Behav Ecol Sociobiol (2011) 65:1581–1593
DOI 10.1007/s00265-011-1168-4

ORIGINAL PAPER

Individual specific contact calls of pallid bats (*Antrozous pallidus*) attract conspecifics at roosting sites

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Received: 13 October 2010 / Revised: 28 January 2011 / Accepted: 23 February 2011 / Published online: 15 March 2011

Abstract In several bird and mammal species, contact calls are utilized to maintain group cohesion and coordinate group movement. From a signal design perspective, contact calls typically exhibit acoustic features that make them easily localizable and encode information about individual or group identity. Pallid bats (*Antrozous pallidus*) are unusual among vespertilionids in that they often emit a loud, partially audible frequency-modulated social call several times in rapid succession while in flight. This call appears to function as a contact call in that it is frequently given when bats return from foraging and perform circular flights before entering a crevice roost. However, the degree to which pallid bats respond to the calls of conspecifics and what information is provided in the call is unknown. Thus, the goal of this study was to investigate pallid bat calling behavior to determine if calls attract roostmates or elicit responses from them and provide sufficient information for individual recognition. In playback studies, we found that contact calls elicit calls and approaches and that free-flying bats respond more to familiar than unfamiliar calls. In addition, analysis of frequency and temporal measurements of calls collected from multiple sites and spectral cross correlation analysis of calls recorded from the same radio-tagged bats on multiple evenings revealed that the frequency pattern of contact calls is highly repeatable over time within individuals but exhibits significant differences among individuals. Thus, contact call structure appears to be unique to individuals and stable through time, which makes these calls well-suited for roostmate recognition.

Communicated by G. Jones

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Keywords Communication · Signature call · Fission–fusion · Vespertilionid bat

Benefits of group living in animals include predator detection, information transfer about foraging sites, and social thermoregulation (Krebs and Davies 1993). To obtain these benefits, a mechanism to maintain group cohesion is necessary, especially when individuals in the group are highly mobile. One such mechanism utilized by several bird and mammal species is the use of a specialized vocal signal, typically designated as a contact call. From a signal design perspective, contact calls are often high in amplitude and easily localizable, with the broadcast range of the call often closely tied to the dispersion of the group. In addition, variation in frequency modulation, temporal pattern, and harmonic structure can encode information about the individual or the social composition of its group (Bradbury and Vehrencamp 1998). For example, northern resident killer whales (*Orcinus orca*) live in stable family groups and produce contact calls that are specific to groups, and to a lesser extent, individuals (Nousek et al. 2006).

Alternatively, in more fluid societies, there is little benefit to maintain group signatures due to the frequent immigration and emigration of individuals. Thus, contact calls often encode individual signatures, which may aid in maintaining non-random associations among group members (Cortopassi and Bradbury 2006). For example, fission–fusion social structure is characteristic of many avian and mammalian societies where subgroups are part of a larger group that frequently splits or merges together (Couzin 2006), and many species with this type of social system produce individually specific contact calls [e.g., spider monkeys, *Ateles geoffroyi* (Ramos-Fernandez 2005); orange-fronted parakeets, *Aratinga canicularis* (Cortopassi and Bradbury

2006); and brown-throated conures, *Aratinga pertinax* (Buhrman-Deever et al. 2008)]. One well-studied species that utilizes contact calls and exhibits fission–fusion social structure is the bottlenose dolphin, *Tursiops truncatus* (Tyack 2003). In this species, individually distinct whistles are produced in both captive and free-living contexts (Sayigh et al. 2007) and are thought to mediate interactions and maintain social bonds within the group (Tyack 2003; Watwood et al. 2005).

Given their relatively dark aquatic habitat where light is quickly attenuated, acoustic signals enable dolphins to orient in their environment and interact with group members. Echolocating bats face similar challenges when flying at night necessitating the use of acoustic signals for both orientation and communication. Calls utilized for social communication in bats have been shown to function as contact calls to locate group members prior to foraging (Wilkinson and Boughman 1998) and recruit roostmates in species that exhibit high roost lability (Chaverri et al. 2010; Schoner et al. 2010). In addition, the information encoded in bat contact calls ranges from group specific via call convergence in stable *Phyllostomus hastatus* social groups (Boughman 1998) to individually specific calls of white-winged vampire bats, *Diaemus youngi* (Carter et al. 2008).

However, the extent to which social calls are used for mediating interactions within and among social groups is largely unknown for most bat species. Here, we report on social calls and associated behaviors of free-ranging pallid bats (*Antrozous pallidus*), a species where individuals in the colony switch roosting sites frequently and thus may benefit from a mechanism to locate roostmates as they return to the maternity colony from foraging at night. Our study includes observational data on the behavioral context of social calls, playback data, and an analysis of the variability and repeatability of social calls to determine if calls contain sufficient information to allow for individual discrimination at the roost site.

Pallid bats range throughout western North America from British Columbia south to central Mexico (Barbour and Davis 1969). In the summer, female pallid bats form maternity colonies in large rock outcroppings near a source of water to give birth and nurse their pups while males typically roost away from the maternity colony in smaller groups (Hermanson and O'Shea 1983). In addition, telemetry data show that pallid bats within a maternity colony exhibit high roost lability, switching among multiple rock crevice roosts within the larger cliff complex every 1–2 days, on average, with inconsistent group association (Lewis 1996). Thus, pallid bats appear to conform to a fission–fusion social structure model similar to that found in other vespertilionid bat species (Kerth 2008).

Although the roost switching behavior of pallid bats is a relatively common phenomenon among bats (Lewis 1995), pallid bats are unusual among vespertilionids in that they often produce a loud, audible call several times in rapid succession while in flight. This directive call (as described by Orr 1954) differs from echolocation calls in both structure and context by having lower frequencies and by occurring in rapid bursts rather than being continuously emitted (Fig. 1). Interestingly, pallid bats exhibit greater auditory sensitivity between 5 and 15 kHz than many other bat species (Brown et al. 1978), which is notable because low-frequency hearing in bats is associated with the use of low-frequency calls for social communication (Bohn et al. 2006). Pallid bat directive calls are frequently given both when bats leave the roost in the evening and when they return from foraging and perform "rallying flights" in which individuals give repeated calls as they fly back and forth along the roosting area while being joined by other calling bats (Vaughan and O'Shea 1976). While pallid bat directive calls are also given in other contexts, such as parent-offspring recognition (Brown 1976), several lines of evidence indicate that calling outside the roost does not function solely for this purpose. For example, rallying behavior occurs during all phases of the maternity season (including prior to the birth of pups) with calls typically produced away from the roosting crevice (personal observation). In addition, adult males produce calls that are similar in structure to calls given by females outside the maternity roost (personal observation). Thus, we will hereafter refer to the audible calls given by pallid bats in flight as "contact calls" since the term "directive call" is typically associated with maternal social calls directed at offspring (Altringham and Fenton 2003).

Alternatively, low-frequency calls produced by bats outside roosting crevices may have a limited social function in that calls could potentially be utilized as a specialized autocommunication signal to enhance crevice detection. Playback studies are thus critical for determining if there is a causal relationship between the call and the response of the receiver (Falls 1992). While playback studies on bats in the field have been conducted infrequently, they have been used to examine social call function in *Pipistrellus pipistrellus* (Barlow and Jones 1997), *P. hastatus* (Wilkinson and Boughman 1998), *Thyroptera tricolor* (Chaverri et al. 2010), and *Myotis bechsteinii* (Schoner et al. 2010). Thus, our first objective was to assess the extent to which calling behavior assists in forming roosting groups by observing the context in which pallid bats give contact calls to determine whether calling is more frequently associated with approaching and entering rather than while exiting a crevice roost. In addition, we utilized playbacks to address the following three predictions. First, if calls have a social function, we expect bats to respond more to playbacks of contact calls than to white noise. Second, if calling behavior in pallid bats is associated with roost advertisement, we predict that bats would be attracted or respond more to the calls of multiple

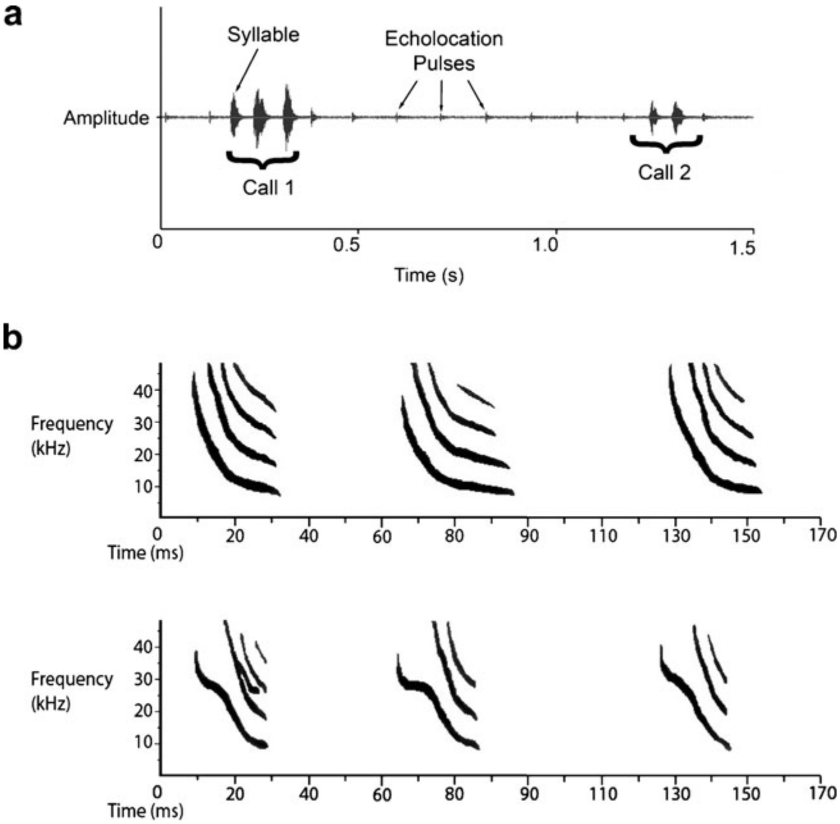

Fig. 1 Examples of contact calls recorded from free flying adult pallid bats. **a** Waveform showing a "call bout" consisting of two contact calls flanking a series of echolocation pulses recorded from a single bat flying away from the microphone. **b** Spectrograms of contact calls recorded from two different bats

than single bats outside the roost since larger roosting groups offer a greater thermoregulatory benefit to cavity-dwelling bats (Willis and Brigham 2007). Third, we test if bats can recognize and respond preferentially to familiar calls by broadcasting calls recorded from bats at the same or a different colony.

Our second objective was to analyze recordings from free-flying individuals to determine if the acoustic structure of contact calls contains information about individual identity. While the stability of pallid bat social groups is not well known, telemetry data collected by Lewis (1996) showed a greater roosting association among lactating bats than pregnant bats. Thus, given the potential benefits of group roosting for lactating pallid bats [e.g., social thermoregulation (Trune and Slobodchikoff 1976)], Lewis (1996) suggested that contact calls function in roostmate recognition, which would require individually specific call structure with high inter-individual and low intra-individual variability (Beecher 1989).

To examine whether contact calls contain sufficient information for roostmate recognition, we used calls recorded from unmarked free-flying bats at different colonies to determine the proportion of call variation explained at different levels of social affiliation (e.g., differences among colonies and differences among bats within a colony) and the information capacity present in the call (Beecher 1989). In addition, we used calls recorded on multiple days from free-flying bats carrying radiotransmitters to test whether individual differences in contact calls are present and stable through time, as expected if contact calls are utilized for social communication and roostmate recognition.

Methods

Site locations

We conducted field work at four different colonies in the Clarno basin of central Oregon, USA (44.94° N lat., 120.38° W long.). Two colonies [designated as Cove Creek North (CCN) and Cove Creek South (CCS)] are located in the Pine Creek Conservation Area, which is managed by the Confederated Tribes of Warm Springs, and the remaining two colonies are located in the Clarno Unit (CU) and Painted Hills Unit (PHU) of the John Day Fossil Beds National Monument (Fig. 2). The habitat in this area is typical of shrub-steppe desert in central Oregon with common vegetation consisting of sagebrush (*Artemisia tridentata*), juniper trees (*Juniperus virginianus*), and cheat grass (*Bromus tectorum*) (Verts and Carraway 1998) and moderate to steep topography with numerous large cliff formations each of which typically contains multiple roosting crevices suitable for pallid bats.

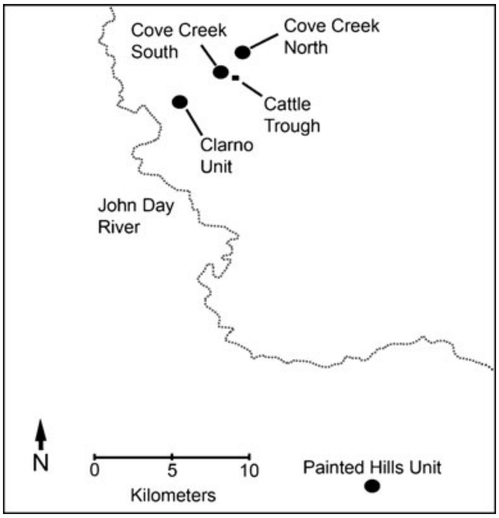

Fig. 2 Map showing the relative location of the study sites in central Oregon, USA

Call terminology

Pallid bat contact calls typically consist of a series of 2–4 vocalizations with frequency modulated (FM) sweep structure separated by short periods of silence (avg. 40 ms). Following Kanwal et al. (1994) and Bohn et al. (2008), we refer to the elements of the call as “syllables,” a “call” as a group of syllables each separated by less than 80 ms, and a call “bout” as two or more calls separated by at least 500 ms of silence (see Fig. 1).

Calling behavior

We videotaped bats entering and exiting seven different roosting crevices for 1 h on each of nine nights at the CCN and CCS colonies using a Sony DCR-TRV320 night shot digital video camera along with an LED infrared spotlight (model # 15-IL07, Cop Security System Corp., Taiwan) to illuminate the roosting area. Video recording times varied but were typically between midnight and 0500 hours when bats returned from foraging. Vocalizations were recorded into the video camera with a shotgun microphone (model AT4071A, Audio Technica, Japan) that was oriented toward the roost approximately 6 m above ground on extension poles. For each 1 h video recording, we scored call occurrence, approaches of a bat to the roosting crevice, and entries into the roosting crevice. We scored calls as being associated with approaching or entering the roost if the call occurred less than 5 s before either event on tape. Videotapes were scored using JWatcher v. 1.0 (JWatcher.ucla.org).

To determine if calling is associated with bats exiting a roost, on 25 nights we counted the number of bats that did or did not call as they exited 12 different roosts using a night scope (Noctron V, Varo, Inc. Garland, TX, USA) and the LED spotlight. Counts were carried out until no bats exited for more than 5 min or until bats began to return to the roost after foraging. We determined if calling behavior is associated with approaching, entering, and exiting the roosting crevice using a two-way contingency table analysis conducted using JMP v.5.0 (SAS Institute Cary, NC, USA).

Response to call playback

We conducted playbacks on 21 different evenings and pre-dawns in 2006 and 2008 at the CCN and CCS colonies. On each night or pre-dawn, we conducted two to five trials in a 1-h period (80 total trials). Each trial consisted of a series of calls from either a single bat or multiple bats that were recorded from the same or a different colony as the playback site. For a control stimulus, we broadcast pulses of white noise equivalent to the duration of a call. All playback files were 30 s long and consisted of calls recorded from free-flying bats at the CCN, CCS, and PHU colonies. All calls utilized for playback consisted of 2–5 syllables per call and only calls with sufficient signal-to-noise ratio were selected. To determine whether bats respond more to recordings from multiple bats than an equal number of repeated recordings of a single bat, we created playback sound files using the program Raven Version 1.3 (Cornell University Lab of Ornithology, Ithaca, NY, USA). Single bat recording files consisted of the same call recorded from a single bat repeated 13 times in the following pattern: two bouts consisting of calls repeated five times with each call spaced approximately 1.2 s apart followed by 5 s of silence and finishing with one bout with the call repeated three times. Multiple bat playback files consisted of single calls recorded from three different bats with calls from two bats repeated five times and calls from one bat repeated three times with the same silent intervals as the single bat treatment. For the multiple bat treatment, call order was randomly determined.

Calls were broadcast using a Marantz PMD671 flash recorder (sampling frequency 96 kHz, Marantz Inc., Mahwah, NJ, USA) connected to a Radio Shack 40-W stereo amplifier and a Realistic portable loudspeaker (flat frequency response to 45 kHz) mounted on a 6 m extension pole above ground or lowered from the top of the cliff using a pulley. All playback stimuli were equalized to have amplitudes similar to calls made by free-flying bats (approximately 50–54 dB at 6–8 m).

All playback trials were videotaped using a Sony nightshot video camera (Sony Inc.) focused on the speaker, which was illuminated with infrared light. The number of social calls and passes of bats by the speaker were counted 1 min prior to the initiation of each trial to assess background activity. Responses were scored as the difference between the 1-min playback and the 1 min background level. If there was no bat activity either prior to the playback or after the playback, the observation was removed from the analysis. Both passes by the speaker and calls in response were analyzed using a mixed effects model Analysis of Variance (ANOVA) with day and trial included as random effects and colony (CCN or CCS), time of day (evening or pre-dawn), call treatment (contrast between all bat call playback files together and the white noise control), bat number (single or multiple), and colony origin (same or different colony) included as fixed effects.

Assessment of call variability

Recording methods

We conducted 39 recording sessions outside pallid bat crevice roosts between June and August 2005–2008. Although recording sessions often lasted throughout the night, the majority of calls were recorded between 2100 and 2300 hours as bats exited the day roost and 0300 and 0500 hours as bats returned to the day roost. We recorded calls using the high-frequency output of an Ultrasound Advice S-25 bat detector (Ultrasound Advice Inc., London, UK) and a custom built filter/amplifier (bandpass 4–100 kHz) connected in 2005 to a Gateway laptop (Gateway, Inc., Irvine, CA, USA) with a DAQ i508 sound card sampling at 250 kHz (INEES Inc., New South Wales, Australia) running Batsound Pro (Pettersson Elektronik AB, Sweden) or in 2006–2008 to the Marantz PMD671 flash recorder sampling at 96 kHz. The microphone was positioned 6 m in the air using extension poles to get it as close as possible to free-flying bats, which were typically at or near the top of the rock formation (approx. 10–20 m above ground depending on the site).

Pallid bat contact calls are partially audible which allowed the observer to easily determine that a call was given and often permitted observing the bat that called. However, because not all bats were individually marked, we limited recordings to a single calling bout. To minimize the chance of analyzing multiple calling bouts from the same bat, we included no more than three calling bouts separated by at least 5 min per recording session (range 3–8 h of recording). A total of 189 calls (58 calls from CCN, 57 calls from CCS, 55 calls from CU, and 19 calls from PHU) from 74 calling bouts with at least two calls per bout were analyzed (range 2–5 calls per bout). Calls used for the analysis had sufficient signal relative to noise to measure frequency and time variables. In situations where a recording file contained calls from multiple bats, we used amplitude differences and syllable intervals to assign calls to bat.

Call measurements

We performed spectrographic analyses using Raven Version 1.3 (Cornell University Lab of Ornithology, Ithaca, NY, USA) with a 128-point Hanning window and 512-point Fast Fourier Transform. Pallid bat contact calls contain multiple harmonics (Fig. 1b). However, because contact calls were recorded from flying bats at different heights and trajectories above the recording setup, we could only reliably measure the fundamental frequency of each syllable from each call. Three variables were measured from the waveform of the call (call duration, syllable duration, and inter-syllable interval) and 23 frequency, time, and amplitude variables were measured from the spectrogram of the first and last syllable of each call (see Table 1 for the description of variables measured). Variables were log transformed to meet the assumption of normality if necessary.

Statistical analyses

Prior to analysis, we examined the correlation matrix for all call variables and found that the first and last syllable first quartile frequency and time, as well as the first and last syllable third quartile frequency and time, were highly correlated ($r>0.8$) with the center frequency and time measurements. Thus, we removed the first and third quartile measurements from the subsequent analyses since any attempts to include these variables resulted in a singular covariance matrix. To reduce the dimensionality of the dataset, we performed a factor analysis with varimax rotation in SAS v 9.1 (SAS Institute, Cary, NC, USA) to extract orthogonal factors. After applying the selection criteria outlined in Tabachnick and Fidell (2001), we retained six factors, which explained 78% of the variation in the data. These six factors were then included in a multivariate analysis of variance (MANOVA) to test if call characteristics differed among bats and colonies, both of which were designated as random effects. Finally, we used Proc Varcomp in SAS v. 9.1 to estimate the variance explained by colony, bats within colony, and calls within bat for each retained factor using restricted maximum likelihood. The variance estimates for between bat differences (S_B^2) and within bat differences (S_W^2) were then used to calculate the total variance (S_T^2) and the information capacity for each factor [$H_i=\log_2(S_T/S_W)$] as well as the total information capacity present in the call [$H_s=\sum H_i$] (Beecher 1989). Finally, these estimates were also used to calculate the repeatability of each factor as $S_B^2/(S_B^2+S_W^2)$.

Temporal stability of calls

Recording methods

Ten pregnant or lactating female pallid bats were captured using mist nets placed at a spring fed water trough located between the CCN and CCS colonies (Fig. 2) during the 2007 and 2008 field seasons. Each bat was weighed and

Table 1 Description of variables measured from pallid bat contact calls

Variable measured	Description
Call duration	Duration of call measured from waveform
First inter-syllable interval	Time between first and second syllable
First and last syllable duration	Duration of syllable measured from waveform
First and last syllable mid-time frequency	Frequency measured at the middle time of the syllable
First and last syllable end frequency	End frequency of the syllable
First and last syllable peak frequency	Peak frequency of the syllable
First and last syllable center frequency	Frequency that divides the syllable into two intervals of equal energy
First and last syllable center time	Time of the center frequency
First and last syllable first quartile frequency	Frequency that divides the syllable into 25% and 75% of the total energy in the syllable
First and last syllable first quartile time	Time of the first quartile frequency
First and last syllable third quartile frequency	Frequency that divides the syllable into 75% and 25% of the total energy in the syllable
First and last syllable third quartile time	Time of the third quartile frequency
First and last syllable inter-quartile range (IQR) bandwidth	Difference between first and third quartile frequencies
First and last syllable inter-quartile range (IQR) duration	Difference between first and third quartile times

marked with a numbered band (National Band and Tag, Newport, KY, USA) so that individuals could be identified if recaptured during future mist net sessions. Radiotransmitters were built (Wilkinson and Bradbury 1988), marked with colored reflective tape (3M Inc., St. Paul, MN, USA), and placed in the interscapular region of each bat using Skinbond adhesive (Torbot Group, Inc., Cranston, RI, USA). To minimize disruption to normal flight behavior, transmitters weighed less than 5–8% of total body weight (Aldridge and Brigham 1988). We tracked each bat to their roosting crevice during the day and set-up recording equipment (Marantz PMD671 and high-frequency microphone, see above) to attempt to record a contact call from the bat as it either exited or returned to the day roost during the night. We were able to verify that the bat wearing the radio called by monitoring the pulse from the radio with a telemetry receiver (Custom Electronics, Inc., Urbana, IL, USA) and using a spotlight to highlight the colored reflective tape on the radio to identify the location of the bat with respect to the microphone after the call occurred. Since radio-tagged bats often returned to the roost several times in a night, we were able to reliably assign calls to the radio-tagged bats by using calls recorded when the bat either returned or exited by itself or in small groups (less than three bats).

Statistical analyses

For six bats, we recorded at least two contact calls during the same recording session and one contact call on an additional day. Thus, we had at least three calls recorded for six bats to examine differences in call structure within bats over time. Each call spectrogram was first partitioned into separate spectrograms for each syllable and then band-pass filtered between 5 and 45 kHz to remove excess noise present in the recordings. To compare the similarity of syllable structure among and within bats, we used spectrographic cross-correlation analysis (SPCCA) (Clark et al. 1987) in Raven. In this procedure, two spectrograms are overlapped in time and cross-correlated frame by frame. The peak of the resulting correlation function represents the time frame where the two sounds are most similar.

We performed SPCCA on all possible combinations of each syllable from each radio-tagged bat's call. To test whether calls recorded from the same bat have a higher peak cross-correlation value than calls recorded from different bats, we conducted a permutation test (Manley 1997) using R (V. 2.7.2, http://www.R-project.org). Here the observed test statistic was computed as: $\overline{X}_{\text{(peak r same bat)}} - \overline{X}_{\text{(peak r different bat)}}$ and tested for significance against the permuted distribution (10,000 permutations). Since calls recorded on the same day and at the same site could artificially inflate within bat similarity, we only included the two calls recorded on different days and different sites in this analysis. If calls from the same bat are structurally similar across time, we predicted that there should be no difference in correlation values between calls recorded from the same bat on different days and calls recorded from the same bat on the same day. To test this prediction, we used a second permutation test in R. Here we computed the observed test statistic as: $\overline{X}_{\text{(peak r same day)}} - \overline{X}_{\text{(peak r different day)}}$ and tested for significance against the permuted distribution (1,000 permutations).

Results

Calling behavior

Calling was not independent of the position of a bat relative to the crevice in that calls occurred more frequently when bats were approaching (χ^2=312.82, P<0.0001) and entering a roost (χ^2=132.88, P<0.0001) than while exiting the roost (Table 2). The number of calls emitted when approaching versus when entering the roost did not differ (χ^2=1.02, P=0.314).

Response to call playback

Bats both called in response ($F_{(1,\ 366)}$=27.67, P<0.0001) and flew past the speaker [$F_{(1,\ 366)}$=8.09, P=0.0047] significantly more often during playbacks of contact calls than of white noise (Fig. 3). There was no significant effect of either the location where the playbacks were conducted [calls in response ($F_{(1,\ 366)}$=0.567, P=0.452), passes by speaker [$F_{(1,\ 366)}$=0.676, P=0.412] or time of day [calls in response ($F_{(1,\ 366)}$=0.499, P=0.48, passes by the speaker ($F_{(1,\ 366)}$=0.001, P=0.92)].

There was a significant effect of colony origin in that bats called in response more frequently to the playbacks of calls recorded from their own roosting area ($F_{(1,286)}$=6.036, P=0.0146) while colony origin had no significant effect on of the number of bats flying by the speaker ($F_{(1,286)}$=1.38, P=0.241). The number of bats included in the playback file had no significant effect on either calls in response ($F_{(1,286)}$= 3.196, P=0.075) or passes by the speaker ($F_{(1,\ 286)}$=0.167, P=0.683) (Fig. 3).

Variability of calls among bats and colonies

In general, the intensity of pallid bat contact calls recorded in the field was high, allowing us to make recordings even when bats were flying 20 m above the recording apparatus. The majority of the recorded contact calls consisted of two to four syllables, although several recordings contained up to six syllables. In addition, the frequency modulation pattern of the syllables within each call was relatively consistent with correlations of the first and last syllable measurements ranging from 0.69 to 0.81. Thus, pallid bat contact calls appear to consist of a single FM syllable type repeated two to six times. The mean, standard error, and range of the temporal and frequency variables measured from the contact calls are summarized in Table 3.

Table 2 Occurrence of contact calls outside a roost categorized by context

Bat behavior	Call occurrence	
	Yes	No
Approaching roost	897	790
Entering roost	202	199
Exiting roost	247	956

Factor analysis revealed that temporal and frequency variables tend to load independently on each factor with mid-time, peak, and center frequency loading predominantly on factor 1, syllable duration and center time loading on factor 2, and end frequency loading heavily on factor 3 (Table 4). Together, the first three factors explained 55%, and the six extracted factors explained 78% of the variation in the calls. MANOVA using the six extracted factors as variables in the analysis showed that there were significant differences among bats but not among colonies (Colony–Wilks' Lambda=0.80, $F_{(18,\ 184.33)}$=0.84, P=0.66; Bat–Wilks' Lambda=0.000027, $F_{(420,\ 667.22)}$=7.63, P<0.0001). This result is consistent with nested univariate ANOVAs, which revealed that the majority of the variance in call structure as measured by the six factors is explained by differences among bats with little to no variance explained by differences among colonies (Table 5). The variance estimates for differences among bats for all six factors equates to a total information capacity of H_S=7.83 bits (Table 5).

Temporal stability of calls within bats

The spectrograms of contact calls recorded from the same bat were visually similar with consistent frequency modulation patterns and syllable durations, while differences in these call features are evident when comparing calls recorded from different bats (cf. examples of syllable spectrograms from radio-tagged bats BB# 49 and BB# 76 are shown in Fig. 4). The permutation test confirmed that SPCCA values of calls recorded from the same radio-tagged bat on different days and recording sites were significantly greater than SPCCA values calculated from recordings between bats $\left[\overline{X}_{(\text{peak r same bat})}=0.714,\ \overline{X}_{(\text{peak r different bat})}=0.586, (P=0.0063)\right]$. In addition, a second permutation test to examine temporal stability of contact calls showed that the peak correlation for syllables from calls recorded from the same bat on different days did not differ from the peak correlation of calls recorded from the same bat on the same day $\left[\overline{X}_{(\text{peak r different day})}=0.714,\ \overline{X}_{(\text{peak r same day})}=0.802, P=0.11)\right]$.

Discussion

Social function of pallid bat contact calls

Pallid bat contact calls have been suggested to function in facilitating roosting group formation (Vaughan and O'Shea 1976) either by advertising the location of a suitable crevice for roosting or by recruiting individuals to maintain social

Fig. 3 Histograms showing the response of pallid bats to the playback treatments (**a** contrast between call treatments and white noise control; **b** contrast between same and different colony playbacks; **c** contrast between single and multiple call playbacks)

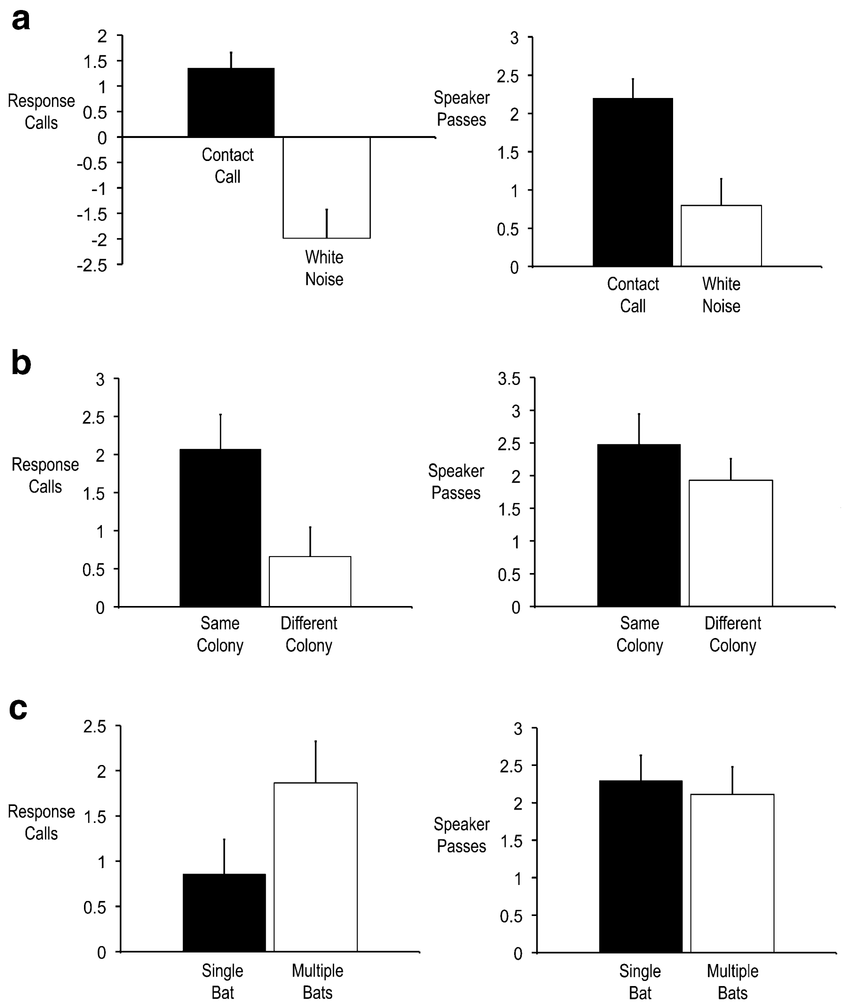

Table 3 Descriptive statistics for variables measured from contact calls

Call variable measured	Mean±SE	Range
Call duration (ms)	138.83±3.04	68–281
First inter-syllable interval (ms)	38.67±0.64	23–79
First syllable duration (ms)	22.89±0.40	13–47
Last syllable duration (ms)	24.30±0.39	15–42
First syllable mid-time frequency (kHz)	15.46±0.27	9.36–27.70
Last syllable mid-time frequency (kHz)	17.33±0.30	9.03–32.92
First syllable end frequency (kHz)	7.55±0.06	5.72–13.34
Last syllable end frequency (kHz)	7.76±0.06	5.92–11.82
First syllable peak frequency (kHz)	21.54±0.33	9–33
Last syllable peak frequency (kHz)	21.94±0.28	13.5–35.25
First syllable center frequency (kHz)	22.00±0.26	11.25–30.75
Last syllable center frequency (kHz)	22.55±0.24	15.75–31.25
First syllable center time (ms)	9.05±0.22	3.3–20
Last syllable center time (ms)	10.07±0.26	3.7–23
First syllable IQR bandwidth (kHz)	6.98±0.23	1.56–17.25
Last syllable IQR bandwidth (kHz)	6.64±0.21	0.78–16.41
First syllable IQR duration (ms)	7.07±0.21	2–18.6
Last syllable IQR duration (ms)	6.83±0.17	2–14.1

Table 4 Varimax-rotated loadings for the first six factors extracted from contact call measurements

Variable measured	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6
Call duration	−0.08	−0.07	−0.29	0.03	−0.34	**0.54**
First inter-syllable interval	0.01	0.02	0.02	−0.10	**0.73**	−0.11
First syllable duration	−0.15	**0.79**	−0.14	−0.21	0.12	−0.06
Last syllable duration	−0.04	**0.86**	−0.17	−0.11	0.15	0.01
First syllable mid-time frequency	**0.78**	0.14	0.44	−0.03	−0.07	−0.12
Last syllable mid-time frequency	**0.73**	0.38	0.35	−0.09	−0.24	−0.02
First syllable end frequency	0.12	−0.05	**0.91**	0.05	0.10	−0.07
Last syllable end frequency	0.14	0.01	**0.90**	0.06	−0.00	−0.01
First syllable peak frequency	**0.69**	−0.20	0.01	0.06	0.35	0.14
Last syllable peak frequency	0.49	−0.12	0.05	0.09	0.08	**0.69**
First syllable center frequency	**0.88**	−0.19	0.02	0.15	0.08	0.11
Last syllable center frequency	**0.75**	−0.16	0.16	0.13	−0.11	0.45
First syllable center time	−0.25	**0.77**	0.26	0.00	−0.22	−0.04
Last syllable center time	0.17	**0.88**	0.07	0.07	−0.08	−0.20
First syllable IQR bandwidth	−0.09	−0.04	0.04	**0.81**	−0.27	0.18
Last syllable IQR bandwidth	0.24	−0.11	0.05	**0.86**	0.13	−0.07
First syllable IQR duration	**−0.59**	0.46	0.19	0.07	0.17	0.26
Last syllable IQR duration	−0.33	0.47	0.20	0.29	0.44	0.21

Call variables with loadings greater than 0.5 are shown in *bold*

bonds. However, low-frequency calls could potentially function as a specialized echolocation signal to detect roosting crevices as bats approach the roost. Since pallid bat calling behavior has yet to be thoroughly investigated in the field, one of the objectives of this study was to determine the context in which contact calls occur using observations and playbacks and then infer the extent to which contact calls perform a social function.

First, if contact calls are used to facilitate roosting group formation, we expected that calling behavior would be associated with bats approaching or entering a crevice more than when bats exit a roosting crevice. In addition, if calls are being used to advertise roost location, one might expect that calling would occur almost ubiquitously with approaching, while if bats are using calls to maintain contact with other bats, calling may occur opportunistically depending on the bat's motivation to locate roostmates. While bats were more likely to call when entering or approaching a crevice than when exiting, there were 247 instances of bats calling while exiting the roost, and the frequency of bats approaching silently was almost equal to that of bats calling while approaching (Table 2). These results suggest that calls have a social function to maintain contact with roostmates in that if calls were utilized as a method of autocommunication to locate roosting crevices or roost advertisement, we would expect few bats to approach silently or call while exiting a crevice roost.

The playback data also support the hypothesis that contact calls serve a social function. For example, bats

Table 5 Variance component estimates, repeatabilities, and information content in bits, H_i, for factors extracted by factor analysis of contact calls

	Colony (N=4)		Bat (N=74)		Call (N=189)		
	F^a	VCE[b]	F^a	VCE[b]	VCE[b]	Repeatability	H_i
Factor 1	1.6	0.03	9.35*	0.76	0.23	0.77	1.49
Factor 2	0.96	0	11.81*	0.80	0.20	0.80	1.58
Factor 3	0.76	0	16.64*	0.87	0.13	0.87	1.83
Factor 4	1.25	0	3.12*	0.47	0.55	0.46	0.95
Factor 5	0.33	0	5.34*	0.62	0.38	0.62	1.18
Factor 6	0.5	0	2.48*	0.35	0.65	0.35	0.80

[a] F values for random effects univariate ANOVA conducted on each factor.

[b] Variance component estimates obtained by restricted maximum likelihood indicate the proportion of variance explained by differences among colonies (Colony), among bats within colony (Bat) and calls within bats (Call)

VCE variance component estimates

*$P<0.0001$

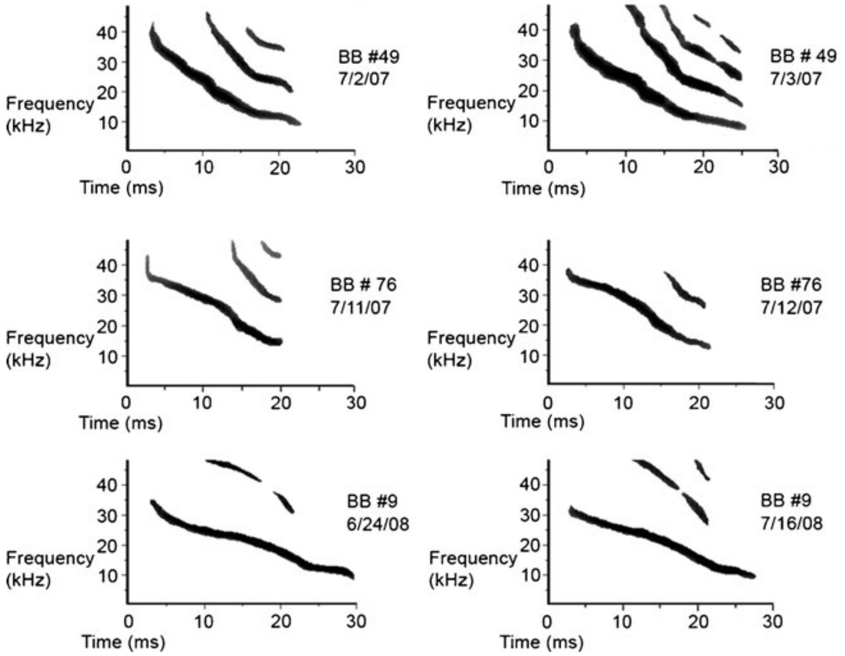

Fig. 4 Spectrograms showing the similarity of contact calls recorded from the same pallid bat on multiple days. Numbers designate bat identity. For presentation purposes, only one syllable from each contact call is shown

responded both by calling in response and passing by the speaker more during playback of call stimuli than during white noise as expected if they are utilizing the calls for social communication. Interestingly, playbacks of calls recorded from the same colony as the location of the playback elicited significantly more calls than playbacks of calls from a different colony, which suggests that bats can differentiate familiar from unfamiliar calls as has been shown in playbacks of orange-fronted parakeets (*A. canicularis*) (Vehrencamp et al. 2003) and lesser bulldog bats (*Noctilio albiventris*) (Voigt-Heucke et al. 2010). However, there was no significant difference between passes by the speaker for playbacks of colony versus non-colony member calls, which could be due to a tendency for bats to approach the source of an unknown call to obtain more information about the calling bat. Finally, neither calling nor passes by the speaker differed when playback stimuli contained calls from one or more than one bat. This result also suggests that calls are used more for roostmate identification than for advertisement of a roosting area. If the latter was correct, then bats would be expected to be more attracted to the calls of multiple bats if they were searching for an occupied roost.

Evidence for signature calls in adult pallid bats

Both enhanced variability among individuals and reduced variability within individuals are key characteristics of signature calls in acoustically mediated recognition systems (Beecher 1989). If contact calls are used for individual recognition by pallid bats, we would expect calls to exhibit significant differences among individuals and stereotypy within individuals. We characterized the variability in adult pallid bat contact calls by analyzing recordings of 189 calls from 74 bats from four colonies to determine the level of information provided in the call. In addition, we used radio-telemetry to find and record the same bat repeatedly over a period of at least 2 days to examine temporal stability of call structure, which has yet to be reported for any bat species in the field.

Random effects nested ANOVAs using factors extracted from acoustic characteristics of calls recorded from bats at multiple colonies showed that most of the variability in call structure is explained by differences among bats and little to no variability is explained by differences among colonies. The second and third factors showed the highest variance explained by differences among bats (80% and 87%) and, therefore, the highest repeatabilities (Table 5). These factors are loaded heavily by both temporal variables (factor 2—syllable duration and syllable center time) and frequency characteristics (factor 3—mid-time frequency and end frequency) indicating that both temporal and frequency characteristics of the call carry individual information and may be important for distinguishing among bats. Since these calls are given predominantly while bats are flying outside the roost (Vaughan and O'Shea 1976), features of the call that will be less susceptible to distortion over distance will be most beneficial for carrying information about the sender. Thus, syllable duration, mid-time frequency, and end frequency may be especially useful for individual discrimination of different bats because, unlike high-frequency portions of the call, they will be less affected by attenuation as the distance from the receiver to the sender increases (Bradbury and Vehrencamp 1998).

Encoding of individuality by differences in the frequency and temporal structure of pallid bat contact calls is similar to how individual distinctiveness arises among pup isolation calls in both evening bats (*Nycticeius humeralis*) (Scherrer and Wilkinson 1993) and greater spear-nosed bats (*P. hastatus*) (Bohn et al. 2007) where the majority of information is carried by the spectral features of the call while temporal characteristics also carried significant, but lesser amounts of information. One hypothesis for the development of adult contact calls in pallid bats is that they are derived from infant isolation calls. Evidence in support of this hypothesis comes from Brown (1976) who reported that pallid bat pup isolation calls decrease in frequency and resemble contact calls after 8 weeks of age and Esser and Schmidt (1989) who reported that maternal directive calls resemble the isolation calls of pups in the lesser spear-nosed bat, *Phyllostomus discolor*. However, isolation calls of both evening bats (Scherrer and Wilkinson 1993) and greater spear-nosed bats (Bohn et al. 2007) increase in frequency as pups age. Furthermore, isolation calls are given only by pups at rest while contact calls are primarily given by bats in flight. Thus, more longitudinal studies are needed to determine if contact calls are ontogenetically related to or distinct from isolation calls in pallid bats.

The total information capacity of pallid bat contact calls is 7.83 bits, which would allow for the identification of approximately 228 unique call signatures (Beecher 1989). Colony size in pallid bats typically varies depending on maternal period, and groups of up to 200 bats and their young have been reported (Hermanson and O'Shea 1983). Based on roost exit counts at both CCN and CCS colonies at the study area using an infrared spotlight and night vision spotting scope, roosting group sizes ranged from 7–100 (average 48) bats in the same crevice with bats occupying up to four different crevices within the same colony at a given time (B. Arnold, unpublished data). Thus, the information content provided by the signal is consistent with the potential discrimination required by the roosting habits of pallid bats in central Oregon. When compared to other acoustically mediated individual recognition systems, the information content encoded in pallid bat contact calls also falls well within the range expected for individual recognition in a gregarious species. For example, similar analyses conducted on mew calls in cooperatively breeding bell miners (*Manorina melanophrys*) (McDonald et al. 2007) and pup isolation calls in Mexican free-tailed bats (*Tadarida brasiliensis*) (Wilkinson 2003) found a total information capacity of 9 bits. In addition, the information capacity of alarm calls in yellow-bellied marmots (*Marmota flaviventris*) was calculated as 3.37 bits (Blumstein and Munos 2005), the latter of which has been shown to discriminate between calls of different individuals (Blumstein and Daniel 2004) even though the estimated information content is relatively low.

Finally, SPCCA of calls recorded from bats wearing radiotransmitters also supports the contention that adult pallid bat contact calls encode individual signatures in that calls recorded from the same individual are significantly more correlated than calls recorded from different bats. One advantage of SPCCA over the MANOVA approach is that it considers all features of the spectrogram rather than an arbitrary set of acoustic variables. Thus, it may provide a better representation of the information available to a bat as it extracts information from another individual's contact call.

By recording the same bat on multiple days, we also demonstrated that contact call structure is maintained across time, i.e., calls recorded on different days and at different sites are correlated no less than calls recorded on the same day. Although the calls used for this analysis were recorded over the course of up to only 3 days, we also obtained evidence that call structure is maintained over longer periods of time. During the study, a bat designated as BB# 9 was captured and recorded as it called immediately after being released and then recaptured and recorded again over 2 weeks later, at which time it gave a structurally similar call (Fig. 4). Thus, our evidence indicates that pallid bat contact calls contain enough information and are sufficiently repeatable to function as signature calls.

Social communication in bats

While we describe contact calls as “social calls” throughout this paper, distinguishing between vocalizations used for social communication or for echolocation can be difficult, since any call can potentially be used by conspecifics to gain information about the sender (Fenton 1985). Furthermore, echolocation calls have been shown to encode individual identity both in the lab [e.g., *Eptesicus fuscus* (Kazial et al. 2001)] and in the field [e.g. African large-eared free-tailed bats, *Otomops martiensseni* (Fenton et al. 2004)]. However, Siemers and Kerth (2006) failed to find evidence of individual signatures in *M. bechsteinii*, a bat species where females live in closed groups that are stable across years (Kerth et al. 2000). Arguably, echolocation calls may be poorly designed for encoding individual identification given their relatively simple acoustic structure. In addition, some bats vary call structure depending on the context in which the call is given to maximize returning information (Fenton 2003). In contrast, several studies that have analyzed variation in acoustic structure of social calls in adult bats have found evidence for individual signatures (Balcombe and McCracken 1992; Pfalzer and Kusch 2003; Carter et al. 2008). This study adds a new dimension to this body of work by using calls recorded from radio-tagged individuals in the field to assess call stability over time and by demonstrating with playbacks that calls preferentially attract familiar individuals.

Potential benefits of calling in pallid bats

Pallid bats are often regarded as highly social in that females have been reported to preferentially place juveniles in the center of a roosting group (Trune and Slobodchikoff 1978), guard juveniles (Beck and Rudd 1960), and guide mothers to distressed offspring (Brown 1976). While most of the evidence for cooperative behavior is limited to bats in captivity, the potential for contact calls to function in maintaining roosting associations among bats and to facilitate kin-selected (Hamilton 1964) or reciprocity-based (Trivers 1971) cooperative behavior warrants further study. Although relatively little is known about the stability of pallid bat social groups, mist-netting efforts in the study area have resulted in recapture of 20 banded female bats in more than one field season and telemetry data have confirmed that bats roost in the same colony in multiple years (B. Arnold, unpublished data). Thus, the available evidence to date indicates that female pallid bats are philopatric to their maternity colony. In addition, pallid bats have been reported to live over 9 years in the wild (Tuttle and Stevenson 1982), which along with female philopatry increases the possibility that calling behavior may facilitate the maintenance of multigenerational social groups. Future studies incorporating playbacks of calls in pallid bats to test whether bats can discriminate between individually specific calls of other bats will be necessary to determine the role they may play in maintaining social structure.

Acknowledgments All field protocols were approved by the University of Maryland Institutional Animal Care and Use Committee (Protocol R-08-39). We would like to thank Emily Muns and Stephanie Rihl for assistance with field work, Tom Rodhouse for help with locating study sites, Kevin Misner for assisting with the videotape analysis, and Jason Douglas for help measuring calls. We are also grateful to the Confederated Tribes of Warm Springs and the National Park Service for allowing access to the field sites as well as the staff at Hancock Field Station in Clarno, Oregon for providing support during the field season. Finally, we would also like to thank Jackie Metheny, Beatrice Mao, Julie Samy, Genevieve Spanjer Wright, and two anonymous reviewers for comments that helped to improve the manuscript. This work was supported by research grants from Sigma Xi, the Cosmos Club Foundation of Washington DC, the American Society of Mammalogists, and the American Philosophical Society to B.D.A. as well as summer support provided by the BEES graduate program at the University of Maryland to B.D.A.

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