



# Contact calling in context: intra- and intergroup variation in vocalization rates depend on a call's function

Gloriana Chaverri<sup>1,2</sup> · Yimen G. Araya-Ajoy<sup>3</sup> · Maria Sagot<sup>4</sup>

Received: 17 July 2018 / Revised: 7 April 2020 / Accepted: 14 April 2020  
© Springer-Verlag GmbH Germany, part of Springer Nature 2020

## Abstract

To maintain group cohesion while coordinating group movements, individuals might use signals to advertise the location of a route, their intention to initiate movements, or their position at a given time. In highly mobile animals, the latter is often accomplished through contact calls that are emitted at different rates by group members. Here, we describe and quantify intra- and intergroup variation in contact calling rates in Spix's disc-winged bats (*Thyroptera tricolor*), a species that employs distinct inquiry and response calls to coordinate group movements during flight and while announcing roost locations. We evaluate the extent to which groups are composed of individuals with similar calling rates and estimate variation among and within groups. Our results show large variation in response calling rates among and within groups, both in terms of calling rates and the probability of being vocal or not; for example, a large portion (35%) of bats sampled did not produce these signals. For inquiry calls, we found that variation in calling rates was greater within than among groups, and in contrast to response calls, only a few individuals (3%) did not produce inquiry calls. Overall, we found support for the existence of intra- and intergroup differences in the context of contact calling in disc-winged bats, and our results suggest that different mechanisms may promote the evolution and maintenance of varying calling rates for the two types of calls studied.

## Significance statement

Animal communication networks are comprised of individuals with different vocal behaviors. However, we still do not fully understand the mechanisms that facilitate individual and group variation in vocal behavior and how these differences affect group cohesion in highly mobile organisms. Here, we describe and quantify contact calling behavior in Spix's disc-winged bats (*Thyroptera tricolor*) and evaluate whether vocal behavior is associated with group membership and call type. We found consistent individual differences in contact calling rates, as well as among-group variation in calls associated to roost finding. Our study provides a baseline for generating hypotheses regarding the costs and benefits of contact call production during group movements.

**Keywords** Communication · Contact call · Repeatability · *Thyroptera tricolor*

---

Communicated by M. Knoernschild

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s00265-020-02837-w>) contains supplementary material, which is available to authorized users.

✉ Gloriana Chaverri  
gloriana.chaverri@ucr.ac.cr

<sup>1</sup> Sede del Sur, Universidad de Costa Rica, #4624 Alamedas, Golfito 60701, Costa Rica

<sup>2</sup> Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, República de Panamá

<sup>3</sup> Department of Biology, Centre for Biodiversity Dynamics (CBD), Norwegian University of Science and Technology (NTNU), N-7491 Trondheim, Norway

<sup>4</sup> Department of Biological Sciences, State University of New York at Oswego, Oswego 13041, NY, USA

## Introduction

Social behaviors such as aggression, spacing, gregariousness, and grooming are unstable phenotypic traits (Lott 1991; Blomberg et al. 2003; Georgiev et al. 2013; Carter and Wilkinson 2015) that may vary within and among individuals and groups across observations (e.g., Gero et al. 2009; Pruitt and Riechert 2011). Variation in such behaviors may occur in response to variable ecological, physiological, and developmental conditions (Snowdon and Boe 2003; Réale et al. 2007; Groothuis and Trillmich 2011; Carter and Wilkinson 2015) or in response to selective pressures favoring coexistence of different behavioral types within social groups (Dall et al. 2004).

Variation in social behaviors can be expected in species that coordinate group movements. During group foraging, individuals often maintain cohesion by producing contact calls (Kondo and Watanabe 2009). In a few species, it has been reported that some group members are consistently more vocal, while others seldom produce contact calls (Guillette and Sturdy 2011; Friel et al. 2016). In other species such as the green woodhoopoes (*Phoeniculus purpureus*), all group members are equally likely to produce vocalizations during group movement (Radford 2004). In those cases, continuous emission of contact calls by all group members may function as a means to announce location and thus remain in contact with group members. Notwithstanding, when an individual finds an important resource, for example, a feeding patch or shelter, or when deciding a specific traveling direction, group cohesion can be affected by a lack of consensus if several group members vocalize. In such cases, group cohesion and coordination might be more efficiently preserved if only one or a few individuals vocalize, particularly those that are more experienced or better informed of the location of resource (Couzin et al. 2005). Thus, we expect individual differences in contact calling behavior, specifically calling rates, to depend on the context in which these sounds are used.

In this study, we first describe and quantify contact calling behavior, focusing on calling rates, in Spix's disc-winged bats (*Thyroptera tricolor*). Second, we estimate differences in calling rates within and among groups to determine if production of social calls is determined by group membership and/or call type. *Thyroptera tricolor* is a highly mobile animal species that employs acoustic signaling to coordinate group movements during flight and while locating roosts. This species forms small, cohesive and highly related groups of an average of five individuals (range = 2–12) that remain together for several years (Findley and Wilson 1974; Vonhof et al. 2004; Chaverri 2010; Chaverri and Kunz 2011; Buchalski et al. 2014). In addition, *T. tricolor* uses a unique roosting resource, the developing furled leaves of plants such as *Heliconia* spp. and *Calathea* spp. which are suitable as a roosting site for very short periods of time (approximately 24 h; Vonhof and Fenton 2004). Such an ephemeral resource, which is only used by one

social group at a time, forces bats to find a new roost daily while maintaining contact with group members.

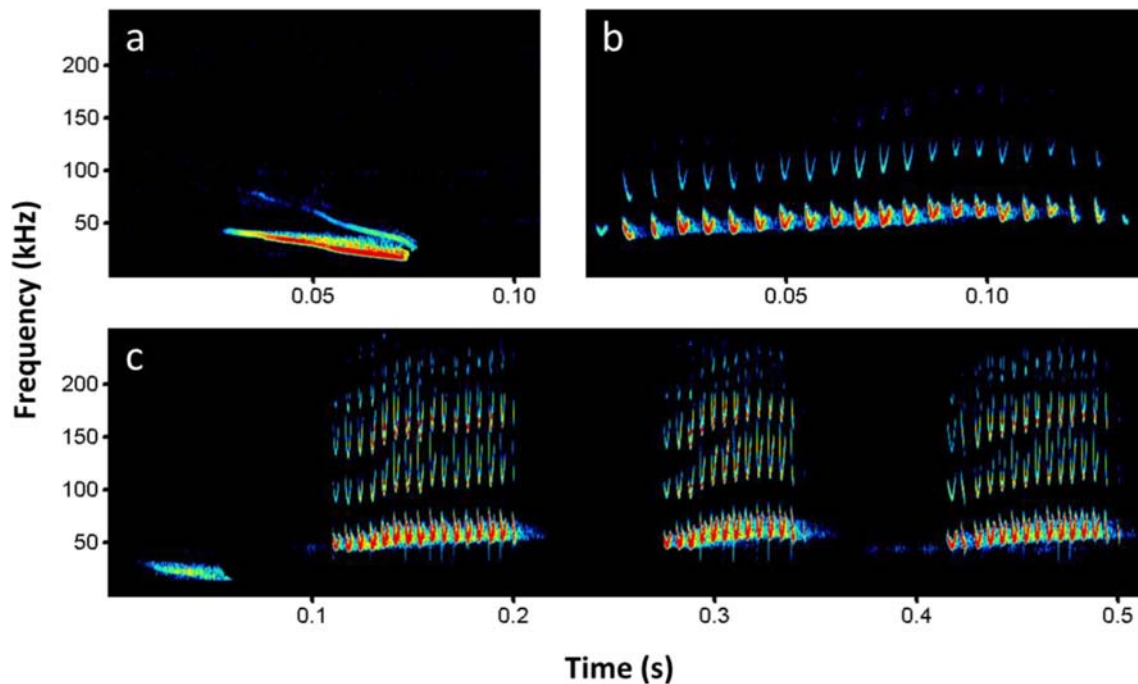
Acoustic experiments have shown that *T. tricolor* uses two types of calls to maintain contact with roosting bats and other flying group members (Chaverri et al. 2010). During flight, bats emit, in addition to echolocation calls, a simple downward frequency modulated acoustic signal termed an inquiry call (Fig. 1a). This call attracts group members, allowing flying individuals to remain in close contact. When an individual locates and occupies a suitable furled leaf, it rapidly produces a series of more complex signals, termed response calls (Fig. 1b). These calls are produced after hearing an inquiry call emitted by bats flying nearby and provide greater information capacity than inquiry calls (Gillam and Chaverri 2012). This exchange of acoustic signals results in group members rapidly locating and entering the occupied furled leaf (Chaverri et al. 2010, 2013). The inquiry and response calls have individual signatures that might allow bats to discriminate between the signals of group and non-group members; however, while bats preferentially join their own group while searching for roosts, bats inside furled leaves do not preferentially respond to group members (Gillam and Chaverri 2012; Chaverri et al. 2013). Furthermore, Spix's disc-winged bats exhibit strong individual differences in calling rates, and their vocal behavior is consistent over time (Chaverri and Gillam 2015). For instance, some bats have not produced response calls (non-vocal bats) during the time in which they have been studied, while some individuals consistently produce calls at varying rates (vocal bats). It has also been found, in both experimental settings and in the wild, that groups find roosts faster when a vocal bat is inside, and bats that are more exploratory while searching for roost-sites produce calls at higher rates (Sagot et al. 2018).

Here, we estimate variation in inquiry and response calling rates within and among groups of varying sizes of *T. tricolor* using a set of complementary analyses. We use a variance partitioning approach to estimate the proportion of variation among versus within groups for the two call types. We then proceed to use randomizations to determine if observed variation in calling rates within groups reflects the variation in the entire population. Overall, this study aims to determine if there are group differences in behaviors associated with the maintenance of group cohesion.

## Methods

### Field and acoustic methods

We collected data on contact calling production for 142 individuals, from 33 different social groups (i.e., bats using the same roost at the same time), in the Barú Biological Station in Southwestern Costa Rica, from January 2017 through January 2019. All acoustic trials were conducted during the daytime,



**Fig. 1** Spectrograms showing **a** an inquiry call and **b** a response call. **c** A bout spanning from the emission of the inquiry call ( $n = 1$ ) until the last response call ( $n = 3$ )

as this is the period during which bats are actively searching for roost sites if they become flushed from their roost sites (Chaverri et al. 2010). Each sampling day, we looked for social groups by locating furled leaves that can potentially be used as roosting sites by *T. tricolor* (Vonhof and Fenton 2004). Once a roost was located, we captured all the bats within the furled leaf and placed them into a cloth holding bag. We sexed, aged, and determined reproductive condition for all bats captured. All adults were fitted with transponders (Mini HPT8; Biomark Inc., ID, USA), injected subcutaneously in the mid-dorsal area for individual identification.

A total of 42 individuals from 11 social groups were sampled for inquiry call production within a small portable flight cage ( $3 \times 3 \times 2$  m). To record inquiry calls, we released a single bat and kept the rest of the group in a cloth bag in a cool shaded area, at least 10 m away from the cage to avoid acoustic interference during test trials. We allowed bats to fly for a maximum of 5 min while recording them; after this period, we captured them using a hand net. Inquiry calls emitted by flying bats were recorded with an Avisoft condenser microphone (CM16, Avisoft Bioacoustics, Berlin, Germany) through Avisoft's UltraSoundGate 116Hm onto a laptop computer running Avisoft-Recorder software (sampling rate 500 kHz, 16-bit resolution). We repeated this process for all group members. We performed 113 recording sessions of inquiry calling behavior. Few bats (8) were sampled only once; the remaining individuals (34) were sampled for up to five times (Supplementary Fig. S1).

For response calls, we ran trials with a total of 141 individuals from 33 social groups. During trials, we placed individual bats within a tubular structure made of either a natural leaf blade or transparent plastic; in both situations, bats remained safely attached to the interior's smooth surface. Because bats only produce response calls after an inquiry call has been emitted (Chaverri et al. 2010), we broadcasted previously recorded inquiry calls to elicit and record response calls to the bats inside the tubular structure. These inquiry calls were collected from five individuals flying within a large flight cage ( $3 \times 4 \times 9$  m) for a total of 1 min; none of these individuals were later included in our response calling trials. The aforementioned inquiry signals were used so that all test subjects were exposed to the same stimulus, an unrelated and unfamiliar set of conspecifics, as bats within social groups are generally unrelated to bats in neighboring groups (Buchalski et al. 2014). A total of 67 inquiry calls were identified in the 1-min recording; hence, while we present data on the number of response calls per minute, we are referring to the number of calls produced in response to these 67 inquiry calls. We broadcasted this set of inquiry calls through an Avisoft UltraSoundGate Player to a broadband loudspeaker (Ultrasonic Omnidirectional Dynamic Speaker Vifa, Avisoft Bioacoustics, Berlin, Germany) to single bats placed inside the tubular structure. To prevent the bats' escape, we placed a circular piece of mesh in the upper portion of the leaf; this does not affect their calling behavior as previous studies suggest that a bat's behavior is consistent among trials with and without the mesh (Sagot et al. 2018; GC unpublished data).

We placed the microphone near the entrance of the furled leaf, and we recorded response calls onto a laptop computer following the same procedure for recording inquiry calls. We broadcasted the 1-min recording of inquiry calls for 1, 5, or 10 min. We performed 234 recording sessions of response calling behavior. For the response call trials, most bats were sampled only once (63%), and 37% of individuals were sampled for up to four times (Supplementary Fig. S1). After each trial, we provided mealworms (*Tenebrio molitor*) and water to all the individuals.

We analyzed recordings for both trial types in SASLab Pro (Avisoft Bioacoustics, Berlin, Germany). It was not possible to record data blind because our study involved focal animals in the field, and the person analyzing the data and the person that collected the data on the focal animals were the same. For each inquiry call trial, we measured the number of calls produced per minute, which was estimated based on the number of calls produced during the period in which the bat was flying in the flight cage. For each response call trial, we measured the average number of response calls produced per minute or the number of calls produced in response to the 67 inquiry calls (see previous paragraph). These two different estimates of calling behavior are suitable to understand individual differences within social groups, as previous studies have found that average calling rates are highly repeatable (i.e., individual differences are maintained over time) in *T. tricolor* (repeatability for inquiry calling rates, 0.46 [95% CI = 0.25–0.68]; repeatability for response calling rates: 0.49 [0.39–0.70]; Chaverri and Gillam 2015). Also, we used different measures of calling rates as inquiry calls are emitted spontaneously by bats during flight without the need to first broadcast other signals, whereas response calls are only emitted by bats after hearing an inquiry call.

## Statistical analyses

### Coefficient of variation

To estimate differences in variation between inquiry and response calling rates among individuals, we computed the within-group coefficient of variation (i.e. intragroup variation in call emission rates) based on the maximum number of inquiry and response calls registered per individual in any trial. We performed a two-way ANOVA with coefficient of variation as the dependent variable and call type (inquiry and response), group size (ranging from 3 to 6 bats for response calls and 3 to 4 for inquiry calls), and the interaction as factors. We only used these group sizes because we had at least 3 replicates (i.e., separate groups with the same number of individuals) for them in our data set. For this analysis, we worked on a total of 9 groups and 31 individuals for inquiry calling trials and 28 groups and 119 individuals for response calling trials. We performed all analyses in R 3.0.2.

### Variance partitioning approach

To understand the relative contribution of groups and individuals on variation of inquiry and response contact calling rates, we used mixed effect models. We estimated the amount of variation associated to among-group differences, as well as differences within groups among individuals, by fitting random intercepts for individual identity ( $n = 141$  individuals) and group identity ( $n = 33$  social groups). Moreover, because multiple studies have found that age and sex can predict variation in vocal behavior (e.g., Baptista and Petrinovich 1986; Kipper and Kiefer 2010), in our models, we fitted these factors as fixed effects. Age was treated as a categorical variable, and bats were classified as either adults or subadults; the former classification is based on signs of previous reproductive activity (Racey 1988; Chaverri and Vonhof 2011).

We estimated repeatability of group calling behavior as the ratio between the variance explained by the random effect group and the total phenotypic variance (Nakagawa and Schielzeth 2010). For the response calls, we calculated the residual variance following Nakagawa and Schielzeth (2010). We assumed a Gaussian error distribution for call rate; thus, we applied a square root transformation on call rate to approximate normality in the residuals. In many instances, individuals did not emit response calls, leading to zero inflation. Thus, we analyzed probability of responding as a binary trait. We fitted a generalized linear model, where we modeled the probability of responding or not in a given recording. We fitted the models in the R package lme4 (Bates et al. 2015) to estimate a posterior distribution of the parameter estimates using the R package arm (Gelman and Hill 2006). We present the mean and 95% confidence intervals of these posterior distributions. We used log-likelihood ratio tests to determine the statistical significance of the random effects (Pinheiro and Bates 2000).

### Randomization approach

To determine if variation in call rate of inquiry and response calls within social groups reflects the overall variation in the population, we used a randomization approach. For this, we randomly permuted the number of calls produced by all the individuals per group size (ranging from 3 to 6 bats for response calls and 3 to 5 for inquiry calls; see sample size in methods section “Coefficient of variation”) and assigned them to randomly created groups of the same size. This procedure was replicated 1000 times for each group size, using the mean number of calls produced by individuals across recording sessions. We then compared the mean and standard deviation in calling rates between observed and randomly created groups.



## Data availability

The datasets analyzed during the current study are available in the Figshare repository (<https://doi.org/10.6084/m9.figshare.9916127.v2>).

## Results

### Variation in calling rates

The average number of bats found within social groups was 4.27 ( $\pm$ SD = 1.26, range = 2–7). Bats emitted an average of 5.98 inquiry calls ( $\pm$  5.38, 0–25) and an average of 18.57 response calls per minute ( $\pm$ 32.97, 0–159). We found that the overall coefficient of variation in calling rates was greater for response calls ( $CV_{\text{inquiry}}$ , 62.13;  $CV_{\text{response}}$ , 116.96). The two-way ANOVA showed a significant effect of call type on the coefficient of variation ( $F_{1/31} = 10.56$ ,  $p = 0.002$ ) but no differences in CV among-group sizes ( $F_{3/31} = 1.08$ ,  $p = 0.37$ ) nor in the interaction between group size and call type ( $F_{1/31} = 2.15$ ,  $p = 0.15$ ; Table 1). Therefore, individuals within groups produced response calls at very different rates compared with inquiry calls, with many individuals producing few or no response calls and others producing more than 100 per minute (Fig. 2). Also, we found significant differences between the proportion of vocal (i.e., produced at least one call during any trial) and non-vocal (i.e., did not vocalize in a trial) bats for both inquiry and response calling ( $\text{Chi}^2 = 17.08$ ,  $df = 1$ ,  $P < 0.001$ ); only a few (i.e., 3%) bats were non-vocal during inquiry calling trials, whereas a larger portion of individuals (i.e., 35%) did not produce response calls (Fig. 3).

### Sources of variation in contact calling

Males produced more inquiry and response calls than females (Table 2). However, age did not affect the production of inquiry or response calls. We found consistent group differences in inquiry calling rate ( $\sigma^2 = 0.20$  [95% CI = 0.08, 0.40];  $p = 0.02$ ) and response calling behavior ( $\sigma^2 = 1.57$  [0.92, 2.34];  $p < 0.01$ ). Group repeatability for

inquiry calling was 0.13 (95% CI = 0.05, 0.23) and for response calling rate was 0.15 (0.09, 0.22). We also found that within each group, individuals produced inquiry calls at different rates, and those differences were maintained over time ( $\sigma^2 = 0.48$  [0.30, 0.71];  $p < 0.01$ ). We found the same pattern in response calling behavior ( $\sigma^2 = 0.97$  [0.76, 2.34];  $p < 0.01$ ). Individual repeatability for inquiry calling was 0.31 (0.22, 0.39) and for response calling was 0.09 (0.07, 0.12). In summary, we found that 31 and 9% of the variation in inquiry and response calling rates, respectively, are associated to individual differences, while 13 and 15% of the variation in inquiry and response calling rates are explained by differences among groups. These results show that individuals within groups differ in their vocal behavior (i.e., there are individuals that consistently call more than others) and that there are among-group differences in vocalization rates (i.e., there are groups that call more than others) (Table 2).

### Randomization tests

For inquiry calls, group variation in calling rates did not differ from randomly created groups after accounting for group size ( $t_{2,02} = -0.231$ ,  $p = 0.838$ , Fig. 4). Similarly, variation in response calling rates in randomly created groups did not differ from observed variation ( $t_{3,20} = 0.752$ ,  $p = 0.503$ ). These results show that variation in inquiry and response calling rates within groups is similar to the variation observed in the entire population, yet there is a wider dispersion of within-group variation in real data, which suggests that calling rates are similar in some groups but very different in others (Fig. 4).

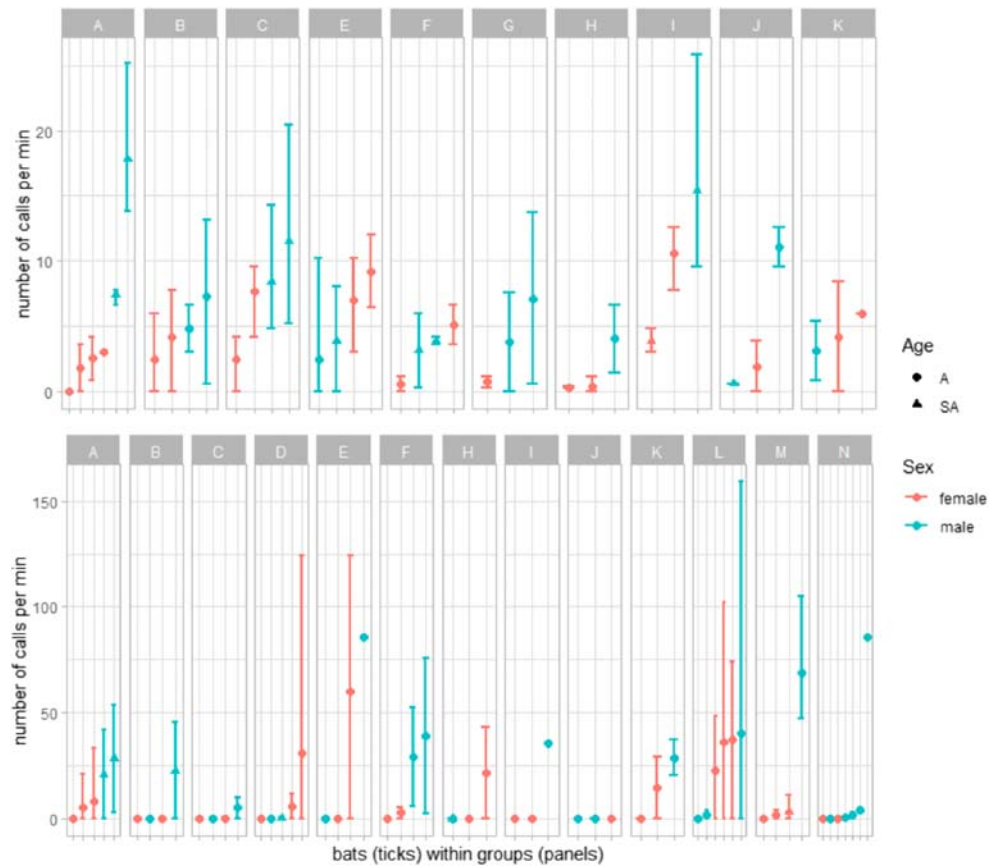
## Discussion

In this study, we show that Spix's disc-winged bats exhibit within- and among-group variation in contact calling rates; our results thus corroborate and extend previous findings by Chaverri and Gillam (2015) on variation in contact calling behavior in *T. tricolor*. More specifically, we confirm that call rates differ among individuals for inquiry and response calls, and we additionally demonstrate among-group differences for inquiry and response calls. Interestingly, our results point to different mechanisms promoting the appearance and maintenance of vocal behavior for the two types of calls studied. The results of our randomizations and the variance partitioning approach confirm both within- and among-group variation in both inquiry and response calling rates. However, the coefficient of variation suggests that there is more within-group variation in response calling rates than for inquiry calling rates. In summary, our results demonstrate a small variation in inquiry calling rates within and among groups

**Table 1** Coefficient of variation (CV) for inquiry and response calling rates within groups of varying sizes

Group size	CV inquiry	CV response
3	82.80	125.04
4	41.46	140.65
5		106.02
6		96.15

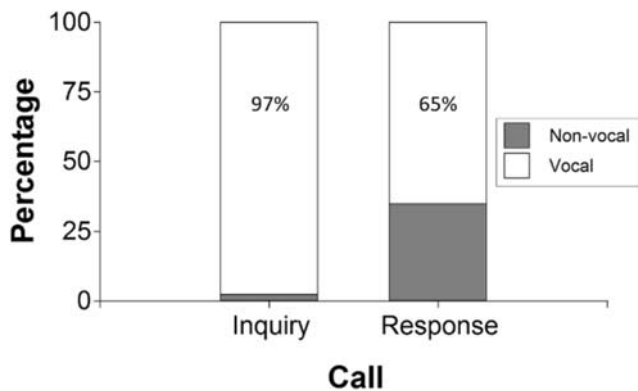
**Fig. 2** Mean number of inquiry (upper panel) and response (lower panel) calls emitted per individual according to age (A, adults; SA, subadults) and sex. Error bars indicate the minimum and maximum number of calls. We present data for individuals that we tested at least twice



and a larger variation in response calling within and among groups, both in terms of calling rates and the probability of being vocal or not.

In *T. tricolor*, groups seem to be composed of a mixture of vocal and non-vocal individuals in the context of response calling, where many bats do not produce this type of acoustic signal. Having a mix of vocal and non-vocal individuals in response calling behavior can potentially promote coordination of social groups, by facilitating informed decisions and consensus on the location of suitable roosts (Couzin et al.

2005). Efficient roost finding based on informed decisions may be achieved by following vocal individuals that disproportionately contribute to the location of these resources; in support of this, previous studies show that individuals which produce more response calls tend to be more

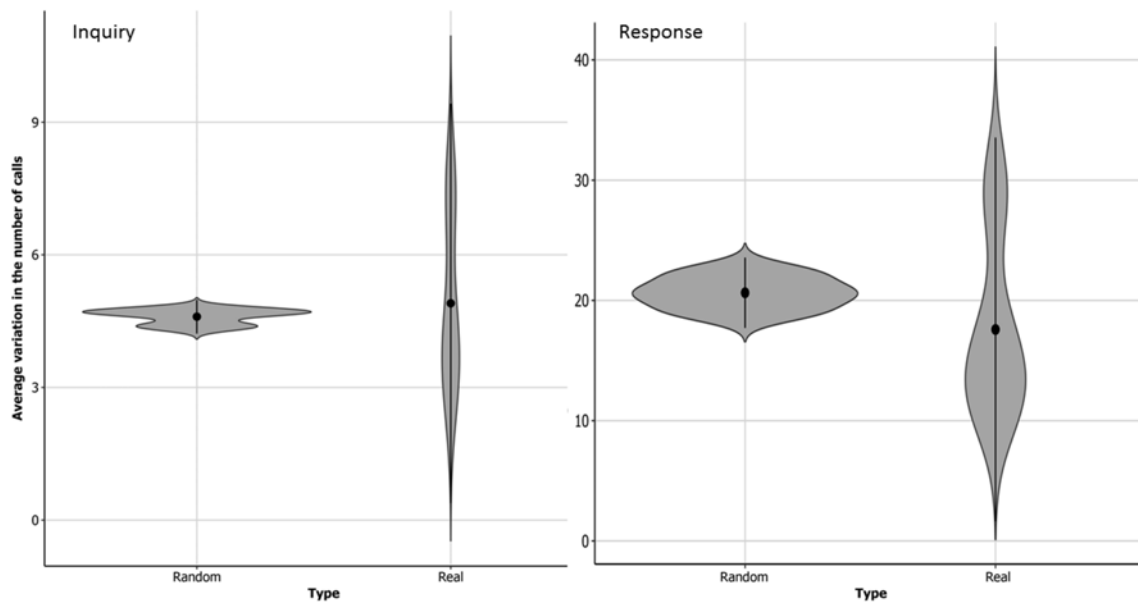


**Fig. 3** Percentage of individuals that were vocal (produced at least one call) or non-vocal (did not produce a call) for inquiry and response calling trials

**Table 2** Estimates for the mixed effect models to study the sources of variation in contact calling behavior

	Inquiry calls	Response calls
Fixed effects ( $\beta$ )		
Intercept	1.68 (1.23, 2.15)	-0.47 (-1.11, 0.18)
Age (subadult)	0.21 (-0.56, 0.96)	0.51 (-0.76, 1.76)
Sex (male)	0.70 (0.01, 1.36)	1.28 (0.56, 2.03)
Random effects ( $\sigma^2$ )		
Individual	0.48 (0.30, 0.71)	0.97 (0.76, 2.34)
Group	0.20 (0.08, 0.40)	1.57 (0.92, 2.34)
Residual	0.87 (0.66, 1.14)	-
Repeatability ( $R^2$ )		
Individual	0.31 (0.22, 0.39)	0.09 (0.07, 0.12)
Group	0.13 (0.05, 0.23)	0.15 (0.09, 0.22)

Inquiry calls were modeled assuming a Gaussian error distribution, while response calls were modeled assuming a binomial error distribution. We present the mean and the 95% confidence intervals in parenthesis



**Fig. 4** Average variation (represented by the standard deviation, SD) in the number of inquiry and response calls produced per minute in randomized and observed social groups

exploratory and locate more roosts on a daily basis (Sagot et al. 2018). However, having many vocal bats may counter-intuitively make the group less efficient because there can be conflicts in the process of decision-making (i.e., which roost to go to), especially when there is more than one suitable roost available within the group's home range. Indeed, Couzin et al. (2005) found that accuracy of group movements toward the preferred direction increased asymptotically as the proportion of informed individuals increased, but as group size became larger, the relationship was increasingly nonlinear because individuals might not reach consensus.

We also observed variation in inquiry calling rates, yet unlike response calls whereupon many individuals did not vocalize, most bats sampled in our study produced some inquiry calls during our trials. Inquiry calls are emitted by bats to maintain contact with group members during flight (Chaverri et al. 2010, 2013; Gillam and Chaverri 2012; Montero and Gillam 2015), suggesting that each bat benefits by consistently producing these signals. Many studies show that information transfer becomes less efficient as groups become more dispersed (Sueur et al. 2011). Thus, having a larger number of individuals vocalizing during group movements may decrease uncertainty and increase social coordination (Bousquet et al. 2011).

Individual differences in both inquiry and response calling rates might be associated with available energy reserves. It has been shown that call production is energetically intense for bats (e.g., Speakman et al. 1989; Ophir et al. 2010; Dechmann et al. 2013); correspondingly, Spix's disc-winged bats in low body condition/weight or in energetically demanding periods, such as during

lactation, are also less likely to produce contact calls (Chaverri and Gillam 2015; Sagot et al. 2018). Other potential sources of variation in calling rates, including differences in the ratio of males to females, juveniles to adults, or relatedness among group members, should also be addressed in further studies, particularly since a large portion of the variation in inquiry and response calling rates (56 and 76%, respectively) was unexplained by individual or group differences. Understanding the sources of variation in calling behavior will provide important insights into the mechanisms generating different vocal phenotypes within and among groups.

In this study, we found support for the existence of intra- and intergroup differences in contact calling rates in disc-winged bats. While our current results and those of previous studies (i.e., Chaverri and Gillam 2015) suggest that individuals behaved in a specific manner over multiple trials, we cannot conclude that individuals maintain their vocal behavior throughout their lifespan nor have we looked at the role of reproductive condition and resource availability in contact calling rates. In the future, we intend to more closely monitor individuals and measure short- and long-term trends in contact calling rates to explore the role of learning, individual condition, energy limitation, and relatedness in contact call variability, to elucidate the mechanisms facilitating the evolution of phenotypic variation in the context of social communication.

**Acknowledgments** We would like to thank Jose Pablo Barrantes, Silvia Chaves-Ramírez, Giada Giacomini, Andrés Hernández-Pinsón, and Abigail J. Jago, who greatly contributed to data collection. Julio Bustamante and Lilliana Rubí Jimenez provided valuable guidance during research permit application. We also thank Ronald Villalobos for

logistics support and the Centro Biológico Hacienda Barú for their continuous support of our research. Lastly, we greatly appreciate the insightful comments of Erin Gillam, Gerry Carter, and several anonymous reviewers; this manuscript has significantly improved because of them.

**Funding information** GC was funded by the University of Costa Rica, and YA-A was supported by the Research Council of Norway (SFF-III 223257/F50).

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interests.

**Ethical approval** For the handling of animals, we followed the ABS (Animal Behavior Society)/ASAB (Association for the Study of Animal Behavior) “Guidelines for the treatment of animals in behavioral research and teaching.” 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-INV-008-2017. Protocols were also approved by the University of Costa Rica’s Institutional Animal Care and Use Committee (CICUA-42-2018).

## References

- Baptista LF, Petrinovich L (1986) Song development in the white-crowned sparrow: social factors and sex differences. *Anim Behav* 34:1359–1371. [https://doi.org/10.1016/S0003-3472\(86\)80207-X](https://doi.org/10.1016/S0003-3472(86)80207-X)
- Bates D, Mächler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48. <https://doi.org/10.18637/jss.v067.i01>
- Blomberg SP, Garland T Jr, Ives AR (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57:717–745. <https://doi.org/10.1111/j.0014-3820.2003.tb00285.x>
- Bousquet CAH, Sumpter DJT, Manser MB (2011) Moving calls: a vocal mechanism underlying quorum decisions in cohesive groups. *Proc R Soc Lond B* 278:1482–1488
- Buchalski MR, Chaverri G, Vonhof MJ (2014) When genes move farther than offspring: gene flow by male gamete dispersal in the highly philopatric bat species *Thyroptera tricolor*. *Mol Ecol* 23:464–480
- Carter GG, Wilkinson GS (2015) Intranasal oxytocin increases social grooming and food sharing in the common vampire bat *Desmodus rotundus*. *Horm Behav* 75:150–153. <https://doi.org/10.1016/j.yhbeh.2015.10.006>
- Chaverri G (2010) Comparative social network analysis in a leaf-roosting bat. *Behav Ecol Sociobiol* 64:1619–1630
- Chaverri G, Gillam EH (2015) Repeatability in the contact calling system of Spix’s disc-winged bat (*Thyroptera tricolor*). *R Soc Open Sci* 2:140197. <https://doi.org/10.1098/rsos.140197>
- Chaverri G, Kunz TH (2011) All-offspring natal philopatry in a Neotropical bat. *Anim Behav* 82:1127–1133. <https://doi.org/10.1016/j.anbehav.2011.08.007>
- Chaverri G, Vonhof MJ (2011) Reproduction and growth in a neotropical insectivorous bat. *Acta Chiropterol* 13:147–155
- Chaverri G, Gillam EH, Vonhof MJ (2010) Social calls used by a leaf-roosting bat to signal location. *Biol Lett* 6:441–444. <https://doi.org/10.1098/rsbl.2009.0964>
- Chaverri G, Gillam EH, Kunz TH (2013) A call-and-response system facilitates group cohesion among disc-winged bats. *Behav Ecol* 24:481–487. <https://doi.org/10.1093/beheco/ars188>
- Couzin ID, Krause J, Franks NR, Levin SA (2005) Effective leadership and decision-making in animal groups on the move. *Nature* 433:513–516
- Dall SRX, Houston AI, McNamara JM (2004) The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol Lett* 7:734–739
- Dechmann DKN, Wikelski M, van Noordwijk HJ, Voigt CC, Voigt-Heucke SL (2013) Metabolic costs of bat echolocation in a non-foraging context support a role in communication. *Front Physiol* 4:66
- Findley JS, Wilson DE (1974) Observations on the Neotropical disk-winged bat, *Thyroptera tricolor* Spix. *J Mammal* 55:562–571. <https://doi.org/10.1126/science.95.2469.427-b>
- Friel M, Collins LM, Friel M, Kunc HP, Griffin K, Asher L, Collins LM (2016) Acoustic signalling reflects personality in a social mammal. *R Soc Open Sci* 3:160178. <https://doi.org/10.1098/rsos.160178>
- Gelman A, Hill J (2006) Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge
- Georgiev AV, Klimczuk ACE, Traficonte DM, Maestriperi D (2013) When violence pays: a cost-benefit analysis of aggressive behavior in animals and humans. *Evol Psychol* 11:678. <https://doi.org/10.1016/j.biotechadv.2011.08.021.Secreted>
- Gero S, Engelhaupt D, Rendell L, Whitehead H (2009) Who cares? Between-group variation in alloparental caregiving in sperm whales. *Behav Ecol* 20:838–843. <https://doi.org/10.1093/beheco/arp068>
- Gillam EH, Chaverri G (2012) Strong individual signatures and weaker group signatures in the contact calls of Spix’s disk-winged bat, *Thyroptera tricolor*. *Anim Behav* 83:269–276
- Groothuis TGG, Trillmich F (2011) Unfolding personalities: the importance of studying ontogeny. *Dev Psychobiol* 53:641–655. <https://doi.org/10.1002/dev.20574>
- Guillette LM, Sturdy CB (2011) Individual differences and repeatability in vocal production: stress-induced calling exposes a songbird’s personality. *Naturwissenschaften* 98:977–981. <https://doi.org/10.1007/s00114-011-0842-8>
- Kipper S, Kiefer S (2010) Age-related changes in birds’ singing styles: on fresh tunes and fading voices? *Adv Stud Behav* 41:77–118
- Kondo N, Watanabe S (2009) Contact calls: information and social function. *Jpn Psychol Res* 51:197–208. <https://doi.org/10.1111/j.1468-5884.2009.00399.x>
- Lott DF (1991) Intraspecific variation in the social systems of wild vertebrates. Cambridge University Press, Cambridge
- Montero BK, Gillam EH (2015) Behavioural strategies associated with using an ephemeral roosting resource in Spix’s disc-winged bat. *Anim Behav* 108:81–89. <https://doi.org/10.1016/j.anbehav.2015.07.014>
- Nakagawa S, Schielzeth H (2010) Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biol Rev* 85:935–956
- Ophir AG, Schrader SB, Gillooly JF (2010) Energetic cost of calling: general constraints and species-specific differences. *J Evol Biol* 23(7):1564–1569
- Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-PLUS. Springer-Verlag, Berlin
- Pruitt JN, Riechert SE (2011) How within-group behavioural variation and task efficiency enhance fitness in a social group. *Proc R Soc Lond B* 278:1209–1215. <https://doi.org/10.1098/rspb.2010.1700>
- Racey PA (1988) Reproductive assessment in bats. In: Kunz TH (ed) Ecological and behavioral methods for the study of bats. Smithsonian Institution Press, Washington, pp 31–45
- Radford AN (2004) Vocal mediation of foraging competition in the cooperatively breeding green woodhoopoe (*Phoeniculus purpureus*). *Behav Ecol Sociobiol* 56:279–285. <https://doi.org/10.1007/s00265-004-0785-6>
- Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ (2007) Integrating animal temperament within ecology and evolution. *Biol Rev* 82:291–318



- Sagot M, Schöner CR, Jago AJ, Razik I, Chaverri G (2018) The importance of group vocal behaviour in roost finding. *Anim Behav* 142:157–164
- Snowdon CT, Boe CY (2003) Social communication about unpalatable foods in tamarins (*Saguinus oedipus*). *J Comp Psychol* 117:142–148. <https://doi.org/10.1037/0735-7036.117.2.142>
- Speakman JR, Anderson ME, Racey PA (1989) The energy cost of echolocation in pipistrelle bats (*Pipistrellus pipistrellus*). *J Comp Physiol A* 165(5):679–685
- Sueur C, King AJ, Conradt L, Kerth G, Lusseau D, Mettke-Hofmann C, Schaffner CM, Williams L, Zinner D, Aureli F (2011) Collective decision-making and fission-fusion dynamics: a conceptual framework. *Oikos* 120(11):1608–1617
- Vonhof MJ, Fenton MB (2004) Roost availability and population size of *Thyroptera tricolor*, a leaf-roosting bat, in northeastern Costa Rica. *J Trop Ecol* 20:291–305
- Vonhof MJ, Whitehead H, Fenton MB (2004) Analysis of Spix's disc-winged bat association patterns and roosting home ranges reveal a novel social structure among bats. *Anim Behav* 68:507–521

**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.