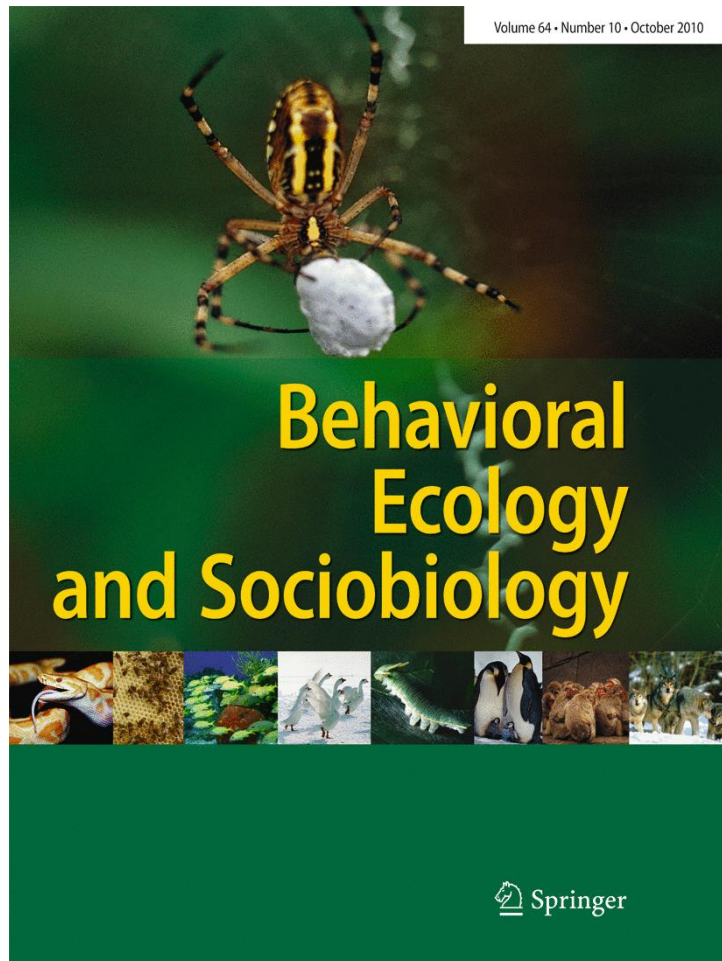


**ISSN 0340-5443, Volume 64, Number 10**



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# Individual recognition and potential recognition errors in parent–offspring communication

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Received: 15 November 2009 / Revised: 4 March 2010 / Accepted: 16 April 2010 / Published online: 30 April 2010  
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**Abstract** The recognition of food-provisioning parents is crucial for fledglings of many bird species. Vocalizations are the most commonly used cues in avian parent–offspring communication, and it has been shown in several species that fledglings respond specifically to their parents' contact calls. However, fledglings occasionally also react to unrelated adults. Such responses may reflect recognition errors or alternatively a strategy of fledglings to obtain food or other direct benefits from unrelated adult birds. In a playback experiment, we tested whether zebra finch *Taeniopygia guttata* fledglings perceive variation in adult call signatures to recognize their parents and whether the propensity to respond to unrelated individuals is related to the gender of adults and to signal properties of male and female calls. Male calls are learnt and show high intra-sexual variation, which may improve the accurate recognition of the father's individual signature. In contrast, calls of adult females are innate, show lower intra-sexual variation such that the mother's call is more likely to be confused

with another female call. We demonstrate that fledglings are able to recognize their parents. In addition, fledglings reacted more strongly to unrelated females compared with unrelated males. Our findings suggest that responses to unrelated adults may reflect recognition errors and indicate the importance of variation in identity signals for individual recognition processes in parent–offspring communication.

**Keywords** Parent–offspring recognition · Brood division · Begging · Parental care · Bioacoustics · *Taeniopygia guttata*

In many animal species, parents provide resources to their offspring before independence (Clutton-Brock 1991). By providing parental care, parents invest time and energy into their progeny thereby increasing their own fitness via producing viable offspring. From an offspring's perspective, the amount of resources they receive from their parents positively affects their survival (e.g., Perrins 1965) and the likelihood to reproduce and recruit into the breeding population (Both et al. 1999; Tinbergen and Boerlijst 1990). The importance of parental care for the fitness of offspring has led to accurate recognition systems where fledglings use specific cues to recognize their parents.

Vocalizations are commonly used recognition cues in birds since they can be used over long distances (e.g., Charrier et al. 2001) and when visual contact is restricted. Many chicks of colonially breeding species like penguins (Jouventin and Aubin 2002; Searby and Jouventin 2005; Searby et al. 2004), murrelets (Jones et al. 1987; Lefevre et al. 1998), and swallows (Leonard et al. 1997; Medvin and Beecher 1986; Medvin et al. 1992, 1993) use acoustic cues to identify their parents. Such recognition systems are

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Communicated by M. Hauber

**Electronic supplementary material** The online version of this article (doi:10.1007/s00265-010-0965-5) contains supplementary material, which is available to authorized users.

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especially likely to evolve where offspring could potentially confuse their own mother and father with other food-provisioning parents. This is the case in large breeding colonies and in species showing extended post-fledging care where parents can no longer use spatial cues, i.e., the nest, to locate their brood (Tibbetts and Dale 2007). Recognition cues may also evolve whenever parents show specific preferences in their long-term interactions with their offspring, feeding only a subset of fledglings within a brood (“brood division”, reviewed in Leedman and Magrath 2003). Thus, parent–offspring recognition may involve class-level recognition (i.e., class being both parents) as well as individual recognition (i.e., individual parents). While there is ample evidence that fledglings of many species recognize their parents, it remains unexplored whether offspring actually use “family” or individual signatures in parent–offspring communication.

Despite the evidence that fledglings recognize and specifically respond to their parents' calls, it is also known that fledglings sometimes respond to unrelated adults. These responses may reflect a strategy of fledglings in order to obtain food and other direct benefits from adult birds (Sealy and Lorenzana 1997; Shy 1982). Alternatively, responding to unrelated adults may reflect recognition errors where fledglings confuse unrelated adults with their parents. This definition of recognition error is based on studies demonstrating that parents recognize their offspring using acoustic cues (Beecher et al. 1981a; Buckley and Buckley 1972; Draganoiu et al. 2006; Lessells et al. 1991) and that responding to unrelated adults incurs costs. Adults are known to attack unrelated offspring that solicit extensively for food (Beecher et al. 1981b; Hauber 2002; Proffitt and McLean 1991). In addition, enhanced calling, without parental food rewards, needlessly increases the risk of attracting predators (Briskie et al. 1999; Haskell 1994; Lima 2009; McDonald et al. 2009). Such recognition errors are expected to be common in communication systems with low signal variation and whenever the identity signal is close to the modal, i.e., the most common signature. Selection for accurate parent–offspring recognition should favor individuals or parents with distinct signals, since these individuals will be more easily recognized and less likely to be confused with others (Dale et al. 2001).

Here, we use a captive population of Australian zebra finch *Taeniopygia guttata* which is an opportunistic breeder with biparental care (Zann 1996) to study individual recognition in parent–offspring communication after fledging. Zebra finches are ideal study organisms since they breed in loose colonies (Zann 1996), and offspring are fed during an extended post-fledging phase by their parents (Zann 1996). Recognition systems are expected to evolve under such breeding conditions, where offspring could potentially confuse their own mother and father with other

food-provisioning parents, and we predict the spread of individual signatures in distance calls. After fledging, offspring start to elicit this specific distance call that is used in the context of parent–offspring communication and is replaced by the begging call once the parents have approached (also called “long tonal call” in Zann (1996)). This distance call is not only used in the context of food-provisioning but also whenever fledglings try to re-unite with their parents. In addition, individual signatures in distance calls may be important during social interactions within a flock and for mate recognition at the adult stage (Vignal et al. 2008).

Such a communication system allows testing critical hypotheses of parent–offspring recognition and identity signaling. Specifically, we test whether offspring can discriminate between distance calls of their own parents (mother and father) and unrelated adults. We predict that fledglings are able to recognize their parents and will respond stronger to their parents than to non-parents. A stronger response can be manifested through an increase in number of response calls, shorter latency to respond, and/or changes in call characteristics related to call urgency or motivational status (Morton 1977). In addition, we test whether an offspring's response to unrelated individuals is related to the gender of adult calls. It is known that male distance calls are learned and show high variability while female calls are innate and show relatively low variation (Forstmeier et al. 2009; Zann 1996). In the light of these sex-specific developmental trajectories of adult calls, we predict that offspring will commit more recognition errors in relation to female calls and will therefore respond more often to unrelated female than unrelated male calls. Alternatively, the response pattern to unrelated adults may reflect a chick's strategy due to behavioral differences, namely aggressiveness or discriminatory abilities in feeding behavior, of males and females. Here, we collect data about adult call variability and adult behavior to assess whether a fledgling's response pattern to unrelated adults is more likely to reflect recognition errors or a feeding strategy.

## Methods

### Subjects and housing

Fledgling zebra finches (*T. guttata*) used in the present study were from a captive population held at the Max Planck Institute for Ornithology in Seewiesen, Germany (imported from Sheffield University/UK). All fledglings tested in this study are descendants from birds breeding in one of six aviaries each of which held six breeding pairs. The sex of the offspring was determined using molecular methods (Griffiths et al. 1998). Temperature in the rooms

was maintained at  $24 \pm 1^\circ\text{C}$  and relative humidity ranging 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 November 2007 and February 2008. Nestlings were weighed and color-banded with a brood-specific plastic color ring at 8 days of age. Aviaries were checked twice a day for newly fledged birds.

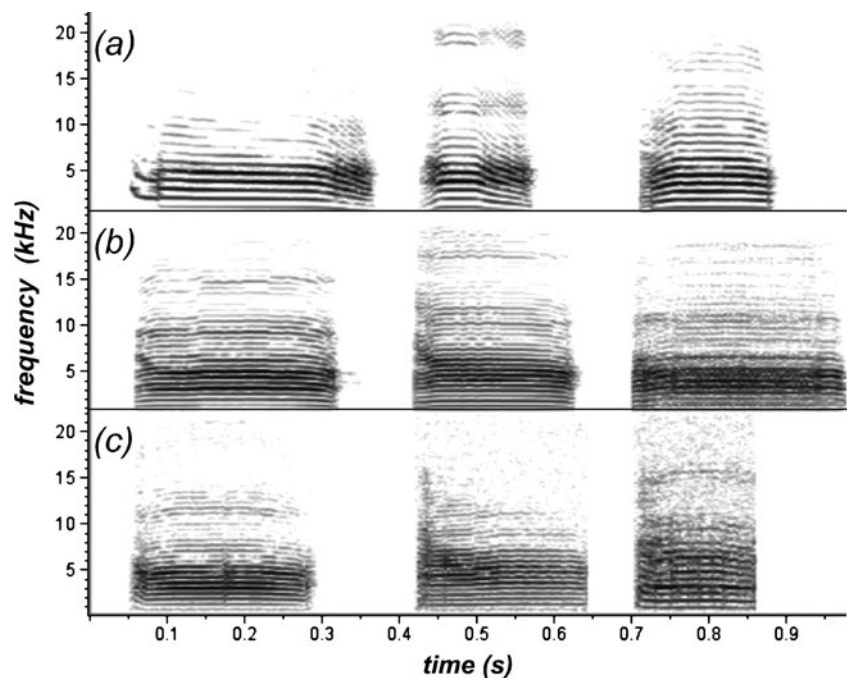
#### Playback protocol

The playback experiment was intended to simulate a situation where a fledgling lost visual and acoustic contact to its parents. In this context, fledglings are expected to react to distance calls of their parents (Zann 1996). Recently, fledged chicks ( $4.59 \pm 2.01$  days after fledging, range 1–9 days) were transferred from their natal aviary to a sound-attenuated chamber ( $70 \times 50$  and 50 cm) equipped with a small metal wire cage containing a single perch, a microphone (C2, Behringer GmbH, Willich), and a small loudspeaker (I-Trigue, Creative Ltd., Dublin). We recorded (sampling rate, 44 kHz; amplitude resolution, 16 bit) the fledglings' response calls with a microphone that was connected to a solid state recorder (Microtrack II, M-Audio, Irwindale). Fledglings were allowed a 2-min "acclimation phase" in the new experimental cage, before the recognition trials started. Preliminary tests had shown

that fledglings calm down shortly after transferring them to the sound-attenuated chamber and the relatively short "acclimation period" of 2 min proved to be long enough for testing a fledgling's response to adult calls.

In a playback experiment, we investigated a fledgling's acoustic response to its social parent's calls and to calls of unrelated adults (for examples of distance calls see Fig. 1). The stimulus calls of the genetically unrelated female and male (mean relatedness between chicks and unrelated adults:  $r=0.019$ , max  $r=0.125$ . Relatedness was measured based on a pedigree of five generations and calculated with the software Pedigree Viewer 5.1.) were calls of randomly chosen adults from this study population that lived in a different, acoustically separated room than the fledglings. For each fledgling within a brood, we played back different unrelated adult calls. To find the most representative call recording for each individual, we proceeded as follows (see Forstmeier et al. 2009 for details). We extracted from each call recording of every bird recorded in our population ( $N=13,815$  calls of 806 individuals) 33 call parameters that are routinely calculated by SAP version 2.063 (Tchernichovski et al. 2004) as well as the first 12 mel-frequency cepstral coefficients calculated by Voicebox (Speech Processing Toolbox for MATLAB, written by M. Brookes, Imperial College, UK; <http://www.ee.ic.ac.uk/hp/staff/dmb/voicebox/voicebox.html>). These 45 call parameters were reduced to 12 principal components with Eigenvalues larger than one, and we calculated for every individual the centroid in this 12-dimensional space across its repeated recordings. We then took the euclidian distances of each

**Fig. 1** Sonograms showing inter-individual variation in distance calls of three different males (a), females (b), and fledglings (c)



call from the individual's centroid and selected the recording that showed the smallest deviation. The same adult stimulus call was repeatedly used for all playback trials with the same fledging subject. Using a single call per individual will lead to inflated variance components of the random terms (i.e., individual and brood) but will lead to correct test statistics of the fixed effects, hence our analyses do not face the problem of pseudoreplication. Each fledgling was only tested once and presented with four series of different stimulus calls: mother, father, unrelated female, and unrelated male. Each series lasted 30 s and contained a first part of 10 s where the stimulus call was repeatedly played back three times at intervals of 5 s (i.e., at 0, 5, and 10 s from the start of the series). The playback phase was followed by a silent period of 20 s and followed by a new series with another stimulus call. The four series were broadcasted at random and repeated once, i.e., we investigated a fledgling's acoustic response to six stimulus calls of its father, mother, and unrelated male and female. We tested for order of presented stimuli effects on the absolute and relative response to both parents and to calls of unrelated adults. Order effects never explained a significant part of the variation and were not included in the final models.

#### Fledgling call rate

We quantified the acoustic response of fledglings (83 individuals from 30 broods) to stimulus calls by measuring (1) the number of calls within 5 s following the stimulus calls and (2) the latency (milliseconds), measured as the time between the end of the stimulus call and the chick's first response call. Six out of 83 chicks never responded to any stimulus call and were excluded from further analyses. If a chick did not respond to a stimulus call, we scored number of response calls as 0, while latency was not scored. Accordingly, sample sizes and therefore also denominator degrees of freedom in the analyses differ when analyzing treatment effects on call number and call latency. In cases where the chick's response call overlapped the stimulus call, latency was scored as zero. Latency and the number of calls are correlated ( $r = -0.451$ ,  $p < 0.001$ ,  $N = 209$ ), i.e., the more a chick responded to a stimulus, the shorter the latency. For analysis, both parameters were combined by calculating the first PC of the principal components analysis. Principal component 1 explained 71.85% of the variation.

#### Fledgling call characteristics

In addition, we quantified acoustic parameters of the fledglings' response calls using Sound Analysis Pro (SAP) software (Tchernichovski et al. 2004, [http://ofer.sci.ccnycunyu.edu/html/sound\\_analysis\\_pro](http://ofer.sci.ccnycunyu.edu/html/sound_analysis_pro)).

SAP is specifically developed for the analysis of spectral-based features of zebra finch vocalizations. Compared with other methods that use visually assessed measurements from spectrograms, SAP uses complex algorithms to calculate values for each millisecond of the call and provides means and variances of those values (Tchernichovski et al. 2004). For all our analysis, we used the default settings of SAP. Response calls were selected and analyzed using the batch module of Sound Analysis Pro. For analysis, we used the response call with the best signal-to-noise ratio (i.e., the loudest call) elicited after each stimulus call. We refrained from analyzing all acoustic parameters and focused on acoustic parameters that are suggested to relate to motivational status and call urgency in birds (Morton 1977). These parameters were mean amplitude (decibels), amplitude modulation, call length (millisecond) (Ficken 1990; Leavesley and Magrath 2005), mean frequency (Hertz; Ficken 1990; Leavesley and Magrath 2005), and frequency modulation. Frequency modulation is estimated based on time and frequency derivatives across frequencies. If the frequency derivatives are much higher than the time derivatives, frequency modulation is low and vice versa (for details see Tchernichovski et al. 2004). Amplitude modulation is the overall time-derivative power across all frequencies within a range (for details see Tchernichovski et al. 2004). Mean frequency provides a smooth estimate of the center of derivative power. In contrast to peak frequency, mean frequency does not “stick” to any frequency trace (for details see Tchernichovski et al. 2004).

#### Adult behavior in parent–offspring interactions

Observations of adult behavior were carried out throughout the breeding season (50 sessions of 5 min for each of the six aviaries, i.e., 25 h in total). We recorded (1) whether adult birds fed their own or unrelated offspring and (2) aggression of adult birds towards fledglings. In total, we recorded 56 feeding events by 15 different males and 49 events by 17 different females. Adult attacks on fledglings were observed 330 times involving 34 out of the 36 males and 32 out of the 36 females.

#### Statistical analyses

##### *General statistical methods*

All statistical analyses were performed with R2.8.0 (R Development Core Team 2008). The standard model diagnostics of non-normal errors, non-constant error variance, and the presence of outliers were performed on each of the final models according to Fox (2002). In all mixed model analyses, we used a stepwise backward procedure

and tested the significance of predictor variables in a hierarchical fashion, retaining lower-order effects in the analyses in case a higher-order term was significant.

#### *Fledgling call rate and call characteristics*

To analyze the effects of stimulus calls on a fledgling's quantitative (number of response calls, time to first response call) and qualitative (call parameters) response, we used linear mixed-effects models (package *nlme*, Pinheiro et al. 2006) with the sex of the adult (two levels; i.e., male, female), relatedness (two levels, i.e., parents, unrelated) and the sex of the offspring (two levels; i.e., male, female) as fixed factors, and individual nested within brood (i.e., social pair, 30 levels) as a random factor. Age after fledging was initially included as a covariate in all analyses. As it never explained a significant part of the variation, it was excluded from the final models. The denominator degrees of freedom of the test statistics of mixed models are computed according to Pinheiro and Bates (2000, page 91).

We tested whether fledglings responded to both parents with the same number of response calls or showed a preference towards one parent. For this analysis, we run separate chi-square tests for each chick, comparing the number of response calls towards mother and father. Fisher's combined probability was used to combine probabilities of chi-square tests of each chick.

#### *Sex differences in call variability*

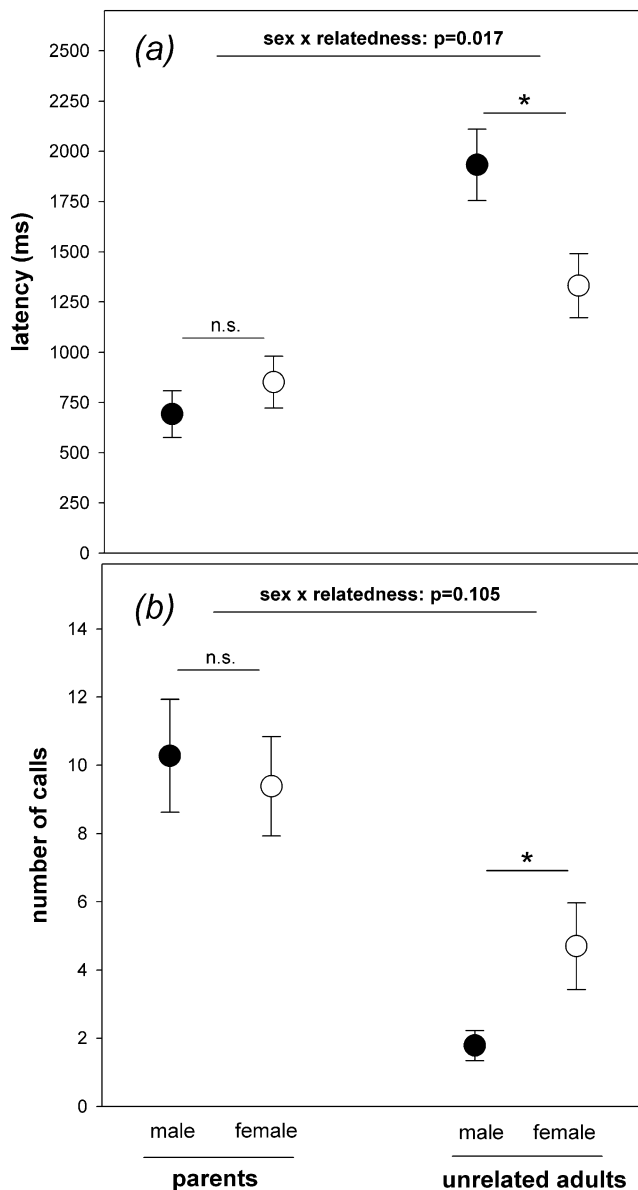
To test for sex differences in adult distance calls and to quantify individual differences in distance calls for both adult females and males, we performed three separate discriminant function analyses (DFAs; package *MASS*, Venables and Ripley 2002). All DFAs were done using ten acoustic parameters (call duration, mean pitch, mean principal contour, mean frequency modulation, mean entropy, mean pitch goodness, mean frequency, variance in frequency modulation, variance in entropy, and variance in amplitude modulation). Parameters were BoxCox transformed prior to the DFA to approach a normal distribution. For the DFA on sex differences, we used a randomly selected single call from 30 adult females and 30 adult males. For the DFAs on intra-sex differences, we used ten calls per individual and a total of 27 individuals per sex. The calls were randomly selected for each individual. For all DFAs, a cross-validated (leave-one-out) procedure was used to fit a left out call into the multidimensional signal space calculated from all calls but the one left out. The correct assignment rate was calculated as the percentage of calls assigned to the correct sex or individual, respectively.

## Results

### Vocal recognition in parent–offspring communication

From a total of 83 tested fledglings, six chicks did not respond to any adult call. Fifty-nine fledglings responded to both the calls of parents and unrelated adults. Fourteen fledglings reacted to their parents only, while four individuals responded to unrelated adult calls only and not to their parents' calls. In a first model, we analyzed the effect of relatedness on a fledgling's response. Fledglings reacted faster (call latency; relatedness:  $F_{1,153.3}=34.48$ ,  $p<0.001$ ) and with more calls (number of calls: relatedness:  $F_{1,245}=31.40$ ,  $p<0.001$ ) towards distance calls emitted by their parents than to distance calls of unrelated adult calls (Fig. 2). In a second step, we analyzed a fledgling's response in relation to the gender and relatedness of adult calls. The latency of a chick's first response call depended on the relatedness but additionally on the sex of the adult stimulus call (sex x relatedness,  $F_{1,154}=5.98$ ,  $p=0.017$ , Fig. 2a). In a post hoc approach, we analyzed the reaction towards parents and unrelated adults separately. The reaction towards father and mother did not differ ( $F_{1,61.8}=1.07$ ,  $p=0.31$ , Fig. 2a), whereas fledglings reacted faster towards unrelated females versus unrelated males ( $F_{1,48.1}=6.83$ ,  $p=0.01$ , Fig. 2a). A similar response pattern was found in relation to number of response calls. The reaction towards father and mother did not differ ( $F_{1,82}=0.19$ ,  $p=0.67$ , Fig. 2b), whereas fledglings reacted faster towards unrelated females versus unrelated males ( $F_{1,82}=5.63$ ,  $p=0.02$ , Fig. 2b). The interaction between sex and relatedness for call number was not significant (sex x relatedness,  $F_{1,246}=2.73$ ,  $p=0.10$ , Fig. 2b). Combining both measures using a principal component analysis, we found that the reaction towards adult calls depended on the relatedness but additionally on the sex of the adult (PC1; sex x relatedness,  $F_{1,152}=4.57$ ,  $p=0.034$ ). The sex of the offspring had no effect on call latency ( $F_{1,62.3}=1.90$ ,  $p=0.17$ ) and the number of response calls ( $F_{1,79.70}=0.10$ ,  $p=0.76$ ) or PC1 ( $F_{1,65.80}=0.41$ ,  $p=0.52$ ).

The response pattern of fledglings towards calls of unrelated adults might be related to the frequency of male versus female feedings of unrelated offspring or to male versus female aggressiveness towards fledglings. On average, males were feeding fledglings that were not their social offspring in 41% of their feedings ( $N=56$  feeding observations on 15 males), and females fed non-social offspring in 65% of their feedings ( $N=49$  observations on 17 females). Male and female feeding behavior did not differ significantly (glm with quasibinomial error distribution;  $t_{30}=-1.48$ ,  $p=0.15$ ). Throughout all of our observation sessions, the average male was seen to attack a fledgling 5.2 times, while the average female attacked



**Fig. 2** Fledglings' response **a** call latency, **b** number of response calls, in relation to distance calls of their parents and unrelated adults. Shown are means $\pm$ SE. Significance is indicated with *asterisks*, where *one asterisk* means  $p < 0.05$

fledglings 4.0 times. Again, aggressiveness towards fledglings was not significantly different between males and females ( $t$  test on sqrt-transformed data;  $t_{70} = 1.28$ ,  $p = 0.21$ ).

Call characteristics of fledglings differed in their response to parents and unrelated adults. For the comparison of call characteristics, we only used individuals that responded to their parents and to the same sex of unrelated adults. There were 40 fledglings that reacted to both female calls and 29 individuals that reacted to both male calls. Individuals that responded to both female calls, responded louder, at a higher mean frequency, and the calls were longer towards their mother while there were no effects on

frequency modulation and amplitude modulation (Table 1). The same pattern was found in individuals that responded to both male calls. Calls emitted towards their father were louder, at a higher mean frequency, and the calls were longer while there were no effects on frequency modulation and amplitude modulation (Table 1). Overall, the calls emitted towards parents were of a higher urgency compared with response calls towards unrelated adults. The sex of the offspring had no effect on any of the measured call characteristics (all  $p > 0.12$ ).

#### Individual recognition in parent–offspring communication

Figure 3 illustrates the proportion of response calls each nestling emitted towards its mother and father. Thirteen (nine male, four female) fledglings reacted towards the mother only, whereas 13 (eight males, five females) fledglings responded only towards the father. The sex of the offspring did not affect the relative reaction towards both parents (Mann–Whitney U Test,  $U = 562.5$ ,  $p = 0.36$ ). Visual inspection of Fig. 4 indicates a “complex” distribution with two distinct peaks around 0 and 1. Fledglings either reacted to their father (i.e., values close to 0), their mother (i.e., values close to 1), or to both parents (i.e., values between 0 and 1). The response pattern clearly deviates from a normal, unimodal distribution (Fisher's Combined Probability,  $722.22 > 176$ ,  $p < 0.001$ ;  $\chi_{0.001, 122}^2 = 176$ ) and fledglings that responded to a single parent only (13 towards mother, 13 towards father) are highly overrepresented. These findings indicate that at least some fledglings use individual signatures, possibly in combination with signatures that code for the sex of an adult bird, to recognize their parents.

#### Response to unrelated adults

The response to unrelated females depended on a fledgling's relative response towards its parents. Fledglings that showed a preference for their mother also reacted more towards unrelated females than unrelated males. Out of 27 fledglings that showed a preference for their mother, 24 responded significantly more towards an unrelated female (binomial test,  $p < 0.001$ ). In contrast, a preference for their father had no effect on reaction towards unrelated males and females. Out of 21 fledglings that reacted stronger towards their father, only 12 responded more to unrelated males (binomial test,  $p = 0.66$ ).

The response to unrelated adults depended on whether fledglings responded to one or both parents. Out of those 26 individuals that responded to a single parent only, 12 also reacted towards unrelated parents. In contrast, 42 out of 47 fledglings that reacted to both parents also reacted to unrelated adults. Individuals that reacted to both parents

**Table 1** Means±SE, estimates, and test statistics of response calls of fledglings towards distance calls of parents (mother, father) and unrelated adult (female, male) calls

	Mother	Father	Female	Male	Comparison	Estimates	SE	df	<i>t</i>	<i>p</i>
Amplitude (dB)	32.11±1.00	29.48±1.34	29.96±0.93	26.08±1.31	Mother vs. female Father vs. male	2.15 3.00	0.92 1.06	39 28.36	2.34 2.82	0.025 0.009
Call length (ms)	215.80±11.67	201.39±168.70	190.43±9.88	168.70±10.67	Mother vs. female Father vs. male	25.38 31.11	10.32 13.90	39 28.77	2.46 2.24	0.019 0.033
Mean frequency (Hz)	3991.85±81.53	3819.32±101.49	3764.68±84.37	3553.20±89.14	Mother vs. female Father vs. male	218.20 238.80	84.09 98.65	38.08 28.66	2.60 2.42	0.013 0.022
Frequency modulation	16.23±1.37	15.84±1.68	16.37±1.34	15.02±1.25	Mother vs. female Father vs. male	0.19 0.63	1.45 1.64	33.61 28.87	0.13 0.38	0.90 0.70
Amplitude modulation (1/ms)	0.0092±0.0005	0.0092±0.0007	0.0093±0.0005	0.0079±0.0006	Mother vs. female Father vs. male	0.0004 0.001	0.0006 0.0007	34.42 28.59	0.07 1.67	0.94 0.11

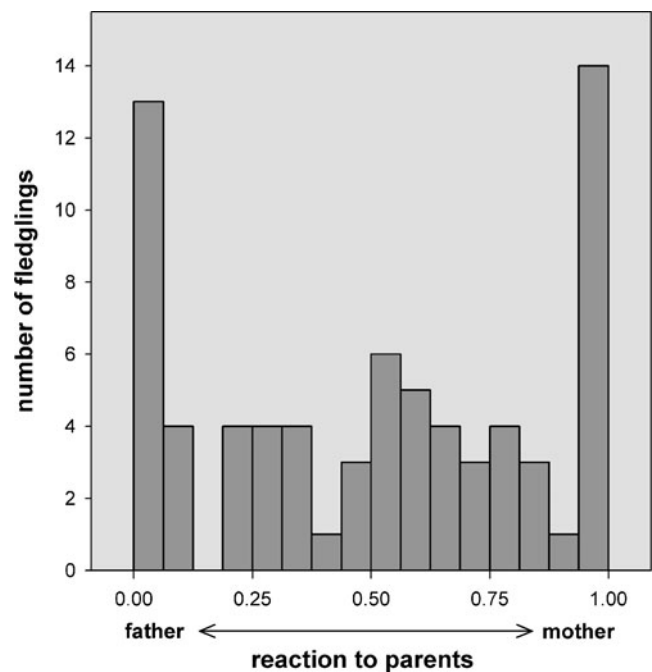
Note that frequency modulation does not have a unit

were more likely to respond to unrelated adults compared with fledglings that reacted to a single parent only (Fisher's exact test:  $p < 0.001$ , odds ratio=9.42). Body mass at day 8, as an indicator of past growing conditions, did not predict whether fledglings responded to one or both parents ( $t$  test,  $t_{1,70}=0.10$ ,  $p=0.92$ ).

#### Recognition errors—call variability of female and male calls

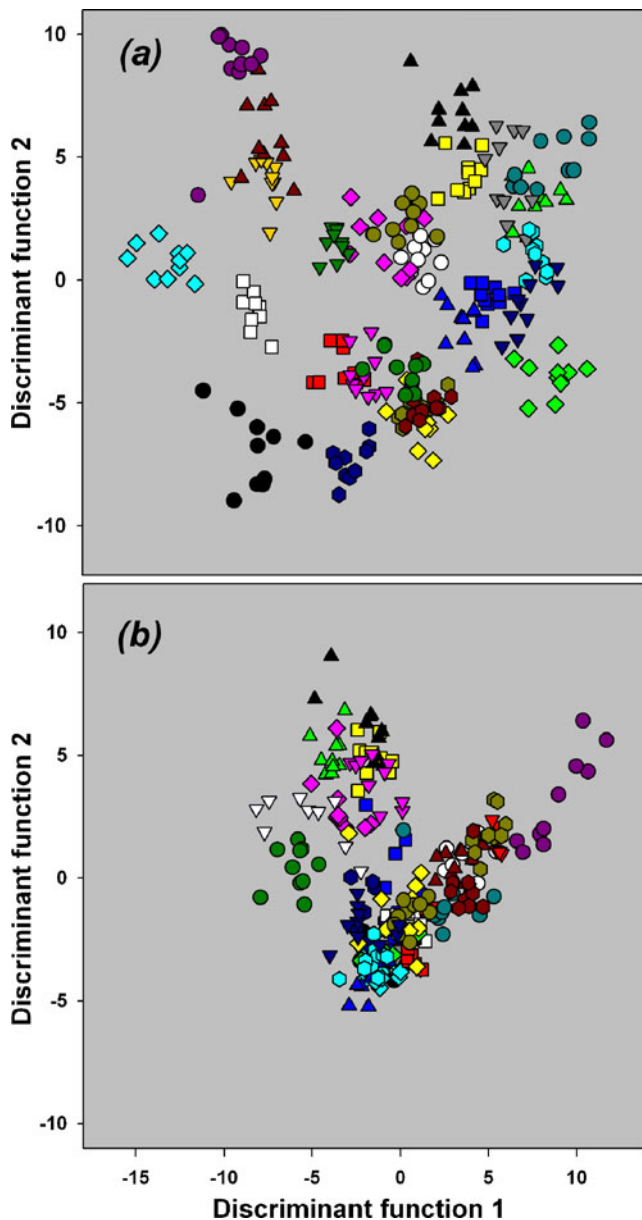
A DFA using a single call of 60 individuals (30 individuals/sex) reveals that 54 calls (26 male calls, 28 female calls, overall 90%) got assigned to the right sex. The calls of both sexes are highly distinctive and can be discriminated better than by an expected 50% correct assignment by chance (binomial test,  $p < 0.001$ ).

In a second step, we investigated sex-specific variation in distance calls. Some 72% of the female calls (194 out of 270) were assigned to the correct individual while male calls showed a 95% (257 out of 270) correct assignment rate (Fig. 4a, b). In both sexes, calls are individually distinct, but the assignment probability for male calls is significantly higher than for female calls ( $t$  test,  $t_{52}=4.03$ ,  $p < 0.001$ ).



**Fig. 3** Frequency distribution of fledglings' response pattern towards their mother and father. Illustrated is the relative response in proportions, where values of 0 and 1 refer to fledglings that reacted to a single parent only. Note that one bin covers 6.25%, e.g., the last bin covers the range from 93.75% to 100%





**Fig. 4** Discriminant analyses based on 27 males (**a**) and females (**b**). Plotted are the two first discriminant functions that explain 68.8% (DF1, 42.7%; DF2, 26.1%) of the variation in males and 67.7% (DF1, 36.0%; DF2, 31.7%) of the variation in females. Note that the DFA's produced ten discriminant functions and the figure therefore underestimates the differences in call signatures between individuals

## Discussion

Our study demonstrates that zebra finch fledglings recognized their parents and that many fledglings responded to distance calls of unrelated adults. The significant interaction term between sex and relatedness on latency and our combined measure of response latency and the number of response calls (i.e., PC1) demonstrates that offspring reacted more towards unrelated females than unrelated males. This sex-specific response to unrelated adults may

reflect a strategy of fledglings but may additionally be related to differences in signal variation among sexes. Female calls show low intra-sexual variation and are more similar to each other than male calls. We further discuss whether the higher response rate to unrelated females may be attributed to recognition errors or a strategic investment of fledgling birds.

### Individual recognition versus class-recognition

Fledglings reacted faster and emitted more response calls towards their parents than to unrelated adults. In addition, the response to their parents differed among fledglings, where around a third of the individuals reacted only towards one individual parent, irrespective of the parent's sex. This response pattern demonstrates that at least some fledglings are able to discriminate among two equally familiar adult calls and use individual signatures, in contrast to class-signatures (e.g., relatedness), to recognize their mother and father. These individual signatures are most likely learnt and may be composed of components that encode the sex in combination with components encoding the individual. Such a fine discrimination of parental calls can be facilitated by the mere exposure or familiarity to the stimuli or alternatively result from differential reinforcement at a similar exposure of the different stimuli. A preference towards one of the parents may reflect the history of previous parent–offspring interactions among individuals. In several species, individual adults feed a subset of the brood, rather than each adult feeding all young (Draganoiu et al. 2006; Leedman and Magrath 2003). A recent study in black redstarts *Phoenicurus ochruros*, a species that shows “brood division” after fledging, demonstrates that individual parents only responded to the subset of distance calls of fledglings they were feeding (Draganoiu et al. 2006). In line with these results, the observed response pattern of young zebra finches may reflect brood division where a fledgling only or mainly responded to the parent that was feeding it. Alternatively, a stronger reaction towards one parent may reflect the absolute amount of investment in offspring feeding of the mother or the father. Both scenarios are possible, not mutually exclusive, and more detailed behavioral observations of parent–offspring interactions after fledging are needed to distinguish among both hypotheses.

Not only did fledglings react more to their parents, but they also altered call characteristics. It is widely known that the motivational status of a signaller affects call structure (Morton 1977). In situations of high urgency, bird and mammal species have been shown to produce longer calls and vocalizations of higher frequency (Anderson et al. 2010; Ficken 1990; Furrer and Manser 2009; Leavesley and Magrath 2005). Here, we propose that changes in these call

parameters in relation to an increasing urgency likely reflect the consequence of selection for call loudness. The amplitude of calls is expected to be a main call character under selection because of its direct effect on detection probability (Brumm and Slabbekoorn 2005). Call amplitude is mainly determined by the air pressure in a bird's air sacs, which affects the airflow through the syringeal systems (Plummer and Goller 2008). By increasing the airflow through the syrinx, a bird will not only change vocal amplitude but calls will additionally be altered in length and frequency (Plummer and Goller 2008). These accompanied changes highlight that the expression of each call parameter within a complex multi-component signal can be limited by selection on other call components. How these constraints on signal production affect the perception of single call component is unknown, and receivers may use the accompanied changes in frequency or call length and not the trait under selection, i.e., amplitude to assess the urgency of a call.

#### Responses to unrelated adults in parent–offspring communication

Many fledglings responded to unrelated adult calls. Most importantly, the reaction was more common towards unrelated females than males. Our findings are in line with previous studies that have shown a stronger vocal response (Vicario et al. 2001) and neuronal activation (Gobes et al. 2009) of adult birds towards female distance calls. The stronger response towards unrelated females is most likely not due to behavioral differences between the sexes. Males and females did not differ significantly in the likelihood to allocate food to unrelated fledglings or in the aggressiveness towards fledglings. The observed percentage of adult feedings to unrelated fledglings was surprisingly high and unexpected. The occurrence of extra-pair paternity and egg dumping did not explain these observed cases (unpublished data). Therefore, these results may rather be the consequence of the housing situation, which may not mimic the natural conditions perfectly. In our aviaries, parent–offspring interactions may be complicated through limited space where family units (i.e., food-provisioning adult and its offspring) cannot easily escape from unrelated food-soliciting fledglings.

The stronger reaction towards female calls can also be discussed in the light of recognition errors. Female calls show lower intra-sexual variation, and individual female voices are more difficult to discriminate than male voices, at least in a statistical approach using discriminant function analyses. In our study, female calls were assigned to the correct individual in about 72% of the cases, while male calls were assigned to the correct individual in almost all cases (95%). An assignment rate of 72% is still high and

demonstrates that female calls possess individually distinctive features (see also Vignal et al. 2004). However, it also shows that a substantial proportion of female calls (28%) were statistically assigned to the wrong female which could account for the relatively high number of responses to unfamiliar female calls in our study. The proximate reason for intersexual differences in variation in distance calls might be due to different selection pressures acting on male and female voices. Male calls are learnt and show high intra-sexual variation (Forstmeier et al. 2009). Learning processes are often not perfectly precise thereby adding variance to the learnt trait and facilitating the accurate recognition of the father's individual signature. In contrast, distance calls of adult females are innate (Forstmeier et al. 2009), show low intra-sexual variation, and the mother's call is more likely to be confused with another female call.

Another result supports the idea that recognition errors are mainly due to low between-individual variation in female calls. Fledglings, which showed a preference for their mother, also reacted stronger to unrelated females. This relationship was only observed in reactions to the mother, i.e., fledglings that reacted more to their father did not react more strongly to unrelated males. This sex-specific response rate indicates that fledglings will commit recognition errors in relation to female calls as long as they respond to their mother. In cases where fledglings responded to a single parent only, they responded significantly less to unrelated adult calls than fledglings that responded to both parents. Fledglings that responded to both parents show an environmentally induced or genetic predisposition to be less choosy. Individuals in states of high need may adopt more risk-prone strategies, trying to solicit food from unrelated individuals or the existence of highly consistent heritable individual variation in behavioral strategies, also referred to as personalities, may account for the differences in responsiveness towards adult calls among fledglings (Drent et al. 2003).

This study highlights the importance of responses to unrelated adults in understanding parent–offspring communication specifically and recognition processes in general. While many studies have demonstrated that offspring recognize their parents, it remains an open question how signal properties facilitate or complicate recognition processes. To conclusively demonstrate that calling towards unrelated adults reflects recognition errors and not a strategy of fledglings, we still need careful experiments linking a fledgling's responsiveness with the similarity in adult signal properties important in individual recognition. Such studies will yield insight into costs and benefits of individual signatures and test fundamental assumptions of the spread of individual signatures via negatively frequency-dependent selection.

**Acknowledgements** We want to thank Katrin Martin, Edith Bodendorfer, Annemarie Grötsch, Johann Hacker, and Jenny Minshull for technical assistance. Additionally, we wish to thank M. Hauber and two anonymous reviewers, Bart Kempenaers for providing facilities and Holger Schielzeth for statistical advice. This project was partly funded by an Emmy-Noether Fellowship (DFG: FO 340/1-2 to W.F.), a research grant from the Volkswagen Foundation (I/82-747 to H.R.) and through a research grant from the Swiss National Science Foundation (PA00A-111437 to A.J.).

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