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Original Article

Socially foraging bats discriminate between group members based on search-phase echolocation calls

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Animals have evolved diverse strategies to use social information for increasing foraging success and efficiency. Echolocating bats, for example, can eavesdrop on bats foraging nearby because they shift from search-phase calls to feeding buzzes when they detect prey. Feeding buzzes can directly convey information about prey presence, but it is unknown whether search-phase calls also convey social information. Here, we investigated whether search-phase echolocation calls, distinct calls produced by some bat species to scan large open areas for prey, can additionally convey individual identity. We tested this in *Molossus molossus*, a neotropical insectivorous bat that forages with group members, presumably to find ephemeral insect swarms more efficiently. We caught *M. molossus* from six different social groups and recorded their search-phase calls during a standardized release procedure, then recaptured and tested 19 marked bats with habituation–dishabituation playback experiments. We showed that they can discriminate between group members based on search-phase calls, and our statistical analysis of call parameters supported the presence of individual signatures in search-phase calls. Individual discrimination is a prerequisite of individual recognition, which may allow *M. molossus* to maintain contact with group members while foraging without using specialized signals for communication.

Key words: **bioacoustics, echolocation, individual discrimination, social foraging, social information.**

INTRODUCTION

In most animals, foraging efficiency is crucial for fitness (Morse and Fritz 1987). Many animals can increase their foraging efficiency by using social information (Giraldeau and Caraco 2000). When food is difficult to find yet abundant when found, the benefits of acquiring social information about where food is located can outweigh the cost of having to share the food resource with group members (Ranta et al. 1993). These benefits are greatest for animals that exploit patchy ephemeral resources, which are unpredictable in space or time and, thus, unlikely to be encountered when searching alone (Pulliam and Millikan 1982; Clark and Mangel 1984; Deygout et al. 2010; Bhattacharya and Vicsek 2014). For such animals, social information transfer not only increases the chance of discovering food patches but also allows foragers to optimize their timing in leaving patches before they are exhausted, thus increasing individual foraging efficiency (Hancock and Milner-Gulland 2006).

The way information is transmitted between social foragers depends on their life history and ecology (Marler 1967). Many seabirds, for example, use visual cues: flocks of seabirds diving for schools of fish can alert others to the presence of prey from kilometers away (Rosenthal and Ryan 2000; Boyd et al. 2016). Nocturnal foragers, however, cannot use long-distance visual cues and instead rely predominantly on olfaction or sound (Beauchamp 2007). Olfactory cues can transmit information about food sources away from the foraging area, such as the smell of food on the breath of group members at a day roost (O'Mara et al. 2014). Yet olfactory information about the location of food may only be useful if the food source persists long enough to allow following of group

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members (Marler 1967; Bradbury and Vehrencamp 1998; O'Mara et al. 2014). Acoustic information on the other hand, although limited in range, can rapidly transmit information about short-lived food sources at night (Beauchamp 2007). If nocturnal animals strongly depend on social information, they could benefit from remaining within hearing distance of conspecifics to maintain access to such cues (Pöysä 1992; Valone 1993; Templeton and Giraldeau 1996; Bhattacharya and Vicsek 2014).

The acoustic social information transfer exhibited by echolocating bats has attracted considerable attention over the last several decades (reviewed in both Jones and Siemers 2011 and Gager 2018). When foraging, many echolocating bats primarily produce two types of echolocation calls. When searching for prey, they produce long-range search-phase calls to scan the landscape. When they encounter prey, they produce feeding buzzes, which are call sequences of high pulse repetition to precisely localize prey for capture. Thus, feeding buzzes can serve as inadvertent but honest cues alerting other bats to the presence of prey (Barclay 1982; Fenton 1985; Fenton 2003). Many bats are attracted to playbacks of feeding buzzes while foraging, particularly species that feed on shareable food, for example, insect swarms versus single insects (Barclay 1982; Balcombe and Fenton 1988; Gillam 2007; Dechmann et al. 2009; Ubernickel et al. 2013; Lewanzik et al. 2019). Some of these species are also attracted to search-phase calls (reviewed in Gager 2018), but the exact role of search-phase calls in social information transfer among foraging bats remains poorly understood. Unlike feeding buzzes, search-phase calls do not inherently reveal information about prey presence. They may, however, convey social information about the bat producing the calls, which could be useful for bats that forage near conspecifics.

Compared to communication sounds, echolocation should have limited capacity for conveying identity because it is shaped largely by ecological factors, resulting in call structure that varies by species and ecological niche (Jones and Siemers 2011; Denzinger and Schnitzler 2013). This design leaves little room for intraspecific variation. Yet, there is increasing evidence that bat echolocation calls can vary among individuals enough to play a communicative role (Jones and Siemers 2011; Dechmann et al. 2013). Call frequency and structure can encode information about sex, age, body condition, group membership, and individual identity in various species (reviewed in Jones and Siemers 2011; Knornschild et al. 2012; Finger et al. 2017; Lewanzik et al. 2019). Playback studies show that some species can use this information to discriminate between males and females, familiar versus unfamiliar bats, and even individuals (Kazial and Masters 2004; Kazial, Kenny, et al. 2008; Yovel et al. 2009; Voigt-Heucke et al. 2010). However, a challenge for playback studies is that the full range of echolocation call types bats produce in the wild cannot be easily recorded in captivity to use in playbacks because echolocation is strongly influenced by the task a bat is performing and the environment in which it is calling (Schnitzler et al. 2003; Grilliot et al. 2009). Conversely, calls recorded in the wild cannot be easily attributed to a single bat or to a bat with particular attributes (sex, colony membership, individual identity, and so forth). These two challenges complicate our ability to test the extent to which bats can vocally discriminate in different natural contexts, such as foraging versus roosting. Such context-dependent call variation is especially strong for bats that forage in open space, which includes the majority of social foraging bats studied to date (Schnitzler et al. 2003; Gager 2018). In these species, search-phase calls are often highly distinct from calls produced in nonforaging contexts, for example, at a roost entrance or in captivity because these environments greatly differ in the amount of clutter or obstacles present, changing the echolocation task the bats must perform (Schnitzler et al. 2003). To understand the social information available to socially foraging bats, one must play back the call types available to the bats while they forage, an approach which to date has not been tested.

We investigated individual discrimination of search-phase calls in *Molossus molossus*, a small insectivorous bat that preferentially forages within hearing distance of its social group members (Dechmann et al. 2010). *Molossus molossus* produces distinct search-phase echolocation calls as it forages in open space. It specializes on ephemeral insects that are unpredictable in their spatial distribution and only available for a brief time at dusk and dawn (Rydell et al. 1996; Safi and Kerth 2007). Group cohesion may give these bats continuous access to social information conveyed by the feeding buzzes of their group members, increasing their chance of discovering insect swarms. However, to forage with group members, the bats must keep track of each other's movements and stay within their hearing range of up to 54 m while flying at high speeds in the dark (Dechmann et al. 2010). Although many animals produce contact calls for this purpose (Kondo and Watanabe 2009), search-phase calls could inadvertently serve a similar purpose if they convey individual identity or group membership. We hypothesized that spectral features of search-phase echolocation calls contain individual signatures, but not group signatures, and that *M. molossus* can use this information to discriminate between individuals. Verifying the presence and use of individual information in search-phase calls is an important prerequisite for individual recognition, which may allow *M. molossus* to coordinate flight with their group members without using specialized signals for communication.

METHODS

We conducted this study from January to March 2018 in Gamboa, Panama, where small social groups of *M. molossus* roost in building crevices (mean group size of 9.6 ± 6.7 adults; Gager, Gimenez, et al. 2016). *Molossus molossus* from the study site weigh on average 10.2 g for females and 11.4 g for males and have forearms measuring 36.7 mm for females and 37.4 mm for males (Gager, Tarland, et al. 2016). Social groups have a harem structure, consisting of several females with stable membership and fewer males that have less stable membership (Gager, Gimenez, et al. 2016). Since 2013, several roosts have been equipped with PIT-tag (Passive Integrated Transponders) readers, which provide information about which bats enter or exit the roosts (e.g., social group membership). Roosts are repeatedly captured to PIT-tag new individuals (Gager, Gimenez, et al. 2016).

We captured six social groups in mist nets as they exited from their roosts just after sunset. We recorded mass, forearm length, sex, age, and reproductive status. No females were pregnant or lactating. We recorded the transponder number of previously PIT-tagged individuals (n = 9) and marked each new individual with a unique subcutaneous PIT tag (n = 37; Trovan ID-100, Euro ID, Weilerswist, Germany). The impacts of PIT tags appear to be minimal, including the brief moderate pain caused by the PIT-tagging procedure (Schlicht and Kempenaers 2018). Our bats rarely struggle or show other signs of stress when PIT tags are injected, a process that takes just a few seconds. We caught and tagged many new individuals for this study because the study population was less intensively monitored in 2016 and 2017, and individuals in the population are short-lived (Gager, Gimenez, et al. 2016).

In addition, a few roosts were abandoned during that time, so, in 2018, at the start of this study, we searched for and discovered several new roosts to replace the roosts that had been abandoned. We caught 38 female and 8 male adults and recorded their calls upon release. We later recaptured the five largest social groups and tested 25 females and 4 males in experiments. We only included females in later analyses because four out of five social groups contained only one male.

Call recordings

After measurement and marking, we placed each bat on a 2-m-high platform against a wall and allowed it to orient and fly away freely. From the moment we placed each bat on the platform until it flew away and left the area, we recorded and digitized its vocalizations at a 250 kHz sampling rate and 16-bit resolution using an Avisoft ultrasonic condenser microphone (CM16/CMPA, sensitivity range: 10–200 kHz) and Avisoft UltraSoundGate 116 with Avisoft-Recorder USHG software (Avisoft Bioacoustics, Germany) on an Acer Aspire ES1-331 laptop. The microphone was positioned 5 m from the platform and 1.5 m from the ground. The setup against the wall constrained bats' direction of flight so that all individuals were facing the microphone from approximately the same direction during recordings. We used this method to ensure that we recorded search-phase echolocation calls, which bats do not produce in the flight cage or in the hand (Surlykke and Moss 2000). To ensure that we only recorded the targeted individual, we released bats at least 2 h after the end of this species' average foraging period (37.6 ± 2.06 min after dusk; Dechmann et al. 2010) to minimize the possibility that conspecifics were flying nearby. Released individuals did not remain in the recorded area, and we were confident that the previous bat had left before we released and recorded the next individual. In total, we recorded 46 bats in this first round of roost captures.

By visualizing calls in Avisoft-SASLab Pro (Avisoft Bioacoustics, Germany), we classified two distinct types of echolocation calls from released bats, with a sequence of ambiguous calls transitioning from one type to the other. The first calls produced after bats flew from the platform were always steep broadband pulses of short duration with a prominent harmonic (Figure 1a). We term these "approach calls" following similar designs described for *M. molossus* near roosts both in Gamboa (Gager, Tarland, et al. 2016) and in Cuba (Mora et al. 2004). The second call type had a narrower bandwidth, longer duration, and a weaker harmonic and was produced in pairs alternating between an upper and a lower frequency (mean peak frequency: lower = 37.52 Hz, upper = 41.95 Hz; Figure 1b). This type could be unambiguously classified as a "search-phase call" because it had the same structure and two-toned arrangement described for *M. molossus* foraging echolocation calls (Koessl et al. 1999; Gager, Tarland, et al. 2016). It also matched the calls we observed *M. molossus* producing while foraging, interspersed with feeding buzzes, near our study site. While our primary interest was individual discrimination with search-phase calls, we experimentally tested both call types to explore the extent to which *M. molossus* can detect information about individual identity in the diversity of their echolocation call repertoire. However, we focused our statistical analysis on individual signatures in search-phase calls because these calls are stereotyped, whereas approach calls vary greatly according to the immediate surroundings of the caller during flight.

In order to preserve all potentially informative qualities from call recordings, such as interpulse interval or variation in relative call amplitudes, we kept partial sequences intact when constructing playbacks. First, we divided entire recordings into approach calls and search-phase calls by excluding the transitionary periods where calls could not be unambiguously classified as either approach or search-phase. Next, we divided each sequence into two halves containing the same number of pulses to create two unique sets per individual for each echolocation call type to present in our playback experiments. Then, we ran a band-pass filter to remove frequencies below 28 and above 100 kHz for search-phase calls and below 28 and above 110 kHz for approach phase calls. This processing produced files of varying lengths, which we repeated to produce standard-length playback files for the experiments (details below).

Habituation–dishabituation experiments

For playback experiments, we recaptured the five largest social groups with the method described above and kept them in captivity for 5–7 days. We only kept and tested bats that readily ate in captivity. Typically, one to two individuals from each roost did not eat readily in captivity, so we released these individuals to return to their roosts on the night of capture. These individuals did not return to roosts without any other group members because we did not manage to recapture all individuals when capturing roosts for experiments. We housed bats from each roost together in a 28 × 28 × 28 cm mesh insect tent, fed them 2 g (~20% body mass) of mealworms and/or wet cat food per night, and provided water ad libitum (see also Stockmaier et al. 2015). Experiments were conducted

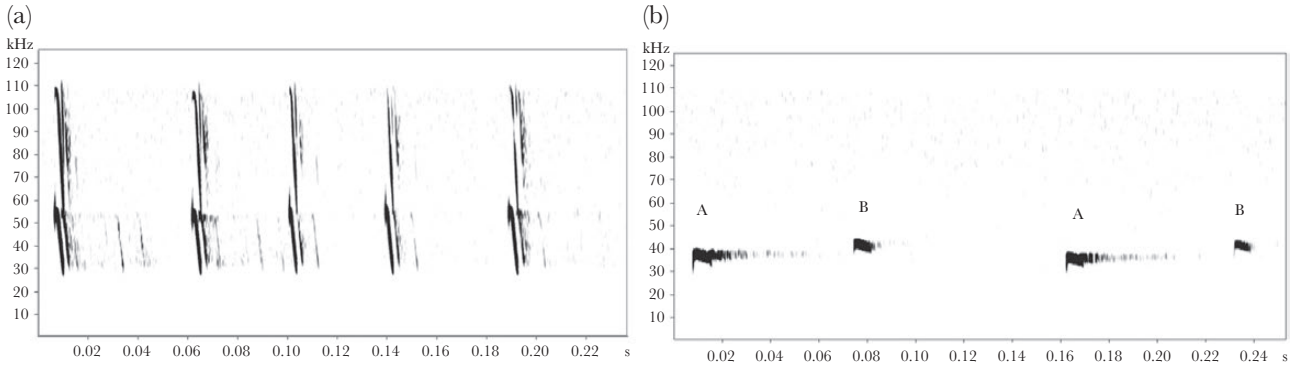

Figure 1
Example spectrograms of approach calls (a) and search-phase calls (b) recorded during release. Search-phase calls alternate between a lower pulse frequency (A) and an upper pulse frequency (B).

in a 5 × 5 m outdoor flight cage and began the second night after roost capture. We observed responses of unrestrained subjects in a small cage (20 × 15 × 8 cm) with soft mesh walls while playbacks were emitted from an Avisoft ultrasonic speaker positioned 70 cm in front of the bats. We started the first trial of each night at dusk when *M. molossus* typically begin their first foraging bout (Dechmann et al. 2010). Group members were released on the same night after all trials for all individuals were completed.

We used a habituation–discrimination method adapted from previous studies (Kazial, Kenny, et al. 2008; Finger et al. 2017). Each bat underwent one to two trials per day from a set of five trials in randomized order (Table 1). Each trial consisted of three phases of differing acoustic playbacks: 1) 10 min habituation phase, 2) 40 s dishabituation phase, and 3) 40 s rehabituation phase. Each trial ended with 10 s of white noise as a control to test if nonresponding bats were unresponsive in general (Figure 2). The phases were separated by short pauses of 20–100 s and a new phase only began when the bat was not grooming to ensure that it was attentive. For all trials, we recorded infrared video with a Sony NightShot Plus camcorder (DCR-SR45) and infrared lights (IR Illuminator CM-IR100B) and ultrasonic audio with the same setup described under Call recordings. An observer was seated 1 m behind the setup to observe the bat while operating the video camera and controlling playbacks during trials.

Playback files differed by trial type (search-phase calls or approach calls), trial treatment (test or control), and trial phase (habituation, dishabituation, and rehabituation; Table 1). Habituation playbacks were constructed using either the first or second unique half of echolocation pulses (see above) chosen randomly and repeated for 10 min with 3 s of silence between repeats. Dishabituation playbacks in test trials were constructed of the same sequence half (first or second) as their corresponding habituation playback to control for potential inherent differences between calls at the beginning versus the end of a sequence. Dishabituation playbacks in control trials were the first 40 s of the corresponding habituation playback. To present new call pulses produced by the same bat, rehabituation playbacks were constructed of the opposite sequence half (first or second) to that used for the corresponding habituation playback. We ensured that bats were not tested with calls of the same group member in different trial types and otherwise assigned playbacks randomly. In case bats respond differently to particular group members, we tested subject bats with search-phase calls in two trials, each with a different group member's calls (Individual Test 1 and 2; Table 1). Habituation and rehabituation playbacks were kept the same between these two trials while dishabituation playbacks changed. Lastly, we ran a 3 s fade-in/fade-out at the beginning and end of playbacks so that they did not stimulate a startle response in listening bats (Finger et al. 2017). To ensure realistic intensity of sound, the volume for playbacks was adjusted so that they were emitted from the speaker at approximately the same amplitude at which the recorded bat had produced them at the same distance.

Table 1

Combinations of playbacks presented to each bat in five trials of habituation–dishabituation experiments in randomized order for each subject bat

	Trial 1	Trial 2	Trial 3	Trial 4	Trial 5
	Search-phase Call Control	Search-phase Call Test 1	Search-phase Call Test 2	Approach Call Control	Approach Call Test
Habituation	Individual 1	Individual 1	Individual 1	Individual 4	Individual 4
Dishabituation	Individual 1	Individual 2	Individual 3	Individual 4	Individual 5
Rehabituation	Individual 1	Individual 1	Individual 1	Individual 4	Individual 4

The experimental design allowed us to interpret several responses. If a subject bat breaks habituation to the dishabituation playback, then this is evidence that it perceives a difference between the habituation and dishabituation playbacks. If, instead, it maintains habituation to the dishabituation playback, then this is evidence that it perceives no salient difference between the calls (e.g., the calls appear to be coming from the same individual as heard in the habituation playback). If the subject bat resumes habituation to the rehabituation playback, then this is evidence that either it perceives no difference between the rehabituation and the original habituation playbacks or it detects the same individual signature in these two playbacks even though they contain different calls. Thus, the rehabituation phase controls for the possibility that individuals respond to any new playback instead of perceiving individual differences or similarities between playbacks.

We quantified behavioral responses during four segments of each trial: 1) first 40 s habituation ("prehab"), 2) last 40 s habituation ("posthab"), 3) 40 s dishabituation ("dishab"), and 4) 40 s rehabituation ("rehab"). We use these abbreviations to distinguish the three trial phases from the four segments of behavioral scoring. During preliminary video analysis, we observed that the most noticeable and consistent behavioral response to playbacks were "head waggles" defined as "rapid head movements that change the orientation of the ears and are proposed to amplify auditory cues used for target localization" (Corcoran and Moss 2017). *Eptesicus fuscus* waggle their heads when listening to retuning echoes while tracking moving objects and increase the frequency of head waggles with more complex motion-tracking tasks (Wohlgemuth et al. 2016). Using BORIS software v. 6.0.5 (Friard and Gamba 2016), we scored the number of head waggles in each trial segment. The scoring was done blind to both trial treatment and timing of playbacks.

We chose to run the habituation phase for 10 min in all trials because we could not always confidently determine when bats were sufficiently habituated to playbacks while conducting trials. This resulted in some trials where bats were not habituated to stimuli by the end of the 10-min habituation phase, so we excluded trials in which bats did not meet habituation criteria (decrease number of head waggles by 50% from prehab to posthab), a threshold used in similar studies (Kazial, Kenny, et al. 2008). We also excluded trials in which bats did not respond to white noise playback, the positive control for attentiveness.

We fit general and generalized linear mixed models to test for the fixed effects of trial segment (prehab, posthab, dishab, and rehab) and treatment (test and control) on head waggle number for both search-phase call trials and approach call trials. We visualized distributions of model residuals and performed Shapiro–Wilk tests to assess normality of the model residuals. We used nonparametric bootstrapping ("boot" R package, 5000 iterations) to calculate 95% confidence intervals (CIs) around mean responses during test and control trials. To control for trial differences in activity, we centered head waggle number by trial by subtracting the trial mean from all response values. Finally, to compare the effects of playbacks on head waggle number across specific trial segments, we performed permutation *t*-tests on noncentered response values (*t*-statistic, 4999 permutations). To control for multiple comparisons, we adjusted *P*-values with sequential Bonferroni correction. We conducted all statistical analyses in R (version 3.4.3).

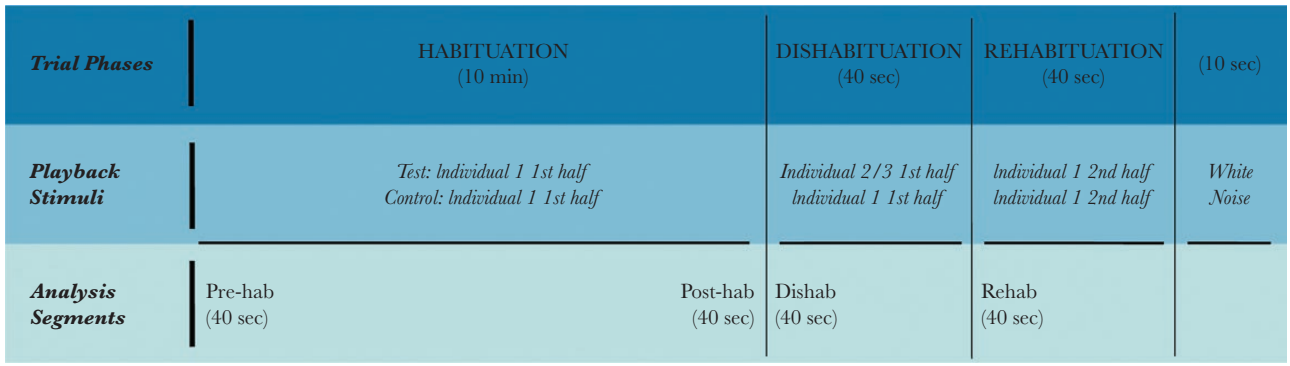

Figure 2
Scheme of an example trial in the habituation–dishabituation experiment and subsequent analysis. Adapted from (Finger et al. 2017).

We performed experiments with 25 female *M. molossus* from five different roosts. Each bat underwent all five trials, but the videos for 22 out of 125 trials were not scored due to problems with the trial or video. We excluded the 50 trials where bats did not meet the habituation threshold requirement (50% reduction in response from prehab to posthab) in subsequent analyses. Thus, we analyzed a total of 34 trials from 19 individuals (20 test trials and 14 control trials) for individual discrimination based on search-phase calls and 19 trials from 14 individuals (10 test trials and 9 control trials) based on approach calls.

Call signatures

We conducted a linear discriminant function analysis (DFA) using spectral and temporal call features to determine if individual and group identity can be assigned to calls with greater-than-chance success. We extracted peak frequency, minimum frequency, and maximum frequency from each search-phase call, each taken at the maximum amplitude of the pulse and also at 12 points at regular intervals over the call duration using Avisoft-SASLab Pro (Supplementary Figure S1). We analyzed the calls used in playback experiments, as well as calls from a subset of tested bats that we were able to record a second time, during their release after playback experiments. This allowed us to analyze calls recorded on two different dates for some individuals and, subsequently, test whether calls from different sessions with the same bat were more similar than calls from different bats. We obtained two recording sessions for 11 bats and, for eight of these individuals, both recording sessions contained sufficient numbers of pulses to be included in this analysis. We included these pulses recorded on a second night, even though they were only obtained for some individuals, to have a larger sample size and, thus, higher statistical power. However, we also tested whether these calls contributed proportionally higher to misclassifications rates by running the DFA with and without these calls.

Search-phase call sequences consist of pulse duplets at alternating frequencies, so we labeled each pulse within a duplet as either A or B according to its relative frequency and tested them separately (Figure 1b). Spectrograms were constructed in Avisoft-SASLab Pro with a Flat-top window, fast Fourier transformation (FFT) length of 512 points, 75% frame, and 93.75% temporal overlap, resulting in a frequency resolution of 488 Hz and temporal resolution of 0.128 Hz. To detect and measure calls with good signal-to-noise ratio (SNR), we used the Automatic Parameter Measurement function in Avisoft to determine the start and end of each pulse using three thresholds: overall −59 dB, start −10 dB, and end −8 dB, with a hold time of 2 ms, manually adjusting when necessary. We recorded A-pulses with good SNR from 34 individuals. On average, we measured 20.7 A-pulses per individual (range: 7–47 pulses per bat). We recorded B-pulses with good SNR from 19 individuals. On average, we measured 17.1 B-pulses per individual (range: 7–38 pulses).

The following parameters were used in subsequent analyses: 1) peak frequency at maximum amplitude, 2) minimum frequency at maximum amplitude, 3) maximum frequency at maximum amplitude, and 4) call curvature. To measure call curvature, we used principal component analysis to extract the first three principal components of the peak frequencies taken at 11 intervals over each pulse, excluding the start and end intervals because these are susceptible to the pulse's beginning and end designation in the spectrogram, which can be affected by varying call amplitude. We previously excluded individuals with less than seven pulses because this is fewer than the number of parameters used in the DFA.

To test for individual signatures in both A- and B-pulses separately, we used DFA in the R package "MASS" (Venables and Ripley 2002) with cross-validation (leave-one-out classification). Leave-one-out classification computes discriminate functions for as many observations as are in the data, each time leaving out one observation in order to calculate a discriminate function on the rest of the data. It then uses this function to classify the excluded observation (e.g., the excluded call to the correct bat). In this way, data used to create the classifier are never used to test the classifier. We then compared our observed correct classification rate (proportion of total calls that were correctly assigned to bats) to a distribution of classification rates expected from the null hypothesis. We generated this null distribution using the same procedure applied to 1000 randomized data sets where calls were randomly assigned to bats. The one-sided *P*-value was then the proportion of random classification rates that were greater than or equal to the observed classification rate.

Next, we used permuted discriminate function analysis (pDFA) to test whether we could correctly assign A-pulse calls to social groups while accounting for variation between individuals (Mundry and Sommer 2007). This permutation procedure uses two nested resampling steps to control for variation within and across individuals while assigning calls to groups of individuals (see Mundry and Sommer 2007; Carter et al. 2008, 2012). We then compared our observed classification rate (both with cross-validation and without cross-validation) against a null distribution of classification rates for 999 data sets where bats were randomly assigned to groups. The *P*-value was then the proportion of random classification rates that

were greater than or equal to the observed classification rate. We included rates with and without cross-validation to compare both conservative and high estimates of the correct classification rate. We did not test B-pulses because the sample size was too low.

Finally, to test if individual signatures can be completely explained by recording session, we performed a DFA using recording session rather than bats. We tested if the misclassifications in the DFA were predicted by the recording sessions sharing the same bat. To do this, we calculated the DFA confusion matrix, which shows the number of calls in each session (rows) that were classified to every other session (columns). We then created a same-bat matrix, which has a 1 if the recording sessions in the row and column shared the same bat and a 0 if the two sessions used different bats. To make the confusion matrix symmetrical, we averaged the two misclassification rates for each pair of sessions. We used a Mantel test (5000 permutations) to test if the same-bat cases were correlated with higher misclassification rates. A significant correlation in the Mantel test shows that calls recorded from the same individual on different sessions (nights) were more similar than expected by chance.

All methods conformed to the ASAB/ABS Guidelines for the Use of Animals in Research and were approved by the Ministerio del Ambiente (SE/A-32-17, SE/A-29-18) and the Institutional Animal Care and Use Committee of the Smithsonian Tropical Research Institute (2017-0815-2020).

RESULTS

Habituation–dishabituation experiments

Molossus molossus used search-phase echolocation calls to discriminate between individual group members. After habituating to calls from one group member in the prehab phase, bats dishabituated to calls from a second group member: they responded with 14 more head waggles on average in a 40 s period (test trial posthab to dishab: Bonferroni-adjusted $P = 0.0008$, $n = 20$, Hedges's $g = 0.993$; Tables 2 and 3; Figure 3). Bats subsequently rehabituated to new calls from the first caller by responding on average with eight less head waggles (test trial dishab to rehab: Bonferroni-adjusted $P = 0.0016$, $n = 20$, Hedges's $g = -0.834$; Tables 2 and 3; Figure 3). This change in response shows that they perceived a difference between the two callers rather than just between the three different playbacks.

In control trials, after habituating to calls from one caller, bats remained habituated to calls of that group member even though there was a short pause between the habituation playback being stopped and the dishabituation playback being started (Table 2; Figure 3). However, they broke this habituation during the rehabituation phase when hearing new calls from the same caller (control trial dishab to rehab: Bonferroni-adjusted $P = 0.0168$, $n = 14$, Hedges's $g = 0.867$; Tables 2 and 3; Figure 3). Bats responded with nine more head waggles on average, which shows that bats were also able to discriminate between unique sequences of calls from the same caller. This increase during the rehabituation phase of the control trials contrasts with the decreased response during test trials. Finally, the change in the number of head waggles was greater when bats heard a new group member in test trials than when they heard the same group member in control trials (dishab in test vs. control trial: mean effect = 15 more head waggles during test trial dishab segments; Bonferroni-adjusted $P = 0.0080$, $n = 12$, Hedges's $g = 1.124$; Tables 2 and 3; Figure 3). This contrast confirms that bats do not spontaneously dishabituate after about 10 min of habituation and that dishabituation in test trials was indeed a direct response to the change in the playbacks.

We did not detect evidence that *M. molossus* discriminated between group members based on approach calls. We analyzed a total of 19 trials from 14 individuals (10 test trials and 9 control trials) for individual discrimination based on approach calls. In test trials, subject bats tended to respond with more head waggles from posthab segments to dishab segments but the 95% CIs of the mean response rates were overlapping (Table 4; Supplementary Figure S2). They did not respond with less head waggles during the rehab segment.

Call signatures

The observed classification rate for assigning A-pulses to individuals was 15.6%, significantly greater than the expected-by-chance classification rate (mean expected rate = 5.5%, $P < 0.001$; Supplementary Figure S3). A-pulses, therefore, contain enough information for individual identification. The coefficients of the linear discriminant functions revealed that maximum frequency and peak frequency contributed most to classification of A-pulses (Supplementary Table S1). This result also stands if the pulses recorded in a second recording session for some individuals are removed. The classification rate remains almost the same, 16.7%.

The observed classification rate for assigning B-pulses to individuals was 20.9%, significantly greater than expected by chance (mean expected rate = 10.1%, $P < 0.001$; Supplementary Figure S3). B-pulses also contain enough information for individual identification. The coefficients of the linear discriminant functions revealed that minimum frequency and maximum frequency contributed most to classification for B-pulses (Supplementary Table S2). Calls from bats recorded on two different nights were more likely than expected by chance to be classified to the correct bat on the wrong night than to the wrong bats, demonstrating that individual signatures cannot be fully explained by recording night (Mantel test, $r = 0.079$, $P = 0.0166$).

We tested for evidence of group signatures in search-phase echolocation calls of individuals from five different social groups, but we did not find evidence of group signatures. Groups were represented by 3–12 individuals each (35 individuals total) and 54–210 calls each. The pDFA correctly assigned 14.17% of calls in the cross-validated procedure and 10.4% of calls without cross-validation, but neither was significantly greater than the expected random classification rates (Supplementary Figure S4).

Table 2

Means, bootstrapped 95% CIs, and sample sizes for head waggle number and relative head waggle number (centered by trial) in each phase of habituation–dishabituation trials with search-phase echolocation calls

Treatment	Segment	Lower (raw)	Mean (raw)	Upper (raw)	Lower (relative)	Mean (relative)	Upper (relative)	*n*
Test								
	Prehab	12.050	18.450	24.000	2.250	6.050	9.938	20
	Posthab	2.200	4.050	5.699	−11.213	−8.350	−5.063	20
	Dishab	10.800	17.650	23.500	2.025	5.250	8.525	20
	Rehab	3.601	9.450	14.450	−5.775	−2.950	−0.138	20
Control								
	Prehab	12.929	17.500	21.714	6.072	8.518	10.839	14
	Posthab	1.071	2.214	3.286	−8.911	−6.768	−4.357	14
	Dishab	1.000	3.429	5.571	−7.518	−5.554	−3.821	14
	Rehab	6.357	12.786	18.286	−0.143	3.804	7.482	14

DISCUSSION

As hypothesized, the search-phase echolocation calls of *M. molossus* contained individual signatures and the bats were able to use them to discriminate between group members. Individual discrimination is a prerequisite for individual recognition, which is the ability to identify an individual according to its individually distinct characteristics and use learned cues for identification in future interactions (Tibbetts and Dale 2007). Our results suggest that these echolocation calls could have a social function for *M. molossus* in addition to their primary function to detect prey. Specifically, they could convey identities of bats to nearby foraging group members.

In contrast to search-phase calls, *M. molossus* did not discriminate between individuals using approach calls. Approach calls are characterized by short durations and steep frequency modulations as a response to environments with more obstacles or clutter (Broders et al. 2004) and may be too short and dependent on the environmental context to contain identity information. Alternatively, our sample size (n = 19 trials) was insufficient to detect true but subtle differences in the responses of bats during playback trials.

The rehabituation phase of our habituation–dishabituation experiments verified that bats discriminated between individual group members and not simply between different playback sequences. In test trials, bats transferred habituation from one sequence of search-phase calls to a sequence of new calls from the same individual after dishabituating to calls from a second individual in between. In the rehabituation phase of control trials, we also expected bats to transfer habituation to a playback of new calls from the same individual. Instead, they dishabituated and responded with significantly more head waggles. Although unexpected, this actually confirmed that *M. molossus* could distinguish between two unique sequences of search-phase calls from the same individual. Only when presented with calls from a second individual, in test trials, did bats evaluate calls at the individual rather than at the call-sequence level.

We quantified the responses of bats to playbacks by counting their head waggles. *Molossus molossus* consistently responded with head waggles when hearing the search-phase calls of a group member for the first time in each trial (during prehabituation and dishabituation segments in test trials). This stereotyped head motion helps bats localize the source of calls in space (Corcoran and Moss 2017). Perhaps, foraging *M. molossus* use head waggles to localize the position of foraging group members based on their search-phase calls. In contrast to other bat species in playback experiments, most of our subject bats did not respond to playbacks

Table 3

Permutation test results for comparison of head waggle number between segments in search-phase echolocation call habituation–dishabituation trials

Test	Mean response change	n	P	Bonferroni-adjusted P
Test trial posthab to dishab	14	20	<0.0002	0.0008
Test trial dishab to rehab	−8	20	0.0004	0.0016
Dishab in test vs. control trial	−15	12	0.002	0.0080
Control trial dishab to rehab	−9	14	0.004	0.0168

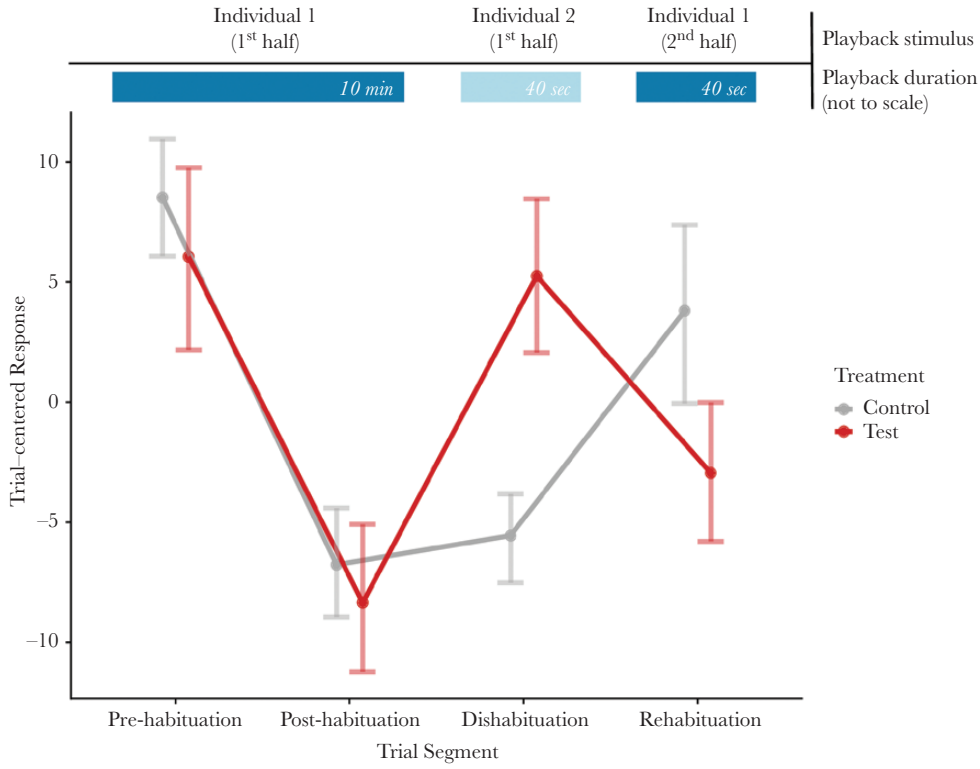

Figure 3

Change in mean number of head waggles during habituation–dishabituation trials with search-phase echolocation calls. Errors bars are bootstrapped 95% CIs around the means. Colored bars represent the playback being presented during trial segments. Test trials: n = 20; control trials: n = 14.

Table 4

Means, bootstrapped 95% CIs, and sample sizes for head waggle number and relative head waggle number (centered by trial) in each phase of habituation–dishabituation trials with approach calls

Treatment	Segment	Lower (raw)	Mean (raw)	Upper (raw)	Lower (relative)	Mean (relative)	Upper (relative)	*n*
Test								
	Prehab	11.700	19.800	27.500	1.300	7.950	15.699	10
	Posthab	0.700	3.500	6.000	−12.975	−8.350	−3.425	10
	Dishab	3.403	12.300	19.900	−4.650	0.450	5.050	10
	Rehab	1.700	11.800	19.200	−7.224	−0.050	5.500	10
Control								
	Prehab	10.889	19.111	26.778	4.056	7.861	11.222	9
	Posthab	1.333	5.889	9.556	−7.222	−5.361	−3.556	9
	Dishab	0.556	9.778	16.889	−6.888	−1.472	2.611	9
	Rehab	7.333	10.222	13.667	−5.000	−1.028	3.444	9

by vocalizing with either echolocation or social calls (Kazial and Masters 2004; Carter et al. 2008; Kazial, Kenny, et al. 2008; Voigt-Heucke et al. 2010). *Molossus molossus* might rely more on passive listening than active communication to discriminate between calling conspecifics. Indeed, the majority of the auditory cortex in *M. molossus* is tuned to the dominant frequencies of their search-phase calls, indicating the importance of processing these call types (Macías et al. 2009). The use of social calls by bats in social foraging contexts has received little attention. While the use of social calls would not negate the benefit of social information conveyed by search-phase echolocation calls, they may provide advantages, such as facilitating reunion if group members lose contact or recruiting group members to a food patch (Wilkinson and Boughman 1998). On the other hand, social calls might present some cost to foraging bats, requiring a trade-off between scanning the landscape with echolocation and social calling, because both call types cannot be emitted simultaneously. The use of social calls certainly presents an interesting line for future research.

In addition to bats perceiving individual differences between search-phase calls of group members, we confirmed individual differences statistically. Our analyses of call parameters supported the presence of individual signatures and not group signatures as predicted. Discriminant function analyses revealed consistent differences between individuals, assigning calls to the correct individuals significantly better than expected by chance. In addition, we confirmed that calls recorded from the same individual on nights separated by more than 2 weeks are more similar than expected by chance, suggesting that individual signatures are not an artifact of recording session. However, rate of misclassification was relatively high in comparison to studies with similar methods and numbers of individuals (see Knornschild et al. 2012; Finger et al. 2017 for comparison). Therefore, the spectral features of search-phase calls vary within an individual bat in addition to varying between bats, making it difficult to reliably assign calls to individuals. Molossids have highly flexible echolocation call design in comparison to other bat families (Kingston et al. 2003; Mora et al. 2004; Jung et al. 2014). Jung et al. (2014) suggested that this flexibility may be adaptive for enhancing communicative potential as molossids also adjust echolocation call design in the presence of conspecifics (Ulanovsky et al. 2004; Gillam 2007). No study has yet investigated *M. molossus* call plasticity at the interindividual or intraindividual level, but individual signatures may be the result of a "flexible echolocation system that meets various sensorial challenges while conserving sender identity" (Jung et al. 2014). We did not expect group signatures to be encoded in search-phase calls for several reasons. Group members are typically unrelated (Gager, Gimenez, et al. 2016), so group signatures would require learned vocal convergence in adult bats, whereas individual signatures only require variation in the development of vocal structures. The greater the vocal individuality, the more difficult it is to form group signatures. Individual recognition of groupmates via individual signatures can provide the same benefits as group signatures. Finally, individual signatures are found in echolocation calls for many bat species, but evidence for group signatures is rare (Jones and Siemers 2011).

The way in which echolocation is flexible to meet diverse sensory challenges may also enable it to meet diverse social tasks. In some species, echolocation calls produced while roosting provide more social information to roostmates (sex and reproductive state) than echolocation calls produced while flying (Kazial, Kenny, et al. 2008; Kazial, Pacheco, et al. 2008; Grilliot et al. 2009). In addition, individual bats can adjust their echolocation calls in social contexts to facilitate social communication, for example, the echolocation "honk" calls of *Noctilio leporinus* to avoid collisions with conspecifics (Suthers 1965; Hiryu et al. 2006; Chen et al. 2016). Yet search-phase echolocation calls, especially for bats that produce distinct search-phase calls because they forage in open space, should be less flexible because they are under strong selective pressure to accomplish the same foraging task in all conspecific individuals (Schnitzler et al. 2003), which could reduce consistent individual differences in call structure (Jones and Siemers 2011). To the extent that severe ecological constraints on individual variation exist, individually distinct search-phase calls in *M. molossus*, and their ability to discriminate between them, could be an adaptive trait related to social foraging in accordance with the "social function hypothesis" (Shapiro 2010). Alternatively, individuality in echolocation calls might be inherent in the individuality of the vocal tracts or behavioral repertoires of individual bats and the ability to vocally discriminate between individuals might be found across all species of echolocating bats, including those that do not forage socially. Noisy miner birds produce a call in a nonsocial context, which has individual signatures and allows for individual discrimination (Farrow et al. 2020). This is consistent with an alternative hypothesis that selection for individual signatures in calls produced in social contexts may facilitate the same selection even in calls that have no social function. Most bat species are gregarious and many produce social calls in addition to echolocation, for example, individually distinct pup isolation calls. Individual signatures in echolocation could be facilitated by selection on social calls. Comparative studies comparing such abilities across bats that vary in foraging strategy could test these hypotheses. Under either scenario, echolocation calls may serve an essential role in social information transfer for *M. molossus* while they forage.

The ability to discriminate between individuals with search-phase echolocation calls might be particularly advantageous for *M. molossus* and other bats that forage alongside group members. Dechmann et al. (2010) hypothesized that the extreme sociality (small stable social groups) of *M. molossus* hinges on their social foraging behavior. Social foraging may allow them and other species to exploit unpredictable, ephemeral insect swarms efficiently enough to meet their daily energetic needs in as little as 1 h/day (Dechmann et al. 2009, 2011), which, in turn, reduces energy needed for their costly flight (Norberg and Rayner 1987; O'Mara et al. 2017). By coordinating flight, *M. molossus* could remain within

earshot of their group members' feeding buzzes. This would allow them to increase the area in which they can detect prey from 2 m via active echolocation, up to 54 m, the distance from which they can hear conspecific calls (Dechmann et al. 2010). Foraging with consistent group members, rather than opportunistically eavesdropping on bats encountered on the landscape, could ensure that they have continuous access to social information about prey for the entire foraging period and share the same level of satiation and, thus, motivation to forage as their foraging partners. A potential trade-off, compared to solitary foraging, is the cost of keeping track of the movements of their foraging partners, which may be a challenging task that diverts some of their attention away from looking for insect swarms. In a similar way, once bats converge on an insect swarm and occupy a smaller area at higher density, they may also need to divert attention from foraging to avoiding collisions with other bats and to distinguish their echoes from those of other bats as shown in (Cvikel et al. 2015).

A similar social foraging strategy has been hypothesized for *Noctilio albiventris*, another neotropical bat that seems to coordinate foraging with group members while hunting for ephemeral insects over open water (Dechmann et al. 2009). *Noctilio albiventris* also produces echolocation calls that serve a dual function. They emit calls while perched in a flight cage that permit discrimination between familiar and unfamiliar individuals (Voigt-Heucke et al. 2010). In a similar way, individual discrimination of search-phase echolocation calls may help both species identify group members while foraging to maintain contact with them and fly as a cohesive unit—a complicated and challenging task.

As technology advances, devices such as miniaturized GPS units and on-board ultrasonic microphones will enable us to experimentally test whether social foraging bats are attracted to the search-phase echolocation calls of group members while they fly in the wild. Bats that forage socially are already being tracked with increasing temporal and spatial resolution, showing that species foraging on ephemeral resources intentionally search for prey patches collectively with conspecifics rather than being simply attracted to feeding buzzes (Cvikel et al. 2015; Egert-Berg et al. 2018). If echolocation can convey information about identity, social foraging could be a coordinated effort with particular individuals rather than an opportunistic process with unknown conspecifics for many species. We may well be underestimating the level of coordination and complexity of foraging behavior in bats, which has implications for our understanding of their long-term social affiliations and the evolution of sociality in this taxon.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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