. youngi* call when isolated, and their social calls attract conspecifics and elicit antiphonal responses. Bats called within 500 ms of a conspecific more than expected based on a random calling model. These findings are the first evidence of antiphonal calling among adult bats. We found significant individual variation in call structure, and show that bats can discriminate individual identity using social calls alone. We hypothesize that *D. youngi* use these antiphonal contact calls to mediate social interactions among individuals outside the roost.

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In individualized societies, simply advertising one's identity can be an adaptive strategy for influencing conspecifics (Rendall & Owren 2002). Vocalizations labelled 'contact calls' coordinate kin, pair or group actions by honestly conveying identity and location (e.g. Rendall et al. 1996; Wanker et al. 1998; Weiss et al. 2001; Cortopassi & Bradbury 2006). In many group-living vertebrates (bar-headed geese, *Anser indicus*: Lamprecht et al. 1985; budgerigars, *Melopsittacus undulatus*: Brown et al. 1988; Japanese macaques, *Macaca fuscata*: Sugiura 1993, 1998; cottontop tamarins, *Saguinus oedipus*: Weiss et al. 2001; Jordan et al. 2004; African elephants, *Loxodonta africana*: Soltis et al. 2005; bottlenose dolphins, *Tursiops truncatus*: Janik & Slater 1998; killer whales, *Orcinus orca*: Miller et al. 2004; naked mole-rats, *Heterocephalus glaber*: Yosida et al. 2007), contact calls

from two individuals may form simple antiphonal duets, composed of a call followed by a precise response. The adaptive function of antiphonal calling remains unclear, because many other contact calls do not elicit precise responses.

Antiphonal calling between mothers and pups has been reported in at least two bat species. To reunite with mothers, bat pups living in colonial roosts typically produce individually distinct contact calls termed 'isolation calls' (e.g. Gelfand & McCracken 1986; Balcombe 1990; Scherrer & Wilkinson 1993; Bohn et al. 2007). In some species, mother bats may vocally respond with 'directive calls' (e.g. Gould et al. 1973; Brown 1976; Fenton 1985; Balcombe & McCracken 1992). Matsumara (1981) found that mother and pup greater horseshoe bats, *Rhinolophus ferrumequinum*, mutually coordinate their calls in time. Brown et al. (1983) reported similar 'duetting' between mother–pup pairs in lesser fishing bats, *Noctilio albiventris*. Such observations suggest that an antiphonal calling pattern may help mothers identify, localize and maintain contact with their pups at roosts (Gould 1977; Matsumara 1981) or in flight (Brown et al. 1983).

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Here we present the first report of antiphonal calling by adult bats and investigate its function. The white-winged vampire bat, *Diaemus youngi*, has a diverse vocal repertoire (G. Carter, unpublished data), and one social call type is commonly exchanged in a duet-like fashion. These calls are commonly produced by groups of *D. youngi* while feeding on chickens, while leaving roosts and when individuals are separated (G. Carter & P. Faure, unpublished data). The calls consist of usually two (sometimes one or three, but rarely more) syllables that are tonal, downward frequency-modulated (FM) sweeps with multiple harmonics (Fig. 1). In other species, this tonal, multiharmonic FM 'double-note' structure has been reported for pup isolation calls (e.g. Gould et al. 1973; Gould 1977; Porter 1979; Brown et al. 1983; Fenton 1985) and adult directive calls (Brown 1976; Porter 1979; Fenton 1985).

Although tonal FM sweep social calls are common, their function among adult bats is ambiguous. Based on behavioural observations, some researchers (e.g. Brown 1976; Leippert et al. 2000; Pfalzer & Kusch 2003) suggested that adults might use FM sweep social calls as contact calls for individual recognition and/or social cohesion in much the same way as mother-pups pairs. In contrast, Barlow & Jones (1997) found that playback of FM sweep-structured social calls of *Pipistrellus pipistrellus* repel conspecifics, and they concluded that such signals function in defending patches of aerial insects. In cases where bats forage as groups, social calls may simultaneously play both roles (i.e. identifying groupmates and forming groups in order to defend foraging sites cooperatively) (Wilkinson & Boughman 1998).

Group-living greater spear-nosed bats, *Phyllostomus hastatus*, use two distinct kinds of contact calls. Pups produce isolation calls that allow individual discrimination by adults (Bohn et al. 2007). Adults, on the other hand, produce group-specific screech calls (Boughman 1997) that allow discrimination of groupmates from nongroupmates, but not individual recognition (Boughman & Wilkinson 1998). The two call types vary completely in structure; isolation calls are double-note FM sweeps, but adult screech calls are bursts of atonal, broadband sound.

Diaemus youngi is an interesting case for comparison because, unlike *P. hastatus*, adult social calls are double-note FM sweeps. The calls do not appear to be used to advertise male quality or attract mates, because calling can occur between two or three females, and nonreproductive white-winged vampire bats also produce these calls (G. Carter, personal observation). We tested whether these vocalizations could act as individual contact calls, much like pup isolation calls, allowing individual recognition of separated individuals. In this case, they should be easy to localize, produced copiously by isolated individuals, and carry information about caller identity. Alternatively, if the signals are alarm calls, they should be given in the presence of conspecifics, when a potential predator is detected. If they advertise or defend food, then calling rates should be affected greatly by presence of food. Finally, if such calls are actually signals to predators or prey, then calling should not occur among bats in the absence of observers or prey.

In isolation experiments, we investigated the effect of conspecifics and prey presence on calling. To examine

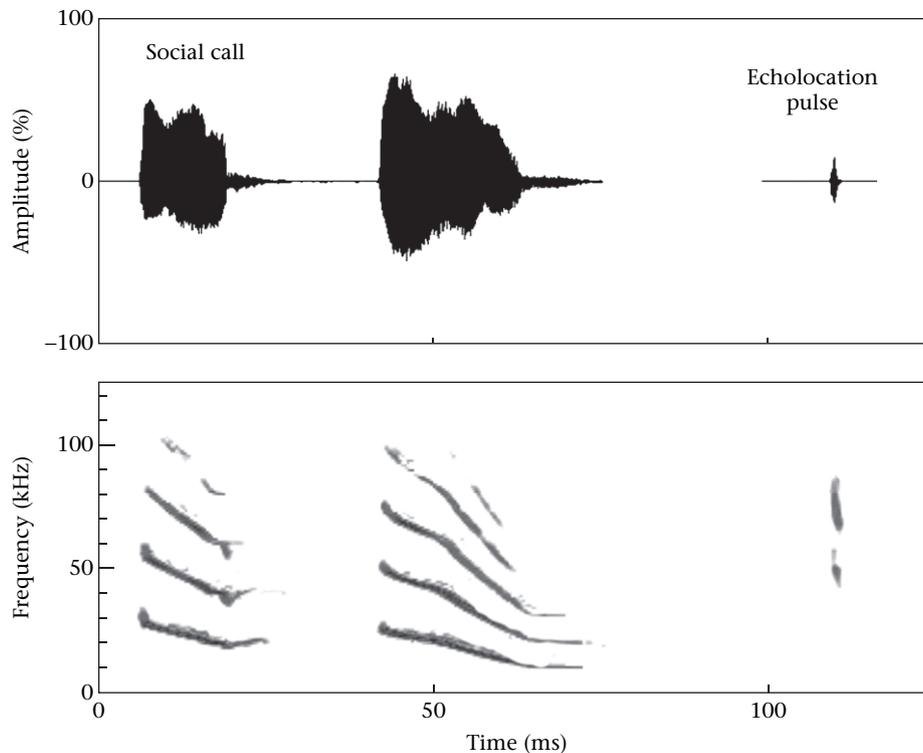


Figure 1. Amplitude envelopes and spectrograms show relative intensity and spectral structure of a typical 'double-note' social call and echolocation pulse. Calls were recorded at the same distance from an adult *Diaemus youngi*. Spectrograms were generated using a 512-point fast Fourier transform and a Hanning window.

whether calls are exchanged antiphonally, we simultaneously recorded the temporal production patterns of four isolated individuals, using synchronized microphones. We investigated vocal individuality using a statistical analysis of call structure. Finally, we tested for individual vocal discrimination using a habituation–discrimination playback experiment.

GENERAL METHODS

Terminology

Because we discuss only one type of social call, we herein use the term ‘social call’ to refer to the *D. youngi* social calls with FM sweep structure, described above (Fig. 1). Following Kanwal et al. (1994), we use the term syllable, rather than note, to describe single continuous elements of a call.

Animals

Eighteen captive *D. youngi* served as subjects. All were housed within a temperature- and humidity-controlled facility in Tijeras, New Mexico, U.S.A. (Exhibitor’s Permit no. 85-C-0021 issued by USDA Animal and Plant Health Inspection Service, Animal Care Division), except for one bat (S) housed at the Rosamund Gifford Zoo in Syracuse, New York, U.S.A. Nine of these bats had been wild-caught in Trinidad in 2003, and nine were born in captivity. Relatedness in all bats was unknown. We marked all individuals with plastic beaded necklaces and wing-punch scars. Walk-in cages housed four separate groups of ‘roostmates’. Live chickens were herded into cages every night to serve as blood donors at a ratio of one chicken per bat, with each chicken parasitized no more than once every 8 days. Our methods adhere to *Animal Behaviour’s Guidelines for the Treatment of Animals in Behavioural Research and Teaching*.

Sound Equipment

We recorded bat calls with CM 16 ultrasound condenser microphones (frequency range 10–200 kHz, Avisoft Bioacoustics, Berlin, Germany) and digitized sounds through an Ultrasoundgate 116 or 416 on to a PC laptop running Avisoft Recorder USG software. Unless otherwise stated, recordings were digitized with 16-bit resolution at a sampling rate of 250 kHz. For all playback, we used an Avisoft Scanspeak ultrasonic speaker (no. 60102, frequency response \pm 12 dB: 1–120 kHz) connected to an Avisoft amplifier (no. 70101). Digital sound files were converted to analogue and played back using BatSound Pro (Pettersson Elektronik AB, Uppsala, Sweden) and a high-speed A/D card (DAQcard 6062E, National Instruments, Austin, TX, U.S.A.). We videorecorded responses using a Sony Nightshot DV Camcorder (30 frames/s), equipped with an infrared light and a Sennheiser K6 microphone (Sennheiser Electronic Corporation, Old Lyme, CT, U.S.A.), and linked directly to a Macintosh G4 PowerBook (Apple Computers, Cupertino, CA, U.S.A.) running the application

iMovie HD. We synchronized clocks on both computers at the start of every night of playback. We conducted playback experiments June–August 2006 and 2007.

Recordings from Individuals

To record social calls from each individual, we isolated a bat in a room (361 \times 150 \times 302 cm) lined with acoustic foam. A mesh cage constrained subjects to within 10–45 cm of the microphone. At the time of recording, a subject bat was spatially but not acoustically isolated from other bats in an adjacent room. Because of large differences in amplitude, we could easily discriminate between calls produced by the subject bat and background calls from other bats, allowing us to unambiguously assign identity. We recorded during June–August and January–March in 2006 and 2007.

ISOLATION EXPERIMENTS

We conducted isolation experiments to determine whether bats produce calls when isolated, and to examine the effects of food and conspecific calls on their vocal behaviour. We isolated each bat ($N = 12$) from the rest of the colony under two conditions: with or without a chicken, alternating the order of presentation. Experiments were located in a different building from where bats were housed, so subjects had no visual or auditory contact with conspecifics. In a third condition, we spatially isolated an individual bat ($N = 16$) with no chicken present, but allowed the bat to hear the calls of roostmates in an adjacent room. Under all conditions, we used the Avisoft system to remotely monitor the number of social calls produced by the isolated bat for 2 h after sunset.

In a second experiment, we sought to examine the effect of social calls on conspecifics by remotely observing whether conspecifics moved towards isolated calling bats. We placed an individual bat ($N = 6$) inside a nylon mesh cage (34 \times 34 \times 56 cm, Apogee Reptarium, Apogee Enterprises, Inc., Minneapolis, MN, U.S.A.), and placed this small cage inside the larger colony cage housing other roostmates (361 \times 122 \times 226 cm). As a control, we also placed an identical but empty cage inside the colony cage. To record social calls from the isolated bat, a microphone was directed towards the isolated individual and directly away from the colony roost. We used three small wireless light-emitting diode (LED) infrared surveillance cameras to remotely monitor activity.

Results

Diaemus youngi produced many social calls only when both spatially isolated and able to hear conspecifics. When completely isolated with no chicken present, one bat out of 12 produced a total of nine social calls. When completely isolated with a chicken present, none of the 12 bats produced social calls. However, when bats were spatially isolated but allowed to hear conspecifics with no chicken present, 16 of 16 called, producing a total of 507 calls.

In the second experiment, bats were attracted to social calls from isolated conspecifics. In all six cases, roostmates approached the cage with a bat inside, but ignored the empty cage. In all six cases, we also recorded social calls after lights were turned off, and in five of these cases, we were certain of rapid social call exchanges between the isolated individual and others. In the last case, caller identity was uncertain because the isolated bat faced away from the microphone.

GENERAL RESPONSE TO PLAYBACK

Methods

We conducted playback experiments to determine whether bats would respond more to social calls than to echolocation calls, and whether they would respond differently based on caller sex or affiliation (roostmate or not). We also presented playback of social calls from one wild-caught male *D. youngi* recorded in 1993 to examine response to an unfamiliar conspecific. Captive-born subjects could not have been familiar with this bat, and wild-born subjects were extremely unlikely to have encountered this bat in the wild because capture sites differed and capture dates were separated by 10 years. As a control, we also presented some echolocation calls from a big brown bat, *Eptesicus fuscus*, recorded with the same equipment.

Playback stimuli

Using Batsound Pro, we constructed playback stimuli of echolocation and social calls from every individual. Because most calling takes place in bouts, and to eliminate temporal variation between stimuli, we spaced playback calls with the following time intervals: 3000, 3000, 2000, 2000, 1000, 1000, 200, 200, 200, 200, 200, 1000, 1000, 2000, 2000, 3000, 3000 ms, followed by silence until the 30 s mark. This sequence was repeated to produce a 60 s stimulus. To produce a 60 s control stimulus, we created and repeated one 30 s file of silence (i.e. equipment noise).

Test design

A playback test consisted of a 60 s control period of silent playback followed by 60 s of either echolocation pulses or social calls. Echolocation stimuli were calls from (1) a same-sex roostmate, (2) a same-sex nonroostmate, (3) an opposite-sex nonroostmate and (4) a heterospecific (*E. fuscus*). Social call stimuli were calls from (5) the above same-sex roostmate, (6) the above same-sex nonroostmate, (7) the above opposite-sex nonroostmate and (8) the one unfamiliar *D. youngi* male.

Each bat ($N=16$) received all eight playback tests, presented randomly in groups of two or three, over three separate days. Testing days for an individual were spaced apart by at least 4 days. Because roostmate group sizes were uneven, it was necessary to use one individual's calls as the same experimental treatment (e.g. different-sex nonroostmate) for two different subjects. Whenever this was the case, we constructed a second unique playback stimulus from this individual.

Test procedure

We conducted tests between 2030 and 2400 hours. We transported a subject individually to an acoustically isolated testing room surrounded by acoustic foam. We placed a subject inside a $76 \times 76 \times 183$ cm cage, with five nylon-mesh sides and one clear acrylic side. Experimenter presence was concealed behind a large fabric screen. A playback test began once a subject was acclimated enough to emerge from a blanket, or at least 9 min after a previous test. Synchronized ultrasound and video recording of responses began upon initiation of playback and continued for 2 min after playback ended. Gains on microphones and the speaker were constant across all trials. To avoid observer bias, the identity of each playback stimulus was kept blind from the experimenter.

Statistics

We used nonparametric statistics in JMP (v.5, SAS Institute, Cary, NC, U.S.A.) to compare the effect of playback stimuli on vocal responses. To control for baseline vocal activity, we calculated the vocal response evoked by playback as: (N during first 3 min)–(N during silent control minute \times 3), where N is the number of social call syllables. Alpha was 0.05.

Results

Only six of 16 bats responded with social calls to any playback test; thus only 18 of the 128 tests evoked responses. Despite this small sample, a few observations are noteworthy. Only two bats responded with social calls ($N=12$ and 31 calls) to echolocation call playback; however, six bats responded to social call playback with a mean \pm SD of 95.26 ± 96.29 calls per vocal response. Furthermore, responses were not limited to *D. youngi* callers of any one category; of 18 positive responses to playback, nine responses were to playback of callers of the opposite sex, eight responses were to callers of the same sex, four responses were to roostmates and 10 responses were to nonroostmates. Of the six bats that replied, three responded to the unfamiliar conspecific. There was only one response to playback of a heterospecific bat; one bat responded to the first echolocation pulse of the *E. fuscus* stimulus but did not respond to the rest of the playback. No bats called during the silent control periods prior to playback.

ANTIPHONAL CALLING EXPERIMENT

Methods

In this experiment, our goal was to determine whether social calls occur as antiphonal exchanges. To test this, we placed a caged bat in each corner of a roughly 4×4 m room lined with acoustic foam, and recorded simultaneously from all four bats using four synchronized microphones (Avisoft Ultrasoundgate 416; 8-bit resolution). Each microphone was placed 5–20 cm from a focal bat, and directed away from other bats. Our set-up allowed unambiguous assignment of calls to individuals. We used 14

bats in seven recording sessions: three with all-male roostmates, one with all-female roostmates, one with a female and three males, and two with a male and three females. We stopped each session when bats seemed habituated as indicated by a decrease in calling activity. Sessions lasted 50–71 min.

To create a database of social call times and sources, we used automated procedures in Avisoft SASLabPro to measure onset time, duration and frequency at maximum amplitude of social calls. We used duration and frequency measurements to exclude echolocation pulses from our data set. We tested and validated this automated approach with 268 hand-measured calls. We calculated interval between calls using onset times and average call length.

We counted antiphonal responses to conspecific calls for each focal bat. We considered calls antiphonal if they occurred less than 500 ms after a conspecific call, but we did not count calls as antiphonal if they overlapped or started within the first 10 ms, the approximate sound travel time to another bat. A 500 ms threshold was determined beforehand based on preliminary observations. For each bat, we calculated the number of antiphonal calls expected by chance (E) using the equation:

$$E = \frac{0.49N_F N_C}{T}$$

where N_F is the number of bat calls from a focal bat, N_C is the number of conspecific calls, and T is the total time recorded. For each conspecific call N_C , there is an antiphonal response ‘window’ of 0.49 s (500 ms window – 10 ms of sound travel time). The number of subject bat calls expected to occur in these windows by chance alone is thus the focal bat’s calling rate (N_F/T) multiplied by window length (0.49 s) and the number of windows (N_C). This approach is mathematically equivalent to another analysis of antiphonal calling (Soltis et al. 2005). We used chi-square tests to compare actual and expected values for all bats in the antiphonal calling experiments. We also applied the above calculations to the data from the previous playback experiment to determine whether those vocal responses to playback were antiphonal more than expected by chance. Alpha was 0.05.

If antiphonal calling is related to physical isolation, then the same four bats should not call when reunited. We tested this prediction by putting all bats together in a single cage after each session and recording any vocalizations for 10–30 min.

Results

Bats did not produce calls randomly with respect to conspecific calls (Fig. 2). The most common interval between a focal bat call and conspecific was ca. 300–350 ms. Ten of 14 bats called during these experiments, but two females were excluded from analyses because of small sample size ($N = 2$ calls each). For all but one of the remaining bats, calls occurred less than 500 ms after a conspecific call significantly more than expected by chance (Table 1). During the playback experiment, three of five bats called during the antiphonal window significantly more often than expected by chance (Table 1).

Antiphonal calling bouts occurred in every session, but decreased in frequency over time. Most antiphonal exchanges (67%) occurred as an initial social call followed by a single response. The longest exchange was five alternating social calls among three bats.

If all calling consists of initial calls followed by a single antiphonal response, then 50% of calls are expected to be antiphonal responses. In contrast, approximately 18% of calls ($N = 1858$) were antiphonal responses. Hence, many calls elicited no response. During the playback experiments, 38.5% of vocal responses were antiphonal (i.e. within 0.5 s of a playback call).

Bats generally called when isolated, but not when we placed them together; social call bouts by isolated bats began immediately after the lights were turned off, but we recorded no social calls from the same bats placed together for 10–30 min.

INDIVIDUAL VARIATION IN CALL STRUCTURE

Methods

From each of the 17 bats, we selected calls with the best signal-to-noise ratio, no clipping of signal, unambiguous caller identity and two syllables (27–64 per individual, 816 total). We marked the beginning and end of each syllable in the program BatSound Pro by hand. We used a custom-designed Matlab program (Skowronski 2007) to automate frame-based measurements. Each hand-labelled note was analysed using 0.5 ms Blackman windows and 512-point FFTs (488 Hz resolution) that overlapped by 50%. Local call features were extracted from each window (e.g. maximum energy, frequency of maximum energy, and temporal slope and concavity of energy and frequency). Global call features were estimated from the local features for the fundamental frequency and all harmonics (e.g. minimum and maximum frequency, bandwidth, duration, median slope and concavity, and frequency percentiles). We estimated 58 global features for each syllable (Skowronski 2007).

We reduced the number of variables per call to 20 for two reasons. First, we found some automated measurements to be unreliable. We therefore removed variables that measured maximum and minimum frequency values, because these measurements might contain inaccurate outliers if beginning or end marks were off by even a single frame. We also removed variables whose frequency distribution could not be transformed to an approximately normal distribution because of the presence of many outliers. Second, the number of variables used in a discriminant function analysis (DFA) must be fewer than the number of levels (calls) in the smallest group (an individual), in this case 27. We therefore removed variables that measured harmonics above the fourth harmonic, as not all recordings included these data. When any two variables were highly correlated (correlation coefficient >0.70), we removed one. We assessed normality using Shapiro–Wilk’s tests and from observing frequency histograms. For each variable, we used transformations that best fit the data to normal distributions, based on Shapiro–Wilk’s W (Table 2).

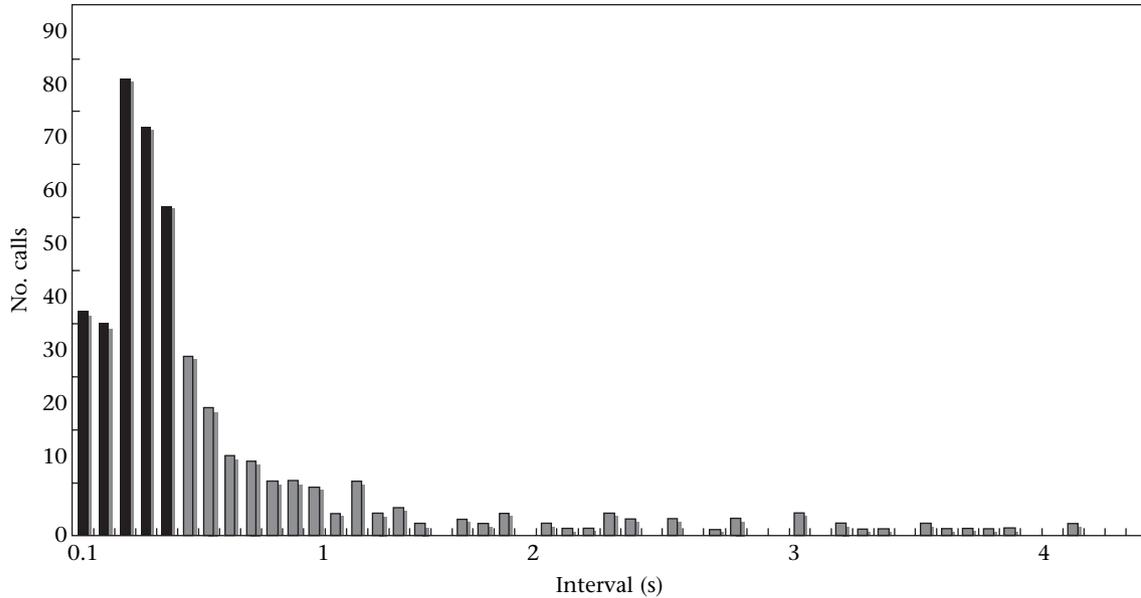


Figure 2. Frequency distribution showing the number of social calls occurring within a 5 s period after a conspecific social call. Black bars represent calls considered antiphonal (latency < 0.5 s).

Statistics

We initially used DFA in SPSS (v.11, Chicago, IL, U.S.A.) to calculate correct classification rates for individual identity of 17 bats. We entered 20 variables together (Table 2). We used a random 75% of calls to derive discriminant functions; the remaining 25% were used as test calls. A DFA can yield a high percentage correct classification to group even for randomly generated ‘groups’, so repeating DFAs with randomized data sets is a necessary test to avoid this problem (e.g. Kazial et al. 2001). To control for recording year as a potentially confounding variable, we then

used a permuted DFA (pDFA, Mundry & Sommer 2007) to test the null hypothesis that subjects cannot be discriminated by their calls. This pDFA permuted calls between subjects but only within years. In addition, permutation was restricted such that all calls of a subject were permuted simultaneously, accounting for the nonindependence of different calls obtained from a subject in a given year.

Table 1. Percentage of social calls occurring as antiphonal responses in eight bats

| Bat | Total no. calls | Responses to live bats within 0.5 s of other calls | | χ^2 | df | P |
|-----------------------|-----------------|--|----------|----------|----|----------|
| | | Expected | Observed | | | |
| B* | 2 | 0.15 | 2 | | | |
| C* | 2 | 0.03 | 0 | | | |
| D | 151 | 0.17 | 10 | 568.41 | 1 | <0.0001 |
| G | 10 | 0.66 | 3 | 8.30 | 1 | 0.0040 |
| H | 552 | 12.52 | 36 | 44.03 | 1 | <0.0001 |
| I | 34 | 2.16 | 4 | 1.57 | 1 | 0.2102** |
| J | 243 | 11.45 | 48 | 116.67 | 1 | <0.0001 |
| M | 38 | 2.37 | 17 | 90.31 | 1 | <0.0001 |
| O | 291 | 12.35 | 101 | 636.34 | 1 | <0.0001 |
| P | 501 | 12.98 | 501 | 422.11 | 1 | <0.0001 |
| Responses to Playback | | | | | | |
| D | 376 | 67.45 | 144 | 86.88 | 1 | <0.0001 |
| H | 24 | 4.14 | 15 | 28.49 | 1 | <0.0001 |
| J | 24 | 5.16 | 8 | 1.56 | 1 | 0.2116** |
| K | 272 | 52.35 | 102 | 47.09 | 1 | <0.0001 |
| P | 7 | 0.83 | 2 | 1.65 | 1 | 0.1989** |

*Excluded from analysis due to small sample size.
 **Not significantly different from random chance.

Each permutation in a pDFA requires two randomizations (Mundry & Sommer 2007). First, the pDFA randomly selects training calls from each individual bat to derive discriminant functions. The pDFA chooses the number of training calls such that the sample of calls for each combination of individual identity and year of recording are balanced. The remaining (testing) calls are then used for validating the discriminant functions (i.e. cross-classification). Because numbers of calls per bat were unequal, we repeated DFAs with 100 different random selections to determine the average number of correct test assignments for the original data set. In the second randomization, the pDFA randomly exchanges between subjects but within years, whereby calls of the same year remain grouped. This is repeated 1000 times, and a DFA is performed each time, revealing the expected distribution of correct test call assignments under the null hypothesis. The proportion of randomized data sets revealing a number of correct assignments at least as large as the original data set equals the one-tailed P value (Mundry & Sommer 2007).

The pDFA was conducted using an R script (written by Roger Mundry). To control for the effect of sex, we performed a pDFA on male and female calls separately. We omitted one bat, born that year, from the analysis because it was recorded in only one year and sex was unknown.

Results

We found individual differences in the structure of social calls. Correct classification rates for the preliminary

Table 2. Variables and transformations used in discriminant function analyses

| Variable | Transformation | |
|--|----------------|--------------|
| | 1st syllable | 2nd syllable |
| Duration (ms) | $\sqrt{x+0.5}$ | None |
| Frequency of the 10th percentile of the fundamental (kHz)* | x^2 | $\log(x+1)$ |
| Frequency of the 50th percentile of the fundamental (kHz)* | None | x^2 |
| Frequency of the 90th percentile of the fundamental (kHz)* | $\sqrt{x+0.5}$ | x^2 |
| Frequency of most energy (FME) of the fundamental (kHz) | $\sqrt{x+0.5}$ | x^2 |
| FME of the 1st harmonic (kHz) | None | x^2 |
| FME of the 2nd harmonic (kHz), 2nd syllable only | None | x^2 |
| FME of the 3rd harmonic (kHz) | None | None |
| Time of FME of the fundamental relative to start (ms) | \sqrt{x} | $\log(x+1)$ |
| Slope of the 50th percentile of the fundamental (kHz/ms) | None | None |
| Interval: ms between end of 1st syllable and start of 2nd | | $\log(x+15)$ |

*Frequency of the *N*th percentile is the frequency at the frame *N* percentage of the way to the end of the syllable.

DFA in SPSS for test calls were 78.3% for females, 73.8% for males, and 67.2% overall. These rates were significantly greater than expected by chance (pDFA; females: $N = 417$, $P = 0.005$; males: $N = 399$, $P = 0.001$). For the single bat excluded from the pDFA, 100% of test calls were correctly classified by the preliminary DFA.

VOCAL DISCRIMINATION EXPERIMENT

Methods

We used a modified habituation–discrimination approach because this test is particularly powerful for showing individual recognition and does not require training (e.g. Rendall et al. 1996; Boughman & Wilkinson 1998; Weiss et al. 2001). Following Rendall et al. (1996), we represented each individual with playback of multiple call exemplars to test for discrimination of individuals, not simply stimuli.

Playback stimuli construction

We only used calls with signal amplitudes between 45% and 99% of maximum recording intensity. Mean amplitude of playback calls from different individuals did not differ significantly. Median interval between calls of a lone bat was 998 ms ($N = 500$), so we spaced playback calls between randomly generated latencies of 900 to 1100 ms. We constructed 16 playback stimuli from individual recordings (Table 3). Although some bats were used several times as habituation stimuli or test stimuli because of call recording availability, every sequence used a unique set of call exemplars.

Each playback sequence (Fig. 3) included a 5 s silent period, followed by a habituation period (30, 60 or 90 s;

Table 3. Playback sequences included in statistical analyses

| | Source of habituation calls | Source of test calls | Length of habituation (s) |
|----|-----------------------------|----------------------|---------------------------|
| 1 | P* | F* | 30 |
| 2 | A | D | 30 |
| 3 | I* | E | 90 |
| 4 | H* | S* | 60 |
| 5 | H* | B | 30 |
| 6 | G* | H* | 90 |
| 7 | F | C | 30 |
| 8 | E | N | 60 |
| 9 | E | G* | 30 |
| 10 | B | S* | 90 |
| 11 | B | R* | 30 |
| 12 | B | L | 60 |
| 13 | B | K | 30 |
| 14 | A | R* | 30 |
| 15 | C | R* | 60 |
| 16 | A | L | 60 |

Letters indicate different bats.

*Males.

Table 3), a test period (10 s) and a rehabilitation period (10 s). The habituation and rehabilitation periods consisted of different call exemplars from one bat, while the test period presented call exemplars from a different bat (see Supplementary Material). We adjusted intensity of playback so that calls recorded simultaneously from a speaker and a live bat produced equal amplitudes on an equidistant microphone, and we maintained this level across all trials.

Playback methodology

We conducted playback tests between 2030 and 2400 hours in complete darkness. We transported subjects inside boxes to an acoustically isolated testing room, where temperature and humidity were maintained at levels similar to those in the housing area. In preliminary trials, we found that bats responded more often to conspecific calls after vocal or physical contact was interrupted. We therefore ‘primed’ subject bats by initially allowing them and the bat corresponding to the habituation stimulus to vocally interact in complete darkness. We placed the subject inside a $13.9 \times 7.6 \times 7.6$ cm testing cage, in which five sides were wire mesh and one side was clear acrylic; we placed the other bat in a different cage nearby. After 2–5 min, we removed the nonsubject bat. After another acclimation period of 0.5–2 min, we broadcast a playback sequence. The speaker was located 79 cm from the subject. The ultrasound microphone faced towards the subject and directly away from the speaker. The microphone gain was constant across all trials.

We monitored and recorded playback responses remotely from an adjacent room. We defined a response as any of the following: (1) vocal response: production of social call, (2) orientation: turning of head and body towards speaker, (3) startle response: change from eyes closed and ears still to eyes open and ears moving. If bats did not respond to the habituation periods or the test period, we played a ‘post-test stimulus’ (following Weiss

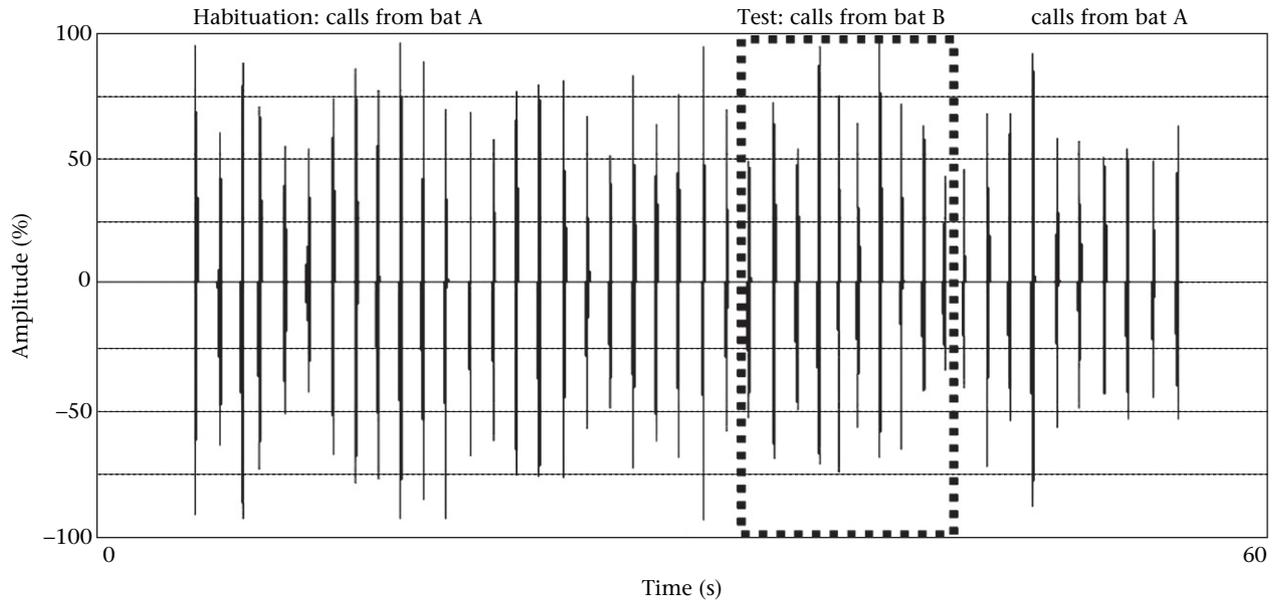


Figure 3. Typical playback sequence of social calls depicted as amplitude over time. Test period is highlighted with a dotted line box.

et al. 2001). The post-test stimulus was a distress call, an aggressive hissing call, a rapid bout of calling, and a series of complex vocalizations, all from different bats. If a subject failed to respond to this series of sounds, then we aborted that trial and discarded those data. Failing the post-test stimulus test indicates a generalized habituation to the entire experimental set-up. Of 135 trials attempted, we aborted 59 when (1) subjects failed to respond to any playback including the post-test stimulus (31 trials), (2) subjects showed no visible decrease in response during the habituation period (23 trials) or (3) the experiment was interrupted, for instance, by an outside noise or equipment malfunction (5 trials).

Response measurement

We measured two responses independently: calling rate and physical response duration. To measure calling, we used the program BatSound Pro to count the number of social call syllables produced by the subject during each 10 s period of the playback sequence starting at the onset of the playback. Subject calls could be unambiguously discriminated from playback calls. To measure physical response duration, we analysed frame-by-frame digital video in the program iMovie HD. For each 10 s period, we marked the starting frame of the response until the response or the period ended, yielding a measurement from 0 to 10 s. We measured all responses blind to the identity of the trial.

Statistical analysis

We used nonparametric statistics to compare the mean response during the 10 s test period to the average of the mean responses during 10 s periods immediately before and after the test period: ((mean response during 10 s before test) + (mean response during 10 s after test))/2. Averaging the mean responses during these two periods is a conservative approach, because some of the response to the 10 s test period may linger into the following 10 s period.

We analysed the responses to the vocal discrimination experiment using two alternative approaches. In the first analysis, we used the number of playback sequences ($N = 16$) as the sample size. For each sequence, we first averaged the responses for multiple trials with the same subject, and then averaged the responses across all subjects. We then entered those sequence averages into a Wilcoxon signed-ranks test. This first approach places priority on showing that several bats' calls can be discriminated from each other, rather than showing that many different bats can perform a vocal discrimination task. However, some researchers argue that subjects are the proper unit of replication. Therefore, we also present a second analysis where we averaged the results for each bat across the sequences played to that bat, and then entered those individual averages ($N = 8$) into the Wilcoxon signed-ranks test. We conducted analyses using JMP (v. 7.0) and SPSS 11. Alpha was 0.05.

Results

We analysed responses to 16 unique playback sequences collected from eight individuals (Table 4). Mean calling rate of subjects during the 10 s test period was significantly greater than the average of the mean calling rates during the habituation period (10 s before) and rehabilitation period (10 s after) (Fig. 4a, Supplementary Material). We found a significant difference regardless of whether using a sample size of sequences (Wilcoxon signed-ranks test: $T = 30$, $N = 16$, $P = 0.005$) or subjects ($T = 14$, $N = 8$, $P = 0.016$). Mean calling rate during the test period did not differ significantly from the first 10 s of habituation (Wilcoxon signed-ranks test: $T = 4.5$, $N = 16$ sequences, $P = 0.772$; or $T = 9$, $N = 8$ bats, $P = 0.156$; Fig. 4a).

Mean duration of physical response during the 10 s test period was significantly greater than the average of the mean durations during the habituation period and rehabilitation period (Wilcoxon signed-ranks test: $T = 49$,

$N = 16$ sequences, $P = 0.003$; or $T = 14$, $N = 8$ bats, $P = 0.016$; Fig. 4b, Supplementary Material). Mean duration during the test period was also greater than the first 10 s of habituation (Wilcoxon signed-ranks test: $T = 41$, $N = 16$ sequences, $P = 0.007$; or $T = 12$, $N = 8$ bats, $P = 0.047$; Fig. 4b).

DISCUSSION

The antiphonal calling behaviour of adult white-winged vampire bats is unlike any vocal behaviour we have seen in other bats (see footage, Supplementary Material). Our results indicate that these antiphonal calls help bats to identify and find each other at a distance. Isolated bats called repeatedly when they could hear conspecifics, and antiphonal calling bouts occurred among simultaneously isolated bats. Moreover, calling declined dramatically when the same bats were put together. Below we describe the temporal pattern of calling, explain evidence for individual discrimination and discuss possible functions of antiphonal calling.

Temporal Pattern of Antiphonal Calling

White-winged vampire bats respond to conspecific social calls with a latency of about one-third of a second. This simple call–answer pattern is found in primate antiphonal contact calls, albeit with longer mean latency periods (e.g. about 3.7 s in cottontop tamarins: Miller et al. 2005). Our antiphonal calling experiments yielded a lower overall percentage of antiphonal calling than when bats replied to playback, because in our antiphonal calling experiments, most responses ceased after a series of initial bouts lasting roughly 20 min, but a few individuals continued to call repetitively with no response from conspecifics.

Evidence for Individual Discrimination

Using permuted DFA, we have shown that individual identity can be assigned with greater than chance probability using call structure. While this result alone does not establish vocal recognition, our playback experiments provide convincing evidence that white-winged vampire bats can discriminate between vocalizations from different individuals. Such discrimination is a prerequisite for vocal recognition, an ability to associate vocalizations with an individual.

Our playback data corroborate other recent evidence that bats can discriminate adult conspecifics using only vocalizations (see also Kazial et al. 2008). Bats were able to discriminate between adult conspecifics with several possible combinations of sex and affiliation (Table 4). For instance, two male subjects (J and I) both discriminated between two other males in the same cage, G and H. In another test, a female (K) in a different cage also discriminated between G and H, even though bats G and H were represented by sequences with different calls in all three tests.

Since relatedness of individuals in our study was unknown, it is theoretically possible that every observed case of a response rebound was actually a case of

Table 4. Results of vocal discrimination playback experiment

| Subject bat and sex | Playback: habituation source to test source | Affiliation: D = different cage, U = unfamiliar, S = same cage, U = unfamiliar | No. of trials | Test period rebound [†] | |
|---------------------|---|--|---------------|----------------------------------|-------------------|
| | | | | Vocal response | Physical response |
| K female | A to R | D to S | 3 | X | X |
| | G to H | D to D | 3 | X | |
| | H to B* | D to D | 1 | | |
| | E to G* | D to D | 1 | | |
| | B to R* | D to S | 1 | X | X |
| | I to E* | D to D | 3 | X | |
| | A to L | D to S | 2 | X | X |
| | B to L | D to S | 1 | X | X |
| | E to N | D to D | 2 | X | |
| | F to C* | D to D | 1 | | |
| F male | H to S | D to U | 1 | X | X |
| | E to G* | S to D | 2 | | |
| | A to R* | S to D | 3 | X | X |
| | B to K | S to D | 3 | | X |
| | O to D* | D to S | 1 | | |
| | H to B* | D to S | 2 | | |
| | I to E* | D to S | 1 | | X |
| D female | H to S | D to U | 1 | X | |
| | B to L | S to D | 1 | X | X |
| | P to F | D to D | 2 | | X |
| | I to E* | D to S | 1 | | |
| | B to K | S to D | 2 | | |
| | F to C* | D to S | 1 | | |
| | A to R* | S to D | 4 | X | X |
| | E to G* | S to D | 1 | | |
| | B to S* | D to U | 1 | X | |
| | G to H | D to D | 1 | | |
| J male | B to R* | S to D | 1 | X | |
| | G to H | S to S | 2 | X | |
| | I to E* | S to D | 2 | | |
| | H to B* | S to D | 1 | | |
| | E to G* | D to S | 1 | | |
| | P to F | D to D | 1 | | |
| | F to C* | D to D | 1 | | |
| H male | I to E* | S to D | 3 | X | |
| | E to G* | D to S | 1 | | X |
| | A to R* | D to D | 2 | | X |
| | O to D* | D to D | 1 | | |
| P male | H to S | S to U | 1 | | X |
| | A to R* | D to D | 1 | X | |
| | C to R* | D to D | 1 | X | X |
| | G to H | D to D | 1 | | |
| O male | E to G* | D to D | 1 | | X |
| | H to B* | D to D | 1 | | X |
| | E to G* | D to D | 1 | | |
| I male | B to R* | D to D | 1 | X | X |
| | E to G* | D to S | 1 | | |
| | G to H | S to S | 2 | | X |
| | H to B* | S to D | 1 | | X |

Letters are different bats. A–E, K, L and N are females. F–J, M, O, P and R are males.

*Indicates that the sex of bat changed between habituation and test stimuli sources.

†An X indicates that the mean response during the last 10 s habituation period was 0 and that the mean test period response was greater than 0. Mean response during the last 10 s habituation period never exceeded the mean test period response.

discriminating kin from nonkin rather than discriminating individual identity. However, our results are unlikely to be due to kin discrimination alone for two reasons. First, several subjects could discriminate between the same

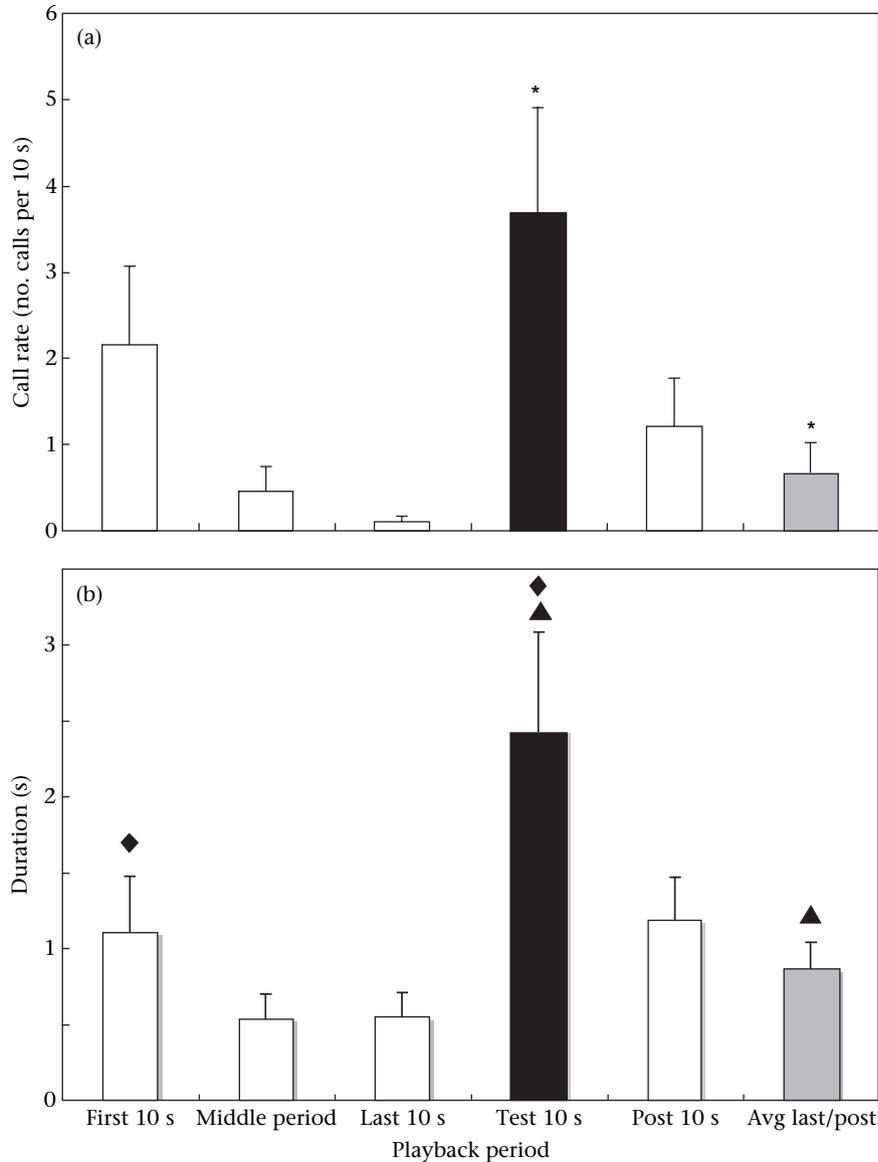


Figure 4. Mean + SE (a) vocal and (b) physical responses to periods of a habituation–discrimination playback sequence. Response during the ‘middle’ period is the average response per 10 s period between the first and last habituation periods. ■: mean response during the 10 s test period, when the identity of the caller changed. □: average of the responses during the periods before and after the test period. See text for test statistics. * $P = 0.005$; ◆: $P = 0.007$; ▲: $P = 0.003$.

pair of bats. For example, five subjects discriminated playback of bat R from bat A (Table 4), and all five responded more to playback of bat R. If bats can only vocally discriminate kin from nonkin, then all five of these subjects must be related to one bat, but not the other. Second, another bat (S) was almost certainly unrelated to all subjects, yet four subjects could discriminate its calls from those of others (Table 4). Likewise, if bats can only vocally discriminate kin from nonkin, then all four subjects in this case must have been related to the first bat presented in the sequence. It is far more likely that subjects discriminated these calls based on identity. In particular, bat R was born 4 months prior and may have evoked a particularly strong response because of its age or unfamiliarity, and bat S was unfamiliar to all subjects.

In a typical habituation–discrimination test, the initial response to the habituation stimulus is expected to be greater than, or equal to, the test stimulus (e.g. Rendall et al. 1996). In our results, however, mean response was greater during the test period than during the initial habituation period (Fig. 4). This bias makes sense since the habituation playback period was often preceded by some prior habituation, occurring when subjects were exposed to calling from the same live bat from which they would later hear playback calls. In other words, the first measured response occurred when the playback began even though the bats were allowed to interact prior to this. Hence, from a subject’s point of view, these first playback calls may have represented a continuation of calling. Indeed, in four trials, subjects seemed to be already habituated before

playback began. They ignored the initial playback and only responded during the test period when the caller's identity changed.

Function of Social Calls

Several results suggest that *D. youngi* social calls are contact calls that allow long-distance vocal recognition. In some bats, such as vespertilionids, high-intensity echolocation calls can carry information on identity long distances (e.g. Kazial et al. 2001, 2008), but for phyllostomids, such as vampire bats, echolocation calls have relatively low intensity and thus cannot serve well in this role. Social calls, on the other hand, are more intense and have a lower frequency than echolocation calls (Fig. 1), so they travel further distances. *Diaemus youngi* social calls were not correlated with the presence or absence of food. Unlike alarm calls, social calling was not elicited by disturbances, but rather stopped when a person appeared (G. Carter, personal observation). Antiphonal social calls occur year-round among and between captive bats of both sexes (personal observation), and we also recorded them from bats as young as 4 months. Their basic double-note structure is common in bat pup isolation calls (Gould et al. 1973; Gould 1977). Social calls are most reliably recorded from isolated bats that can hear conspecifics, and conspecifics are attracted to the calls. Lastly, calls are individually distinct and can be individually discriminated by conspecifics. These observations suggest that antiphonal calling behaviour between adult *D. youngi* is similar to, and perhaps originates from, the antiphonal contact calling that sometimes occurs between a mother bat and her pup (Matsumara 1981; Brown et al. 1983).

Social calls are not only produced during isolation. Captive white-winged vampires also produce them while emerging from roost boxes, while feeding on chickens, and in some putative social dominance interactions. For example, we observed one bat calling while atop another individual. These observations support the notion that adult contact calls may be used in a variety of contexts. Further study is needed to determine how *D. youngi* use these social calls in the wild.

Possible Functions of Antiphonal Responses

Responding antiphonally to contact calls might be advantageous to listeners for several reasons. Kin or reciprocal altruists might be seeking to minimize the time that the caller must wait for a response (Sugiura 1993; Hall 2004). Another possibility is that listeners use antiphonal responses to actively elicit 'updates' of acoustic information. In theory, intervals between actions will normally be shorter among paired or grouped animals than in lone animals (Dostalkova & Spinka 2007). Accordingly, individual calling rates should be higher during an antiphonal calling bout than during a lone calling bout. Therefore, listeners that also rapidly reply will increase a caller's signalling rate, providing additional cues for caller location and identity. Consider a mother bat searching

for a pup. By providing rapid vocal feedback, mother bats can manipulate the pup's calling rate, direction and/or intensity, making recognition and localization faster. Our results support this explanation for adult white-winged vampires as well, because bats increased calling rate after receiving antiphonal responses.

Individual Recognition in Vampire Bats

The common vampire bat, *Desmodus rotundus*, is considered the closest living relative to *Diaemus youngi* based on molecular and morphological data (Greenhall & Schutt 1996). Like many social primates, *D. rotundus* live in societies where long-term individual social relationships are important components of reproductive success. Common vampire bats are long-lived (15 years in the wild: Tschapka & Wilkinson 1999), and their social structure conforms to a fission–fusion model of sociality (Wilkinson 2003). In hollow trees, roosting groups typically include 8–12 adult females (up to 20 in caves), their pups, a dominant male and a few subordinate males (Wilkinson 1985a, 1988). Although intragroup relatedness is low (Wilkinson 1985b), individual affiliations are important and maintained partly through allogrooming (Wilkinson 1986). Indeed, such relationships are a prerequisite for the evolutionary stability of the reciprocal altruism that takes place both between kin and between unrelated adults (regurgitated food sharing: Wilkinson 1984; DeNault & McFarlane 1995).

Although social behaviour of the rare white-winged vampires is known only from observations of captive bats (Schutt et al. 1999), several observations strongly suggest that individual identity plays an important social role in *D. youngi* as well. Captive *D. youngi* also perform reciprocal food sharing and allogrooming (G. Carter & C. Coen, unpublished data). Certain pairs of individuals were consistently aggressive to one another, and others consistently roosted in close proximity. Although a group's roosting location might change, an individual's sleeping position in relation to other bats is fairly stable (G. Carter, personal observation).

Interactions such as reciprocal food sharing require individual recognition at short range, but do not explain the need for long-distance vocal recognition. Interestingly, *D. rotundus* do not seem to use similar contact calls and are not nearly as vocal (Schmidt 1972; Sailer & Schmidt 1978; G. Carter, personal observations). We therefore predict that *D. youngi* social interactions differ from those of *D. rotundus* while outside the roost.

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Supplementary Material

Supplementary data associated with this article can be found, in the online version, at doi: [10.1016/j.anbehav.2008.04.023](https://doi.org/10.1016/j.anbehav.2008.04.023).

References

- Balcombe, J. P. 1990. Vocal recognition of pups by mother Mexican free-tailed bats, *Tadarida brasiliensis mexicana*. *Animal Behaviour*, **39**, 960–966.
- Balcombe, J. P. & McCracken, G. F. 1992. Vocal recognition in Mexican free-tailed bats: do pups recognize mothers? *Animal Behaviour*, **43**, 79–88.
- Barlow, K. E. & Jones, G. 1997. Function of pipistrelle social calls: field data and a playback experiment. *Animal Behaviour*, **39**, 960–966.
- Bohn, K. M., Wilkinson, G. S. & Moss, C. F. 2007. Discrimination of infant isolation calls by female greater spear-nosed bats, *Phyllostomus hastatus*. *Animal Behaviour*, **73**, 423–432.
- Boughman, J. W. 1997. Greater spear-nosed bats give group-distinctive calls. *Behavioral Ecology and Sociobiology*, **40**, 61–70.
- Boughman, J. W. & Wilkinson, G. S. 1998. Greater spear-nosed bats discriminate group mates by vocalizations. *Animal Behaviour*, **55**, 1717–1732.
- Brown, P. 1976. Vocal communication in the pallid bat, *Antrozous pallidus*. *Zeitschrift für Tierpsychologie*, **41**, 34–54.
- Brown, P. E., Brown, T. W. & Grinnell, A. D. 1983. Echolocation, development, and vocal communication in the lesser bulldog bat, *Noctilio albiventris*. *Behavioral Ecology and Sociobiology*, **13**, 287–298.
- Brown, S. D., Dooling, R. J. & O'Grady, K. 1988. Perceptual organization of acoustic stimuli by budgerigars (*Melopsittacus undulatus*): III. Contact Calls. *Journal of Comparative Psychology*, **102**, 236–247.
- Cortopassi, K. A. & Bradbury, J. W. 2006. Contact call diversity in wild orange-fronted parakeet pairs, *Aratinga canicularis*. *Animal Behaviour*, **71**, 1141–1154.
- DeNault, L. A. & McFarlane, D. A. 1995. Reciprocal altruism between male vampire bats *Desmodus rotundus*. *Animal Behaviour*, **49**, 855–856.
- Dostalkova, I. & Spinka, M. 2007. Synchronization of behaviour in pairs: the role of communication and consequences in timing. *Animal Behaviour*, **74**, 1735–1742. doi:10.1016/j.anbehav.2007.04.014.
- Fenton, M. B. 1985. *Communication in the Chiroptera*. Bloomington: Indiana University Press.
- Gelfand, D. L. & McCracken, G. F. 1986. Individual variation in the isolation calls of Mexican free-tailed bat pups (*Tadarida brasiliensis mexicana*). *Animal Behaviour*, **34**, 1078–1086.
- Gould, E. 1977. Echolocation and communication. In: *Biology of Bats of the New World Family Phyllostomatidae* (Ed. by R. J. Baker, J. K. Jones & D. C. Carter), pp. 247–279. Lubbock: Texas Tech University Press.
- Gould, E., Woolf, N. K. & Turner, C. 1973. Double note communication calls in bats: occurrence in three families. *Journal of Mammalogy*, **54**, 998–1001.
- Greenhall, A. M. & Schutt, W. A. 1996. *Diaemus youngi*. *Mammalian Species*, **533**, 1–7.
- Hall, M. L. 2004. A review of hypotheses for the functions of avian duetting. *Behavioral Ecology and Sociobiology*, **55**, 415–430.
- Janik, V. M. & Slater, P. J. B. 1998. Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Animal Behaviour*, **56**, 829–838.
- Jordan, K., Weiss, D., Hauser, M. & McMurray, B. 2004. Antiphonal responses to loud contact calls produced by *Saguinus Oedipus*. *International Journal of Primatology*, **25**, 465–475.
- Kanwal, J. S., Matsumara, S., Ohlemiller, K. K. & Suga, N. 1994. Analysis of acoustic elements and syntax in communication sounds emitted by moustached bats. *Journal of the Acoustical Society of America*, **96**, 1229–1254.
- Kazial, K. A., Burnett, S. C. & Masters, W. M. 2001. Individual and group variation in echolocation calls of big brown bats, *Eptesicus fuscus* (Chiroptera: Vespertilionidae). *Journal of Mammalogy*, **82**, 339–351.
- Kazial, K. A., Kenny, T. L. & Burnett, S. C. 2008. Little brown bats (*Myotis lucifugus*) recognize individual identity of conspecifics using sonar calls. *Ethology*, **114**, 469–478. doi:10.1111/j.1439-0310.2008.01483.x.
- Lamprecht, J., Kaiser, A., Peters, A. & Kirchgessner, C. 1985. Distance call duets in bar-headed geese (*Anser indicus*): co-operation through visual relief of the partner? *Zeitschrift für Tierpsychologie*, **70**, 211–218.
- Leippert, D., Goymann, W., Hofer, H., Marimuthu, G. & Balasingh, J. 2000. Roost-mate communication in adult Indian false vampire bats (*Megaderma lyra*): an indication of individuality in temporal and spectral pattern. *Animal Cognition*, **3**, 99–106.
- Matsumara, S. 1981. Mother–infant communication in a horseshoe bat (*Rhinolophus ferrumequinum nippon*): vocal communication in three-week-old infants. *Journal of Mammalogy*, **62**, 20–28.
- Miller, C. T., Iguina, C. G. & Hauser, M. D. 2005. Processing vocal signals during antiphonal calling in tamarins. *Animal Behaviour*, **69**, 1387–1398.
- Miller, P. J. O., Shapiro, A. D., Tyack, P. L. & Solow, A. R. 2004. Call-type matching in vocal exchanges of free-ranging resident killer whales, *Orcinus orca*. *Animal Behaviour*, **67**, 1099–1107.
- Mundry, R. & Sommer, C. 2007. Discriminant function analysis with nonindependent data: consequences and an alternative. *Animal Behaviour*, **74**, 965–976. doi:10.1016/j.anbehav.2006.12.028.
- Pfalzer, G. & Kusch, J. 2003. Structure and variability of bat social calls: implications for specificity and individual recognition. *Journal of Zoology*, **261**, 21–33.
- Porter, F. L. 1979. Social behavior in the leaf-nosed bat, *Carollia perspicillata* II. Social communication. *Zeitschrift für Tierpsychologie*, **50**, 1–8.
- Rendall, D. & Owren, M. J. 2002. Animal vocal communication: say what? In: *The Cognitive Animal* (Ed. by M. Bekoff, C. Allen & G. M. Burghardt), pp. 307–314. Cambridge, Massachusetts: MIT Press.
- Rendall, D., Rodman, P. S. & Emond, R. E. 1996. Vocal recognition of individuals and kin in free-ranging rhesus monkeys. *Animal Behaviour*, **51**, 1007–1015.
- Sailler, H. & Schmidt, U. 1978. Social calls of the common vampire bat *Desmodus rotundus* during aggressive behavior at the feeding place in the laboratory. *Zeitschrift für Säugetierkunde*, **43**, 249–261.
- Scherrer, J. A. & Wilkinson, G. S. 1993. Evening bat isolation calls provide evidence for heritable signatures. *Animal Behaviour*, **46**, 847–860.
- Schmidt, U. 1972. Social calls of juvenile vampire bats *Desmodus rotundus* and their mothers. *Bonner Zoologische Beiträge*, **23**, 310–316.

- Schutt, W. A., Muradali, F., Mondol, N., Joseph, K. & Brockmann, K. 1999. Behavior and maintenance of captive white-winged vampire bats, *Diaemus youngi*. *Journal of Mammalogy*, **80**, 71–81.
- Skowronski, M. 2007. Acoustic analysis of bat calls: methods for read_marks Matlab program. Available from: <http://publish.uwo.ca/~mskowro2/>.
- Soltis, J., Leong, K. & Savage, A. 2005. African elephant vocal communication I: antiphonal calling behaviour among affiliated females. *Animal Behaviour*, **70**, 579–587.
- Sugiura, H. 1993. Temporal and acoustic correlates in vocal exchanges of coo calls in Japanese macaques. *Behaviour*, **124**, 207–225.
- Sugiura, H. 1998. Matching of acoustic features during the vocal exchange of coo calls by Japanese macaques. *Animal Behaviour*, **55**, 673–687.
- Tschapka, M. & Wilkinson, G. S. 1999. Free-ranging vampire bats (*Desmodus rotundus*, Phyllostomidae) survive 15 years in the wild. *Zeitschrift für Säugetierkunde*, **64**, 239–240.
- Wanker, R., Apcin, J., Jennerjahn, B. & Waibel, B. 1998. Discrimination of different social companions in spectacled parrotlets (*Forpus conspicillatus*): evidence for individual vocal recognition. *Behavioral Ecology and Sociobiology*, **43**, 197–202.
- Weiss, D. J., Garibaldi, B. T. & Hauser, M. D. 2001. The production and perception of long calls by cotton-top tamarins (*Saguinus oedipus*): acoustic analyses and playback experiments. *Journal of Comparative Psychology*, **115**, 258–271.
- Wilkinson, G. S. 1984. Reciprocal food sharing in the vampire bat. *Nature*, **308**, 181–184.
- Wilkinson, G. S. 1985a. The social organization of the common vampire bat *Desmodus rotundus* I. Pattern and cause of association. *Behavioral Ecology and Sociobiology*, **17**, 111–122.
- Wilkinson, G. S. 1985b. The social organization of the common vampire bat *Desmodus rotundus* II. Mating system genetic structure and relatedness. *Behavioral Ecology and Sociobiology*, **17**, 123–134.
- Wilkinson, G. S. 1986. Social grooming in the common vampire bat, *Desmodus rotundus*. *Animal Behaviour*, **34**, 1880–1889.
- Wilkinson, G. S. 1988. Social organization and behavior. In: *Natural History of Vampire Bats* (Ed. by A. M. Greenhall & U. Schmidt), pp. 85–97. Boca Raton, Florida: CRC Press.
- Wilkinson, G. S. 2003. Social and vocal complexity in bats. In: *Animal Social Complexity* (Ed. by F. B. M. de Waal & P. L. Tyack), pp. 322–341. Cambridge, Massachusetts: Harvard University Press.
- Wilkinson, G. S. & Boughman, J. W. 1998. Social calls coordinate foraging in greater spear-nosed bats. *Animal Behaviour*, **55**, 337–350.
- Yosida, S., Kobayasi, K. I., Ikebuchi, M., Ozaki, R. & Okanoya, K. 2007. Antiphonal vocalization of a subterranean rodent, the naked mole-rat (*Heterocephalus glaber*). *Ethology*, **113**, 703–710.