



## Vocal individuality in cohesion calls of giant otters, *Pteronura brasiliensis*



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Social calls conveying identity yield several advantages in managing social group living. Signalling identity to conspecifics and the perception of the calling individual by receivers allow for appropriate behavioural responses based on experience of previous interactions. Contact calls help maintain group cohesion and often provide individual signatures. Giant otters, endemic to Amazonian rainforests and wetlands, are a highly social and vocally active species. Their family groups consist of a monogamous alpha pair with offspring of different ages, and elder siblings assist in rearing the young. During collective fishing bouts, individuals frequently become separated from their group. Giant otters use two types of cohesion calls. The 'contact call' is often uttered when the otters are visually separated, and is then followed by the reunion of group members. The 'hum' is produced in close proximity to manage group movements. We predicted giant otters would have individually distinct cohesion calls and be able to discriminate between the cohesion calls of different individuals. We recorded and measured calls from wild and captive individuals and conducted habituation–dishabituation playbacks with two captive groups. Our results provided statistical evidence for a strong individual signature in contact calls but not in hums. Nevertheless, the giant otters were able to distinguish individuals in both cohesion calls tested. We conclude that individual signatures seem to be advantageous in terms of managing group movements. Giant otters might additionally benefit from discriminating individuals within their social group, where kin recognition is insufficient to identify equally related individuals that cooperate in hunting and rearing of the young.

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Acoustic communication is a prominent channel for signalling individual identity to conspecifics (Bradbury & Vehrencamp, 1998). Vocal individuality, defined as interindividual variation exceeding intraindividual variation in acoustic parameters (Falls, 1982), is widespread among diverse taxa (Terry, Peake, & McGregor, 2005). Vocal signatures are shaped by physical, anatomical and cognitive constraints (Fitch & Hauser, 1998; Janik & Slater, 2000; Tibbetts & Dale, 2007). However, they have behavioural relevance only if conspecifics are able to differentiate and recognize the signature information (Boughman & Moss, 2003; Freeberg, Dunbar, & Ord, 2012; McCowan & Reiss, 2001; Townsend, Hollén, & Manser, 2010). Individuality can be perceived through recognition and discrimination (Cheney & Seyfarth, 1982; Tibbetts & Dale, 2007). True individual recognition is defined as a learned unique and often multimodal inner template of another individual, which the receiver matches with identity signals of this individual (McComb,

Moss, Sayialel, & Baker, 2000; Tibbetts & Dale, 2007). Individual discrimination, on the other hand, is achieved when receivers use the similarity or dissimilarity of vocalizations to discriminate between senders, for example different known individuals or known and unknown individuals (Miller & Bee, 2012; Tibbetts & Dale, 2007). Regrettably, the definitions for recognition and discrimination differ between authors and are not always strictly separated (following Tibbetts & Dale, 2007). Whenever unspecified, in this paper we use the term 'recognition' for both mechanisms, being aware that the experimental design of our study was targeted to investigate discrimination.

Social calls conveying information on the individuality of the sender offer one possibility to deal with the challenges of social group living. Contact calls serve in coordinating group movements, finding and reuniting separated animals or keeping a group together, even when group members are out of sight. The social functions of contact calls are enhanced by vocal signatures that facilitate individual or group recognition by conspecifics (for a review see Kondo & Watanabe, 2009). These characteristics of contact calls emphasize their special importance in social group living and

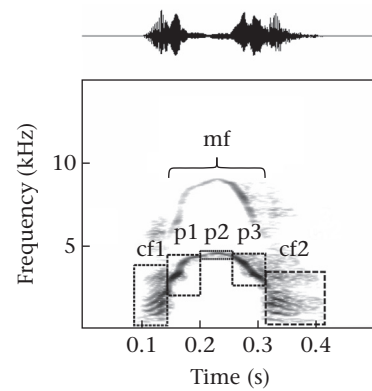
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may explain their wide distribution among taxa (bats: Carter, Logsdon, Arnold, Menchaca, & Medellín, 2012; Gillam & Chaverri, 2012; Wilkinson & Boughman, 1998; birds: Berg, Delgado, Okawa, Beissinger, & Bradbury, 2011; Buhrman-Deever, Hobson, & Hobson, 2008; Cortopassi & Bradbury, 2006; Wanker & Fischer, 2001; carnivores: Durbin, 1998; Maurello, Clarke, & Ackley, 2000; Townsend et al., 2010; dolphins: Janik & Slater, 1998; lemurs: Oda, 2002; primates: Cheney, Seyfarth, & Palombit, 1996; Stewart & Harcourt, 1994). The level of recognition involved in the perception of contact calls depends on their social function (Gillam & Chaverri, 2012; Kondo & Watanabe, 2009). Finding an individual in larger groups such as breeding colonies, herds or flocks may require mate or true individual recognition (Charrier, Mathevon, Jouventin, & Aubin, 2001; Jouventin, Aubin, & Lengagne, 1999; Tibbetts & Dale, 2007; Wanker & Fischer, 2001). However, the reunion of family members generally requires only kin recognition (Insley, 2001) or group recognition (Boughman, 1997; Wilkinson & Boughman, 1998). Contact calls are referred to as cohesion calls when they facilitate group coordination (Janik & Slater, 1998). Cohesion calls need not be individually distinct as long as the animals are moving in close proximity to each other (Bouchet, Blois-Heulin, Pellier, Zuberbühler, & Lemasson, 2012) but may encode the caller's identity (Janik, Sayigh, & Wells, 2006) and distance (Kondo & Watanabe, 2009; Oda, 1996) after spatial and visual separation (Janik & Slater, 1998; Stewart & Harcourt, 1994).

Giant otters are a suitable study species for investigating vocal individuality in cohesion calls. Endemic to the Amazon rainforests and wetlands of Southern America (Kruuk, 2006, p. 265; Staib, 2002), giant otters live in a habitat with high background noise. Mobile species inhabiting noisy environments tend to have stronger individual signatures than can be explained by genetic variation alone (Janik & Slater, 1998). Furthermore, individual calls are favoured in stable social groups with a complex structure, where animals frequently interact in varying social situations (Pollard & Blumstein, 2011). Giant otters belong to the socially most complex and vocally most active species within the Lutrinae (Ben-David et al., 2005; Bezerra, Souto, Schiel, & Jones, 2010; Hwang & Larivière, 2005; Kruuk, 2006, p. 265; Larivière, 2001a, 2001b). The basic social unit of giant otters is a family group with usually five to seven individuals (Duplaix, 1980; Hajek & Groenendijk, 2008, p. 160; Staib, 2002), comprising the reproductive alpha pair and their offspring of different ages (Duplaix, 1980; Duplaix et al., 2012; Staib, 2002). Giant otter groups are stable, have a strong association index (Duplaix, 1980; Leuchtenberger & Mourão, 2008) and cooperate in hunting, breeding and territorial defence (Carter & Weber Rosas, 1997; Leuchtenberger & Mourão, 2008, 2009; Staib, 2002). All activities such as fishing, territorial marking, grooming and resting are done together (Carter & Weber Rosas, 1997; Duplaix, 1980; Leuchtenberger & Mourão, 2009).

Depending on the social context, giant otters may use different modalities to identify conspecifics. First, olfaction plays an important role in the social life of all mustelids (Kruuk, 1992, 2006, p. 265) and olfactory cues will provide sufficient information for giant otters about other individuals in close proximity (Duplaix, 1980). Furthermore, visual cues such as the unique throat markings can be used over a greater distance when individuals are still visible to each other. Additionally, vocal recognition may be used when giant otters are separated at large distances with animals out of sight of each other. In these situations, two types of cohesion calls are produced by giant otters (for audio files SA1 and SA2, see [Supplementary material](#)). The 'contact call' (Fig. 1) is produced in situations of visual separation and subsequent reunion of group members. The 'hum' (Fig. 2) is uttered in close contact situations and is used for managing movements and soothing group members



**Figure 1.** Contact call of a captive adult female (see also audio file S1 in the [Supplementary material](#)). Selected sections for contact call measurements: cf1, cf2: parts with constant or quasiconstant frequency; mf: modulated frequency; p1–p3: three subunits of the modulated part. The spectrogram depicts frequency over time and was generated using a 1024-point fast Fourier transform and a Hann window with 87.5% overlap. The oscillogram shows changes in voltage over time.

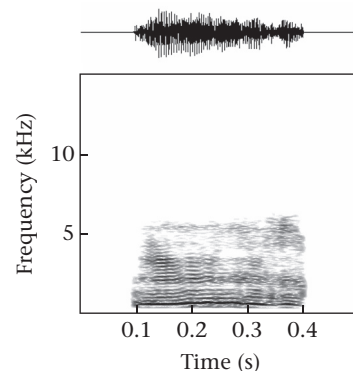
(Duplaix, 1980; Hajek & Groenendijk, 2008, p. 160; Staib, 2002). The two cohesion calls can be readily distinguished by their respective behavioural context.

In this study, we investigated vocal individuality in the cohesion calls of giant otters. We measured the acoustic properties of both cohesion call types from different individuals belonging to two wild and three captive giant otter groups and hypothesized we would find individual vocal signatures when analysing the acoustic parameters. Moreover, we predicted giant otters would be able to discriminate conspecifics by their cohesion calls. Therefore, we conducted habituation–dishabituation playback experiments on vocal discrimination with two captive giant otter groups.

## METHODS

### Study Sites and Study Animals

We recorded two wild and four captive giant otter groups. Group size varied from two to eight individuals, covering all age classes from juveniles to adults (giant otter age classes according



**Figure 2.** Hum of a wild adult male (see also audio file S2 in the [Supplementary material](#)). The spectrogram depicts frequency over time and was generated using a 1024-point fast Fourier transform and a Hann window with 87.5% overlap. The oscillogram shows changes in voltage over time.

to Sykes-Gatz, 2005). The vocalizations of wild giant otters were recorded at two oxbow lakes in the Peruvian Amazon region. Both lakes, Cocha Cashu (11°53'04"S, 71°24'28"W) and Cocha Salvador (11°59'46"S, 71°13'59"W), are located along the Manu River within the Manu National Park, in Cusco and Madre de Dios Departments, Peru. Recordings took place from September to December 2011. The vocalizations of captive giant otters were recorded in three German zoos in 2009 and 2011. Calls analysed or broadcast in playback experiments in the present study were recorded at Tierpark Hagenbeck (April 2009, May 2011 and July 2011), Zoo Duisburg (March 2011) and Zoo Dortmund (March 2009 and April 2011). Playbacks were conducted with four individuals at Tierpark Hagenbeck in 2012 and four individuals at Zoo Leipzig in 2013. All zoos had indoor and outdoor enclosures, except Zoo Leipzig, where two different indoor areas were located inside the large Gondwanaland hall. The public access area inside Gondwanaland had natural light with additional artificial light. The outdoor enclosures (natural light) in the other zoos were always open for visitors, whereas the indoor enclosures (artificial light) mainly served as retreat areas for the giant otters. Feeding times were three to five times per day. Each giant otter received 2–6 kg of fish (trout, whiting and roach) with supplementary fruit and vegetables as an enrichment.

### Animal Welfare

Giant otters are listed as endangered with a decreasing population trend (Duplaix et al., 2012). For field work in Peru, we had an official research permit (No. 014 S/C-2011-SERNANP-PNM) provided by SERNANP (Servicio Nacional de Areas Naturales Protegidas), the Peruvian nature conservation authority. The permit allowed us to follow and observe wild giant otter groups. We did not chase the animals and kept a minimum observing distance of 10–50 m, depending on the giant otters' activities. This distance was increased when newborn cubs were present. To prevent the giant otters from suddenly being frightened by our presence, we did not hide our activities from them and they became habituated to us.

To conduct recordings and playback experiments in the zoos, permission was obtained from the respective persons in charge (zoo director, head curator or veterinarian). The captive giant otter groups were not separated for recordings or for playback experiments, since no regular animal training was conducted and the giant otters were used to being together all day. When a litter was born, recordings were abandoned to avoid stressing the animals.

### Recording

We recorded giant otter vocalizations with a directional microphone (Sennheiser, MKH 416-P48U3) connected to a digital audio recorder (Zoom H2 Handy Recorder; 48 or 96 kHz sampling rate, 24 bit depth resolution). The behavioural context of the vocalizations was documented by spoken notes and video recordings (Sony, DCR SR-35 camcorder). We identified individuals by their unique throat markings either directly during recording or subsequently when analysing the video recordings.

To follow the free-ranging giant otters in Peru, we used one-person kayaks. Two observers monitored the otters' daily activity period from sunrise to sunset (around 0500 to 1700 hours) with four alternating 3 h shifts. Daily recording sessions in the zoos lasted around 3 h and covered the giant otters' activity period in the morning, afternoon or evening in alternating recording sessions.

### Call Analysis

Contact calls and hums were selected from the original recordings in Raven Pro (version 1.4, The Cornell Laboratory of Ornithology, Ithaca, NY, U.S.A.). Only calls with a good signal-to-noise-ratio that were not overlapped by other calls and for which we had additional information on individual and behavioural context were chosen for analyses. Whenever possible, we selected calls from different recording dates for each individual to reduce the effect of very similar or graduated calls within calling bouts of the same individual (Siemers & Kerth, 2006). We conducted noise reduction in WavePad Sound Editor (version 4.52, NCH Software, [www.nchsoftware.com](http://www.nchsoftware.com)) and erased bird calls or loud background noise with AviSoft SASlab Pro (version 5.1.23, R. Specht, Berlin, Germany). AviSoft SASlab Pro automatically reduced the resolution to 16 bit. Prior to evaluating the calls in Raven Pro, we normalized the volume of the calls in WavePad. Frequency parameters were measured from a spectrogram and a selection spectrum with high frequency resolution (fast Fourier transform: 1024 point; window: Hann; overlap: 87.5%; Hop size: 2.67 ms; DFT size: 1024 samples; grid spacing: 46.9 Hz).

### Measurements of Contact Calls

To look for statistical evidence of an individual vocal signature in contact calls, we only selected giant otters from which we had at least five calls of sufficient quality for measurements (for individual contact calls see Fig. A1, in the Appendix). This resulted in nine individuals (48 contact calls in total), from both wild and captive groups (for details on social classes of focal individuals see Table 1). Contact calls were analysed both over the entire call and within five subunits, referring to constant frequency and modulated frequency parts (Fig. 1). Entire calls were measured by selecting the spectrogram section with the fundamental frequency in Raven Pro. We measured three temporal parameters (duration, time to peak frequency, time to peak amplitude), four spectral parameters (minimum and maximum frequency, peak frequency, peak power), one waveform-derived parameter (peak amplitude) and average entropy (Charif, Waack, & Strickman, 2010). Additionally, we measured the same parameters in two parts with constant or quasiconstant frequency at the beginning and the end of the calls (cf1, cf2) and the modulated frequency part (mf) in the middle of the calls separately. The modulated part was further subdivided into three units of equal duration (p1–p3) that were measured separately. For each of the three subunits, we measured peak frequency at the beginning, the

**Table 1**

Number, distribution of social classes and origin of individuals contributing calls to our study and of focal individuals in the playback experiments

Number of	Contributing calls for analysis		Stimulus donors in playbacks		Focal otters in playbacks
	Contact call	Hum	Contact call	Hum	
Individuals	9	9	12	8	8
Males	7	5	7	4	4
Females	2	4	5	4	4
Wild otters	4	2	0	0	0
Captive otters	5	7	12	8	8
Juveniles	4	0	3	0	0
Subadults	3	1	4	1	4
Adults	2	8	5	7	4

Eight otters were the focal animal in both hum and contact call playbacks, one otter was the focal animal only in contact call playbacks and another only in hum playbacks. Thus, sample size for both playbacks was seven each. Age classes are according to Sykes-Gatz (2005).

middle and the end to describe the frequency contour of the modulated frequency part (Fig. 1). As the peak frequency at the end of p1 was identical to the peak frequency at the beginning of p2 (the same applied to the peak frequency at the end of p2 and the peak frequency at the beginning of p3), we described the frequency contour of the modulated frequency part with seven peak frequency measurements. Finally, we measured the mid time of the subunits, as well as the overall peak frequency and the time of this peak frequency in each of the three subunits, resulting in nine more parameters for the modulated frequency part. In total, we obtained 52 acoustic parameters to describe contact calls (for details, see Table S1 in the Supplementary material).

### Measurements of Hums

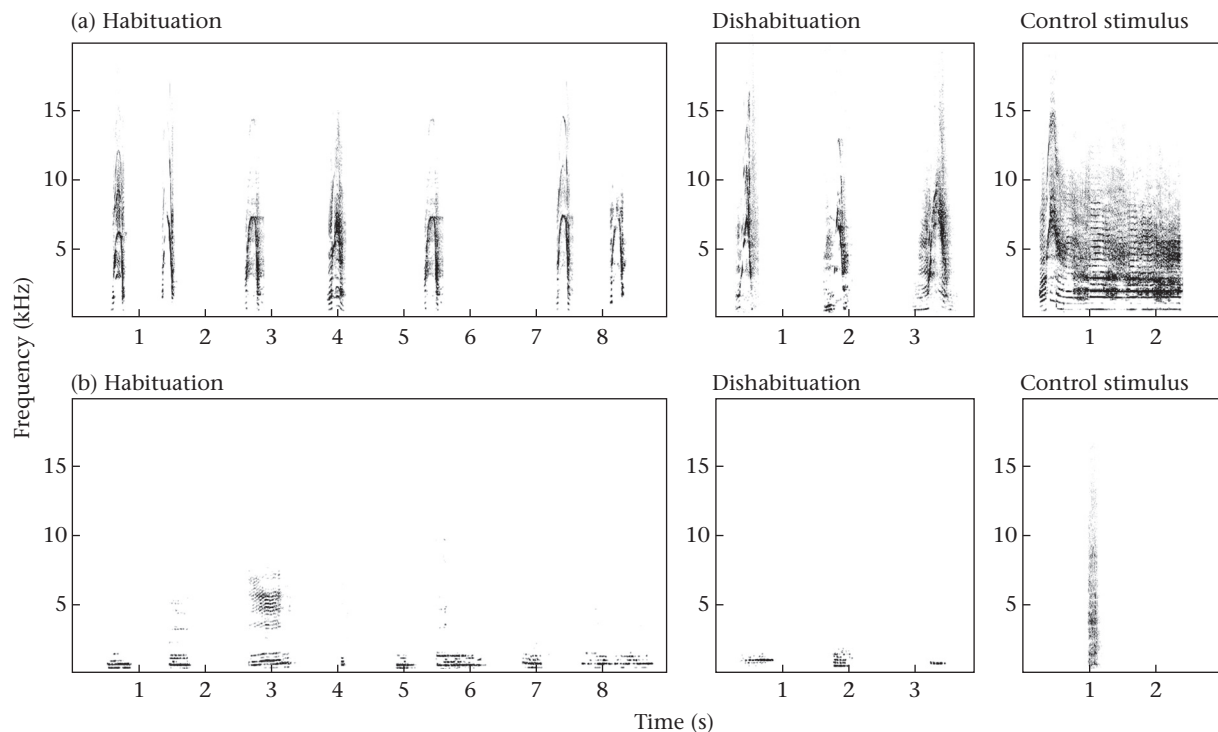
Hums were soft, low-frequency calls with a (quasi-) constant frequency. Owing to the simpler acoustic structure and the lack of a prominent frequency modulation, the quality of the recorded hums did not allow for detailed measurements comparable to those of contact calls. We only selected giant otters from which we had at least five calls of sufficient quality for measurements and thus measured hums from nine individuals (68 calls in total), from both wild and captive groups (for details on social classes of focal individuals see Table 1). The hums were analysed by selecting a spectrogram section from the highest to the lowest visible frequency (narrower when no harmonics were present and wider when harmonics were present) in Raven Pro. Over the entire call, we measured three temporal parameters (duration, time to peak frequency, time to peak amplitude), four spectral parameters (minimum and maximum frequency, peak frequency, peak power), one waveform-derived parameter (peak amplitude) and disorder in the hums, measured as average entropy (Charif

et al., 2010). This resulted in a total of nine acoustic parameters describing hums (for details, see Table S2 in the Supplementary material).

### Habituation–Dishabituation Playback Design

In the habituation–dishabituation playbacks, habituation stimuli (e.g. calls from individual ‘A’) were repeatedly broadcast until the study subjects habituated, that is, no longer reacted to the stimuli. Subsequently, dishabituation stimuli (e.g. calls from individual ‘B’) were broadcast to test whether the study subjects could discriminate between them and the habituation stimuli (see also Cheney & Seyfarth, 1988; Hauser, 1998). After the dishabituation stimuli, we broadcast a control stimulus (one call per playback, e.g. from individual ‘C’) to monitor attentiveness and motivation, to test whether the giant otters were listening to the broadcast stimuli throughout the whole playback. We chose alarm calls as control stimuli because we expected them to elicit a strong response when heard owing to the exciting nature of these calls. For contact call playbacks, we used the alarm call ‘waving scream’, for hums the alarm call ‘snort’ (Duplaix, 1980; see Fig. 3).

Each playback consisted of habituation calls of one individual, dishabituation calls of a different individual and one control stimulus call from a third individual (see also video S1 of a playback trial in the Supplementary material). All calls used as playback stimuli were recorded in 2009 and 2011 at Zoo Dortmund, Zoo Duisburg and Tierpark Hagenbeck (Table 1). We selected only high-quality calls for playbacks. For contact call playbacks, we used 12 captive giant otters as stimulus donors (3–17 different calls per stimulus donor). For hum playbacks, we used eight captive giant otters as stimulus donors (3–64 different calls per stimulus donor). We broadcast all possible combinations of sexes during the habituation



**Figure 3.** Examples of the experimental design of habituation–dishabituation playbacks of contact calls and hums. (a) Contact call. (b) Hum. Habituation calls from individual ‘A’, dishabituation calls from individual ‘B’ and control stimulus call from individual ‘C’. Habituation sequences are only excerpts. The spectrograms depict frequency over time and were generated using a 1024-point fast Fourier transform and a Hann window with 87.5% overlap.



and dishabituation phases of different playback trials (i.e. male versus male, female versus female and female versus male donors), to test whether discrimination was influenced by the sex of the stimulus donor. Moreover, we selected only current nongroup members as stimulus donors to exclude an influence of group membership. Some of the nongroup members were known to the focal individuals, since they came from Tierpark Hagenbeck zoo, which is one of the two giant otter breeding lines in German zoos and the offspring had been transferred to the zoos Duisburg, Dortmund and Leipzig.

The time intervals between all calls in the playback sequences were based upon measurements of natural call sequences (0.2–2.0 s for contact calls and 0.2–2.5 s for hums). Within this range, call intervals were chosen at random. Prepared habituation sequences lasted up to 4 min (even though focal animals normally habituated much faster; for details see below) and dishabituation sequences lasted 3.26–9.51 s (mean for contact calls = 5.41 s, mean for hums = 6.76 s). All randomly selected numbers (call intervals, playback order and call order) were obtained from the random number generator in Microsoft Excel 2007. We conducted no more than seven playbacks per day. Trials were separated by a break of at least 10 min and trial days were separated by 1 day.

The playback experiments were conducted in the outdoor enclosure of Tierpark Hagenbeck (November 2012) and in the indoor enclosure 'Gondwanaland' at Zoo Leipzig (February 2013). Playback stimuli were broadcast from a Hama active speaker (Sonic Mobil 400 Alu, frequency range 100 Hz–20 kHz) connected to a notebook (Lenovo ThinkPad L412). The speaker was hidden at the fence of the enclosure and we randomly varied its position. We documented the otters' responses to the playbacks with two Sony Handycams (DCR-SR35), one hand-held and the other mounted on a tripod (see video S1 in the [Supplementary material](#)). A playback experiment started when the otters were not too engaged in other activities such as playing, begging for food, eating, mating or sleeping or distracted by the presence of animal keepers. The habituation phase consisted of different calls of one stimulus donor (Fig. 3) that were broadcast in random order (3–64 different calls per stimulus donor). Habituation calls were broadcast until the animals were habituated (habituation phase mean  $\pm$  SD duration in contact calls:  $86 \pm 40$  s; hums:  $85 \pm 46$  s), that is, no longer showed any reaction towards the speaker and started to engage in other activities. At this point, the dishabituation stimuli were presented. The dishabituation stimuli always consisted of three different calls per stimulus donor (Fig. 3) that were broadcast in a balanced order. After the dishabituation stimuli, we broadcast one control stimulus from a different stimulus donor to those in the earlier playback phases. Playbacks were abandoned when disturbances from aeroplanes or passing zoo cars occurred or when the giant otters showed obvious distracted behaviour.

### Response Measures

We extracted the audio tracks as wave files from the videos using Any Video Converter (version 5.0.3, Anvsoft Inc., [www.anvsoft.com](http://www.anvsoft.com)) to measure reaction latency until the first reaction and the duration of the response behaviour to the dishabituation stimuli in Raven Pro. We measured the duration of the reaction as metric data and the type of movement towards the speaker as categorical data (0: no movement; 1: raising or turning the head; 2: turning the whole body; 3: walking 4: moving fast), the latency until the first reaction and the duration of the whole reaction. No visible movement (category 0) was rated as no response and any movement towards the speaker (category 1–4) was rated as a response. The reaction to the control stimulus was classified

bimodally ('response' and 'no response'). This was done to rate playbacks as either valid (reaction to dishabituation and control stimulus or only to control stimulus) or invalid (no reaction), and to distinguish a discriminative response (reaction to dishabituation and control stimulus) from no discrimination between habituation and dishabituation (reaction only to control stimulus). The individuals' behavioural responses were analysed in Windows Movie Maker. Responses to the dishabituation stimuli were examined from the beginning of the first dishabituation stimulus to the start of the control stimulus.

### Statistics

To look for statistical evidence of an individual vocal signature, we considered contact calls and hums separately. We used principal component analyses with varimax rotation to reduce the number of measured variables and to decrease the difference in the number of measured variables in contact calls and hums. The principal component analyses fulfilled Kaiser–Meyer–Olkin (KMO) and Bartlett's test criteria. For contact calls, 15 principal components (PCs) with eigenvalues greater than one were extracted (four PCs of the entire call, six PCs of the cf parts and five PCs of the mf parts). Subsequently, we performed a stepwise discriminant function analysis (DFA) with leave-one-out cross-validation which selected five of the 15 PCs. For hums, we extracted five PCs with eigenvalues greater than one and used them in a discriminant function analysis with leave-one-out cross-validation; in this analysis, all five PCs were used simultaneously. We tested whether DFA classification results differed significantly from a random classification by conducting one-tailed binomial tests (following Mundry & Sommer, 2007).

For statistical analyses of the playback experiments, we focused only on the individual that first reacted to the respective dishabituation phase, since the subsequent reactions of other otters could have been influenced by the behaviour of the individual that reacted first. Thus, focal animals were chosen retrospectively. If we had more than one valid playback for a given individual and stimulus combination, we selected the playback with lowest background noise for further analyses. When analysing only playbacks with the lowest background noise, we found seven focal animals that reacted to all four different sex combinations for contact calls and hums, respectively.

We conducted both a general and a generalized linear model with sex combinations and individuals as fixed factors to test whether the seven focal animals or the sex of stimulus donors influenced the otters' responses to the playbacks. We used a Shapiro–Wilk test to ascertain that standardized residuals of the models did not deviate from a normal distribution. The two models were applied to separate behavioural response measures. The metric response variables used in the general linear model were response duration and reaction latency (which consisted of a PC combining latency until first reaction, latency until raising the head and latency until turning the head). The categorical response variable movement type was used in the generalized linear model (GLM). To test for differences in response behaviour between contact calls and hums, we used a Wilcoxon signed-ranks test for the metric variables and a sign test for the categorical variable. To examine the influence of the different control stimuli on the proportion of valid playback trials and on the proportion of discriminative responses within valid trials, we ran chi-square tests. Chi-square tests were performed on all playback experiments for a given individual and stimulus combination, not only on the ones with the lowest background noise. Thus, the sample size was 56 valid and 11 invalid trials for contact calls and 52 valid and 17 invalid trials for hums. To assess the proportion of

**Table 2**  
Assessment of model fit of the discriminant function analyses on contact calls and hums

Function	Eigenvalue	Percentage variance	Test of function	Wilks's lambda	Chi-square	df	P
Contact calls							
1	3.238	47.3	1–5	0.02	151.29	40	<0.0001
2	2.100	30.7	2–5	0.10	93.53	28	<0.0001
3	0.646	9.4	3–5	0.30	48.28	18	<0.001
4	0.572	8.4	4–5	0.50	28.34	10	0.002
5	0.292	4.3	5	0.77	10.23	4	0.037
Hums							
1	0.964	47.2	1–5	0.21	93.23	40	<0.0001
2	0.711	34.8	2–5	0.42	52.73	28	0.003
3	0.193	9.5	3–5	0.71	20.50	18	0.305
4	0.125	6.1	4–5	0.85	9.89	10	0.451
5	0.048	2.4	5	0.95	2.82	4	0.588

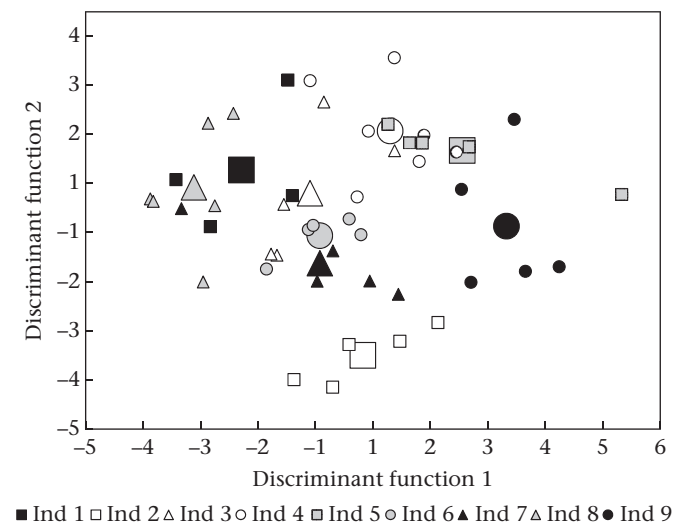
Function: discriminant function. Eigenvalue: discriminative ability of a function. Percentage variance: the function's eigenvalue divided by the sum of all the eigenvalues  $\times 100$ . Test of functions: functions included in a test with the null hypothesis that canonical correlations (i.e. between predictor variables and groupings) associated with a given function, and all that follow, are equal to zero. Wilks's lambda: proportion of the total variance in the discriminant scores not explained by differences between groups (i.e. individuals). Chi-square: tests the null hypothesis that a function, and all functions that follow, have no discriminating ability (i.e. canonical correlations are equal to zero). *df*: effect degrees of freedom for a given function (based on the number of groups and discriminant variables). *P*: *P* value associated with the chi-square statistic.

discriminative responses within valid trials, we compared the number of valid playback trials with a discriminative response (reaction to dishabituation and control stimulus) and without a discriminative response (reaction only to control stimulus). For contact calls, a discriminative response was found in 48 of 56 valid trials; for hums, a discriminative response was found in 49 of 52 valid trials. With the exception of the chi-square tests (Preacher, 2001), all statistical tests were performed with SPSS (version 17, SPSS Inc., Chicago, IL, U.S.A.).

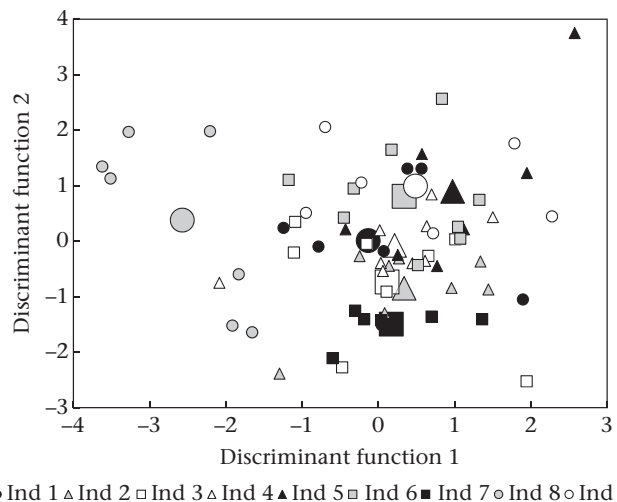
## RESULTS

### Individual Signature in Cohesion Calls

In total, 48 contact calls from nine individuals and 68 hums from nine individuals were analysed (for detailed DFA results, see



**Figure 4.** Signal space of contact calls defined by the first two discriminant functions. Large symbols: group centroids. Small symbols: contact calls.



**Figure 5.** Signal space of hums defined by the first two discriminant functions. Large symbols: group centroids. Small symbols: hums.

Table 2, Figs 4, 5). For contact calls, 56.3% of the cross-validated calls were allocated to the correct individual. This classification result differed significantly from a random classification (11.1%; one-tailed binomial test:  $P = 0.002$ ). Only 23.5% of the cross-validated hums were assigned to the correct individual, which did not differ significantly from a random classification (11.1%; one-tailed binomial test:  $P = 0.254$ ).

### Playback Experiments on Individual Discrimination

We conducted 67 contact call and 69 hum playback experiments. Of the contact call playbacks 56, and of the hum playbacks 52, met our criteria for validity (i.e. at least a reaction to control stimulus). In the majority of trials, the habituated otters showed a discriminative response (contact calls: 48 of 56 trials; hums: 49 of 52 trials). Thus, our results clearly indicate that giant otters were able to discriminate between individuals based on their contact calls or hums.

The sex of the stimulus donors had no significant effect on response duration and reaction latency (general linear model: contact calls: Wilks's  $\lambda = 0.659$ ,  $F_{6,34} = 1.312$ ,  $P = 0.279$ ; hums: Wilks's  $\lambda = 0.882$ ,  $F_{6,34} = 0.368$ ,  $P = 0.894$ ) or movement type (GLM: contact calls:  $X^2_3 = 1.209$ ,  $P = 0.751$ ; hums:  $X^2_3 = 4.240$ ,  $P = 0.237$ ). The identity of the focal animals also had no significant effect on response duration and reaction latency (general linear model: contact calls: Wilks's  $\lambda = 0.674$ ,  $F_{12,34} = 0.617$ ,  $P = 0.813$ ; hums: Wilks's  $\lambda = 0.466$ ,  $F_{12,34} = 1.315$ ,  $P = 0.255$ ) or movement type (GLM: contact calls:  $X^2_6 = 4.486$ ,  $P = 0.611$ ; hums:  $X^2_6 = 9.279$ ,  $P = 0.158$ ).

The otters' response duration did not differ significantly between contact calls and hums (Wilcoxon test:  $Z = -0.676$ ,  $P = 0.499$ ); however, the latency until the first reaction was significantly shorter for contact calls than for hums (Wilcoxon test:  $Z = -2.366$ ,  $P = 0.018$ ; mean  $\pm$  SD: contact calls:  $0.99 \pm 0.26$  s; hums:  $1.56 \pm 0.62$  s). No differences between contact call and hum playbacks were found in the movement type (two-tailed sign test:  $P = 0.999$ ).

The different control stimuli did not affect the proportion of valid playback trials (chi-square test:  $X^2_1 = 0.161$ ,  $P = 0.688$ ) or the proportion of discriminative responses within valid playback trials (chi-square test:  $X^2_1 = 2.138$ ,  $P = 0.144$ ).

## DISCUSSION

Our study provides convincing evidence that giant otters have individually distinct cohesion calls. By analysing the acoustic properties of the cohesion calls, we found an individual signature in contact calls but not in hums. According to the ‘distance communication hypothesis’ (sensu Bouchet et al., 2012), the degree of vocal individuality in cohesion calls should be positively correlated with an increasing distance between the calling animal and the receiver, and with frequently occurring separations (Bouchet et al., 2012; Mitani, Gros-Louis, & Macedonia, 1996; Rendall, Rodman, & Emond, 1996). Our results could be in concordance with the ‘distance communication hypothesis’ by showing an individual signature in the long-range contact calls and no individual signature in hums, which are used for short-range communication. However, the better DFA classification success obtained for contact calls compared with hums is probably caused by the different number of parameters measured for the two call types, which can influence the detectability of an individual vocal signature (Beecher, 1989). Furthermore, the giant otters readily discriminated nongroup members in both calls tested despite the fact that we only found statistical evidence of an individual signature in contact calls but not in hums. This result corresponds to a study of mongoose, *Mungos mungo*, contact calls, where Müller and Manser (2008) stated that a low DFA classification result on individual calls does not imply the lack of individual recognition.

Like most mammalian vocalizations (Titze, 1994), cohesion calls of giant otters are produced in the larynx (i.e. the ‘source’) and radiated through the vocal tract (i.e. the ‘filter’). This source filter theory (sensu Fant, 1960) is crucial for understanding mammalian call production mechanisms. Acoustic variation leading to vocal individuality may be created in the source (e.g. bottlenose dolphins, *Tursiops truncatus*; Janik et al., 2006) or in the filter (e.g. chacma baboons, *Papio cynocephalus ursinus*; Rendall, 2003) or in both. However, most mammals encode their individual distinctiveness with source characteristics such as frequency and amplitude contours, duration and harmonic structure. Modulations of the fundamental frequency are particularly important for source-induced individual variability in mammals (reviewed in Taylor & Reby, 2010). In this study, we measured only source-induced characteristics which created sufficient interindividual variation to encode individual signatures in cohesion calls.

In our habituation–dishabituation playbacks, the otters’ response duration did not differ significantly between contact call and hum playbacks, but the focal animals took significantly longer to respond in hum playbacks than contact call playbacks. Since giant otters produce the hum in situations in which they are visible to each other (Hajek & Groenendijk, 2008, p. 160), this call serves to maintain contact in close proximity. In this situation, discrimination may already have occurred, making a fast reaction and thus a short latency unnecessary. Nevertheless, the giant otters were able to discriminate between hums of conspecifics, indicating that they convey identity information. This leads us to the conclusion that hums probably contain subtle parameters suitable for individual discrimination which we did not detect with our measurements. Correspondingly, Owren and Rendall (2001) reported that close-range calls in primates often include information on the senders’ individuality. These vocalizations may allow the senders to influence the receivers’ affective state (Owren & Rendall, 2001), and allow the receivers to respond appropriately to the senders’ intention based on previously experienced interactions (see also Briefer, 2012). This process facilitates social interactions in groups with a dominance hierarchy, since the

animals can avoid conflicts by basing their behavioural decisions on an already established hierarchy. It is likely that giant otters use this process as well and benefit from signalling identity, even when in visual range. To date, no general study of the hierarchy system in giant otter groups exists, but naturally the alpha pair represents the dominant individuals, with sometimes the alpha female, sometimes the alpha male being more dominant (Evangelista, 2004). The lack of intragroup aggression in giant otters (Duplaix, 1980) may be mediated through the process of dominant individuals signalling their identity and subordinates responding accordingly.

In the playback experiments, we only used calls from current nongroup members to test for vocal discrimination. We did not have sufficient calls from group members to test additionally for discrimination between group members or between group members and strangers. Discriminating between nongroup members represents a more difficult task than distinguishing between group members present during the playback and strangers, since current familiarity cannot be used as a cue. This emphasizes the well-developed ability of individual vocal discrimination in giant otters. Some of the stimulus donors were known to the focal animals; for instance the alpha female from the Tierpark Hagenbeck group was the mother of the alpha male in the Zoo Leipzig group. The former acquaintance may have facilitated the categorization process on a basis of a prior association mechanism, enabling animals to discriminate familiar relatives from unknown individuals (Mateo, 2004). However, there is no information on how and for how long giant otters store information on other individuals no longer belonging to the group. Since giant otters were able to differentiate conspecifics within the category ‘stranger’ and since the sex of the stimulus donors had no influence on the discrimination success, we assume that the giant otters in our study distinguished the stimulus donors on a basis of individual-level categorization (sensu Tibbetts & Dale, 2007).

In the context of group cohesion, a vocal group signature might be considered to be generally sufficient for recognition and reunion processes (compare Boughman, 1997). Nevertheless, several species have individual cohesion calls (Benson-Amram, Heinen, Dryer, & Holekamp, 2011; Durbin, 1998; Frommolt, Goltsman, & MacDonald, 2003; Frommolt, Kruchenkova, & Russig, 1997; Tooze, Harrington, & Fentress, 1990). Individuality in cohesion calls probably facilitates intragroup interactions (Gillam & Chaverri, 2012), making an individual signature more advantageous than a group signature. The faculty of individual discrimination may not only facilitate group coordination in giant otters, but could also be important in terms of indirect fitness gains for helpers within the cooperative breeding system (Komdeur, Richardson, & Burke, 2004). Both helpers and parents could simply rely on the decision rule to feed and care for all cubs within the nest, group or natal territory (Komdeur et al., 2004; Mateo, 2004). In a giant otter family, helpers and dependent cubs usually have the same degree of relatedness (siblings, after Staib, 2002) and, so far, no extrapair paternity has been reported (Hajek & Groenendijk, 2008, p. 160; Sykes-Gatz, 2005). However, helpers in social groups show various degrees of helping effort, depending on their social rank, age or sex (Cant & Field, 2001, 2005; Clutton-Brock et al., 2000). Under these circumstances, kin recognition alone will not be sufficient to distinguish between different cubs, or between equally related helpers with differing degrees of helping effort (Komdeur et al., 2004; Müller & Manser, 2008). In the giant otters’ helping system, in which elder siblings help their parents rear the current young (Duplaix, 1980; Evangelista & Weber Rosas, 2011; Staib, 2002), adult offspring sometimes even support older family members with food



(Davenport, 2010). This role-reversed helping behaviour of offspring helping their parents very likely demands that giant otters are not only able to discriminate between kin and nonkin but are also able to recognize individuals.

The same situation may apply to other otter species. Contact calls of Asian small-clawed otters, *Aonyx cinerea*, appear to have a similar frequency contour to the contact calls of giant otters (compare Lemasson, Mikus, Blois-Heulin, & Lodé, 2013). In both otter species, the contact calls are individually distinct (at least in male Asian small-clawed otters, Lemasson et al., 2013), and both species show vocal discrimination. The social organization of Asian small-clawed otters is similar to that of giant otters. Groups are composed of the alpha pair and their offspring of different ages. Both parents contribute to rearing the young, show a strong pair bond (Hussain, Gupta, & de Silva, 2011) and elder offspring may act as helpers (Larivière, 2003; Lemasson et al., 2013). A group includes up to 12 individuals (Larivière, 2003) and a vocal repertoire of 12 vocalizations has been reported (Timmis, 1971). Therefore we think that Asian small-clawed otters, like giant otters, may profit from signalling their identity to conspecifics, especially if helpers and dependent cubs show the same degree of relatedness and helpers differ in their amount of helping effort.

Thus, otters are a highly interesting taxon for further investigations of their communicative and cognitive abilities. Otters offer the opportunity to study species within this mustelid sub-family that show a wide variety of social organizations. If the socially more demanding groups of giant otters or Asian small-clawed otters display a more advanced communication system than more solitary species, as for instance the Eurasian otter, *Lutra lutra*, it would further support the 'social complexity hypothesis for communicative complexity' (Freeberg et al., 2012), which so far has been shown only for a selected few species (Blumstein & Armitage, 1997; Freeberg, 2006; McComb & Semple, 2005).

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## Supplementary Material

Supplementary material associated with this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2013.12.005>.

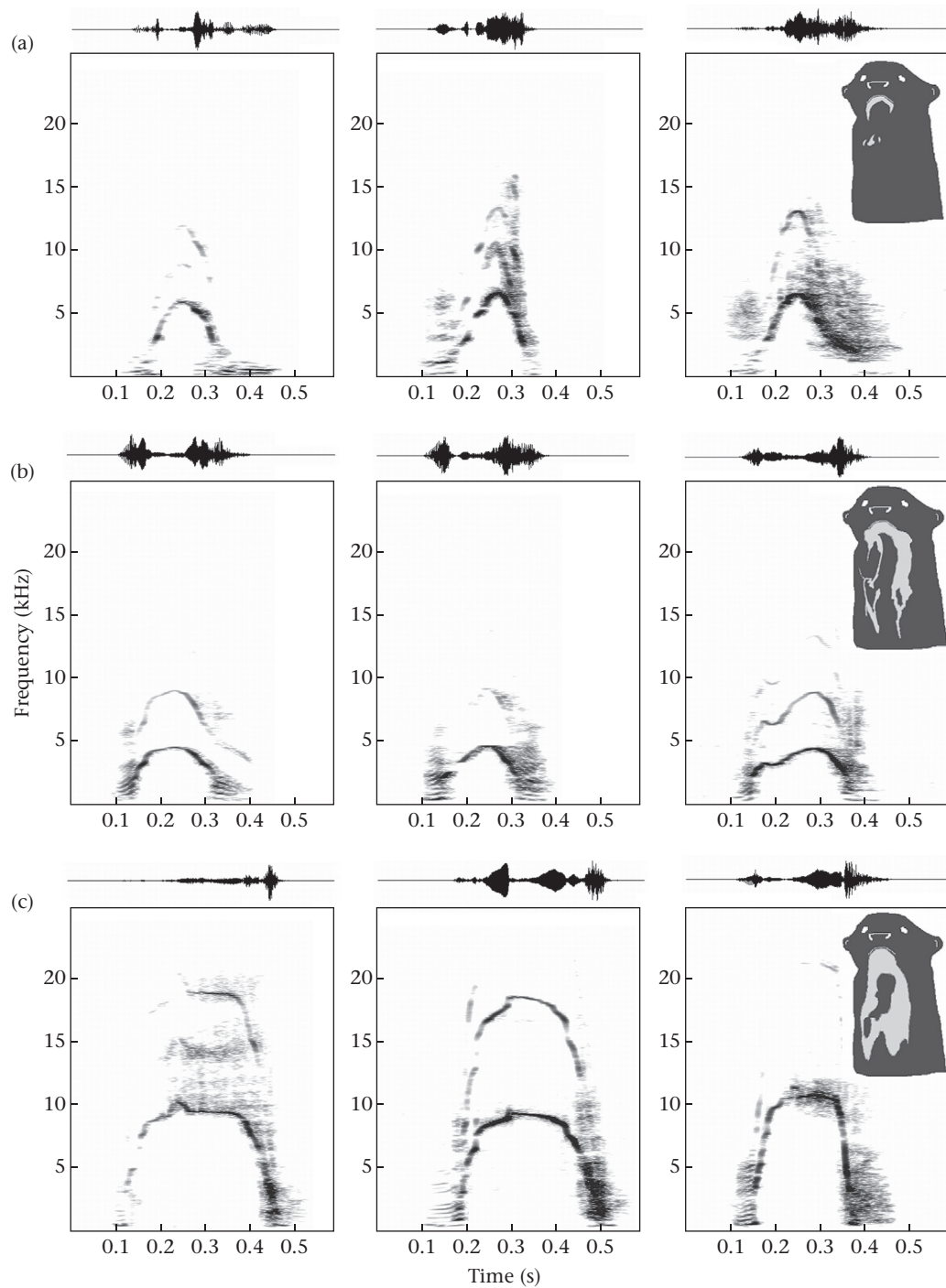
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## APPENDIX



**Figure A1.** Three examples of contact calls for each of three giant otters. (a) Adult male, Zoo Dortmund, (b) adult female, zoo Tierpark Hagenbeck, (c) juvenile male, Cocha Salvador. The spectrogram shows frequency over time and was generated using a 1024-point FFT and a Hann window with 87.5 % overlap. The oscillogram illustrates changes in voltage over time.