



Common vampire bat contact calls attract past food-sharing partners



Gerald G. Carter^{a,*}, Gerald S. Wilkinson^b

^a Smithsonian Tropical Research Institute, Gamboa, Panama

^b Department of Biology, University of Maryland, College Park, MD, U.S.A.

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Animals living with kin and nonkin should make social decisions based on the consequences for both direct and indirect fitness. Common vampire bats, *Desmodus rotundus*, invest in stable cooperative relationships that benefit both components of inclusive fitness. To disentangle these two factors, we conducted two types of playback trials using a captive group of familiar common vampire bats with mixed kinship and varying rates of dyadic food sharing. We presented each subject with two speakers, playing contact calls from two different familiar conspecifics. In 'past donor trials', 15 vampire bats chose between calls recorded from either a frequent or rare food donor, but both callers were related to a similar degree with the subject. In 'kinship trials', 31 vampire bats chose between calls recorded from either a close or distant relative, but both callers were matched for food-sharing history with the subject. We found that vampire bats were attracted to contact calls of frequent food donors when controlling for kinship, but not to calls of kin when controlling for food-sharing history. Responses and acoustic analyses suggested that bats recognized individuals from vocalizations. These results corroborate past findings that prior food sharing can overshadow relatedness in determining the social decisions of vampire bats. Common vampire bat contact calls allow food-sharing partners to recognize and find each other at a distance, which likely enables them to switch roosts together in the wild.

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Several social birds and mammals, including some corvids, primates, carnivores, cetaceans and bats, form individualized and enduring social relationships that involve multiple forms of cooperation (Brent, Chang, Gariépy, & Platt, 2014; Carter, 2014; Seyfarth & Cheney, 2012). These cooperative social bonds can provide indirect and direct fitness benefits, so animals should invest in them based on kinship cues (Hamilton, 1964), past experiences of reciprocal cooperation (Trivers, 1971), or both (Wilkinson, 1984). However, kinship and reciprocal help are often correlated and confounded. An understanding of why animals invest in cooperative relationships can therefore require teasing apart their relative importance (Carter & Wilkinson, 2013a; Schino & Aureli, 2010).

Among adult common vampire bats, *Desmodus rotundus*, enduring reciprocal relationships appear to stabilize regurgitated food sharing (Carter & Wilkinson, 2013a, 2013b; Wilkinson, 1984, 1985a, 1986). Food sharing has inclusive fitness consequences because vampire bats often fail to feed and can starve to death after missing only two to three nightly meals of blood (Wilkinson, 1984,

1988). Food-sharing rates among dyads in a social network are predicted by several correlated factors: kinship, association, allogrooming and reciprocal sharing. The relative roles of kinship versus social experience have been assessed by Monte Carlo simulation (Wilkinson, 1988) and by testing predictors of food sharing among bats observed under natural conditions (Wilkinson, 1984), among unrelated bats with different levels of association (Wilkinson, 1984) and among familiar bats with different levels of relatedness (Carter & Wilkinson, 2013a). Food donation sizes in the wild and in captive experiments are similar (Wilkinson, Carter, Bohn, & Adams, 2016), and together these tests have shown that past experiences of food sharing or social grooming can overshadow kinship for predicting food donation rates among adults (Carter & Wilkinson, 2013b). The hypothesis that food sharing provides reciprocal benefits is further supported by the observation that vampire bats that feed more nonkin maintain a larger and more robust network of donors (Carter & Wilkinson, 2015). However, the most common and crucial context for food sharing involves mothers feeding their dependent offspring, suggesting that regurgitated food sharing may have evolutionary origins in maternal care.

Another possibly neotenous social behaviour in vampire bats is contact calling. In all bat species, pups produce isolation calls that allow mothers to recognize and retrieve them (Balcombe, 1990;

* Correspondence: G. G. Carter, Smithsonian Tropical Research Institute, Attn: Gerry Carter (Rachel Page Lab, Gamboa), P.O. Box 0843-00153, Republic of Panama.
E-mail address: gerry@socialbat.org (G. G. Carter).

Bohn, Moss, & Wilkinson, 2006; Carter & Wilkinson, 2013c; Gould, 1971; Gould, Woolf, & Turner, 1973; Scherrer & Wilkinson, 1993; Wilkinson, 2003). In all three vampire bat species, contact calls are also produced by isolated adults (Carter, Logsdon, Arnold, Menchaca, & Medellín, 2012). These calls are longer and of lower frequency than echolocation pulses and so travel farther distances. They also vary substantially in acoustic structure both among and within individuals (Fig. 1). Contact calls appear to allow bats to find and recognize familiar group-mates. In playback studies, white-winged vampire bats, *Diaemus youngi*, showed vocal discrimination: vocal responses occurred more often when playbacks of different contact calls shifted to a novel caller (Carter, Skowronski, Faure, & Fenton, 2008) and also when two or three isolated group-mates called from swapped spatial positions rather than from each of their original locations (Carter, Fenton, & Faure, 2009). Vocal discrimination has not yet been experimentally demonstrated among adult common vampire bats.

To determine the social factors that influence responses to contact calls in common vampire bats, we conducted two kinds of playback trials. In 'past donor trials', we compared the attraction of subjects to calls recorded from two individuals matched by kinship but differing in their history of donating food to the subject. We predicted that the isolated subjects would be attracted to calls of the more frequent donor.

In 'kinship trials', we compared the attraction of subjects to calls recorded from bats matched in food-sharing history but contrasting in kinship with the subject. Since we previously found that reciprocal food sharing is eight times more important than kinship for predicting donation rates (Carter & Wilkinson, 2013a), we predicted that responses during kinship trials would show a weaker effect size compared with past donor trials. In summary, we predicted that isolated vampire bats would seek out past food donors more strongly than relatives.

METHODS

Subjects

Subjects were 31 common vampire bats from five matriline and three zoo populations, housed and cared for during the study by the Organization of Bat Conservation at the Cranbrook Institute of

Science (Bloomfield Hills, MI, U.S.A.) under permits from the U.S. Department of Agriculture (34-C-0117) and the U.S. Fish and Wildlife Service (MB003342-0). Unrelated bats from the different populations were introduced as adults. Bats were housed at 25–28 °C with >33% humidity on a 12:12 h light:dim light cycle in a 3 × 1.5 × 2 m cage with a soft paper bedding floor that allowed flight and free association among cage-mates. Bats were fed on physically or chemically defibrinated bovine blood that was available ad libitum and changed twice daily. All procedures with animals adhered to the ASAB/ABS Guidelines for the Use of Animals in Research and were approved by the University of Maryland Institutional Animal Care and Use Committee (Protocol R-10-63).

Social Data

Measures of food-sharing history were derived from a food-sharing network involving 355 trial-donations and more than 1250 regurgitation observations made during 2010–2014. To quantify food sharing history we used a food-sharing index from individual A to individual B, which we calculated as the $\ln(x + 1)$, where x is the food-sharing rate from A to B (seconds of mouth licking per h per experimental trial). To calculate relatedness, we genotyped 19 microsatellite markers (Carter & Wilkinson, 2015) and used Wang's (2002) estimator in the R package 'related' (Pew, Muir, Wang, & Frasier, 2015). We defined kinship by substituting zeros for all negative relatedness values and replacing relatedness values of known maternal kin with the appropriate pedigree kinship values (e.g. mother = 0.5, grandmother = 0.25). Findings remained the same whether we used kinship or relatedness.

Playback Stimuli

Isolated vampire bats produce multiharmonic contact calls that are variable between and within individual bats (Fig. 1; Carter et al., 2012). We recorded contact calls by placing an adult individual in a small soft-mesh butterfly cage at a distance of 10–30 cm from a CM16 ultrasound condenser microphone (frequency range 10–200 kHz, Avisoft Bioacoustics, Berlin, Germany) inside an acoustic recording booth (plastic bin lined with acoustic foam) for 1–24 h. Due to these ideal recording conditions (e.g. ultrasonic microphone close to the bat's mouth, low gain, semi-anechoic

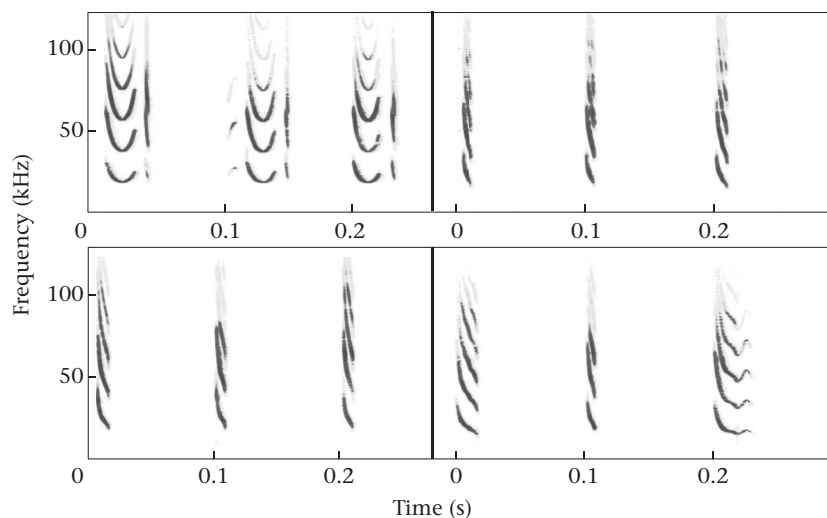


Figure 1. Example contact calls from common vampire bats. Three calls recorded from an 8-year-old female (top left), a 10-year-old female (top right), a 6-year-old male (bottom left) and a 2.5-year-old female (bottom right). Darkness in spectrogram shows relative intensity. All bats were individually isolated during recording. See Carter et al. (2012) for descriptions of call structure variation.

chamber), the noise level was low (<0.5% amplitude). We selected the first 17–30 contact calls that were between 10% and 99% amplitude (100% amplitude signals are clipped) to use in playbacks. Sounds were digitized with 16-bit resolution at a sampling rate of 250 kHz through an Avisoft Ultrasoundgate 116 to a laptop running the program Avisoft Recorder.

We created 19 playback sequences from 19 different vampire bats. For each sequence, we used Batsound Pro (Pettersson Elektronik AB, Uppsala, Sweden) to partition contact calls at random intercall intervals, varying from 1 s to 3 s, and then adjusted intervals so that 30 calls would fit in a 60 s sequence. To remove sounds below 1 kHz, we used a high-pass Butterworth filter (filter order = 2). Each 60 s playback sequence was presented and repeated four times in a trial through one of two Avisoft UltrasoundGate Player BL Pro units (henceforth 'speakers'), each containing an integrated digital-to-analogue converter, amplifier and ultrasonic speaker driver (see www.ultrasoundgate.com for frequency response curves). To equalize the intensity of the two speaker signals, we used the Avisoft recording system described above to simultaneously monitor the amplitudes of sounds from the two speakers playing the same contact call repeatedly at equal distances to the microphone, and we then adjusted the speaker gains until the signal amplitudes matched.

Playback Experiment

Trials took place in darkness and were filmed with an infrared spotlight (IRlamp6, Wildlife Engineering, La Crosse, WI, U.S.A.) and a Sony Nightshot DCR-SR85 camcorder. In each trial, a subject bat was placed in a 76×76 cm plastic mesh experimental 'maze' with five arms that allowed the subject bat in the centre of the maze to move forwards, backwards, left, right, or upwards (Fig. 2). The bat was placed in the arm farthest from the camera, equidistant to the two speakers. After moving forwards, it could enter the arms to the left or right, with each option leading towards a speaker simultaneously playing calls from either a control bat or a test bat. The bat could also move straight backwards or forwards away from either

speaker, or climb upwards, which bats typically do as an escape response. These options allowed us to remove cases where bats were not motivated to move towards either speaker.

Playback trials were of one of two types: 'past food donor trials' and 'kinship trials'. In past food donor trials, a subject with a history of food sharing ($N = 12$ females, 3 males) was presented with a choice between approaching contact calls from a frequent food donor (test bat) and an infrequent donor or nondonor (control bat). Test and control bats differed in their food donation rates to the subject, but were matched by age and kinship (Table 1).

In kinship trials, a subject ($N = 12$ females, 19 males) was presented with a choice between contact calls from a close relative (test bat) and a distant or nonrelative (control bat). Test and control bats differed in their pairwise kinship with the subject, but they were closely matched wherever possible by age and past food-sharing experience (Table 1).

Each trial lasted 10 min. If the bat did not make a choice within the first trial, the trial was discarded and a new trial began. Test stimuli were presented on the left or right randomly. The maze was rotated 90° clockwise between each trial. We presented the two trial types on a random schedule to remove order effects. Each subject experienced a unique playback combination of test and control bat except for one test–control combination that was presented to two different male subjects in the kinship trials; however, removing either one of these observations does not change our conclusions.

Playback Response Analysis

Responses were measured from videos by observers that were blind to the playback treatments and design. The blind observers recorded (1) the number of seconds that bats spent in either the left or right arm of the maze and (2) the latency in seconds from the start of a trial until the bat first entered either the right or left arm. If the bat never entered the arm, latency was scored as 600 s. Response data were non-normal, so we calculated P values using bootstrapping. Using the R package 'boot', we resampled the mean

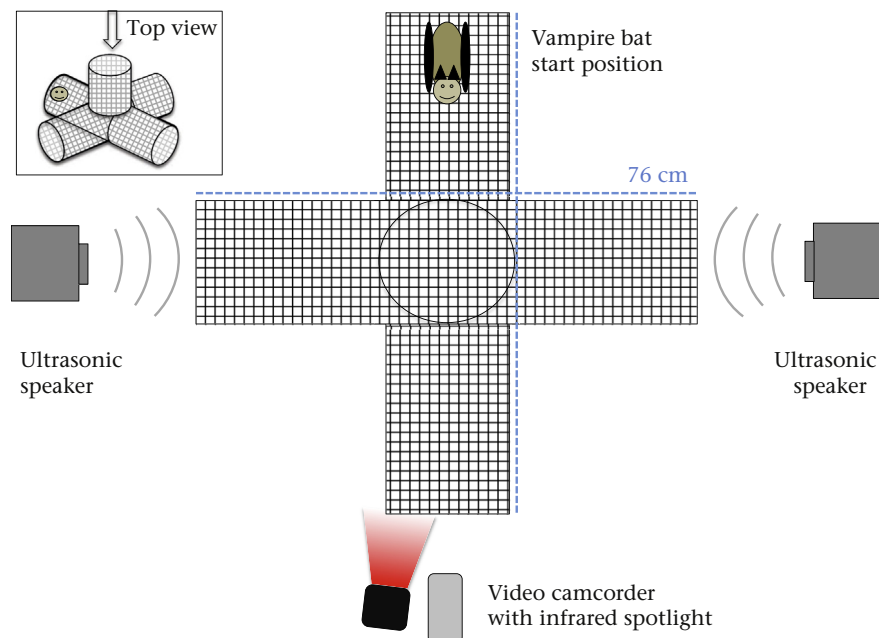


Figure 2. Playback maze. Not shown to scale. Laptops for running each speaker were located in an adjacent room. The cage and the camcorder with infrared light were elevated using a small table and tripod, respectively. The camera was further from the maze than depicted such that the bat could be seen anywhere in the maze.

Table 1
Food sharing and kinship of callers with subject bat

Playback treatment	Food-sharing index			Kinship		
	Median	Range	N	Median	Range	N
Past donor						
Test bat	4.9	2.5–6.2	15	0	0–0.3	15
Control bat	0	0–5.0	15	0	0–0.5	15
Test–Control	4.8	0.8–6.2	15	0	–0.5–0.3	15
Kinship						
Test bat	5.5	0–7.4	24 ^a	0.5	0.4–0.6	31
Control bat	0	0–4.9	19 ^a	0	0–0.3	31
Test–Control	0	0–7.3	18 ^a	0.5	0.1–0.6	31

^a Food-sharing records were not available for all 31 bats used for playbacks because some males were not fasted.

differences (test–control) for both the subject's time in each arm and the subject's latency to enter each arm, and calculated the one-sided *P* value as the proportion of the 5000 sample means that exceeded the observed mean. We calculated 95% confidence intervals (CI) using the BCa method (Puth, Neuhäuser, & Ruxton, 2015). Like all inferences, resampling tests can be problematic when a sample is too small to properly capture the variation of the population. For inferences based on small sample sizes (<20), we therefore also present more conservative *P* values calculated using a nonparametric Wilcoxon signed-ranks test. All response data are available on FigShare (<https://dx.doi.org/10.6084/m9.figshare.1613493>).

Acoustic Analysis of Playback Stimuli

We performed acoustic analyses of the playback stimuli to help interpret our behavioural results. A bias towards frequent donors or kin could indicate vocal recognition. Alternatively, without vocal recognition, an attraction towards kin or frequent donors could occur if kin or frequent donors sound more alike and subjects were attracted to more similar-sounding group-mates. We therefore tested whether the pairwise relatedness or food-sharing index

between the callers predicted the acoustic distance between all possible pairs of 19 playbacks. To measure acoustic distance, we used automated measures in Avisoft SASLab Pro to extract syllable duration, distance to maximum amplitude and peak frequencies at the call's start, end and maximum amplitude (FFT 512, frame size = 100%, Hann window), then entered these variables into a linear discriminant function analyses in R. We defined 'acoustic distance' as the natural log of the Mahalanobis distance between the centroids for each playback.

We also tested the null assumptions that the absolute difference in either acoustic distance or mean peak-to-peak amplitude between the test and control playbacks did not differ by (1) treatment, (2) the subject's time in the test arm or (3) the subject's latency to enter the test arm. To test these assumptions, we used permutation tests applied to general linear models using ImPerm package (Wheeler, 2010) in R. Such an unconstrained randomization approach can have higher power than a Mantel test (Legendre & Fortin, 2010) for detecting potential effects of acoustic distance or amplitude difference on bat responses. We calculated the percentage difference in relative intensity between test and control playbacks by subtracting the mean amplitude of the control playback from that of the test playback, and then dividing by the highest recorded amplitude. Finally, to confirm individuality of the playbacks, we performed jackknifed linear discriminant function analysis in R.

RESULTS

Vampire bats placed in the test arena typically walked and echolocated towards one speaker and then the other, alternating between them. In past donor trials, subjects were more attracted to calls of more frequent donors compared to less frequent donors. They spent on average 51 s longer in the test arm than in the control arm (95% CI = 12–91 s; permutation: *P* = 0.0014; Wilcoxon signed-ranks test: *S* = 44, *N* = 15, one-sided *P* = 0.005; Fig. 3a). Attraction to the frequent donor was still evident even when only using the nine trials where the test bat was unrelated to the subject (test kinship < 0.02; mean time in test arm = 57 s, 95% CI = 16–151 s;

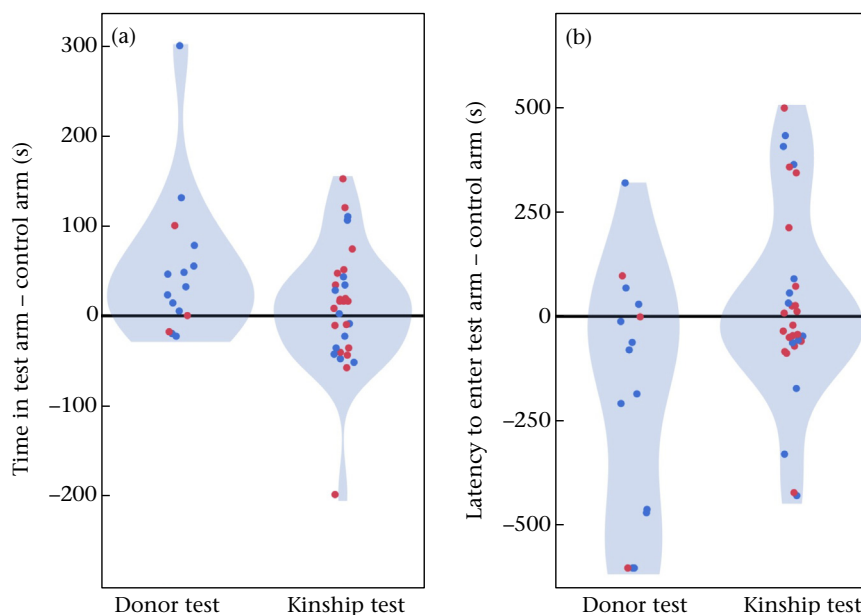


Figure 3. Results of playback tests showing (a) the difference in time spent in each arm and (b) the difference in latency to enter each arm for male (●) and female (●) vampire bats in response to calls from frequent food donors (donor test) and close relatives (kinship test). Shading shows the probability density function. Results remained the same with or without the two outliers in (a).

permutation: $P = 0.007$; Wilcoxon signed-ranks test: $S = 15.0$, one-sided $P = 0.039$). Subjects also entered the test arm on average 184 s sooner (95% CI = 42–331 s; permutation: $P = 0.0066$; Wilcoxon signed-ranks test: $S = 34.5$, one-sided $P = 0.025$; Fig. 3b).

In contrast, subjects in kinship trials did not spend longer in the test arm with calls from kin compared to the control arm with calls from nonkin (95% CI of difference: -13 – 33 s; $N = 31$, $P = 0.192$; Fig. 3a). The subjects' latency to enter the test arm also did not differ (95% CI = -47 – 114 s; Fig. 3b). Subjects were not attracted to the eight related nondonors (95% CI = -58 – 51 s), and we detected no kinship preference in either male subjects (95% CI = -28 – 37 s) or female subjects (95% CI = -18 – 43 s), and no bias for adults towards their mothers ($N = 19$, 95% CI = -37 – 23 s). However, five of the six mothers spent more time near the calls of their adult offspring than near the calls of a control bat ($N = 6$, 95% CI = 7 – 86 s; permutation: $P = 0.0074$; Wilcoxon signed-ranks test: $S = 8.5$, one-sided $P = 0.047$).

The absolute difference in relative intensity between test and control playbacks did not differ from zero (95% CI = -2 – 4%), and neither the relative intensity difference nor acoustic distance between the test and control playbacks correlated with behavioural response times or test type (Table 2). The ln-transformed centroid distance also did not correlate with either relatedness ($R^2 = 0.005$, $N = 171$, $P = 0.36$) or food-sharing ($R^2 = 0.013$, $N = 88$, $P = 0.28$) between the two bats used for the playbacks. Although neither kinship nor food-sharing history predicted acoustic similarity between playbacks, correct assignment rates of playback calls to bat was greater than chance (5% with random chance versus 20% of training set or 18% cross-validated; Wilks' $\lambda = 0.389$, $\chi^2_{90} = 688.43$, $P < 0.001$).

DISCUSSION

The common vampire bats in this study were attracted to the contact calls of frequent donors, even when controlling for kinship. In contrast, they were not attracted to contact calls of relatives when controlling for food-sharing history. The exception was that mothers were attracted to calls of their adult male offspring. We conducted more kinship trials than past donor trials, so a lack of power is unlikely to explain the difference in responses between the trial types. Findings from a previous study using this same captive group revealed that reciprocal sharing and social grooming can overshadow kinship for determining food-sharing decisions (Carter & Wilkinson, 2013b), and our results here suggest that the same is true for decisions about responding to contact calls.

In female greater spear-nosed bats, *Phyllostomus hastatus*, social affiliation leads to convergence in contact call structure, and females are attracted to group-specific contact calls without

individual vocal recognition (Boughman & Wilkinson, 1998). In contrast, we found no evidence that attraction to frequent donors occurred because frequent donors sound more alike and that subjects were merely attracted to more similar-sounding group-mates. Instead, attraction to frequent donors is consistent with individual vocal recognition. No alternative explanation easily accounts for the playback responses that we observed. Playbacks in the kinship trials were not acoustically more similar than those in past donor trials, and we did not detect weaker behavioural responses when the test and control bats were more acoustically similar in frequency or intensity. We also did not find evidence indicating that playbacks from related bats or frequent donors sounded more similar to each other, suggesting that responses were not based on self-phenotype matching of calls.

Measures of only a few acoustic parameters (duration, distance to maximum amplitude and peak frequency at three points) provided better than chance classification of call to individual, and bats probably use a much richer set of acoustic information in these richly harmonic calls, such as formant-like spectral features shaped by the vocal tract (Yovel, Melcon, Franz, Denzinger, & Schnitzler, 2009). Rather than merely being attracted to certain call characteristics, the acoustic and behavioural results suggest that bats were matching calls to a memory of a specific group-mate, and basing their decisions on caller identity. This ability would not be surprising given the experimental evidence that white-winged vampire bats can discriminate among familiar conspecifics using similar contact calls (Carter et al., 2008, 2009), greater spear-nosed bats, *P. hastatus*, can recognize individual pups using isolation calls (Bohn, Wilkinson, & Moss, 2007), and greater mouse-eared bats, *Myotis myotis*, can recognize individuals using voice characteristics of echolocation calls (Yovel et al., 2009), which function primarily for biosonar.

With regard to kin discrimination, the results here are consistent with two interpretations. Either the bats were not able to use calls to recognize kinship, or any perceived kinship was overshadowed by social experience. This latter hypothesis is consistent with prior evidence on social decision making by vampire bats. Free-ranging female vampire bats both positively assort and share food with close kin, and this pattern is unlikely to result from simple mechanisms for kin-biased association, such as spatial location or familiarity (Penn & Frommen, 2010), because female common vampire bats develop multiyear stable associations with kin and nonkin even when frequently switching roosts (Tschapka & Wilkinson, 1999; Wilkinson, 1984, 1985a, 1985b). The mechanisms of kin discrimination in vampire bats remain unclear. Given the results presented here, a parsimonious explanation is that vampire bats learn the calls of maternal kin based on early life experiences (prior association) and do not recognize or favour unfamiliar kin (phenotype matching). However, there is growing recognition that social vertebrates may have multiple forms of kin discrimination, including both prior association and phenotype matching (Breed, 2014; Cornwallis, West, & Griffin, 2009; Green et al., 2015; Mateo, 2010; Mateo & Hauber, 2015; McDonald & Wright, 2011; Pfefferle, Kazem, Brockhausen, Ruiz-Lambides, & Widdig, 2014). Different kin recognition mechanisms may be used in different contexts (e.g. inbreeding avoidance versus nepotism) and might interact with past experience to influence social decisions (Breed, 2014; Daniel & Rodd, 2015; Delton, Krasnow, Cosmides, & Tooby, 2011; Mateo, 2010; Mateo & Hauber, 2015; McDonald & Wright, 2011; Penn & Frommen, 2010; Zöttl, Heg, Chervet, & Taborsky, 2013). Like most mammals, bats appear to use olfaction for social recognition at close range (Bloss, Acree, Bloss, Hood, & Kunz, 2002; De Faniis & Jones, 1995; Englert & Greene, 2009; Gustin & McCracken, 1987; Safi & Kerth, 2003), but a system of kin recognition based on acoustic phenotype matching (Kessler, Scheumann, Nash, &

Table 2
Acoustic comparisons between playbacks or behavioural responses

	R^2	df	F	P
Acoustic distance by:				
Test type (kinship vs donor)	0.03	1, 44	1.4	0.24
Time spent in test arm in donor test	0.02	1, 14	0.2	0.63
Latency to enter test arm in donor test	0.01	1, 14	0.2	0.67
Time spent in test arm in kinship test	0.01	1, 14	0.4	0.52
Latency to enter test arm in kinship test	0.01	1, 14	0.4	0.28
Absolute difference in mean amplitude by:				
Test type (kinship vs donor)	<0.001	1, 44	0.02	0.88
Time spent in test arm in donor test	0.01	1, 14	0.2	0.69
Latency to enter test arm in donor test	0.002	1, 14	0.03	0.86
Time spent in test arm in kinship test	<0.001	1, 14	<0.01	0.98
Latency to enter test arm in kinship test	0.002	1, 14	0.04	0.83

Zimmermann, 2012; Levréro et al., 2015; Pfefferle, Ruiz-Lambides, & Widdig, 2014) would allow for recognition of unfamiliar or paternal relatives at a distance, which would be necessary for co-roosting preferentially with unfamiliar kin over unfamiliar non-kin. Analysis of call variation using better feature extraction across a larger sample of calls and bats is therefore needed to determine whether there are subtle kinship cues that can be used to discriminate unfamiliar (paternal) kin.

Common vampire bats are likely to use contact calls in at least two cooperative contexts. First, common vampires, like many forest-dwelling bats, possess 'fission–fusion' social dynamics where stable relationships are maintained despite frequent regrouping and roost switching (Aureli et al., 2008; Kerth, Perony, & Schweitzer, 2011; Popa-Lisseanu, Bontadina, Mora, & Ibáñez, 2008; Willis & Brigham, 2004). In Costa Rica, particular females often end up in the same roost despite frequently moving among as many as six hollow tree roosts (Wilkinson, 1985a). Given the importance of acoustic communication for bats, and the time and energy it would take to visit multiple trees to smell roost-mates in each, it seems most likely that vampire bats use vocalizations to coordinate these co-roosting associations, as has been found in other bat species (Arnold & Wilkinson, 2011; Chaverri, Gillam, & Kunz, 2012; Kerth & Reckardt, 2003). Second, contact calls might be used within the roost. Food donors often initiate and approach hungry bats to feed them (Carter & Wilkinson, 2013b). In fact, they will sometimes fly to trapped hungry partners, and even feed them through cage bars (Carter, 2016), suggesting that vampire bats can recognize a needy partner from a distance.

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