



Who wants food? Individual characteristics in raven yells

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Discriminating between different individuals is considered as prerequisite for any forms of social knowledge. In birds, discriminating between conspecifics based on individual characteristics has been tested mainly in the auditory domain with territorial calls and songs for neighbour and kin discrimination but little is known about discriminating between signallers in food calls. Ravens utilize a large set of calls and show individually distinctive call repertoires. Moreover, they show advanced social tactics during foraging, suggesting that they are capable of dealing with conspecifics on an individual basis. When confronted with food that is difficult to access, ravens produce particular calls ('haa', yells); these calls attract other ravens and, thus, have been hypothesized to serve as 'functionally referential signals'. We here examined whether ravens are able to differentiate between individuals on the basis of these food calls. We first analysed individual differences in call parameters, using 424 food calls recorded from 18 individually marked wild ravens in the Austrian Alps. We then tested 18 captive ravens for recognition of individual differences in food calls with playbacks, using a habituation-dishabituation design. We found evidence that food calls show individual call characteristics in fundamental frequency and intensity-related measurements providing ravens with the opportunity to respond according to these individually distinct features. Furthermore, ravens discriminated between unfamiliar ravens in the habituation-dishabituation experiment, indicating that they may discern individual differences. Our results suggest that raven food calls are individually distinct and that the birds may be capable of differentiating between food-calling individuals.

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Animal calls are complex acoustic signals and often carry a variety of characteristics about the sender simultaneously (Blumstein & Munos 2005; Neff 2007; Searcy & Andersson 2007). Call characteristics about sex, age and social status (Tibbetts & Dale 2001) are often encoded in call characteristics.

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call characteristics should be highly advantageous for species with repeated and complex social interactions (Cheney & Seyfarth 1980). One index of social complexity, social group size (Dunbar & Shultz 2007), constrains individual discrimination as there should be a negative correlation between group size and simplicity of individual discrimination. Simply designed signals contain fewer features to enable discrimination, and complex signals offer the possibility of more distinct patterns. Thus the difficulty of differentiating between specific individuals in large groups can be compensated for by producing complex signals that increase individual information and variability (Pollard & Blumstein 2011).

A certain class of vocal signals, commonly denoted as functionally referential signals (Macedonia & Evans 1993; Evans et al. 1992).

By referring to external objects such as predators or food these signals elicit receivers' corresponding behavioural responses as if directly responding to the external cue (Seyfarth et al. 1980; Evans & Evans 2007). In the case of food calls, which have been described for many primates (reviewed in Slocombe & Zuberbühler 2006; Clay & Zuberbühler 2009) and birds (e.g. Evans 1982; Soma & Hasegawa 2003; Mahurin & Freeberg 2008), conspecifics are usually attracted to the site where the calling individual is feeding. Considering the disadvantages of increased competition, the benefits of food calls range from reduced vigilance (Elgar 1986) and increased foraging efficiency (Brown et al. 1991) to accessing resources defended by others and/or defending resources from other species (Bugnyar et al. 2001; Slocombe & Zuberbühler 2006; Clay & Zuberbühler 2009). Although individual recognition is not necessary to recruit conspecifics to foraging sites, listeners may profit by using information they gain from discriminating between callers. Specifically, assessing information about the sender's

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reliability of signalling the location and/or quality of food (Bugnyar & Kotrschal 2001; Bugnyar et al. 2001) and its relative rank to the listener as well as the identity and hierarchy of individuals associated with the caller could increase the fitness of listeners. Little is known about individual information in food calls. In birds specifically, caller discrimination and individual recognition have mainly been tested in social contexts such as neighbour and kin discrimination (Beer et al. 1970; Beecher 1989; Wanker et al. 2005; Tibbetts & Dale 2007) but to our knowledge not in referential signals.

Common ravens show advanced cognitive skills during foraging (Bugnyar & Kotrschal 2002b; Heinrich 2011) and conflict management (e.g. Fraser & Bugnyar 2011), indicating the capability of dealing with complex social environments and repeated interactions based on individual recognition. In experiments, they are able to differentiate between ignorant and knowledgeable conspecific competitors (Bugnyar & Heinrich 2005; Bugnyar 2011) as well as human experimenters (Bugnyar et al. 2007). Furthermore, ravens utilize a large set of calls and display individually distinctive call repertoires (Enggist-Dueblin & Pfister 2002). However, to our knowledge, it has been suggested (Heinrich & Marzluff 1991) but not yet proven that ravens have individually distinct call characteristics within one call type. This is surprising because one of the most characteristic features of young, nonbreeding ravens is the recruitment to food, which at short distance works via calls (Heinrich & Marzluff 1991). Raven food calls or 'yells' come in two types (Heinrich 1988; Heinrich & Marzluff 1991), a long version ('haa') is given when subordinate birds face defended and/or potentially dangerous food sources, whereas a short version ('who') is given by dominants when landing at the food (Heinrich & Marzluff 1991; Bugnyar & Kotrschal 2001; Bugnyar et al. 2001). This specific usage of calls suggests different meanings, with 'haa' having the potential to serve as functionally referential signals (Bugnyar et al. 2001). Senders may benefit by attracting others as it increases the chance to overpower the food defence of a few dominant individuals or dangerous predators (Marzluff & Heinrich 1991); moreover, it offers the chance to kleptoparasitize those that have already secured a food item and/or pilfer the others' food caches (Bugnyar & Kotrschal 2002a, b). Receivers may learn about the location of feeding opportunities (Heinrich & Marzluff 1991) and, by distinguishing between callers, may be able to predict the likelihood of competition and the need for cooperation by particular individuals, respectively. Knowing who is calling may thus help ravens in their decision in whether or not to join a feeding crowd. Territorial ravens, on the other hand, are interested in keeping nonbreeders away from their food sources and aggressively prevent young birds from giving 'haa' calls (Heinrich & Marzluff 1991). Being able to tell individuals apart on the basis of their calls may enable them to coordinate their food defence.

We investigated the individual call characteristics within one food call type, the 'haa', determining distinct parameters that could be utilized to differentiate between conspecifics. Based on fundamental frequency- and amplitude-related measurements we predicted that raven 'haa' calls would differ according to the caller's identity. We then tested the birds' response to 'haa' calls of different unknown individuals, determining whether ravens can perceive the acoustic differences, in a habituation–dishabituation paradigm.

METHODS

Food Call Analysis

Food calls ('haa') were recorded from wild, free-ranging ravens between summer and winter 2010 in the Cumberland Wildpark in Grünau (47°48'N, 13°57'E) while they were foraging at the enclosure of wild boars, *Sus scrofa*. Boars are usually fed between 0700

and 0900 hours and are joined by 20–120 ravens, most of which are members of a highly dynamic nonbreeder flock (Braun et al. 2012). At the time of the study, approximately 100 individuals of the flock had been marked individually. In the course of marking, the birds' body weight was measured and age class assigned from morphological characteristics (juvenile, subadult, adult), notably the colour of eyes and inner beak (Heinrich & Marzluff 1992).

To identify vocalizing individuals we videorecorded the feeding sessions with a Camcorder (Canon HF-11 HD, Canon Inc., Japan) and simultaneously audiorecorded all vocalizations via a directional microphone (Sennheiser K6/ME67, Sennheiser Electronic GmbH & Co. KG, Wedemark, Germany) connected to a portable solid state digital recorder (Marantz PMD-670, D&M Holdings Inc., Kanagawa, Japan) with a sampling rate of 48 kHz and 16 bits amplitude resolution, at distances of 3–10 m. Resulting audio files (WAV files: sampling rate = 48 kHz, amplitude resolution = 16 bit) were moved to a MacBook Pro. A total of 424 calls of 18 individuals (Table 1) were analysed after removing all calls with interfering background noise.

Acoustic analysis was conducted with PRAAT 5.1.25 (Boersma & Weenik 2011). Analysed call parameters were mean fundamental frequency (mean F0; Hz) based on a forward cross-correlation method (settings: time step = 0.01 s; expected F0 frequency range = 300–950 Hz; maximum number of candidates = 15; silence threshold = 0.03; voicing threshold = 0.65; octave cost = 0.01, octave-jump cost = 0.35; voiced/unvoiced cost = 0.14), slope from the maximum F0 to the end of the call (Slope M–E; Hz/s), number of inflections/s, harmonicity (dB) representing the relative energy of the signal lying in the harmonic part of the sound in relation to the energy of the noise (harmonicity = $10 \times \log$ (% of energy periodic part/% of energy in the noise, Boersma 1993)), amplitude modulation (Hz), dB range (maximum dB–minimum dB) and sum of variation (the sum of all F0 changes measured/call length; Hz) where the sum of F0 change is the cumulated variation of F0 over the total duration of the call (Reby & McComb 2003). For F0 analysis we manually excluded parts of the recordings from the analysis, which PRAAT tracked because of background noise such as wild boar grunts. The retrieved F0 track was lowpass filtered with a cutoff frequency of 25 Hz in order to track only large changes of F0 and excluding small fluctuations.

Discriminant function analysis (DFA) was performed to test for individuality based on acoustic features of food calls. For DFA analyses a subset of the original data set was used to prevent

Table 1
Name, age class and sex of recorded wild ravens

Individual	Age class	Sex	Number of calls	Analysis
Boszi	Juvenile	Female	47	1
Captain	Subadult	Male	4	
Ford	Subadult	Male	1	
Gertl	Adult	Female	66	1
Gonzo	Adult	Female	8	1
Hampel	Subadult	Female	59	1
Karli	Juvenile	Male	29	2
Karruso	Subadult	Male	1	
Kassiopeia	Adult	Female	2	
Laura	Subadult	Female	72	1
Marvin	Adult	Male	12	2
Monique	Juvenile	Female	40	1
Nemo	Adult	Female	16	1
Punky	Subadult	Female	1	
Sherry	Subadult	Male	1	
Sieglinde	Adult	Female	5	1
Tichy	Adult	Female	138	1
Zafrau	Adult	Female	2	

Only individuals with more than five recordings entered the analysis. Individuals with analysis = 1 were included in the first discriminant function analysis, whereas individuals with analysis = 2 were included in the second analysis.

pseudoreplication, as some individuals were represented in two age classes. Additionally, we calculated two DFAs with 277 calls of nine individuals excluding males (Table 1) and a second DFA including males with 290 calls of 11 individuals in order to show that call classification based on identity can be calculated with and without differences in acoustic features based on sex. We calculated the two DFAs to investigate whether high classification values are due to sex differences or to mere individual differences. We used the reclassification method, the more conservative leave-one-out cross-validation procedure and the hold-out-sample method where we selected a 25% random sample of each individual and tested it against models trained with the remaining 75%. Uncorrelated parameters with univariate significant differences between individuals (Kruskal–Wallis test) were entered in the DFA whereby the criterion for minimum partial F to enter was 3.84 and maximum partial F to remove was 2.71. Prior probabilities were calculated via group sizes. Additionally, we calculated a generalized linear mixed model (GLMM) with the original data set ($N = 424$); individual identity was used as a multinomial response variable. As previous investigations (M. Boeckle, G. Szpl & T. Bugnyar, unpublished data) on differences dependent on sex, age and weight demonstrated sex and age influences on food calls, we additionally entered sex and age as fixed factors to correct classification results for their influences, and chose the same call variables as applied in the DFAs as covariates. For the GLMM we weighted the cases with the inverse of the percentage representation of each individual in the data set. Results are presented despite quasicomplete separation as the variables in the model, the coefficients, SEs and test statistics for the remaining variables still have valid maximum likelihood estimates (Allison 2008). We present the full model with quasicomplete separation as it tests for effects of factors while controlling for other predictor variables (Allison 2008).

Playback Experiment

An average of nine samples of six individuals with little background noise and no distracting or interfering sounds of the previously analysed food calls were selected and used for playback experiments. Eighteen captive individuals housed in male–female pairs at different zoos, game parks and private owners (Table 2) were presented with calls of ravens unfamiliar to the focal individual in a habituation–dishabituation design. Each raven pair was presented with two playback experiments, one in the morning and

one in the afternoon, consisting of stimuli matched for sex and age with the focal individual. Before the presentation of habituation stimuli a 15 min baseline was conducted followed by a presentation of three interspecies stimuli common to all focal individuals (a goose or a rooster) with a 1 min interval to test for the ravens' ability to differentiate between inter- and intraspecific acoustic stimuli playbacks. After the 1 min intermission time, five food calls of one individual were presented. After a further 1 min intermission interval, again five food calls were presented. The five samples were randomly chosen from a set of calls of the same individual (range 8–20) and randomly sorted within one presentation. We repeated the procedure of 1 min interval and five calls until habituation was reached. Habituation criterion was defined as three consecutive call responses being under half the maximum number of calls of the first three presentations or by a decreased behavioural response (see below; for a schematic of the protocol see Fig. 1). Once the focal individual reached the habituation criterion, the dishabituation stimulus was presented. Dishabituation stimuli varied between conditions in order to test for the influence of playback location on response levels: condition 1: habituation and dishabituation stimuli were presented from two individuals at the same location; condition 2: stimuli of the same individual were played from differing locations; condition 3: both location and individual were altered from habituation to dishabituation.

Playback stimuli were presented with speakers (Ion Block Rocker, Ion Audio, LLC. US, www.ionaudio.com; 70 Hz–50 kHz \pm 3 dB) connected to a MacBook Pro using Quick Time Player Pro (V:7.6.9). All experiments were audiorecorded (Marantz PMD-660, D&M Holdings Inc., Japan; Sennheiser Me 67, Sennheiser Electronic GmbH & Co. KG, Germany) and videorecorded (Sony handycam DCR-HC23, Sony Co., Tokyo, Japan).

Responses were videocoded during the 1 min intermission intervals and 1 min after the dishabituation playback with Solomon coder (Péter 2011, copyright by András Péter; <http://solomoncoder.com>). All calls were counted and categorized as long-distance calls, soft calls and self-aggrandizing displays, a typical display of ravens that increases visually perceived body size by feather erection, most often accompanied by an acoustic signal, which is called 'Imponieren' or 'self-assertive-display' (Gwinner 1964; Heinrich 2007). Behavioural responses were categorized as (1) no reaction, (2) head lifting, (3) looking in the direction of the playback, (4) flying in the direction of the playback and (5) flying to the fence close to the playback and searching.

To reduce data dimensionality of response variables, a principal component analysis (PCA) was calculated using numbers of long-distance calls, soft calls and self-aggrandizing displays, behavioural responses and highest behavioural response category. A varimax-rotated correlation method was used and a minimum eigenvalue of 1.0 was set for components to be extracted. Differences between reactions to the different stimuli categories were calculated with a GLMM. To correct for differences between playback individuals and for the presentation order a nested term was included (focal individual(session(call))). Phases of the experiment were divided into baseline before, interspecific playback (including three presentations), first habituation phase (including two presentations of five food calls), second habituation phase (all presentations except the first two and the last two), third habituation phase (last two habituation presentations). After the final playback, the dishabituation stimulus (one presentation) and a baseline after the playback consisting of 15 min of data collection, the experiment was finished. The original and full model included sex, condition, phase time of day and an interaction between sex and sex of the played-back individual as fixed factors. The interaction between sex of the focal and sex of the played-back

Table 2
Name, age class, sex and location of housing of captive ravens

Pair	Individual	Age class	Sex	Keeping
1	Af	Subadult	Female	WP Altenfelden
1	Am	Subadult	Male	WP Altenfelden
2	Kr	Adult	Female	Scharnstein
2	Ar	Adult	Male	Scharnstein
3	Gf	Adult	Female	WP Goldau
3	Gm	Adult	Male	WP Goldau
4	Lu	Subadult	Female	WP Haag
4	Kä	Adult	Male	WP Haag
5	Fl	Adult	Female	Zoo Innsbruck
5	Pa	Adult	Male	Zoo Innsbruck
6	Mf	Adult	Female	Zoo München
6	Mm	Adult	Male	Zoo München
7	Ju	Subadult	Female	Selm
7	To	Subadult	Male	Selm
8	Ro	Adult	Female	Weidling
8	Ru	Adult	Male	Weidling
9	Kf	Adult	Female	VP Turnersee
9	Km	Adult	Male	VP Turnersee

Birds used in the playback study were kept in pairs at various public zoos and game/bird parks (WP = Wildpark, VP = Vogelpark) and private keepers.

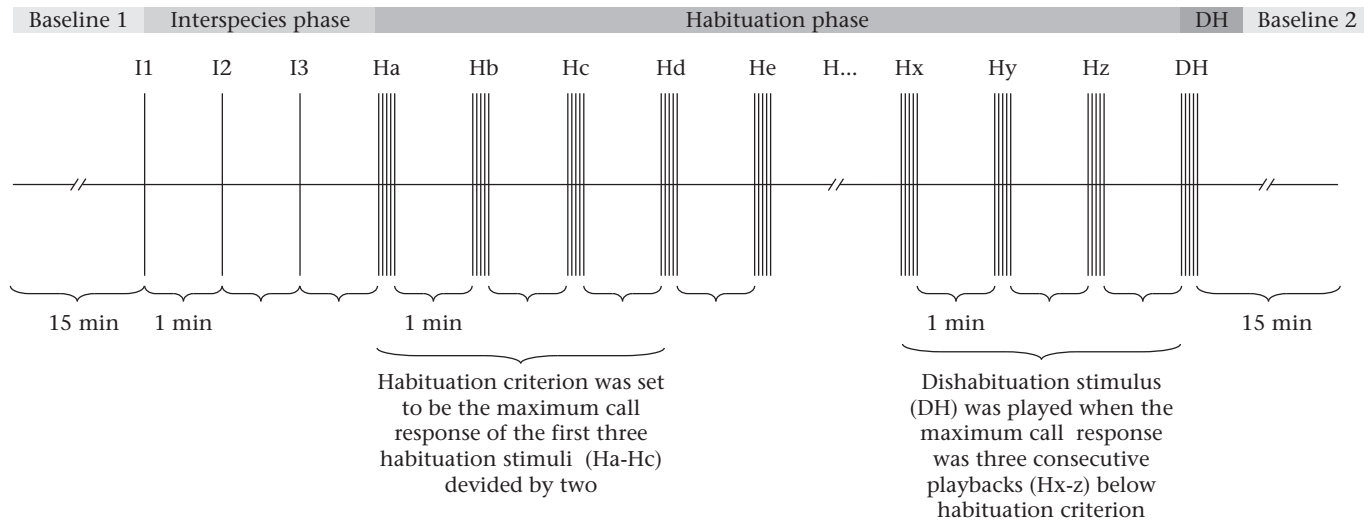


Figure 1. Schematic of the experimental procedure. Playback protocol started with a 15 min Baseline (Baseline 1) followed by interspecies stimuli (1–3) and respective 1 min intermission intervals. The habituation phase (Ha–Hz) lasted until the habituation criterion was reached, which could require different amounts of habituation stimuli (H...). After the response of the focal individual was three times below the habituation criterion the dishabituation stimulus (DH) was played followed by a 15 min baseline (Baseline 2).

individual was used to detect differences between intrasex or intersex responses. Responses of both individuals in the pair were used as a response variable within the GLMM in order to be able to calculate differences between responses to intersex and intrasex stimuli. We used least-square mean differences for post hoc tests without Bonferroni correction of *P* values in order to make the test less conservative (Nakagawa 2004). We tested for differences between conditions with a Kruskal–Wallis test with the differences between the last habituation stimulus and dishabituation. All statistical analyses were conducted using IBM SPSS for Mac 19 (SPSS Inc., Chicago, IL, U.S.A.).

Ethical Note

Captive ravens in Austria, Germany and Switzerland were kept according to the legal rules of the respective countries. Animal trapping and marking were performed with the permission of the Austrian Government (BMWF-66.006/0010-11/10b/2009). Ravens were caught in drop-in traps (Engel & Young 1989), which were positioned next to their main feeding sites so that caught birds remained in visual and auditory contact with conspecifics. Moreover, traps were placed under large trees, protecting the birds from direct sun, rain and snow. The traps were checked every hour and water and food were available ad libitum. Caught birds were handled by trained humans for the minimum amount of time needed for measuring and banding, which was usually <30 min per individual. Banded individuals are monitored intensively (4–6 days/week, start of the programme in 2008). We have no indication that the catching and marking procedure has any negative effects on the birds' behaviour. Already in the first few days after catching, they can be observed from a close distance by humans and about half of the banded birds revisit the trap.

RESULTS

Call Characteristics

Individual distinctiveness was successfully determined by the means of seven acoustic parameters of food calls (for an example spectrogram see Fig. 2). Descriptive statistics for calls are presented

in Table 3. Differences between individuals were confirmed by discriminant functions 1 and 2 (equality test, Table 4; discriminant function, Table 4). DFA reclassified 71.0% (72.6% when including males) of the calls and 61.5% (62.0% including males) when the more conservative method of leave-one-out cross-validated reclassification was applied (Table 5). With the hold-out-sample method, we excluded a subset of the calls, which then had to be classified by the rest of the sample; 62.3% (63.4% including males) were correctly classified confirming that a random sample was possible to assign individually to the trained sample. The characteristics contributing most to the individual distinctiveness were mean pitch and the sum of variation in factor 1 and HNR and amplitude ratio in factor 2. The GLMM using the same variables as the DFA and additional factors for sex and age classified 83.3% of the individuals correctly.

Playback Experiment

As expected, all tested pairs showed a similar pattern of response to the playback of conspecific food calls: (1) compared to

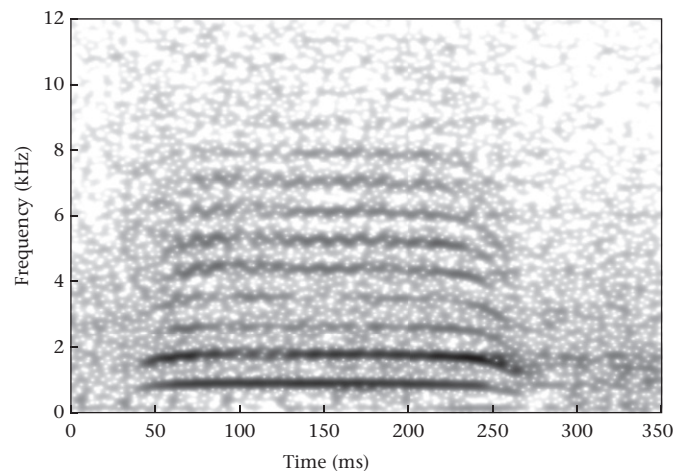


Figure 2. Spectrogram of a food call of a common raven (FFT method, window length = 0.01, time step = 700, frequency step = 250, Gaussian shape).

Table 3
Call parameters

	Mean	SD	K–W χ^2	K–W P	Wilks's λ	$F_{10,197}$	P
Mean F0	655.7	69.9	143.0	<0.001	0.263	55.2	<0.001
Slope Max F0–End	–1410.9	863.9	101.8	<0.001	0.620	12.1	<0.001
Number of inflections/s	11.0	6.5	31.5	<0.001	0.900	2.2	0.019
Harmonicity	14.4	4.0	132.0	<0.001	0.370	33.5	<0.001
Amplitude modulation	34.6	17.2	27.7	0.002	0.889	2.5	0.008
dB range	8.3	3.4	52.0	<0.001	0.719	7.7	<0.001
Sum of variation	88.5	30.6	83.9	<0.001	0.651	10.6	<0.001

Data are presented of all parameters included in the discriminant function analysis. Descriptive statistics are shown for 11 individuals represented in 290 calls. Univariate statistics show significant differences between individuals (K–W χ^2 , K–W P value) and differences between means (Wilks's λ).

the baseline and interspecific controls, they strongly responded to the calls of an unknown raven, (2) with repeated presentation, they habituated to the calls of that raven but (3) dishabituated when hearing the calls of a different unknown individual (Fig. 3). PCA revealed two components in their overall response (Bartlett's test of sphericity: $\chi^2_{10} = 220.2$, $P \leq 0.001$). Component 1 explained 31.2% and component 2 explained 22.0% of the variance, in total 53.0%. On component 1 the variables long-distance calls, self-aggrandizing displays, highest behavioural reaction and number of behavioural reactions loaded and thus are labelled 'territorial behaviour'. All calls (long-distance calls, soft calls, self-aggrandizing displays) loaded on component 2 and are labelled 'vocal response' (Table 6).

The final model investigated differences in the sex of test subjects (GLMM: $F_{1,612} = 10.85$, $P \leq 0.001$), time of day (GLMM: $F_{1,612} = 24.88$, $P \leq 0.001$), phase (GLMM: $F_{6,612} = 7.25$, $P \leq 0.001$) and sex of the playback stimulus (GLMM: $F_{1,612} = 4.57$, $P = 0.033$) on 'territorial behaviour'. Post hoc testing revealed that males reacted more to playbacks than females (t test: $t_{612} = 3.29$, $P \leq 0.001$) and that both sexes showed an increased response to female food calls (t test: $t_{612} = 2.14$, $P = 0.033$). Birds responded less in the afternoon than in the morning (t test: $t_{612} = -4.99$, $P \leq 0.001$). Most importantly, ravens increased 'territorial behaviour' from the last habituation to the dishabituation phase (t test: $t_{612} = -1.97$, $P = 0.050$), whereas baseline, interspecific calls and habituation phases conveyed territorial responses fitting our hypothesized levels, that is, baseline levels were low and interspecific calls evoked little response. We did not find any difference in the measured behaviours between the three tested conditions (Kruskal–Wallis test: $P > 0.05$).

Table 4
DFA structure matrix

	Discriminant function				
	1	2	3	4	5
Mean F0	0.879	0.197	0.117	–0.416	–0.042
Harmonicity	–0.194	0.755	–0.353	0.025	0.516
Amplitude modulation	0.056	–0.233	–0.038	–0.182	–0.052
Number of inflections/s	0.085	0.070	0.241	–0.007	0.236
Sum of variation	0.175	0.213	0.372	0.886	–0.019
dB range	0.114	0.114	–0.419	0.787	0.423
Slope Max F0–End	–0.104	–0.338	0.589	–0.201	0.698

Pooled within-groups correlations among discriminating variables and the first five standardized canonical discriminant functions are shown for discrimination between 11 individuals (290 calls).

DISCUSSION

This study demonstrates that the long version of raven food calls ('haa') shows individually distinctive characteristics based on acoustic parameters such as pitch and harmonicity. Correct classification ranged from 61.5% to 72.6% in the DFA depending on the type of method and data set, whereas correct classification in the GLMM with a correction for age and sex reached up to 83.3%. Importantly, when captive ravens were presented with food calls of two unknown individuals in the habituation–dishabituation experiment, they increased their territorial behaviour not only at the beginning of the habituation phase but also during dishabituation, indicating that they can discriminate between unfamiliar callers. Thus, functionally referential food calls of ravens exhibit individual features that might enable receivers to differentiate between calling individuals.

Call Characteristics

The DFA correctly reclassified individuals, on the basis of temporal and spectral parameters of food calls. Mean F0, spectral slope from maximum F0 to the end of the call, number of inflections/s, harmonicity, amplitude modulation, amplitude ratio and the sum of frequency variation were used to calculate individual differences, but mean F0 and harmonicity seemed to be the most important variables for discriminating between individuals. F0-related measurements are important cues to identity in many birds (Wanker et al. 2005; Nelson & Poessel 2007) and in other corvids (Yorzinski et al. 2006; Kondo et al. 2010). Owing to the highly harmonic structure of the calls with a mean F0 at 650 Hz and the expected formant dispersal of 1308 Hz (based on estimated vocal tract length of 13 cm in ravens) it was impossible to measure formants. Formant dispersal is an important cue for individual identification in human and nonhuman mammals (*Homo sapiens*: Bachorowski & Owren 1999; *Phascolarctos cinereus*: Charlton et al. 2011; *Papio hamadryas ursinus*: Owren et al. 1997; Rendall 2003; *Cervus elaphus*: Reby et al. 2006); in birds, only a few studies have concentrated on individuality including formants and formant dispersal (Suthers 1994).

When we classified individuals with a GLMM and thereby corrected for age class and sex, the percentage of correct classification rose to 75.3%. This result is in accordance with another study (M. Boeckle, G. Szípl & T. Bugnyar, unpublished data) where influences of sex and age class on raven call characteristics were found. Raven yells may thus allow receivers to extract essential social features about the caller, that is, whether it is young or old and male or female. In addition, receivers may pay attention to the caller's individual characteristics. 'Haa' calls are suggested to develop from begging calls (Heinrich & Marzluff 1991) and might convey individually distinct information from the early developmental stages; they may be used by parents to localize (particular) offspring after fledging. In the course of their first year of life, young ravens come to adjust the timing, context and context specificity of food call production (Bugnyar & Kotrschal 2001; Bugnyar et al. 2001), indicating that they are capable of usage learning (Janik & Slater 2003). During this phase, some individuals may be more skilled and/or reliable than others in giving food calls at the appropriate time. Preliminary data indicate that wild ravens of all age classes (juvenile, subadult, adult) show stable intraindividual but highly variable interindividual call rates (G. Szípl, M. Boeckle & T. Bugnyar, unpublished data). This effect can only partially be explained by previously reported suppression of food calling by higher ranking individuals (Heinrich & Marzluff 1991) or the signallers' inhibition of food call production (Bugnyar et al. 2001). Hence, it seems plausible that different individuals respond to a given situation

Table 5
Confusion matrix

Subject	Boszi	Gertl	Hampel	Karli	Marvin	Nemo	Sieglinde	Tichy	Gonzo	Laura	Monique
Boszi	93.3	6.7	0	0	0	0	0	0	0	0	0
Gertl	0	67.6	0	0	0	0	0	32.4	0	0	0
Hampel	0	0	100	0	0	0	0	0	0	0	0
Karli	0	0	0	100	0	0	0	0	0	0	0
Marvin	0	20	0	0	80	0	0	0	0	0	0
Nemo	0	0	0	0	0	100	0	0	0	0	0
Sieglinde	0	0	0	0	0	0	100	0	0	0	0
Tichy	0	8.3	0	0	2.8	2.8	0	68.1	1.4	16.7	0
Gonzo	0	0	0	0	0	0	0	60	20	20	0
Laura	0	0	0	0	0	0	0	33.3	0	66.7	0
Monique	0	0	0	0	0	0	0	0	0	0	100

Percentage of correct classification and misattributions for each subject is shown for all individuals.

with a different rate of calling. Differences in call characteristics demonstrated in this study in combination with different individual calling rates should allow receivers to gain individually based knowledge about food call characteristics of birds they encounter regularly.

Utilizing Individual Information

Captive territorial ravens were able to differentiate between two unknown individuals, when calls were matched for sex and age in the habituation–dishabituation experiment, which suggests that their discrimination abilities are based on individual call characteristics. An alternative possibility would be that the distinction is based on regional dialects. We consider this explanation to be highly unlikely since all of our playback stimuli used in this study were recorded from one population of free-flying ravens at the same location in Austria. Moreover, we only tested birds with playbacks that were kept at a large distance to this site and hence never had vocal contact with the stimulus birds. Importantly, males and females were able to differentiate/be differentiated, suggesting

that sex differences did not play a role. Furthermore, playback location did not have an influence on differentiation abilities.

So far individuality in functionally referential signals has been shown in alarm calls of mammals (Blumstein & Munos 2005; Matrosova et al. 2011). Functional differences within alarm calls vary depending on predator type (Evans et al. 1997) or perceived risk (Blumstein & Arnold 1995; Warkentin et al. 2001). Individual identity within alarm calls might thus be important for the perceiver to react appropriately to the reliability or the kinship of the signaller (Cheney & Seyfarth 1992; Manser 2001; Blumstein et al. 2004; Leavesley & Magrath 2005). Similar effects of caller identity, rank, sex and kinship (reviewed in Clay et al. 2012) might be important in food-associated calls and have been suggested for *Cebus capucinus* (Gros-Louis 2006) and *Saguinus oedipus* (Roush & Snowdon 1999). To our knowledge, this study demonstrates for the first time individuality in food calls of birds and suggests that identity and social information based on the identity of the caller might be relevant for the perceivers.

As scavengers, ravens rely on scarce and ephemeral food sources that are heavily competed for (Heinrich & Pepper 1998). Particularly during winter, carcasses and kills are highly defended by dominant territorial breeders, making it difficult for individual birds to access the food. As a consequence, they start yelling (Marzluff & Heinrich 1991). By testing adult captive pairs, we simulated such a 'territorial' intrusion by hungry nonbreeders. This helped us to assess responses to different individuals by increased territorial behaviour of our focal subjects. Most likely, individuals of a nonbreeder flock would respond to our playbacks with increased attraction to the feeding site. Perceiving calls from different individuals as being different could be advantageous in either context: territorial ravens could make use of this information for coordinating their food defence; nonbreeding ravens might use it for deciding whether or not to join a foraging group. Based on our acoustic analysis we may even speculate that ravens could also learn to identify particular individuals on the basis of their calls. This would require that there is variation in the reliability of individuals' calling in response to (different degrees of) food competition and/or food quality, for example some birds only yell when the food is heavily defended and/or of high quality whereas others yell

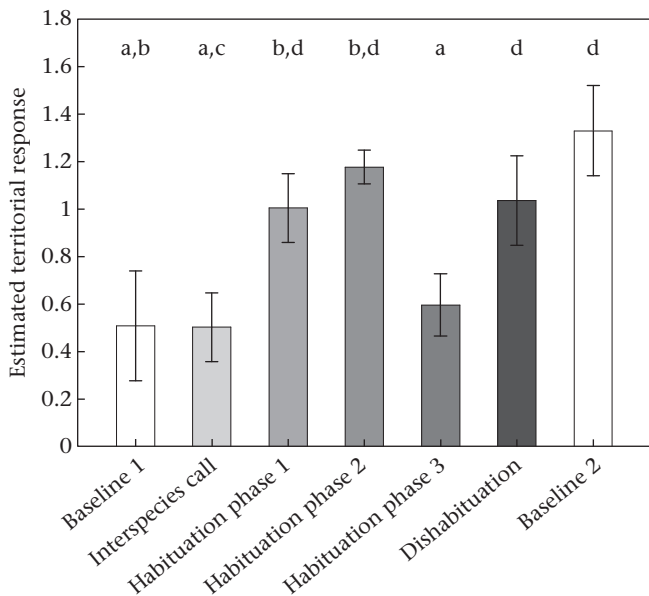


Figure 3. Estimated territorial response \pm SE during the phases of the playback experiment. Habituation phase 1 consisted of the first two playback stimuli, habituation phase 3 of the last two; habituation phase 2 included all stimuli apart from phases 1 and 3. Different letters above the bars designate significance between the phases ($P < 0.05$) whereas same letters represent no statistical difference. For details also see Fig. 1.

Table 6
Component matrix for the playback experiment

	Component 1 territorial component	Component 2 vocal component
Long-distance calls	0.279	-0.653
Soft calls	-0.012	0.630
Self-aggrandizing display	0.322	0.526
Highest reaction	0.874	-0.002
No. of reactions	0.777	0.028

at almost any time. Preliminary findings support this assumption (Marzluff & Heinrich 1991). In the visual domain, ravens routinely take individual characteristics into account to judge the competitiveness of conspecifics for hidden food (Heinrich & Pepper 1998; Bugnyar & Heinrich 2006; Bugnyar et al. 2007) and even hetero-specifics such as human experimenters for access to objects (Bugnyar et al. 2007). It still needs to be shown that foraging ravens also make use of individual characteristics in the auditory domain. Given the relatively high degree of fission–fusion dynamics found in nonbreeding raven groups (Braun et al. 2012), questions such as how long it may take birds to assign specific call characteristics to individuals and which conditions promote this form of learning are promising topics for future studies.

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