



# Food-associated calls in disc-winged bats

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## Abstract

Animals that engage in social foraging can produce food-associated calls (hereafter “food calls”) that elicit two main responses in receivers: the recruitment of other individuals to a foraging site, and an increase in feeding-related behaviors in conspecifics. Spix’s disc-winged bat, *Thyroptera tricolor*, is a highly gregarious species that lives in stable social groups and relies on group call-and-response vocalizations to find ephemeral roosting sites. Because this bat also is known to feed on resources that are abundant but ephemeral – for example insect swarms – we hypothesized that it likewise emits vocalizations that serve to recruit conspecifics to a foraging site and elicit food consumption. We found that indeed, feeding bats emitted distinct vocalizations exclusively while consuming an abundant prey item, a call type that has not been previously described in the acoustic repertoire of any bat to date. We also observed that these food calls prompted responses typically associated with food calling: they increased both feeding-related behaviors and social recruitment. Specifically, we observed that the onset of the consumption of novel prey items was strongly associated with the emission of food calls but not with other types of sounds. In addition, individuals approached a speaker broadcasting food calls, especially when these calls had not been broadcast before, while other types of sounds did not consistently prompt inspection. Taken together, these results suggest that *T. tricolor* coordinates foraging behavior through the emission of food calls.

## Significance statement

Disc-winged bats (*Thyroptera tricolor*) are a highly social species known to rely on vocal communication to coordinate group cohesion as individuals locate ephemeral roosting resources on a daily basis. However, whether these bats use other types of calls to coordinate foraging activities is unknown. Here, we show that this species emits distinct vocalizations, termed “food calls”, exclusively while consuming prey, allowing us to identify a novel call type not previously documented in bats. We found that these calls increase feeding-related behaviors, since the initiation of the consumption of novel prey items was strongly associated with their emission. Furthermore, we observed that food calls stimulate social recruitment, as flying bats approached speakers broadcasting these acoustic signals. These findings expand our understanding of social foraging and vocal repertoires in elusive animals such as bats.

**Keywords** Communication · Food calls · Social foraging · Sociality · *Thyroptera tricolor*

## Introduction

Social foraging occurs when interactions among individuals, either cooperative or exploitative, involve foraging (Giraldeau and Caraco 2000). Organisms that engage in social foraging feed near other foragers. Close spatial proximity of individuals that consume similar food items, however, can result in significant costs given the depletion of available resources with increasing group size and aggressive interactions that may ensue (Johnson 2004; Grove 2012; Rose and Soole 2020). Foraging in groups can also provide many benefits, however, including an increase in the sensory ability

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to detect patchily distributed prey (Dechmann et al. 2010; Cvikel et al. 2015; Kohles et al. 2022), a reduction of individual investment in vigilance (Elgar 1989), a decrease in the per-capita risk of predation (Foster and Treherne 1981), and the recruitment of conspecifics for the defense against potential predators and intruders (Marzluf and Heinrich 1991; Wilkinson and Boughman 1998; Cunha et al. 2017). As expected given these advantages, social foraging has been observed across a wide range of taxa, including cliff swallows (*Hirundo pyrrhonota*; Brown 1988), capuchin monkeys (*Cebus apella*; di Bitetti and Janson 2001), and guppies (*Poecilia reticulata*; Day et al. 2001).

When individuals within foraging groups encounter profitable foraging patches, they often emit food-associated calls (hereafter referred to as “food calls”). The emission of food calls is known to elicit two main responses in receivers: an increase in feeding-related behaviors, and the recruitment of other individuals to the foraging site (Clay et al. 2012). In domestic fowl (*Gallus gallus*), for example, males emit food calls when discovering food, and this causes rapid recruitment of females (Marler et al. 1986; Evans and Marler 1994). Food calls have also been considered to be arousal stimuli that prompt feeding-related behaviors, such as searching (Evans and Evans 2007), pecking (Wauters and Richard-Yris 2002), and consuming provisioned food (Kitzmann and Caine 2009). Most authors agree that the presumed function of these acoustic signals is to inform conspecifics of the location of shareable food sources (Giraldeau and Caraco 2000; Clay et al. 2012). By recruiting group members to a feeding patch, individuals may gain some of the aforementioned benefits of social foraging, in addition to increasing inclusive fitness by aiding close kin locate a profitable food source (Hauser and Marler 1993; Judd and Sherman 1996), enhancing social status (Krunkelsven et al. 1996), or strengthening social bonds (Slocombe et al. 2010). The latter benefits may be particularly relevant for species that form socially stable groups (Clay et al. 2012).

A species in which we would predict both social foraging and food-associated calling (or “food calling”) is Spix’s disc-winged bat, *Thyroptera tricolor*. This species forms cohesive groups that are comprised of philopatric males and females, which are known to remain within their natal groups for several years and are thus closely related (Chaverri 2010; Chaverri and Kunz 2011; Buchalski et al. 2014). Disc-winged bats use highly ephemeral roosting resources that force individuals to locate a new site almost daily (Vonhof and Fenton 2004). Despite these constant movements, individuals are able to maintain group cohesion by exchanging acoustic signals during flight and also when bats locate a new roost site (Chaverri and Gillam 2016). When bats are flushed from a roost during the day, individuals constantly emit “inquiry calls”, which allow them to remain in close contact with other group members during flight. When one

individual locates and enters a roost, it usually starts emitting “response calls” after hearing inquiry calls; flying bats then quickly enter this roost (Chaverri et al. 2010). Both types of acoustic signals have strong individual signatures, and bats seem to discriminate among the calls of group and non-group members, preferentially joining the former (Gillam and Chaverri 2012; Chaverri et al. 2013; Araya-Salas et al. 2020). Inquiry calls are emitted by bats in flight not only during the day, but also at night (Montero and Gillam 2015), suggesting that individuals actively maintain group cohesion not just for roost finding but also while foraging.

The diet of *T. tricolor* includes various arthropods, such as jumping spiders (Aranea) and insects, particularly hemipterans within the family Fulgoridae and various species of diurnal Diptera and wingless larval Lepidoptera and Hymenoptera, among others (Whitaker and Findley 1980; Dechmann et al. 2006). Some of these insects occur in large swarms, for example termites during nuptial flights (Dechmann et al. 2006). The latter is relevant for understanding bat social interactions while foraging, given that clumped feeding resources can reduce the costs of sharing resources and can thus facilitate social foraging (Giraldeau and Caraco 2000; Clay et al. 2012). Notably, we have observed *T. tricolor* produce audible calls when feeding on mealworm larvae (*Tenebrio molitor*), which prompts consumption of provisioned food in conspecifics. Given what we know about *T. tricolor*’s social structure, its feeding habits, and the constant emission of acoustic signals in various social contexts, in this study we wanted to determine if individuals emit food calls. Specifically, we aimed to 1) describe the calls emitted while feeding and 2) test their effect on conspecifics. We predicted that, if the signals we recorded were indeed food calls, their playback would elicit consumption of provisioned food items and recruitment.

## Methods

### Field methods

During the afternoon, we searched for groups of bats in Soberanía National Park near Gamboa, Panamá. Individuals were captured within their roosts, the developing tubular leaves of plants in the order Zingiberales. Upon capture, bats were placed in cloth bags. All individuals were marked with passive integrated transponders (Mini HPT8 Pit Tag, Biomark Inc.). These markers have a unique numbering that allows individual identification of each animal with a digital reader (HPR Lite, Biomark). These tags are small (1.4×8.5 mm) and weigh just 0.09 g (ca. 2% of the bat’s body mass). All individuals were sexed and aged, and we registered the location of each group with a GPS (GPSMAP 64csx, Garmin).

## Food-call emission

In previous projects, we had heard *T. tricolor* produce audible calls when hand-fed mealworm larvae (*Tenebrio molitor*). To investigate these calls, we held bats individually and recorded them as we hand-fed them mealworms. We made all recordings using a CM16 microphone connected to an UltraSoundGate Recorder (model 116 Hme, Avisoft) connected to a laptop computer running Avisoft Recorder software with 500 kHz sampling rate, and a resolution of 16 bits. Bats were recorded 10 cm from the microphone, and the USG recorder's gain was set at medium. Each bat was recorded three times, once in the late afternoon (between 16:00–17:00 h), then again after sunset (around 18:00), and then once more after flying for ca. 15 min in a small flight cage. During each of the three recording sessions bats were fed 2–4 mealworms. After the third trial bats were released at their capture site (see below).

## Playback files

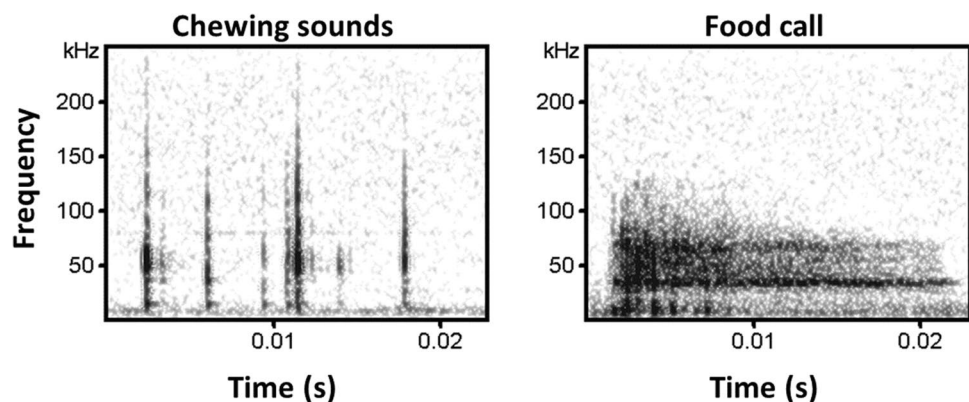
We recorded a total of 15 individuals from 8 different social groups while feeding on mealworms. From these individuals we extracted recordings of chewing sounds from 4 bats, while high quality (i.e. those with high signal-to-noise ratio) food calls were collected from 6 individuals (Fig. 1, Supplementary Table 2). These food calls ( $n=19$ ) and chewing sounds ( $n=4$ ) were then used to create sound files used in playback experiments. We created 5 different sets of files, each 60 s long: 1) food calls only, 2) food calls + chewing sounds, 3) chewing sounds only, 4) pink noise, and 5) silence. In pink noise the energy of the sound decreases with frequency, which simulates natural sounds better than white noise (Hernandez et al. 2012). All playback files were generated using a 500 kHz sampling rate and a resolution of 16 bits. During playback trials, the amplitude was set to similar levels as the original recording. We created 10 playback files for each of the first 3 sets (food calls, food calls + chewing sounds, chewing sounds)

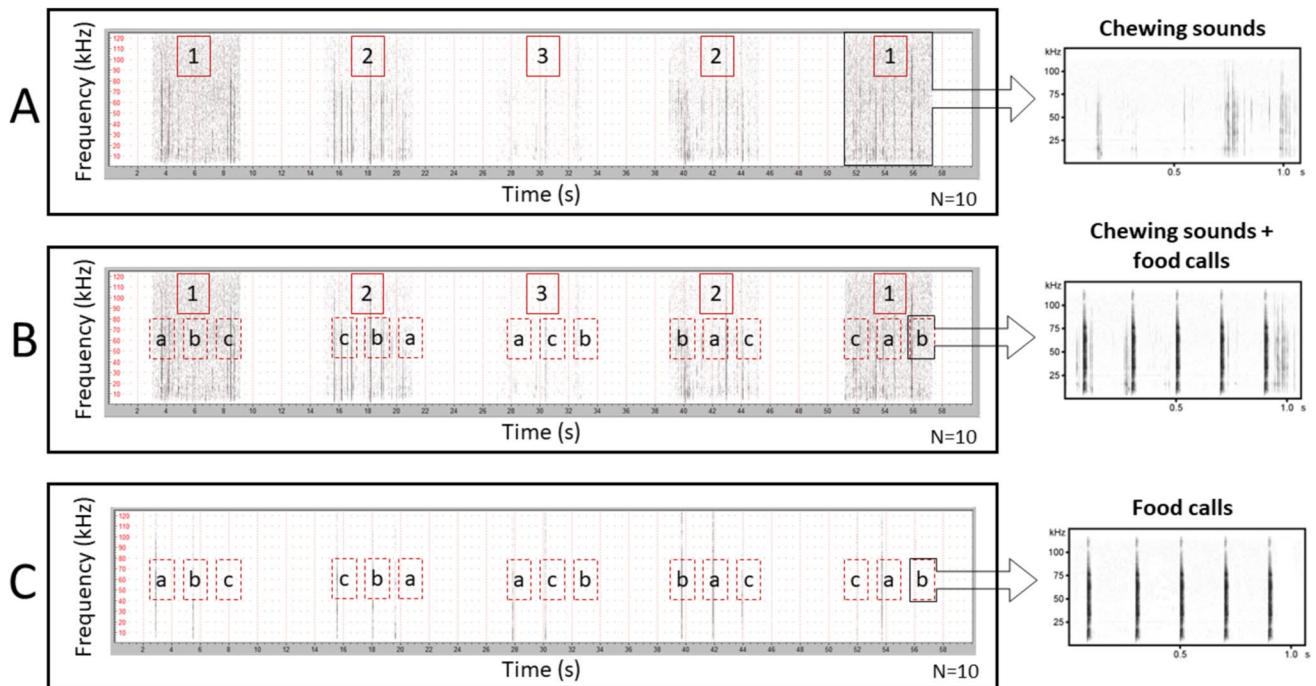
for a total of 30 files; each file contained 5 different food calls and/or 3 chewing sound bouts from different individuals. We created one pink noise file and one silence file, each 60 s long.

Playback files were generated as follows. First, we created 10 files with chewing sounds only. Each file had 5 bouts of chewing sounds, each 6 s long (Fig. 2). For each playback file we randomly selected three 6-s bouts of chewing sounds from different individuals and combined them so that in the end we would have 2 sounds repeated twice, for a total of 5 in a single playback file. Each playback file then contained first a period of silence (2.5 s), then one 6-s chewing bout, then 6 s of silence, then another 6-s chewing bout, and so on until completing 60 s (Fig. 2a). After the chewing-only playback files were created, we added the food calls to those same 10 files (Fig. 2b). Within each 6-s chewing bout we added 3 different food calls (from different individuals), each broadcast in a rapid succession of 5 calls (with a call interval of ca.  $0.20 \text{ s} \pm 0.02 \text{ s}$ , as recorded when hand-feeding bats), such that each 6-s bout had 15 food calls in total. For each of the other bouts we repeated the same process, using the same calls but in random order. Finally, we removed the chewing sounds from the files, leaving the food calls to create the food-call-only files (Fig. 2c).

Using these 32 sound files (10 chewing sounds, 10 food calls, 10 chewing sounds + food calls, 1 pink noise, 1 silence), we generated 40 playlists in Avisoft Recorder USGH software. We randomized the order in which each type of sound was emitted and the sound file that was used for chewing sounds, food calls, and chewing sounds + food calls stimuli. In addition to these 5 files, each playlist also included a 15 s silence period before the start of experiments, then a short 0.5 s sound (slow upward frequency sweep, 5 to 7 kHz) to indicate the start of playback. We also included a short 0.2 s sound (fast upward frequency sweep, 5 to 10 kHz) to indicate the transition between stimuli, and another (slow downward frequency sweep, 5 to 3 kHz) to indicate the end of the playback trial.

**Fig. 1** Spectrograms showing examples of chewing sounds (left) and food calls (right). Both sounds are produced by *Thyroptera tricolor* when eating mealworm larvae. Other examples of food calls are shown in supplementary materials (Fig. S1)





**Fig. 2** The setup of files used for playback experiments. **A** First, we generated a 60 s wav file with 5 chewing sound bouts of 6 s each from 3 different individuals (shown in different numbers). In this example, we include two chewing sound bouts from individual 1, two bouts from individual 2, and one from individual 3. **B** To the same file, A, we added 75 food calls, 15 per bout. Each call (e.g., c from the first

bout) was emitted in bouts of 5, in rapid succession (time interval  $\approx 0.20$  s). The calls were obtained from 5 different individuals (e.g., a, b, c, d, e), and when possible, we used 3 different calls per individual. **C** Finally, we removed the chewing sounds from the files used in B, keeping the 45 food calls with the same time intervals. A total of 10 files were created for each playback type (A, B, and C)

### Experiment 1: onset of eating

We investigated two possible effects of food calls on receivers: (1) a shift in the onset of eating novel prey (mealworms), and (2) a shift in exploratory or approach behavior. To test for the first effect, we captured naïve bats (adult individuals that had never been fed mealworms) and broadcast food calls while holding them with a mealworm next to their mouths. For these experiments we individually placed bats at 10 cm from a speaker (Vifa, Avisoft Bioacoustics) connected to a USG Player (UltraSoundGate Player 116H, Avisoft Bioacoustics) and under a video camera (SONY FDR-AX53) using night-vision mode. All experiments were conducted under red light. We also placed a CM16 microphone directed towards the speaker and near the bat. The microphone was connected to an UltraSoundGate Recorder (model 116 Hme, Avisoft), and both the USG Player and Recorder were connected to a laptop computer running Avisoft Recorder software. The headphone outlet of the USG recorder was connected to the microphone inlet of the video camera, which allowed us to synchronize the video with the audio that was broadcast for the following analyses. We only include results for bats that fed during our playback trials ( $n = 15$  out of 19). We defined the onset of food consumption as the time when

an individual accepted and began eating the offered mealworm. Videos were analyzed using the software BORIS (Friard and Gamba 2016) to determine which stimulus prompted the onset of food consumption.

### Experiment 2: approach and exploration

In the second experiment, we investigated whether the playback of food calls or chewing sounds would elicit exploratory or approach behaviors. None of the bats used in this experiment were included in Experiment 1. Each focal bat was placed individually in a small pyramid-shaped cage (1.5 m long  $\times$  1.5 m wide, 1.5 m from base to apex) lined with mosquito net. Inside the cage we placed a plastic container (30 cm high), covered in cloth, in one corner of the flight cage. Next to the top of the container, and outside the cage, we placed a speaker (Vifa, Avisoft Bioacoustics). Next to the speaker we placed a CM16 microphone; this allowed us to synchronize the video with the audio that was being played back, as in the previous experiment. We traced two semicircles from the corner where the speaker was placed, the first one was placed at 50 cm from the corner, and the other at 75 cm.

Each bat was fed one mealworm shortly before the onset of the first trial. Trials started at 6:30 pm, when a single bat was released within the flight cage. We started playback upon the bat's release; after the playback ended, we captured the bat using a hand net. All other bats were kept in an acoustically isolated location to avoid interference. Each bat was tested in three separate occasions, each time using a different playback list. At the end of each trial, we fed each bat a small mealworm and provided water ad libitum. At the end of the third trial, bats were fed mealworms ad libitum. Video recordings were analyzed in BORIS (Friard and Gamba 2016) to determine the amount of time bats spent in the 75 cm area. We also counted the number of occasions in which individuals entered the 50 cm region. We did not estimate the time spent within the 50 cm region given the fleeting nature of each visit.

## Data analyses

We compared the number of food calls emitted by bats based on their sex, whether they were feeding on mealworm larvae for the first time (naïve = yes) or not (after bats had eaten mealworms on a previous night the bats were no longer naïve = no), and trial number (first, second or third). Given the presence of several outliers in our results (individuals that emitted a large number of calls; see results), we fitted a robust linear mixed-effects model using the function `rlmer` in the R package `robustlmm` (Koller 2016). Traditional estimation methods can be highly sensitive to outliers, leading to biased parameter estimates and inaccurate inference. Robust estimation techniques are designed to mitigate the influence of outliers by reducing their impact on the parameter estimates (Yu and Yao 2017). The model we implemented included the three explanatory variables sex, naïve, and trial number, and their interactions, and bat id as the random effect. To assess model significance, we generated a null model that did not include any of the predictors and compared them using the function `modelsummary` in the R package `modelsummary` (Arel-Bundock 2022). If the model that included all predictors had a lower root mean squared error (RMSE) and higher  $R^2$  values than the null model, we interpreted this as there being an effect. To determine which predictors may influence the number of calls emitted, we used the R package `marginalEffects` (Arel-Bundock et al. 2024) to generate average (marginal) estimates using the function `avg_comparisons` and plotted them using the function `plot_predictions`.

To extract spectral and temporal parameters of food calls, we used SASlab Pro (Avisoft Bioacoustics). We retained only the best quality signals, i.e. those with high signal-to-noise ratios. We manually labelled the calls and then measured peak, minimum and maximum frequencies, in addition to entropy, for the following positions: center of element,

maximum amplitude of element, and mean spectrum of entire element. Spectrograms were analyzed using an FFT length of 512 kHz (bandwidth resolution = 977 Hz), with an overlap of 93.75% (temporal resolution = 0.06 ms).

We analyzed our results of the first experiment by first comparing the number of times a given stimulus prompted the onset of eating during that trial. We first used a generalized linear model (function “`glm`” in the R package `lme4`; Bates et al. 2015) with a binomial distribution, with onset of eating as our response variable, where 1 was assigned to a stimulus in which feeding occurred for the first time, while 0's represented either no feeding or feeding did not occur then for the first time. As explanatory variables we used stimulus type (silence, pink noise, chewing sounds, food calls, chewing sounds + food calls) and trial number (first, second, third, fourth or fifth) in an interaction model. For post-hoc tests we used the function “`lsmeans`” in the R package `lsmeans` (Lenth 2016). For the latter we transformed data to percentage, and values of 0 (a stimulus in which the onset of eating never occurred) were increased to 1 (out of 100) to avoid errors in the estimate. We present results based on estimates of the R function “`pairs`”, which generates pair-wise comparisons after `lsmeans`.

In our second experiment we tested whether the amount of time spent within the 75 cm region varied based on stimulus broadcast. For this analysis, we used time as the response variable and various explanatory variables, including stimulus, stimulus order (1 through 5), and trial number (first, second or third trial per individual). To address the possibility of a lingering effect from the previous stimulus on the tendency of bats to approach the speaker, we also included as a potential explanatory variable the stimulus broadcast immediately prior to the stimulus under analysis. For example, when analyzing the effect of pink noise on time spent in the 75 cm region, we determined whether food calls had been played back before this pink noise stimulus. We named these variables “pre-calls” and “pre-chew”. Because of the number of potential explanatory variables ( $n=5$ ), we created a global model that could include additive effects of all predictor variables or up to 4-way interaction effects using the function `lmer` (model 1) in the R package `lme4`, with bat identity as the random variable. We then used the `dredge` function of the R package `MuMIn` to generate a table of models that include every possible combination of predictor variables. We compared models using the delta AIC, and kept the best models based on delta values  $< 5$ . For that subset of models, we applied the function `sw` in `MuMIn`, which provides an estimate of the relative importance of each predictor variable given the number of times that variable was included in the best models. To interpret the relationship between explanatory and response variables, we created a model in which we kept only the explanatory variables, and their interactions, that were present in at least 50% of

the best models (i.e., those with  $\Delta AIC < 5$ ), based on their relative importance. With this latter model, we determined which predictors significantly explained our response variable (i.e., time spent within the 75 cm region) based on comparison of regression coefficients using the function `plot_model` in the R package `sjPlot` (Lüdtke 2024).

Our approach for testing whether stimulus type affected the number of visits to the 50 cm region did not follow the latter one, given that we encountered problems with model convergence when generating 2, 3 or 4-way interaction effects. However, since time spent in the 75 cm region was best explained by an additive, not an interaction, model (see Results), we feel confident that excluding interaction effects to understand how our various predictors explain time spent in the 50 cm region is appropriate. To confirm that the number of visits to the 50 cm region was explained by a similar model as time spent in the 75 cm region, we generated 4 models with the function `glmer` (`family = poisson`) in the R package `lme4`, with bat identity as the random variable. The first model was a null model that excluded all predictors, the second was a model that excluded our predictor of interest (stimulus), the third model included all predictors (stimulus, trial, stimulus order, pre-calls and pre-chew), and the fourth one was identical to the one used to explain time spent in the 75 cm region (predictors: stimulus, trial, stimulus order and pre-calls). These models were compared with the function `anova`. We retained the model with the lowest Akaike Information Criterion (AIC) value, as long as it was significantly different from the first (null) and the second models. With the best model we determined which predictors significantly explained the number of visits to the 50 cm region based on comparison of regression coefficients using the function `plot_model`.

## Ethical notes

We captured Spix's disc-winged bats in the wild by searching furred leaves of various plant species in the order Zingiberales. To avoid disturbing bats while in their roosts, we approached the leaf very quietly and searched for bats with an extendable mirror; if the presence of bats was confirmed, we placed a transparent plastic bag at the opening of the leaf and carefully pinched the leaf at the bottom slowly moving towards the top, which caused the bats to crawl to the opening and into the plastic bag. Once the bats were in the plastic bag, they were transferred into cloth bags for transportation.

While performing flight cage experiments, we kept each social group together in the same bag to avoid social disturbance. Keeping individuals together like this does not result in conflict; it mimics natural social conditions and appears to decrease stress. Moreover, we kept bags in a ventilated area with no direct exposure to sunlight. If bats were participating

in individual trials, after the trial we returned them to the same bags.

At the end of the experiments, we provided mealworm larvae (*Tenebrio molitor*) and water to all individuals. We released the entire social group by placing all the individuals inside the same or a nearby leaf where they were found roosting earlier in the day. We have used this technique for returning bats to their habitat for over a decade, and individuals remain calm and in their natural roosting positions immediately after their return.

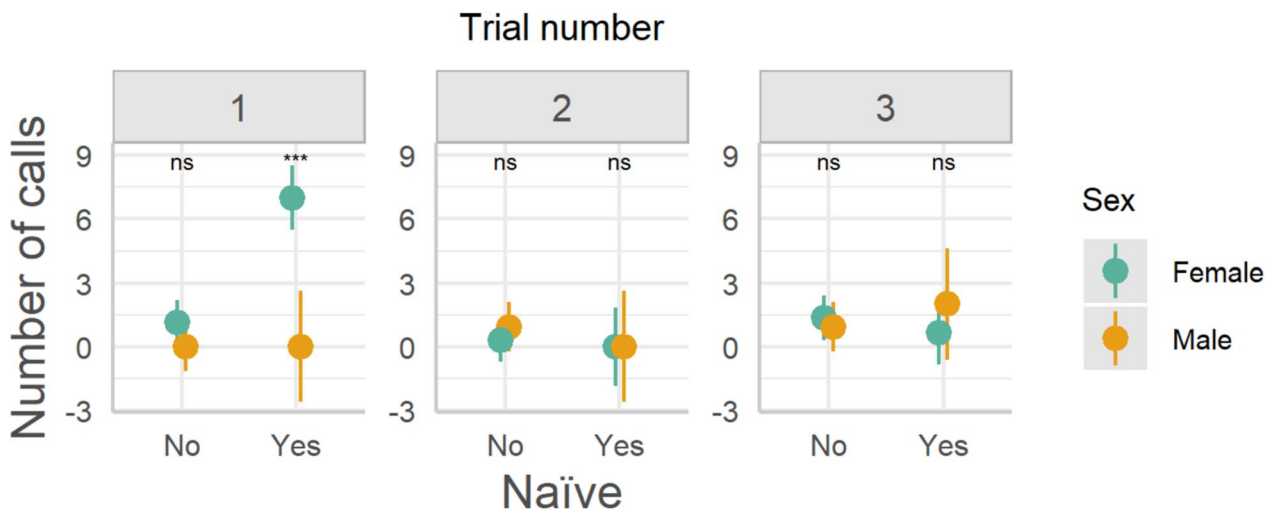
To minimize observer bias, blinded methods were used when all behavioral data were recorded and analyzed.

## Results

We recorded a total of 15 bats from 8 different social groups as they were feeding on mealworms, to determine if they produced food calls. All individuals produced vocalizations except two, and bats typically emitted only a few calls per bout (Supplementary Table S1). The results of the robust linear mixed-effects model show that the model that included all predictors and their interactions was better than the null model (model with all predictors:  $R^2$  marginal and conditional = 0.62, RMSE = 9.26; null model:  $R^2$  marginal and conditional = 0, RMSE = 10.19). Naïve females emitted significantly more calls in their first trial compared to non-naïve females and compared to males (naïve or not; Fig. 3; Supplementary Table S2).

From the recordings of these vocal individuals, we were able to obtain 19 calls of sufficiently good quality for analysis (i.e., those with high signal-to-noise ratios). Mean duration of calls was 0.017 s (standard deviation:  $\pm 0.005$ ), with a mean peak frequency of 46 kHz ( $\pm 15.47$ ) and a mean amplitude of -20.25 dB ( $\pm 4.63$ ) at the maximum amplitude of the call (Supplementary Table S3). Minimum and maximum peak frequencies and amplitudes ranged between 10 and 72 kHz and -28 and -9 dB, respectively. Given these estimates of amplitude, and the specifications provided by the manufacturer for the equipment used to record calls, we estimate that food calls are emitted at approximately 64.75 dB SPL at 10 cm (range 57–76 dB SPL; R. Specht, personal communication). The average entropy of calls, at the call's maximum amplitude, was 0.43 ( $\pm 0.07$ ). For further details see Supplementary Table S3.

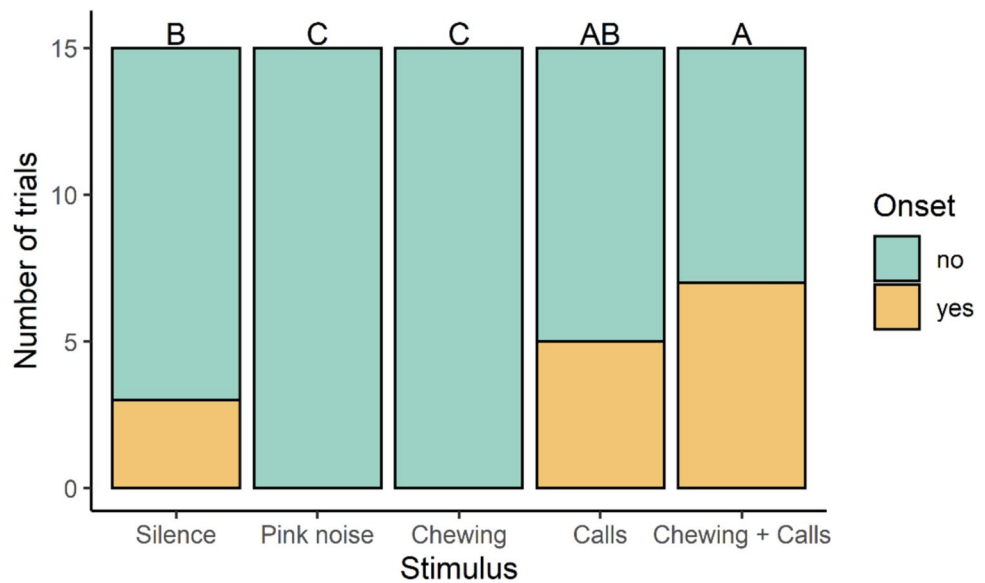
The results of the generalized linear model, where we tested the effect of stimulus and trial number on the onset of eating (Experiment 1), show that only stimulus had a significant effect ( $p$ -values: stimulus  $< 0.001$ , trial = 0.07, stimulus\*trial = 0.96). We found that the stimulus that prompted the onset of eating was most often the food calls, either alone or in combination with chewing sounds (Fig. 4, Supplementary Table S4).



**Fig. 3** Predicted number of food calls emitted by hand-held bats being offered mealworms, based on results of the robust linear mixed-effects model. Results are divided by trial number, sex and whether bats were feeding on mealworms for the first time (naïve=yes) or

not (naïve=no). Error bars represent the standard error. We show the results of the contrasts between the predicted number of calls emitted by females and males for each combination of trial and naïve ( $p$ -value > 0.05: ns,  $p$ -value < 0.001: \*\*\*)

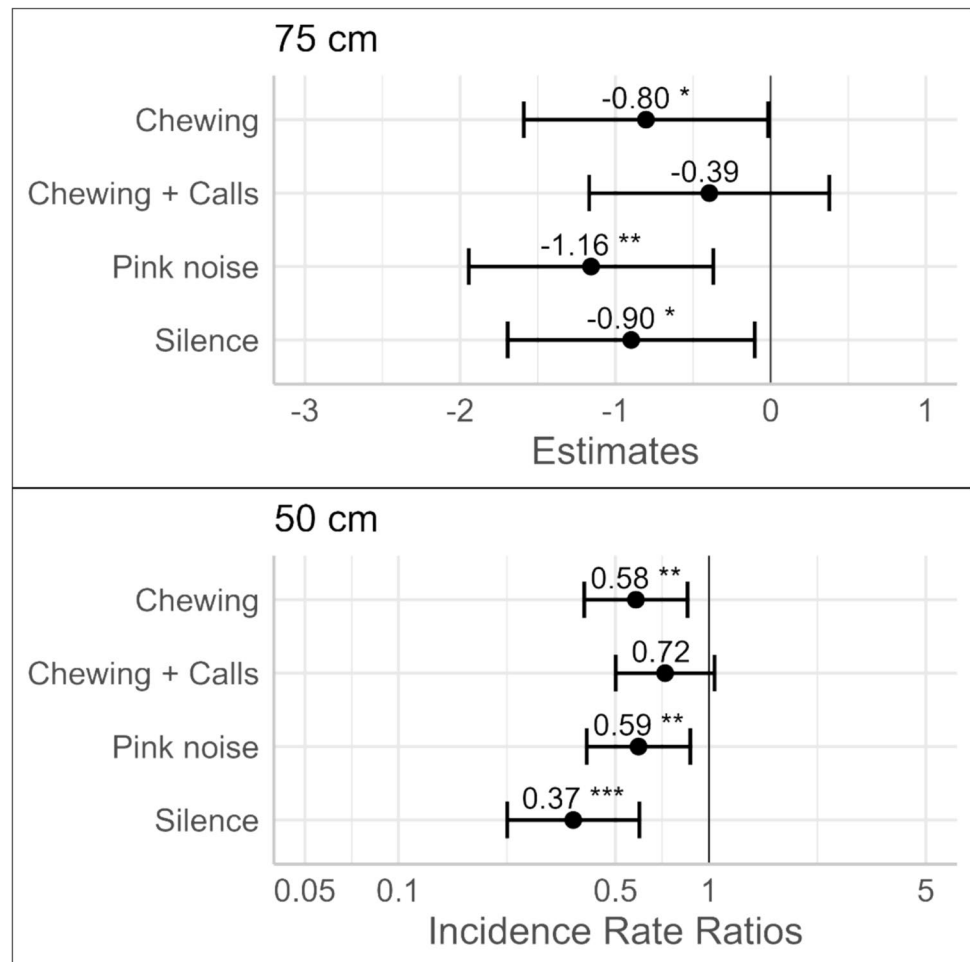
**Fig. 4** Number of trials in which a given stimulus prompted the onset of feeding. Different letters above bars denote significant differences among stimuli



The results of model selection to determine how our explanatory variables influenced time spent near the 75 cm area around the speaker show that the best models (16 models with delta values < 5) primarily include the variables stimulus ( $n=9$ ), trial number ( $n=16$ ), pre-calls ( $n=9$ ) and stimulus order ( $n=16$ ) as additive effects (Supplementary Table S5). The results of the linear model show that bats spent more time near the speaker during playback of food calls compared to most stimuli except food calls in combination with chewing sounds (Fig. 5). Bats also spent increasingly more time near the speaker with each new trial (Supplementary Fig. S2), and they also

spent more time near the speaker during the playback of the fourth stimulus. The variable pre-calls did not have a significant effect on the time bats spent near the speaker. We found the same trends when analyzing the data for the number of times bats entered the 50 cm region (Supplementary Table S6): food calls, either by themselves or in combination with chewing sounds, prompted the highest number of approaches (Fig. 5) compared to other stimuli. Trial and stimulus order, but not pre-calls, also influenced the number of times bats visited the 50 cm region (Supplementary Fig. S2).

**Fig. 5** Coefficients of the effect of stimulus type on social recruitment. Upper panel represents the results of the model based on the time bats spent in the 75 cm region; lower panel shows the results of the model representing the number of times bats visited the 50 cm region. Each stimulus shown is compared to the reference level, which in this case is our stimulus of interest, food calls. Dots represent the mean and error bars the 95% confidence intervals. Numbers on top show the mean value of the coefficient and  $p$ -values ( $p < 0.05$ : \*,  $p < 0.01$ : \*\*,  $p < 0.001$ : \*\*\*). Vertical line indicates no effect



## Discussion

In this study we hypothesized that if the acoustic signals emitted by *T. tricolor* while feeding are indeed food calls, then their playback should elicit the consumption of provisioned food items in attending bats and the recruitment of conspecifics during flight. Our recordings of feeding bats show that many individuals emitted distinct vocalizations while consuming an abundant prey item. This type of call has not been previously described in disc-winged bats (Montero and Gillam 2015; Chaverri and Gillam 2016; Chaverri et al. 2018, 2021), and is markedly different from calls emitted by this species in situations of distress (Chaves-Ramírez et al. 2023). We also observed that vocalizations prompted two responses in receivers which are typically associated with food calling (Clay et al. 2012), namely increasing feeding-related behaviors and social recruitment. Specifically, we observed that the onset of consumption of novel prey items was strongly associated with the emission of food calls but not with other types of sounds. Individuals also approached a speaker broadcasting food calls when flying in a tent, especially when calls had not been played-back before, while

other types of sounds did not consistently prompt inspection. Taken together, these results strongly suggest that *T. tricolor* emits food calls.

Food calling has been observed in several social species, including fowl (*G. gallus*), ravens (*Corvus corvax*), chimpanzees (*Pan troglodytes*), and white-faced capuchin monkeys (*Cebus capucinus*), among others (Clay et al. 2012). In these species, authors reported that calls are emitted exclusively in a feeding context, prompt social recruitment, may change with food characteristics, and can encode information about the characteristics of food, such as quality and quantity (Marler et al. 1986; Hauser and Wrangham 1987; Heinrich and Marzluff 1991; Hauser et al. 1993; Bugnyar et al. 2001; Gros-Louis 2004a, b, 2006; Slocombe and Zuberbühler 2006; Boinski and Campbell 2010). In bats, only one study to date has reported vocalizations that may be considered food calls. Wilkinson and Boughman (1998) found that greater spear-nosed bats (*Phyllostomus hastatus*) emit “screech” calls while traveling to, and at, feeding sites, and primarily if individuals travel in groups. The emission of these calls prompts recruitment of conspecifics, both at feeding sites and also at the entrance of roosts (Wilkinson



and Boughman 1998), and could also help recruit conspecifics when mobbing predators (Knörnschild and Tschapka 2012). Therefore, the production of “screech” calls in this species, while strongly associated with foraging activities, is not considered to be exclusively associated with a feeding context (Clay et al. 2012). In contrast, the evidence we collected, together with results of previous studies (Montero and Gillam 2015; Chaverri and Gillam 2016; Chaverri et al. 2018, 2021; Chaves-Ramírez et al. 2023), shows that food calls in *T. tricolor* are emitted exclusively in a feeding context, and that calls prompt social recruitment. Future studies are needed to confirm that *T. tricolor* emit food calls while freely foraging, particularly in swarm-feeding situations, and to test whether these calls are modulated by, and may encode information about, specific food characteristics.

Food calling has only been observed in species that engage in social foraging. Social foraging is more likely to occur when food is abundant and clumped (Giraldeau and Caraco 2000; Clay et al. 2012). In bats, social foraging is also associated with resource ephemerality (Kohles et al. 2022) and has been observed in species known to have strong social bonds (McCracken and Bradbury 1981; Egert-Berg et al. 2018; Ripperger and Carter 2021). *Thyroptera tricolor* lives in social groups with strong cohesion and high relatedness (Chaverri 2010; Buchalski et al. 2014), and individuals often consume prey items found in large, yet ephemeral, insect swarms (Dechmann et al. 2006). Therefore, given its food calling and combination of habits and traits, *T. tricolor* is an excellent candidate for social foraging (Kohles et al. 2022). To provide further evidence of social foraging we not only need to track group members at night (e.g., Egert-Berg et al. 2018), but also explore in greater detail the diversity of prey items in *T. tricolor*'s diet using DNA metabarcoding (Sousa et al. 2019) to determine if food sources are typically found in abundant and clumped patches. Diet overlap within groups, and differences among groups, would provide further confirmation of social foraging (van der Post and Hogeweg 2006).

While many bats in our study produced food calls, we also found large inter-individual differences in the emission of these vocalizations. Specifically, we found that naïve females produced a greater number of food calls than males in their first trial. Individuals could be emitting a larger number of food calls in the first trial if food calling reflects a signaler's level of arousal in response to a feeding event (Caine et al. 1995). Females could be vocalizing more than males to help close kin, especially their younger pups, locate a profitable food source. *Thyroptera tricolor* lives in matrilineal societies, exhibiting high levels of relatedness, particularly among females (Buchalski et al. 2014). Similarly, rhesus macaques (*Macaca mulatta*) live in matrilineal societies (Chepko-Sade and Sade 1979), and females are known to produce more food calls than

males (Hauser and Marler 1993). Female *T. tricolor* might similarly produce a larger number of food calls than males if these vocalizations provide their close kin with information about food availability and quality, especially if mothers and pups are together at foraging sites, as has been seen in other species of bats (Patriquin and Ratcliffe 2023). If so, this could explain why food calls did not consistently prompt social recruitment, as this could primarily function during mother–pup interactions, which we did not test in our study. To understand the causes and consequences of the variation in the emission of food-associated calls within and among individuals, future studies could focus on testing call emission during different seasons (Hernández-Pinsón et al. 2021), audiences (Dahlin et al. 2005), and type of food (Hauser et al. 1993; Gros-Louis 2004b).

In conclusion, we found strong evidence that *T. tricolor* emits food calls. However, the particular benefits that disc-winged bats may derive from emitting these signals, which may include better detection of patchily distributed prey, the recruitment of conspecifics for the defense against conspecific intruders, and enhancement of social status, among others, remain to be tested. While the primary advantage of food calling is presumably to convey the location of food sources that can be shared among conspecifics, calling to recruit conspecifics can also protect the emitter from potential intruders (Giraldeau and Caraco 2000; Clay et al. 2012). Given that many species of bats are social (McCracken and Wilkinson 2000; Kerth 2008), that their food sources are often abundant and clumped (Kohles et al. 2022), and that social recruitment could potentially aid in the defense of these resources (Chaverri et al. 2018), it is puzzling that no other studies have provided evidence of food calling in this large mammalian order. Some of the main problems precluding further advances in this topic probably relate to the nocturnal habits of many species, their high mobility, and their small size. Direct observations of feeding behaviors and associated acoustic signals are often more feasible in diurnal species. Fowl and rhesus macaques, for example, can be followed on foot by researchers, enabling the direct pairing of observations between feeding and the emission of calls. Some species of bats can be fitted with GPS-microphone devices that provide great spatial resolution and the ability to record the vocalizations emitted throughout an individual's foraging activities. Unfortunately, these devices are still too heavy for most species of bats, including *T. tricolor* (which weigh approximately 4 g), precluding us from recording the calls emitted by individuals while foraging freely in nature. Further efforts to decrease the size of GPS-microphone tags, coupled with semi-captive observations and experiments, are needed to better understand food calls, the context in which they are produced, and the information they convey in *T. tricolor* and other species of bats.

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**Author contributions** Conceptualization: GC, RAP; Data curation: GC; Formal analysis: GC; Funding acquisition: GC, RAP; Investigation: GC, RAP; Methodology: GC, RAP; Project administration: GC; Resources: GC, RAP; Visualization: GC; Writing—original draft: GC; Writing—review and editing: GC, RAP.

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**Data availability** A full data set and the code can be found at the GitHub platform: <https://github.com/morceglo/Food-calling-Thyroptera.git>.

## Declarations

**Ethics approval** All sampling and experimental protocols followed guidelines approved by the American Society of Mammalogists for capture, handling and care of mammals (Sikes 2016) and the ASAB/ABS's "Guidelines for the Treatment of Animals in Behavioural Research and Teaching" (2012). This study was conducted in accordance with the standards of the Government of Panamá (Ministerio de Ambiente permit number: ARG-278–2022). Experimental protocols were also approved by the Smithsonian Tropical Research Institute's Animal Care and Use Committee (IACUC protocol number: SI-23001).

**Conflict of interests** The authors declare no competing or financial interests.

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