Common vampire bat contact calls attract past food-sharing partners

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Animals living with kin and non-kin should make social decisions based on the consequences for both direct and indirect fitness. Common vampire bats invest in stable cooperative relationships that benefit both components of inclusive fitness. To disentangle these two factors, we conducted two types of playback trials in a captive group of familiar common vampire bats (*Desmodus rotundus*) with mixed kinship. 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 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 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.

Keywords: bats, cooperation, communication, food sharing, individual recognition, kin recognition, social calls, vampire bats, vocal recognition, vocalisations

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 2-3 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). 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 non-kin 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 neonotous 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; 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, & Medellin, 2012). These calls can be recorded by isolating an individual for a prolonged period, they are longer and lower-frequency than echolocation pulses and so travel farther distances, and they vary substantially in acoustic structure both among and within individuals (Fig. 1). Contact calls appear to allow bats to find and recognize familiar groupmates. In white-winged vampire bats (*Diaemus youngi*), vocal discrimination was evident because vocal responses occurred more often when playbacks of different contact calls shifted to a novel caller (Carter, Skowronski, Faure, & Fenton, 2008), and also when 2-3 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 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 sum, we predicted that isolated vampire bats would seek out past food donors more strongly than relatives.

METHODS

Subjects

Subjects were 31 common vampire bats (*Desmodus rotundus*), 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, Michigan) under permits from the USDA (34-C-0117) and the US Fish and Wildlife Service (MB003342-0). Unrelated bats from the different populations were introduced as adults. Bats were housed at 25-28 degrees Celsius with >33% humidity on a 12 h light/dim light cycle in a 3 x 1.5 x 2 m cage with a soft paper bedding floor that allowed flight and free association among cagemates. 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 Animal Behavior Society 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 from 2010—2014. To quantify food sharing history we used a food sharing index from A to B, which we calculated as the natural log of $(X+1)$ where X is the food sharing rate from A to B (s of mouth-licking per 1 h of experimental trial). To calculate *relatedness*, we genotyped 19 microsatellite markers (Carter & Wilkinson, 2015) and used the Wang estimator (Wang, 2002) calculated 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 multi-harmonic 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 to 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 chamber), the noise level

was low ($<0.5\%$ amplitude). We selected the first 17-30 contact calls that were between 10-99% 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, Sweden) to space apart contact calls at random inter-call intervals varying from 1-3 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”), which each contain 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, USA) and a Sony Nightshot DCR-SR85 camcorder. In each trial, a subject bat was placed in a 76 x 76 cm plastic mesh experimental ‘maze’ with five arms that allowed the subject bat in the center of the maze to move forwards, backwards, left, right, or upwards (Figure 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—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 toward either speaker.

Playback trials were of one of two types: past donor trials and kinship trials. In past 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 or non-donor (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 non-relative (control bat). Test and control bats differed in their pairwise kinship with subject, but 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 differences (test-control) for both the subject's time in each arm and subject's latency to enter them, 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 non-parametric Wilcoxon signed ranks test. All response data are available on FigShare (Carter 2015).

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 if 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) time the subject spent in the test arm, or (3) latency for the subject to enter the test arm. To test these assumptions, we used permutation tests applied to general linear models using lmPerm package (Wheeler, 2010) in R. Such an unconstrained randomisation approach can have higher power than a Mantel test (Legendre & Fortin, 2010) for detecting any potential effects of acoustic distance or amplitude difference on bat response. We calculated 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 51 s longer in the test arm than in the control arm (95% CI=12—91 s; n=15, permutation p=0.0014; Wilcoxon S=44, one-sided p=0.005, Figure 3A). Attraction to the

frequent donor was still evident even when only using the 9 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, permutation $p=0.007$; Wilcoxon $S=15.0$, one-sided $p=0.039$). Subjects also entered the test arm 184 s sooner (95% CI= 42—331 s; permutation $p=0.0066$; Wilcoxon $S=34.5$, one-sided $p=0.025$, Figure 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 non-kin (95% CI of difference: -13—33 s; $n=31$, $p=0.192$, Figure 3A). The latency to enter the test arm also did not differ (95% CI= -47—114s, Figure 3B). Subjects were not attracted to the eight related non-donors (95% CI= -58—51 s), and we detected no kinship preference in either male (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 to calls from a control bat ($n=6$, 95% CI= 7—86 s, permutation $p=0.0074$; Wilcoxon $S=8.5$, 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 relative intensity difference nor acoustic distance between the test and control playbacks correlated with behavioural response times or test type (Table 2). Natural-log-transformed centroid distance also did not correlate with either the relatedness ($n=171$, $R^2=0.005$, $p=0.36$) or food-sharing ($n=88$, $R^2=0.013$, $p=0.28$) 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 vs. 20% of training set or 18% cross-validated; Wilks' Lambda = 0.389, $\chi^2 = 688.43$, $df = 90$, $p < 0.001$).

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. Past findings in this same captive group found 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. Playback responses are not easily explained by alternative explanations. 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 are likely using 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 groupmate, and basing their decisions on caller identity. This ability would not be surprising given the experimental evidence that white-winged vampire bats (*Diaemus youngi*) can discriminate among familiar conspecifics using similar contact calls (Carter et al., 2009; Carter et al., 2008), greater spear-nosed bats (*Phyllostomus 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 regards 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 multi-year stable associations with kin and non-kin even when frequently switching roosts (Tschapka & Wilkinson, 1999; Wilkinson, 1984; Wilkinson, 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 could 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 vs. nepotism) and might interact with past experience in various ways to influence social decisions (Breed, 2014; Daniel & Rodd, 2015; Delton, Krasnow, Cosmides, & Tooby; 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 Fanis & 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, & 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 if 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 ended up in the same roost despite frequently moving among 1-6 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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FIGURE CAPTIONS

Figure 1. Example contact calls from common vampire bats. Three calls recorded from an 8-year old female (A), 10-year old female (B), 6-year old male (C), and 2.5-year old female (D); all bats were isolated during recording. See Carter et al. 2012 for descriptions of call structure variation.

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.

Figure 3. Vampire bats were attracted to contact calls from past donors of similar kinship but not to close kin of similar food-sharing history. Time spent (A), or latency to enter (B), the test arm shown for males (red) and females (blue) when calls from frequent donors (donor test) or close relatives (kinship test) were broadcast from the test arm. Blue shading shows probability density function. Results remained the same with or without the two outliers in Panel A.

TABLES

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	0.5	0.4—0.6	31
	Control bat	0	0—4.9	*19	0	0—0.3	31
	Test - Control	0	0—7.3	*18	0.5	0.1—0.6	31

*Food sharing records do not exist for all 31 bats used for playbacks because some males were not fasted.

Table 2. Acoustic comparisons between playbacks or behavioural responses

Acoustic distance by:	R ²	df	F	p
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

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Figure 1

Vampire bat
start position

76 cm

Ultrasonic
speaker

Ultrasonic
speaker

Video camcorder
with infrared spotlight

Vampire bat
start position

76 cm

Ultrasonic
speaker

Ultrasonic
speaker

Video camcorder
with infrared spotlight

Figure 3 BW

Figure 3 Colour