Begging calls provide social cues for prospecting conspecifics in the wild Zebra Finch (*Taeniopygia guttata*)

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ABSTRACT

Social information can spread fast and help animals adapt in fluctuating environments. Prospecting on the breeding sites of others, a widespread behavior, can help to maximize reproduction by, for instance, settling in the same area as other successful breeders. Previous studies have shown that successful broods have the highest number of prospectors and that they are visited most when offspring in nesting sites are already old, making the information more reliable. In this field study, we experimentally tested how prospectors are attracted to successful nest sites. We presented wild Zebra Finches (*Taeniopygia guttata*) with different visual or acoustic cues in nest boxes, simulating the presence of small or large clutches or broods. More Zebra Finches visited experimental nests that were associated with playback recordings of begging calls of large broods (7 chicks) as opposed to begging calls of small broods (3 chicks) and controls (white noise and silence). On the other hand, visual cues (nests with different numbers of eggs or rocks), representing nests at early stages, did not influence either the probability of visits, nor number or duration of visits. We present the first evidence that begging calls of chicks in the nest, a signal intended for kin communication, can also provide social information to unrelated prospecting conspecifics. This information could potentially be used for a fast initial assessment of the quality of a breeding site.

Keywords: acoustic cues, honest signal, inadvertent social information, information use, public information, *Taeniopygia guttata*

Bettelrufe von Nestlingen dienen als soziale Information für prospektierende Artgenossen in freilebenden Zebrafinken (*Taeniopygia guttata*)

ABSTRAKT

Durch soziales Lernen können sich Informationen zwischen Individuen schnell verbreiten. Das hilft Tieren dabei sich in einer ständig ändernden Umwelt anzupassen. Mögliche Brutplätze vorab zu „prospektieren" ist eine weit verbreitete Verhaltensweise, die dabei helfen kann einen qualitativ hochwertigen Standort zu identifizieren, an dem andere Individuen bereits erfolgreich brüten. Dadurch kann der eigene Fortpflanzungserfolg gesteigert werden. Studien haben bereits gezeigt, dass besonders erfolgreiche Nester auch besonders häufig prospektiert (d.h. besucht) werden und das vermehrt zu einem Zeitpunkt, an dem die Nachkommen im Nest bereits älter sind, was vermutlich eine verlässlichere Informationsquelle darstellt. Wir haben in einem Freilandversuch getestet welche Hinweise prospektierende Individuen nutzen, um bestimmte Nester gezielt zu besuchen. Dazu wurden freilebenden Zebrafinken (*Taeniopygia guttata*) verschiedene visuelle und akustische Reize in Nistkästen präsentiert, um jeweils die Präsenz von kleinen oder großen Gelegen oder Bruten zu simulieren. Mehr Zebrafinken besuchten experimentelle Nistkästen, in denen ein Playback mit Bettelrufen von großen Bruten (7 Nestlinge) abgespielt wurden, als solche mit den Bettelrufen kleiner Bruten (3 Nestlinge) oder einer Kontrolle (weißes Rauschen oder kein Ton). Die visuellen Reize (Nester mit unterschiedlicher Anzahl Eier oder Kieselsteine), die Nester in einem früheren Stadium repräsentierten, hatten hingegen keinen Einfluss auf die Wahrscheinlichkeit von Besuchern. Mit diesem Versuch konnten wir zum ersten Mal zeigen, dass die Bettelrufe von Nestlingen – ein Signal das normalerweise zur Kommunikation mit Verwandten genutzt wird – also sozialer Stimuli für nicht verwandte, prospektierende Artgenossen dienen kann. Diese Information könnte genutzt werden, um schnell die Qualität von Brutstätten zu evaluieren.

Schlagwörter: Bettelrufe, ehrliche Signale, prospektieren, soziales Lernen, soziale Information, *Taeniopygia guttata*, Zebrafinken

INTRODUCTION

The quality of the environment can be difficult for an individual to assess and, therefore, continuously gathering information from conspecifics is a good way to stay up-to-date with breeding conditions in an ever-changing environment. The information that individuals can gain in this way will ultimately guide their decision-making (e.g., Danchin et al. 2004). Reducing uncertainty through this social information increases evolutionary fitness (e.g., McNamara and Dall 2010). Individuals can collect personal information by directly sampling the environment (e.g., Danchin et al. 2004, Dall et al. 2005), but using social information should be favored if personal information is costly or not available (e.g., Laland 2004). Social information can be derived from observing the interactions of others with the environment, comprising their actions, their decisions as well as their performance (Danchin et al. 2004). Social information use has been identified in many behaviors of adaptive significance, such as mate choice (e.g., White 2004, Drullion and Dubois 2011), foraging (e.g., Templeton and Giraldeau 1995, Coolen et al. 2005), depredation avoidance (e.g., Ward et al. 2011) and habitat and breeding-site selection (e.g., Doligez et al. 2002, Loukola et al. 2012, Kelly et al. 2018). While experimental evidence suggests that social information can, in certain scenarios, even lead to maladaptive behavior (Laland and Williams 1998), it can also help animals to adjust more rapidly to changing conditions (e.g., Danchin et al. 2004, Jaakkonen et al. 2013).

When discussing the costs and benefits of social information, the argument is often made that socially acquired knowledge might be less reliable and more prone to deception (e.g., Koops 2004, Kendal et al. 2005). However, the same argument should not apply to social information derived from inadvertently produced signals. Such signals, not produced with the intention to serve as social cues, can be seen as reliable, because they have to maintain the value for the producer (e.g., Danchin et al. 2004). Begging calls of nestlings, for example, are honest indicators of offspring needs and used in both parent–offspring (e.g., Godfray 1995, Glassey and Forbes 2002) and also sib–sib communication (e.g., Roulin et al. 2000, Dreiss et al. 2010). Eavesdropping predators can use these cues as inadvertent social information to locate nests (e.g., McDonald et al. 2009, Haff and Magrath 2011). While begging calls of chicks serve as signals for the parents and siblings and (inadvertently) also as cues for heterospecific predators, it is unknown whether begging calls can also function as cues for non-kin conspecifics. What we know about the use of conspecific vocalizations as social information for breeders stems from studies focusing on the period after fledging (e.g., Waas et al. 2005, Betts et al. 2008, Kelly and Schmidt 2017).

A widespread strategy to obtain information on the reproductive performance of conspecifics (or even heterospecifics, reviewed in Seppänen et al. 2007) is to visit their breeding sites (e.g., reviewed in Reed et al. 1999). Such prospecting at the nests of others can help to assess potential breeding sites in advance (e.g., Doligez et al. 2004, Pärt et al. 2011) or to decide how much to invest into one's own reproduction (e.g., Forsman et al. 2008, 2011). In the Collared Flycatcher (*Ficedula albicollis*), for example, it was experimentally shown that local reproductive success predicts both immigration and emigration rates of conspecifics in forest patches (Doligez et al. 2002). If it is the aim of prospectors to find areas of high quality for their own breeding, we can expect that prospectors might visit successful nests at higher rates, spend more time there and choose the time where information is most reliable (Doligez et al. 2004). To date, several researchers found support for these predictions in both experimental and correlational studies. Several studies show evidence for higher prospecting activity at nests with larger broods, for example, in Common Goldeneyes (*Bucephala clangula*; Zicus and Hennes 1989) and Pied Flycatchers (*F. hypoleuca*; Schuett et al. 2017). Other studies found that prospecting activity was positively correlated with parental feeding rate in Collared Flycatchers (*F. albicollis*; Pärt and Doligez 2003, Doligez et al. 2004; but see in *F. hypoleuca*; Schuett et al. 2017), suggesting that prospectors can preselect to visit successful nests preferentially, by cueing on the provisioning activity of parents (which in turn is associated with the intensity of nestling begging calls [e.g., Ottosson et al. 1997, Leonard and Horn 2001]). Regarding the timing of prospecting visits, the highest frequency was observed at late stages of chick rearing in Black-legged Kittiwakes (*Rissa tridactyla*), presumably because this is the time when nests provide the most reliable information on local reproductive success (e.g., Boulinier et al. 1996). Further evidence for this was found in a brood size reduction experiment on Spotless Starlings (*Sturnus unicolor*), which revealed that the positive correlation between brood size and number of visiting prospectors was most pronounced at the latest stage of chick rearing (Parejo et al. 2008), suggesting that nests with older chicks provide the most reliable information on reproductive success. Despite many studies on prospecting, the proximate mechanisms underpinning this behavior—which cues prospectors use to gather information on reproductive success—remain unclear.

Wild Zebra Finches (*Taeniopygia guttata*) in the semi-arid zones of Australia prospect on the nests of conspecifics (Mariette and Griffith 2012a, Brandl et al. 2018), but little is known about the mechanisms of social information use in this species and whether the predictions from the numerous studies on species of temperate zones apply to them (e.g., correlation of prospecting activity with brood

size and nest stage; see previous paragraph). Zebra Finches have relatively low parental feeding rates of as little as 1 visit per hr and high synchrony between parents (Mariette and Griffith 2012b). Hence, parental feeding rates of Zebra Finches might not serve as a sufficient indicator of their reproductive success. Living in the arid and semiarid zones of Australia, Zebra Finches are faced with the distinct ecological challenges of a highly fluctuating environment. In particular, rainfalls in the Australian deserts are underlying exceptionally strong temporal and spatial variation that leads to unpredictably fluctuating primary productivity (Morton et al. 2011). Zebra Finches are granivores, which means that their reproduction is strongly linked to the ripening of grass seeds, and thus to the unpredictable rainfalls. These ecological conditions lead to the opportunistic breeding pattern of the Zebra Finch. Opportunistic breeding means that while Zebra Finches breed with some degree of seasonality, they breed over a long potential breeding period, and can breed multiple times in a single year. This generates a number of additional challenges over the timing of and investment into reproductive events for the breeders relative to species in more predictable and seasonal environments. Opportunistic breeding is widespread throughout Australia (Duursma et al. 2017) and probably in other poorly studied parts of the world. The well-studied Zebra Finch therefore provides a good model to investigate the mechanisms through which social information can be assessed by species living in ecologically challenging environments.

In a field experiment, we aimed to test which social cues from the nests of Zebra Finches attract prospecting conspecifics. We will thereby gain insight as to what social information Zebra Finches might use for their reproductive decisions in an unpredictable habitat. In 2 separate experiments, we presented wild Zebra Finches with either acoustic cues (playback of chick begging calls) or visual cues (eggs) of conspecifics with either small or large broods/clutches. Using playbacks of chick begging calls or nests with unhatched eggs, respectively, allowed us to completely discern clutch and brood size from parental activity. Previous studies suggest that playbacks of conspecific courtship calls can function as social cues affecting reproductive parameters (breeding schedule and clutch size in Zebra Finches: Waas et al. 2005; sexual and agonistic interactions in Royal Penguins [*Eudyptes schlegeli*]: Waas et al. 2000). Similarly, fledgling calls of Veeries (*Catharus fuscescens*) have been shown to function as social cues for conspecifics who are more likely to settle in patches where such calls were played, presumably because the calls of fledglings provide evidence for prior nest success (Kelly and Schmidt 2017). We aimed at adding to the small number of studies demonstrating that begging calls can serve as inadvertently produced social information for non-kin conspecifics. Further, this is to our knowledge the

first study investigating the direct reaction of prospectors to begging calls (i.e. asking whether begging calls affect which nests are visited). If the presence of fledglings in an area alone, as simulated in the study on Veeries (Kelly and Schmidt 2017), would provide all relevant information for conspecifics, there would be no need to prospect on their nests beforehand. However, as Zebra Finches visit the nests of their conspecifics frequently (Mariette and Griffith 2012a), it is highly likely that nests already provide additional and/or different information at earlier stages. In addition to giving cues on successful breeding sites (Doligez et al. 2002), nests at earlier stages could potentially provide information to help, for example, synchronize nesting (Emlen and Demong 1975, Stempniewicz et al. 2000) or to adjust clutch size and egg mass (Forsman et al. 2011). We therefore believe that it is highly relevant to expand our understanding on conspecific social information use in the pre-fledging period. It is further conceivable that prospecting is a hierarchical strategy where individuals collect information over time, from various stages of the nesting cycle (e.g., number of eggs, nestlings, and fledglings) and integrate the information to be more comprehensive and reliable.

With this field experiment, we tested the hypothesis that chick begging calls can serve as a source of social information for prospecting Zebra Finches. If this is the case, we predicted that Zebra Finches will visit nests with begging call playbacks more than controls (silence and noise). If the begging calls can also serve as indicators for breeding success, Zebra Finches should visit larger (and potentially more successful) clutches per broods of conspecifics more than small ones, as clutch size is correlated with reproductive success in Zebra Finches (Zann 1996). Clutch size of Zebra Finches seems to be tightly linked to the nutritional state of the female (Zann 1996). That means that a large clutch in a nest might be the result of the female's response to high resource availability and as such would be useful information to the prospectors. We further predict the acoustic cues (representing nests at later stages) may be perceived as more reliable (see, e.g., Boulinier et al. 1996) than visual cues (i.e. nests at early stages) and hence the distinction between small and large broods should be more pronounced in the nests with chick calls as cues than those with egg cues.

METHODS

Study Species and Field Site
Zebra Finches are small, sexually dimorphic passerines with a strong pair bond and biparental brood care (Mariette and Griffith 2012b). They are monogamous, but highly social and live in loose colonies (Zann 1996). The mean clutch size in wild Zebra Finches in this study population

is 5 eggs, ranging from 2 to 8 eggs (Griffith et al. 2008). The study was performed at Gap Hills, located at Fowlers Gap, University of New South Wales (UNSW) Arid Zone Research Station (31.086972°S, 141.704836°E), New South Wales, Australia, between October 11 and November 27, 2016. The study site (~1.5 × 2 km in area) has a dam with a relatively permanent water body in the center. In the surrounding of the dam, 180 wooden nest boxes (12 cm front height, 18 cm back height, 9.3 cm width, 14 cm depth; entry hole 3 cm diameter) attached to metal stakes were installed, which are preferred nesting locations of Zebra Finches and lead to significantly reduced nest depredation rates (Griffith et al. 2008). The nest boxes were arranged in 5 areas of 30 nest boxes each (mean ± SE distance to nearest neighboring area: 413.62 ± 63.62 m; mean distance to nearest neighboring nest box within areas: 10.36 ± 1.98 m). The observed number of natural nests outside of the nest boxes was low during the study period.

General Experimental Procedure
The experimental setup for each trial consisted of 4 wooden nest boxes attached to metal stakes (same as the ones provided for breeding). The 4 nest boxes were set up in a roughly square configuration (mean ± SE distance between experimental nest boxes = 47.91 ± 2.92 m, $n_{nest boxes}$ = 110; distances not measured in every trial) in the morning, within 1 of the 5 nest box areas (i.e. the experimental nest boxes were set up in between the permanent breeding boxes). The 2 different experiments (acoustic cues or visual cues, see below) were never conducted in the same area on the same day. The same experiment was never set up in the same area on consecutive days. In addition, on each day only 1 trial per experiment was conducted. In total, 30 trials were run for each experiment, 6 trials per area.

All experimental nest boxes were erected south of a big bush or small tree to provide shade and to standardize the setup. The nest box openings were facing towards the shrub with ~1 m distance in between and at a height of ~1.5 m. An action camera (GoPro, San Mateo, California, USA; Rollei, Norderstedt, Germany) was attached to a branch of the respective plant so that the nest box was in the center of the camera's view. The nest boxes were then prepared according to the respective experiment and treatment (see below). Once the setup of all 4 boxes of an experiment was completed, the cameras were started. Each trial lasted as long as each camera would record (mean 2.5 ± 0.03 hr SE, $n_{nest boxes}$ = 232). Once all cameras had stopped recording, the complete setup including the stakes and nest boxes was removed. Trials of the experiment with acoustic cues were started between 0700 and 1118 hours and ended between 0820 and 1310 hours. The visual cue trials were started afterwards for logistical reasons, with starting times between 0724 and 1127 hours and end times between 0836 and 1411 hours. Across both experiments,

the starting times of the recording/playback at the first and last box within a trial were mean 12.62 ± 0.98 min SE apart.

Experiment with Acoustic Cues
For the experiment with acoustic cues, a speaker (JBL Clip+, JBL by Harman, Northridge, California, USA; 3.2 W, 160 Hz–20 kHz) was placed inside each nest box. The speakers were covered with a thin layer of nest material that had previously been collected from abandoned Zebra Finch nests. A digital audio player (Intenso Video Scooter Digital Player, Intenso International, Vechta, Germany) was attached to each speaker, each containing the sound file for 1 of the following 4 treatments: "3 chicks" (begging calls of 3 chicks); "7 chicks" (begging calls of 7 chicks); "noise" (white noise); and "silence" (no sound). The assignment to the nest boxes was randomized by blindly allocating the players to the nest boxes. Once all boxes and devices had been set up, all speakers, audio players and cameras were started. When the video recordings were analyzed, we ensured that all playbacks were audible throughout and until the end of each trial.

White noise and silence files were both created using the respective function in the software Audacity (Audacity Team 2014). The playback files were previously recorded with a Zoom H4n digital recorder (Zoom North America, New York, New York, USA) in Waveform Audio File Format (WAV) in nests with 3 chicks (n_{nests} = 4) and 7 chicks (n_{nests} = 4). Chicks were recorded in their nest boxes between day 8 and day 10 after hatching. To ensure that chicks were hungry and hence motivated to utter begging calls, we checked the state of their crops. Depending on the fill level, we then blocked the entrance of the nest boxes with a cloth for 10–90 min, to prevent parents from feeding, until crops were empty. To elicit begging calls from all chicks of the brood, we carefully touched the beaks of the chicks with a small stick before the start of recording and during the recording session if some of the chicks had stopped begging. Two recordings were made at each selected nest in 1 session. Each recording lasted for 2 min with a 2 min break in between when the lid of the nest box was closed. The recorder was held at a distance of 10 cm from the chicks, and we used the same settings for all recordings. We edited the recordings with Audacity (Audacity Team 2014). We copied and pasted different sequences of begging calls from the recordings to create the playback files. Three-hr playback files were assembled by alternating 45 s sequences of begging calls with 90 s sequences of silence. Each file was created using only the files from 1 recording session at 1 nest box (4 min). We cut the recordings in 45 s sequences with different starting points and randomly assembled them within the playback file. We measured the amplitudes of all sound files using a sonometer (A setting, 1 m, SPL meter, Castle GA206 sound level meter). The mean (± SE) amplitude of the treatments

playing sound were: 3 chicks: 51.5 ± 1.55 dB, n = 4; 7 chicks: 56 ± 1.35 dB, n = 4; noise: 56 dB, n = 1 (Figure 1).

We did not modify the audio files in other ways than described here; the difference in amplitude between "3 chicks" and "7 chicks" recordings reflect the natural occurring difference. During the experiment, the 8 different begging call playback files were paired in different combinations (see Appendix Table 1). Begging call playback files were never used in the same area where they had been recorded. It was unfortunately not possible to record more nests before and during the study period, as no more nests of the right brood size were available. Nevertheless, using fewer source exemplars than playback stimuli also has advantages as it allows to test for effects a specific exemplar may have and thus has been suggested as 1 of the many possible playback designs (Wiley 2003).

Experiment with Visual Cues
In this experiment, we applied the same general procedure as described before. However, the following visual cues were presented inside the 4 nest boxes in each trial: "3 eggs" (a nest containing 3 Zebra Finch eggs); "7 eggs" (a nest containing 7 Zebra Finch eggs); "3 rocks" (a nest containing 3 rocks); and "empty" (the nest box remained empty). The empty box and the rocks served as controls. The purpose of the rocks was to present a visual stimulus other than the eggs. The nest material and eggs used in the experiment had previously been collected from abandoned nests of Zebra Finches breeding in nest boxes. We only collected nests that had been abandoned before chick rearing (i.e. nest material was relatively clean). For each trial, 3 nests were assembled inside the experimental nest boxes, while the fourth box stayed empty. In the center of each of the 3 nests, we neatly arranged 3 eggs, 7 eggs, or 3 rocks, respectively. The rocks we selected for the experiment were of light color and matched sizes of Zebra Finch eggs as closely as possible. Nest material, eggs and rocks were exchanged between trials, and treatments were shuffled between nest boxes.

Data Analysis
Six different observers who were blind to the purpose of the experiment viewed the complete video material, coding the behavior of the birds. Four behavioral categories were identified: "at box" (a Zebra Finch appears in close vicinity to the nest box, but has no physical contact with it); "sits" (a Zebra Finch sits on top of the nest box); "hangs" (a Zebra Finch hangs at the entrance of a nest box with at least 50% of his or her body being outside); and "in box" (a Zebra Finch is inside the nest box with more than 50% of his or her body). The duration of each behavior was noted. Each bird appearing in a video was assigned a unique ID code. As long as an individual was clearly identifiable, the same ID code was used. Once a bird left the camera's

field of view, we assumed any bird appearing to be a new individual. Where a count of individuals is mentioned, throughout the article, it refers to this approximated value. In a separate study (H.B. Brandl personal communication) involving a smaller number of Zebra Finches tagged with passive integrated transponders, use of radio-frequency identification readers at nest boxes suggests that the majority of visits to nest boxes while prospecting are made by different individuals. The mean number of individuals appearing per hr ("mean number of IDs per hr") was then calculated for each treatment by dividing the total number of individuals by the total duration of each trial [hr]. In the same way, the mean duration of visit per individual ("mean duration of visit per ID [s]") was calculated to reflect how much time 1 Zebra Finch interacted with a nest box on average. Both variables were calculated for each of the 4 behavioral categories separately, as well as in total.

The data were analyzed in 2 steps and separately for each experiment. First, we fitted a generalized linear mixed effect model (GLMM) with binomial error structure to assess if the treatment affected whether boxes were visited at all during a trial. In the GLMM, we used the binomial variable "visitation" (1 or more birds visited the box = yes; no birds visited the box during the trial = no) as response variable, and the day of the experiment and the area where it was conducted as random effects. Tukey's post hoc test was performed for significant results.

Second, for the further analysis comparing number and duration of visits between treatments we did not run GLMMs because data were highly zero inflated. Instead, we conducted a Friedman rank sum test, using each variable (mean number of IDs per hr and mean duration of visit per ID [s]) as response. In the Friedman test, treatment was used as the grouping factor; the day of the experiment was included as a blocking factor. When the result of the Friedman test was significant, we additionally conducted a multiple pairwise comparison (symmetry test; Hedderich and Sachs 2011) to establish which treatments significantly differed from each other. Kruskal-Wallis tests were performed to examine if the use of different exemplar recordings had an effect on the mean number of IDs per hr or the mean duration of visit per ID [s] in each of the 2 treatments of the experiment with acoustic cues using chick begging calls as playback (3 chicks and 7 chicks). We calculated the eta-squared estimates (η^2) as a measure of effect size for the Kruskal-Wallis tests (Cohen 2008, Tomczak and Tomczak 2014).

In some of the trials, not all 4 treatments could be tested successfully, due to technical issues with the cameras or playback equipment (8 setups in 4 trials of the acoustic experiment; 4 setups in 3 trials of the visual experiment). Since the Friedman test requires a balanced complete block design, no data from these trials could be included in the analysis. For the Friedman test we additionally removed

trials where none of the 4 nest boxes had any visit at all (2 trials of the experiment with acoustic cues and 5 trials with visual cues) from the data, as they contained no informational value.

All statistical analyses were conducted with R (R Core Team 2017): for GLMMs we used the package LME4 (Bates et al. 2015); for multiple pairwise comparisons we used the packages MULTCOMP (Hothorn et al. 2008a) and COIN (Hothorn et al. 2008b). Statistics are presented as mean ± SE (standard error of the mean) and median ± IQR (interquartile range).

RESULTS

Experiment with Acoustic Cues

The experiment using playbacks as acoustic cues for Zebra Finches consisted of 30 trials (112 nest box setups that were included in the analysis), lasting a total of 287.09 hr. In this period, a total of 607 visits of Zebra Finches (2.11 visits per hr; 328 visits by males, 166 visits by females, and the remainder by birds of unidentified sex) were recorded at the experimental boxes across all treatments. Interactions with the nest boxes during these visits summed up to 8.74 hr. The treatment significantly affected whether a nest box was visited by Zebra Finches during a trial or not (binomial GLMM: $\chi^2 = 15.78$, df = 3, $P = 0.001$, $n_{trials} = 30$; Figure 2A). Tukey's post hoc tests revealed a significantly higher likelihood that a box with 7 chicks playback had any visitors, compared with 3 chicks ($P = 0.011$), noise ($P = 0.003$), and silence ($P = 0.001$, $n_{trials} = 30$). The probability of finding 3 statistically significant tests (with $P \leq 0.011$) of 6 due to chance alone (calculated via a Bernoulli process: Moran 2003) is $P < 0.001$.

Further, the mean number of IDs per hr also differed between treatments (Friedman test: $\chi^2 = 8.69$, df = 3, $P = 0.034$, $n_{trials} = 24$; Figure 2B). Post-hoc pairwise comparisons for the mean number of IDs per hr showed a significant difference between the following treatment pairs: 7 chicks playback boxes were visited more often than 3 chicks ($P = 0.010$), noise ($P = 0.012$), and silence playback boxes ($P = 0.044$, $n_{trials} = 24$). The probability of finding 3 statistically significant tests (with $P \leq 0.044$) of 6 due to chance alone is $P < 0.002$. No significant differences were found between the other treatment pairs. The mean duration of visit per ID [s] was not different between treatments (Friedman test: $\chi^2 = 5.78$, df = 3, $P = 0.12$, $n_{trials} = 24$) but the order of the treatments was in accordance with mean number of IDs per hr (Figure 2C).

Analyzing the behavioral categories separately, only the birds being in close proximity to the box without touching it (at box) differed significantly between treatments, in both number and duration of visits (Table 1). Post-hoc testing revealed a significantly higher number of birds being "at box" in the 7 chicks treatment than in 3 chicks ($P = 0.002$) and noise ($P = 0.009$, $n_{trials} = 23$) treatment boxes. There was also a marginally non-significant trend for more birds being "at box" in "7 chicks" boxes compared with "silence" boxes ($P = 0.054$, $n_{trials} = 23$). The probability of finding 2 statistically significant tests (with $P \leq 0.009$) of 6 due to chance alone is $P < 0.002$. Furthermore, birds spent significantly more time per visit "at box" at the 7 chicks playback boxes than at the 3 chicks boxes ($P = 0.010$), the noise boxes ($P = 0.017$), and the silence boxes ($P = 0.023$, $n_{trials} = 23$). The probability of finding 3 statistically significant tests (with $P \leq 0.023$) of 6 due to chance alone is $P < 0.001$.

There were no significant differences between the 4 exemplar recordings used in either of the begging call treatments on mean number of IDs per hr (3 chicks: Kruskal-Wallis: $\chi^2 = 1.74$, df = 3, $P = 0.70$, $n_{trials} = 24$, $\eta^2 = 0.063$; 7 chicks: Kruskal-Wallis: $\chi^2 = 2.96$, df = 3, $P = 0.47$, $n_{trials} = 24$, $\eta^2 = 0.002$) or the mean duration of visit per ID [s] (3 chicks: Kruskal-Wallis: $\chi^2 = 1.41$, df = 3, $P = 0.70$, $n_{trials} = 24$, $\eta^2 = 0.079$; 7 chicks: Kruskal-Wallis: $\chi^2 = 2.96$, df = 3, $P = 0.63$, $n_{trials} = 24$, $\eta^2 = 0.002$). This indicates that none of the exemplars were unusually attractive or unattractive for the birds.

Experiment with Visual Cues

We ran 30 trials of the experiment with visual cues in the nest boxes (120 nest box setups), which had a total runtime of 293.32 hr. During this time, 536 visits (1.83 visits per hr; 125 visits by females, 363 visits by males, the remaining 48 visits by individuals of unknown sex) were made at the nest boxes, lasting a total duration of 8.76 hr. Treatment did not significantly affect whether a nest box was visited at all or not (binomial GLMM: $\chi^2 = 1.40$, df = 3, $P = 0.71$, $n_{trials} = 31$; Figure 3A). There was no significant difference in the mean number of IDs per hr (Friedman test: $\chi^2 = 2.65$, df = 3, $P = 0.45$, $n = 23$; Figure 3B) or the mean duration of visit per ID [s] (Friedman test: $\chi^2 = 0.25$, df = 3, $P = 0.97$, $n = 23$; Figure 3C) between treatments.

Additionally, no significant differences were found in mean number of IDs per hr or mean duration of visits between treatments in any of the 4 behaviors that Zebra Finches showed at the experimental nest boxes (Table 2).

DISCUSSION

In this field study, we used 2 different experimental setups to test whether wild Zebra Finches react differently to neighboring nest boxes, depending on different acoustic and visual cues. Our results demonstrate that the playback of large broods begging indeed attracted more visitors than the begging calls of small broods. This result is in accordance with the hypothesis that prospectors preferentially visit more successful broods (e.g., Cadiou et al. 1994,
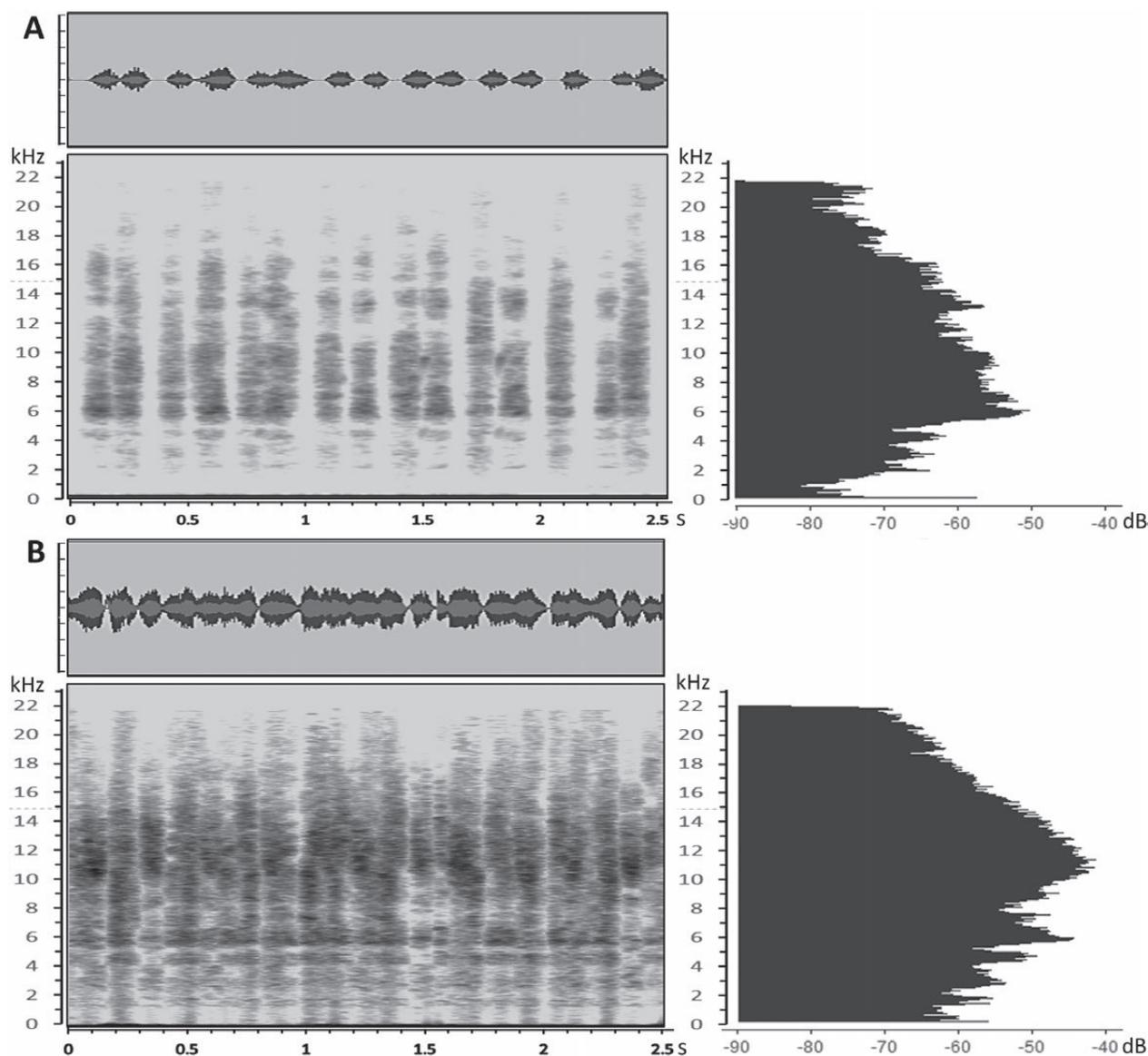
FIGURE 1. Waveform (top left), spectrogram (bottom left) and average power spectra (right) of exemplary 2.5 s sequences of playback recordings of (**A**) begging calls of 3 chicks and (**B**) begging calls of 7 chicks. The files were recorded with 44.1 kHz sampling frequency, and sonograms were created with a window of 4,096 samples using a hanning filter. Therefore, the time resolution is 92.9 ms, which equals a frequency resolution of 10.8 Hz.

Schuett et al. 2017). The chick begging calls alone provided social information for unrelated conspecifics, which can potentially be used to infer on their breeding success. If the information obtained through prospecting is used to identify high quality breeding habitats (see, e.g., Brown et al. 2000, Doligez et al. 2002, Boulinier et al. 2008), being able to identify them quickly will have energetic benefits. Loss of time and energy are presumably costs of prospecting that can be avoided and used for activities by being able to assess the success of nests from a distance. Additionally, having to visit fewer nests of low informational value will

reduce the risk of becoming a victim of depredation and can potentially also minimize conflicts with conspecifics. However, territorial defense behavior in Zebra Finches is limited to the direct protection of their nest (Zann 1996) and we have never observed strong aggression between conspecifics.

Clutch and brood size in wild Zebra Finches are strongly associated with the reproductive success (Zann 1996), thus, nest prospecting could be used to assess the reproductive output of a patch. The mechanism determining the clutch size of Zebra Finches is not fully
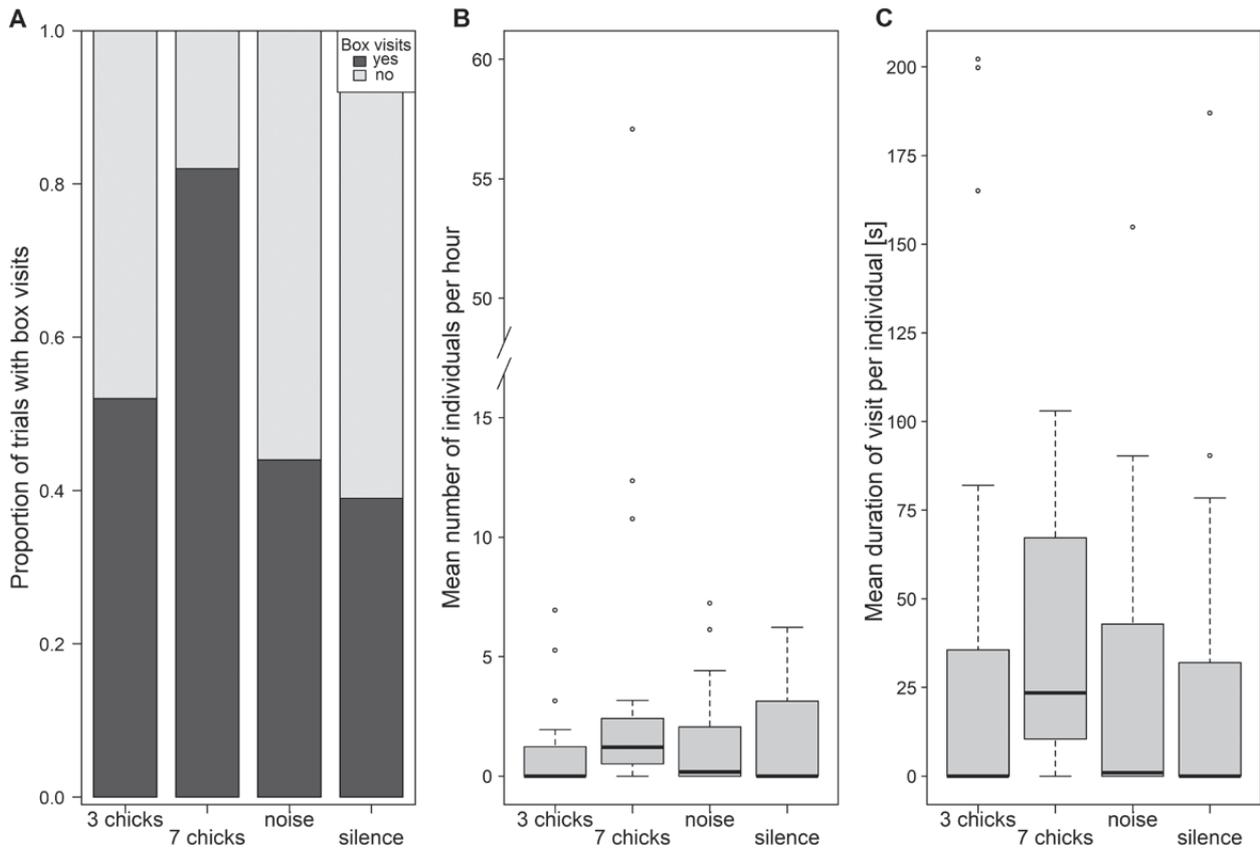
FIGURE 2. Proportion of trials in which the nest box of each treatment was visited by Zebra Finches (**A**), the medians of the mean number of individuals per hr (**B**), and the mean duration of visits [s] (**C**) at nest boxes playing different acoustic cues. The *y*-axis in plot B was truncated for plotting an extreme value.

TABLE 1. Effects of treatment on mean number of IDs per hr and mean duration of visit per ID [s] calculated for different behaviors during the experiment with acoustic cues. Medians, IQRs and the results of Friedman tests are shown. Four different behaviors that Zebra Finches displayed at the experimental nest boxes were identified in the video material: *at box, in box, sits*, and *hangs*. Number of trials (*n*) vary because trials with zero visits in all treatments are not included. Significant *P*-values are highlighted in bold.

Behavior	Variable	Median	IQR	*n*	χ^2	df	*P*
at box	mean number of IDs per hr	0.38	1.63	23	11.459	3	**0.009**
	mean duration of visit per ID [s]	1.00	1.20	23	8.866	3	**0.031**
in box	mean number of IDs per hr	0.00	0.64	7	0.509	3	0.92
	mean duration of visit per ID [s]	0.00	1.00	7	1.824	3	0.61
sits	mean number of IDs per hr	0.44	1.99	19	3.281	3	0.35
	mean duration of visit per ID [s]	7.50	15.65	19	6.671	3	0.08
hangs	mean number of IDs per hr	0.33	1.29	13	3.058	3	0.38
	mean duration of visit per ID [s]	1.57	9.75	13	1.835	3	0.61

understood, but it can be affected by the nutritional state of the female (Zann 1996), both in early life (Haywood and Perrins 1992) and in the period preceding reproduction (Lemon 1993). Abiotic environmental factors such as density and abundance of grass seeds are strongly associated with the onset of reproduction in Zebra Finches (Zann et al. 1995, Zann 1996). Nevertheless, the link between habitat quality and clutch size is not well studied

in Zebra Finches, but considerable variation in clutch sizes between breeding sites and breeding periods can be observed (e.g., Zann 1996, Griffith et al. 2008). Further, quality and quantity of food fed to the nestlings during the rearing period can affect growth rate and adult size of nestlings, and their future egg and clutch size (Zann 1996). While multiple factors might be involved in determining the clutch size of Zebra Finches and further study
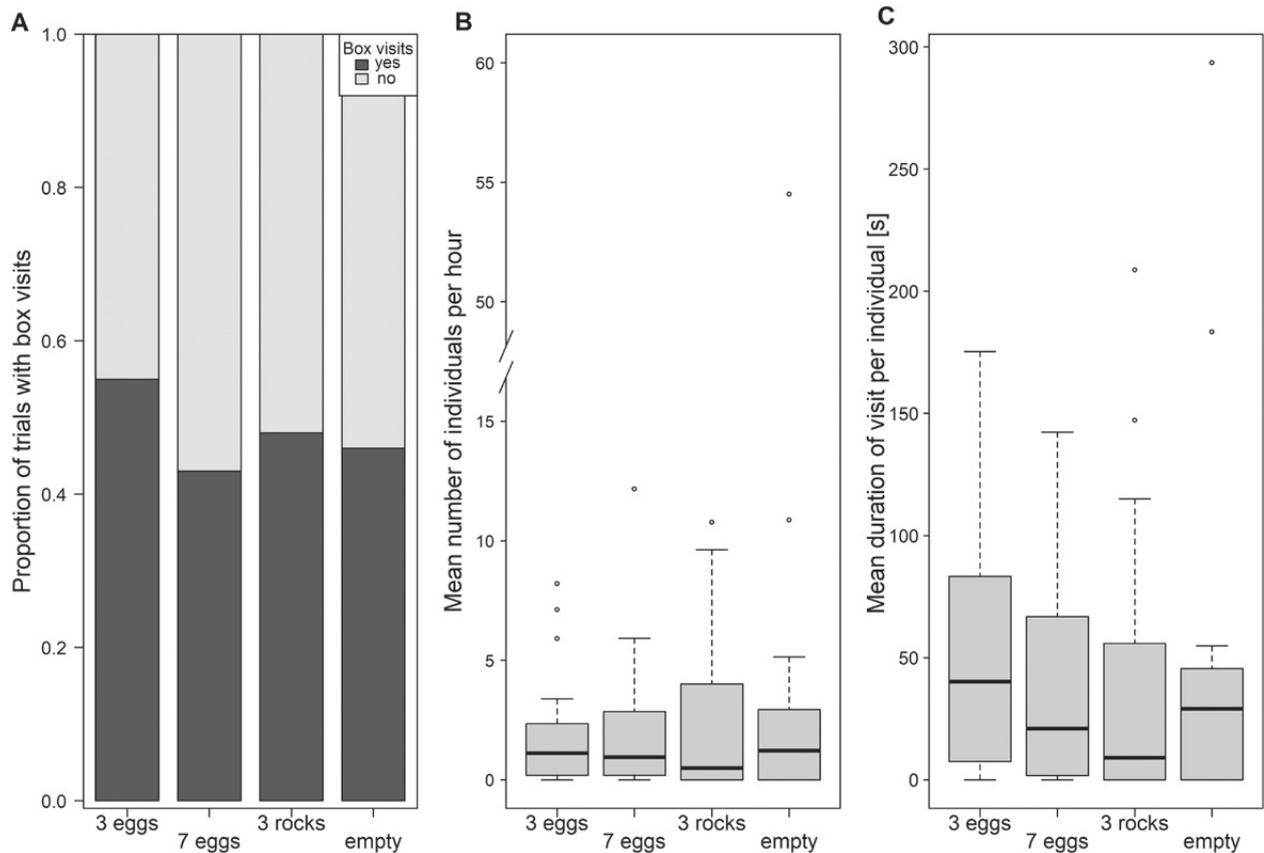
FIGURE 3. Proportion of trials in which the nest box of each treatment was visited by Zebra Finches (**A**), the mean number of individuals per hr (**B**), and the mean duration of visits [s] (**C**) at nest boxes containing different visual cues. The *y*-axis in plot **B** was truncated for plotting an extreme value.

TABLE 2. Effects of treatment on mean number of IDs per hr and mean duration of visit per ID [s] calculated for different behaviors during the experiment with visual cues. Medians, IQRs and the results of Friedman tests are shown. Four different behaviors that Zebra Finches displayed at the experimental nest boxes were identified in the video material: *at box, in box, sits,* and *hangs*. Number of trials (*n*) vary because trials with zero visits in all treatments are not included.

Behavior	Variable	Median	IQR	*n*	χ^2	df	*P*
at box	mean number of IDs per hr	0.70	1.91	22	1.894	3	0.56
	mean duration of visit per ID [s]	8.50	27.50	22	1.742	3	0.63
in box	mean number of IDs per hr	0.38	0.96	15	2.140	3	0.54
	mean duration of visit per ID [s]	18.00	65.00	15	1.209	3	0.75
sits	mean number of IDs per hr	0.39	1.54	17	1.571	3	0.67
	mean duration of visit per ID [s]	6.00	15.79	17	1.047	3	0.79
hangs	mean number of IDs per hr	0.53	2.28	22	2.436	3	0.49
	mean duration of visit per ID [s]	14.25	22.36	22	0.866	3	0.83

is necessary to understand these interactions, it overall appears that the current habitat quality (at least in terms of food availability) affect the reproductive output of individuals breeding there. In consequence, prospecting at nests of conspecifics to assess the quantity, and perhaps also the quality and state, of the offspring can in turn give insight to the habitat and its (current) suitability as a breeding site. More males than females visited the boxes in our experiment and it is possible that the sexes use the social information in slightly different ways. The male, which leads the female in the nest site search (Zann 1996), could gain information on the suitability of the area, while the female might rather glean information to adjust the clutch size according to resource availability.

From the view of a breeding pair receiving prospecting visits, the prospecting activity and, in consequence, the chance of a prospecting pair settling in the area are unlikely to have strong adverse effects. Zebra finches, as a non-territorial, monogamous species, are likely to benefit from additional breeding birds around and the advantages associated with coloniality (e.g., predator detection, dilution effects, group foraging; Møller 1987, Waas et al. 2005, Mariette and Griffith 2012a). Hence, loud begging calls and the attracting of prospectors to nests is not likely to be a problem for conspecifics.

The amplitude of the playbacks of 7 chicks begging and white noise were identical, which makes it highly unlikely that this was a contributing factor as to why some boxes were visited more. The difference we observed between 7 chicks and noise treatment can, hence, be likely attributed to the character and informational value of the signal. Also, in accordance with our predictions, the boxes of the 7 chicks treatment were significantly more likely to be visited than the silence boxes. The probability that 3 chicks playback nest boxes were visited was not significantly higher than in the control treatments. This could be contributed either to the lower amplitude of the signal or the lower information value of these nests, or potentially a mix of both. For this experiment, we decided to play the calls at the amplitude they are produced, instead of adjusting them to equal amplitudes. This allowed us to closely mimic the natural call properties, but we were therefore not able to discriminate between effects caused by differences in the absolute amplitude (i.e. how well the signal could be detected) and the spectral content (i.e. the acoustic character of the signal). Thus, it is possible that the 7 chicks boxes attracted more visitors than those of the 3 chicks treatment because the signal could be detected more easily and over a longer distance. The noise played at the same amplitude as the 7 chicks calls perhaps did not represent a biologically relevant signal and thus was not visited as much.

There is also a possibility that prospectors would usually react differently to chicks of different hunger levels, which affects begging intensity (e.g., Ottosson et al. 1997). In our experiment, however, we were probably able to control for this by only recording chicks with empty crops, i.e. at an equally high level of hunger. Reactions to the recordings of chicks from different broods were similar. Nevertheless, prospectors sometimes also looked inside the nest boxes, which could be used to gain additional visual information on nestling hunger and overall condition. Further, prospecting at the nestling stage might also be a part of a more comprehensive information gathering strategy, which could involve visiting a nest at multiple stages. It is also possible that the Zebra Finches visiting the nest boxes consisted of a mix of birds prospecting for information at conspecific nests and looking for empty nest boxes to breed in, which would also explain a certain level of visits to the control boxes.

We did not observe a difference in the number or duration of visits at the nest boxes containing only visual cues. Obviously, in this scenario birds could not preselect which box to visit, as they were identical from the outside and no other cues, such as parental activity, were available. However, birds that had already inspected the content of the nest box could have returned to the box more frequently or spend more time inspecting it, had they distinguished between more and less successful nests based on clutch size. Our finding follows the line of what can be predicted from another study, where a difference in prospecting rate between smaller and larger broods was only pronounced at late chick stages, presumably because information is more reliable then (e.g., Parejo et al. 2008). However, we cannot completely rule out that our result could have been different if the experimental trial had been running for a longer time. Birds could have revisited certain boxes again at a later point in time. Further, our method of video analysis did not allow for individual identification once an individual had left the field of view. The number of birds appearing at the box, which we used as a proxy for the number of individuals, might not be fine-scaled enough in this context. Another point is that we do not know how a non-incubated clutch, as we presented it, was perceived. It could appear as an unfinished or abandoned nest, which might not provide valuable information in this stage. We performed the experiment at non-incubated nests to dissociate all influence from parental activity, but this also brings along some restrictions. We therefore have to be careful with the interpretation of this negative result.

Overall, our study provides the first evidence that wild birds can use begging calls from chicks at the pre-fledging stage, an acoustic signal intended for kin communication, as social signal. This social information could be an important cue to infer on conspecifics' breeding success. Even though the parental feeding activity at nests is a known indicator of breeding success in some species (Pärt and Doligez 2003, Doligez et al. 2004; but see Schuett et al. 2017), the value of the begging calls in the nest as inadvertent social information has previously not been demonstrated. Our findings highlight the importance to further expand research on social information use, in particular on mechanisms that might have been previously overlooked.

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APPENDIX TABLE 1. Summary of assignment of the 4 different playback recordings of each treatment (3c = 3 chicks; 7c = chicks) to the 6 trials conducted in each area. The area where the begging calls were recorded and thus not used for playback is given in parentheses after the file name. Recording 4 of the 7 chicks treatment (7c - rec. 4) was recorded in a nest in an area which was not used in the experiment. Parentheses around an x indicate that the respective trial was not included in the analysis (see Methods section for details).

	3 chick begging call playback files				7 chick begging call playback files			
	3c - rec. 1 (A)	3c - rec. 2 (D)	3c - rec. 3 (E)	3c - rec. 4 (C)	7c - rec. 1 (D)	7c - rec. 2 (D)	7c - rec. 3 (E)	7c - rec. 4
Area								
A								
Trial 1		(x)			(x)			
Trial 2		x				x		
Trial 3		x			x			
Trial 4			x				x	
Trial 5				x				x
Trial 6				x				x
B								
Trial 1	x				x			
Trial 2	x				x			
Trial 3		x				x		
Trial 4			x		x			
Trial 5	x						x	
Trial 6				x				x
C								
Trial 1	x				x			
Trial 2	x				x			
Trial 3		x				x		
Trial 4			x				x	
Trial 5	x							x
Trial 6		x			x			
D								
Trial 1			x				x	
Trial 2			x				x	
Trial 3	x						x	
Trial 4			x					x
Trial 5				x				x
Trial 6				x			x	
E								
Trial 1	x				(x)			
Trial 2		x				x		
Trial 3		x				x		
Trial 4				x		x		
Trial 5				x				x
Trial 6				x	x			