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# MASTERARBEIT

Titel der Masterarbeit

„Common ravens (*Corvus corax*) show differential responses to SADs (self-aggrandizing displays) depending on call type and identity of caller”

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## **Zusammenfassung**

In komplexen Sozialstrukturen treten häufig individuell unterschiedliche Displays auf.

Hierbei ist von besonderer Bedeutung, welche Information sie beinhalten und ob sie ein und derselben Bedeutungskategorie zugeordnet werden.

Displays wie beispielsweise Pant-hoot-Rufe von Schimpansen oder 'Wahoo'-Wettbewerbe unter männlichen Pavianen signalisieren kompetitive Eigenschaften und bewirken, dass verschiedene Klassen von Rivalen unterschiedlich behandelt werden. Sowohl die Identität des rufenden Tieres als auch der Kontext, in welchem der Ruf produziert wird, könnten die Reaktion des Empfängers beeinflussen.

Seit langer Zeit wird von Autoren „verbeugendes“ und „würgeähnliches“ Verhalten bei Raben, *Corvus corax*, beschrieben und mit Imponiergehabe assoziiert.

Diese Status anzeigenden Displays (im Folgenden SADs) weisen fixe Bewegungsmuster auf, welche von spezifischen, zwischen Gruppen und Individuen variierenden Ruftypen begleitet werden. SADs treten meist im Zuge von Balzverhalten oder agonistischen Interaktionen auf.

Raben zeigen eine Vielfalt von SAD-Ruftypen, lernen vokal voneinander und sind bei der Präsentation von Playback-Rufen in der Lage, andere Raben individuell zu erkennen. Aufgrund dieser Merkmale eignen sich Raben besonders für die Erforschung von Displays.

In sozialen Verbänden gehaltene Raben nahmen an zwei Habituations-Dishabituations-Experimenten teil und hörten SAD-Rufe von bekannten Individuen. Sowohl bei einem unerwarteten Wechsel des Ruftypes als auch bei einem Wechsel des rufenden Artgenossen zeigten die Tiere abweichende Verhaltensreaktionen. Das Geschlecht des Playback-Individuums schien die Häufigkeit von Territorialrufen und Schnabelwetzen zu beeinflussen. Diese Studie zeigt, dass Raben zu individueller Diskriminierung, sowie zur unterschiedlichen Wahrnehmung von verschiedenen SAD-Ruftypen fähig sind. Meine Resultate liefern grundlegende Erkenntnisse zur Wahrnehmung von SADs und deuten auf die Komplexität in der Kommunikation von Kolkraben hin.

**Abstract**

Individually distinct displays often occur in complex social groups and raise the question of what information is encoded and whether they are perceived as one category of meaning. Pant-hoot displays in chimpanzees or 'wahoo' displays in male baboons give signals of competitive ability, causing that distinct categories of rivals are treated differently. Both identity of the caller and the context in which vocalization is produced might affect the receiver's responses. For a long time, different authors have been mentioning 'bowing' and 'gulping-like' behaviour in ravens, *Corvus corax*, associated with showing off. These self-aggrandizing displays (hereafter SADs) are patterns of posture movements accompanied by specific call types that vary among individuals and groups. They occur both in the course of courtship and agonistic interactions. Thus, it is assumed that SADs are meant to impress conspecifics and express dominance. Ravens show a variety of SAD call types, learn vocally from one another and are capable of individual recognition. Hence, they are particularly interesting when inquiring the intrinsic meaning of displays and their relevance for the receiver.

Captive ravens were presented with SAD calls of known individuals in two habituation-dishabituation experiments. They reacted differently when the SAD type was switched as well as when the identity of the caller changed unexpectedly. Furthermore, the sex of caller influenced the frequency of beak wipes and loud calls given by the subjects. This study demonstrates that ravens are capable of individual vocal discrimination as well as distinctive perception of different SAD types.

## Introduction

Living in socially and physically complex environments creates both challenges and opportunities. The pressure to respond to these may have selected for large brains and complex cognition in both apes and corvids (Seed et al., 2009).

In complex social groups, different types of displays can be found. Generally, displays have one essential aim, which is to give signals of competitive ability that are difficult to fake (Cheney & Seyfarth, 2007). Pant-hoot displays in chimpanzees for instance are highly individually distinctive (Notman & Rendall, 2005). Within-group similarity suggests that the calls converge in structure as a consequence of vocal learning (Marshall et al., 1999). To assert their dominance, baboon alpha males may initiate 'wahoo' display contests, containing two-syllable 'wahoo' calls and threatening behaviour (Cheney & Seyfarth, 2007). Male baboons discriminate loud call displays between rivals of different relative ranks. This shows that they treat distinct categories of rivals differently (Kitchen et al., 2005).

For a long time, different authors have been mentioning 'bowing' and 'gulping-like' behaviour in ravens, *Corvus corax*, associated with showing off (Lorenz, 1939; Gwinner, 1964; Coombs, 1978; Pfister, 1988; Boeckle et al., 2012; Massen et al., 2014), calling it 'ear tuft intimidation' (Coombs, 1978) as well as 'self-assertive' or 'self-aggrandizing display' (hereafter SAD) (Gwinner, 1964; Heinrich, 1999). While uttering specific call types, e.g. creaking or clicking sounds, the ravens lower their necks, stretching forward their beak, slightly lift up their wings and sometimes seesaw with their spread tail feathers. They simultaneously increase visually perceived body size by fluffing their throat and head feathers, often forming ear tufts. If a bird continues with these stereotyped SADs, it may rhythmically shift its head slightly up and down while vocalizing. These patterns of posture movements and vocalization tend to occur both in the course of courtship and agonistic interactions (Coombs, 1978; Gwinner, 1964), e.g. when displacing each other. Therefore, it makes sense to conclude that these directed displays have one essential aim, namely presenting dominance and impressing one's opponent. In a mild conflict, ravens may show SADs that are often followed by submissive calls and body posture of a subordinate individual (Massen et al., 2014). They also present SADs in a non-directional way, typically when they have temporarily left or are about to join a group (Massen et al., 2014). The diversity of SAD vocalizations among individuals could represent a cognitively rich set of meanings. Larger SAD call type repertoires could also have an influence on how ravens are perceived by others.

Ravens not only show a variety of SAD calls, but also learn vocally from one another (Enggist-Dueblin & Pfister, 2002) and are capable of individual vocal recognition (Boeckle & Bugnyar,

2012). Hence, they are particularly interesting when inquiring the intrinsic meaning of displays and their relevance for the receiver. Ravens are very adaptive and show sophisticated social mechanisms, like recruitment to food or tactical deception (Boeckle & Bugnyar, 2012). While adult ravens are long-term monogamous and territorial, juveniles live in a fission-fusion-like social system (Heinrich, 1988). During their immature phase of about three years and after settling down as a breeding pair, ravens interact with many individuals (Enggist-Dueblin & Pfister, 2002). Interestingly, their sophisticated social knowledge as non-breeders may still exist in their territorial breeding stage (Boeckle & Bugnyar, 2012). Loretto et al. (2012) revealed that at four to five months post-fledging, a linear dominance rank hierarchy emerges and that siblings share a greater degree of tolerance in accordance with kin selection theory. These findings suggest participation in sophisticated social behaviours and formation of stable relationships already in the first year of a raven's life.

### Individual recognition

In stable social units, group members often recognize one another individually and remember previous interactions. Individual recognition has been widely studied, showing this ability across a variety of taxa (Tibbetts & Dale, 2007), e.g. in cooperatively breeding meerkats (Reber et al., 2013) or domestic horses (Proops et al., 2008). In a habituation-dishabituation experiment, Boeckle et al. (2012) found evidence that ravens discriminate between unfamiliar conspecifics on the basis of individual food call characteristics. When presenting playbacks of long-distance calls, it was shown that adult ravens did not only discriminate between unfamiliar conspecifics and previous group members that they hadn't seen for up to three years; among the familiar birds they even distinguished between former affiliates and non-affiliates according to the relationship quality they had shared with those subjects as juvenile non-breeders a long time ago (Boeckle & Bugnyar, 2012). Until lately, recognizing others' affiliates and adjusting interactions to recent events among others was only shown in primates, e.g. in female monkeys (Cheney & Seyfarth, 1999).

### Vocalization

Acoustic signals are emitted in diverse social contexts and show acoustic properties that differ among individuals of the same species (Hauser, 1991). In many bird species, vocalization is important in reproductive contexts and for the maintenance of hierarchies and territories. Ravens are systematically assigned to the passerine birds and are well known for their acoustic learning abilities. Ethologists have been dealing with both diversity and complexity of common raven vocal capabilities for decades (e.g. Lorenz, 1939; Conner, 1985; Heinrich & Marzluff,



1991). Enggist-Dueblin & Pfister (2002) examined the impact of cultural transmission on the composition of their vocal repertoires. According to Heyes (1993), cultural transmission is defined as the spread of behaviour among individuals by social learning. The distribution of call types among individuals revealed that the main pathway of transmission was within sexes and therefore led to a distinct sexual dimorphism in acoustic signalling (Enggist-Dueblin & Pfister, 2002). Besides, transmission also emerged between raven pair partners, as well as neighbouring and more distant pairs (Enggist-Dueblin & Pfister, 2002). This indicates that ravens are vocal learners. However, there are reasons to believe that not all call types are vocally learned. In the 1970s, Conner (1985) recorded more than 1,000 vocalizations of wild ravens and observed their accompanying behaviour in Southwestern Virginia. He identified 18 call types and associated them with e.g. excitement, agonistic interactions, alert, courtship or submission. In addition, these individuals shared six call types with hand-reared, captive ravens in Germany, which is why he suggested that the use of these call types may be innate (Conner, 1985). Food calls for example are often given by vagrant ravens in response to food guarded by territorial ravens (Heinrich & Marzluff, 1991) and have a fixed meaning (Bugnyar et al., 2000; Boeckle et al., 2012).

In contrast, only little is known about SAD vocalizations. Their variation and their emergence in similar contexts raise the question how they could be classified and what kind of information is encoded in SADs. Calls in general may contain information about the caller, such as his motivational state or identity, and about stimuli within the environment (Bugnyar et al., 2000).

I conducted playback experiments designed to investigate whether common ravens perceive different types of SADs produced by a single familiar individual as an autonomous display. In addition, I tested whether subjects discriminate among conspecifics within a single SAD type. Using the habituation-dishabituation paradigm, I looked at observable differences in ravens' behaviour while presenting recorded SADs of familiar individuals. Prior to recent studies (e.g. Proops et al., 2008; Reber et al., 2013), this paradigm was used to investigate individual recognition e.g. in vervet monkeys (Cheney & Seyfarth, 1988), baboons (Cheney & Seyfarth, 1999) and macaques (Rendall et al., 1996).

### Hypotheses

According to the structure of the experiments, I formulated the following hypotheses (<sub>I</sub> refers to condition 'individual' and <sub>T</sub> to condition 'type'):

H<sub>I0</sub>: It will not make a difference if the identity of the SAD caller is changed.

H<sub>II</sub>: It will make a difference if the identity of the SAD caller is changed.

H<sub>T0</sub>: It will not make a difference if the SAD type is switched by the same individual.

H<sub>T1</sub>: It will make a difference if the SAD type is switched by the same individual.

### Potential outcomes

If the ravens only discriminate between individuals, this will support the hypotheses that it makes a difference if the calling individual changes (H<sub>II</sub>) and that it does not make a difference if the SAD type changes (H<sub>T0</sub>). That would imply that ravens categorize SAD vocalizations as one meaning.

In case they only distinguished between SAD types, this would confirm the hypotheses that it does not make a difference if the identity of the caller is changing (H<sub>I0</sub>) and that it makes a difference if the calling individual switches SAD types (H<sub>T1</sub>). These results would not correspond to previous studies on individual discrimination but would underline the complexity of ravens' social structures and communication.

The subjects might discriminate between both individuals and SAD types. These results would support the hypotheses that it will make a difference if the identity of the caller is changing (H<sub>II</sub>) as well as if the calling individual switches SAD types (H<sub>T1</sub>). This would support the hypotheses that ravens are capable of individual discrimination as well as perception of different SAD types - also a hint at complex social proficiency in ravens.

They might not differentiate between either individuals or SAD types. This would lead to the hypotheses that it neither makes a difference if the identity of the caller is changing (H<sub>I0</sub>) nor if the SAD type is switched (H<sub>T0</sub>). In this case, I would assume that the habituation-dishabituation experiment itself failed.

### Predictions

It should be beneficial to pay attention to the caller's identity whereas information given by a single individual that is just switching SAD types might be of minor importance. Ravens should differentiate between displaying individuals as they do in conspecifics giving food calls. Therefore, I predict that when the individual changes ravens will show a behavioural reaction that varies in intensity, e.g. resulting in modified looking and approaching durations or a change in call frequency when comparing habituation and dishabituation phase.

Since the accompanying body posture itself always remains the same, I assume that ravens group various SAD calls given by the same individual as one category of meaning. Hence, I do not expect to see a behavioural change between habituation and dishabituation when SAD types are switched.

## Methods

### Study site and subjects

Eleven male and seven female captive ravens, *Corvus corax*, aged one to two years were tested individually at the Haidlhof research station in Bad Vöslau, Austria (Tab.1). They were kept together in groups of eight and ten non-breeding birds respectively and lived in hearing and partly visual range of each other. All birds were marked with coloured rings for identification and habituated to human observers at close range.

The subjects formed two groups (Tab.1) that participated in the study consecutively within one season each (December - May). Therefore, the experiments took place over a period of two years in total (December 2012 - May 2014). As the subjects were juveniles, they themselves did not exhibit stereotyped SADs yet. Each subject was tested on two consecutive days. In agreement with Prof. Thomas Bugnyar and Stephan Reber, BSc, MSc, only seven male and seven female individuals were included in the analysis. Two of them - Lellan and Max - only participated in SAD experiment 'type'. The four remaining male subjects - Thor, Matte, Ray and Orm – have not been analysed due to exceeding effort and time constraints (Tab.1).

**Table 1.** Group affiliation, name, sex, ring colour, raising conditions and year of birth of the subjects that participated in the playback experiments. Ravens highlighted in grey have not been included in the analysis due to time constraints. Condition 'type':  $n=14$ , condition 'individual':  $n=12$ .

Group	Subject	Abbrev.	Sex	Ring colour	Raised	Birth
1	Astrid	AS	f	red	Hand raised	2010
1	Joey	JO	f	yellow	Hand raised	2010
1	Thor	TH	m	blue/white	Parent raised	2011
1	Skadi	SK	f	blue/silver	Parent raised	2011
1	Lellan	LN	f	green/white vertical	Hand raised	2011
1	Matte	MA	m	white	Hand raised	2011
1	Ray	RY	m	pink	Hand raised	2011
1	Orm	OR	m	black	Hand raised	2011
2	Adele	AD	f	white/black horizontal	Hand raised	2012
2	Tom	TO	m	white/black triangle	Hand raised	2012
2	Laggie	LA	m	white/black X	Hand raised	2012
2	Horst	HO	m	yellow/black horizontal	Hand raised	2012
2	Louise	LO	f	yellow/black diagonal	Hand raised	2012
2	Nobel	NO	f	no ring	Hand raised	2012
2	George	GE	m	yellow/black triangle	Hand raised	2012
2	Max	MA	m	red/white triangle	Hand raised	2012
2	Paul	PA	m	red/white horizontal	Hand raised	2012
2	Rufus	RU	m	orange/white square	Hand raised	2012

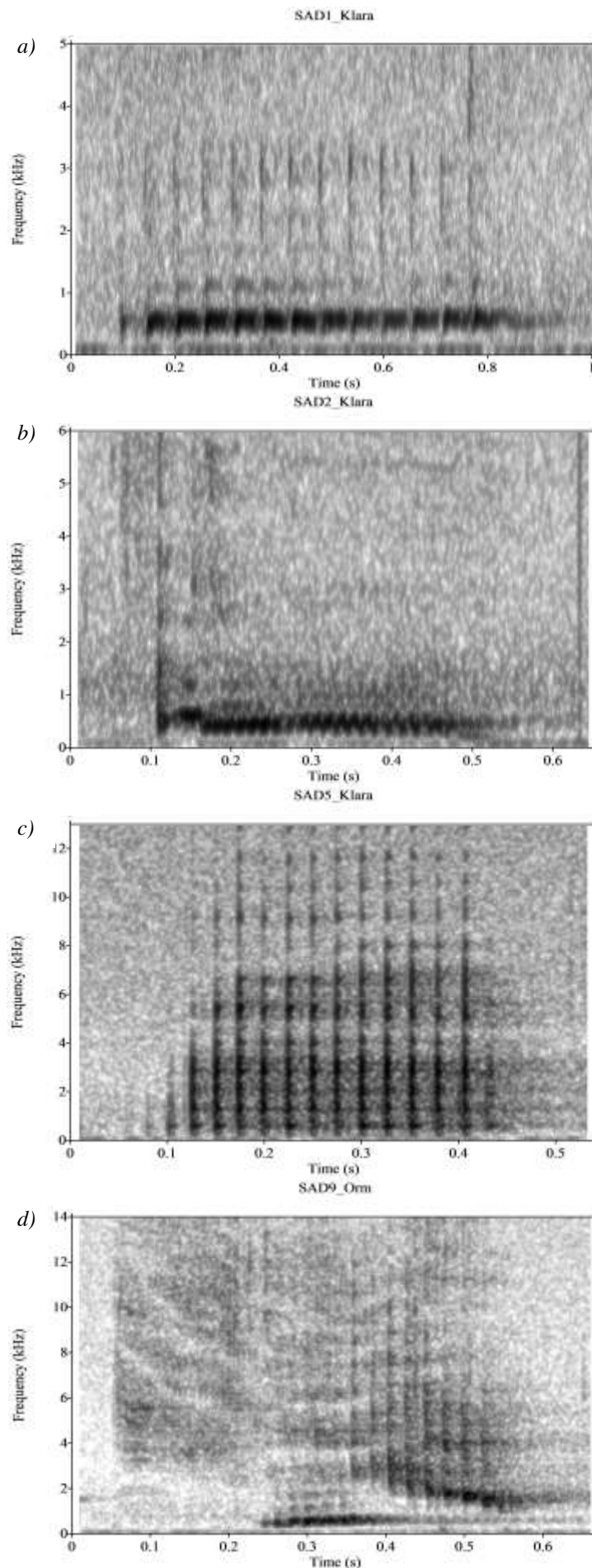
### Recording and preparation of the playback stimuli

Stimuli collection focused on SAD vocalizations and loud calls of six captive ravens, more precisely four males and two females. They were familiar to the focal individual but not kept at Haidlhof anymore at the time of testing. Recordings were mainly taken in the morning and in the afternoon from outside the aviaries at Haidlhof research station and KLF Grünau, using a Sennheiser ME 66 directional microphone (Sennheiser electronic GmbH & Co. KG, Wedemark, Germany) connected with a Zoom H4n Digital Recorder (Zoom Corporation, Tokyo, Japan). I used a 16-bit quantization and a 44.10 kHz sampling rate at a distance of approximately 1-3 m to the chosen individual. The samples were transferred to a computer via a Sony SF-16NX SD card (Sony Europe Limited, Surrey, Great Britain) to extract the calls from the recorded material using the acoustic software 'Praat' (Version 5.3.57, Boersma & Weenink, University of Amsterdam, Netherlands, <http://www.fon.hum.uva.nl/praat/>). Per call type and individual, I chose at least six recordings with the highest possible quality and minimal interfering background noise to avoid pseudo-replication. To exclude low frequency background or system noise, the selected recordings were filtered with a high-pass filter at 100 Hz. This frequency range does not overlap with the range of ravens' vocalizations (frequency range of stimuli: 200-3000 Hz, Tab.2). Sound editing such as fading out the on- and offset of a call, equalizing peak amplitude to a level of -9 dB SPL and combining single calls into stimuli bouts was done with Adobe Audition CC for Mac OS (Adobe Systems Software Ireland Ltd.). One bout consisted of three single calls of the same call type given by the same individual. After the third call, the bout file was complemented with artificially created silence so that all bout files took exactly 1 min (Fig.5). Altogether, I created ten stimuli bouts per call type and individual; the playbacks were assembled randomly out of the single bouts using a Python Script (programmed by Jinook Oh, Version 2.7.6, Python Software Foundation, OR, USA). In the course of audio recording, I registered a total of six SAD types (Tab.2) among which two were shared by the females and two by two males, respectively (Orm & Ray, Anton & Jakob). Tab.2 provides a summary of the individuals' SAD vocalizations sorted by SAD type. In addition, a large amount of long-distance calls was recorded for each individual. The females sometimes produced SADs lacking the typical accompanying body posture. However, the sample size of one female's calls (Sophie) was small, and therefore I included these recordings as their occurrence matched with the common production contexts of SADs. Since I only needed two shared SAD types within each sex, the remaining SAD recordings were not included in the following experiments. Most of the ravens' call types are modulated in frequency and amplitude (Pfister, 1988) and thus are defined via their appearance in a

spectrogram and by description based on the acoustic perception of the observer. In this study, I predominantly classified SAD types according to these two features (Tab.2, Fig.1a)-d)).

**Table 2.** SAD types, acoustic perception by the human observers, individual characteristics according to their spectrograms and individuals uttering them. Italicized SAD types were used for the playback experiments.

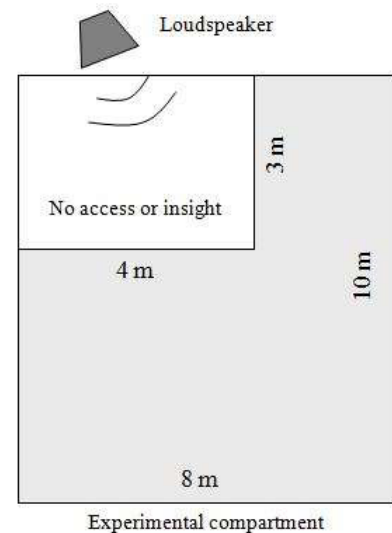
<b>SAD type</b>	<b>Description</b>	<b>Frequency range (Hz)</b>	<b>Call length (s)</b>	<b>Individuals</b>
<i>SAD1</i>	rolling 'R'	500-1000	0.869	Klara
<i>SAD2</i>	gru' like a pigeon	200-600	0.376	Klara, Sophie
SAD3	short grunt, also used in succession, not very vocal	-	-	Orm, Ray
<i>SAD5</i>	deep grunt, lasting about 0,5-1s	1000-1250	0.361	Klara, Orm, Ray, Sophie
SAD6	like tongue clicking	-	-	Klara, Orm
<i>SAD9</i>	zirp' with no/one/two low intros	370-3000	0.616	Orm, Ray



**Figure 1 a) - d).** Spectrograms of SAD types that were used in the playback experiments (FFT with Gaussian shape, sampling frequency=44100 Hz, window length=0.01 s, bandwidth=130 Hz, time step=0.7 s, frequency step=250 Hz; Call lengths: a) 0.861 s, b) 0.405 s, c) 0.340 s, d) 0.527 s).

### Playback experiments

I examined spontaneous reactions in previously separated ravens to playbacks of SADs broadcasted by a loudspeaker (Wireless Portable Sound System, LD Systems, Adam Hall GmbH) at a call intensity of approx. 80 dB<sub>C</sub> at 1 m distance (measured with the sound level meter SL-100, Voltcraft, Conrad Electronic AG). The loudspeaker was approximately 3 m away from the experimental compartment (Fig.2) and out of the focal individual's sight. Via a transmitter-receiver device (Sennheiser eW100 G3, Germany) the speaker was connected with an iPod touch (Apple Inc., CA, USA) that contained the stimuli playlists. I



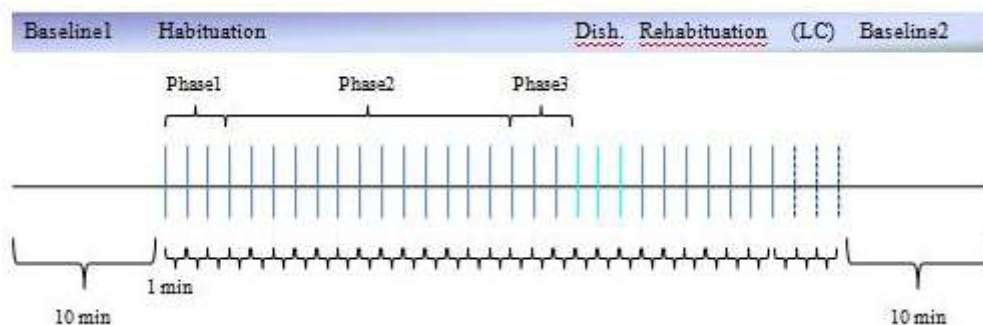
**Figure 2.** Experimental compartment and position of the loudspeaker.

used a second loudspeaker of the same type positioned away from the playback loudspeaker and directed at the group's enclosure. For the time of the experiments, this loudspeaker broadcasted white noise to mask other ravens' calls from the neighbouring aviaries.

Experiments were filmed with a camcorder (Canon HD Legria HFG10, Canon Inc., Japan) and simultaneously audio-recorded via a directional microphone (Sennheiser ME66, Sennheiser Electronic GmbH & Co. KG, Wedemark, Germany). The microphone was connected to a portable Zoom H4n Digital Recorder (Zoom Corporation, Tokyo, Japan), using a sampling rate of 44,100 Hz and 16-bit quantization, at approximate distance of 0.5 m to the compartment. The experiments followed the habituation-dishabituation paradigm. Per subject, only male or female stimuli were picked for playback experiments. Depending on the trial, the ravens experienced two different SAD call types of the same individual (condition 'type') or one SAD call type of two different individuals of the same sex (condition 'individual') (Fig.3). Apart from two subjects (Lellan & Max), each one was presented with both conditions, one on the first day of separation and the other on the following day. The order of trials was counterbalanced, so that half of the subjects heard condition 'type' first and the others heard condition 'individual' first. The selection of playbacks allowed that both male and female stimuli were used equally often and in a way that male as well as female subjects were presented playbacks of the same sex or the other.

		No. of intervals (min.)	Period	Phase	Played back call
Condition	individual	3	Habituation	Phase 1	SAD 1 of individual 1
		variable	Habituation	Phase 2	SAD 1 of individual 1
		3	Habituation	Phase3	SAD 1 of individual 1
		3	Dishabituation	Dishabituation	SAD 1 of individual 2
		variable	Rehabilitation	Rehabilitation	SAD 1 of individual 1
	type	3	Habituation	Phase 1	SAD 1 of individual 1
		variable	Habituation	Phase 2	SAD 1 of individual 1
		3	Habituation	Phase3	SAD 1 of individual 1
		3	Dishabituation	Dishabituation	SAD 2 of individual 1
		variable	Rehabilitation	Rehabilitation	SAD 1 of individual 1
		3	LC Phase	LC Phase	LC of individual 1

**Figure 3.** This figure shows the standardized procedure of the playback experiments for both conditions. In condition ‘type’, I switched SAD type while in condition ‘individual’, I switched the played back individual. The sequence of playback periods or phases always remained the same. Period habituation was split artificially into three phases (Phase1-3) to facilitate the analysis. Loud call (LC) phase only appeared in condition ‘type’.



**Figure 4.** Schematic of the experimental procedure. Playback protocol started with a 10 min baseline (Baseline1) followed by habituation phase (Phase1 - Phase3) which could include different amounts of habituation stimuli. When habituation criterion was reached, the dishabituation phase (Dish.) was played. Rehabilitation also varied in length, depending on how fast the subject habituated again. Finally, a 10 min baseline (Baseline2) was recorded.



**Figure 5.** Example waveform of a playback bout (= 60 s) consisting of three SAD5 calls by Ray.



In the beginning, a 10 min baseline ('Baseline1' in Fig.4) was recorded, followed by a presentation of at least 14 stimuli bouts until the bird habituated ('Habituation' in Fig.4). Habituation criterion was defined as three consecutive bouts causing a decreased behavioural response (a minor or no reaction) compared to the three strongest responses. Within an experiment, bouts of the habituation phase always consisted of the same SAD type given by the same individual. As ravens participated in two different experiments, I alternated at least the SAD type or the caller's identity per subject for the two habituation phases. Thereby, I prevented same habituation conditions per raven for the two experiments. Once the focal individual habituated, the dishabituation phase ('Dish.' in Fig.4) started. The phase transitions were performed as accurately as possible to prevent a temporal deviation of the 1 min bout intervals. Dishabituation stimuli consisted of three bouts and varied between conditions in order to test for the relevance of different SAD types or different individuals on response levels:

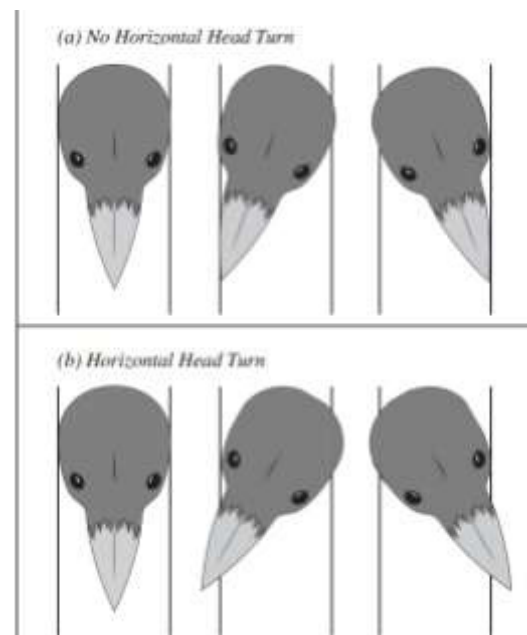
(1) condition 'type': habituation and dishabituation stimuli were presented from one individual changing SAD type; (2) condition 'individual': stimuli of two different individuals uttering the same SAD type were played (Fig.3). Condition 'type' examined whether ravens perceive SADs either as one category of meaning or discriminate between SAD types. In contrast, condition 'individual' was conducted to control whether ravens also differentiate between displaying individuals.

In the rehabilitation phase ('Rehabilitation' in Fig.4), at least seven bouts of the same individual and SAD type were presented as they had been in the habituation phase before; again until the subject reached habituation. Only in condition 'type', the rehabilitation was followed by three bouts of loud calls ('LC' in Fig.4) of the same individual. This control should exclude that the subject habituated to all vocalizations, and not only SADs, of the played back individual. Finally, a 10 min baseline ('Baseline2' in Fig.4) was recorded at the end of each playback session.

## Analysis

Videos were analysed by two stages in steps of 0.2 s with Solomon Coder Version beta 14.03.10 (Péter, 2014; <http://solomoncoder.com>). First, I coded them without sound to enable blind coding; then, I coded the calls that had occurred. Response variables used are given in Appendix I. Responses were video-coded during the presentation of the playback bouts and during intermission intervals within and between the different phases. Behavioural responses of particular importance were (1) looking in the direction of the playback, (2) horizontal and vertical head turns, (3) locomotion, (4) approaching the loudspeaker, and (5) calls of the subjects.

Horizontal head turns (hereafter HHT) were defined as a turn in an angle bigger than  $10^\circ$  to one side starting from the longer axis of the raven's head (Fig.6). Orientation towards the loudspeaker did not have to start or end with a definite HHT towards the speaker. In fact, the beak of the bird had to be directed to the playback, which could also be achieved by head movements below our HHT criterion. The orienting response was used in part to facilitate comparison with previous studies (e.g. Cheney & Seyfarth, 1999; Proops et al., 2008; Boeckle et al., 2012). All calls given by the subjects were categorized as long-distance calls (= loud calls), food calls ('Ha'-calls), soft calls or SAD vocalizations. After completing video-coding, Excel output files with frequencies and durations of the response variables were generated.



**Figure 6.** Definition of a horizontal head turn (HHT): Moving the beak sideways within the boundaries of two imaginary lines (a) running parallel to the initial position of the 'sagittal suture' at the lateral edge of the raven's head was not counted as a HHT; if the beak tip crossed these lines on either side (b), a HHT was recorded. Drawings by Nadja Kavcik. (Reber et al., *in submission*)

The raw data of each experiment got sorted by the experiment's minutes, so that I could divide the habituation phase into three artificial parts: Phase1 covered the first three minutes of the habituation, phase3 the last three minutes and phase2 the midsection, which varied in duration as the length of the habituation phase depended on how fast a subject finally habituated to the given calls (Fig.3, Fig.4). The same applied to the rehabilitation phase, which also differed in duration. To make all the experimental phases comparable, I corrected for the amount of minutes, calculating the mean values for each response variable within each

experimental phase. Furthermore, I used correction factors to straighten out interval deviations of more than 3 s within phase changes. If an interval took e.g. 50 s instead of 60 s, I calculated  $60/50 = 1.20$ . This correction factor was multiplied with all behavioural variables within that interval.

### Statistics

Initially, I calculated and reduced GLMMs for all response variables using R Studio version 3.1.2. They gave an overview which variables indicate significant differences between the phases of the experiments (a), between conditions (b), and between sex of caller (c); furthermore, I checked for the interaction of condition and phase (d). (a) - (d) represent the four fixed factors applied in the GLMM. Because I had repeated measures, a subject was added as random factor nested within group (1 | Group: Subject).

If one of the fixed factors resulted in  $P \leq 0.05$  ( $F \geq 2$ ) for a variable, I conducted post-hoc tests in R. To assess whether a difference in phase was located between phase3 and dishabituation, I did exact Wilcoxon signed-rank tests (Mundry & Fischer, 1998). Concerning response variables that differed between conditions, I performed an exact Wilcoxon signed-rank test with the delta-values (hereafter  $\Delta$ -values) of the test phase (dishabituation minus phase3). To examine correlations regarding the sex of caller, I conducted exact Wilcoxon rank-sum tests (Mann-Whitney U test). Wilcoxon tests also revealed the direction of behavioural changes.

Besides that, I ran a principal component analysis (hereafter PCA) for a list of partly composite behaviours using R Studio to reduce data dimensionality. This PCA excluded data of the loud call phase, which only acted as control. With each of the resulting components, I reduced GLMMs in R Studios to see which of the fixed factors - 'phase', 'condition', 'sex of caller' and 'phase\*condition' - had the main influence. Afterwards, I performed exact Wilcoxon signed-rank tests with the components as I had previously done for the single response variables (if  $P \leq 0.05$ ).

Additionally, a second PCA was conducted to test for the loud call control in condition 'type'. For that reason, all the experimental phases were included. For the component that correlated with factor 'phase' ( $P \leq 0.05$ ), an exact Wilcoxon signed-rank test was performed.

Although statistics were done in R, additional cross-examination was conducted in SPSS.

## Results

Generalized linear mixed models (hereafter GLMMs) were calculated and reduced according to AIC criterion for all of the 31 response variables. The fixed factors - 'phase', 'condition', 'sex of caller', 'condition\*phase' - that were finally included in the reduced model had the strongest influence on a variable. The final GLMMs showed that variables VHT (vertical head turn) and LookLSpF/D (looking towards the loudspeaker frequency/duration) were affected by the experiment's phase, whereas self-directed behaviour and VHT-VHTDirAtLSp (vertical head turns not directed to the speaker) were affected by condition ('type' vs. 'individual'). The caller's sex seemed to have an effect on variables Beak wipe, Loud calls and VHT-VHTDirAtLSp. Regarding the interaction of condition and phase, no correlation could be found. For all results of the final GLMMs see Tab.3.

**Table 3.** This table shows the results for all response variables when reduced in a GLMM. Data printed in bold are significant, meaning that  $P$  is below significance level ( $P \leq 0.05$ ). VHT was almost significant and therefore included in further analysis. Since for factor 'condition\*phase' no correlation could be found, it was excluded from the table. SAD=self-aggrandizing display; HHT=horizontal head turn; VHT=vertical head turn; LSp=loudspeaker; F=frequency; D=duration; - =minus.

No.	F/D	Response Variable	df	Phase	Condition	SexOfCaller
1	F	HA (food) call	1, 1		F=0.0680, $P=0.7851$	F=0.0623, $P=0.7872$
2	F	SAD	1			F=0.3172, $P=0.5469$
3	F	Loud call	1			<b>F=5.9794, <math>P=0.01688</math></b>
4	F	Soft call	1		F=2.8302, $P=0.08433$	
5	D	Manipulation food	1			F=0.6981, $P=0.3737$
6	D	Manipulation object	1			F=1.1441, $P=0.2617$
7	D	Manip. food&object	1		F=0.4493, $P=0.4807$	
8	F	Beak wipe	1			<b>F=9.1132, <math>P=0.005133</math></b>
9	D	Preen	1		<b>F=7.2935, <math>P=0.008257</math></b>	
10	D	Scratching	1		<b>F=4.9588, <math>P=0.02515</math></b>	
11	D	Preen & scratching	1		<b>F=7.7085, <math>P=0.006583</math></b>	
12	D	Digging	1			F=0.4579, $P=0.4683$
13	D	Stretching	4	F=1.9239, $P=0.1001$		
14	F	Structure peck	1		F=1.7786, $P=0.1796$	
15	F	Body shake	1		F=3.3920, $P=0.0652$	
16	F	Head shake	1		F=3.4175, $P=0.06109$	
17	F	Body & head shake	1		<b>F=4.9798, <math>P=0.0238</math></b>	
18	D	Branchhop	1		F=1.8896, $P=0.1664$	
19	D	Flying	1, 1		F=0.0007, $P=0.9914$	F=0.0064, $P=0.9304$
20	D	Walking	1		F=2.1786, $P=0.138$	
21	D	Locomotion-Approach	1			F=1.0252, $P=0.3414$
22	F	HHT	1			F=1.0002, $P=0.2928$
23	F	HHTDirAtLSp	1			F=1.0451, $P=0.2698$
24	F	HHT-HHTDirAtLSp	1		F=1.6076, $P=0.1978$	
25	F	VHT	4, 1, 1	<b>F=2.2112, <math>P=0.05895</math></b>	F=2.7998, $P=0.08191$	F=3.1965, $P=0.06702$
26	F	VHTDirAtLSp	4	<b>F=3.0232, <math>P=0.01645</math></b>		
27	F	VHT-VHTDirAtLSp	1, 1		<b>F=5.4885, <math>P=0.01743</math></b>	<b>F=3.8363, <math>P=0.04684</math></b>
28	F	Looking at LSp F	4	<b>F=2.6653, <math>P=0.02862</math></b>		
29	D	Looking at LSp D	4	<b>F=3.1581, <math>P=0.01598</math></b>		
30	F	Approaching LSp F	1		F=1.6226, $P=0.1939$	
31	D	Approaching LSp D	1		F=2.3575, $P=0.1207$	

## PCA

(Significance codes: '\*\*\*'  $P < 0.001$  '\*\*'  $P < 0.01$  '\*'  $P \leq 0.05$ )

Based on the results of GLMMs, a principal component analysis (hereafter PCA) was conducted for a list of partly composite behaviours. All in all, the PCA reduced 15 response variables into four components (RC1 - 4, Tab.5), which explained 58% of the overall variance (eigenvalues=1.55 - 3.02, rotation: varimax). These four components were extracted in the PCA following Kaiser's criterion, which was preceded by a factor analysis (Tab.4) and a Bartlett's test on the correlation matrix ( $df=105$ ,  $\chi^2=209.96$ ,  $P < 0.001$ \*\*\*). Kaiser's criterion implies that the amount of factors to be maintained equals the amount of eigenvalues  $> 1$ . Extractions were also performed on the basis of scree-plot investigation. On occasion it is recommended to use a KMO-test for PCAs; however, to date there is no R-package that contains the necessary algorithms. Hence, I did not conduct it.

'Beak wipe' was not correlated with any other variable and would have loaded on a principal component alone (which was confirmed by trial and error). Therefore, it was excluded from the PCA, but could still be used for analysis by itself (see results of factor 'sex of caller').

Subtractions like HHT-HHTDirAtLSp (horizontal head turn - horizontal head turn directed at loudspeaker) and VHT-VHTDirAtLSp (vertical head turn - vertical head turn directed at loudspeaker) were done to use variables that are as independent from each other as possible.

The same applied to the use of LookLSpD and ApproachLSpD but exclusion of LookLSpF and ApproachLSpF.

**Table 4.** Correlation matrix for all the response variables used for the principal component analysis. Values between 0.3 and 0.8 were assumed as ideal; - =minus.

	SAD	LoudC	SoftC	Manip F&O	Preen& scratch	Digging	Structure peck	B&H shake	Locom-App	HHT-HHTDirAtLS	HHTDirAtLSp	VHT-VHTDirAtLS	VHTDirAtLSp	Look LSp D	App LSp D
SAD	1.00	0.12	0.12	-0.15	-0.23	-0.15	-0.07	-0.12	-0.19	0.05	-0.04	0.20	-0.11	0.03	-0.19
LoudC	0.12	1.00	0.09	-0.13	-0.16	-0.10	-0.05	-0.11	-0.14	0.06	-0.06	0.09	-0.13	-0.04	-0.10
SoftC	0.12	0.09	1.00	-0.03	-0.06	0.00	0.05	0.12	-0.10	-0.03	-0.14	0.24	-0.15	-0.18	-0.12
ManipF&O	-0.15	-0.13	-0.03	1.00	-0.16	0.37	0.24	0.07	0.36	-0.25	-0.21	0.32	0.26	-0.09	0.19
Preen&scratch	-0.23	-0.16	-0.06	-0.16	1.00	-0.08	-0.06	0.15	-0.25	0.10	-0.12	0.08	-0.09	-0.26	-0.23
Digging	-0.15	-0.10	0.00	0.37	-0.08	1.00	0.42	0.45	0.37	-0.13	-0.13	0.24	0.10	-0.14	0.15
Structure peck	-0.07	-0.05	0.05	0.24	-0.06	0.42	1.00	0.43	0.14	-0.02	-0.12	0.28	0.03	-0.15	-0.03
B&H shake	-0.12	-0.11	0.12	0.07	0.15	0.45	0.43	1.00	0.11	0.12	0.10	0.33	0.06	-0.15	0.01
Locom-App	-0.19	-0.14	-0.10	0.36	-0.25	0.37	0.14	0.11	1.00	-0.15	0.20	0.10	0.46	0.25	0.75
HHT-HHTDirAtLSp	0.05	0.06	-0.03	-0.25	0.10	-0.13	-0.02	0.12	-0.15	1.00	0.41	0.16	-0.02	-0.18	-0.11
HHTDirAtLSp	-0.04	-0.06	-0.14	-0.21	-0.12	-0.13	-0.12	0.10	0.20	0.41	1.00	-0.12	0.39	0.41	0.38
VHT-VHTDirAtLSp	0.20	0.09	0.24	0.32	0.08	0.24	0.28	0.33	0.10	0.16	-0.12	1.00	-0.02	-0.43	-0.02
VHTDirAtLSp	-0.11	-0.13	-0.15	0.26	-0.09	0.10	0.03	0.06	0.46	-0.02	0.39	-0.02	1.00	0.54	0.56
Look LSp D	0.03	-0.04	-0.18	-0.09	-0.26	-0.14	-0.15	-0.15	0.25	-0.18	0.41	-0.43	0.54	1.00	0.44
App LSp D	-0.19	-0.10	-0.12	0.19	-0.23	0.15	-0.03	0.01	0.75	-0.11	0.38	-0.02	0.56	0.44	1.00

**Table 5.** Principal component analysis (PCA) for a list of behaviours. Loadings of the variables on the four components are shown. Loadings exceeding  $\pm 0.5$  are printed in bold; - =minus.

Response variable	RC1	RC2	RC3	RC4	h2	u2
SAD	-0.09	-0.09	0.09	<b>0.71</b>	0.52	0.48
LoudC	-0.09	-0.08	0.05	<b>0.55</b>	0.32	0.68
SoftC	-0.20	0.23	-0.02	0.43	0.27	0.73
ManipFoodObject	0.26	0.45	<b>-0.54</b>	-0.04	0.56	0.44
AutoPreenScratching	-0.44	0.06	0.23	<b>-0.59</b>	0.60	0.40
Digging	0.17	<b>0.69</b>	-0.27	-0.14	0.59	0.41
StructPeck	0.01	<b>0.66</b>	-0.09	-0.03	0.45	0.55
Body/HeadShake	0.01	<b>0.71</b>	0.27	-0.18	0.62	0.38
Locomotion - Approach	<b>0.76</b>	0.31	-0.21	-0.09	0.72	0.28
HHT - HHTDirAtLSp	-0.08	0.13	<b>0.82</b>	0.07	0.70	0.30
HHTDirAtLSp	<b>0.55</b>	-0.11	<b>0.69</b>	-0.05	0.79	0.21
VHT - VHTDirAtLSp	-0.12	<b>0.71</b>	0.09	0.32	0.63	0.37
VHTDirAtLSp	<b>0.77</b>	0.05	0.08	-0.15	0.62	0.38
LookLSpD	<b>0.69</b>	-0.44	0.03	-0.02	0.67	0.33
ApproachLSpD	<b>0.85</b>	0.06	-0.04	-0.09	0.73	0.27
Eigenvalue	3.02	2.52	1.72	1.55		
Proportion Var	0.20	0.17	0.11	0.10		
Cumulative Var	0.20	0.37	0.48	0.59		
Proportion Explained	0.34	0.29	0.19	0.18		
Cumulative Proportion	0.34	0.63	0.82	1.00		

Extraction method: Principal component analysis

Rotation method: Varimax with Kaiser's normalization

### *Principle components*

Following the loadings of the response variables higher than  $\pm 0.5$ , the first component (RC1) was assigned to behaviour directed towards loudspeaker and locomotion in general, whereas the second component (RC2) corresponded to self-directed behaviour and object orientation. The third component (RC3) had a focus on horizontal head turns in general and the fourth component (RC4) was characterized by vocalizations. Loadings of the variables on the different components are shown in Tab.5. Variables that exceeded  $\pm 0.5$  were considered as having a crucial impact on a component. Factors 'phase' and 'condition' loaded on different principal components (RC1, RC2).

#### • RC1

GLMM indicated an effect of factor 'phase' on RC1 ( $df=4$ ,  $F=3.52$ ,  $P=0.007^{**}$ ). Behaviour directed towards the loudspeaker and locomotion increased when the SAD type was switched (exact Wilcoxon signed-rank test for condition type:  $n=14$ ,  $Z=-2.54$ ,  $P=0.009^{**}$ ; condition individual:  $n=12$ ,  $Z=-1.65$ ,  $P=0.110$  (Fig.7)).

- RC2

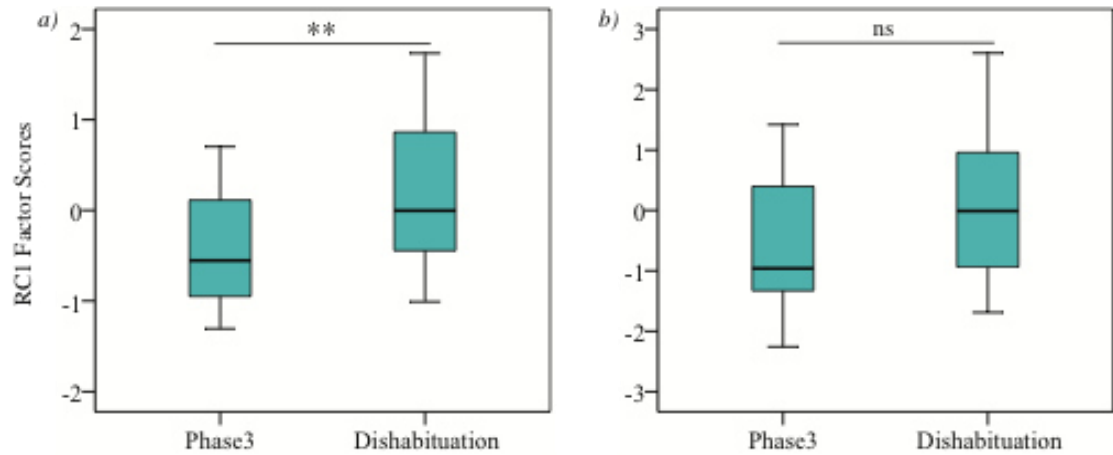
Factor 'condition' had an influence on RC2 (GLMM:  $df=1$ ,  $F=6.47$ ,  $P=0.011^*$ ). Two forms of post-hoc tests were done for RC2. The first test compared all of the phases except LC phase. It revealed that ravens gave more self-directed behaviour and object orientation when the calling individual changed than when the SAD type switched (exact Wilcoxon signed-rank test:  $n=12$ ,  $Z=-2.11$ ,  $P=0.034^*$  (Fig.8a)). The second test was conducted with  $\Delta$ -values of phase3 and dishabituation. In these two phases, I could not show any difference between conditions (exact Wilcoxon signed-rank test:  $n=12$ ,  $Z=-1.33$ ,  $P=0.204$  (Fig.8b)).

- RC3 and RC4

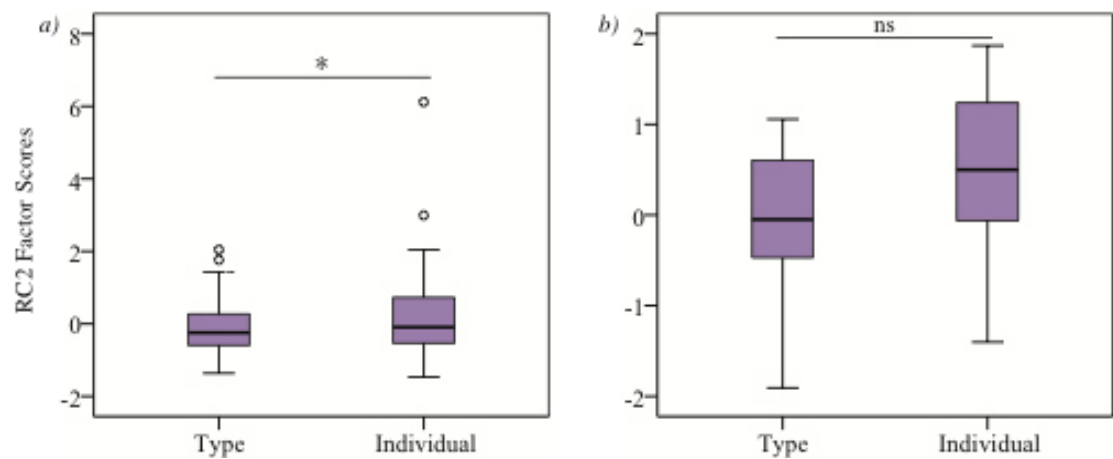
For RC3 and RC4, no correlations could be found (RC3:  $df=1$ ,  $F=1.30$ ,  $P=0.243$  for factor 'condition'; RC4:  $df=1$ ,  $F=3.05$ ,  $P=0.072$  for factor 'sex of caller').

### *Loud call control*

To test for the loud call (LC) control phase in condition 'type', a second PCA of all 'type' experiments including the loud call phase was done. Its component RC1 correlated with factor 'phase' ( $df=5$ ,  $F=2.94$ ,  $P=0.009^{***}$ ). When I compared rehabilitation and LC phase for RC1, no significant difference could be shown (exact Wilcoxon signed-rank test:  $n=14$ ,  $Z=0.97$ ,  $P=0.358$ , rehabilitation:  $v_{mean}=0.04$ ,  $\sigma=0.91$ ; LC:  $v_{mean}=0.42$ ,  $\sigma=0.98$ ). However, component RC2 of the second PCA also correlated with factor 'condition' ( $df=1$ ,  $F=4.86$ ,  $P=0.026^*$ ), as did RC2 of the initial PCA.



**Figure 7.** Ravens showed more behaviour directed towards the loudspeaker and increased locomotion when the SAD type was switched a), but not so when the calling individual was changed b).



**Figure 8.** When comparing all phases between conditions a), ravens showed more self-directed behaviour and object orientation in condition 'individual'. b)  $\Delta$ -values (dishabituation-phase3) did not differ significantly between conditions.

Boxplots represent 25<sup>th</sup> and 75<sup>th</sup> percentiles, centre line indicates the median, whiskers represent non-outlier range and dots are outliers (\*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P \leq 0.05$ , ns=non-significant).



### Single response variables

If  $P \leq 0.05$  ( $F \geq 2$ ) in GLMM (Tab.3), I conducted post-hoc tests for the single variables.

#### *Factor 'phase' - phase3 vs. dishabituation*

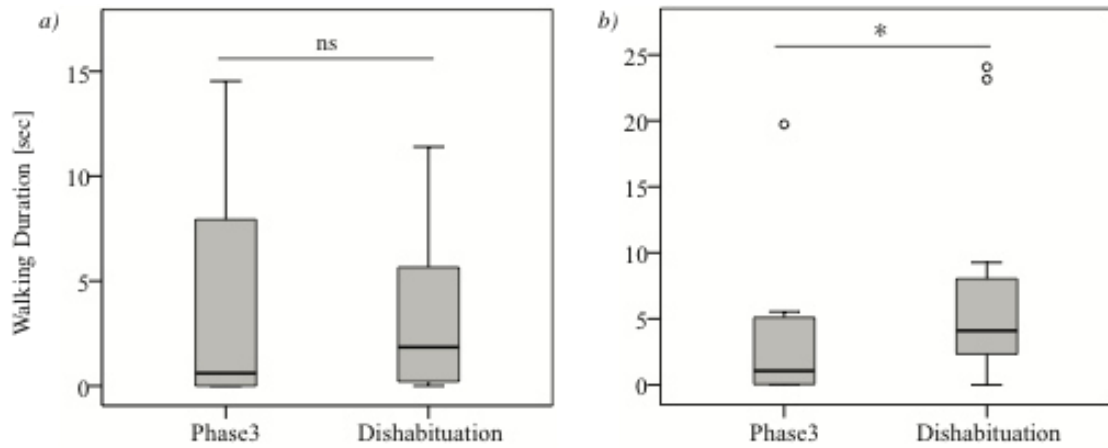
- VHT (vertical head turn) and VHTDirAtLSp (vertical head turn directed at loudspeaker)  
VHT was almost significant in GLMM and therefore included in further analysis. Ravens showed more VHT and VHTDirAtLSp both when the SAD type was switched and when the calling individual was changed (exact Wilcoxon signed-rank tests for VHT: type:  $n=14$ ,  $Z=-2.45$ ,  $P=0.011^*$ ; individual:  $n=12$ ,  $Z=-1.96$ ,  $P=0.050^*$  (Fig.9) and VHTDirAtLSp: type:  $n=14$ ,  $Z=-2.67$ ,  $P=0.005^{**}$ ; individual:  $n=12$ ,  $Z=-2.09$ ,  $P=0.037^*$  (Fig.10))

- LookLSpF/D (looking towards loudspeaker, frequency and duration)  
Ravens looked longer and more often towards the loudspeaker when the SAD type was changed (exact Wilcoxon signed-rank tests for LookLSpF: type:  $n=14$ ,  $Z=-2.64$ ,  $P=0.006^{**}$ ; individual:  $n=12$ ,  $Z=-1.77$ ,  $P=0.081$  and LookLSpD: type:  $n=14$ ,  $Z=-2.92$ ,  $P=0.002^{**}$ ; individual:  $n=12$ ,  $Z=-1.10$ ,  $P=0.301$  (Fig.11)).

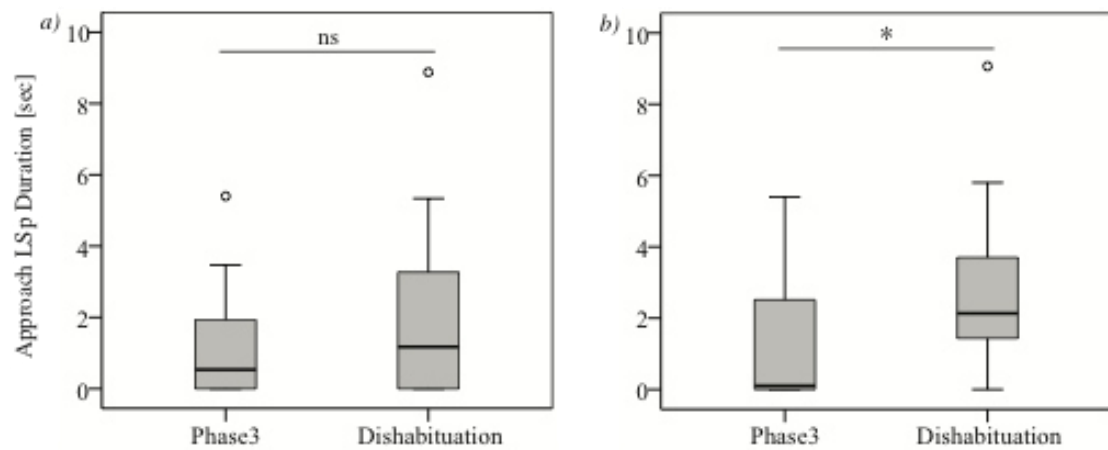
- Walking and ApproachLSpD (approaching the loudspeaker, duration)  
Although GLMM resulted in  $P > 0.05$  for variables Walking and ApproachLSpD (Tab.3), post-hoc tests indicated that the subjects both walked and approached the loudspeaker for a longer period of time when the calling individual was changed (exact Wilcoxon signed-rank tests for Walking: type:  $n=14$ ,  $Z=-0.16$ ,  $P=0.9023$ ; individual:  $n=12$ ,  $Z=-2.32$ ,  $P=0.019^*$  (Fig.12) and ApproachLSpD: type:  $n=14$ ,  $Z=-1.68$ ,  $P=0.102$ ; individual:  $n=12$ ,  $Z=-2.39$ ,  $P=0.014^*$  (Fig.13)).

#### *Factor 'condition' - condition 'type' vs. 'individual'*

GLMM results showed a difference between conditions for VHT-VHTDirAtLSp and self-directed behaviour like variables Preen, Scratching, Preen & scratching and Body & head shake (Tab.3). Post-hoc tests performed with  $\Delta$ -values (dishabituation - phase3) could not reveal any significant differences (results of exact Wilcoxon signed-rank tests see Tab.6). The difference between condition 'type' and 'individual' was not located within these two phases.



**Figure 12.** Ravens increased the duration of walking when the calling individual was changed b), but not when the SAD type was switched a).



**Figure 13.** Ravens approached the loudspeaker for a longer period of time when the calling individual was changed b), but made no difference in approaching duration when the SAD type was switched a).

Boxplots represent 25<sup>th</sup> and 75<sup>th</sup> percentiles, centre line indicates the median, whiskers represent non-outlier range and dots are outliers (\*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P \leq 0.05$ , ns=non-significant).

**Table 6.** This table shows the results of exact Wilcoxon signed-rank tests for the  $\Delta$ -values of phase3 and dishabituation ( $n=12$ ). No significant differences could be found between conditions.

Response variable	Results
Soft call	$Z=-1.39, P=0.172$
Preen	$Z=0.51, P=0.648$
Scratching	$Z=-0.49, P=0.656$
Preen & scratching	$Z=-0.04, P=1.00$
Body shake	$Z=-0.79, P=0.465$
Head shake	$Z=-1.17, P=0.266$
Body & head shake	$Z=-0.98, P=0.347$
Walking	$Z=-1.49, P=0.151$
VHT	$Z=-0.71, P=0.519$
VHT-VHTDirAtLSp	$Z=-1.10, P=0.301$

*Factor 'sex of caller' - male vs. female caller*

To compare variables between male and female playback presentation, I conducted exact Wilcoxon rank-sum tests (equivalent to Mann-Whitney U test) within each of the two conditions on the one hand and throughout all experiments on the other hand.

• VHT-VHTDirAtLSp (VHT minus VHTDirAtLSp)

GLMM indicated an influence of sex of caller on VHT non-directed towards the loudspeaker (GLMM:  $df=1, F=3.84, P=0.047^*$ ; Tab.3). However, no difference could be found in post-hoc tests (exact Wilcoxon rank-sum tests within conditions: type:  $n=7, Z=-1.00, P=0.318$ ; individual:  $n=6, Z=-1.34, P=0.180$ ; exact Wilcoxon rank-sum test comparing all experiments:  $n=13, Z=-1.69, P=0.091$ ).

• LC (loud calls)

Subjects uttered more loud calls when hearing female SADs (GLMM:  $df=1, F=5.98, P=0.017^*$ ; exact Wilcoxon rank-sum tests within conditions: type:  $n=7, Z=-1.53, P=0.125$ ; individual:  $n=6, Z=-1.85, P=0.065$  (Fig.17); exact Wilcoxon rank-sum test comparing all experiments:  $n=13, Z=-2.62, P=0.009^{**}$  (Fig.15)).

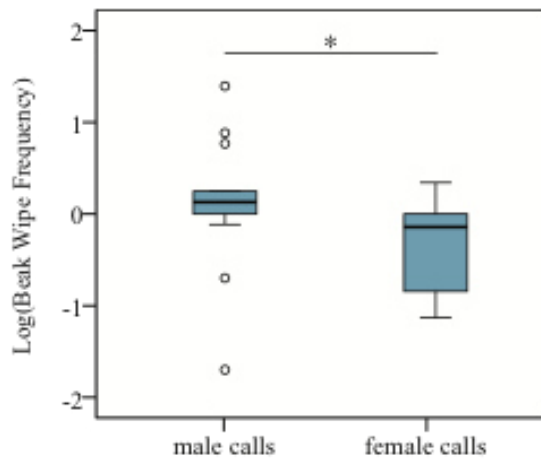
• Beak wipe

Ravens wiped their beak more frequently when they were exposed to (the change of) male playback calls (GLMM:  $df=1, F=9.11, P=0.005^{**}$ ; exact Wilcoxon rank-sum tests within conditions: type:  $n=7, Z=0.13, P=0.902$ ; individual:  $n=6, Z=-2.57, P=0.009^{**}$  (Fig.16); exact Wilcoxon rank-sum test comparing all experiments:  $n=13, Z=2.11, P=0.034^*$  (Fig.14)). The raw data for the variable Beak wipe showed large differences in distributions and histograms; the two-tailed Kolmogorov-Smirnov test was highly significant ( $df=13, Z=0.38, P\leq 0.001^{***}$ ). Therefore, I log-transformed the data for variable Beak wipe which equalized the distribution

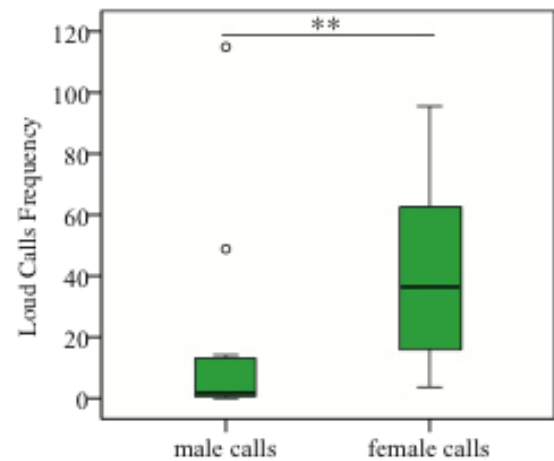
(Kolmogorov-Smirnov-test,  $df=13$ ,  $F=0.23$ ,  $df=13$ ,  $P=0.054$ ). Then I conducted exact Wilcoxon rank-sum tests with the values of the log-transformation.

*Factor 'condition\*phase'*

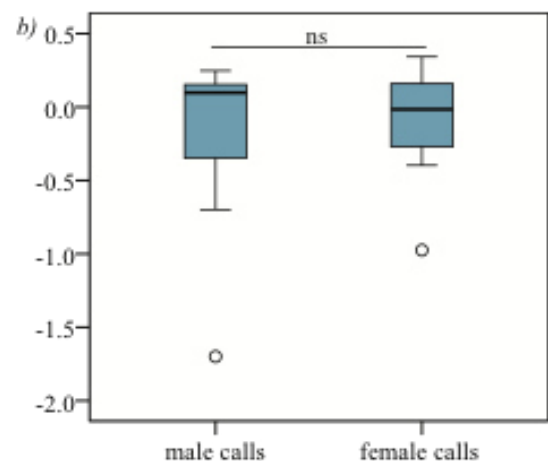
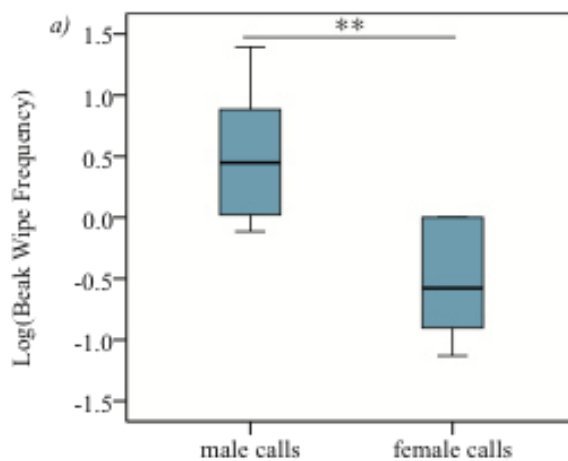
Since models did not show any interaction effect between condition and phase, factor 'condition\*phase' was excluded from the illustration (Tab.3).



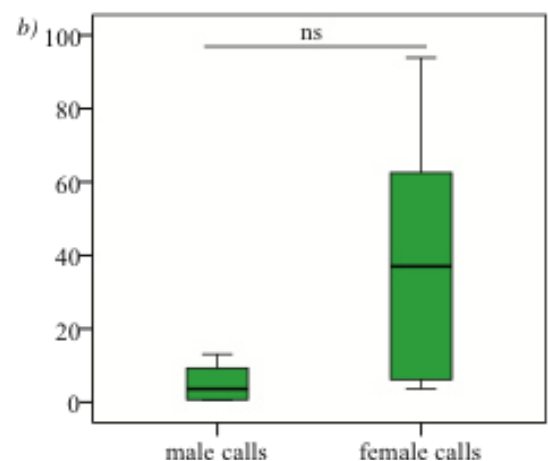
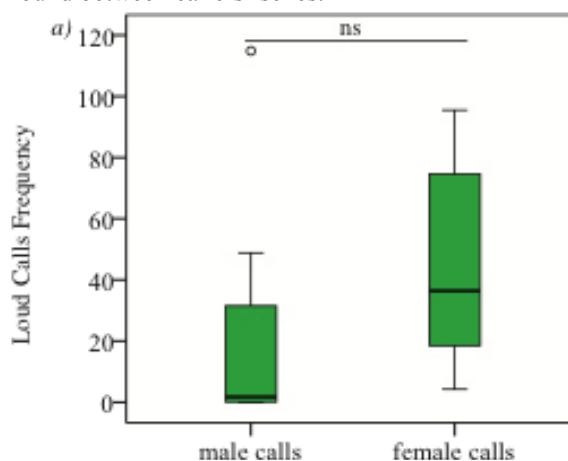
**Figure 14.** Comparing all experiments, ravens showed more beak wipes (log-transformed) when they heard male SADs.



**Figure 15.** Comparing all experiments, ravens uttered more loud calls when they were exposed to female SADs.



**Figure 16.** Within condition 'individual' *a)*, frequency of variable Beak wipe (log-transformed) was higher when subjects heard (the change of) male callers. In condition 'type' *b)*, no significant difference could be found between callers' sexes.



**Figure 17.** When comparing within conditions, frequency of variable Loud calls showed no influence by the caller's sex, neither in condition 'type' *a)*, nor in 'individual' *b)*.

Boxplots represent 25<sup>th</sup> and 75<sup>th</sup> percentiles, centre line indicates the median, whiskers represent non-outlier range and dots are outliers (\*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P \leq 0.05$ , ns=non-significant).

## Discussion

When captive ravens were presented with SAD calls of known individuals in two habituation-dishabituation experiments, they reacted differently both when the SAD type was switched as well as when the calling individual was changed. The difference between habituation and dishabituation phase confirms that the habituation-dishabituation paradigm worked. Subjects discriminated between playbacks by directing behaviours towards the loudspeaker or through an increase of activity. Depending on the condition ('type' or 'individual'), distinct response variables caused a behavioural reaction in the dishabituation phases, respectively.

Additionally, loud calls were uttered more often when hearing female calls, probably indicating arousal. In contrast, beak wipes occurred more frequently when subjects were exposed to male calls. This might represent stress and beak wipes could be seen as a dominance display. The results demonstrate that ravens are capable of individual vocal discrimination as well as distinctive perception of different SAD types.

In the following, I discuss first the findings of the PCA and then of the single variables.

### *Principle components*

Although I had predicted that ravens will not show a behavioural change to different SAD types given by the same individual, subjects responded differently (Fig.7a). Behaviours directed towards the loudspeaker and locomotion increased when the SAD type was switched, indicating that ravens discriminate between SAD types. Orientation towards the speaker represents a direct reaction to the playback and is of particular importance. In contrast, I could not find a difference between phase3 and dishabituation when the playback individual was changed (Fig.7b). This means that the phase difference (indicated by GLMM) is to be found between other phases than the two main test phases. Hence, this result does not support individual discrimination in ravens.

Overall, ravens showed more self-directed behaviour and object orientation when the calling individual changed than when the SAD type was switched (Fig.8a). More self-directed behaviour and object orientation may represent a higher degree of arousal. Surprisingly, this difference between conditions could not be shown explicitly in the main test phases (phase3 and dishabituation) (Fig.8b). That means the difference between conditions is to be found in other experimental phases.

No correlations could be found for horizontal head turns (RC3) and vocalizations in general (RC4). However, GLMM offered a weak tendency for vocalizations (RC4) to be influenced by

the sex of caller. This was confirmed by individual analysis of variable Loud call (see *Factor 'sex of caller'*).

#### *Loud call control*

No difference was found when I compared rehabilitation and loud call (LC) phase in condition 'type'. Ravens did not show a rebound in response when playback individuals suddenly uttered loud calls instead of SAD vocalizations. This control was conducted in case subjects would not differentiate between SAD types. Then I could have excluded that subjects habituated to all vocalizations and not only SADs of the played back individual.

However, components RC1 and RC2 of the second PCA correlated with the same factors as RC1 and RC2 of the first PCA did. When including additional data (LC phase), similar correlations in GLMM could be found. This outcome supports the results of my initial PCA.

#### Single response variables

##### *Factor 'phase' - phase3 vs. dishabituation*

Behaviours like approaching and looking towards the loudspeaker represent a direct reaction to the playback and are of particular importance. Responses directed to loudspeakers are often used within playback experiments (Benson-Amram et al., 2011; Cheney & Seyfarth, 1999; Boeckle et al., 2012; Reber et al., 2013). Non-orienting variables, such as self-directed behaviour or locomotion in general provide information about the effects of different playbacks, too. They might be seen as supplement to the orienting response and help determining whether the subject's behaviour was influenced by the presented playback (Cheney & Seyfarth, 1999). Depending on the condition ('type' or 'individual'), partly distinct response variables caused a behavioural reaction in the dishabituation phase, respectively. This underlines that ravens discriminated between SAD type as well as identity of the caller.

- Vertical head turn and vertical head turn directed at loudspeaker

Contrary to expectations, subjects responded to the dishabituation phase in both conditions. They showed more vertical head turns and vertical head turns directed at the loudspeaker when the SAD type was switched as well as when the calling individual was changed (Fig.9; Fig.10). While vertical head turns could represent levels of activity and vigilance, vertical head turns directed at the speaker refer to a direct response to the playback. These results underline that ravens discriminate among individuals within a single SAD type and among SAD types given by the same individual.

- Looking towards loudspeaker, frequency and duration

Ravens looked more frequently and for a longer period of time at the loudspeaker when the SAD type changed (Fig.11). This direct reaction to the speaker implies that ravens do not categorize acoustically distinct SAD types as one meaning. SAD types seem to have individual meanings.

- Walking and approaching the loudspeaker, duration

Subjects both walked and approached the loudspeaker for a longer period of time when the calling individual was changed (Fig.12; Fig.13). Again, this result confirms that ravens discriminate among vocalizing conspecifics giving the same SAD type. Walking may represent a higher degree of activity, while approaching the loudspeaker can be seen as strong orienting response.

#### *Factor 'condition' - condition 'type' vs. 'individual'*

Vertical head turns not directed to the speaker and self-directed behaviours like auto-preening, scratching, body and head shake showed a difference between conditions (Tab.3). However, post-hoc tests performed with  $\Delta$ -values (dishabituation - phase3) could not reveal any differences (Tab.6). Thus, the difference between condition 'type' and 'individual' was not located within these two phases. In principle, ravens discriminated between conditions, as different response variables showed a rebound in dishabituation of condition 'type' compared to 'individual'.

#### *Factor 'sex of caller' - male vs. female caller*

- Loud calls

I found that the loud call rate was influenced by the caller's sex when comparing all experiments. Ravens gave more loud calls when they heard female playbacks compared to male playbacks (Fig.15), which could be an indication for arousal. Szípl et al. (2014) simultaneously presented calls of a male and a female conspecific in a playback experiment and could show that ravens responded strongest to playbacks of familiar individuals and within these, they preferred female stimuli. Generally, ravens tended to approach the speaker that played back calls of conspecifics lower in rank than themselves (Szípl et al., 2014). Usually, females are dominated by males (Braun & Bugnyar, 2012) which might be the reason for a stronger calling response towards female playbacks. But the majority of food yells at carcasses is produced by females, maybe to obtain social support at a food source (Szípl & Bugnyar, 2014). Besides, Boeckle & Bugnyar (2012) showed that familiarity is coded in the number of calls given by a responding individual. However, the subjects should be equally familiar with



male and female stimuli birds. Therefore, I assume that familiarity cannot be used to explain the increased loud call frequency regarding female playbacks.

- Beak wipe

In addition, ravens showed more beak wipes when exposed to a change of male callers as compared to female callers. This was the case within experiment 'individual' (Fig.16a).

Overall, frequency of beak wipes was influenced by the caller's sex when all experiments were compared (Fig.14). The rate of beak wipes might be an indicator for stress or be used as a dominance display. For male ravens, SAD calls of male conspecifics could be perceived as threatening gesture. They may suggest that a competitor is close by and that he may be ready for a contest regarding one's partner or territory. In general, males are higher in rank than females. Thus, from a female's point of view, a male giving SADs means that a bird higher in rank than oneself presents showing off behaviour. While a male receiver might get directly involved in a fight, females may be disadvantaged if the existing rank hierarchy in their group changes or if their partners fail to assert themselves. The increased risk of agonistic interactions and the potential threat to the existing rank hierarchy in one's group might be the reason why male calls elicited more beak wipes.

Finally, I want to point out that within subjects, the sex of the played back individuals always remained the same. Hence, this study was dealing with inter-individual comparisons.

### Individual discrimination

Based on previous research, it is already known that ravens are capable of individual recognition (Boeckle & Bugnyar, 2012). Results of single response variables underline that ravens discriminate among individuals within a single SAD type. Vertical head turns (Fig.9b), vertical head turns directed at the speaker (Fig.10b), walking (Fig.102b) and approaching the speaker (Fig.13b) increased when the calling individual was changed. The increase of vertical head turns directed at the speaker and approaching is particularly convincing as these are behaviours oriented towards the speaker. Moreover, vertical head turns and walking may stand for an overall increase of vigilance and activity in the dishabituation. The sudden change of an acoustically perceived conspecific might induce stress. Massen et al. (2014) showed that ravens increased activity levels when listening to a simulated group rank reversal and assessed this raised activity as related to stress (Massen et al., 2014).

Proops et al. (2008) stated that a receiver might form a multi-modal perception of an individual and then react strongly to the change because of its acoustic contrast and cross-modal impression of another individual. Ravens could well be able to associate characteristic cues

with previously stored information on an individual. Just like functionally referential food calls (Boeckle et al., 2012), SAD vocalizations of ravens might possess individual features that enable listeners to differentiate between individuals.

### SAD type discrimination

I predicted that ravens will not show a behavioural change to different SAD types given by the same individual. My prediction was based on previous findings, e.g. by Cheney & Seyfarth (1988) who revealed that vervet monkeys, *Cercopithecus aethiops*, learned to ignore acoustically different calls given by one unreliable conspecific, if the calls had similar referents.

In my study, results of PCA (RC1, Fig.7a) and single response variables confirmed that ravens discriminate among perceived SAD types. They habituated to a specific SAD type but did not transfer habituation to another SAD type when the signaller remained the same. Again, orienting behaviours like vertical head turns directed at the speaker (Fig.10a), looking at the speaker frequency/ duration (Fig.11a) were involved and might represent a direct reaction to the playback. Subjects looked more frequently and for a longer period of time at the loudspeaker when the SAD type changed. Furthermore, they increased vigilance and activity levels based on vertical head turns. These results imply that ravens do not categorize acoustically distinct SAD types as one meaning. SAD types seem to have individual meanings. According to Seyfarth et al. (2010), several studies exhibited that on one side, acoustically distinct calls can elicit similar responses but on the other, acoustically similar calls can cause different responses. Different responses elicited by distinct SAD vocalizations may be due to acoustic variation. In natural group surroundings, reactions might also be affected by diverse contexts in which SADs are given, e.g. relative rank difference between caller and listener or current events within a group. This also relates to findings in other species, e.g. baboons. Rendall et al. (1999) revealed that grunts of wild baboons, *Papio cynocephalus ursinus*, can function as referential signal, but that the context of production and social identity of the caller also affect receiver's responses.

Meaning is based on discrete properties like rank, call type or identity that are combined to a mental representation (Cheney & Seyfarth, 2007). Competition for high rank is of major importance for example in a male baboon's life because it refers directly to its reproductive success (Cheney & Seyfarth, 2007). Pant-hoot displays in chimpanzees seem to function in both dissociating neighbouring groups (Wilson et al., 2001) and maintaining cohesion within groups (Mitani & Nishida, 1993). In general, SADs may indicate the quality of a reproductive partner. Larger call type repertoires could have an influence on how ravens are perceived by

others. Besides, SADs may also play a role in regulating spatial relationships among ravens between and within groups. However, further studies will be needed to encode the meaning of SADs in ravens as it has already been done for loud calls and food calls.

#### Problems & suggestions for further investigations

Horizontal head turns directed at loudspeaker did not show any difference in the main test (phase3 and dishabituation) while vertical head turns directed at the speaker did. One reason might be that it is problematic to interpret horizontal head turns directed at the speaker in ravens. Unfortunately, I cannot think of any better standardized definition for this variable than using the orientation of the beak towards the playback. It is almost impossible to determine the orientation of ravens' eyes.

It might have been even better to add an evaluation of immediacy for the behavioural reactions, since it could make a difference if a response occurs immediately after a playback presentation or up to 1 min later. However, this procedure would have raised still more efforts for the analysis.

One can argue that taking the duration of approach into account is deficient, as it would take longer if a bird slowly walks towards the loudspeaker by chance as compared with racing or flying towards it. In the latter case, the duration would be shorter, although the intensity of the reaction could be assessed as higher.

During separation from their group, ravens differed vastly in their coping styles. While 'reactive' ones were static and also did not move after hearing a playback stimulus, others got very agitated and flew back and forth in the testing compartment (personal observation).

However, almost all of the subjects increased their calling rate, also regarding SADs. One reason could be that ravens made use of being alone to experiment and practice their vocalizing skills. Usually, they may be suppressed by higher-ranked group members. Massen et al. (2014) stated that SADs occur in a non-directional way when ravens have temporarily left a group.

This might particularly be a sphere of interest for future investigation.

## Appendix I.

### Response variables used for video-coding:

<b>Vocalization</b>			<i>calls from other birds are not noted</i>
HA	frequency	food/begging call	
SAD	frequency	defined call types (SAD1,2,3,5,6,9) or new ones, also if not accompanied by specific body posture	
Loud Call	frequency	long-distance call	
Soft Call	frequency	everything that is low, except SADs	
<b>Self-directed</b>			
Manip.Food	duration	includes "eating"	
Manip.Object	duration	playing with objects, e.g. ball/bowl/etc., taking an object with its beak or destroying it	
Beak wipe	duration	bird wipes its beak on a structure	
Auto-preening	duration	bird preens itself (feathers)	
Scratching	duration	scratching head with leg; scratching feet/pecking at rings with beak (not auto-preening)	
Digging	duration	caching/retrieving objects/food; usually parallel with caching	
Stretching	duration	stretching legs/wings in the air	
Wall/StrucPeck	frequency	against wall/branch	
Body-shake	frequency	can occur simultaneously with head shake	
Head-shake	frequency	can occur simultaneously with body shake	
<b>Locomotion</b>			
Flying	duration		
Walking	duration		
Branchhop	duration	bird hopping on the same branch or from one branch to another	
<b>Head movement</b>			
HHT	frequency	horizontal head turn, independent from direction	
VHT	frequency	vertical head turn, head lifting only	
LookLoudS	duration	actual time bird spends on looking towards loudspeaker; beak directed towards speaker	
<b>Approach</b>			
Loudspeaker	duration	bird is approaching loudspeaker	
<b>Direction</b>			
At LoudS	duration	amount of time that bird invests in a behaviour directed at the loudspeaker; beak directed at speaker	

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# Curriculum Vitae

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## Education

10/2012 – Postgraduate studies: Behavioural-, Neuro- & Cognitive Biology at the Univ. of Vienna  
2012 **Bachelor of Science – Degree Biology**  
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2009 – 2012 Undergraduate studies: Biology, focused on Zoology  
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03/2013 – 06/2013 Research internship at the Tiergarten Schönbrunn:  
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03/2012 – 06/2012 Research internship on archer fish at the Haus des Meeres:  
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## Language Skills

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