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Naturwissenschaften
The Science of Nature

ISSN 0028-1042
Volume 100
Number 3

Naturwissenschaften (2013)
100:275-279
DOI 10.1007/s00114-013-1022-9



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Social partner discrimination based on sounds and scents in Asian small-clawed otters (*Aonyx cinereus*)

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Received: 11 December 2012 / Revised: 24 January 2013 / Accepted: 30 January 2013 / Published online: 10 February 2013
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Abstract Ability to discriminate familiar conspecifics is an essential competence in any group-living species, ensuring socio-spatial cohesion, but in many animals, such as mustelids, the relative importance of the different communicative modalities for discrimination is poorly understood. In otters, there is evidence of intra-specific variation in physical appearance and in feces chemical profile, but the potential for acoustic identity coding as well as for identity decoding in visual, acoustic and olfactive domains remains unexplored. We investigated the acoustic structure of contact calls in five captive groups of small-clawed otters and found that it is possible to reliably assign one particular call to a given adult male caller. Females discriminated between familiar and unfamiliar adult males based on their sound (playback) and smell (feces) but not based on their picture, suggesting abilities to memorize and use acoustic and olfactive signatures in their daily social life.

Keywords Individual acoustic variability · Auditory discrimination · Olfactory discrimination · Visual discrimination · Playback · Mustelids

Communicated by: Sven Thatje

Electronic supplementary material The online version of this article (doi:10.1007/s00114-013-1022-9) contains supplementary material, which is available to authorized users.

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Introduction

Social living habits imply the ability to discriminate between familiar and unfamiliar conspecifics. Discrimination may be based on different modalities, depending on species morphology, sensory and cognitive abilities, as well as habitat quality. Discrimination of familiar individuals based on acoustic (elephant—McComb et al. 2000; horse—Lemasson et al. 2009; baboon—Lemasson et al. 2008), olfactive (ant—D'Ettore and Heinze 2005; panda—Hagey and MacDonald 2003; penguin—Coffin et al. 2011) and visual (wasp—Tibbetts 2002; cow—Coulon et al. 2011; chimpanzee and macaque—Parr et al. 2000) cues have been shown in a large range of animals.

Some mustelid species, like otters, form extended family groups; however, little is known about the sensory cues on which they rely to identify each other. Mustelids are well-known for their marking behaviour (Roper et al. 1993), and chemical analysis revealed individual differences in feces (Zhang et al. 2005; Brinck et al. 1983; Buesching 2002; Trowbridge 1983). Acoustic differences between individuals belonging to different age classes have also been shown in otters (Lemasson et al., submitted), but whether the voices of individuals also vary within these age–sex classes remains in question. There is also evidence to suggest that physical differences between individuals may enable visual identity coding (mink—Thom et al. 2004; otter—Hattori et al. 2003). For example, Duplaix (1980) suggested that giant otters are able to discriminate each other visually at a 50-m distance using the colour of the fur in the neck. In sum, although a few observations have already suggested that otters communicate with a series of vocal, visual and olfactive signals (e.g. *Lontra canadensis*—Kruuk 2006), little is known concerning the relative importance of each sensory modality in the familiarity decoding mechanism. More

generally, several studies have investigated the roles of calls in fission–fusion societies or the importance of olfactory communication in carnivores, but very few studies have focused on multimodal signalling in these species.

We studied captive groups of small-clawed otters. In the wild, this species forms small or extended family groups composed of one adult couple and their offspring from several generations, the oldest being sometimes described as helpers (Hussain et al. 2011). We tested (1) whether adult males differed in their voices amongst themselves and (2) which modalities were involved in discrimination for adult females when presented with acoustic, olfactory and visual cues from familiar and unfamiliar adult males. We hypothesized that unfamiliar stimuli would attract the female's attention more than familiar stimuli (Lemasson et al. 2009).

Methods

Study animals

To address our first question, we recorded and analyzed the calls of five adult males (M1–M5) originating from different French zoological park facilities (Table 1). We collected the feces of four of them (M1–M4). Then, we tested the discrimination ability of their unrelated adult female mates (F1–F4). Otters from different zoos had never met. When a group from any one zoo housed two adult males or females, the dominant individual (as designated by zoo-keepers) was selected as subject. Within a group, males and females have known each other for more than 1 year. Enclosures were enriched with vegetation, a pond (>4 m²,

1 m in depth) and shelter with straw litter, in which all group members were locked at night. Otters were fed daily with fish, meat, insects and pellets.

Stimulus collection and acoustic analysis

Feces

For each male (M1–M4), five to eight fresh feces were collected and immediately stored at –18 °C. A sample was thawed out at 4 °C 24 h prior to each trial, and 6 g were brought to room temperature 1 h before the trial.

Pictures

Pictures were taken (Canon E0560D, 18 million pixels) to obtain, for each male, two different photos in comparable postures (body showing its right side with head facing, as in Blumstein et al. 2009, see examples in ESM 1). Images were printed on HD paper (UltraPhoto 1200dpi 160 g) at 1:1 size ratio, cut to shape and mounted on a stand-alone cardboard cut-out.

Calls

Adult male calls (M1–M5) were recorded outdoors (from <5 m) with a Marantz® PMD661 recorder connected to a Sennheiser® K6/ME66 directional microphone (sample rate 48,000 Hz, resolution 16 bits, recording duration per male 47±8 min). The second male of La Boissière almost never called. Spectrograms were drawn using Praat® (FFT, number of time/frequency steps 1,000/250). Only U3 contact calls (*N*=40 per

Table 1 Subject characteristics (females: F1–F4, males: M1–M5) and housing conditions of our captive small-clawed otters and chronology of stimulus collection and experiment

Zoo name (French zip code)	Group composition [date of birth, code name]	Enclosure size in m ² [other species]	Stimulus collection	Experiment
La Boissière du Doré (44430)	♀ [01/08/2001, F1] ♂ [25/01/2009, M1] ♂ [25/01/2009]	2,000 [with gibbons and orangutans]	Calls and feces: February 2012	March 2012
Les sables d'Olonne (85100)	♀ [6/10/2007, F2] ♂ [14/12/2003, M2]	220	Calls and feces: March 2012	April 2012
Doué la Fontaine (49700)	♀ [5/01/2007, F3] ♂ [9/05/2002, M3]	70	Calls and feces: February 2012	April 2012
Champrépus (50800)	♀ [14/07/2006, F4] ♀ [11/09/2007] ♂ [13/07/2009, M4]	70	Calls and feces: February 2012	April 2012
Planète Sauvage (44710)	♀ [in 2001] ♂ [in 1998, M5] 8 offspring	240	Calls: April 2011	The female of this group was not tested as the male died prior to the experiment

male) were used as these are associated with relaxed and affiliative contexts (Lemasson et al., submitted).

First, seven acoustic parameters were measured on the 40 calls from each male (Fig 1). We tested for individual acoustic differences by running a discriminant factorial analysis (DFA) using Statistica 10. Second, acoustic stimuli were assembled and consisted of four series of nine different calls per male, randomly selected and separated by a silent gap of 2 s (average intra-individual inter-call delay in spontaneous calling events = 2 ± 0.2 , $N=63$). Each acoustic stimulus was played back only once in order to avoid pseudoreplication. The amplitude of each stimulus was adjusted to 65 db in order to achieve natural sound intensity.

Stimulus presentation

Each female (F1–F4) was tested eight times using pairs of stimuli (two modality combinations “Call+Feces, Call+Picture” $\times 2$ types of male “unfamiliar [randomly attributed], mate” $\times 2$ modes of presentation “the two stimuli are from the familiar or from an unfamiliar male [congruent], one stimulus is from the familiar male while the other is from an unfamiliar male [incongruent]”). Stimulus pairs were presented in a random order, not more than once per day, at the time of their release from the shelter (morning). All experiments occurred 1 h prior to the first feeding time.

Pairs of stimuli (picture, feces, loudspeaker) were presented simultaneously from within a wired cage ($80 \times 35 \times 35$ cm; mesh, 40 mm) with a PVC bottom. The cage was cleaned with alcohol between trials. The cage was installed 3 m from the shelter by a caretaker, 30 min before the release of resident otters (cage position was slightly modified at each trial to limit habituation). The sound (in .wav format) was broadcast using an Asus G53J computer connected to a Nagra Kudelski speaker as soon as the female subject's body emerged from the shelter. After 2 min and 45 s, the caretaker removed the cage from the

enclosure. For 15 min, the experimenter filmed (Sony HDR XR155E) the subject from a fixed station.

Behavioural response analysis

As the number of subjects was too low to test stimulus congruency effect, we focused on the influence of familiarity (with the male) on female reaction to each of the three signal modalities (visual, auditory, olfactory). Starting time (T0) was assigned to the moment when the female emerged from the shelter (auditory and visual stimuli) or came within 1 m of the cage (olfactory stimulus; two trials were excluded because the female did not approach the cage). The occurrence frequency and duration analysis was performed on a 2-min 30-s sample (auditory and visual stimuli) or 1 min (olfactory), ending when the caretaker entered the enclosure. Several variables were measured using (1) focal and (2) scan sampling methods (every 5 s); (1) focal sampling included number of gazes (>1 s), number of sniffing directed at the cage and duration of first glance toward the cage; (2) scan sampling included number of contacts with the cage, with the male in the group and movements to the latrine (sampling time extended to 15 min for the latrine).

Results

Individual acoustic variability

Acoustic variability between individuals was found in U3 acoustic structures (ESM 2). A DFA confirmed the reliability of our call-to-caller assignment method (88 % of correct classification, ESM 3). Functions 1 and 2, respectively, explain 76.4 and 19.5 % of the variance and were highly correlated with F0max and F0end, respectively. This DFA was done using 20 calls per male as the training sample and 20 calls per male as the test sample. We have replicated this analysis using another random subset of 100 calls to create the DFA model and found again a high percentage (81 %) of correct classification.

Reaction to familiar vs. unfamiliar stimuli

The level of familiarity with visual stimuli did not influence the female's response when presented with a photographic portrait of a male; on the other hand, level of familiarity significantly influenced the female's response to both acoustic and olfactory stimuli (Table 2). The duration of the female's first gaze towards the loudspeaker following the broadcast of an unfamiliar male's call was twice as long as the first glance elicited by a familiar male's call. Females went twice as often to seek contact with the latrine of their enclosure after exposition to an unfamiliar male's odour.

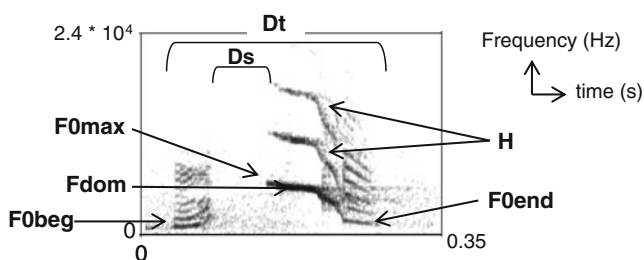


Fig. 1 Spectrogram of small-clawed otter's contact call and illustration of the acoustic measurements performed. Definition of acoustic measurements: duration of the call (Dt), duration of the silent break (Ds), number of harmonics (H), fundamental frequency at the beginning (F0beg), end (F0end) and top (F0max) of the call, dominant frequency where the intensity was the highest (Fdom)

Table 2 Behavioural response of small-clawed otter subjects to the presentation of familiar vs. non-familiar social stimuli using auditory, visual and olfactory signals. The *first* and *second lines* of each cell presents *P* and *Z* values of the one-tailed Wilcoxon matched-pair tests, comparing the responses to stimuli coming from familiar vs. unfamiliar males (*bold type*: significant results). The *third* and *fourth lines* presents the mean (\pm SE) response scores to familiar (F) and unfamiliar (NF) males

		Sound (<i>N</i> =16)	Picture (<i>N</i> =8)	Smell (<i>N</i> =6)
Number of contact to the cage	<i>p</i>	0.700	0.704	0.767
	<i>Z</i>	0.524	0.535	0.730
	F (mean \pm SE)	3.31 \pm 1.48	3.38 \pm 2.11	2.33 \pm 1.17
	NF (mean \pm SE)	2.81 \pm 1.32	3.13 \pm 2.10	1.83 \pm 1.47
Number of contact to the male	<i>p</i>	0.608	0.583	0.395
	<i>Z</i>	0.275	0.210	0.267
	F (mean \pm SE)	4.44 \pm 0.96	5.38 \pm 1.85	1.5 \pm 0.96
	NF (mean \pm SE)	4.25 \pm 0.99	5.00 \pm 1.38	1.83 \pm 0.79
Number of contact to the latrine	<i>p</i>	0.06	0.071	0.014
	<i>Z</i>	1.556	1.468	2.201
	F (mean \pm SE)	3.25 \pm 1.06	1.88 \pm 1.08	4.33\pm2.72
	NF (mean \pm SE)	5.6 \pm 1.59	5.88 \pm 1.77	8.33\pm2.47
First gaze duration (s)	<i>p</i>	0.008	0.500	0.977
	<i>Z</i>	2.430	0.000	1.992
	F (mean \pm SE)	1.19\pm0.40	1.24 \pm 0.43	3.56 \pm 1.22
	NF (mean \pm SE)	2.09\pm0.51	1.31 \pm 0.48	0.91 \pm 0.18
Number of gazes to the cage	<i>p</i>	0.541	0.500	0.888
	<i>Z</i>	0.103	0.000	1.213
	F (mean \pm SE)	9.69 \pm 2.47	9.38 \pm 3.30	6.00 \pm 1.83
	NF (mean \pm SE)	9.13 \pm 1.88	8.38 \pm 2.66	3.84 \pm 1.22
Number of smells to the cage	<i>p</i>	0.964	0.791	0.827
	<i>Z</i>	1.804	0.809	0.944
	F (mean \pm SE)	5.13 \pm 1.45	4.13 \pm 1.60	5.00 \pm 1.59
	NF (mean \pm SE)	3.38 \pm 1.03	3.38 \pm 1.72	3.00 \pm 1.55

Discussion

Contact calls produced by adult male small-clawed otters presented a high potential for acoustic identity coding. Given their affiliative function, it was likely that these call types, more than others, would encode identity (Lemasson and Hausberger 2011). The differences in the frequency of male voices may reflect slight morphological variations (size, weight); such correlations between pitch and morphometry have been reported across a wide range of mammals (monkey spp.—Ey et al. 2007; orca—Kremers et al. 2012; horse—Lemasson et al. 2009). Investigating more acoustic parameters, notably vocal tract related parameters, is now necessary to understand what the primary source of between male variations is.

Furthermore, our experiment showed that females were able to discriminate between familiar and unfamiliar adult males via these calls as well as through feces scent; however, they appeared to be unable to do so using life-size photographic representations. Otter response to broadcast calls differed in the duration of the “immediate first gaze”, a common measure in acoustic cognitive experiments (Lemasson et al. 2008). The response to scents was usually delayed and was expressed by a varying number of contacts

with the latrine over a 15-min period; this was potentially used for olfactory comparison or marking reinforcement. Photo-discrimination at the species (marmot—Blumstein et al. 2009) and individual (cow—Coulon et al. 2011; macaque/chimpanzee—Parr et al. 2000) levels has been documented in non-human animals, but this capacity does not appear wide-spread across taxa (birds—Dawkin 1996; Ryan and Lea 1994). Comparative studies, using different protocols (e.g. using videos or 3D models), are now needed to confirm the inability to discriminate pictures of conspecifics in otters. In sum, these results confirm the key role played by vocal and olfactory signals in the social life of otters. Hence, vocal signals may be used by otters to coordinate group vigilance and travelling, notably at the time of predator attack or conspecific aggression, as well as mother–cub interactions (Duplaix 1980). Discriminating familiar from unfamiliar conspecifics using multimodal signals is particularly important for carnivores with frequent inter-group encounters and visually closed habitats.

As none of our subjects were genetically related, females could not have used any potential kin signature to discriminate males. Hence, females may have learned individual acoustic structures and chemical profiles from experience in order to achieve subsequent discrimination. This supports

previous findings in polecats which showed that familiarity, more than kin relatedness, influences social behaviours (Lodé 2008). In mustelids, the ability to memorize individual signatures would enhance social cohesion.

Acknowledgments This study was funded by the French Ministry of Research, the C.N.R.S. and the 'Institut Universitaire de France'. We thank the staff of the French zoos for their logistical support. We are grateful to Françoise Cardou for correcting our English.

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