



Research



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Calling to the collective: contact calling rates within groups of disc-winged bats do not vary by kinship or association

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Many group-living animals coordinate social behaviours using contact calls, which can be produced for all group members or targeted at specific individuals. In the disc-winged bat, *Thyroptera tricolor*, group members use 'inquiry' and 'response' calls to coordinate daily movements into new roosts (furled leaves). Rates of both calls show consistent among-individual variation, but causes of within-individual variation remain unknown. Here, we tested whether disc-winged bats produce more contact calls towards group members with higher kinship or association. In 446 experimental trials, we recorded 139 random within-group pairs of one flying bat (producing inquiry calls for roost searching) and one roosting bat (producing response calls for roost advertising). Using generalized linear mixed-effect models (GLMM), we assessed how response and inquiry calling rates varied by sender, receiver, genetic kinship and co-roosting association rate. Calling rates varied consistently across senders but not by receiver. Response calling was influenced by inquiry calling rates, but neither calling rate was higher when the interacting pair had higher kinship or association. Rather than dyadic calling rates indicating within-group relationships, our findings are consistent with the hypothesis that bats produce contact calls to maintain contact with any or all individuals within a group while collectively searching for a new roost site.

This article is part of the theme issue 'The power of sound: unravelling how acoustic communication shapes group dynamics'.

1. Introduction

Group-living animals often use acoustic signals to coordinate costly, risky or challenging collective behaviours, such as group hunting [1–3], formation

of coercive alliances or coalitions [4], cooperative predator mobbing [5] and cooperative defence of resources [6]. Acoustic signalling between group members can not only facilitate cooperation but also itself be a form of cooperative behaviour that can either provide a return benefit or be exploited. In these cases, the signals should therefore be directed to a particular set of receivers. As expected, many vocal species exhibit directed contact call exchanges that occur between parents and offspring, mated pairs or group members (e.g. [7]). These vocal interactions can establish a distinct caller–receiver relationship that maintains inter-individual physical proximity despite constant movements, limited visual input or a noisy background [8–11]. For example, in Mexican free-tailed bats *Tadarida brasiliensis*, which form the largest bat colonies in the world, each mother bat uses vocal exchanges to find her pup by identifying its calls among many thousands of other calling pups in a completely dark cave [12,13].

Vocal interactions can function at multiple social levels: a caller could be targeting a whole group, a subgroup (e.g. matriline) or a single receiver [7,9]. In a group setting, it is often difficult for researchers to identify the intended versus unintended receivers, and this challenge can mask the amount of social complexity shaping vocal communication [14]. One solution is to capture and split a social group into caller–receiver pairs and estimate the calling and responding rates for each pair [15]. This procedure allows the construction of a within-group ‘vocal interaction network’, where individuals are network nodes and the calling rates are network edges. The results from such a procedure can help identify the factors predicting vocal exchange rates among conspecifics. For example, vocal exchange rates might differ by pairwise dominance, familiarity or kinship [15,16]. Given the role of communication in the maintenance of social interactions (e.g. [17,18]), measuring social relationships through the lens of communication can provide a deeper understanding of animal societies [19].

In this study, we decompose social groups into caller–receiver pairs during vocal exchanges that ensue as individuals search for roosts. Our focal species is Spix’s disc-winged bat, *Thyroptera tricolor*. This small neotropical species forms small groups of about five bats (mean = 4.60, s.d. = 2.18, range 2–9) that roost inside the young, developing tubular leaves of plants in the order Zingiberales, such as heliconias and bananas [20–22]. The tubular structure of these leaves unfurls after approximately one day [21]. Given the ephemeral nature of their roosts, the bats must rapidly find new roost sites. To do this while maintaining group cohesion, they rely on a call-and-response contact calling system [23,24]. When a single individual, or a group, is searching for a new tubular leaf, they produce ‘inquiry’ calls, which help maintain contact with group members [25]. When one or several individuals find and enter a roost, they often produce a distinctive ‘response’ call in reply to inquiry calls [26–28]. Response calls have not been recorded in any context besides responding to inquiry calls from a live bat or a playback speaker [27,29]. For both call types, there are large, repeatable inter-individual differences in calling rates, yet there is also substantial within-individual variation [30,31], which has yet to be explained.

Here, we sought to explain the within-individual variation in calling rates of *T. tricolor* by testing whether calling rates from a sender to a receiver were predicted by the kinship or co-roosting association rates of that within-group dyad (pair). *Thyroptera tricolor*’s mixed-sex social groups have the highest known kinship of any bat [32]. Social groups are mostly composed of close kin, and females typically have higher within-group relatedness than males, suggesting a matrilineal group structure [33] that seems to be sustained by high levels of offspring philopatry for both sexes [34]. Mean pairwise relatedness between females and other group members ranges between 0.24 and 0.29, while for male relatedness, it ranges between 0.15 and 0.20 [33]. Despite high levels of all-sex natal philopatry and kinship, dispersal and subsequent merging of matrilineal groups occur occasionally [34]. *Thyroptera tricolor* also exhibits high levels of group cohesion [32]. Individuals rarely roost with members of other social groups, resulting in high levels of within-group association over extended periods of time [22,35]. However, groups may often split, especially if roosting resources are scarce [36]. As a result, the mean within-group simple ratio index—the proportion of time that two individuals spent in co-roosting association after accounting for sampling effort—is about 0.66 (s.d. = 0.21) [22].

To test the hypothesis that within-group calling rates in *T. tricolor* differ by partner kinship or association, we recorded calls from groupmate pairs that we experimentally placed into the roles of a flying bat that could produce inquiry calls and a roosting bat, placed inside a leaf, that could produce response calls. Although previous studies suggest that individuals may preferentially respond to some inquiry calls more than others [31], it remains unclear whether calling is targeted to close relatives or to group members with whom focal individuals are more closely associated.

If rates of contact calling vary among caller–receiver relationships within the group, then we expected that higher association and kinship would predict higher counts of inquiry calls and response calls. We tested this prediction while controlling for partner calling rates, since response calling is prompted by the emission of inquiry calls [26]. Effects of kinship and association on calling rates are predicted based on observations from other group-forming taxa, where individuals often produce a greater number of calls directed towards kin and familiar individuals and receivers of these signals typically exhibit stronger reactions [37–40].

Alternatively, contact calling rates may not be explained by the individual identity of the receivers. In some taxa, call rates are influenced by the risk of becoming separated from one’s group [41,42]; thus, contact calls may be produced for the entire group, not targeted at a single receiver, to remain in close contact with group members [43,44] or to avoid inter-group interactions, which could result in aggression [45]. In that case, we expect the best predictor of calling rate to be the caller, rather than the receiver or its kinship or association with the caller.

2. Methods

(a) Field methods

We collected data from January 2021 until December 2022 at Hacienda Barú Biological Research Station. Hacienda Barú is located within the Barú National Wildlife Refuge, Savegre district in southwestern Costa Rica. We consistently sampled social groups (a group is defined as a set of individuals sharing a roost at the same time) in a predetermined focal area of *ca* 6 ha (electronic supplementary material, figure S1). In 2021, we captured a total of 76 bats that were sampled between 1 and 39 days (mean = 17.71, s.d. = 9.35). In 2022, we also captured 76 bats, and individuals were sampled between 1 and 16 days (mean = 9.18, s.d. = 4.22; electronic supplementary material, table S1). The total number of individual bats identified and tagged within our focal area was 106.

To determine the location of social groups, we conducted daytime surveys across the study area. During these surveys, we meticulously inspected potential roost sites (developing tubular leaves of plant species such as *Heliconia* spp., *Calathea* spp. and *Musa* spp.). We used an extendable mirror to verify the presence of bats. Upon locating a group, all individuals were captured by closing the entrance to the leaf and then covering it with a plastic bag. As bats exit the roost, they enter the plastic bag, allowing us to gently transfer them as a group into a cloth bag for subsequent processing. For accurate geospatial information, we used a GPS to record the precise location of each bat and social group.

Upon the first capture, bats over two months old were tagged with passive integrated transponder tags. These tags are very small (1.4 × 8.5 mm) relative to the size of the bat (*ca* 4 g) and weigh only 0.09 g. Each tag has a unique alpha-numeric code, allowing the precise recognition of individuals with a digital reader (Biomark HPR Plus, Inc., Idaho, USA). For each bat, we registered information about forearm length, sex, age and reproductive condition. We also collected two 3 mm wing tissue samples from each bat, procuring one sample per wing. We placed the tissue samples in vials containing silica gel as a desiccant, to preserve DNA integrity until extraction.

(b) Estimating co-roosting associations

For each sampling day, we recorded which individuals were associated (i.e. in the same roost), then used the R package *asnipe* [46] to construct co-roosting association networks with edges defined by the simple ratio association index (SRI) [47,48]. The SRI calculates the proportion of time that two individuals spent in association after accounting for a sampling of both individuals, with values spanning from zero (no association) to one (always observed together). Because SRI estimates are imprecise with only a few observations, we did not estimate SRI values for the 14 bats (out of 106 sampled) that were seen only 1–3 times.

We also used the *igraph* R package to create undirected and weighted association networks [46,49]. After creating the networks, we identified communities, which are defined as sets of individuals more closely associated with each other than with the rest of the population [50]. Communities differ from groups as the latter are composed of individuals sharing a roost on a given day, while the former are defined based on long-term data of sustained co-roosting associations among group members. To determine community membership, we implemented the commonly used ‘fastgreedy’ algorithm [51], which performs well when the underlying community structure in the network is well defined and modular [50]. To verify the latter, we calculated modularity, which measures what proportions of connections among individuals (based on co-roosting events) are intra-community, rather than inter-community [52,53]. Modularity ranges between 0 and 1, with higher values indicating dense intra-community and sparse inter-community connections [51]. Additionally, we estimated the average local clustering coefficient, which represents the probability that the neighbours of a node are connected to each other. Higher values of this coefficient indicate a more cohesive social structure [54].

(c) Estimating kinship

DNA extractions were conducted at the University of Minnesota Genomics Center (<https://genomics.umn.edu/services/gbs>) using the Qiagen DNeasy 96 Blood & Tissue Kit (Cat. No./ ID: 6958) following the manufacturer’s instructions.

(i) Genotyping-by-sequencing

Sequencing was performed at the University of Minnesota Genomics Center using a double enzyme digestion protocol. Briefly, extracted DNA was quantified using Picogreen® (Thermo Fisher Scientific, MA, USA) and normalized to 10 ng/μL. A total of 100 ng of DNA per sample were digested with 10 units of *Bam*HI + *Nsi*II (New England Biolabs®, Inc., MA, USA) restriction enzymes and incubated at 37°C for 1 h, and then heat-inactivated at 80°C for 20 min. The DNA samples were then ligated with 200 units of T4 ligase (New England Biolabs®, Inc., MA, USA) and phased adaptors with –GATC and –TGCA overhangs at 22°C for 1 h and heat-killed. The ligated samples were then purified with solid-phase reversible immobilization beads and amplified for 18 cycles with 2× NEB Taq Master Mix to add the barcodes. Libraries were quantified and pooled. Fragments of 300–750 bp were selected and diluted to 1 nM for sequencing on Illumina NovaSeq™ 6000 (Illumina, CA, USA) using single-end 100 bp reads. The sequencing depth was 2 M reads per sample.

(ii) Data cleaning, de novo alignment, and variant discovery

The raw FASTQ files were demultiplexed using the Illumina *bcl2fastq* software (Illumina, CA, USA). To trim 5' padding sequences from the sequencing facility (0–10 bases at the start of each read) and to trim all reads to a length of 90 bp using

cutadapt, we used the script GBStrim.pl (<https://bitbucket.org/jgarbe/gbstrim>). Stacks v. 2.4 was used for de novo alignment of sequences and to generate genotypes [55]. First, we used process_radtags to clean the trimmed raw files. Then, we ran a pilot analysis with eight samples to optimize parameters based on the 'r80' method [47] and settled on $M = 4$, $n = 5$ and $m = 3$. Next, the wrapper program denovo_map.pl was used on all samples, which executes each of the Stacks pipeline components (ustacks, cstacks, sstacks and tsv2bam) individually [55]. We filtered and exported variant data using the populations command, conserving only a single nucleotide polymorphism (SNP) per RAD site to avoid including linked SNPs in pedigree analysis. To convert the Stacks VCF file to plink format and filter to representative variant sites based on missingness (0.05) and minor allele frequency (0.45), we added contig names using a custom script and then used a combination of plink2 and plink with the arguments --RecodeA, --set-all-var-ids and --allow-extra-chr [48].

(iii) Estimating pedigree and pairwise kinship

To build a pedigree and relatedness matrix from the genotype data, we used the R program Sequoia [48], which incorporates sex and birth year information using selected SNPs across individuals. We attempted to reduce pedigree error using genomic relatedness as determined by GRM with GCTA [48], but doing so did not improve estimates of group relatedness, so these results are not reported.

(d) Recording vocal interactions

To identify pairwise response calling interactions within groups, we captured focal groups during the morning hours and transported them in cloth bags to the research centre (electronic supplementary material, figure S1) with a flight cage ($3 \times 4 \times 9$ m). Using a custom R script, we randomly selected the dyads, from a single group, that would be tested each day. We allowed the first bat from each dyad to fly inside the flight cage for a maximum of 5 min until it located and entered a tubular leaf. Once inside the leaf, we placed a large mesh cover around the leaf to prevent the second bat from entering the roost. The second bat was then allowed to fly for 5 min while we recorded both response and inquiry calls from the roosting and flying bats, respectively. Flight times varied because 70 out of 446 trials ended before 5 min when the responding bat would not remain within the leaf, and four trials were accidentally longer than 5 min (5.02–6.00 min) because researchers failed to stop the recording on time. This procedure was repeated until all pairwise response calling interactions within a group had been recorded but without repeating individuals in a single task in a single day (flying or roosting) to decrease the risk of habituation. After each trial, we provided mealworms (*Tenebrio molitor*) and water to all individuals before returning them to their roosts on the same day.

We recorded sounds with three or four omnidirectional microphones (Knowles FG-O) and digitized them using an Avisoft UltraSoundGate 416 connected to a computer running Avisoft-Recorder software (sampling rate 500 kHz, 16-bit resolution). For all recordings, we counted the number of inquiry and response calls using Raven Pro 1.6 [56] to get a sum for each trial. We only tested how bats in the roost responded to flying bats when the latter had produced at least one inquiry call. We excluded from analysis seven trials where neither bat called ($n = 5$) or where the sound file was lost ($n = 2$).

(e) Measuring individual differences in calling rates

We first used GLMM to partition the sources of variation in rates of inquiry and response calling to assess (i) consistent individual differences in the sender and (ii) how much the receiver affected the vocal production of the sender. For the inquiry calls, we fitted random intercepts for the individual flying (sender) and the individual roosting (receiver). For the response calls, we fitted random effects for the individual roosting (sender) and the individual flying (receiver). Both models had a within-year group as a random effect and no fixed effects and were fitted as a negative binomial model with the package lme4 [57] within R. Repeatability estimates were calculated on the observed scale [58] (see electronic supplementary material, text S1 'Derivation for the repeatability formula based on the variance estimates of a negative binomial mixed-effect model').

(f) Measuring the effect of flight times on calling rates

To assess the relationship between flight times and inquiry calling, we fit a negative binomial GLMM with flight minutes as the fixed effect and inquiry call count as the response. Random intercepts were the flying bat, roosting bat and within-year group. To assess the relationship between flight times and response calling, we fit a zero-inflated negative binomial GLMM with the same random effects, response call count as the response, and flight minutes and inquiry call count as fixed effects. For fitting these models, we used the R package glmmTMB [59] and assessed overdispersion and zero inflation using the R package performance [60]. For inferences, we used the Profile (likelihood-based) method to get 95% confidence intervals (CIs) for model fixed effects using the R package broom.mixed. This method for estimating 95% CIs is based on the asymptotic χ^2 distribution of the log-likelihood ratio test statistic, and it outperforms the function's default Wald's method, which is faster but less reliable.

(g) Measuring the effect of inquiry calling on response calling

To assess the relationship between inquiry and response calling ('vocal responsiveness'), we fit a zero-inflated negative binomial model (using the R package glmmTMB). The dependent variable was the count of response calls. Random intercepts were the

within-year group and IDs for the flying bat and roosting bat. Fixed effects were the count of inquiry calls and the log flight time of the bat as an offset term to control for sampling time. To visualize the response calling rate while controlling for inquiry calling and flying time, we used the difference between the observed and predicted counts from this model to define and plot the ‘residual response call variation’ as a dependent variable.

(h) Kinship and association as predictors of dyadic calling rates

To assess predictors of response calling rates, we fit a zero-inflated negative binomial GLMM (using the R package *glmmTMB*). Random intercepts were the within-year group and IDs for the flying bat and roosting bat. Fixed effects were kinship, association (SRI), their interaction, the count of inquiry calls as a covariate and the log flight time of the bat as an offset term to control for sampling time. We initially included the interaction term to assess whether the effect of association rates on calling rates was lower among kin and greater among non-kin (a negative interaction). This scenario might occur if kin always have high calling rates, regardless of their co-roosting association rate. However, in all these models, we did not detect any evidence of a negative interaction between association and kinship: the interaction coefficient was not significant, it was positive rather than negative and it did not clearly improve our metrics of model performance (below). Given that any effect of association on calling rates did not appear to be greater among non-kin or differ with kinship, we fit the models without the interaction term.

To assess predictors of inquiry calling rates, we fit a negative binomial GLMM (using the R package *glmmTMB*) similar to the one above except with the count of inquiry calls as the dependent variable and the count of response calls as a covariate. We fit this model of inquiry calling with all trials and again when excluding trials with zero response calls. In both the response calling and inquiry calling models, we scaled predictors to convert units to standard deviations. To evaluate and compare model performance, we used Akaike information criterion (AIC), Bayesian information criterion (BIC) and R^2 between the observed counts and predicted counts.

To assess fixed effects, we fit zero-inflated models, assuming that there were multiple causes of zero response call counts. We assumed this because previous work found that about a third of bats do not make response calls [30] and suggested that some bats are in a current state of not producing response calls (‘non-vocal bats’), while others do make response calls at varying rates (‘vocal bats’). Our assumption was consistent with the `check_zeroinflation()` function (from the R package *performance*), which suggested ‘probable zero inflation’ indicating that a negative binomial model was underfitting zeros. The AIC and BIC values for the zero-inflated model were also better than the same model without zero inflation. We did not expect that the hypothesized effects on calling rates would differ by sex of caller and receiver; to confirm this, we plotted the effects of kinship and association separately for each combination of sex and role (e.g. flying male and roosting female, flying male and roosting male, etc.).

3. Results

(a) Associations, kinship and calling rates

Within our study area of *ca* 6 ha, we identified 76 bats in 2021 and 2022 (106 unique individuals) that belonged to 11 and 12 social groups, respectively (electronic supplementary material, table S1). The average number of individuals observed in the same roost at the same time was 4.25 (electronic supplementary material, table S2). However, based on the community assignment of all individuals observed in our study site, not just those observed on more than three occasions, the community size was ≈ 6 (figure 1; electronic supplementary material, table S1). Communities were highly distinct and cohesive, with modularity values of 0.86 and 0.89, and average local clustering coefficients of 0.92 and 0.93 (electronic supplementary material, table S1). For individuals who were observed on more than three occasions, the average within-group association (SRI) ranged from 0.34 to 1 (electronic supplementary material, table S2).

Across 12 groups containing 76 individuals in either 2021 or 2022, the SNP-based pedigree analysis estimated a mean group relatedness of 0.32 ± 0.14 (electronic supplementary material, table S2). Within each group, a mean of 1.2 ± 1.1 individuals were not detected to be kin of other group members.

Across 446 trials, we collected vocal interaction data from 139 experimental pairs of bats (254 directed flying–roosting pairs) from 23 groups (defined within each year, 11 in 2021 and 12 in 2022). All of the experimental pairs were from the same group. Bats emitted, on average, 71 (range = 1–280) inquiry calls and 99 (range = 0–859) response calls during trials. Inquiry calling rates (calls per minute) ranged from 0.2 to 160 (average = 15), whereas the average number of response calls per inquiry call ranged from 0 to 125 (average = 2). We had association rates from 133 pairs and relatedness data from 82 of 139 pairs (24 pairs with $r = 0.5$, 8 pairs with $r = 0.25$ and 50 non-kin pairs with $r = 0$). For experimental pairs, mean within-group kinship was 0.23 (0.16–0.31) (bootstrapped 95% CI) and mean within-group association (SRI) was 0.51 (0.47–0.55). Association rates tended to be higher in kin pairs than in non-kin pairs (for kinship = 0.5: mean SRI = 0.720 (0.640–0.802); for kinship > 0: mean SRI = 0.694 (0.629–0.759); for kinship = 0: mean SRI = 0.582 (0.517–0.638); electronic supplementary material, figure S2).

(b) Repeatability of inquiry and response calling

For the number of inquiry calls produced during a trial, 49% of the variance was explained by the identity of the sender (flying bat); the variance explained by the identity of the receiver (roosting bat) was negligible. This implies that some flying

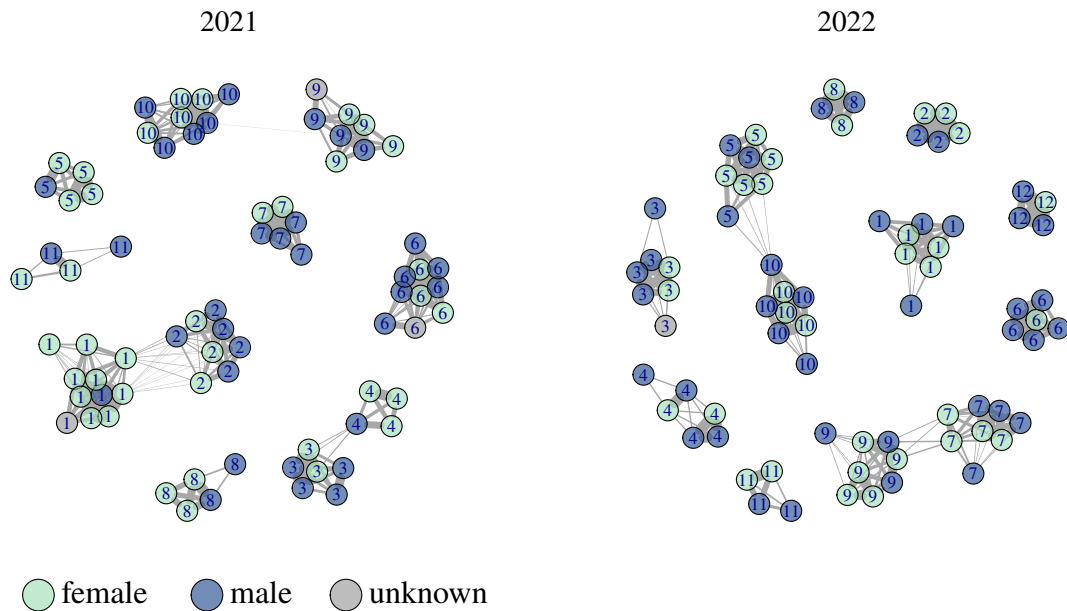


Figure 1. Network diagrams displaying associations of focal *Thyroptera tricolor* bats observed in 2021 and 2022. Line width indicates the strength of the association based on the SRI. Numbers within nodes denote community identity. Node colour represents the sex of an individual. We included all individuals observed in each year for the construction of these diagrams, not only those observed on more than three occasions.

bats produce more inquiry calls than others, while the identity of the roosting bat does not explain the number of inquiry calls emitted by flying bats. For the number of response calls, 51% of the variance was explained by the identity of the sender (roosting bat), and the variance that was explained by the identity of the receiver (flying bat) was also negligible. This implies that some of the roosting bats are more responsive than others, while the identity of the flying bat has little effect on the number of response calls produced by roosting bats.

(c) Flight times and calling rates

The inquiry call count increases by a factor of 1.43 (1.36–1.49) (95% CI) for every minute of flight time (electronic supplementary material, figure S3). When controlling for inquiry calling, response call count increased by a factor of 1.67 (1.34–2.03) for every minute of flight time. Because call counts increased with flight time, we included flight time as an offset exposure variable, similar to sampling effort, in our subsequent GLMMs.

(d) Kinship and association as predictors of calling rates

In our model of response calling, the observed values explained 47% of the variation in predicted response call counts. As expected from vocal exchanges, response calling increased with inquiry calling, even when controlling for flight time (figure 2). Contrary to our predictions, neither inquiry calling nor response calling was higher for kin pairs or more associated pairs (electronic supplementary material, figure S4). The lack of a positive relationship was evident overall (figure 3) and within combinations of sex (electronic supplementary material, figure S5). We also confirmed that neither association nor kinship predicted response calling as single predictors, when not including the other effect (association coefficient = -0.04 , $z = -0.33$, $p = 0.74$; kinship coefficient = 0.04 , $z = 0.36$, $p = 0.72$).

For the model of inquiry calling, the observed counts explained 71% of the variation in the predicted inquiry call counts (or 81% when excluding trials without response calling). Regardless of whether we included or excluded trials without response calls, we detected no clear effects of response calls, kinship or association (figure 4). We also confirmed that neither association nor kinship predicted more inquiry calling when not including the other effect (all trials: association coefficient = -0.04 , $z = -1.31$, $p = 0.19$; kinship coefficient = -0.06 , $z = -1.72$, $p = 0.09$; trials with non-zero response calls: association coefficient = -0.01 , $z = -0.32$, $p = 0.75$; kinship coefficient = -0.03 , $z = -0.69$, $p = 0.49$). Instead, inquiry calls were predicted by the identity of the flying bat. Of the total variance explained by the random effects, the flying bat explained 84%, the group explained 16% and the roosting bat explained $<0.00001\%$.

4. Discussion

In this study, we assessed in *T. tricolor* whether within-individual variation in calling rates during caller–receiver vocal interactions was explained by kinship or association. As found in previous studies [30,31], we observed consistent individual variation in both inquiry and response calling rates. The identity of the sender explained much of the variation in the number of calls bats produced. We also found that response calling rates were strongly influenced by partner inquiry calling rates. For

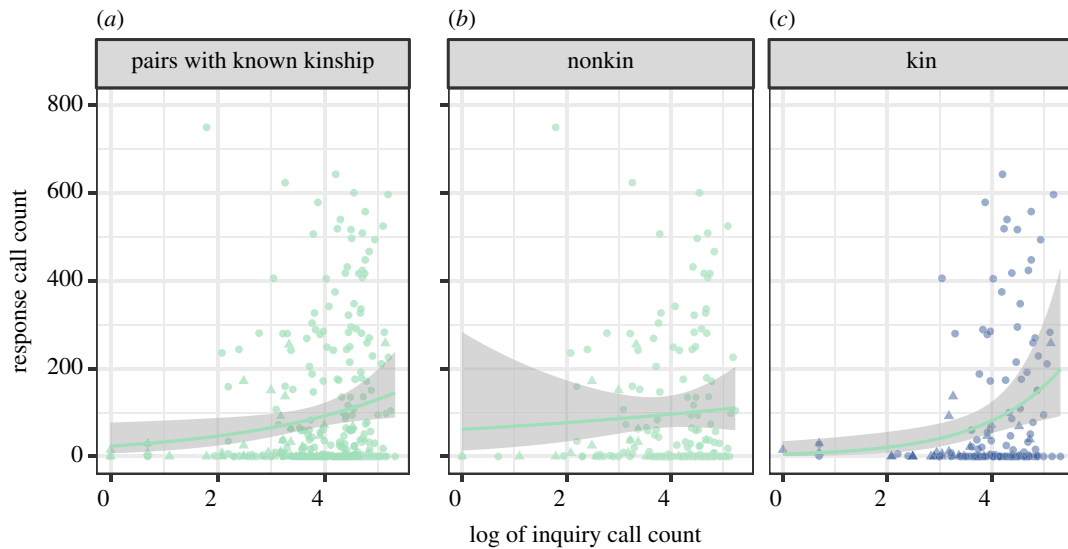


Figure 2. Relationship between inquiry calling and response calling. Panel (a) shows how response calling by the roosting bat increases with inquiry calling by the flying bat. Panels (b,c) show the relationship for only non-kin pairs and only kin pairs. Triangles represent trials that ended before the established 5 min period because the roosting bat left the roost. Inquiry call count is shown with a natural log transformation for better visualization. The lines shows negative binomial fit.

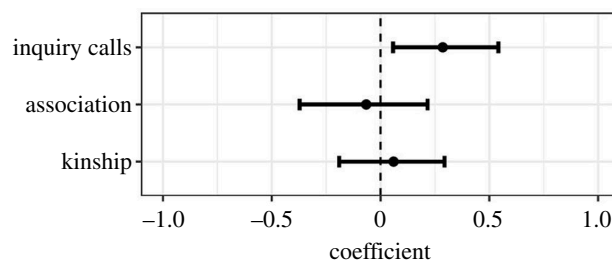


Figure 3. Response calling is not predicted by kinship or association. Estimates of fixed effects (coefficients) of how response calling by the roosting bat is predicted by inquiry calling, association and kinship with the flying bat. Fixed effects were scaled to convert units to standard deviations. Additional details are provided in the electronic supplementary material, table S3.

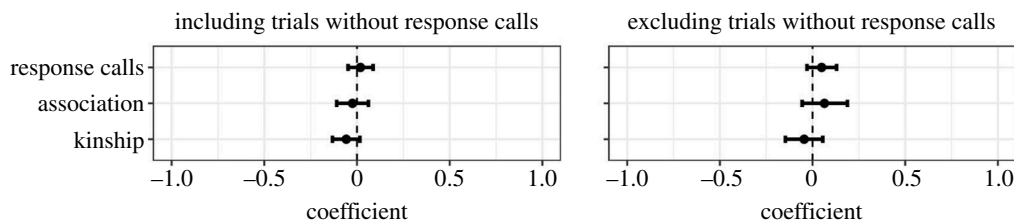


Figure 4. Inquiry calling is not predicted by kinship or association. Estimates of fixed effects (coefficients) of how inquiry calling by the flying bat is predicted by response calling, association and kinship with the roosting bat. Fixed effects were scaled to convert units to standard deviations. Additional details are provided in the electronic supplementary material, table S4.

both call types, however, the identity of the receiver did not determine how much an individual vocalized. Calling rates did not increase dramatically when the pair of group mates had higher kinship or association. These findings suggest that contact calls might not be targeted at specific individuals but rather broadcast to the entire group so that group mates remain in close contact while collectively searching for a new roost site.

Our results are consistent with several non-mutually exclusive hypotheses. First, contact calls might be produced for any or all group members rather than for specific partners within each group, especially if the mutual benefits of recruitment, or the avoidance of inter-group interactions, occur at the group level. Within-group nepotism is rare in cooperative breeding groups of birds and mammals where mean group kinship is high and variance in kinship is low [61,62]. In such species, individuals might often produce calls that benefit multiple group members. Although there are no cooperatively breeding bats [63], *T. tricolor* has the highest mean group kinship ($r = 0.2$) known for any group-forming species of bats [32,33] and groups are highly stable and cohesive relative to other well-studied bats [22,32,35]. In contrast, kin-biased contact calling is predicted when individuals live in less stable groups and regularly interact with both kin and non-kin. For example, in common vampire bats (*Desmodus rotundus*), co-roosting groups have mixed kinship (mean within-group kinship = 0.08) and are highly fluid and unstable, changing composition from day to day [32,64,65]. Cooperative relationships are nepotistic, reciprocal and highly differentiated within groups [66–68]. Cooperative behaviours are targeted at specific group members, and individuals preferentially move towards contact calls of specific group members, such as food-sharing partners [37,69,70].

A second explanation for the lack of strong effects of kinship and association on response calling is that vocal recognition might simply be too difficult for roosting bats. Although inquiry and response calls vary by individual and group [27,28], roosting bats in past studies did not show a clear preference to respond to groupmate calls [25]. This might be explained by the acoustic properties of the leaf roost, which significantly distorts incoming inquiry sounds and thus could hinder recognition [71]. If recognition is difficult, then bats might increase the call rate to gather more social information when the identity of the other bat is less clear or unfamiliar, rather than when the partner identity is known. Recognition seems easier for flying bats, which are more likely to enter a roost if a response call comes from a group member, and also prefer to approach inquiry calls emitted by group members in flight [25].

Finally, it is possible that intra-individual variation in calling rates is not primarily explained by kinship and/or association but rather by other factors not considered in our study, such as energetic limitations and the complexity of the physical or social environment. The production of response calls in *T. tricolor* is energetically costly [72], so individuals may only emit these signals when not constrained by food shortages [73]. Also, given the vital role of contact calls in maintaining group cohesion, bats could increase calling rates when individuals perceive a higher risk of becoming separated from conspecifics. For example, Japanese macaques (*Macaca fuscata*) produce higher rates of contact calls when individuals forage in areas with poor visibility [41]. Bats could also increase call emission when individuals are harder to localize. In white-winged vampire bats (*Diaemus youngi*), rates of contact calling and rates of responding among group members increased when bats were moved to new locations compared to when they were moved the same distance back to the same location [74]. The social context is also likely to modulate the emission of contact calls. Swinhoe's White-eyes (*Zosterops simplex*), for instance, change their contact calling rates with experimental modifications of group size [75]. Meerkats (*Suricata suricatta*) adjust their calling rates to the number and distance of neighbours [44]. Further work is needed to disentangle the role of these, and other factors in modulating contact call emission in disc-winged bats. Moreover, if calling rates are not explained by actor–receiver relationships, then bats might recognize and selectively call specific groupmates in ways that do not impact calling rates. Future work could investigate, for instance, whether call design is modified for different intended receivers within the same group.

Besides contact calling, another mechanism that allows these bats to maintain cohesive social groups with few changes in membership over time is that *T. tricolor* groups use, and potentially defend, a small roosting home range [22,36]. When searching for roosts, individuals probably target those areas, which would reduce the probability of flying bats accidentally joining other groups and roosting bats responding to non-groupmates. The events would be costly because individuals entering a roost occupied by another group face the risk of aggression [45].

In conclusion, our work shows that individual variation in calling rates during dyadic interactions within *T. tricolor*'s social groups is primarily influenced by the identity of the caller rather than the level of relatedness or association with the receiver. Contrary to our initial expectation that vocalizations would be directed towards more closely related or associated groupmates, the findings suggest that inquiry and response calls appear to serve the purpose of maintaining group cohesion rather than being specifically targeted at particular individuals to maintain or strengthen within-group affiliations. Our findings underscore the importance of understanding communication within the broader context of group dynamics and collective behaviours, shedding light on the social strategies employed by these bats during their collective search for roosting sites [76–79].

Ethics. This study was conducted in accordance with the ethical standards for animal welfare of the Costa Rican Ministry of Environment and Energy, Sistema Nacional de Áreas de Conservación, permit no. SINAC-ACOPAC-RES-045-2021. Protocols were also approved by the University of Costa Rica's Institutional Animal Care and Use Committee (CICUA-015-2021).

Data accessibility. The data and code that support the findings of this study are openly available at [80].

Electronic supplementary material is available online [81].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. G.C.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, visualization, writing—original draft, writing—review and editing; M.S.: data curation, funding acquisition, investigation, writing—original draft, writing—review and editing; J.L.S.: data curation, formal analysis, investigation, writing—original draft, writing—review and editing; M.A.-S.: investigation, methodology, visualization, writing—review and editing; Y.A.-A.: conceptualization, formal analysis, writing—review and editing; M.N.: writing—review and editing; M.K.: writing—review and editing; S.C.-R.: investigation, writing—review and editing; N.S.: investigation, writing—review and editing; M.S.-C.: data curation, investigation, writing—review and editing; Y.J.-T.: data curation, investigation, writing—review and editing; D.U.-S.: data curation, investigation, writing—review and editing; H.S.-H.: investigation, writing—review and editing; G.G.C.: conceptualization, formal analysis, methodology, visualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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