



Acoustic similarity to parental calls promotes response to unfamiliar calls in zebra finch fledglings



Hendrik Reers^{a,1}, Wolfgang Forstmeier^{a,2}, Alain Jacot^{a,b,c,*}

^aBehavioural Ecology and Evolutionary Genetics Group, Max Planck Institute for Ornithology, Seewiesen, Germany

^bSwiss Ornithological Institute, Field Station Valais, Sion, Switzerland

^cUniversity of Bern, IEE-Conservation Biology, Bern, Switzerland

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Individual recognition, using acoustic, visual or olfactory individual signatures, is crucial for the coordination of social interactions and its occurrence has been demonstrated experimentally in many taxa. In this context, mistaking one individual for another is expected to be costly, for example through misdirected parental care or social punishment. To minimize the occurrence of such false responses, individual signatures should be distinct and selection should act on receivers to perceive these differences. However, it is largely unknown how precise signal perception is and whether similarity between individual signatures influences the occurrence of false responses. We used acoustic parent–offspring recognition in zebra finches, *Taeniopygia guttata*, to test how acoustic similarity between individuals affects a chick's response behaviour. In a playback experiment, fledglings were presented with calls of parents as well as calls of nonparents that varied systematically in their similarity to the parents' calls. The acoustic similarity between calls of parents and unrelated adults partly explained the response pattern of fledglings. Offspring preferentially responded to adult calls that were similar to their parents' call. The response pattern further seemed to incorporate a baseline responsiveness to conspecifics since most fledglings responded to very dissimilar adults. These findings demonstrate that the strength of response is related to signal similarity, which is potentially an important underlying mechanism shaping distinctiveness in signal design.

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It is well established that birds and other taxa use contact calls to coordinate their social interactions and that these calls facilitate recognition between individuals (for a review see [Kondo & Watanabe 2009](#)). Individual recognition is selectively advantageous in a variety of repeated social interactions, for example to ensure that investments reach the correct recipient in parental care ([Jouventin et al. 1999](#)), or to enable mates to recognize one another ([Vignal et al. 2008](#)). Selection for individual recognition is expected to act on both the distinctiveness of individuals and the ability of the receiver to perceive differences between individuals ([Tibbetts & Dale 2007](#)).

Distinctiveness in identity traits can evolve through negative frequency-dependent selection, which promotes distinctive or rare signals/phenotypes ([Dale et al. 2001](#); [Sheehan & Tibbetts 2009, 2010](#)). As soon as a 'rare' phenotype evolves, this might give the

bearer a selective advantage by being more easily recognizable ([Tibbetts & Dale 2007](#)). This trait is then expected to spread, until the trait becomes common and a new rare phenotype evolves, resulting in large intraspecific variation in identity signalling traits ([Tibbetts & Dale 2007](#)). While negative frequency-dependent selection is expected to increase variation in the selected trait within the population, selection for distinctiveness is likely to be counterbalanced by the need for species recognition or sexual selection processes ([Ryan & Rand 1993](#)).

Comparative studies on penguins ([Jouventin & Aubin 2002](#)), gulls ([Mathevon et al. 2003](#)) and swallows ([Medvin et al. 1993](#)) suggest that the ability to perceive individual differences and the distinctiveness of signals are related to the degree of coloniality of a species, because coloniality also increases the risk of mistaking one individual for another. Distinctiveness, as well as the ability to recognize differences between individuals, is thought to have evolved to minimize the risk of costly false responses, i.e. recognition errors ([Dale et al. 2001](#)). Costs related to recognition errors could result in misdirected parental effort for parents, inability of parents and young to reunite, social punishment of young approaching unrelated adults or attraction of predators through increased unselective signalling (e.g. begging or contact calls).

* Correspondence: A. Jacot, University of Bern, IEE-Conservation Biology, 3012 Bern, Switzerland.

E-mail address: alain.jacot@vogelwarte.ch (A. Jacot).

¹ E-mail address: hreers@gmail.com.

² E-mail address: forstmeier@orn.mpg.de.

However, whereas the selective advantage of individual recognition is intuitive, virtually no study has addressed the potential costs of recognition errors.

While there is ample evidence that recognition, using various sensory pathways, exists between familiar (e.g. parents, group members) and unfamiliar individuals (acoustic, e.g. Charrier et al. 2001; Sharp et al. 2005; visual, e.g. Parr & De Waal 1999; Tibbetts 2002; olfactory, e.g. Bowers & Alexander 1967; Carazo et al. 2008), these studies also demonstrate that recognition processes are not perfect and that false responses occur. Specifically in zebra finches, *Taeniopygia guttata*, we (Jacot et al. 2010) have found that fledglings respond to nonparental calls and we proposed that such responses to nonparents could be recognition errors, related to acoustic similarity between parents and nonparents. Surprisingly however, few studies have specifically tested the effect of similarity on the precision of acoustic recognition processes (Fallow et al. 2011). Such studies are of crucial importance since costly recognition errors are likely to be an important driving force shaping distinctiveness in signal design.

In this study on captive zebra finches, we investigated how fledglings responded to nonparental adult distance calls that varied systematically in their overall acoustic similarity to the parents' distance calls. Zebra finches are opportunistic breeders with biparental care that nest in loose colonies of up to 100 pairs, and offspring are fed during an extended postfledging phase by their parents (Zann 1996). Acoustic recognition is an important component of the zebra finch's communication system; adult zebra finches of both sexes have been shown to recognize individuals of the other sex in a mate recognition context (Vignal et al. 2004, 2008). It has also been shown that young zebra finches preferentially respond to parental calls, suggesting that they are able to recognize their parents acoustically (Jacot et al. 2010; Mulard et al. 2010). One of the main calls used in social interactions is the distance call, a contact call used if birds are not close to each other or in visual contact (Zann 1996). Young fledglings use long tonal calls that gradually develop into a distance call at around the age of 30 days; these calls are most similar to female distance calls (Zann 1996).

A fledgling's response behaviour to unrelated adults may incorporate several, nonmutually exclusive components. First, it may reflect true recognition errors. Second, responding to unrelated adults may be part of social interactions where fledglings try to socialize with conspecifics. Third, it may reflect a fledgling's strategy to cheat on unrelated adults that are acoustically similar to their parents. This last hypothesis assumes that those similar unrelated adults produce offspring that are acoustically similar to the cheating fledglings and in turn will mistake them for their own fledglings. We used recently fledged zebra finches in a playback experiment, in which we visually and acoustically isolated fledglings from their parents and aviary members. As playback stimuli we used calls with known similarity between parent calls and calls of unrelated adults. This allowed us to test systematically a fledgling's response towards unrelated adults, depending on their acoustic similarity to its parents. First, we predicted that fledglings would react more strongly towards calls from their parents. Second, we predicted that responses to calls of unrelated adults would be less strong as acoustic similarity to parental calls decreased. In both predictions we expected that young birds would change the number of response calls and adjust call characteristics that are related to motivational status (Jacot et al. 2010).

METHODS

Subjects and Housing

Fledgling zebra finches used in the present study originated from a captive population held at the Max Planck Institute for

Ornithology in Seewiesen, Germany. All fledglings tested in this study were descendants from birds breeding in aviaries that held six breeding pairs. Even though in this study we focused on recognition of social parents (recognition of the parent raising the fledglings), we also had information on the genetic origin of fledglings (Forstmeier et al. 2011). Of 120 fledglings in our study, 75 were within-pair offspring, 42 had been sired by extrapair fathers and three originated from dumped eggs. The sex of the offspring was determined using molecular methods (Griffiths et al. 1998). Temperature in the rooms was maintained at 23–25 °C and relative humidity from 40 to 60%. Rooms were illuminated by full-spectrum fluorescent light (Osram Lumilux T5 FH 28W/860 Daylight) and the light:dark period was 14:10 h. All birds received a millet seed mixture, cuttlefish, grit, water ad libitum on a daily basis and a multivitamin supplement once per week. All recognition trials were conducted between May and August 2009. Aviaries were checked twice a day for newly fledged birds. Nestlings were individually marked by numbered alloy bands.

Acoustic Similarity between Individuals

To calculate similarities between individuals, we used distance call recordings of 100 male and 94 female zebra finches (total number of calls: $N_{\text{males}} = 1576$, $N_{\text{females}} = 990$; number of calls/individual: mean \pm SD: males: 15.76 ± 6.29 ; females: 10.53 ± 1.71). These calls had been recorded previously as described by Forstmeier et al. (2009), using the same playback-recording set-up as for our experiment (see below) from individuals that were unfamiliar to the tested fledglings. The calls were analysed with Sound Analysis Pro software (Tchernichovski & Mitra 2004) using standard settings. We extracted the following acoustic features to characterize the acoustic structure of each call: (1) call duration (ms), (2) variance in amplitude modulation (1/ms), (3) mean frequency (Hz), (4) mean frequency modulation (°), (5) variance in frequency modulation (°), (6) mean entropy, (7) variance in entropy, (8) mean pitch, (9) mean pitch goodness and (10) mean principal contour (for details see Tchernichovski & Mitra 2004; Reers & Jacot 2011).

To investigate the effect of acoustic similarity on the probability of a chick responding, we used stimulus calls with known similarity to parental calls. The acoustic similarities (i.e. the inverse of acoustic distances) between calls were calculated for both sexes from two separate linear discriminant function analyses using all 10 acoustic features ($N_{\text{males}} = 100$, $N_{\text{females}} = 94$; R-package: MASS, Venables & Ripley 2002). Using the discriminant scores for each call, the centre for an individual (i.e. the centroid) was calculated as the mean of each discriminant score for all calls from one individual (mean intraindividual variation in distance of calls to centroid: mean \pm SD: males: 3.31 ± 1.29 ; females: 4.49 ± 2.24). In the next step, the 'most representative call' for each individual was then defined as the call with the shortest Mahalanobis distance to its centroid (distances to centre of group; mean \pm SD: males: 0.86 ± 0.44 ; females: 1.43 ± 1.08 ; Mahalanobis 1936; Medvin et al. 1992).

In the following, we only use this one selected call from each of the 194 adults. As a measure of acoustic similarities between individuals, we calculated the Mahalanobis distances between the representative calls of all individuals, separately for each sex. For each individual parent we picked from the pool of other same-sex parents the five most similar calls (similarity 1, ranked 1–5 in distance; mean \pm SD: male: 4.21 ± 3.50 ; female: 4.65 ± 2.77), five calls with intermediate similarity (similarity 2, ranked 40–44 in distance; mean \pm SD: male: 11.72 ± 5.73 ; female: 11.83 ± 4.09) and five calls that were dissimilar (similarity 3, ranked 80–84 in distance; mean \pm SD: male: 19.35 ± 6.73 ; female: 19.14 ± 4.85) as

stimulus calls for the playback experiment. By picking five calls per adult and similarity level, we were able to test all of a pair's fledglings with a unique combination of nonparental stimulus calls. We chose to limit the distance rank range to 84 out of 100 males, or 94 females, to avoid putting too much emphasis on outlier adults with extreme call characteristics.

To investigate the cheating hypothesis, we tested for a relationship between the acoustic similarity of fledglings and the acoustic similarity of their mothers and fathers. In other words, we tested whether parents that are very similar to each other also produce broods that sound similar to each other. For this, we compared the distance of representative calls for fathers and mothers of 13 broods and the centroids of their respective broods with each other. Distances were calculated following the above-described methods of extracting Mahalanobis distances and centroids from discriminant function analysis on males, females and broods. The discriminant function analysis on broods was performed on 40 fledglings from 13 broods, using their representative calls (number of fledglings per nest: mean \pm SD: 3.1 ± 1.0). As representative calls of fledglings we only used long tonal calls (i.e. fledgling distance call) that were given in response to their parents in the playback experiments. Centroids for broods were calculated as the mean of the discriminant scores for each fledgling's representative call.

Playback Protocol

To stimulate fledglings to respond to playbacks of distance calls, we simulated a situation in which a fledgling lost visual and acoustic contact with its parents, by placing the fledgling in a visually and sound-attenuated recording box (70 \times 50 cm and 50 cm high). This recording box was equipped with a small metal wire cage containing a single perch, a microphone (C2, Behringer GmbH, Willich, Germany) approximately 20 cm from the perch and a small loudspeaker (V20, Logitech, Morges, Switzerland) next to the microphone (recording conditions as in Forstmeier et al. 2009). The microphone was connected to a preamplifier (SM Pro Audio, Melbourne, Australia) from which we recorded directly through an M-Audio Delta 44 (AVID Technology GmbH, Hallbergmoos, Germany) sound card onto the hard drive of a computer at a sampling rate of 44 kHz and 16 bit amplitude resolution using Audacity 1.3.7 (D. Mazzoni, Canada, <http://audacity.sourceforge.net/>). Audacity was used to play back distance calls and to record the fledgling's acoustic response.

As test subjects we used 120 recently fledged young from 48 broods from 28 families ($N_{\text{females}} = 61$, $N_{\text{males}} = 59$; age: 24.7 ± 1.1 days; days fledged: 6.7 ± 2.0 days). For each individual fledgling we built its own playback stimulus (see Fig. 1). Each playback stimulus consisted of representative calls of the fledgling's mother and father and a unique combination of representative calls of three nonparent females and males, one of each similarity level. For each

female and male we built a sequence in which the representative call was played three times, separated by 5 s of silence and followed by 20 s of silence. This sequence was 30 s long and defined as an 'individual unit' (see Fig. 1). For each sex we combined the 'individual unit' of the parent and the 'individual units' of the three nonparents into a 'sex unit', which was then 2 min in total (see Fig. 1). The order of 'individual units' was randomized within each 'sex unit'. The final step was to combine 'sex units' randomly twice in an alternating fashion (i.e. first female, second male, third female, fourth male or the other way around). The result was a playback stimulus in which the representative call of each individual was played six times (i.e. twice three times), and thus a total of 48 stimulus calls were played within this 8 min long playback stimulus. To allow for acclimation of the fledgling to the recording box, we added 2.5 min of silence to the beginning of the playback stimulus (Jacot et al. 2010). Immediately after these 10.5 min (i.e. 2.5 min of silence and 8 min of playback stimulus) we transferred the fledgling back to its natal aviary.

Response Analysis

The fledgling's acoustic response was measured as the number of calls within 5 s from the start of each stimulus call and the latency to respond as the time from the start of the stimulus call to the fledgling's first response call. In cases where fledglings did not respond to a stimulus, the count of response calls was 0 and latency could not be scored.

To investigate whether fledglings adjust their calls to playbacks of different similarity levels, we measured call features for the response call after each stimulus with the best signal-to-noise ratio (i.e. the loudest call). We limited our analysis to those call features that are suggested to relate to motivational status and call urgency in birds (Morton 1977; Jacot et al. 2010). These parameters were (1) call length (ms) (Ficken 1990; Leavesley & Magrath 2005), (2) mean amplitude (dB), (3) mean amplitude modulation, (4) mean frequency (Hz) (Ficken 1990; Leavesley & Magrath 2005), (5) mean frequency modulation ($^{\circ}$) and (6) mean entropy. As in the previous analyses, all call features were analysed using SAP with standard settings. The quality of response calls was assessed using 1859 individual calls (responses to different similarity levels: $N_{\text{parent}} = 577$; $N_{\text{similarity 1}} = 450$; $N_{\text{similarity 2}} = 441$; $N_{\text{similarity 3}} = 391$).

Statistical Analysis

All statistical analyses were performed with R 2.8.0–R 2.12.0 (R Development Core Team 2008). To analyse the effects of stimulus similarity on the number of response calls (Poisson distribution), latency to respond (square-root-transformed, Gaussian distribution) and call features (Gaussian distribution) we used generalized linear mixed-effects models (GLMM; R-package: lme4, Bates & Maechler 2011). Mean amplitude modulation was square-root-

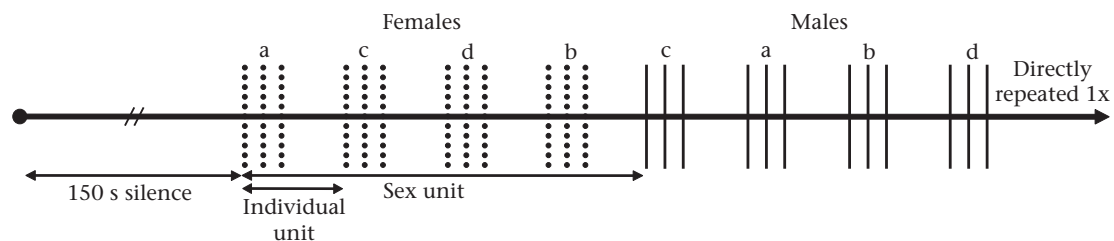


Figure 1. Playback design: three identical calls (individual unit) for four different adults (a, b, c, d) per sex (sex unit) were used. The order of individual units (a, b, c, d) within a sex unit was randomized for every fledgling. The order of sex units (i.e. whether male or female stimuli were played first) was altered between playbacks. Each sex unit was played twice, keeping the individuals within a sex unit in the same order.

transformed and mean frequency modulation was log-transformed to approach normality.

We used the GLMMs to test both our predictions: (1) that fledglings respond more strongly to parents than to the most similar nonparent and (2) that, among nonparents, fledglings decrease their response with decreasing acoustic similarity to their parents. For each prediction we performed eight GLMMs (i.e. one for each response variable: latency, number of responses and six measures of call structure). For all 16 GLMMs we simultaneously included as fixed factors the factorial variables sex of the fledgling, sex of the adults and parentage (full genetic offspring or extrapair/dumped egg), and as a continuous variable the similarity levels ranging from one to three. The similarity levels were treated as a continuous variable and not as a categorical variable, since similarity reflects a continuum and since we were interested in an overall relationship between the similarity of adult calls and the strength of a fledgling's response. As random effects, we added fledgling identity, brood, parent identity and nonparent stimulus identity.

To investigate the cheating hypothesis, we tested whether the acoustic similarity among fledglings of different broods is related to the acoustic similarity among their mothers or fathers. We used two GLMMs (i.e. one for each sex of parent) with distances as fixed factors and identity of adults and broods as random factors to control for pseudoreplication due to multiple comparisons.

The standard model diagnostics of non-normal errors, nonconstant error variance and the presence of outliers were performed on each of the models according to Fox (2002). Using a single (i.e. representative) call per individual as stimulus will lead to inflated variance components of the random effects but will lead to correct test statistics of the fixed effects; hence our analyses do not face the problem of pseudoreplication (Jacot et al. 2010).

Ethical Note

This study complied with local laws and was carried out under the housing and breeding permit no. 311.4-si (by Landratsamt Starnberg, Germany). From all fledglings we took a 20–100 μ l blood sample from the brachial vein for molecular sexing (Griffiths et al. 1998) and paternity analysis. After the playback experiment, which lasted for a maximum of 15 min all fledglings were transferred back to their natal aviary and there were no signs of aggression of the parents towards their offspring.

RESULTS

In the playback experiment 100 of 120 individual fledglings ($N_{\text{females}} = 51$, $N_{\text{males}} = 49$; $N_{\text{genetic}} = 61$, $N_{\text{extrapair}} = 36$, $N_{\text{dumped}} = 3$) responded to stimuli at least once. Those 20 ($N_{\text{females}} = 10$, $N_{\text{males}} = 10$) trials in which fledglings did not respond were discarded from further analysis. Of the 100 fledglings that did respond, nine responded to males only and nine to females only. Two of 100 fledglings responded to parental calls only, while six fledglings responded to unrelated adults only. From the 94 fledglings that did respond to parental stimulus calls, 16 fledglings responded to their fathers only, 12 to their mothers only.

Fledglings responded differently towards parents and towards the most similar nonparents. The responses were fewer (GLMM: $b \pm SE = -0.67 \pm 0.12$; $t = -5.83$, $N = 100$, $P < 0.0001$; Fig. 2a) and slower (GLMM: $b \pm SE = 6.39 \pm 1.16$; $t = -5.510$, $N = 97$, $P < 0.0001$; Fig. 2b) to calls of the most similar nonparents (i.e. similarity 1) than to parental calls. In addition, fledglings called more loudly towards their parents and their calls were longer and of higher frequency (Table 1, Fig. 3 and Appendix Table A1).

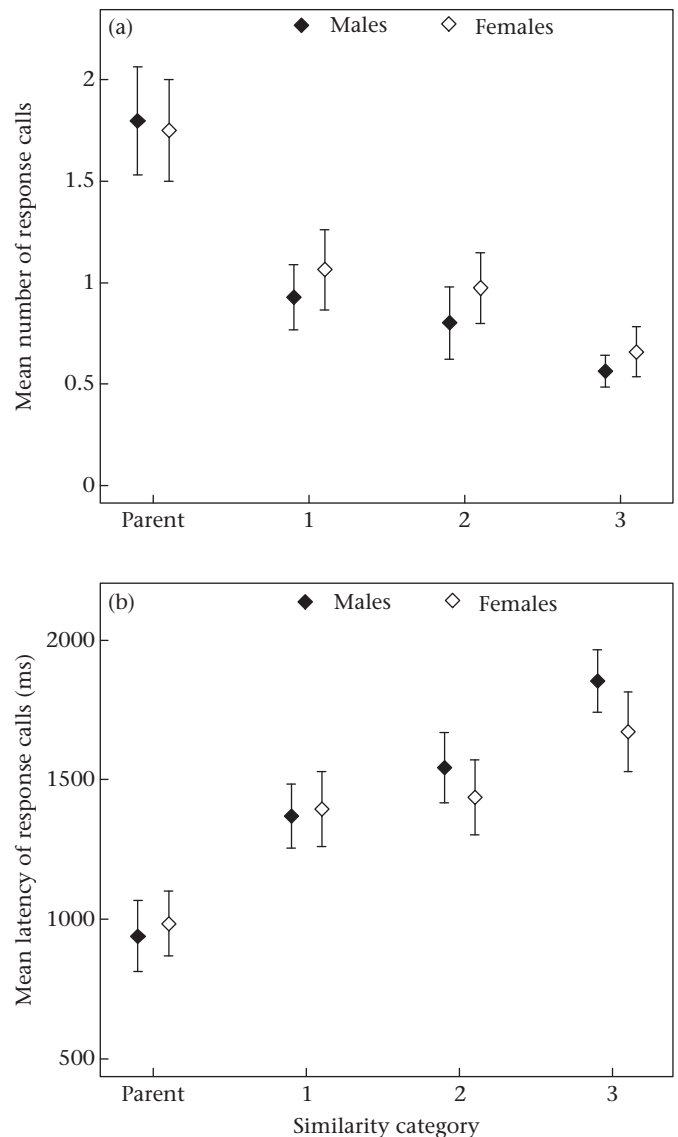


Figure 2. Mean \pm SE (a) number of response calls and (b) latency to respond for fledglings of both sexes in response to parental calls and increasingly dissimilar nonparent calls (1–3).

Among the three different similarity levels of nonparents, the acoustic similarity of nonparental calls to parental calls affected a fledgling's response pattern. Fledglings gave fewer calls in response (GLMM: $b \pm SE = -0.18 \pm 0.05$; $t = -3.45$, $N = 100$, $P = 0.0006$; Fig. 2a) and the response was slower (GLMM: $b \pm SE = 2.22 \pm 0.63$; $t = 3.54$, $N = 97$, $P = 0.0004$; Fig. 2b) towards the most dissimilar calls than towards the most similar calls. Calls towards the most similar nonparental calls were of higher urgency, that is, they were louder and longer, while the frequency did not change significantly (Table 2, Fig. 3 and Appendix Table A2). Fledglings still responded to calls of the most dissimilar nonparents. The latency of these response calls was roughly twice as long and these calls were around three times fewer than towards parents' calls (Fig. 3).

In a further step we analysed whether the sex of the adults, the sex of the chicks or their genetic background (i.e. within-pair, extrapair, dumped egg) had an effect on any of the measured call characteristics of the response calls. Some tests reached borderline significance (see Appendix Tables A1 and A2) but all these results became nonsignificant after controlling for multiple testing.

Table 1Means \pm SE, estimates and test statistics of response calls of fledglings towards distance calls of parents and the most similar nonparent calls

Call parameter	Parent (N=577)	Most similar (N=450)	Estimate	SE	t	P
Call duration (ms)	198.96 \pm 2.91	177.80 \pm 2.87	-17.68	4.35	-4.06	<0.001
Mean amplitude (dB)	46.78 \pm 0.30	45.00 \pm 0.33	-1.34	0.40	-3.32	<0.001
Mean amplitude modulation (1/ms)	0.0114 \pm 0.0002	0.0119 \pm 0.0002	0.0023	0.0011	2.11	0.035
Mean frequency (Hz)	3668.83 \pm 21.34	3546.49 \pm 23.77	-109.44	28.36	-3.86	<0.001
Mean frequency modulation ($^{\circ}$)	15.11 \pm 0.31	15.56 \pm 0.32	0.044	0.021	2.12	0.034
Mean entropy	-2.44 \pm 0.02	-2.33 \pm 0.03	0.104	0.034	3.03	0.002

Acoustic similarity of distance calls between fathers or between mothers of different broods did not predict the mean acoustic similarity of distance calls between their respective broods (GLMM: fathers: $b \pm SE = -0.01 \pm 0.02$, $t = -0.21$, $N_{\text{comparisons}} = 78$, $P = 0.84$; mothers: $b \pm SE = 0.01 \pm 0.02$, $t = 0.35$, $N_{\text{comparisons}} = 78$, $P = 0.73$; Fig. 4).

DISCUSSION

In this study we have shown that fledgling zebra finches responded more strongly to their parents than to the most acoustically similar nonparents. Most importantly, our results demonstrate that a fledgling's strength of response is positively related to the acoustic similarity of nonparental distance calls to its parents' distance calls.

Previous studies have already indicated that fledglings often respond to contact calls of unrelated conspecifics (e.g. Sealy & Lorenzana 1997; Jacot et al. 2010). However, it remained largely elusive why and to whom offspring respond. In this study, we have provided experimental results that allow insights into how similarity of acoustic signals shapes the response pattern in the receiver. Acoustic recognition of parents by fledglings seems very accurate in zebra finches. Fledglings responded significantly more strongly to calls of parents than to those of the most acoustically similar nonparent. This finding is interesting since the most similar

nonparents appeared very similar to the actual parents. Their acoustic distances were close to or within the individual acoustic variability of a fledgling's parents. We have to assume, though, that the actual differences perceivable for a fledgling are magnitudes higher than those measured by our comparably simple statistical method.

Fledglings responded significantly more strongly to similar than to dissimilar nonparental calls. This response pattern demonstrates a positive relationship between the acoustic similarity of a distance call to the calls of the fledgling's parents and the strength of response. Such a relationship was found for quantitative response measures (i.e. number of calls and latency to respond), and also for qualitative aspects (i.e. changes in call features) of the response call given by fledglings. A similar relationship between acoustic similarity and strength of response has been found in the reaction of superb fairy-wrens, *Malurus cyaneus*, to heterospecific alarm calls with varying acoustic similarity to their own alarm calls (Fallow et al. 2011). These studies demonstrate that the acoustic similarity of signals affects the precision of recognition processes, while the exact mechanism behind this response pattern remains elusive. Both the differential response pattern relative to call similarity and a striking level of responsiveness towards the most dissimilar nonparental calls can be interpreted in three ways. First, these responses are true recognition errors, indicating that recognition is not perfect. Second, fledglings follow a cheating strategy to solicit

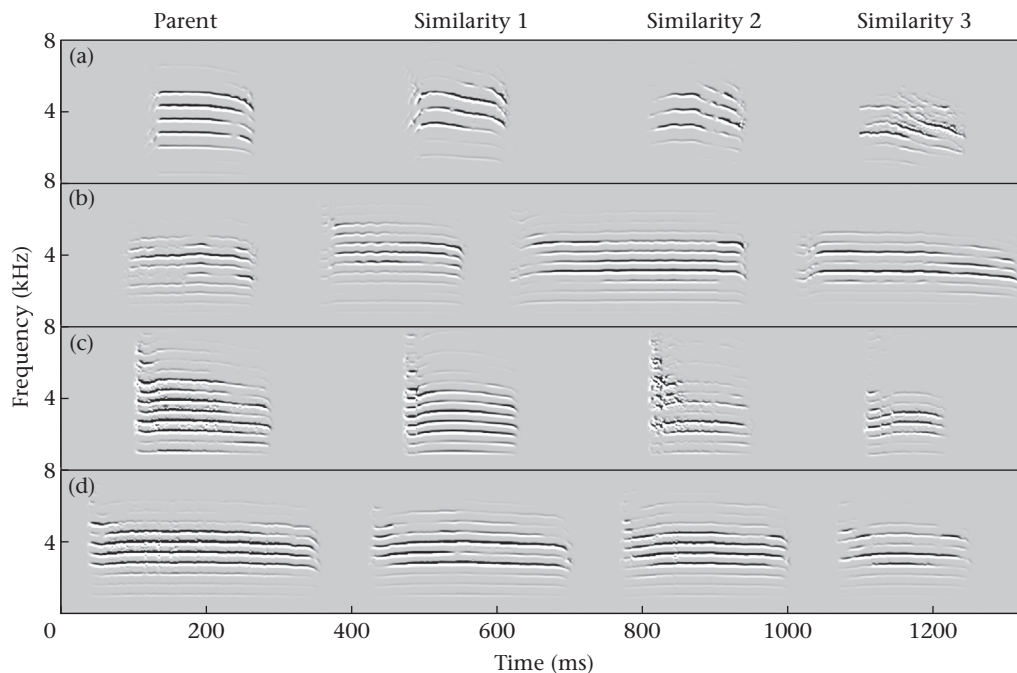


Figure 3. Representative adult stimulus calls of (a) a male parent and (b) a female parent and the respective calls of nonparent adults of different similarity levels 1–3. (c, d) Response calls of two fledglings to a parent call and nonparent calls from similarity levels 1–3. For the fledgling response, note the decrease in call length and in amplitude with decreasing similarity of nonparental calls compared to response calls to parental calls. Spectrograms were produced in Sound Analysis Pro.

Table 2
Means \pm SE, estimates and test statistics of response calls of fledglings towards distance calls of adults varying in similarity

Call parameter	Similarity 1 (N=450)	Similarity 2 (N=441)	Similarity 3 (N=391)	Estimate	SE	t	P
Call duration (ms)	177.80 \pm 2.87	170.21 \pm 2.93	161.01 \pm 2.68	-6.99	2.01	-3.47	<0.001
Mean amplitude (dB)	45.00 \pm 0.33	44.85 \pm 0.33	44.30 \pm 0.36	-0.53	0.20	-2.64	0.008
Mean amplitude modulation (1/ms)	0.0119 \pm 0.0002	0.0128 \pm 0.0002	0.0130 \pm 0.0002	0.0015	0.0006	2.59	0.010
Mean frequency (Hz)	3546.49 \pm 23.77	3549.49 \pm 24.85	3508.72 \pm 27.10	-14.93	15.51	-0.96	0.336
Mean frequency modulation ($^{\circ}$)	15.56 \pm 0.32	16.15 \pm 0.33	16.32 \pm 0.31	0.027	0.011	2.36	0.018
Mean entropy	-2.33 \pm 0.03	-2.35 \pm 0.03	-2.30 \pm 0.03	0.031	0.017	1.91	0.056

In all analyses similarity is treated as a continuous variable.

food from nonparents by responding to any adult. Third, fledgling responses can be interpreted as an urge for social interactions with conspecifics, with familiar calls triggering a higher response than unfamiliar calls. Disentangling these three alternatives is very difficult and our results do not allow us to reject any of these explanations. Most importantly, these explanations are not mutually exclusive and the response pattern of fledglings may incorporate several factors or motivations at the same time.

Whether acoustic responses to unrelated adults are recognition errors or represent a cheating strategy to solicit food largely depends on the ability of parents to recognize their own young. False responses are potentially costly in terms of attracting predators (e.g. Briskie et al. 1999; Lima 2009) and adults are known to attack unrelated offspring that solicit extensively for food (Proffitt & McLean 1990; Hauber 2002). If parents are not able to recognize their own offspring acoustically from unrelated young, however, fledglings are not expected to face the cost of attacks by nonparents. In such a scenario cheating is likely to occur. In previous studies on zebra finches we found a significant number of fledglings being fed by unrelated adults within the same aviary (Jacot et al. 2010), as well as indications that parents might not be precise at recognizing their own young acoustically (Reers et al. 2011). Adopting a cheating strategy under such 'environmental conditions' might be beneficial where fledglings can plastically adjust their response pattern in relation to positive or negative feedback of adult birds. Such a cheating strategy might be more widespread and not be limited towards similar-sounding unrelated adults, since we found no relationship between adult call similarity and call similarity among their offspring (Fig. 4).

Implicit in the cheating hypothesis is a potential benefit for a responding fledgling. While the benefit in the cheating hypothesis is an additional amount of food, a responding chick may get any other social reward in our third 'social urge' hypothesis. A certain

level of responsiveness even to very dissimilar nonparents can be interpreted as baseline responsiveness to conspecifics, with familiar calls triggering a higher response than unfamiliar calls. Baseline responsiveness may be beneficial in a social context, for example to maintain contact within a flock (Zann 1996). This interpretation is supported by the finding that precision of recognizing parents is rather high in fledglings, making recognition errors unlikely, unless there is a high degree of similarity. Baseline responsiveness to conspecifics in a social context, and this may include potential food rewards, may therefore be a likely explanation for responses to dissimilar adult calls.

Our study provides some interesting insights into the process of acoustic recognition in fledgling zebra finches specifically and, in a more general way, into the role of acoustic similarity in communication among conspecifics. These findings may have wider implications in other communication systems and further studies with elaborate experimental designs are clearly needed to clarify the exact mechanism responsible for an increased response relative to signal similarity.

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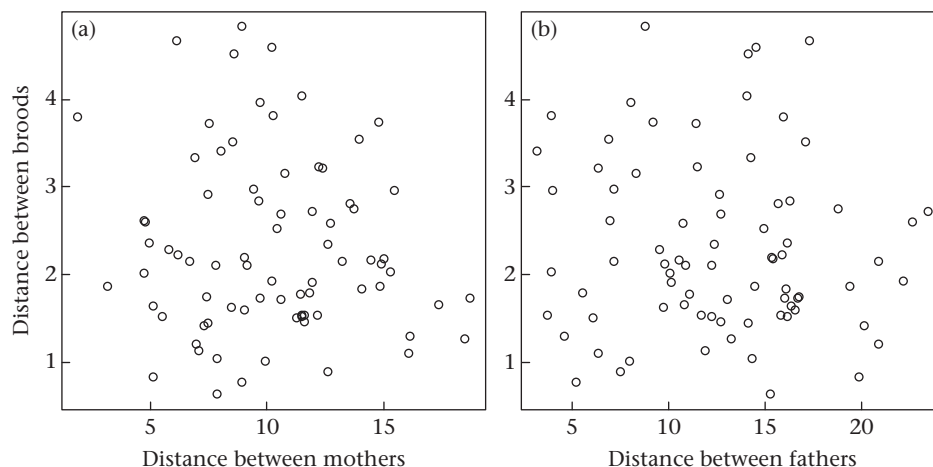


Figure 4. Acoustic similarities between (a) mothers of two broods and among their respective broods and (b) fathers of two broods and among their respective broods, for all possible comparisons (13 broods, 78 possible comparisons).

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Appendix

Table A1

Test statistics for GLMMs on responses of fledglings towards parents and similarity category 1

		Estimate	SE	t	P
Number of calls (Poisson distribution)	Intercept	0.2624	0.2927	0.8965	0.370
	Sex of parent	−0.0542	0.1152	−0.4708	0.638
	Sex of fledgling	0.1534	0.2307	0.6649	0.506
	Dumped egg	0.2599	0.6586	0.3946	0.693
	Extrapair paternity	−0.4072	0.3066	−1.3279	0.184
	Acoustic similarity	−0.6728	0.1153	−5.8327	0
	Latency to respond (square-root-transformed)	Intercept	25.6723	2.5334	10.1334
Sex of parent		−0.0296	1.1754	−0.0252	0.980
Sex of fledgling		−0.9057	1.8313	−0.4946	0.621
Dumped egg		−6.079	4.934	−1.2321	0.218
Extrapair paternity		−0.0872	2.3927	−0.0365	0.971
Acoustic similarity		6.3845	1.1582	5.5122	0
Call duration		Intercept	194.1722	12.2961	15.7913
	Sex of parent	−2.0656	4.4678	−0.4623	0.644
	Sex of fledgling	4.8428	9.7223	0.4981	0.618
	Dumped egg	−11.6794	26.8217	−0.4354	0.663
	Extrapair paternity	−2.0929	13.7358	−0.1524	0.879
	Acoustic similarity	−17.6782	4.3537	−4.0605	<0.001

(continued on next page)

Table A1 (continued)

		Estimate	SE	<i>t</i>	<i>P</i>
Call amplitude	Intercept	45.6209	1.3367	34.1283	0
	Sex of parent	-0.7324	0.4143	-1.7679	0.078
	Sex of fledgling	-0.0138	1.1454	-0.0121	0.990
	Dumped egg	-2.2244	3.2129	-0.6924	0.489
	Extrapair paternity	0.8702	1.5851	0.549	0.583
Call amplitude modulation (square-root-transformed)	Acoustic similarity	-1.3373	0.4024	-3.3235	0.001
	Intercept	0.1091	0.0033	33.4146	0
	Sex of parent	0.0013	0.0011	1.1141	0.265
	Sex of fledgling	-0.0053	0.0024	-2.2233	0.026
	Dumped egg	-0.001	0.0065	-0.1493	0.881
Call frequency	Extrapair paternity	0.0019	0.0036	0.5114	0.609
	Acoustic similarity	0.0023	0.0011	2.1109	0.035
	Intercept	3652.365	85.9832	42.4777	0
	Sex of parent	-21.8202	29.2175	-0.7468	0.455
	Sex of fledgling	0.7699	78.2833	0.0098	0.992
Call frequency modulation (log-transformed)	Dumped egg	-120.726	219.4366	-0.5502	0.582
	Extrapair paternity	23.3381	98.6939	0.2365	0.813
	Acoustic similarity	-109.442	28.3647	-3.8584	<0.001
	Intercept	2.7044	0.0708	38.1941	0
	Sex of parent	0.0172	0.0215	0.7988	0.424
Call entropy	Sex of fledgling	-0.068	0.0643	-1.0587	0.290
	Dumped egg	-0.0811	0.1808	-0.4489	0.654
	Extrapair paternity	0.0115	0.0845	0.1361	0.892
	Acoustic similarity	0.0442	0.0208	2.1236	0.034
	Intercept	-2.3518	0.106	-22.1935	0
	Sex of parent	0.0232	0.0353	0.6586	0.510
	Sex of fledgling	-0.0013	0.0938	-0.0139	0.989
	Dumped egg	0.015	0.2633	0.0571	0.954
	Extrapair paternity	-0.119	0.1227	-0.9696	0.332
	Acoustic similarity	0.1039	0.0343	3.032	0.002

Table A2

Test statistics for GLMMs on responses of fledglings towards nonparents of similarity category 1–3

		Estimate	SE	<i>T</i>	<i>P</i>
Number of calls (Poisson distribution)	Intercept	-0.4564	0.2817	-1.6201	0.105
	Sex of parent	-0.1444	0.0862	-1.6746	0.094
	Sex of fledgling	0.0008	0.2405	0.0035	0.997
	Dumped egg	0.2264	0.6843	0.3309	0.741
	Extrapair paternity	-0.6128	0.3046	-2.0117	0.044
Latency to respond (square-root-transformed)	Acoustic similarity	-0.1806	0.0528	-3.4215	<0.001
	Intercept	31.9479	2.5082	12.7372	0
	Sex of parent	1.3768	1.0388	1.3254	0.185
	Sex of fledgling	0.3729	1.6981	0.2196	0.826
	Dumped egg	-4.0968	4.4135	-0.9282	0.353
Call duration	Extrapair paternity	-0.9252	2.1578	-0.4288	0.668
	Acoustic similarity	2.2207	0.6271	3.5415	<0.001
	Intercept	178.2257	10.6818	16.685	0
	Sex of parent	-3.4721	3.368	-1.0309	0.303
	Sex of fledgling	-1.158	8.3934	-0.138	0.890
Call amplitude	Dumped egg	-17.2439	22.6973	-0.7597	0.447
	Extrapair paternity	-5.375	11.6389	-0.4618	0.644
	Acoustic similarity	-6.991	2.0136	-3.4719	<0.001
	Intercept	44.3714	1.2883	34.4406	0
	Sex of parent	-0.6663	0.3376	-1.9737	0.048
Call amplitude modulation (square-root-transformed)	Sex of fledgling	-1.1275	1.1296	-0.9981	0.318
	Dumped egg	-2.7029	3.1209	-0.8661	0.386
	Extrapair paternity	1.0043	1.5103	0.665	0.506
	Acoustic similarity	-0.5319	0.2012	-2.6435	0.008
	Intercept	0.1084	0.0033	32.9403	0
Call frequency	Sex of parent	0.0006	0.001	0.6096	0.542
	Sex of fledgling	-0.0034	0.0027	-1.2825	0.200
	Dumped egg	-0.0033	0.0072	-0.4541	0.650
	Extrapair paternity	0.0051	0.0037	1.3837	0.166
	Acoustic similarity	0.0015	0.0006	2.5868	0.010
	Intercept	3452.281	89.3854	38.6224	0
	Sex of parent	-18.4815	25.991	-0.7111	0.477
	Sex of fledgling	-41.7127	79.8484	-0.5224	0.601
	Dumped egg	-168.959	219.9906	-0.768	0.442
	Extrapair paternity	24.8021	100.6628	0.2464	0.805
	Acoustic similarity	-14.9308	15.516	-0.9623	0.336

Table A2 (continued)

		Estimate	SE	<i>T</i>	<i>P</i>
Call frequency modulation (log-transformed)	Intercept	2.7016	0.0661	40.8458	0
	Sex of parent	0.0001	0.0191	0.006	0.995
	Sex of fledgling	−0.017	0.0597	−0.2845	0.776
	Dumped egg	−0.1235	0.1649	−0.7489	0.454
	Extrapair paternity	0.0534	0.0749	0.7137	0.475
Call entropy	Acoustic similarity	0.0268	0.0114	2.3595	0.018
	Intercept	−2.2887	0.1012	−22.6265	0
	Sex of parent	0.037	0.0274	1.3509	0.177
	Sex of fledgling	0.0871	0.0919	0.9477	0.343
	Dumped egg	−0.0302	0.2542	−0.1187	0.906
	Extrapair paternity	−0.0363	0.1174	−0.3088	0.757
	Acoustic similarity	0.0311	0.0163	1.9099	0.056