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- Schloegl, C., Schmidt, J., Boeckle, M., Weiß, B. M., & Kotrschal, K. (2012). Grey parrots use inferential reasoning based on acoustic cues alone. *Proceedings Of The Royal Society B-Biological Sciences*, 279(1745), 4135-4142. doi: 10.1098/rspb.2012.1292
- Wascher, C. A. F., Szípl, G., Boeckle, M., & Wilkinson, A. (2012). You sound familiar: carrion crows can differentiate between the calls of known and unknown heterospecifics. *Animal Cognition*, 15(5), 1015-1019. doi: 10.1007/s10071-012-0508-8

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I am the main author on all publications where I am listed as first author and have been responsible for all aspects of experimental design, data collection, and data analysis. In the publications where I am listed as co-author I was essentially involved either in study design, data collection, data analysis, or have essentially contributed in data interpretation.

General Introduction

Background

Research on the evolution of mind in humans and animals has earned a lot of attention in recent years (e.g. Shettleworth 2009). One of the main approaches is to examine selective pressures that lead to the evolution of complex behaviour and cognition. Historically, cognition research focused on primate cognition that started with the advances of Köhler who initiated in 1914 to systematically analyse chimpanzee behaviour (for review see Maestripieri 2005). Recently the focus shifted also to other mammalian taxa like hyena (*Crocuta corcuta*) (Holekamp, Sakai & Lundrigan 2007), meerkats (*Suricata suricatta*) (Kutsukake & Clutton-Brock 2008; Townsend, Allen & Manser 2012), and canines (Gácsi et al. 2009; Kaminski et al. 2011; Range, Huber & Heyes 2011). Latest since the discovery that the avian brain is not inferior to the mammalian brain (Jarvis et al. 2005), the study of bird cognition has gained large interest (Pepperberg 2011). By widening the attention to a variety of taxa a comparative approach to the evolution of cognition started to be attainable, which has the advantage to foster the understanding of selective pressures and convergent evolution. The vast amount of avian species, in combination with their global distribution and their ecological flexibility make comparative studies within birds as well as between other taxa a large but potentially fruitful endeavour.

Cognitive skills help to solve problems in the social and physical environment of a species. Thus, physical cognition is concerned with on the one hand the understanding of space, time, and numbers but might also involve the capability of tackling difficulties of food acquisition (foraging theory of intellect) (Shettleworth 2009). Social cognition addresses skills that help to solve problems that emerge from interacting with others, whereby group size and structure might necessitate different solutions (Shettleworth 2009). Recent studies on parrots

and corvids try to understand the influences of both domains (Heinrich 2011; Mikolasch 2012; Pepperberg 2002; Pepperberg 2011; Schloegl et al. 2009). One of the fundamental mechanisms that underlie the social brain (Dunbar 1992; Humphrey 1976; Jolly 1966) is individual recognition (IR) (Tibbetts & Dale 2007). Different sensory domains are relevant for IR. In bird species that often interact vocally, acoustic communication seems to be an important part of the social world. Thus bioacoustics and ethology seem to be prone to help understand the sociality in birds. The focus of this thesis is to tackle questions concerning the social cognition based on acoustic communication of a socially highly complex corvid species – the raven. Acoustic communication and its means as social interaction are based on the production of the acoustic signals. Investigating production mechanisms as well as the signals are fundamental to understanding the social interactions in acoustic communication.

Vocal Production

In the study of mammalian vocalizations the source filter theory introduced by Fant (1960) that differentiates the vocal source (vocal folds) and the filter (vocal tract) in vocal production, has started to be highly influential. The source is in most tetrapods considered to be the quasi-harmonic vibration of the vocal folds in the larynx, while in birds the vibrating tissue (labiae) are situated in the syrinx, whereby additional sound producing mechanisms are known. Important to note is that the source produces the fundamental frequency (Fitch & Hauser 2002). The quasi periodic vibrations are hypothesized to at least in mammals be based on the myoelastic-aerodynamic theory that is well understood in humans (e.g. Titze 2000). In mammals vibrations that consists of a fundamental frequency with harmonic overtones then travels through the supra-laryngeal vocal tract, that in turn filters some of the frequencies and amplifies others (Reby & McComb 2003). The combination of the two mechanisms is the signal that is analysed in its time and frequency domain. While fundamental frequency is based on the vibrations of the source, vocal tract filtering results in

broad band filters called formants (Fant 1960) that can be seen as dark bands in the spectrogram.

The source-filter theory is highly useful for the analysis of animal signals that are based on similar structures as they help to combine physiological parameters of the vocalizer with acoustic features of the call so that by understanding spectrographic representations inferences about the production mechanism can be made (Elemans, Heeck & Muller 2008b) as well as inferences about the anatomical features of the signaller (Charlton, Reby & McComb 2007; Taylor, Reby & McComb 2009). While the analysis of a spectrogram can lead to inferences about the sound producing mechanism, it cannot lead to unambiguous interpretation of the actual mechanism (Elemans et al. 2008b). Detailed anatomical studies in combination with functional morphological understanding are needed to completely understand and interpret the spectrographical representations of vocalizations. Thus understanding the biomechanical and anatomical features helps to apprehend the function of animal signals.

Production mechanisms are only one of the influences that shape signal structure. Phylogeny (Laiolo & Rolando 2003; Laiolo et al. 2001; Ryan & Brenowitz 1985) and habitat noise (Kirschel et al. 2009; Lema & Kelly 2002; Luther & Baptista 2010; Luther & Derryberry 2012; Morton 1975) are further constraints on signal characteristics. Additionally motivation structural rules have been hypothesized to exist across species (August & Anderson 1987; Morton 1977). Thus calls should decrease in fundamental frequency, tonality, and show increasing chaotic structures with the increase of agonistic state, while an increase in fundamental frequency and tonality should occur with the rise of affiliation or submission (Morton 1977).

In the phylogenetic development of birds the sound producing structure has evolved in different versions. These structures thus differ according to the phylogenetic background the

single species has and furthermore led to the three main versions of syrinxes so far known. Dependent on the localization of the vocal folds within the trachea-bronchial tube, the syrinx is categorized as tracheal, tracheobronchial or bronchial (King 1989; Rüppell 1933). Song birds have a tracheobronchial syrinx (Raikow & Bledsoe 2000) that produces quasi-periodic oscillations via thickened two pairs of labia in the bronchi (Suthers & Zollinger 2004). Syringeal muscles innervate at different regions of the syrinx to allow neural motor control of the signal in its temporal, amplitude und frequency structure (Elemans, Zaccarelli & Herzel 2008a; Elemans et al. 2008b; Elemans et al. 2008c). Integrating neural control with motor patterns of the syrinx and vocal tract filtering are necessary to understand proximate and ultimate functions of these signals (Suthers & Zollinger 2004).

Acoustic Communication

The study of acoustic communication in animals, based on the above-mentioned production mechanisms, tries to understand the function and meaning, as well as the ontogenetic and evolutionary development of these calls. The field has undergone several discussions about what communication is and how it works. The often underlying ‘information theoretical’ approach introduced by Shannon and Weaver (1964) has recently been intensively discussed (Owren, Rendall & Ryan 2010; Rendall, Owren & Ryan 2009; Seyfarth et al. 2010). Main focus of the discussion is whether signallers encode information so that perceivers can decode and respond according to information they gained. This thesis does not focus on the discussion of the theoretical approach to animal communication but rather tries to understand signals in the perspective of the four Tinbergen’s questions. Tinbergen (Tinbergen 1951, 1963) introduced based on (Huxley 1914) four questions to analyse a certain behaviour: How does it work; how does it develop; what is it for; how did it evolve? Animal acoustic communication should try to understand both proximate and ultimate mechanisms. While the functional explanation is based on questions about its physical and

anatomical background, that also introduces questions about the evolution of the structures and their mechanisms, understanding the biological function and its behavioural consequences is a different side of the same coin. Especially animal cognition, ethology, comparative psychology and other related areas of research try to understand among others the meaning of vocalizations and their social function. Thus what is the 'intention' of the signaller and what is the response of the perceiver. The question, what intentionality in animals is, still remains unresolved. Similarly, whether there are levels of intentionality like supposed by Dennett (1983) is highly disputed. A framework to understand and redefine intentionality and animal knowledge can be found in (Boeckle in press).

In addition to questions concerned about production and function of acoustic signals, acoustic communication has turned out to be a useful tool for answering cognitive questions. Playback experiments that test social knowledge in vervet monkeys (Cheney & Seyfarth 1982; Cheney & Seyfarth 1985; Seyfarth, Cheney & Marler 1980) and baboons (Cheney & Seyfarth 1999; Cheney, Seyfarth & Silk 1995) initiated this movement.

Social Life

Understanding the cognitive mechanism of animals, which means understanding information acquisition, processing and behavioural response (Shettleworth 2009), seems especially interesting also in the acoustic domain. With the rise of the idea of natural selection by Darwin (1859) the prime selective pressures were considered to be the ecological niche and sexual selection. Only later selective pressures for the evolution of intelligent behaviour were taken into consideration that include social factors like group size, social network size and complexity (Byrne 1996; Byrne & Whiten 1988; Humphrey 1976; Jolly 1966). The social brain hypothesis or Machiavellian intelligence hypothesis states that the larger the group the larger neo-cortex size should be (Dunbar 1992; Humphrey 1976;

Jolly 1966). The correlation turned out to be true for some mammals (Connor 2007; Dunbar 1992; Dunbar & Bever 1998; Marino 2002; Sawaguchi & Kudo 1990) but could not be found in other taxa (Dunbar & Shultz 2007; Emery et al. 2007). In birds it is hypothesized that complex cognitive abilities are based on long-term monogamous pair bonds (Dunbar & Shultz 2007; Emery et al. 2007) but see Scheiber et al. (2008) for criticism.

Independent of the selective force at work the classification of social partners into classes are necessary for using social knowledge (Cheney & Seyfarth 1982). One of the classifications that is most studied is kin recognition (Hamilton 1963). Thus prerequisite for any forms of complex social cognition seems to be the differentiations of individuals whereby the most demanding is supposed to be individual recognition (IR) (Tibbetts & Dale 2007). Social knowledge and the memory of previous interactions should not only be based on classes but should be based on individuals, so that adequate behavioural responses can be given also in large groups (Dunbar 1992). Thus along with IR comes the integration with memories about previous interactions that help to act adequately to specific individuals. Still, not for all social interactions IR is necessary and gross classifications into groups might be sufficient (Tibbetts & Dale 2007). To differentiate between true individual recognition and class recognition has been of large interest both for the theoretical (Steiger & Müller 2008; Tibbetts & Dale 2007; Tibbetts, Sheehan & Dale 2008) and for empirical work. Best evidence for true individual recognition seem to come from cross-modal studies that either integrate visual and acoustic sensory stimuli (e.g. Kondo, Izawa & Watanabe 2012; Proops, McComb & Reby 2009) or internal representations of time, space and acoustic stimuli (Townsend et al. 2012).

Within species individual recognition has been the focus of various studies while between species individual recognition and class level differentiation has earned less attention. While intra-species pressures are highly discussed for individual differentiation similar effects should be found between species that often interact. It is known that alarm

calls (Fallow, Gardner & Magrath 2011; Ito & Mori 2009; Johnson et al. 2003; Magrath, Pitcher & Gardner 2009), mobbing calls (Fallow & Magrath 2010) and food associated calls (Koda 2012) of heterospecific individuals are exploited. Similarly, it has been shown that some species differentiate between reliable and unreliable food and alarm callers (Blumstein 2002; Blumstein & Daniel 2004; Fitch & Hauser 2002; Nocera & Ratcliffe 2010). Differentiating classes and individuals might show similar benefits in heterospecifics. To the best of our awareness, little is known about heterospecific class-level or individual recognition except differentiating between threatening and non-threatening humans (Cornell, Marzluff & Pecoraro 2012; Lee et al. 2011; Levey et al. 2009).

Study Species

Within the range of birds, corvids are one of the taxons that recently gained much attention as they possess large brains and are therefore attributed with high cognitive abilities (Iwaniuk & Arnold 2004; Iwaniuk & Hurd 2005). Both environmental unpredictability and social pressures are hypothesized to be the driving force of high behavioural flexibility (e.g. Bugnyar 2007; Bugnyar & Kotrschal 2002; Fraser & Bugnyar 2010a, 2011; Heinrich 2011; Marzluff, Heinrich & Marzluff 1996). The largest corvid species, i.e. the raven, with its distribution in the northern hemisphere has a complex social life. With the age of about six months, when parent caregiving ends, juvenile ravens flock in large aggregations (Haffer 1993; Huber 1988; Huber 1991; Ratcliffe 1997). Individuals may stay within these non-breeder flocks for long periods (up to 10 years; personal communication T. Bugnyar). Flocks are highly variable in the number of individuals and group composition during the day (Braun et al. 2012) with large groups formed during feeding and roosting (Cotterman & Heinrich 1993; Dall 2002; Danchin & Richner 2001; Marzluff & Heinrich 2001; Marzluff et al. 1996; Preston & Johnson 2005; Wright, Stone & Brown 2003), which might be interpreted as fission-fusion dynamics (Aureli et al. 2008). During this prolonged non-breeder stage ravens

show various relationships among kin and non-kin individuals (Fraser & Bugnyar 2010b) and might already include bonded pairs. These relationships are maintained over long periods and supported, among others, by post-conflict behaviours (Fraser & Bugnyar 2010a, 2011, 2012). After the prolonged non-breeder stage, ravens search for vacant territories that can comprise up to 10km² (Rösner & Selva 2005), which they occupy and defend as breeding pairs.

During all stages of raven ontogeny acoustic communication plays a crucial role (Gwinner 1964; Pfister 1988; Pfister-Gfeller 1995). In early development begging calls are the predominantly uttered vocalization, that later is hypothesized to develop into food calls (Heinrich 2011). While some information exists about the function of this food associated call (Bugnyar, Kijne & Kotrschal 2001; Heinrich & Marzluff 1991; Heinrich, Marzluff & Marzluff 1993) little is known about correlations to phenotypic characteristics of the vocalizer and its individual differences.

For ravens the long distance calls are most typical. These calls are known to be highly variable and seem to be different between individuals and seem to have regional dialects (Enggist-Dueblin & Pfister 2002). Within long distance calls various subgroups of vocalizations might be found (Conner 1985; Dorn 1972; Gwinner 1964). While descriptive work of these call types has been conducted, little is known about the function and variability of these calls. Additionally, vocalizations with individual variation have the potential to be differentiated not only by conspecifics but also heterospecifics. Especially species that show intraspecific individual discrimination might be likely to show heterospecific individual or class recognition.

Hypotheses

The aim of this thesis is to increase understanding of vocal production and vocal communication in common ravens. Based on the lack of data showing detailed morphological data we first want to provide general morphological descriptions of the raven vocal apparatus. Syrinx and vocal tract as part being crucial for the source-filter theory of call production will be described in chapter 1 “Vocal tract length and syringeal structures of common ravens” (Boeckle et al. in prep.). In addition to the description of the vocal apparatus body-size related measurements of the raven will be correlated with the vocal tract length. Sex, age and size dependent features will also be identified.

Based on the anatomical differences we also predict that some of the morphological differences between sex and age might be prevalent in the acoustic signals of the call. This topic will be addressed in Chapter two “Indicators of sender’s sex and age in raven food calls” (Boeckle, Szípl & Bugnyar submitted). While we hypothesize that class recognition of sex and age are mainly important for individuals unknown to each other, individual differentiation might be more important when having repeated social interactions. Chapter 3 “Who wants food? Individual characteristics in raven yells” (Boeckle, Szípl & Bugnyar 2012) concentrates on individual differences in food associated calls.

Individual differences within call types might give rise to raven’s ability to differentiate both within known individuals but also between unknown individuals. To understand whether perceivers of raven calls can differentiate between two unknown callers we conducted playback experiments with two call types. Chapter 3 describes differentiation between two unknown food callers while chapter 4 “Ravens discriminate unknown individuals in long distance calls” (Boeckle & Bugnyar in submitted) shows the differentiation abilities between two unknown territorial callers.

While most studies concentrate on individual and class recognition within species we here also tested whether heterospecifics might be able to differentiate between individuals. Especially species, which are supposed to have individual recognition should also be able to discern between individual callers of other species. This question will be addressed in chapter 5 “You sound familiar: Carrion crows can differentiate between the calls of known and unknown heterospecifics” (Wascher et al. 2012).

Individual differences might not always lead to true individual recognition but might lead to categorizations that are related to classes like familiar vs. unfamiliar, male vs. female, age class, affiliate vs. non-affiliate. Most studies on individual recognition in birds concentrated on familiar versus unfamiliar birds, as it is related to the dear enemy effect. To answer whether ravens are able to discriminate between these categories we conducted a playback experiment in chapter 6 “Long-term memory for affiliates in ravens” (Boeckle & Bugnyar 2012).

As social knowledge and vocal communication seem to be highly developed in common ravens, we predict that playback experiments might be a useful means to test for social knowledge. Some individual ravens will meet regularly but others only after prolonged periods of time, a feature typically discussed in the framework of fission-fusion dynamics. Because of this dynamic group structure we suggest that ravens might profit from memorizing individuals for long periods. Additionally, long lasting memory for the differentiation between affiliates and non-affiliates, might increase the positive effect. We therefore tested in chapter 6 whether ravens memorize individuals they were living together after a maximum of three years and can differentiate between previous affiliates and non-affiliates.

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Chapter 1:

Vocal Tract Length and Syringeal Structures of Common Ravens

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Abstract

Understanding vocal production in animals helps to better interpret function and meaning of the produced acoustic signals. Acoustic parameters that correlate with phenotypic characteristics of the vocalizer might be utilized as cues by perceivers. It has been shown that based on the source-filter theory various predictions can be made on signal structure. Especially the filter i.e. the vocal tract length has been discussed to be a reliable indicator for body size in many species. Differences in the vocal tract length between individuals as well as changes within individuals during phonation should be perceivable in changing formant frequencies in vocalizations with pulsated or chaotic structures, or in low fundamental frequencies and many harmonics. We here analysed vocal tract length of 23 dead ravens in order to test for correlations with body-size measurements and body weight. Additionally we predict that due to sex dimorphism in size and possible changes of the vocalizing apparatus during maturing, sex and age differences might occur in vocal tract length. We could show that vocal tract length is correlated with body size and age differences are evident. We suggest that vocal tract length influence formant frequencies that can be used by perceivers during decision making processes.*

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Introduction

Many animal calls are complex acoustic signals, which covary with various phenotypic features of the vocalizing individual. An important factor in mating and social behavior of various animals is body size as it may correlate with fitness-related advantages in agonistic and mating behavior (e.g. Brown, Marquet & Taper 1993; Clutton-Brock & Albon 1979; Modig 1996; Parker 1974; Schuett 1997). Based on the source-filter theory (Fant 1960) size dependent features of the vocal organ are hypothesized to correlate with acoustic features of either the source or the filter (e.g. Morton 1977). Covariations of body size and fundamental frequency have been demonstrated in some vertebrate groups (August & Anderson 1987; Hauser 1993; Ryan & Brenowitz 1985). Vocal structures can provide reliable cues to body size (Fitch 1997; Fitch & Reby 2001; Pfefferle & Fischer 2006), which in turn might enable perceivers to respond according to size dependent features (for review see: Fitch & Hauser 2002). Acoustic displays may provide perceivers with a cue to body size and thereby an opponent's ability to compete for resources before physical interactions take place, which could be beneficial for the perceivers fitness.

While correlations between source dependent features like fundamental frequency and body size have been described as reliable interspecific cues (Gingras et al. in press; Preininger, Boeckle & Hödl 2007), intraspecific covariations have also been shown (Morris 1989; Morris & Yoon 1989). For instance in vocalizations of the male cricket frogs (*Acris crepitans*) spectral parameters are inversely related to laryngeal size, which is largely mediated by body size (McClelland et al., 1996), in other words, large frogs produce calls with lower dominant frequency. Between species differences in fundamental frequency are possibly more predictive because of larger body size differences, while for instance small birds might not vary largely between individuals or classes. Thus the reliability of fundamental frequency as cue to body size has been questioned (Fitch & Hauser 2002;

Patel, Mulder & Cardoso 2010) Furthermore, fundamental frequency is easily manipulated by length and tension of the vibrating tissues, which changes during vocalization. Thus, variation within an individual might be larger than variation predicted by body size and therefore might override effects of body size correlations in many species.

Filter related features that highly depend on vocal tract length (VTL) are indicators to caller's size (e.g. Fitch 1997). The primary determinant of formant frequencies is VTL, which often relates to body size of the vocalizer. Additionally, it has been demonstrated that lengthening the vocal tract by elongating the neck or lowering the larynx decreases formant dispersion (i.e. the spacing between adjacent formants), signifying larger body size (Fitch & Reby 2001). Elongation of VTL together with its biological function has been extensively studied in deer where body size is correlated with formant dispersion (Charlton, Reby & McComb 2007a, b; Reby & McComb 2003; Reby et al. 2005a). Hence, acoustic characteristics of animal vocalizations should provide a cue to the size of the vocalizer. The usage of body weight as a proxy for body size was also used by other authors (e.g. Charlton, Zhihe & Snyder 2009).

Vocal repertoires of vertebrate groups range widely, with mammals and birds having high propensity for vocal call complexity. Birds have a large variety of syringeal structures that are responsible for large species differences, and structural differences of vocal organs can be used to analyse phylogenetic relatedness (Raikow & Bledsoe 2000). Several studies focus on influences of the syringeal structures and the VTL on vocal production as well as on the influences of VTL on acoustic characteristics in some avian species (Beckers, Nelson & Suthers 2004a; Brittan-Powell et al. 1997; Fitch & Kelley 2000; Goller, Mallinckrodt & Torti 2004; Nelson 2005; Riede et al. 2006; Suthers 2001; Suthers 1994). However, little is known about the biological function of the VTL in birds and its implications on the call system. Recently, biological interpretation has been added in ravens, where changes in formant

frequencies of response calls relate to the affiliation between signaler and perceiver (Boeckle & Bugnyar 2012).

The so far most studied vocalization in ravens is the 'haa' call, a food related call given by non-breeders when facing problems to access food (Boeckle, Szpl & Bugnyar 2012; Bugnyar & Kotrschal 2001; Bugnyar, Kijne & Kotrschal 2001; Heinrich 1988, 1994b; Heinrich & Marzluff 1991; Heinrich, Marzluff & Marzluff 1993; Marzluff & Heinrich 1991). Due to the harmonic structure and the predicted formant frequencies based on VTL (Hinds & Calder 1971) of ravens these calls do not reveal measurable formants. Vocalizations like the long distance call emitted by territorial breeders (Boeckle & Bugnyar 2012), that show a different harmonic structure or more non-linear phenomena might reveal clear formant frequencies. We predict that not only the affiliative status is correlated with the formant structure but also gross body size. Perceivers could estimate body size from large distances, especially in territorial defense, where the vocalizer might indicate fitness and fighting abilities via formant dispersion or other acoustic parameters. Assessing the size of opponents could be highly beneficial as severe fights in ravens are potentially lethal.

To our knowledge little work has been focusing on the vocal production in corvids (Chamberlain et al. 1968; Tsukahara, Aoyama & Sugita 2006; Tsukahara, Yang & Sugita 2008; Tsukahara et al. 2009) and especially in ravens, except for a general myological description of ravens (Shufeldt 1890) and description of VTL of a single raven (Hinds & Calder 1971). In this study we analyze correlations of gross body measurements and VTL in common ravens. Positive results would not only provide the opportunity to use external morphological measures to predict VTL and analyze specific calls, but could also indicate that call characteristics might be exploited by conspecific perceivers to estimate body size previous to interactions and thus affect social behavior in ravens.

Material and Methods

Dissection

We analyzed a sample of 23 wild ravens that died a natural death (i.e. ravens that were killed by captive predators like wolves, bears, lynxes, foxes, or eagles when cofeeding in their enclosures) in the Cumberland Gamepark in Grünau and were collected between 1996 and 2011. All samples were deep frozen directly after first sight and unfrozen the day before dissection. Of the unfrozen specimen we measured body size related parameters: weight, beak to tail length, first primary, second primary, third primary, beak tip to back head, beak tip to nostril, beak tip to the distal end of the gnathotheka, ulna, humerus, sternum, tibia, tarsometatarsus, first toe, second toe, third toe, fourth toe and first toe to third toe, while other measurements were taken after dissection: tongue, tongue to glottis, glottis, VTL at 0 g, VTL at 10 g, VTL at 20 g, VTL at 30g, VTL at 40g, VTL at 50 g, left Sternotrachealis muscle, right Sternotrachealis, asymmetry between first left and right bronchial ring as well as asymmetry of the last left and right bronchial ring. For co-variation of VTL and weight we used a spring scale and pulled in the horizontal way. All parameters were measured with a caliper to the nearest 0.1 mm; only primaries and beak to tail measures were taken with a measuring tape to the nearest 1 mm.

Computer Tomography (CT) and Micro Computer Tomography (μ CT)

An intact dead raven was scanned for *in situ* analysis of the raven syrinx in Trieste at the Azienda Ospedaliera Universitaria Trieste with a medical CT-scanner (Temax Liquido 15Min, Bauer - Glavine Fabio Svenio 60). Specimen was unfrozen one day before scanning and then positioned with an elongated neck to the front (Fig. 1).

For the CT scan of the excised syrinx we fixated the specimen in a tube with foamed polystyrene and wooden toothpicks. The specimen was filled with NaCl solution at the same

day. The following day NaCl solution was exchanged with a 5% formalin solution for four days. Then it was flushed with aqua dest and stepwise transposed from 70% ethanol to 100% ethanol within one day. The same evening 100% ethanol was then changed to 99% ethanol with 1% iodine following the instructions of Metscher (2009). We conducted μ CT scans at the μ CT (lab of the Department of Anthropology of the University of Vienna (Austria) using a Viscom X8060 NDT x-ray system (Viscom, Hanover, Germany). Images were generated and gray values corresponding to the tissue density were assigned to each voxel. The size of each voxel was $80\ \mu\text{m}^3$.

For both CT and μ CT the 3D reconstruction and imaging were conducted on the resulting images with Osiri-X 4.1.2 64-bit (Geneva, Switzerland; <http://www.osirix-viewer.com/>) or Amira 4.1 software (Mercury Computer Systems, Chelmsford, MA). Images are included here for illustration purposes only (see Fig. 1 and Fig. 2).

Statistics

All body and vocal tract measurements except glottis size (KS: $Z=1.932$ $P\leq 0.001$) were normally distributed (KS: $p\leq 0.2$). Further analysis thus is based on parametric statistics. For the prediction of VTL length via a linear model we excluded seven out of the 23 dissected ravens because of outliers with Cook's distance larger than 4 divided by the number of observations. Missing values were replaced with means of the training partition of the dataset. We used a forward stepwise procedure to derive the final model. For correlations with body size we calculated univariate Pearson correlations (PC). Additionally we calculated multivariate general linear models to check for sex and age differences between the single parameters. Sex was determined by gonadal inspection during dissection and genetically checked by Laboklin Austria. Age was determined by mouth coloration and categorized into

juvenile, subadult, and adult individuals (Heinrich 1994a; Heinrich & Marzluff 1992). All statistical tests were conducted using IBM SPSS statistics 19.

Results

Predicting VTL

Body measurements in ravens are presented in Table 1. We derived the final model with forward stepwise model selection and 0g extension with AIC=-12.369. VTL in ravens was highly predicted by the three external morphometric measurements beak to tail ($\beta=0.283$, S.E.=0.039, $t=7.329$, $P\leq 0.001$), first toe to third toe ($\beta=0.744$, S.E.=0.145, $t=5.141$, $P\leq 0.001$), and humerus ($\beta=0.680$, S.E.=0.136, $t=5.019$, $P\leq 0.001$). For estimated regression lines see Figure 3. VTL was possible to change by attaching increasing weights to the excised specimen and increased with weight (GLMM: $F_{5,70.2}=59.812$, $P\leq 0.001$) (Fig. 4), whereby effect size decreased with the increase of weight (Table 2).

Body size

Similarly, when calculating PC we derived correlations of body weight and first toe length (PC: $r=0.627$, $P=0.005$, $N=18$) third toe length (PC: $r=0.497$, $P=0.026$, $N=20$), first toe to third toe (PC: $r=0.513$, $P=0.025$, $N=19$) beak to tail (PC: $r=0.595$, $P=0.015$, $N=16$), third primary (PC: $r=0.637$, $P=0.014$, $N=14$), and tongue size (PC: $r=0.485$, $P=0.041$, $N=18$) as well as with all VTL measurements (0-50g) (PC: $P\leq 0.05$). Body weight was significantly correlated with general body-size measurements. Extended as well as un-extended VTL significantly correlated with body measurements (Table 3).

Sex and Age differences

Univariate tests revealed that the first primary (df=2, $F=30.87$, $P \leq 0.001$, partial eta squared=0.885), second primary (df=2, $F=5.201$, $P=0.036$, partial eta squared=0.565), tip beak to head (df=2, $F=8.994$, $P=0.009$, partial eta squared=0.692), and tip beak nostril (df=2, $F=5.695$, $P=0.029$, partial eta squared=0.587) differ according to sex.

Age class in univariate testing reveals differences in second primary (df=2, $F=14.854$, $P=0.002$, partial eta squared=0.788), third primary (df=2, $F=12.217$, $P=0.004$, partial eta squared=0.753), ulna (df=2, $F=3.447$, $P=0.083$, partial eta squared=0.463), and VTL at 0g (df=2, $F=4.916$, $P=0.041$, partial eta squared=0.551).

Discussion

We here report that raven VTL is positively correlated with body weight and body size, while some body size measurements vary according to sex and age. In excised samples VTL can be elongated for roughly 1 cm independent of sex and age of the individual. Thus we suggest that body size of a calling individual can be a predictable attribute for ravens perceiving a call that show clear acoustic filter related resonances.

Positive correlations of body size and VTL suggest that formant dispersion in a raven call might provide the perceiver with information on body size of the vocalizing individual. We could show that weight is positively correlated with body size leading to the conclusion that weight might be used as proxy for body size in ravens. Even though weight is underlying seasonal changes and with food availability fluctuations of body weight seem not to influence the general correlation of VTL and body weight. This might be due to the fact that body size differences are still a better predictor than seasonal changes and food availability for body weight. As VTL in general is negatively correlated with formant dispersion in various animals

(Fitch 1997; Reby et al. 2005b) the perception of low formant dispersion in ravens like suggested in Boeckle and Bugnyar (2012) could be used by listening ravens as indicators of body size. Cues to body size in formant dispersion of raven calls might help in decision making processes whether to join, compete etc. or not. Additionally, various correlations of body weight with measurements of toe size and beak to tail measurements might help to better assess VTL in situ when marking and measuring ravens. Predictors of VTL were beak to tail, first toe to third toe and humerus, which we interpret to be the best measurements that should be taken when marking.

A previous study suggests that ravens can change formant frequencies and thus could potentially exaggerate vocally perceived body size (Boeckle & Bugnyar 2012) like it has been observed in deer (Reby & McComb 2003). An alternative explanations of changes in formant structures might also be in accordance with motivation-structural rules (Morton 1977), though the hypotheses are not mutually exclusive and need to be varified. Vocal tract length modification in mammals has been reported to be possible by protrusion of the lips (Hauser & Ybarra 1994) or lowering the larynx (Fitch 1997; Fitch & Reby 2001; Reby et al. 2005b), while in birds various mechanisms for changing formant structure have been suggested like tongue configuration, retraction of the syrinx by the sternotrachealis muscle, changes of the positon of the laryngeal structures (e.g. Beckers, Nelson & Suthers 2004b; Fletcher & Tarnopolsky 1998; Riede & Suthers 2009; Riede & Goller 2010; Riede et al. 2006; Warren, Patterson & Pepperberg 1996). However, to assess these mechanisms in ravens additional functional anatomic studies like xray cineradiography during vocalization are needed. Our results demonstrate that ravens VTL can be increased when elongating by putting weight on them by about 1.5cm from around 14cm to 15.5cm. This corresponds with VTL calculated from formant dispersion in long distance calls of ravens (Boeckle & Bugnyar 2012) between 12.5cm and 15.1cm and 14.9cm reported by Hinds and Calder (1971). The production of long distance vocalization in ravens most often is accompanied by opening the bill (personal observations) and thus VTL could additionally be increased by not opening the bill that far

(Fletcher & Tarnopolsky 1998) and together might result in lower formant dispersion indicating larger body size.

Sex differences were only observed in length of second primary, tip beak to head, and tip beak to nostril. No differences were observed according to VTL. While VTL as such did not differ significantly, differences in beak size and configuration can change formant frequencies (Fletcher & Tarnopolsky 1998). This suggests that previous results of raven vocalization without observable formant frequencies that did not show clear sex differences (Boeckle et al. 2012) might not have shown increased sex differences based on mere VTL differences. Still differences of sexes are perceivable in vocalizations with more chaotic structures and thus include observable and perceivable formant frequencies (Boeckle & Bugnyar in prep.). Additionally, sex differences in vocalizations might still be based on differences according to sex in beak configuration and anatomy as well as on other not measured peripheral organs along the vocal tract like the food pouch, air sacs, etc.

While no differences in VTL were observed between sexes, age differences existed in second primary, third primary, ulna and unextended vocal tract. This is in accordance with previous studies on food calls that showed clear age differences in fundamental frequency (Boeckle et al. 2012). Differences in VTL due to maturing might lead to a clearer age differentiation in calls that show clearer formants and thus might increase the vocally perceivable age differences in raven vocalizations (Boeckle & Bugnyar in prep.).

We show here that VTL length in birds is correlated to body size. As VTL is correlated with formant dispersion body size differences might be perceived by con-specifics (Fitch & Kelley 2000). Additionally previous data on raven vocalizations suggest that these differences are changed dependent on motivational-structural rules (Boeckle & Bugnyar 2012) and also attended to as shown in playback studies where differences of response between male and female stimuli were observed. Future research should focus on

neuromuscular control of VTL changes in birds and raven abilities to differentially respond to changes of formant frequencies. Additionally detailed analyses of the functional anatomic structures and the neuromuscular control of changes in VTL should be conducted to better understand production mechanisms that might have functional relevance for vocalizations.

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Tables

Chapter 1 - Table 1. Body and anatomical measurements of the vocal tract.

	All					Female					Male				
	N	Min.	Max	Mean	StD.	N	Min.	Max	Mean	StD.	N	Min.	Max	Mean	StD.
Weight	21	656	1386	1026,61	196,48	8	730	1336	1041,12	188,40	12	656	1386	1008,17	214,63
beack to tail	16	50,00	64,00	58,63	3,86	7	50,00	62,50	56,43	4,27	8	56,50	64,00	60,56	2,68
1.Primary	18	29,50	35,00	30,53	1,33	6	29,50	32,00	30,33	0,98	11	29,50	31,50	30,23	0,65
2.Primary	18	36,00	43,50	39,25	2,12	6	36,50	41,00	38,67	1,91	11	36,00	43,50	39,18	1,95
3.Primary	14	39,00	44,50	41,64	1,85	5	39,00	44,50	40,90	2,10	8	39,00	44,50	41,81	1,62
TipBeaktoHead	20	11,68	12,94	12,42	0,39	7	11,68	12,70	12,16	0,44	12	12,01	12,94	12,59	0,28
TipBeakNostril	20	4,24	5,08	4,60	0,25	7	4,26	4,77	4,48	0,18	12	4,24	5,08	4,69	0,26
TipBeakMouth	20	6,12	7,68	7,03	0,41	7	6,50	7,23	6,77	0,25	12	6,12	7,68	7,19	0,43
Ulna	20	9,50	14,00	12,53	1,00	7	11,50	13,50	12,56	0,71	12	9,50	14,00	12,55	1,20
Humerus	20	9,96	13,00	11,32	1,05	7	10,00	12,00	10,93	0,73	12	9,96	13,00	11,50	1,21
Sternum	20	7,50	9,00	8,37	0,43	7	7,50	9,00	8,21	0,47	12	7,62	9,00	8,45	0,43
Tibia	20	11,00	13,50	12,37	0,70	7	11,00	12,50	12,00	0,58	12	11,00	13,50	12,55	0,72
Tarsometatarsus	20	5,50	7,00	6,15	0,40	7	5,50	6,41	5,92	0,37	12	5,60	7,00	6,24	0,36
1.Toe	18	3,29	4,96	4,34	0,36	6	3,99	4,49	4,23	0,21	11	3,29	4,96	4,41	0,43
2.Toe	19	2,98	4,70	3,68	0,49	7	2,98	4,50	3,61	0,48	11	3,09	4,70	3,74	0,53
3.Toe	20	3,80	6,00	4,91	0,60	7	3,80	6,00	4,69	0,77	12	4,00	5,61	5,01	0,51
4.Toe	20	3,31	4,80	4,04	0,44	7	3,46	4,70	3,93	0,48	12	3,31	4,80	4,09	0,44
1.Toeto3.Toe	19	7,97	11,26	9,98	0,86	7	8,26	11,20	9,84	0,99	11	7,97	11,26	10,08	0,84
Tongue	18	3,47	4,44	3,82	0,26	6	3,47	3,88	3,61	0,15	11	3,63	4,44	3,94	0,24
tongueTOglottis	18	0,75	2,87	1,36	0,57	6	0,83	1,36	1,15	0,19	11	0,75	2,87	1,47	0,70
glottis	18	1,85	7,17	2,35	1,21	6	1,85	2,19	2,01	0,11	11	1,91	7,17	2,54	1,54
VTL_0g	20	10,00	16,80	13,93	1,71	7	11,60	16,00	13,54	1,80	12	10,00	16,80	14,14	1,78
VTL_10g	15	10,60	17,70	14,10	1,93	4	11,90	13,20	12,58	0,53	10	10,60	17,70	14,70	2,06
VTL_20g	15	10,70	17,90	14,32	1,92	4	12,20	13,40	12,90	0,53	10	10,70	17,90	14,88	2,10
VTL_30g	15	10,90	18,20	14,57	1,94	4	12,40	13,70	13,20	0,59	10	10,90	18,20	15,10	2,14
VTL_40g	15	11,00	18,40	14,79	1,96	4	12,60	14,30	13,55	0,73	10	11,00	18,40	15,28	2,21
VTL50g	15	11,20	18,60	15,00	1,95	4	12,90	14,50	13,83	0,70	10	11,20	18,60	15,45	2,22
sinisterSternotrachealis	15	1,15	3,22	2,17	0,60	3	1,15	2,62	1,75	0,77	11	1,44	3,22	2,28	0,56
dexterSternotrachealis	12	1,67	3,70	2,69	0,59	3	1,67	2,88	2,15	0,64	8	2,29	3,70	2,90	0,50
asymetry1.bronchialring	15	0,00	0,40	0,14	0,09	5	0,10	0,20	0,14	0,04	9	0,00	0,40	0,14	0,12
asymetryLastBronchealRing	13	0,36	0,74	0,48	0,13	4	0,36	0,67	0,47	0,15	8	0,37	0,74	0,50	0,14

Chapter 1 - Table 2. Estimates of elongation of the excised VTL.

Parameter	Estimate	Std. Error	df	t	Sig.
Intercept	15.27	0.41	19.96	37.69	≤0.001
0g weight	-1.34	0.09	70.38	-15.07	≤0.001
10g weight	-0.90	0.09	70.06	-10.15	≤0.001
20g weight	-0.68	0.09	70.06	-7.67	≤0.001
30g weight	-0.43	0.09	70.06	-4.89	≤0.001
40g weight	-0.21	0.09	70.06	-2.41	0.02
50g weight	0	0.00	0.00	0.00	0.00

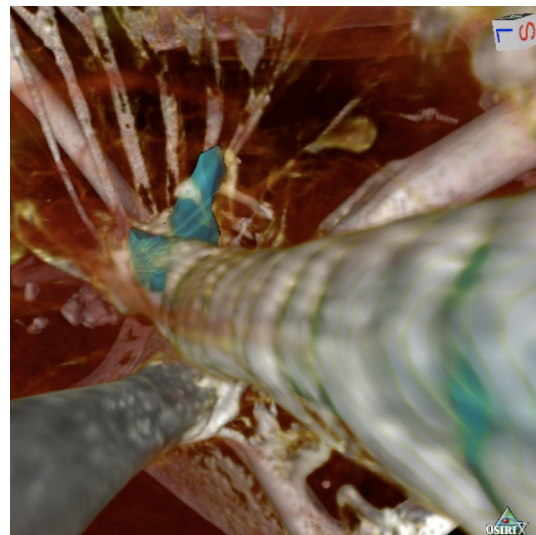
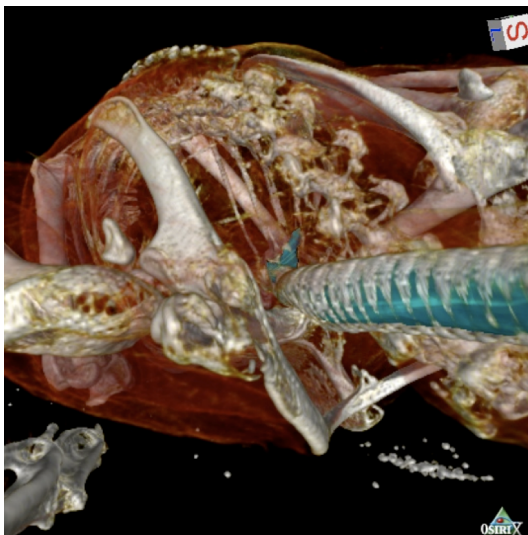
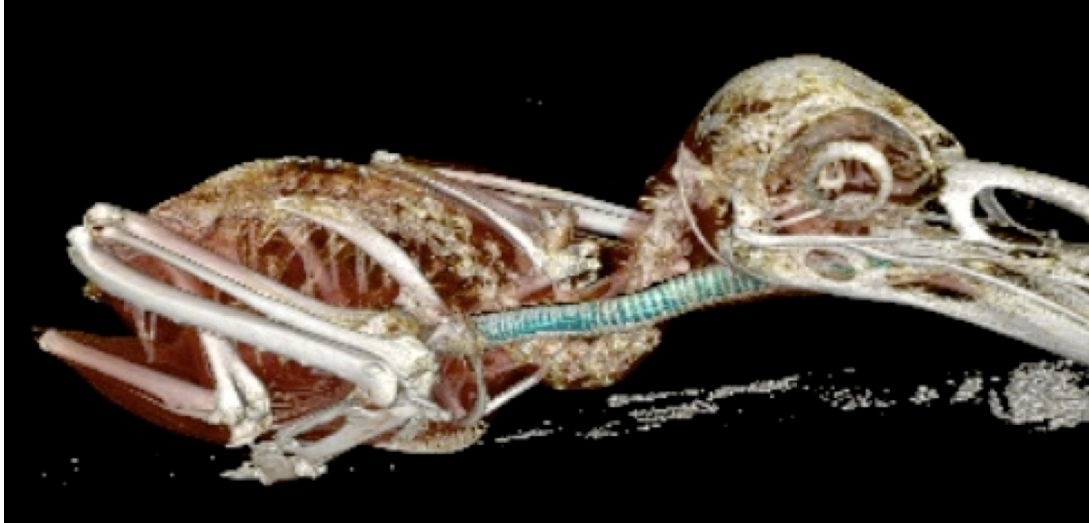
Chapter 1 - Table 3. Pearson Correlations of Vocal Tract length at different weights.

		Weight	beack to tail	2.Primary	3.Primary	1.Toe	4.Toe	1.Toeto3.Toe	Tongue	tongueTOglottis	sinisterSternotrachealis	dexterSternotrachealis
VTL_0g	Pearson Correlation	,608**	,639**	,479*	,650*	,526*	,480*	,568*	,634**	,443	,570*	,615*
	Sig. (2-tailed)	,004	,008	,044	,012	,025	,032	,011	,005	,065	,026	,033
	N		16	18	14	18	20	19	18	18	15	12
VTL_10g	Pearson Correlation	,602*	,698*	,425	,631*	,547*	,619*	,607*	,836**	,614*	,538	,604
	Sig. (2-tailed)	,017	,012	,130	,028	,043	,014	,021	,000	,015	,071	,085
	N	15	12	14	12	14	15	14	15	15	12	9
VTL_20g	Pearson Correlation	,636*	,703*	,410	,613*	,569*	,613*	,595*	,837**	,635*	,543	,602
	Sig. (2-tailed)	,011	,011	,146	,034	,034	,015	,025	,000	,011	,068	,086
	N	15	12	14	12	14	15	14	15	15	12	9
VTL_30g	Pearson Correlation	,644**	,707*	,398	,589*	,588*	,605*	,600*	,839**	,641**	,545	,595
	Sig. (2-tailed)	,010	,010	,158	,044	,027	,017	,023	,000	,010	,067	,091
	N	15	12	14	12	14	15	14	15	15	12	9
VTL_40g	Pearson Correlation	,672**	,698*	,366	,552	,601*	,576*	,583*	,826**	,654**	,520	,575
	Sig. (2-tailed)	,006	,012	,199	,063	,023	,025	,029	,000	,008	,083	,105
	N	15	12	14	12	14	15	14	15	15	12	9
VTL50g	Pearson Correlation	,677**	,684*	,379	,548	,607*	,584*	,596*	,821**	,660**	,510	,549
	Sig. (2-tailed)	,006	,014	,181	,065	,021	,022	,025	,000	,007	,090	,126
	N	15	12	14	12	14	15	14	15	15	12	9

Figures

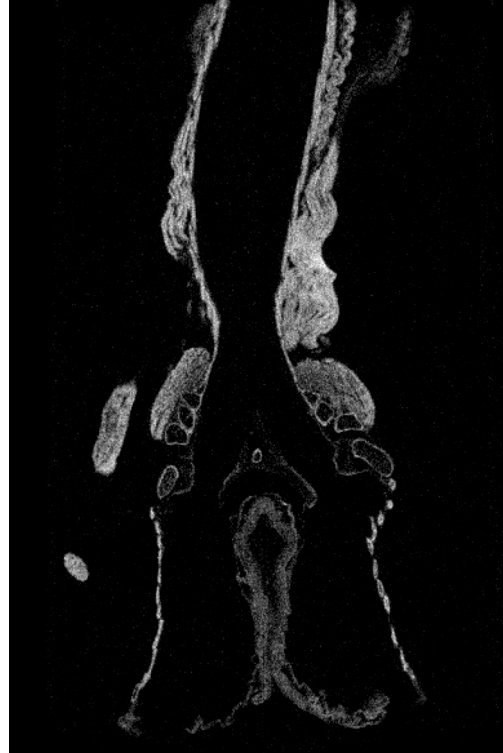
Chapter 1 - Figure 1. CT Scan of an intact raven.

Bones and cartilaginous structures are white and muscles red. Suprasyringeal vocal tract is indicated in green.

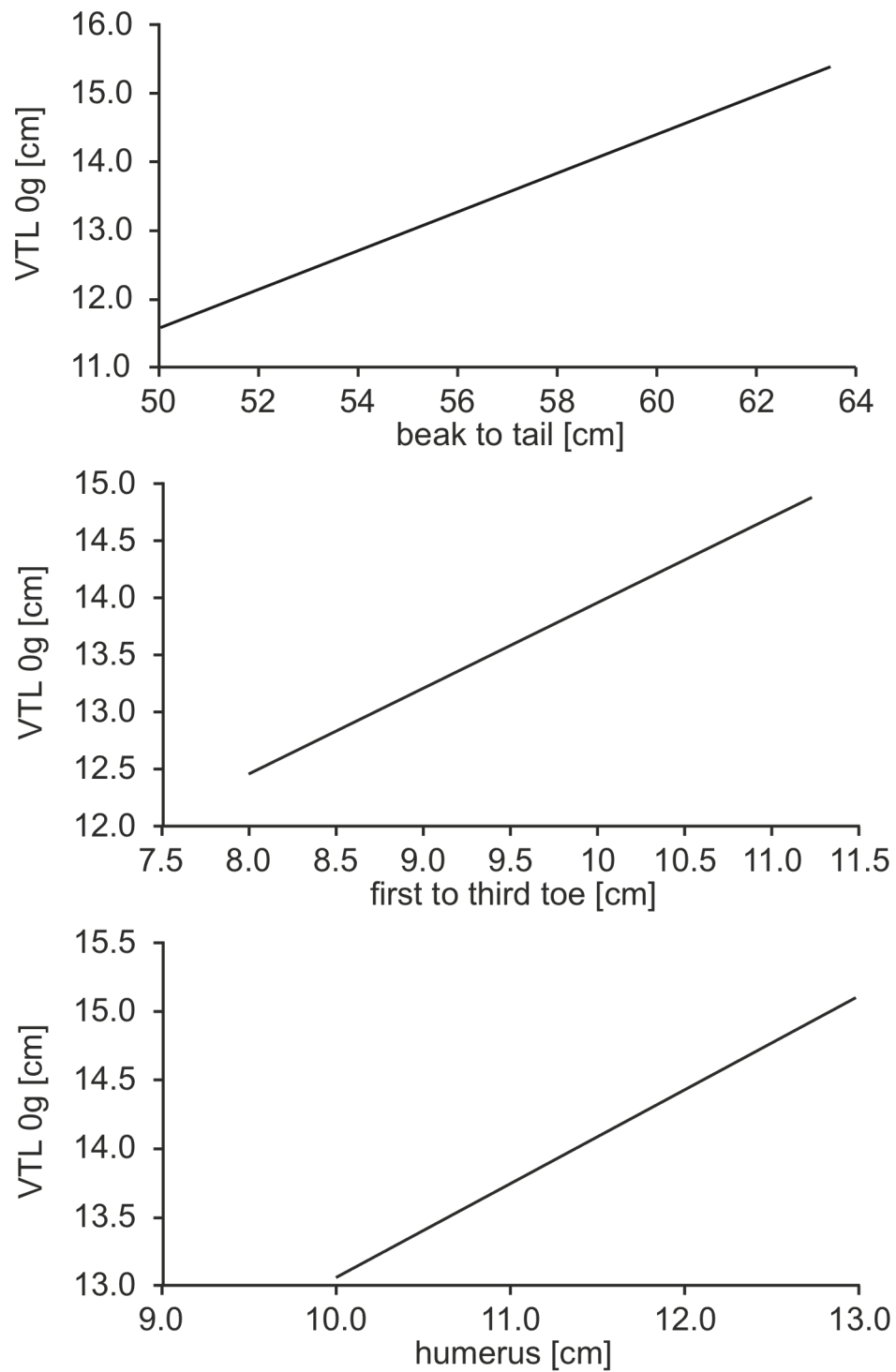


Chapter 1 - Figure 2. Raven Syrinx.

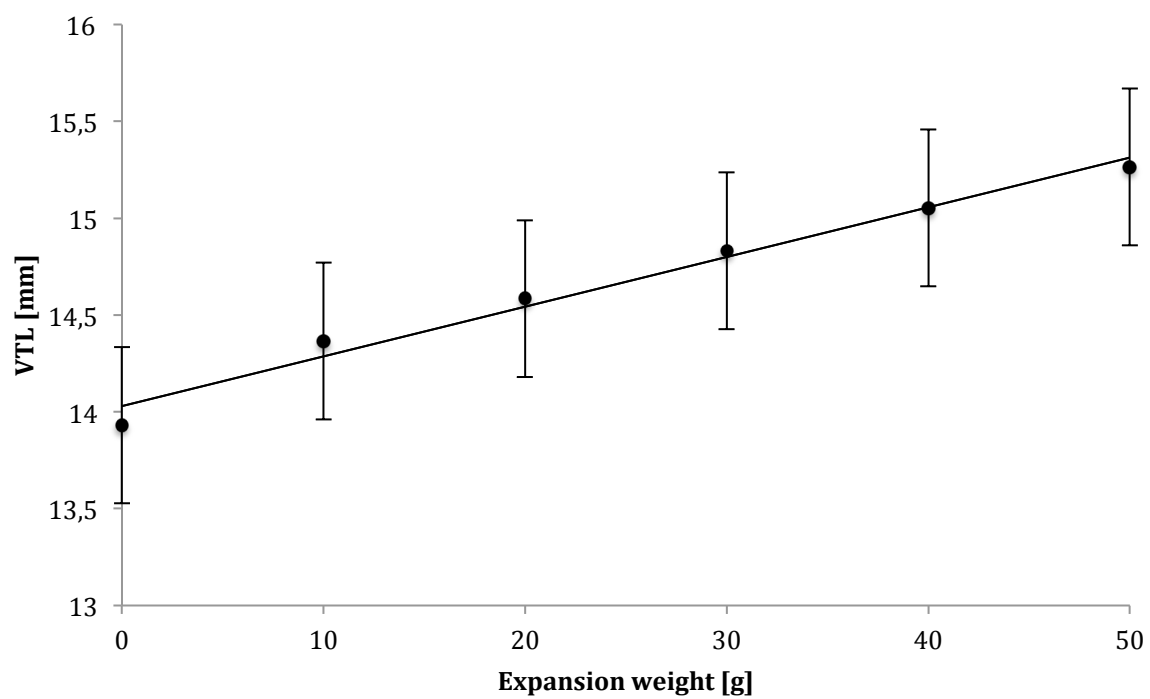
(A) picture of the Syrinx after removal of the Sternum and ribs. (B) Coronal view of a μ CT scan of the syrinx with $80\mu\text{m}^3$ voxel size and Iodine staining conducted with a Viscom X8060 NDT x-ray system (Viscom, Hanover, Germany).



Chapter 1 - Figure 3. Estimated means regression of VTL with the three significant morphometric measurements.



Chapter 1 - Figure 4. Elongation of the excised Vocal Tract with the increase of weight.



Chapter 2:

Indicators of Sender's Sex and Age in Raven Food Calls

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Abstract

Acoustic parameters of animal signals have been shown to correlate with various phenotypic characteristics of the sender. The acoustic characteristics can be learned and categorized and thus are basis for perceivers' recognition abilities. One of the most demanding capacity is individual recognition, achievable only after repeated interactions with the same individual. Still, class level recognition might be potentially important to perceivers who have not previously encountered callers but can classify unknown individuals according to the already learned categories. Especially for species with high fission-fusion dynamics that repeatedly encounter unknown individuals it may be advantageous to have class level recognition. We here want to test whether acoustic parameters of vocalizations emitted by ravens, a species with a high fission-fusion dynamics, are correlated with phenotypic characteristics and thus have the potential for class level recognition. The analysis of 418 food calls revealed that age classes can be correctly classified based on acoustic parameters while sex differentiation cannot be fully proven. Correlations of vocal characteristics and respective sex and age categories suggest class level recognition by the perceiver. Together the results provide evidence for the phenotypic co-variation of raven food calls that can potentially be used by perceivers that are ignorant of the caller's identity.[†]

[†] This abstract or a similar version of it was submitted as conference and workshop applications. In case of acceptance the abstract might be published in the conference booklet and might be found in the internet.

Introduction

The acoustic characteristics of vocalizing animals relate to various attributes of the vocalizer, among others sex (e.g.: Sayigh et al. 1995), age (e.g.: Green 1981), emotional state (e.g.: Morton 1977), dominance rank hierarchy (e.g.: Clark 1993), and reproductive status (e.g.: Pipitone and Gallup Jr 2008). How and which ones of these attributes are obtained by perceivers from acoustic signals has been extensively studied in the last decades (e.g. Bradbury and Vehrencamp 2011).

Based on Fant (1960) and his acoustic theory of speech production, vocal production in humans and mammals (Fitch 1997, Story et al. 1998) and later also in birds (Beckers et al. 2004, Nowicki 1987, Fitch and Kelley 2000, Patterson and Pepperberg 1994) has been considered as a two stage process (source-filter-theory). An acoustic signal is produced by the vibrations of tissue and is filtered by the resonances in the cavities of the vocal tract above the vibrating tissue. Either sound production or subsequent filter mechanism or both in unison have the potential to indicate aspects of the phenotypic attributes of the signaller. In some species vocal features as fundamental frequency, frequency contour, and other source dependent mechanisms provide dependable cues to body size but also to genetic variation and age (Gingras et al. in press, Charlton et al. 2009).

Source related acoustic characteristics in mammals and birds are categorically different because of the differences in producing structures, mammalian vocal folds in the larynx (Fant 1960) and the labia in the bird syrinx (Goller and Larsen 2002). Complexity increases when focusing on the different syrinxes in birds, categorized as tracheal, tracheobronchial or bronchial, dependent on the position of the vocal folds within the trachea-bronchial tube (Rüppell 1933, King 1989). Additionally, birds with bronchial or tracheobronchial vocal folds mostly have paired vocal folds in both bronchi enabling them to vocalize with both vocal fold pairs simultaneously (Goller and Suthers 1995).

Ravens as the largest songbirds have a tracheobronchial syrinx with two pairs of focal folds. Only few studies have focused on vocal production in corvids (Chamberlain et al. 1968, Tsukahara et al. 2006, Tsukahara et al. 2009, Tsukahara et al. 2008, Bock 1978) and species specific vocal production and anatomy of common ravens in particular (Shufeldt 1890) has received little attention. Sex and age dependencies of acoustic signals in ravens might be similar to other bird species (Wallschläger 1980) based on apparent size differences between sexes and age-classes (dos Anjos et al. 2009). Moreover, the acoustic features could be exploited by conspecifics for various forms of decision making, e.g. for joining/avoiding foraging groups. Unlike features that are connected to caller identity (Boeckle et al. 2012), size and age dependent acoustic features might not have to be learned of each single individual as cues to class level recognition (Tibbetts and Dale 2007).

Typical vocalizations of common ravens are food related calls or 'yells', which come in two categorically different versions (Bugnyar and Kotrschal 2001, Heinrich and Marzluff 1991). While short 'who' calls are emitted by dominants when landing close by the food source, long 'haa' calls are produced by subordinates when facing problems in accessing food. 'Haa' calls are individually distinct and might be individually recognizable (Boeckle et al. 2012). However, different age classes differ in their call characteristics (Heinrich and Marzluff 1991, Bugnyar et al. 2001), which points towards size and/or age dependent acoustical features. 'Haa' calls are described to show highly harmonic structures in addition to non-linear phenomena. Resonance frequencies produced by the vocal tract are not possible to measure because of the lacking overlap between fundamental frequency and formant dispersal (Boeckle et al. 2012). Thus any attributes in raven yells that might indicate sex and age are primarily based on source related production mechanisms (i.e. fundamental frequency). We here investigate the dependency of food call characteristics of the common ravens 'haa' call on age classes. We predict that in addition to individual characteristics

ravens sexual dimorphic (Bedrosian et al. 2008) and age differences are detectable in the food related 'haa' call.

Material and Methods

Study Site and Call recording

Between summer 2009 and winter 2010 we recorded food calls of free-ranging common ravens that regularly use the enclosures of the Cumberland Wildpark Grünau for foraging (Drack and Kotrschal 1995). At the time of the study, around 100 birds were individually marked with coloured leg bands and wing tags. From these birds, body measures, weight, sex and age class was known (Braun et al. 2012). Sex was genetically determined from blood samples (Laboklin, Austria). Age classes were identified according to mouth and feather coloration and labelled juvenile (from fledging until end of first year; pink oral cavity), subadult (second and third year of life, until oral cavity has turned black), and adult (> 3 years, black oral cavity; Heinrich and Marzluff 1992, Heinrich 1994).

We recorded calls of individually marked ravens between 0700h and 0900h at the feedings of wild boars *Sus scrofa*. We simultaneously video- and audio-recorded each feeding-session to identify vocalizing individuals (Video-recorder: Canon HF-11 HD; microphone: Sennheizer ME67/K6; solid-state audio-recorder: Marantz PMD-670 with settings: sampling rate = 48 kHz, amplitude resolution = 16 bits) at distances ranging from 3-10 meters. All calls with interfering background noise were removed. Additionally, we removed individuals with less than two calls in the dataset, which provided us with 418 calls of 12 individuals and with 183 calls of 11 individuals when we excluded calls of individuals that were represented in two age classes.

Call Analysis

Acoustic analysis was conducted with PRAAT 5.1.25 (Boersma and Weenik 2011) that automatically logged these variables in an output file. Because of the highly harmonic structure of the call under investigation we mainly used source related acoustic features that are related to the fundamental frequency (F_0). The analysed call parameters are mean F_0 (Mean F_0 ; Hz), maximum F_0 (Max F_0 ; Hz), minimum F_0 (Min F_0 ; Hz), range of F_0 (Range F_0 ; Hz), start F_0 (Start F_0 ; Hz), end F_0 (End F_0 ; Hz), F_0 at the half of call duration (Mid F_0 ; Hz), call duration (s), slope from F_0 start of the call to the F_0 maximum (Slope S-M; Hz/s), slope from the maximum F_0 to the end of the call (Slope M-E; Hz/s), inflex (number of inflections/s), harmonicity (HNR; dB), amplitude range (maximum dB – minimum dB) and sum of variation (sum of all F_0 changes measured/call length; Hz).

Statistical Tests

We calculated a backward-stepwise multinomial logistic regression model (MLR) in order to select the variables differing between predicted classes. Because all parameters deviated from normality (Shapiro Wilk: $W < 0.965$; $p \leq 0.001$) we tested for co-linearities with Spearman correlations for all measured acoustic features. F_0 mean, call duration, slope start max, slope S-M, inflex, hnr mean, jitter, intsumvar, and amplitude modulation were used in the original model (Table 1). We used χ^2 differences in -2 log-likelihoods between the original model and a reduced model at each step to derive at the final model. We calculated MLRs with a reduced dataset where each individual was presented in one age class only to circumvent pseudo-replication. Additionally we calculated multinomial mixed linear regression models (MMLR) where the individual was entered as a random variable to account for repeated measures of the same individual in different age classes. Additionally, in MMLR's we entered for age class and sex categorization the variable that was not entered

as dependent variable as random variables; for sex categorization we used age class as random variable and vice versa. This allows to account for the differences caused by the respective factor and derive with a model that represents classification without influences of the random factor. We used the same variables in MLR and MMLR's in the full model. We used MLR and MMLR's as they are robust against deviations from normality. All statistical tests were analysed using SPSS 19 for Mac.

Results

Mean values of the used call characteristics within age categories are listed in Table 2. No colinearities between acoustic variables were found in the data for the MMLR or the reduced dataset for the MLR ($p < 0.05$).

Age differences

Raven 'haa' calls can be correctly classified according to their age related characteristics, namely mean F_0 , inflex, harmonicity, amplitude modulation, amplitude range, call duration and F_0 slope max-end, whereby amplitude modulation and inflex only show significant influence in MMLR (compare Table 3 and Table 4). Depending on the method used, 88.8 % (MLR) or 91.6 % (MMLR) of raven 'haa' calls were correctly classified. Juvenile calls have been correctly assigned in 87.5 % (MMLR 97.9 %) of the cases, whereby 12.5 % have been wrongly classified as subadult in the MLR and 2.1 % as adult in the MMLR. Subadult calls were correctly classified in 85.4 % (MMLR 60.0 %) whereby 12.2 % (MMLR 36.7 %) have been wrongly categorized as adult calls. Highest classification results are observed in adult calls where 97.6 % (MMLR 92.7 %) have been correctly identified, whereby only 2.4 % (MMLR 7.3 %) have been wrongly classified as subadult calls. When checking for variables responsible for differences in age class we derived at the final model with a MLR

(for stepwise statistics see Table 4) with the remaining variables mean f_0 , amplitude range, harmonicity, slope S-M and call duration. The full mixed model reveals that mean f_0 , slope, harmonicity and amplitude range have significant ($p \leq 0.05$) and inflex a trend on age class differentiation (Table 3). All three age classes differ significantly in intercept and amplitude range (Table 5). Mean F_0 is highest in juvenile yells and lowest in adults while there is only a trend in the differentiation of juvenile and subadult food callers (Table 5). Inflex and slope are important measures for the differentiation between juveniles and subadults and differ between juveniles and adults (Table 5). In the full model harmonicity shows a significant difference between subadults and adults.

Sex differences

For the classification of sex (stepwise statistics see Table 3) we derived the final MLR model including mean F_0 , amplitude range, harmonicity, slope and call duration. Classification of sex with the MLR was 98.8 % whereby the 70.1 % of male calls were classified incorrectly. The classification of the MMLR showed 100 % correct classification for male and female calls, which is based on non-significant effects of the MMLR (Table 3). Still, MLR showed that mentioned acoustic parameters in the final model of MLR are significant (Table 4).

Discussion

We show that ‘haa’ calls, one form of raven yells given at food that is difficult to access, contain phenotypic characteristics in their acoustic parameters. Specifically, age classes can be correctly classified based on acoustic parameters. Additionally indicators for sex differences were found. These results are in line with the possibility of class-level recognition (Tibbetts and Dale 2007), i.e. that naïve ravens listening to food calls may extract information about which age class and, possibly, which sex the callers belong to.

Age differences

While sex related results remain ambiguous, age classification of ‘haa’ calls is highly supported by our data. All acoustic variables apart from amplitude modulation and call duration had significant influence on age classification. We hypothesize that labial flexibility, mass and length, which have been shown to vary with age in mammals (Titze 2000), might change as signallers mature. Structural differences of the vocalizing apparatus in turn determine acoustic features of a vocalization (e.g. Titze 2000). In addition to variations in the vocal organ, maturing of neural structures in a raven might additionally influence acoustic features of calls as shown for birdsong (Zeigler and Marler 2008). These changes may be based on general restructuring of anatomic and neural structures from the juvenile to the subadult stage as well as in changes to sexual maturing from subadulthood to adulthood. Especially the later change might depend on hormonal changes, which has been shown to occur with testosterone induced HVC-growth in females (Nottebohm 1980).

Mean F_0 has age class dependent differences, whereby juveniles show the highest F_0 and adults the lowest. The differences in fundamental frequency can be size dependent as it might be possible that after fledging and gaining weight, developmental changes of internal

structures like ossification of tracheal and syringeal cartilaginous rings take place, and thus can cause post fledging syringeal size dependent changes in F_0 (Appel 1929). Additionally callers developmental stages of neural structures might correlate with our classification in age classes and thus might result in differences in F_0 of yells, like increases of the higher vocal centre (HVC) after sexual maturing can occur (Nottebohm et al. 1986).

Raven yells differ in their slope between juveniles and both other classes while subadult and adults do not differ. These changes might relate to abilities of call production. Older birds have better abilities of call structure manipulation based on better developed HVC. Similarly, inflex does not differ between subadults and adults but juveniles are different compared to both other classes. Again a possible explanation could be better vocal versatility gained over age.

Highest amplitude ranges are found in juvenile ravens and shows a negative correlation with age. Furthermore deterministic chaos, which can be measured for instance by harmonicity of a call, is important in the acoustic communication of animals (Fitch et al. 2002, Suthers et al. 2011) as it can encode urgency or motivation. Baby cries and monkey alarm calls are often changed depending on the urgency of the situation and might be perceived by listening individuals (Stoeger et al. 2012). Hand in hand with maturing we expect decrease of urgency related features in yells that also might relate with the motivation of the caller (Morton 1977). In congruence with this motivation-structural rules, food calls are hypothesized to develop from begging calls (Heinrich and Marzluff 1991). Intra-individual variation of chaotic features of raven yells might additionally correlate with the urgency or motivation i.e. hunger level of the caller.

Sex differences

MLR results show that there are significant differences in sexes based on mean F_0 , amplitude range, harmonicity, slope and call duration. Differences in mean F_0 might be based on syringeal structures and hormonal differences causing faster vibrations of labiae and thus higher fundamental frequencies (Larsen and Goller 2002, Goller and Larsen 2002, Elemans et al. 2008a, Elemans et al. 2008b). Size related differences have been reported for jungle crows (Tsukahara et al. 2006) and other species (Miller et al. 2008), while to our knowledge none such differences are reported in the literature for ravens. However, gross body mass and size differences (dos Anjos et al. 2009) might correlate with differences in syringeal structures and cause sexually dimorphic acoustic features of raven calls. Though it has been discussed that based on small effect sizes F_0 differences have low reliability as indicators for body size in birds (Patel et al. 2010). Hence, F_0 variances might not be good indicators for the sex of the food-calling raven when sex differences are merely based on size dependent differences in syringeal anatomy. The lower predictability in comparison to age classes is also shown in results of the MMLR that lacks significant influence of any entered variable. Thus based on our female biased sample, differences in male and female yells cannot be supported fully. Generally we observed less male food callers in the wild (Szipl G. unpublished data) leaving us with a rather low sample size of males and their calls.

Similarly, differences in hormone levels of male and female birds can change calling behaviour (Wada 1982) and neural song control regions (DeVoogd 1986), while to our knowledge no hormonal caused change of vibrations of labia has so far been described for birds though is found in mammals (Abitbol et al. 1999). Especially bird species with monomorphic singing and calling behaviour are less studied (Jawor and MacDougall-Shackleton 2008) in their differences in HVC structures. Still, seasonal changes and sexually dimorphic neural structures might cause sexually dimorphic calls in ravens, which has to be studied in more detail.

Possible functions

Transmitting cues about the age of the vocalizer might be beneficial for receivers and senders of raven yells. Perceivers might be able to assess signal reliability based on age as previous studies indicate that the emission of yells is more context specific and reliable in older individuals (Bugnyar et al. 2001). The ability of perceivers to selectively respond more to specific classes has been reported for instance in alarm calls of marmots (*Marmota flaviventris*) where juvenile calls are more attended to (Blumstein and Daniel 2004), and in vervet monkeys (*Cercopithecus aethiops*) where reliability of the signaller was learned in a playback study (Cheney and Seyfarth 1988). On the other hand juvenile senders of food calls might profit from indicating their age to unknown individuals. As juvenile food calls (also termed 'chii calls') are supposed to derive from begging calls (Heinrich and Marzluff 1991) they may indicate the hunger level of offspring to still caring parents (Heinrich and Marzluff 1991). Thus perceivers of such calls might take into account that parent ravens could be in the vicinity and defend their young. Dominant adults have been documented to actively inhibit food calling of younger birds (Heinrich and Marzluff 1991).

Perceivers that are familiar with the calling individuals might not have to rely on the acoustic differences between age and sex categories in their food calls. Based on their previous experience with the signalling individual, ravens do classify callers along several domains, including sex, kin and affiliation status (Boeckle et al. 2012, Boeckle and Bugnyar 2012). While features determining class membership might be learned like in 'true' individual recognition (Tibbetts and Dale 2007) classifications of unknown individuals might be possible. Thus, as soon as these categories are formed perceivers that are ignorant about the identity of raven calls would be dependent on call characteristics for classification according to sex and age. In this respect it is worth to reiterate that, compared to females, males tend to show low rates of food calls (Szipl G. et al. unpublished data). This may indicate that giving food calls is most important for females and evolutionary pressures may

work towards individual classification rather than sex categorisation of the signaller. Furthermore, dominant callers may use another food related call ('who'; Bugnyar et al. 2001). This call type might indicate different phenotypic information than the here presented 'haa'.

Taken together, we herewith show that analysing vocal production helps to understand and determine acoustic signals and their possible functions. While differences in the production mechanisms exist between mammals and birds, the relation between anatomical features of the production mechanisms and the acoustic features of the signal seem to be similar. Circumstantiality of the acoustic production still has to be investigated in more detail, especially in birds that show a variation in the anatomical and neural basis of vocal production.

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Tables

Chapter 2 - Table 1. Spearman-Rho Correlationcoefficient of reduced dataset.

	f0_mean	am	rangeAMP	hnr_mean	slopeMaxEnd	f0_call_length	inflex
f0_mean	1	0.075	-0.098	-0.091	-0.069	0.451	-0.205
am	0.075	1	-0.037	-0.086	-0.019	0.117	0.043
rangeAMP	-0.098	-0.037	1	0.233	-0.214	-0.109	-0.089
hnr_mean	-0.091	-0.086	0.233	1	-0.306	-0.329	-0.267
slopeMaxEnd	-0.069	-0.019	-0.214	-0.306	1	0.159	0.254
f0_call_length	0.451	0.117	-0.109	-0.329	0.159	1	-0.173
inflex	0.205	0.043	-0.089	-0.267	0.254	-0.173	1

Chapter 2 - Table 2. Mean acoustic values used in the full model.

	Mean $\pm$ SE					
	Juvenile (N=49;3)		Subadult (N=164;7)		Adult (N=205;7)	
f0_mean	757.430 $\pm$	13.804	685.767 $\pm$	6.536	642.192 $\pm$	3.150
slopeMaxEnd	-1732.230 $\pm$	196.715	-1309.496 $\pm$	62.227	-1624.730 $\pm$	49.202
inflex	11.288 $\pm$	0.987	10.247 $\pm$	0.543	9.475 $\pm$	0.393
hnr_mean	11.659 $\pm$	0.813	14.229 $\pm$	0.257	16.236 $\pm$	0.193
am	31.792 $\pm$	1.306	37.858 $\pm$	1.642	30.909 $\pm$	0.752
rangeAMP	9.413 $\pm$	0.497	9.018 $\pm$	0.376	8.750 $\pm$	0.216
f0_call_length	0.292 $\pm$	0.013	0.218 $\pm$	0.003	0.201 $\pm$	0.002

Calls are analyzed from 12 individuals represented in 418 calls. Five individuals were recorded in two age classes.

Chapter 2 - Table 3. Fixed effects of full multinomial mixed effects logistic regression model with age class or sex as multinomial classifier.

Predictor	Fixed effects	F	Df	P
age	Corrected model	4.528	14; 401	≤ 0.001
	f0_mean	5.194	2; 401	0.006
	f0_call_length	0.352	2; 401	0.703
	slopeMaxEnd	5.671	2; 401	0.004
	inflex	2.712	2; 401	0.068
	hnr_mean	8.271	2; 401	≤ 0.001
	am	0.676	2; 401	0.509
	rangeAMP	23.655	2; 401	≤ 0.001
sex	Corrected model	0.231	7; 409	0.978
	f0_mean	0.074	1; 409	0.785
	f0_call_length	0.132	1; 409	0.717
	slopeMaxEnd	0.159	1; 409	0.690
	inflex	0.284	1; 409	0.594
	hnr_mean	0.776	1; 409	0.379
	am	0	1; 409	0.985
	rangeAMP	0.432	1; 409	0.511

Chapter 2 - Table 4. Backward-stepwise multinomial regression statistics for the classification of age-class and sex of reduced dataset.

Factor	Variable	AIC	BIC	-2 Log-Likelihood	Chi-Quadrat	df	p
Age class	Intercept	205.078	237.389	185.078	78.372	2	0.000
	f0_mean	234.440	266.751	214.440	107.734	2	0.000
	rangeAMP	175.864	208.175	155.864	49.158	2	0.000
	hnr_mean	153.014	185.325	133.014	26.308	2	0.000
	slopeMaxEnd	137.947	170.258	117.947	11.241	2	0.004
	f0_call_length	152.668	184.979	132.668	25.962	2	0.000
Sex	Intercept	205.078	237.389	185.078	78.372	2	0.000
	f0_mean	234.440	266.751	214.440	107.734	2	0.000
	rangeAMP	175.864	208.175	155.864	49.158	2	0.000
	hnr_mean	153.014	185.325	133.014	26.308	2	0.000
	slopeMaxEnd	137.947	170.258	117.947	11.241	2	0.004
	f0_call_length	152.668	184.979	132.668	25.962	2	0.000

AIC, BIC, -2 Log-Likelihood of the final model. Chi2 statistics is based on differences between full and final model.

Chapter 2 - Table 5. Pairwise comparison of full multinomial mixed effects logistic regression model with age class as multinomial classifier.

	Term (Reference level)	Estimate	SE	t	P-Value
Intercept	Juvenile (adult)	-43.057	11.327	-3.801	≤0.001
	Subadult (adult)	-11.426	5.658	-2.019	0.044
	Subadult (juvenile)	24.246	7.820	3.100	0.002
f0_mean	Juvenile (adult)	0.038	0.012	3.198	≤0.001
	Subadult (adult)	0.022	0.009	2.526	0.012
	Subadult (juvenile)	-0.031	0.008	-1.768	0.078
f0_call_length	Juvenile (adult)	-10.777	19.682	-0.548	0.584
	Subadult (adult)	-9.011	10.873	-0.829	0.408
	Subadult (juvenile)	-4.311	14.165	-0.304	0.761
slopeMaxEnd	Juvenile (adult)	-0.003	0.001	-3.339	≤0.001
	Subadult (adult)	0	0	-0.882	0.378
	Subadult (juvenile)	0.002	0.001	3.220	≤0.001
infelx	Juvenile (adult)	0.241	0.104	2.314	0.021
	Subadult (adult)	0.024	0.040	0.594	0.553
	Subadult (juvenile)	-0.157	0.077	-2.040	0.042
hnr_mean	Juvenile (adult)	-0.057	0.237	-0.240	0.810
	Subadult (adult)	-0.425	0.115	-3.706	≤0.001
	Subadult (juvenile)	-0.229	0.169	-0.1357	0.175
am	Juvenile (adult)	-0.038	0.042	-0.913	0.362
	Subadult (adult)	-0.026	0.024	-1.101	0.271
	Subadult (juvenile)	0.014	0.031	0.455	0.649
rangeAMP	Juvenile (adult)	0.981	0.178	5.506	≤0.001
	Subadult (adult)	0.551	0.088	6.272	≤0.001
	Subadult (juvenile)	-0.322	0.122	-2.638	0.009

Chapter 3:

Who wants food? Individual characteristics in raven yells

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Abstract

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

Keywords: *Corvus corax*, food call, functionally referential signal, individual recognition, playback, raven

[‡] This abstract or a similar version of it was submitted as conference and workshop applications. In case of acceptance the abstract might be published in the conference booklet and might be found in the internet.

Introduction

Animal calls are complex acoustic signals and often carry a variety of characteristics about the sender simultaneously (Blumstein & Munos 2005; Nelson & Poesel 2007; Charlton et al. 2009). Besides sex, age and social class, individual identity can also be transmitted (Tibbetts & Dale 2007). Recognizing individuals based on distinctive call characteristics should be highly advantageous for species with repeated and complex social interactions (Cheney & Seyfarth 1980). One index of social complexity, social group size (Dunbar & Shultz 2007), constrains individual discrimination as there should be a negative correlation between group size and simplicity of individual discrimination. Simply designed signals contain fewer features to enable discrimination, and complex signals offer the possibility of more distinct patterns. Thus the difficulty of differentiating between specific individuals in large groups can be compensated for by producing complex signals that increase individual information and variability (Pollard & Blumstein 2011).

A certain class of vocal signals, commonly denoted as functionally referential signals (Macedonia & Evans 1993; Evans et al. 1997), has been proposed to transmit not only characteristics about a sender's physical characteristics or motivational status, but also 'information' about objects in the environment (Marler et al. 1992). By referring to external objects such as predators or food these signals elicit receivers' corresponding behavioural responses as if directly responding to the external cue (Seyfarth et al. 1980; Evans & Evans 2007). In the case of food calls, which have been described for many primates (reviewed in Slocombe & Zuberbühler 2006; Clay & Zuberbühler 2009) and birds (e.g. Evans 1982; Soma & Hasegawa 2003; Mahurin & Freeberg 2008), conspecifics are usually attracted to the site where the calling individual is feeding. Considering the disadvantages of increased competition, the benefits of food calls range from reduced vigilance (Elgar 1986) and increased foraging efficiency (Brown et al. 1991) to accessing resources defended by others

and/or defending resources from other species (Bugnyar et al. 2001; Slocombe & Zuberbühler 2006; Clay & Zuberbühler 2009). Although individual recognition is not necessary to recruit conspecifics to foraging sites, listeners may profit by using information they gain from discriminating between callers. Specifically, assessing information about the sender's reliability of signalling the location and/or quality of food (Bugnyar & Kotrschal 2001; Bugnyar et al. 2001) and its relative rank to the listener as well as the identity and hierarchy of individuals associated with the caller could increase the fitness of listeners. Little is known about individual information in food calls. In birds specifically, caller discrimination and individual recognition have mainly been tested in social contexts such as neighbour and kin discrimination (Beer et al. 1970; Beecher 1989; Wanker et al. 2005; Tibbetts & Dale 2007) but to our knowledge not in referential signals.

Common ravens show advanced cognitive skills during foraging (Bugnyar & Kotrschal 2002b; Heinrich 2011) and conflict management (e.g. Fraser & Bugnyar 2011), indicating the capability of dealing with complex social environments and repeated interactions based on individual recognition. In experiments, they are able to differentiate between ignorant and knowledgeable conspecific competitors (Bugnyar & Heinrich 2005; Bugnyar 2011) as well as human experimenters (Bugnyar et al. 2007). Furthermore, ravens utilize a large set of calls and display individually distinctive call repertoires (Enggist-Dueblin & Pfister 2002). However, to our knowledge, it has been suggested (Heinrich & Marzluff 1991) but not yet proven that ravens have individually distinct call characteristics within one call type. This is surprising because one of the most characteristic features of young, nonbreeding ravens is the recruitment to food, which at short distance works via calls (Heinrich & Marzluff 1991). Raven food calls or 'yells' come in two types (Heinrich 1988; Heinrich & Marzluff 1991), a long version ('haa') is given when subordinate birds face defended and/or potentially dangerous food sources, whereas a short version ('who') is given by dominants when landing at the food (Heinrich & Marzluff 1991; Bugnyar & Kotrschal 2001; Bugnyar et al. 2001). This specific usage of calls suggests different meanings, with 'haa' having the potential to serve as

functionally referential signals (Bugnyar et al. 2001). Senders may benefit by attracting others as it increases the chance to overpower the food defence of a few dominant individuals or dangerous predators (Marzluff & Heinrich 1991); moreover, it offers the chance to kleptoparasitize those that have already secured a food item and/or pilfer the others' food caches (Bugnyar & Kotrschal 2002a, b). Receivers may learn about the location of feeding opportunities (Heinrich & Marzluff 1991) and, by distinguishing between callers, may be able to predict the likelihood of competition and the need for cooperation by particular individuals, respectively. Knowing who is calling may thus help ravens in their decision in whether or not to join a feeding crowd. Territorial ravens, on the other hand, are interested in keeping nonbreeders away from their food sources and aggressively prevent young birds from giving 'haa' calls (Heinrich & Marzluff 1991). Being able to tell individuals apart on the basis of their calls may enable them to coordinate their food defence.

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

Methods

Food Call Analysis

Food calls ('haa') were recorded from wild, free-ranging ravens between summer and winter 2010 in the Cumberland Wildpark in Grünau (47°48'N, 13°57'E) while they were

foraging at the enclosure of wild boars, *Sus scrofa*. Boars are usually fed between 0700 and 0900 hours and are joined by 20–120 ravens, most of which are members of a highly dynamic nonbreeder flock (Braun et al. 2012). At the time of the study, approximately 100 individuals of the flock had been marked individually. In the course of marking, the birds' body weight was measured and age class assigned from morphological characteristics (juvenile, subadult, adult), notably the colour of eyes and inner beak (Heinrich & Marzluff 1992).

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

Acoustic analysis was conducted with PRAAT 5.1.25 (Boersma & Weenik 2011). Analysed call parameters were mean fundamental frequency (mean F0; Hz) based on a forward cross-correlation method (settings: time step = 0.01 s; expected F0 frequency range = 300–950 Hz; maximum number of candidates = 15; silence threshold = 0.03; voicing threshold = 0.65; octave cost = 0.01, octave-jump cost = 0.35; voiced/unvoiced cost = 0.14), slope from the maximum F0 to the end of the call (Slope M-E; Hz/s), number of inflections/s, harmonicity (dB) representing the relative energy of the signal lying in the harmonic part of the sound in relation to the energy of the noise (harmonicity = $10 \times \log (\% \text{ of energy periodic part} / \% \text{ of energy in the noise})$, Boersma 1993), amplitude modulation (Hz), dB range (maximum dB–minimum dB) and sum of variation (the sum of all F0 changes measured/call

length; Hz) where the sum of F0 change is the cumulated variation of F0 over the total duration of the call (Reby & McComb 2003). For F0 analysis we manually excluded parts of the recordings from the analysis, which PRAAT tracked because of background noise such as wild boar grunts. The retrieved F0 track was lowpass filtered with a cutoff frequency of 25 Hz in order to track only large changes of F0 and excluding small fluctuations.

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

have valid maximum likelihood estimates (Allison 2008). We present the full model with quasicomplete separation as it tests for effects of factors while controlling for other predictor variables (Allison 2008).

Playback Experiment

An average of nine samples of six individuals with little background noise and no distracting or interfering sounds of the previously analysed food calls were selected and used for playback experiments. Eighteen captive individuals housed in male–female pairs at different zoos, game parks and private owners (Table 2) were presented with calls of ravens unfamiliar to the focal individual in a habituation–dishabituation design. Each raven pair was presented with two playback experiments, one in the morning and one in the afternoon, consisting of stimuli matched for sex and age with the focal individual. Before the presentation of habituation stimuli a 15 min baseline was conducted followed by a presentation of three interspecies stimuli common to all focal individuals (a goose or a rooster) with a 1 min interval to test for the ravens' ability to differentiate between inter- and intraspecific acoustic stimuli playbacks. After the 1 min intermission time, five food calls of one individual were presented. After a further 1 min intermission interval, again five food calls were presented. The five samples were randomly chosen from a set of calls of the same individual (range 8–20) and randomly sorted within one presentation. We repeated the procedure of 1 min interval and five calls until habituation was reached. Habituation criterion was defined as three consecutive call responses being under half the maximum number of calls of the first three presentations or by a decreased behavioural response (see below; for a schematic of the protocol see Fig. 1). Once the focal individual reached the habituation criterion, the dishabituation stimulus was presented. Dishabituation stimuli varied between conditions in order to test for the influence of playback location on response levels: condition 1: habituation and dishabituation stimuli were presented from two individuals at the same

location; condition 2: stimuli of the same individual were played from differing locations; condition 3: both location and individual were altered from habituation to dishabituation.

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

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

To reduce data dimensionality of response variables, a principal component analysis (PCA) was calculated using numbers of long-distance calls, soft calls and self-aggrandizing displays, behavioural responses and highest behavioural response category. A varimax-rotated correlation method was used and a minimum eigenvalue of 1.0 was set for components to be extracted. Differences between reactions to the different stimuli categories were calculated with a GLMM. To correct for differences between playback individuals and for the presentation order a nested term was included (focal individual(session(call))). Phases of the experiment were divided into baseline before, interspecific playback (including three presentations), first habituation phase (including two presentations of five food calls), second

habituation phase (all presentations except the first two and the last two), third habituation phase (last two habituation presentations). After the final playback, the dishabituation stimulus (one presentation) and a baseline after the playback consisting of 15 min of data collection, the experiment was finished. The original and full model included sex, condition, phase time of day and an interaction between sex and sex of the played-back individual as fixed factors. The interaction between sex of the focal and sex of the played-back individual was used to detect differences between intrasex or intersex responses. Responses of both individuals in the pair were used as a response variable within the GLMM in order to be able to calculate differences between responses to intersex and intrasex stimuli. We used least-square mean differences for post hoc tests without Bonferroni correction of *P* values in order to make the test less conservative (Nakagawa 2004). We tested for differences between conditions with a Kruskal–Wallis test with the differences between the last habituation stimulus and dishabituation. All statistical analyses were conducted using IBM SPSS for Mac 19 (SPSS Inc., Chicago, IL, U.S.A.).

Ethical Note

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

indication that the catching and marking procedure has any negative effects on the birds' behaviour. Already in the first few days after catching, they can be observed from a close distance by humans and about half of the banded birds revisit the trap.

Results

Call characteristics

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

Playback Experiment

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

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

Discussion

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

Call characteristics

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

Owren et al. 1997; Rendall 2003; *Cervus elaphus*: Reby et al. 2006); in birds, only a few studies have concentrated on individuality including formants and formant dispersal (Suthers 1994).

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

Utilizing individual information

Captive territorial ravens were able to differentiate between two unknown individuals, when calls were matched for sex and age in the habituation–dishabituation experiment, which suggests that their discrimination abilities are based on individual call characteristics. An alternative possibility would be that the distinction is based on regional dialects. We consider this explanation to be highly unlikely since all of our playback stimuli used in this study were recorded from one population of free-flying ravens at the same location in Austria. Moreover, we only tested birds with playbacks that were kept at a large distance to this site and hence never had vocal contact with the stimulus birds. Importantly, males and females were able to differentiate/be differentiated, suggesting that sex differences did not play a role. Furthermore, playback location did not have an influence on differentiation abilities.

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

As scavengers, ravens rely on scarce and ephemeral food sources that are heavily competed for (Heinrich & Pepper 1998). Particularly during winter, carcasses and kills are

highly defended by dominant territorial breeders, making it difficult for individual birds to access the food. As a consequence, they start yelling (Marzluff & Heinrich 1991). By testing adult captive pairs, we simulated such a ‘territorial’ intrusion by hungry nonbreeders. This helped us to assess responses to different individuals by increased territorial behaviour of our focal subjects. Most likely, individuals of a nonbreeder flock would respond to our playbacks with increased attraction to the feeding site. Perceiving calls from different individuals as being different could be advantageous in either context: territorial ravens could make use of this information for coordinating their food defence; nonbreeding ravens might use it for deciding whether or not to join a foraging group. Based on our acoustic analysis we may even speculate that ravens could also learn to identify particular individuals on the basis of their calls. This would require that there is variation in the reliability of individuals’ calling in response to (different degrees of) food competition and/or food quality, for example some birds only yell when the food is heavily defended and/or of high quality whereas others yell at almost any time. Preliminary findings support this assumption (Marzluff & Heinrich 1991). In the visual domain, ravens routinely take individual characteristics into account to judge the competitiveness of conspecifics for hidden food (Heinrich & Pepper 1998; Bugnyar & Heinrich 2006; Bugnyar et al. 2007) and even heterospecifics such as human experimenters for access to objects (Bugnyar et al. 2007). It still needs to be shown that foraging ravens also make use of individual characteristics in the auditory domain. Given the relatively high degree of fission–fusion dynamics found in nonbreeding raven groups (Braun et al. 2012), questions such as how long it may take birds to assign specific call characteristics to individuals and which conditions promote this form of learning are promising topics for future studies.

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Tables

Chapter 3 - Table 1. Name, age class and sex of recorded wild ravens

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

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

Chapter 3 - Table 2. Name, age class, sex and location of housing of captive ravens.

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

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

Chapter 3 - Table 3. Call parameters

	Mean	SD	K-W χ^2	K-W P	Wilks's λ	$F_{10,197}$	P
Mean F0	655.7	69.9	143.0	< 0.001	.263	55.2	< 0.001
Slope Max F0–End	-1410.9	863.9	101.8	< 0.001	.620	12.1	< 0.001
Number of inflections/s	11.0	6.5	31.5	< 0.001	.900	2.2	0.019
Harmonicity	14.4	4.0	132.0	< 0.001	.370	33.5	< 0.001
Amplitude modulation	34.6	17.2	27.7	0.002	.889	2.5	0.008
dB range	8.3	3.4	52.0	< 0.001	.719	7.7	< 0.001
Sum of variation	88.5	30.6	83.9	< 0.001	.651	10.6	< 0.001

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

Chapter 3 - Table 4. DFA structure matrix

	Discriminant function				
	1	2	3	4	5
Mean F0	0.879	0.197	0.117	-0.416	-0.042
Harmonicity	-0.194	0.755	-0.353	0.025	0.516
Amplitude modulation	0.056	-0.233	-0.038	-0.182	-0.052
Number of inflections/s	0.085	0.070	0.241	-0.007	0.236
Sum of variation	0.175	0.213	0.372	.886	-0.019
dB range	0.114	0.114	-0.419	.787	0.423
Slope Max F0–End	-0.104	-0.338	0.589	-0.201	0.698

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

Chapter 3 - Table 5. Confusion matrix

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

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

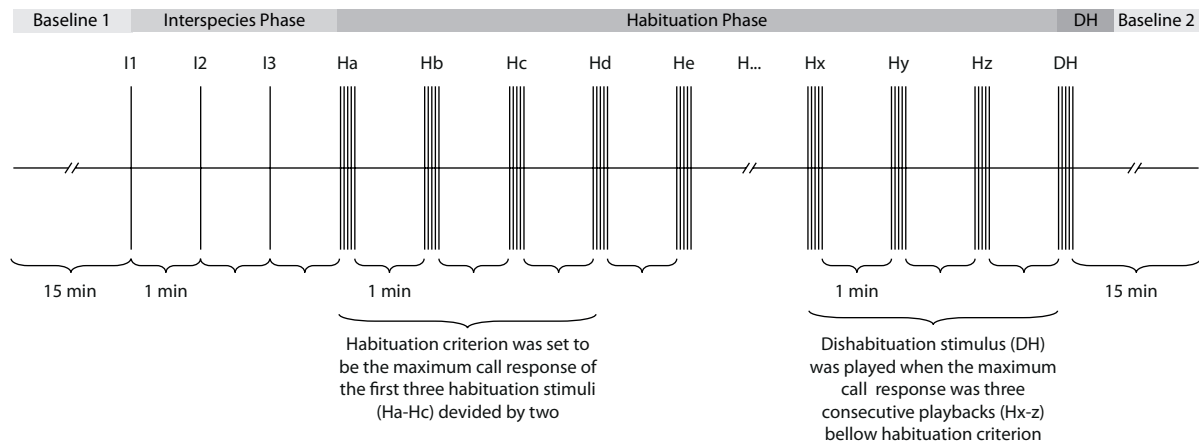
Chapter 3 - Table 6. Component matrix for the playback experiment

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

Figures

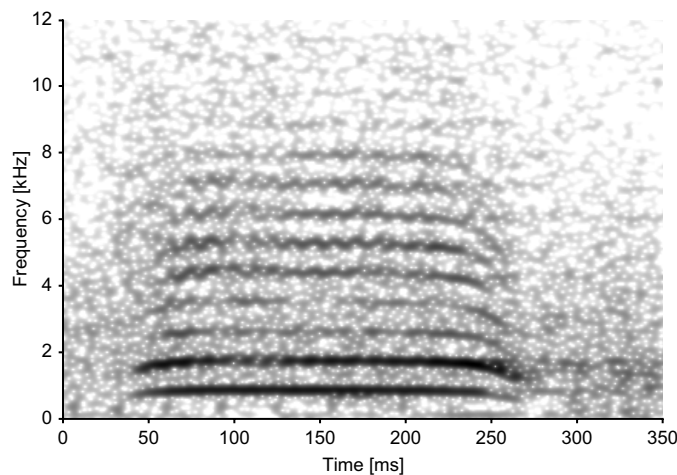
Chapter 3 - Figure 1. Schematic of the experimental procedure.

Playback protocol started with a 15 min Baseline (Baseline 1) followed by interspecies stimuli (I1–I3) and respective 1 min intermission intervals. The habituation phase (Ha–Hz) lasted until the habituation criterion was reached, which could require different amounts of habituation stimuli (H...). After the response of the focal individual was three times below the habituation criterion the dishabituation stimulus (DH) was played followed by a 15 min baseline (Baseline 2).



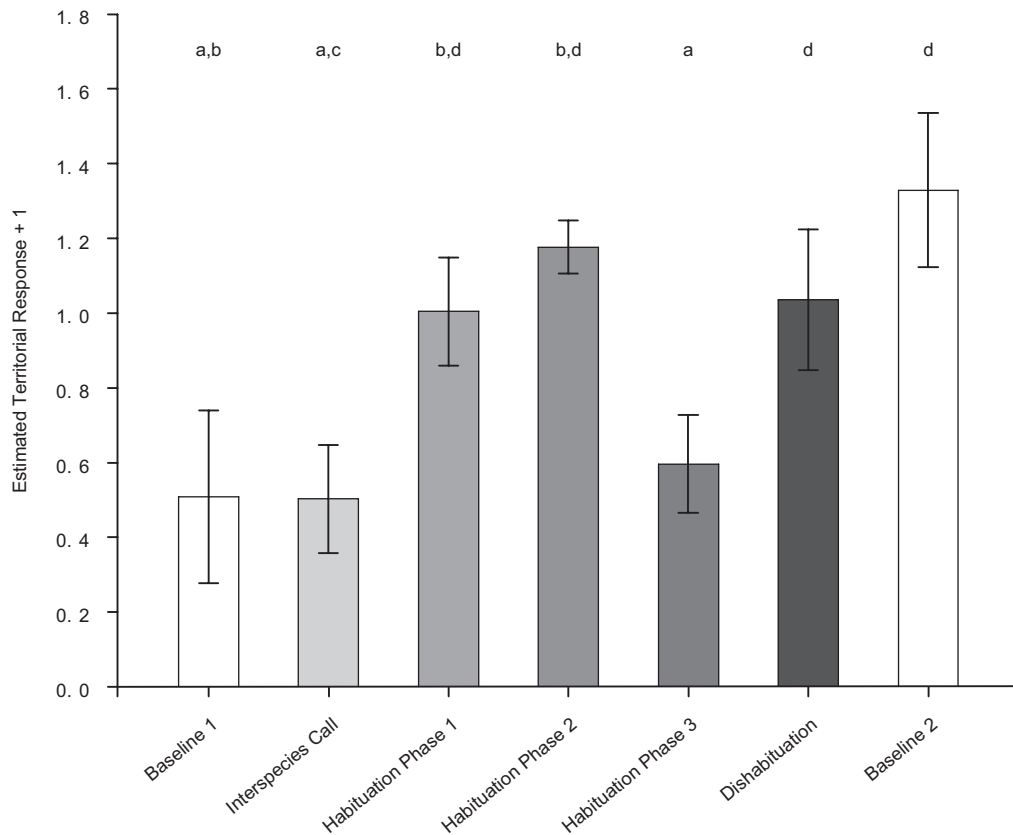
Chapter 3 - Figure 2. Spectrogram of a food call of a common raven

(FFT method, window length = 0.01, time step = 700, frequency step = 250, Gaussian shape).



Chapter 3 - Figure 3. Estimated territorial response $\pm$ SE during the phases of the playback experiment.

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



Chapter 4:

Ravens discriminate long distance calls of unknown individuals in a habituation-dishabituation experiment

Running title: Ravens discriminate long distance calls of unknown individuals

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Abstract

Individual recognition (IR) is considered as prerequisite for many forms of social knowledge. In birds, IR has been tested mainly in the auditory domain for neighbor and kin-discrimination. Common ravens show advanced skills during foraging and conflict management, suggesting that they are capable of dealing with conspecifics on an individual basis. Furthermore, ravens flexibly utilize a large set of calls and show individually distinctive call repertoires. We here examined if ravens are capable of differentiating individuals through distinct call parameters. We tested 16 male and 16 female ravens, kept pair-wise in their home aviaries, with playbacks of long distance calls using a habituation-dishabituation design. Calls of an unfamiliar adult bird were played back repeatedly until responses to calls had reached a previously determined baseline level. After habituation, one of three conditions was presented in the dishabituation phase: (a) the same call-type of a different individual projected from the same location; (b) the same call-type of the same individual from a different location; (c) or changed location and individual. Results suggest that ravens can differentiate individuals by their calls, but their responses are also affected by the location of call presentation. We herewith show that ravens differentiate between unknown individuals and suggest that ravens might be capable of individual recognition.[§]

[§] This abstract or a similar version of it was submitted as conference and workshop applications. In case of acceptance the abstract might be published in the conference booklet and might be found in the internet.

Introduction

Social life has been proposed as one of the main driving forces for brain evolution (Jolly 1966; Humphrey 1976; Dunbar 1992). Notably, groups structured by different types of relationships (Barnard & Burk 1979; Karavanich & Atema 1998; Dugatkin & Earley 2004; Tibbetts & Dale 2007; Izawa & Watanabe 2008) and/or different degrees of fission-fusion dynamics (Aureli et al. 2008) require individuals to deal with various individuals repeatedly, often on a day to day basis. In such iterated encounters, it should be advantageous when the identity of individuals as well as the outcome of previous interactions are memorized (Trivers 1971). One of the outcomes of repeated interactions, and a cognitive prerequisite for many forms of social maneuvers, may be individual differentiation and/or recognition (IR) (Tibbetts & Dale 2007; Steiger & Müller 2008; Tibbetts et al. 2008).

Individual recognition is the perceiver's ability to identify an individual by previously learned signal characteristics (Tibbetts & Dale 2007). Individual recognition has been documented in various domains and vertebrate and invertebrate species e.g. olfactory IR in ants (*Pachycondyla villosa*: D'Ettorre & Heinze 2005) or visual IR in lobsters (*Homarus americanus*: Karavanich & Atema 1998). In birds, IR has been tested mainly in the auditory domain for neighbor (e.g. Godard 1991; Mackin 2005) and kin-discrimination (e.g. Beecher 1988). Long term memory for individuals has been reported primarily from mammals and lasts at least two years in elephants *Loxodonta africana* (McComb et al. 2000) and sheep *Ovis aries* (Kendrick et al. 2001), around four years in pinnipeds *Callorhinus ursinus* (Insley 2000) and monkeys *Saguinus odipus* (Matthews & Snowden 2011).

Common ravens show advanced cognitive skills during foraging (Bugnyar & Heinrich 2005; Bugnyar et al. 2007) and in post conflict management (Fraser & Bugnyar 2010; Fraser & Bugnyar 2011), suggesting that they are capable of dealing with others on an individual basis. Recently, we experimentally demonstrated differentiation between individuals on the

basis of 'yells' (Boeckle et al. 2012), a call emitted in food related situation that typically attracts conspecifics to food bonanzas. However, IR has been reported for various social contexts (e.g. Medvin & Beecher 1986; Bee & Gerhardt 2001; Hare & Atkins 2001; Tibbetts & Dale 2007) and thus food related vocalizations might underlie different selective forces than other raven calls. In the current study we focused on another, frequently given vocalization, the territorial 'rab', and tested if ravens can differentiate between different individuals uttering this call. 'Rabs' are long distance calls emitted by territorial breeders, presumably for indicating territorial ownership, territorial defense, and keeping contact with the pair partner. Previous studies indicated that long distance calls are highly variable (Enggist-Dueblin & Pfister 2002; Boeckle & Bugnyar 2012) and playback studies revealed differential responses to 'rabs' depending on the relationship valence between signaler and receiver (Boeckle & Bugnyar 2012). We thus hypothesized that ravens are able of caller discrimination in long distance calls when tested in a habituation–dishabituation experiment.

Material and Methods

Individuals

We used a total of 32 ravens (16 males, 16 females), which were kept pair-wise in Zoos, gameparks, and private owners across Austria, Switzerland, and Germany (Table 1). All individuals were kept in compliance to the legal regulations of the responsible country.

Playback Stimuli

Long distance calls were recorded between February 2008 and July 2009. Each pair was visited multiple times (min= 2, max= 24) for getting 311 hours of recordings under standard daily life conditions. In addition, we presented pairs with a stuffed male raven at a distance of 10 meters, to experimentally elicit calls used for territorial defence. As expected, the onomatopoetically described call 'rab' was the most prominent response to a simulated

intruder and thus selected for further use. This call type has also been described as the “gewöhnlicher Feindruf” (Gwinner 1964), or “growl like vocalization” (Conner 1985). In addition to the calls emitted directly in response to the stuffed raven, we used ‘rab’ calls from the recordings under standard conditions. This was necessary because some pairs did not show any response to the stuffed raven. Note that it is known that ravens hardly respond to dummies (unpubl. data) even when special care is taken that they are presented as naturally as possible and are not fully visible to the tested birds.

Stimuli consisted of at least ten randomly selected calls recorded at different days and day times to ensure that habituation is not due to specific call characteristics apart from individuality. We used the same method as reported in (Boeckle et al. 2012). Note that in the playback experiment we presented raven pairs with calls of to them unknown individuals only. Pairs received two playback experiments, with either the male or the female being the focal subject. Per playback, we used stimuli from only male or only female individuals that were matched according to sex and age of the focal individual. Male and female playbacks were conducted in the morning (between 8-11 am) and in the afternoon (between 13-17 pm) with the order being counterbalanced across pairs. Baseline duration before stimuli presentation was 15 minutes, after which an interspecies stimuli was presented to determine the birds’ general response to a played back call (Boeckle et al. 2012). After the last 1-minute intermission interval between heterospecific calls, the first raven stimulus consisting of five randomly selected long distance calls were presented with a succeeding 1-minute pause. The stimuli plus the pause were repeated until habituation criterion was reached. Habituation criterion was defined as being the half of the highest response to the first three conspecific stimuli presentations. After habituation we presented dishabituation stimuli that were from a different individual but from the same sex and age class as the calls from the individuals in the habituation. We introduced three conditions in the dishabituation phase to disentangle influences of caller position and determine the influences of caller identity. The underlying idea was that dishabituation stimuli might be interpreted by the focal bird as a different call

type of the same individual instead of it being a different individual calling from the same or a different position. Like in Boeckle et al. (2012) the conditions were the following: (1) the same call-type of a different individual projected from the same location; (2) the same call-type of the same individual from a different location; (3) or changed location and individual. For stimuli presentation we used a MacBookPro with Quick Time Player Pro (V:7.6.9) plugged in speakers (Ion Block Rocker, Ion Audio, LLC. US, www.ionaudio.com; 70 Hz–50 kHz $\pm$ 3 dB).

Data Collection

Both individuals within a pair were audio-recorded (Marantz PMD-660, D&M Holdings Inc., Japan; Sennheiser Me 67, Sennheiser Electronic GmbH & Co. KG, Germany) and video-recorded (Sony handycam DCR-HC23, Sony Co., Tokyo, Japan) by two human experimenters (focusing on the male and female, respectively). We coded responses to stimuli in the 1-minute pause between stimuli presentation with Solomon coder (Péter 2011, copyright by András Péter; <http://solomoncoder.com>). We used the same call categorization - i.e. long-distance calls, soft calls and self-aggrandizing displays - as well as the same behavioural responses - (1) no reaction, (2) head lifting, (3) looking in the direction of the playback, (4) flying in the direction of the playback and (5) flying to the fence close to the playback and searching - as we used in a previous study conducted on food calls (Boeckle et al. 2012).

Statistics

We calculated a varimax-rotated correlation principle component analysis to reduce the number of variables with a minimum of eigenvalue of 1.0 to be part of the final components.

The original variables are number of long-distance calls, soft calls and self-aggrandizing displays, behavioural responses and the highest behavioural response.

For statistical testing we categorized phases of the experiment like in (Boeckle et al. 2012) into the following parts: a 15 min baseline, playback of a goose or a rooster (three presentations), habituation phase one (two presentations of five 'rab' calls), habituation phase two (all habituation stimuli excluding the first two and the last two), habituation phase three (last two habituation stimuli presentations), dishabituation (one presentation) and a final baseline consisting of 15 min (Boeckle et al. 2012).

We calculated a general linear mixed model (GLMM) to check for difference between the phases of the playback experiment. We used a nested term as random factor in order to correct for differences between playback individuals and presentation (focal individual(session(call))). We included sex of the focal, sex of the played-back individual as well as their interaction, age class, condition, phase and time of day as fixed factors in the full model. Both individuals of the pair entered the analysis as response variable in the GLMM to calculate intersex and intrasex stimuli differences. Model selection was based on lowest AICc values in backward step procedure (Burnham & Anderson 2010). No adjustment for multiple comparison was applied reduce over-conservativeness (Nakagawa 2004). Differences between conditions were calculated with a Kruskal–Wallis tests entering the differences between the last habituation stimulus and dishabituation as response variable and condition as factor. Tests were calculated using IBM SPSS for Mac 19 (SPSS Inc., Chicago, IL, U.S.A.).

Results

Habituation criterion was reached after a median of 14.5 playbacks (min=6; max=32). Interestingly, maximal response in behavioural and vocal responses was shown after different numbers of playbacks. Highest behavioural response was shown after a median of two playbacks, and maximum number of behavioural responses after a median of four playbacks. Vocal behaviours peaked after a median of seven playbacks. Accordingly, the number of playbacks, which were required until maximum response was shown by ravens, differed significantly between the two categories, namely number of playbacks needed until highest behavioural response and highest number of vocalizations per minute (Wilcoxon Signed Rank: $df=29$; $Z=-4.463$; $p\leq 0.001$). Similarly, the number of playbacks until the maximum number of behavioural responses that were needed to elicit peak response in vocalizations per minute differed significantly between the two categories (Wilcoxon Signed Rank: $df=29$; $Z=-3.129$; $p=0.002$).

Principle component analysis (Bartlett's Test of Sphericity: $\chi^2=1165.186$; $df\ 10$; $p\leq 0.001$) results in two components. We refer to the resulting component 1 as 'territorial response' because its main loadings are based on parameters related to territorial defence, i.e. territorial calls and height and number of behavioural responses. In its rotated matrix component 1 is comprised of territorial calls per minute (0.281), self-aggrandizing calls per minute (0.168), soft calls per minute (-0.07), highest behavioural response (0.923), and number of behavioural responses (0.911). We name component 2 'within pair communication' as its main loading is based on soft calls. Specifically component 2 is comprised of territorial calls per minute (-0.520), SAD per minute (0.763), soft calls per minute (0.473), highest response (-0.061), and number of responses (-0.064). Cumulative percentage explained by both components is 57.11%, while component 1 explains 36.59% and component 2 20.93% of variance.

The final model reveals significant differences between daytime (morning, afternoon), age class (adult, subadult), phase (habituation, dishabituation), condition (positions), and sex of the stimulus (male, female; Table 1). Crucially for our hypothesis, pairwise posthoc comparison reveals, that responses in the dishabituation phase are higher than in the last two habituation stimuli ($\beta=-0.578$; $SE=0.143$; $t=-4.035$; $p\leq0.001$; Figure 1). Responses in the morning were stronger than in the afternoon ($\beta=0.145$; $SE=0.043$; $t=3.416$; $p\leq0.001$). Although age class reveals a significant effect in F-statistics, post hoc pairwise comparison shows that adult ravens did not respond more than non-adult ones ($p>0.05$). Female calls elicited more responses than male calls ($\beta=0.137$; $SE=0.042$; $t=3.289$; $p\leq0.001$) while female and male receivers did not differ in their response to the playback stimuli ($p>0.05$). Finally, differences between conditions indicate that position of the caller matters (Table 1). Birds showed highest territorial behaviour in condition 2, when the same individual was played back at different locations; condition 1 and 3 did not differ significantly (Condition 1 vs 2: $\beta=-0.22$; $SE=0.063$; $t=-3.497$; $p\leq0.001$; Condition 1 vs 3: $\beta=0.062$; $SE=0.064$; $t=0.957$; $p>0.05$; Condition 2 vs 3: $\beta=0.281$; $SE=0.062$; $t=4.570$; $p\leq0.001$). Despite of these differences, conditions did not vary in their differences between last habituation and dishabituation in any single or compound variable (Kruskal Wallis: $p>0.05$).

Discussion

Our results reveal that ravens respond differentially in a habituation-dishabituation experiment to two unknown individuals based on long distance calls ('rab'). Stimuli response peaked after seven in acoustic and after two (highest behavioural response) or four (number of behavioural response) in behavioural movement parameters. While condition does not show significant variation in the difference between habituation and dishabituation, the highest territorial response could be found in condition 2, when the same individual was

played from a different side. Female stimuli elicited more response than males while both sexes did not show differences in response to our playback experiment.

That ravens can differentiate two unknown individuals based on one of their most common long-distance calls is not surprising from an evolutionary point of view. As territorial breeders they are likely to face a high selective pressure to distinguish between conspecifics, for instance intruders and neighbours or different neighbours (Stoddard et al. 1991; Temeles 1994; Mackin 2005). Since our calls were matched for sex and age class of the birds, it seems that ravens can pick up on subtle individual differences in call structure, which is in line with previous findings on differentiation of familiar ravens (Boeckle & Bugnyar 2012). Additionally it was recently shown that noisy miners (*Manorina melanocephala*) (McDonald 2012) and ravens (*Corvus corax*) (Boeckle et al. 2012) differentiate between unknown individuals. This shows that not only differentiation based on familiarity, which typically is used in the 'dear enemy effect' (e.g. Johnston & Jernigan 1994), is possible but also subtle individual call differences can be quickly acquired and used. Subtle individual differences are already detected in characteristics of fundamental frequency without vocal tract resonances (Boeckle et al. 2012; Mathevon et al. 2012). Males and females might also use different parameters of the fundamental frequency in order to differ from other individuals (Mathevon et al. 2012). While these differentiating abilities are based on single modalities and make true IR hard to prove, cross-modal individual recognition was also shown for jungle crows (*Corvus macrorhynchos*) (Kondo et al. 2012).

Interestingly, the habituation/dishabituation design revealed a temporal separation of behavioural and vocal responses to a calling individual. Presumably, movement responses came first because birds tried to find and/or make visual contact with the simulated intruder. Eventually, they reduced searching for the simulated raven and started to call back in response to the stimuli. A reduced response to playbacks in the afternoon as compared to the morning may reflect motivational differences in interacting with conspecifics across the

day; alternatively, it may indicate that ravens get habituated to the playback setting already after a single experience. Still, it is noteworthy that the reduction in response did not have any measurable effect on the birds' differentiation between the callers.

Differences between conditions showed that ravens responded most in the condition where the same individual called from two different positions. As differences between conditions are found in the GLMM results, this could mean that several phases of the playback were affected. However, a detailed analysis of the last habituation stimulus and the dishabituation stimulus revealed no difference between conditions. This might mean that differential response from last habituation to dishabituation was not dependent on condition or that differences occurred after dishabituation. For instance, differences in the second baseline phase, after the dishabituation, were large. This strong effect might generate differences between the conditions in the estimated means by the GLMM. If this was the case, ravens would respond most in the condition where the same individual calls from two different positions. Calls in the territory from various positions of the same individuals might indicate highest territorial intrusion and cause most territorial behaviour. This interpretation in combination with the difference found between habituation and dishabituation would make true individual identification likely.

As no significant interaction between the sex of the stimulus and the sex of the focal individual was found we can report that neither females nor males show enhanced responses to any of the sexes. Thus there were no stronger responses to inter- or intrasex stimuli in both sexes. However, focal sex showed a significant influence in our model. While the sex of perceiver did not show significant differences, stimuli that were comprised of female calls elicited higher territorial response in comparison to male calls in both sexes. Males signal territory borders more often than females, which in turn might lead to increased territorial response in the resident pair. Additionally playbacks were conducted shortly before the breeding season, where gonadal hormones are supposed to be high in seasonally

breeding birds (Nottebohm et al. 1987). Thus territorial responses might be higher during our experiment exaggerating responses to female calls.

Taken together, we were able to show that ravens differentiate between unknown individuals based on their territorial calls. Our findings fit with the recent literature reporting that ravens can differentiate unknown individuals in food calls (Boeckle et al. 2012) and categorize as well as memorize former affiliates based on long distance calls (Boeckle & Bugnyar 2012). Thus ravens may learn about others and classify them in fine-grained categories within one call type. Alternatively, ravens might remember others on an individual basis. We speculate that true individual recognition (Tibbetts & Dale 2007) may be cognitively less demanding than classifying them according to multiple categories within and between call types. Furthermore, differentiating between affiliative and non-affiliative individuals, long-term memory for affiliations, and caller discrimination might lead to complex recruiting behaviours. Recruitment might be used not only in feeding situations where recruiting affiliates might be highly advantageous but also in conflict situations.

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Tables

Chapter 4 - Table 1. Background information about tested individuals.

Pair	ID	Sex	Housing
1	I	M	WP Grünau
1	O	F	WP Grünau
2	Q	M	NP Bayr. Wald
2	E	F	NP Bayr. Wald
3	H	M	KLF
3	D	F	KLF
4	L	M	Welser Tierpark
4	T	F	Welser Tierpark
5	P	M	Wolkersdorf
5	Mä	F	Wolkersdorf
6	Kä	M	WP Haag
6	Lu	F	WP Haag
7	Ru	M	Weidling
7	Ro	F	Weidling
8	Pa	M	Zoo Innsbruck
8	Fl	F	Zoo Innsbruck
9	Gm	M	WP Goldau
9	Gf	F	WP Goldau
10	Km	M	VP Turnersee
10	Kf	F	VP Turnersee
11	Am	M	WP Altenfelden
11	Af	F	WP Altenfelden
12	Ar	M	Scharnstein
12	Kr	F	Scharnstein
13	Mm	M	Zoo Hellabrunn Munich
13	Mf	F	Zoo Hellabrunn Munich
14	Sm	M	Selm
14	Sf	F	Selm
15	R	M	WP Grünau
15	P	F	WP Grünau
16	J	M	WP Grünau
16	M	F	WP Grünau

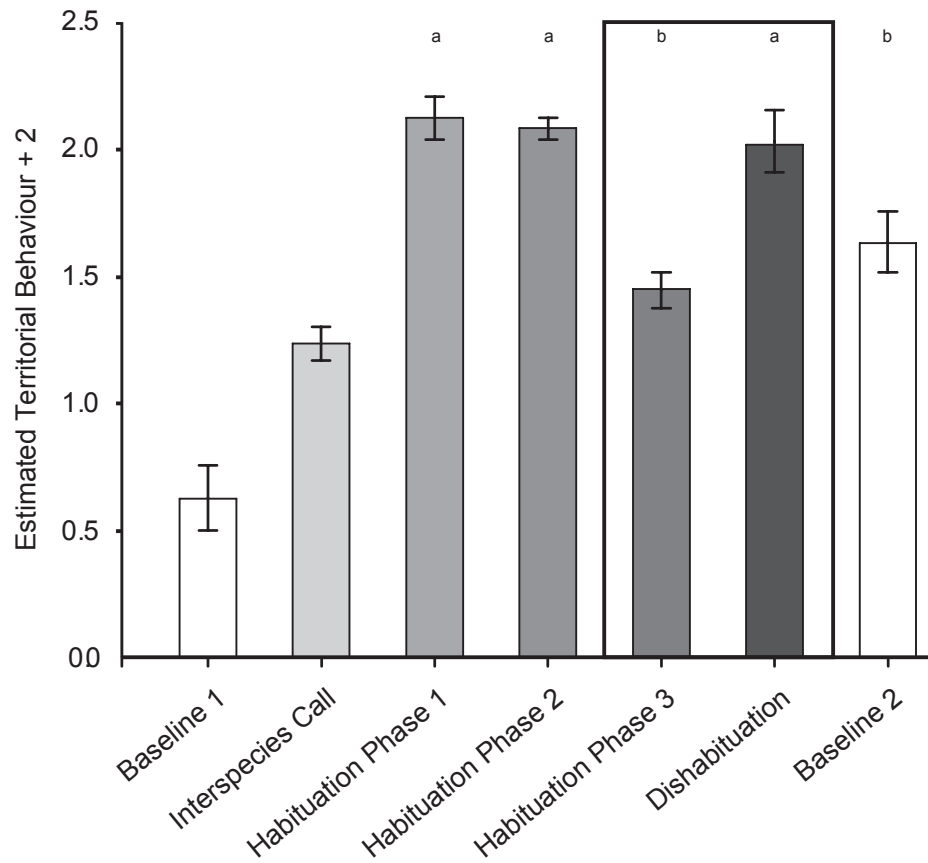
Chapter 4 - Table 2. Fixed effects of final model.

	F	Df1	Df2	P
Intercept	39.323	12	1317	≤0.001
Condtion	11.635	2	1317	≤0.001
Stimulus Sex	10.818	1	1317	≤0.001
Focal Sex	5.111	1	1317	0.024
Age Class	105.909	1	1317	≤0.001
Daytime	11.669	1	1317	≤0.001
Phase	47.296	6	1317	≤0.001

Figures

Chapter 4 - Figure 1. Estimated territorial response ($\pm$ SE) to the different phases of playback presentation.

Habituation phase 1 comprised first two playback stimuli, habituation phase 3 last two, and habituation phase 2 consisted of all other habituation stimuli. Same letters above the bars designate non-significance between the phases ($P > 0.05$) whereas no varying letters represent statistical difference ($P < 0.05$). Differentiation between the two stimuli categories that test for differentiation abilities are highlighted in the box.



Chapter 5:

You sound familiar: carrion crows can differentiate between the calls of known and unknown heterospecifics

Running head: Interspecies recognition in carrion crows

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Abstract

In group-living animals it is adaptive to recognize conspecifics on the basis of familiarity or group membership as it allows association with preferred social partners and avoidance of competitors. However, animals do not only associate with conspecifics but also with heterospecifics, for example in mixed-species flocks. Consequently, between species recognition, based either on familiarity or even individual recognition, is likely to be beneficial. The extent to which animals can distinguish between familiar and unfamiliar heterospecifics is currently unclear. In the present study we investigated the ability of eight carrion crows to differentiate between the voices and calls of familiar and unfamiliar humans and jackdaws. The crows responded significantly more often to unfamiliar than familiar human playbacks and, conversely, responded more to familiar than unfamiliar jackdaw calls. Our results provide the first evidence that birds can discriminate between familiar and unfamiliar heterospecific individuals using auditory stimuli.**

Keywords: interspecies recognition, familiarity, vocal information, playback, carrion crows

** This abstract or a similar version of it was submitted as conference and workshop applications. In case of acceptance the abstract might be published in the conference booklet and might be found in the internet.

Introduction

The ability to differentiate familiar from unfamiliar conspecifics is adaptive as association with familiar individuals decreases aggression (Temeles 1994; Johnsson 2010; Barnard and Burk 1979), increases foraging success (Hojesjo et al. 1998) and can result in enhanced predator detection (Hare 1998). Animals are able to recognize group members on the basis of visual (Parr et al. 2000; Marechal et al. 2010; Wilkinson et al. 2010; Dale et al. 2001), auditory (Clark et al. 2006; Sayigh et al. 1998; Rendall et al. 1996) or olfactory cues (Thom and Hurst 2004; Bonadonna et al. 2007).

In nature animals forage (Powell 1974; Lynnes et al. 2002) and mob predators in mixed-species flocks (Humphrey 1989), interact aggressively with members of other species (Frye 1983; Wallace and Temple 1987; Waite 1984a; Waite 1984b) and recognize and respond appropriately to heterospecific alarm calls (Kitchen et al. 2010; Magrath et al. 2009b; Rainey et al. 2004a). This suggests that animals frequently eavesdrop on information given by heterospecifics (Magrath et al. 2009a; Fallow and Margrath 2010; Lea et al. 2008). Thus, discriminating familiar from unfamiliar individuals of other species is likely to be beneficial for essentially the same reasons as are postulated for individual or class level recognition in conspecifics (Tibbetts and Dale 2007). Recent research has revealed that American crows (*Corvus brachyrhynchos*), magpies (*Pica pica*) and Northern mockingbirds (*Mimus polyglottos*) quickly learn to discriminate between threatening and non-threatening humans (Marzluff et al. 2010; Levey et al. 2009; Lee et al. 2011). However, except in the specific case of predatory situations, very little is known about whether animals are able to discriminate between and respond appropriately to individual heterospecifics. It is therefore particularly interesting to investigate whether they use information about heterospecifics in other contexts and, if so, whether they are able to encode it on an individual level. Contact calls are traditionally thought to encode more information about the caller in order to allow individual recognition than alarm calls in which the animals may respond to a call specific

feature (Chapman and Weary 2005; Snowden and Cleveland 1980) but see (Blumstein and Munos 2005; Hare 1998; Yorzinski et al. 2006).

In the present study, we investigated whether carrion crows (*Corvus corone corone*) could discriminate between voices and calls of familiar and unfamiliar individuals of two heterospecific species, humans and jackdaws (*Corvus monedula*). Crows are social living animals that form long-term relationships with valuable partners and have been shown to recognize individual conspecifics (Kondo et al. 2012 Yorzinski et al. 2006). Free living crows, jackdaws and humans all live in a shared habitat (e.g. cities) and frequently use the same foraging and roosting areas (Waite 1984a; Röell 1978). It can therefore be expected that these species are relevant to each other (e.g. eavesdropping on each other's alarm calls). The crows used in this study are aviary housed and visited by human experimenters and caretakers. A free-living flock of jackdaws forages daily around the Konrad Lorenz research station (KLF) in direct proximity to the crow aviaries. Individuals of both species are thus in regular auditory and visual proximity. Anecdotal observations suggest that the crows do attend to jackdaw calls and, for example, respond with vigilance to jackdaw alarm calls (unpublished observation). This provides an ideal setup to investigate this research question.

Methods

Study subjects and playback stimuli

From June-July 2010 we tested eight captive carrion crows (4 females, 4 males) kept in three large outdoor aviaries at the KLF in Austria.

Five female humans familiar to the crows and five female humans unfamiliar to the crows were recorded saying 'Hey', a frequently used greeting when approaching the crow aviaries. Familiar humans had regularly worked with the animals for at least 2 months;

unfamiliar humans had never met the crows. From each person ten different 'Hey' stimuli were recorded in a standardized way and used in the playbacks. For the jackdaw stimuli 'tchak' contact calls from five familiar and five unfamiliar birds were recorded. Five different calls from each jackdaw were used for the playback. Thus we ensured that each stimulus of either the human or the jackdaw playback was repeated, at maximum, twice per focal individual. Recordings of familiar jackdaws were collected at the KLF from individuals who either bred directly at the KLF in close proximity to the crow aviaries or frequently joined for the daily feedings. This ensured that the individuals were highly familiar to the crows. Contact calls from jackdaws kept at the ornithological station in Radolfzell, Germany, were recorded for the unfamiliar stimuli. One female crow ('Resa') was kept in Radolfzell before coming to Grünau at the end of April 2010. As we do not have any information on whether this bird was kept within auditory distance of the jackdaw aviary in Radolfzell we ran the analysis of the behavioral responses to the jackdaw stimuli both without this individual and with the Radolfzell stimuli as familiar and the KLF stimuli as unfamiliar. In contrast, we made sure that she met and was highly familiar with all the human caretakers used in the present experiment. The period of two months also exactly corresponded with the minimum familiarization period to the humans for the other crows (for additional information see online supplementary materials).

Testing procedure

All birds were tested individually and in auditory isolation from each other. When tested they entered the test compartment on a voluntary basis. We conducted two sessions for each stimulus type (human, jackdaw) per crow. In each session 10 stimuli consisting of five familiar and five non-familiar individuals were presented in pseudo-randomized order. We randomized playback stimuli (humans: 1-10, jackdaws: 1-5) whereby each recording was used only once per session to avoid habituation to specific recordings. The mean duration of

each stimulus was 0.302 ± 0.097 s (mean $\pm$ SD) for the jackdaw calls and 0.476 ± 0.104 s (mean $\pm$ SD) for human vocalizations. The inter-trial interval varied between 45-180 s to ensure that stimulus occurrence was not predictable. In addition, after five stimulus presentations the birds received a ten-minute break in each session. The presentation of five stimuli took 4.212 ± 0.599 minutes (mean $\pm$ SD). The birds were given at least one-week break between the two sessions of each stimulus type. A human experimenter filmed all responses.

Video and statistical analysis

All trials were coded from videotapes by CAFW using SOLOMON Coder v. 11.09 (András Péter, www.solomoncoder.com). Head and body movement towards the speaker, looking up and changes into vigilance position shortly after the playback stimulus (latency to respond mean $\pm$ SE: 0.583 ± 0.174 s) were coded as responses. An inter-observer reliability analysis using the Kappa statistic was performed on 25 percent of the trials, which were coded by a second observer (GS; Cohen's K human stimuli= 0.826, jackdaw stimuli= 0.896). To analyze the data we used generalized linear mixed models (GLMMs) with binomial error distribution and a log link function. Response variable was the individuals' behavioral response in each trial (reaction yes/no). Session, sex, identity of the vocal model and category (familiar/unfamiliar) served as fixed factors. In order to account for repeated measures for each individual, the individual identity was included as random factor. We used second order Akaike's information criterion (AICc) to choose the best model, starting with all main effects and interactions between all factors and individual identity. All factors and interactions remaining in the final model are presented here, irrespective of their significance. All GLMM analyses were performed in SPSS 19.0.

Results

In response to human stimuli, the familiarity of the caller significantly influenced behavioral responses ($n=8$, $df=2$, $F=43.462$, $p<0.001$). Crows responded more often to unfamiliar human stimuli (Fig. 1). The interaction between familiarity of the caller and session remained in the final model, but was not significant ($n=8$, $df=2$, $F=1.515$, $p=0.223$).

Carrion crows' behavioral response to jackdaw calls tended to be influenced by the familiarity of the caller, when one female previously housed in Radolfzell was excluded from the analysis ($n=7$, $df=2$, $F=3.033$, $p=0.052$). Birds responded more to familiar individuals (Fig. 2). The interaction between focal individual and familiarity of the caller remained in the final model but was not significant ($n=7$, $df=12$, $F=0.893$, $p=0.556$). When the additional bird was included in the statistical analysis but with switched familiarity contingencies (KLF stimuli: unfamiliar, Radolfzell stimuli: familiar), the crow's behavioral response was marginally significant ($n=8$, $df=2$, $F=3.053$, $p=0.05$).

Discussion

The present study shows that carrion crows discriminate between familiar and unfamiliar humans and jackdaws on the basis of vocal cues. This is the first evidence that birds can differentiate between familiar and unfamiliar individuals of another species using contact calls. This shows that species living in complex social systems like carrion crows may use heterospecific information in addition to information transmitted by members of their own species. Individuals' responses to heterospecific alarm calls are relatively well investigated (Fallow and Margrath 2010; Kitchen et al. 2010; Magrath et al. 2009b; Rainey et al. 2004b, a), however, this study presents first evidence that crows use information in contact calls of heterospecifics. The use of auditory stimuli may be particularly relevant to

carrion crows as they belong to the order of songbirds. Thus acoustic stimuli and their encoded information might play a significant role in their everyday social life and as such a general sensitivity to acoustic information may have been selected for. Little is known about the function of acoustic communication in carrion crows' social life but they are likely to play a role in the context of everyday social interactions (e.g. affiliative and agonistic encounters), reproduction (e.g. mating, territory defense) and enhance cooperative behaviors (e.g. transmitting information about food and predators, helping behavior in the context of cooperative breeding; Parr 1997).

Our study provided the crows with a very limited amount of auditory information; this is in contrast to everyday situations where individuals can evaluate humans based on a combination of large amounts of visual and auditory information. The stimuli in this study were very short and their presentation was entirely unpredictable for the crows. In addition they were decoupled from visual information, i.e. a human approaching. Still, the crows did respond more often to unfamiliar than to familiar stimuli.

The ability to categorize human individuals based on familiarity might be facilitated by the fact that the crows in this study are captive reared and thus had early and regular exposure to human caretakers. However, the ability to recognize individual humans has been anecdotally described in the free-living bird literature. It is likely that this is facilitated by the fact that crows frequently inhabit human dominated areas and probably does not require close interactions and bonding with humans (Lorenz 1952; Marzluff and Angell 2005).

Interestingly, the behavior of the crows differed depending on the species of heterospecific. Hence, in crows, heterospecific recognition may be based on different mechanisms or serve different functions depending on the species (Hopp et al. 2001). From our results it seems that familiar individuals of both jackdaws and humans have similar relevance and crows are responding to them at approximately the same rates, however, they

are responding more to unfamiliar humans and less to unfamiliar jackdaws. This suggests that responding to familiar jackdaws might facilitate the association with preferred and the avoidance of non-preferred social partners and recognition of highly successful individuals in a foraging flock might be beneficial. There are currently no studies investigating heterospecific social interactions in mixed species flocks and research on this topic would be highly desirable. In contrast, responding to unfamiliar humans may be adaptive given the crow's long history of extensive hunting. In this study we did not find an effect of type of behavioral response (look up, turn head to speaker, move to speaker, vigilance) depending on familiarity. Therefore, we can only speculate about possible functions of the observed behaviors and further work is required in order to investigate the mechanisms controlling this behavior.

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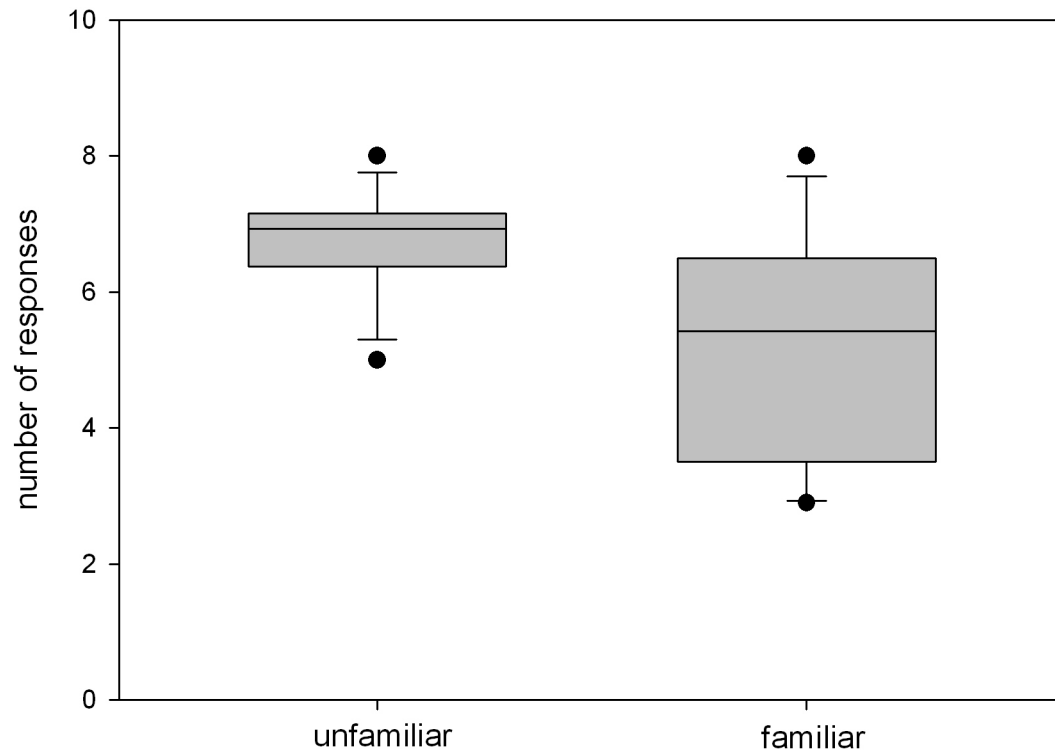
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Figures

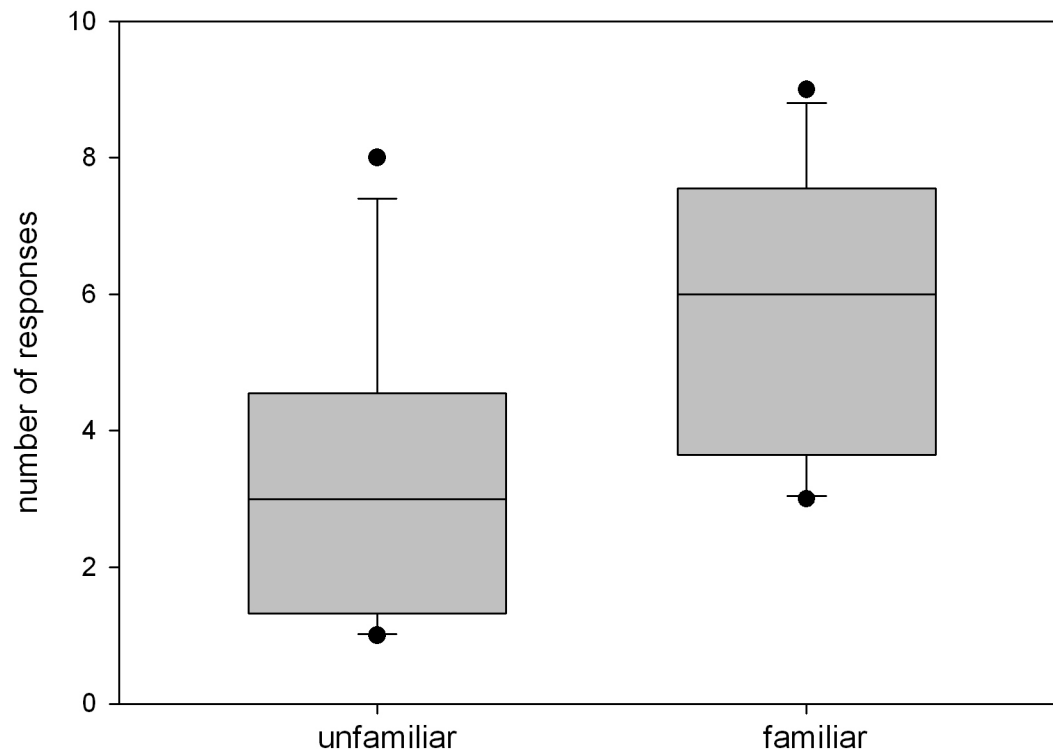
Chapter 5 - Fig. 1. Carrion crows' behavioral responses to familiar and unfamiliar human voices.

Y-axis shows number of behavioral responses to the playback stimuli per focal individual (n=8). Individual identity is indicated with different symbols.



Chapter 5 - Fig. 2. Carrion crows' behavioral responses to calls of familiar and unfamiliar jackdaws.

Y-axis shows number of behavioral responses to the playback stimuli per focal individual (n=7). Individual identity is indicated with different symbols. One individual ('Resa') previously housed in Radolfzell and with switched familiarity has been excluded from the graph.



Supplement: You sound familiar: Carrion crows can differentiate between the calls of known and unknown heterospecifics

Claudia A.F. Wascher, Georgine Szipl, Markus Boeckle & Anna Wilkinson

Methods

Study subjects and playback stimuli

The eight tested carrion crows are kept in two male-female pairs in one aviary separated by a central testing compartment (aviary A) and one group of two males and two females in a separate aviary (aviary B) approximately 10 m away from aviary A.

All playback stimuli were recorded by GS or MB using a Sennheiser ME67 or ME65 directional microphone on a K6 module, and a Marantz PMD661 digital recorder or a Sony TCD-D100 digital audio recorder. Only calls with little background noise were selected and low frequency noise was filtered with a stop-Han-band.

Testing procedure

To prevent any bird other than the focal individual from hearing the playbacks, masking noise was played to all other birds. The noise was recorded from a generator next to the crow aviary and the individuals were familiar to the sound. The focal bird was separated and masking noise was directed towards the back part of the aviary (approximately 5 meters away from the focal birds' position), where the other crows were separated. This ensured proper masking of the other crows in that aviary whereas the focal bird was not affected by the noise due to directionality and sound pressure level (which was highly reduced by the

distance of the focal bird to the source of the noise). For logistical reasons we could not fully randomize the order of the crows and always started with two birds from aviary A, followed by the four birds in aviary B, followed by the last two birds, also in aviary A. Calls were played back from a loudspeaker (ION Block Rocker; frequency response = 70 Hz - 20 kHz $\pm$ 3 dB) connected to a Mac Book Pro using Apple quick time player, approximately three meters from the crow aviaries, not visible to the birds. The sound pressure level was approximately 75 dB (measured at 1 meter) for human voices. This accounts for the distance of the loudspeaker to the focal bird (approximately 3 meters) and matches the SPL of normal speech in humans (approximately 70 dB). Jackdaw stimuli were played back with approximately 82 dB SPL at 1 meter, as these intensities are equivalent to the intensity of naturally occurring jackdaw vocalizations (Szipl et al. unpubl. data).

Sound analysis of human voices and jackdaw calls

We performed a sound analysis of human and jackdaw stimuli in order to test for inter- and intraindividual variation. The stimuli were analyzed using a custom built program in PRAAT (Boersma and Weenink 2011) to measure source- and filter-related acoustic features of each jackdaw and human stimuli. Measured parameters used in the analysis were minimum, maximum, and mean values of the fundamental frequency (F_0) as well as stimulus duration, duration of tonal parts, and the percental time point of maximum amplitude in the call (elapsed). Further, we conducted formant analysis for human 'Hey' stimuli on the vowel 'e'. We measured five formants, and maximum formant value was set at 5500 Hz, matching ranges of the voice of adult females; F_0 settings were set at 160 to 350 Hertz. In jackdaws, we measured mean frequencies of the second (F_2) and the third (F_3) harmonic band. Descriptive measures are given in Table 1.

For analysis of inter-individual and group differences in recordings, we applied Kruskal-Wallis and Mann-Whitney-U tests over all measurements of human voices and jackdaw contact calls, as most of the parameters were not normally distributed. We then tested for inter-correlation between the measured parameters using Spearman rank correlation. Parameters which had the highest significance and were not inter-correlated were used to conduct permutated discriminant function analysis (pDFA) with 1000 permutations and 100 random selections in R (Hornik 2011). We calculated crossed pDFA using individual humans (N=10) or jackdaws (N=10) as test factor and each stimulus per human (N=10) or jackdaw (N=6) as control factor. In order to rule out differences in call characteristics between groups, we calculated nested pDFA with group membership (N=2, familiar or unfamiliar) as test factor and individual identity (N=10) as control factor. The results showed that individual discrimination was highly significant in humans and jackdaws ($p=0.001$), whereas calls could not be classified correctly by group membership (humans: $p=0.206$; jackdaws: $p=0.314$, Table 2), indicating that crows' reactions were unlikely to be based on acoustic differences in the recordings of familiar and unfamiliar humans and jackdaws.

Chapter 5 - Table 1. Descriptive statistics of measurements used for analysis of jackdaw 'tchak' and human 'Hey' stimuli.

With minimum, maximum, maximum difference, mean, standard deviation (SD), coefficient of variation in percent (CV%; calculated as standard deviation/mean*100) and variance for each individual.

parameter	jackdaw	minimum	maximum	max difference	mean	SD	CV%	variance
minimum F ₀	1	633.52	1226.11	592.59	1019.23	238.68	23.42	56967.01
	2	581.67	1127.98	546.31	981.20	203.65	20.76	41473.01
	3	506.25	1159.13	652.88	969.38	242.83	25.05	58968.56
	4	350.67	1083.82	733.15	764.57	309.11	40.43	95546.98
	5	843.40	1017.37	173.97	924.78	73.23	7.92	5361.96
	6	511.80	1231.12	719.32	798.73	251.34	31.47	63171.72
	7	779.21	1824.70	1045.49	981.89	413.53	42.12	171009.14
	8	822.52	1100.87	278.35	910.92	108.73	11.94	11822.74
	9	773.78	1095.78	322.00	947.62	141.44	14.93	20005.07
	10	618.71	1090.08	471.37	792.27	166.16	20.97	27610.71
maximum F ₀	1	872.59	1533.60	661.01	1382.40	252.74	18.28	63878.64
	2	1066.88	1283.13	216.25	1140.96	76.54	6.71	5858.55
	3	1156.14	1382.91	226.77	1212.86	84.42	6.96	7125.96

parameter	jackdaw	minimum	maximum	max difference	mean	SD	CV%	variance
	4	968.86	1312.65	343.79	1127.89	129.69	11.50	16820.70
	5	1138.98	1275.16	136.18	1190.05	48.11	4.04	2314.84
	6	524.37	1592.21	1067.84	1005.84	363.06	36.10	131814.40
	7	1015.76	1948.07	932.31	1257.87	350.78	27.89	123044.12
	8	1062.96	1893.55	830.59	1254.65	324.78	25.89	105483.71
	9	1054.74	1513.36	458.62	1247.60	166.98	13.38	27881.68
	10	666.39	1462.03	795.64	1048.99	255.87	24.39	65468.87
mean F_0	1	677.17	1284.80	607.63	1134.81	232.96	20.53	54268.25
	2	811.36	1196.36	385.00	1049.68	131.07	12.49	17179.65
	3	895.46	1179.96	284.50	1097.18	105.51	9.62	11132.58
	4	626.41	1169.47	543.06	918.47	224.83	24.48	50547.52
	5	1004.96	1084.55	79.59	1033.03	33.26	3.22	1106.55
	6	517.43	1433.46	916.03	899.08	313.63	34.88	98361.33
	7	897.43	1901.34	1003.91	1089.98	398.75	36.58	159003.30

parameter	jackdaw	minimum	maximum	max difference	mean	SD	CV%	variance
	8	928.78	1332.59	403.81	1064.24	161.83	15.21	26189.60
	9	899.48	1194.01	294.53	1061.24	118.00	11.12	13924.37
	10	629.77	1225.08	595.31	892.93	191.54	21.45	36688.58
stimulus	1	0.24	0.36	0.11	0.28	0.04	14.98	0.00
duration	2	0.24	0.59	0.35	0.35	0.13	37.30	0.02
	3	0.15	0.21	0.06	0.19	0.02	12.39	0.00
	4	0.21	0.43	0.22	0.29	0.08	28.32	0.01
	5	0.29	0.33	0.05	0.31	0.02	6.15	0.00
	6	0.17	0.43	0.26	0.28	0.09	33.63	0.01
	7	0.15	0.40	0.25	0.28	0.10	35.23	0.01
	8	0.20	0.49	0.29	0.37	0.10	27.08	0.01
	9	0.24	0.51	0.27	0.36	0.10	28.76	0.01
	10	0.16	0.46	0.31	0.32	0.13	42.01	0.02
duration of	1	0.19	0.29	0.11	0.23	0.04	17.41	0.00

parameter	jackdaw	minimum	maximum	max difference	mean	SD	CV%	variance
tonal parts	2	0.18	0.26	0.08	0.22	0.03	14.84	0.00
	3	0.10	0.16	0.06	0.14	0.02	16.92	0.00
	4	0.13	0.30	0.17	0.20	0.06	31.78	0.00
	5	0.22	0.28	0.06	0.24	0.03	11.41	0.00
	6	0.12	0.17	0.05	0.14	0.02	12.29	0.00
	7	0.09	0.20	0.11	0.17	0.04	26.11	0.00
	8	0.14	0.41	0.27	0.20	0.11	54.86	0.01
	9	0.18	0.28	0.10	0.24	0.04	15.60	0.00
	10	0.09	0.39	0.30	0.23	0.11	48.90	0.01
elapsed	1	18.82	44.50	25.67	34.00	11.32	33.30	128.19
	2	25.01	50.65	25.64	35.71	9.12	25.53	83.11
	3	18.44	25.91	7.47	21.81	3.19	14.63	10.19
	4	16.61	44.70	28.09	24.09	10.53	43.71	110.89
	5	31.73	38.60	6.87	34.39	2.42	7.04	5.86

parameter	jackdaw	minimum	maximum	max difference	mean	SD	CV%	variance
	6	42.45	57.72	15.27	50.00	5.70	11.40	32.48
	7	26.62	37.77	11.15	33.07	3.95	11.94	15.61
	8	18.58	40.50	21.93	26.37	7.74	29.36	59.96
	9	19.37	47.75	28.38	36.61	9.90	27.03	97.98
	10	20.66	53.38	32.72	38.56	11.22	29.10	125.92
mean F_1	1	2293.11	2558.19	265.08	2429.83	86.54	3.56	7489.59
	2	2269.38	2541.77	272.39	2418.95	96.47	3.99	9306.56
	3	2314.23	2492.08	177.85	2392.89	57.71	2.41	3330.06
	4	2041.12	2343.56	302.44	2160.07	122.24	5.66	14941.56
	5	2028.80	2675.79	646.99	2487.00	238.54	9.59	56902.93
	6	2160.64	2707.87	547.23	2503.84	191.69	7.66	36746.81
	7	1606.02	2773.46	1167.44	2397.71	425.19	17.73	180785.88
	8	2088.86	2664.17	575.31	2408.87	208.21	8.64	43350.01
	9	1973.75	2604.53	630.78	2341.91	260.19	11.11	67696.69

parameter	jackdaw	minimum	maximum	max difference	mean	SD	CV%	variance
	10	1980.68	2532.16	551.48	2312.38	202.16	8.74	40868.16
mean F_2	1	3502.68	3988.87	486.19	3749.69	181.12	4.83	32803.40
	2	3816.52	4141.99	325.47	3980.61	112.66	2.83	12692.81
	3	3599.30	4163.56	564.26	3866.29	229.71	5.94	52764.45
	4	3865.77	4338.25	472.48	4071.14	161.06	3.96	25939.35
	5	4041.60	4227.25	185.65	4126.51	85.53	2.07	7316.17
	6	3422.27	4252.91	830.64	3755.63	325.60	8.67	106013.75
	7	4112.22	4283.28	171.06	4190.40	73.71	1.76	5433.79
	8	3575.24	4319.48	744.24	4023.60	259.28	6.44	67224.07
	9	3863.41	4179.46	316.05	3976.16	129.75	3.26	16836.02
	10	3841.96	4342.42	500.46	4129.78	193.10	4.68	37288.12
parameter	human	minimum	maximum	max difference	mean	SD	CV%	variance
minimum F_0	1	162.80	232.50	69.70	211.47	21.68	10.25	470.03
	2	173.26	212.82	39.56	196.19	13.41	6.83	179.75

parameter	jackdaw	minimum	maximum	max difference	mean	SD	CV%	variance
	3	176.20	283.55	107.35	251.15	30.20	12.03	912.22
	4	164.59	237.77	73.18	185.03	26.41	14.27	697.47
	5	172.73	232.76	60.03	204.87	23.30	11.37	542.72
	6	177.63	264.10	86.47	220.43	32.24	14.63	1039.66
	7	172.40	187.31	14.91	178.23	4.42	2.48	19.56
	8	159.92	204.78	44.86	174.06	13.42	7.71	180.10
	9	208.79	227.47	18.68	215.97	7.51	3.48	56.43
	10	165.07	219.07	54.00	193.51	18.67	9.65	348.68
maximum F ₀	1	220.99	279.21	58.22	247.47	18.20	7.35	331.19
	2	221.03	277.84	56.81	242.21	16.28	6.72	264.96
	3	324.20	347.65	23.45	336.99	7.73	2.29	59.81
	4	311.62	349.84	38.22	335.38	13.01	3.88	169.20
	5	233.74	307.87	74.13	259.81	21.27	8.19	452.39
	6	288.50	347.65	59.15	325.20	19.19	5.90	368.31

parameter	jackdaw	minimum	maximum	max difference	mean	SD	CV%	variance
	7	277.28	312.34	35.06	295.31	12.01	4.07	144.28
	8	298.58	349.78	51.20	329.61	14.32	4.34	204.96
	9	272.30	301.55	29.25	288.22	9.23	3.20	85.17
	10	314.46	346.65	32.19	337.29	10.86	3.22	118.03
mean F_0	1	215.06	241.03	25.97	229.65	7.41	3.23	54.86
	2	210.57	238.55	27.98	222.82	9.60	4.31	92.12
	3	279.29	312.30	33.01	294.83	12.64	4.29	159.78
	4	201.73	267.85	66.12	232.21	21.39	9.21	457.42
	5	229.27	257.42	28.15	241.56	8.68	3.59	75.40
	6	240.71	301.73	61.02	275.65	16.20	5.88	262.44
	7	210.36	222.77	12.41	215.84	4.58	2.12	20.95
	8	212.51	282.74	70.23	263.28	19.10	7.26	364.94
	9	249.27	263.99	14.72	253.13	4.20	1.66	17.63
	10	246.20	273.85	27.65	255.35	7.89	3.09	62.25

parameter	jackdaw	minimum	maximum	max difference	mean	SD	CV%	variance
stimulus duration	1	0.31	0.40	0.09	0.36	0.03	8.42	0.00
	2	0.52	0.74	0.22	0.64	0.07	10.32	0.00
	3	0.40	0.58	0.18	0.49	0.05	9.93	0.00
	4	0.39	0.57	0.18	0.48	0.06	12.51	0.00
	5	0.44	0.55	0.11	0.48	0.04	8.06	0.00
	6	0.31	0.55	0.23	0.42	0.09	20.17	0.01
	7	0.27	0.66	0.38	0.37	0.10	28.27	0.01
	8	0.38	0.47	0.10	0.42	0.03	7.08	0.00
	9	0.44	0.51	0.07	0.48	0.03	5.27	0.00
	10	0.57	0.67	0.10	0.62	0.03	5.17	0.00
duration of tonal parts	1	0.28	0.38	0.10	0.32	0.03	9.53	0.00
	2	0.49	0.69	0.20	0.59	0.06	10.27	0.00
	3	0.34	0.53	0.20	0.42	0.05	12.43	0.00
	4	0.37	0.53	0.16	0.45	0.06	13.14	0.00

parameter	jackdaw	minimum	maximum	max difference	mean	SD	CV%	variance
	5	0.40	0.48	0.08	0.43	0.03	6.67	0.00
	6	0.22	0.53	0.30	0.37	0.10	27.71	0.01
	7	0.23	0.34	0.11	0.31	0.03	10.81	0.00
	8	0.32	0.42	0.10	0.35	0.03	8.15	0.00
	9	0.39	0.46	0.07	0.42	0.02	5.04	0.00
	10	0.53	0.61	0.08	0.57	0.02	4.24	0.00
elapsed	1	28.75	64.93	36.18	52.13	9.94	19.07	98.88
	2	20.35	47.51	27.16	33.56	9.20	27.41	84.60
	3	24.12	35.28	11.16	29.25	3.90	13.34	15.23
	4	17.08	44.88	27.79	28.40	9.22	32.48	85.07
	5	18.69	56.74	38.05	35.76	10.37	28.98	107.43
	6	31.61	50.03	18.42	39.85	5.79	14.52	33.49
	7	30.32	42.63	12.32	36.24	4.50	12.41	20.22
	8	19.88	38.98	19.10	27.41	5.88	21.45	34.55

parameter	jackdaw	minimum	maximum	max difference	mean	SD	CV%	variance
	9	35.47	47.95	12.48	42.47	3.94	9.29	15.55
	10	25.53	48.10	22.57	40.70	8.69	21.35	75.48
formant 1	1	301.26	1454.20	1152.94	502.39	340.15	67.71	115701.83
	2	306.68	1029.78	723.10	474.81	209.54	44.13	43908.24
	3	190.58	1976.19	1785.61	820.24	650.45	79.30	423082.02
	4	180.35	971.16	790.81	349.27	238.84	68.38	57046.09
	5	275.40	910.59	635.19	573.77	241.02	42.01	58088.33
	6	424.69	1934.33	1509.64	710.34	451.68	63.59	204010.88
	7	453.45	775.56	322.11	591.90	112.01	18.92	12545.54
	8	375.96	441.11	65.15	412.16	22.33	5.42	498.49
	9	289.85	578.36	288.51	428.19	112.72	26.33	12705.92
	10	414.96	1704.32	1289.36	1032.81	381.30	36.92	145392.98
formant 2	1	1794.69	2046.48	251.79	1911.38	73.08	3.82	5340.77
	2	2104.95	2422.20	317.25	2275.25	95.89	4.21	9195.65

parameter	jackdaw	minimum	maximum	max difference	mean	SD	CV%	variance
	3	2282.46	2421.07	138.61	2346.59	43.99	1.87	1934.80
	4	2010.74	2283.25	272.51	2140.17	82.63	3.86	6826.96
	5	2135.93	2372.11	236.18	2286.81	72.16	3.16	5207.53
	6	2206.70	2537.75	331.05	2415.28	119.32	4.94	14237.05
	7	2066.52	2282.61	216.09	2161.68	72.14	3.34	5204.61
	8	2144.07	2235.29	91.22	2192.67	27.94	1.27	780.37
	9	2284.26	2468.60	184.34	2397.24	58.91	2.46	3470.91
	10	1983.99	2234.41	250.42	2093.24	71.46	3.41	5107.07
formant 3	1	2571.73	2839.04	267.31	2657.68	81.36	3.06	6619.75
	2	2888.47	3213.81	325.34	2981.96	97.90	3.28	9583.74
	3	2895.66	3141.34	245.68	2992.17	71.95	2.40	5177.50
	4	2518.42	2743.47	225.05	2608.21	65.00	2.49	4225.50
	5	2786.30	2962.29	175.99	2887.39	53.95	1.87	2910.40
	6	2963.19	3190.46	227.27	3089.34	78.55	2.54	6170.34

parameter	jackdaw	minimum	maximum	max difference	mean	SD	CV%	variance
	7	2815.59	2967.73	152.14	2867.88	56.38	1.97	3178.16
	8	2596.67	2674.89	78.22	2643.33	25.81	0.98	666.04
	9	3112.74	3167.69	54.95	3137.65	21.88	0.70	478.66
	10	2744.37	2894.94	150.57	2808.27	49.73	1.77	2472.71
formant 4	1	3387.84	3821.84	434.00	3573.21	154.55	4.33	23884.71
	2	3546.09	3909.80	363.71	3745.71	93.99	2.51	8833.97
	3	4013.07	4116.02	102.95	4062.16	38.10	0.94	1451.37
	4	3156.77	3569.12	412.35	3357.18	119.08	3.55	14179.77
	5	3718.55	4376.19	657.64	4153.83	205.93	4.96	42405.23
	6	3718.47	4181.59	463.12	3908.41	133.84	3.42	17913.68
	7	3650.35	3911.27	260.92	3794.03	80.69	2.13	6511.30
	8	3900.72	4058.93	158.21	4006.40	50.39	1.26	2538.90
	9	3949.17	4349.00	399.83	4269.37	119.08	2.79	14181.04
	10	3647.91	3756.31	108.40	3699.48	34.46	0.93	1187.53

Chapter 5 - Table 2. Results of the crossed and nested pDFA for human and jackdaw stimuli.

Showing the number (N) of levels of control and test factors, the number of correct classified call with significance values (p), and the acoustic parameters used in the analysis.

species	jackdaws		humans	
pDFA	crossed	nested	crossed	nested
test factor	individuals	group membership	individuals	group membership
control factor	calls	individual	calls	individual
N test	10	2	10	2
N control	6	6	10	10
N correct classified	33	38	87	75
p =	0.001	0.314	0.001	0.206
parameters	mean F ₀ , mean F ₂ , elapsed, stimulus duration	maximum F ₀ , stimulus duration	maximum F ₀ , formant 3, duration of tonal parts	maximum F ₀ , stimulus duration

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Chapter 6:

Long-Term Memory for Affiliates in Ravens

Running head: Ravens remember relationships they had with others

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Summary

Complex social life requires individuals to recognize and remember group members [1] and, within those, to distinguish affiliates from non-affiliates. Whereas long-term individual recognition has been demonstrated in some non-human animals [2-5], memory for the relationship valence to former group members has received little attention. Here we show that adult, pair-housed ravens not only respond differently to the playback of calls from previous group members and unfamiliar conspecifics but also discriminate between familiar birds according to the relationship valence they had to those subjects up to three years ago as subadult non-breeders. The birds' distinction between familiar and unfamiliar individuals is reflected mainly in the number of calls, whereas their differentiation according to relationship valence is reflected in call modulation only. Compared to affiliates, ravens responded to non-affiliates by increasing chaotic parts of the vocalization and lowering formant spacing, potentially exaggerating the perceived impression of body size. Our findings indicate that ravens remember relationship qualities to former group members even after long periods of separation, confirming that their sophisticated social knowledge as non-breeders is maintained into the territorial breeding stage.^{††}

Highlights:

- Ravens remember former group members for extended time periods
- Aside group membership, relationship valence (affiliates, non-affiliates) is memorized
- Familiarity is coded in the number of calls given in response to playback
- Relationship valence is coded in the modulation of response calls

^{††} This abstract or a similar version of it was submitted as conference and workshop applications. In case of acceptance the abstract might be published in the conference booklet and might be found in the internet.

Results

Humans are able to visually recognize, remember and think about hundreds of different faces over decades or longer, but the neural and evolutionary basis for this ability remains poorly understood. Non-human animals living in social groups and/or facing regular encounters with territorial neighbors may also recognize conspecifics on an individual basis [1, 6] and, sometimes, remember them for years [2-5, 7]. Sheep (*Ovis aries*) for example, are able to differentiate between conspecific faces for two years [4] and fur seal pups (*Callorhinus ursinus*) still remember their mother's calls after four years [2]. Long-term memory has been proposed to be particularly important in societies with a high degree of fission-fusion dynamics [8], as specific individuals may meet regularly but after unpredictably long periods of separation. Likewise, memory load may increase when, in addition to individual identity, the social relationships to (temporarily absent) group members need to be remembered [8]. Although dealing with social relationships is often considered a critical driving force in the evolution of advanced cognition [8-10], our knowledge about long-term memory for social relations is limited. So far, studies have tested only for long-term class-level recognition [1] by using in-group and out-group categories such as kin versus non-kin [11] and territorial neighbor versus unknown conspecific [3, 12].

Ravens *Corvus corax* spend their first years in non-breeder flocks, engaging in sophisticated social maneuvers like recruitment to food [13, 14] and tactical deception for access to food caches [15]. Moreover they regularly participate in complex interactions during and after conflicts [16, 17], providing support predominantly to those individuals with whom they share a valuable relationship [16]. The presence of valuable partners (kin and non-kin affiliates) also affects the birds' thoroughness in exploring novel objects [18] and the likelihood of acquiring skills through social learning [19]. Hence, the valence of relationship among individuals may explain much of the social behavior of non-breeding ravens.

Interestingly, non-breeder flocks are not stable units but show high degrees of fission-fusion dynamics over the day and across months [20]. This complex system of coming and going coupled with the pattern of forming valuable relations would make an extensive memory for individuals and their relationships advantageous for non-breeding ravens. In contrast to the vagrant life of non-breeders, reproductively active ravens are highly local, defending a territory year-round. Yet, they may encounter, and even join, non-breeder groups from time to time [21], suggesting that memory for conspecifics may be useful also in the breeding stage.

Here we tested whether adult captive ravens remember their relationship valence to former group members. We made use of the fact that the birds were kept together in one social group as non-breeders and subsequently were housed pair-wise at different locations in Austria and Germany (see the Supplemental Experimental Procedures available online for details). At each current location, we played back calls from previously familiar ravens with whom the focal birds shared an affiliate or non-affiliate relationship, and from unfamiliar ravens, who the birds had not encountered before. Affiliate relationships consisted of seven kin and eleven non-kin pairings. We predicted that birds would not only respond differently to the calls from familiar and unfamiliar conspecifics, but also discriminate between familiar birds according to the relationship valence they had to those subjects up to three years prior as non-breeders.

Throughout the experiment, ravens emitted a total of 6,934 calls (mean=630 /playback), whereby 5,548 (mean=504 /playback) were long distant calls. The number of calls emitted by individuals when listening to the stimuli categories affiliate, non-affiliate or unknown differed significantly (GLMM: $F_{2,177}=4.576$, $p=0.012$). Ravens called less often to unfamiliar individuals than to the two familiar ones (Pairwise comparison: unfamiliar - non-affiliate $\beta=-3.765$, S.E.=1.615, $df=177$, $t=-2.332$, $p=0.049$; unfamiliar - affiliate $\beta=-4.123$, S.E.=1.701, $df=177$, $t=-2.424$, $p=0.049$; affiliate - non-affiliate $\beta=0.358$, S.E.=2.051, $df=177$,

$t=0.174$, $p=0.862$; estimated means for calls per minute: affiliate=8.7, S.E.=1.6; non-affiliate=8.3, S.E.=1.5; unfamiliar=4.6, S.E.=0.8). A similar, but even stronger, effect was observed when we restricted our analysis to long distance calls (GLMM: $F_{2,177}=5.805$, $p=0.004$; Pairwise comparison: unfamiliar – non-affiliate $\beta=-4.509$, S.E.=1.640, $df=177$, $t=-2.750$, $p=0.020$; unfamiliar-affiliate $\beta=-4.608$, S.E.=1.708, $df=177$, $t=-2.699$, $p=0.020$; affiliate - non-affiliate $\beta=0.099$, S.E.=2.011, $df=177$, $t=0.049$, $p=0.961$; estimated means for long distance calls per minute: affiliate=7.9, S.E.=1.6; non-affiliate=7.8, S.E.=1.5; unfamiliar=3.3, S.E.=0.9).

From the originally recorded response calls we analyzed 1,294 calls without interfering background noises. From these remaining calls we extracted six components from measured call parameters (Table 1). All six variables explained 66.5% of the overall variance of the data (for loadings of the parameters on each component see Table 2). The final models including sex relation, kinship and affiliation (Table S1) of components 1, 3, 4, 5, and 6 differed significantly between treatments. In the main text we only present results for component 5 (for further details see Table S2).

Component 5 revealed a highly significant difference between the three affiliation categories (GLMM: $F_{2,1291}=12.368$, $p\leq 0.001$) when corrected for the other two fixed factors, kinship and sex relation. Notably, pairwise comparison indicated a significant effect of relationship valence (affiliate – non-affiliate: $\beta=0.651$, S.E.=0.235, $df=1291$, $t=2.772$, $p=0.011$), along with the difference between familiar and unfamiliar birds (affiliate - unfamiliar: $\beta=0.942$, S.E.=0.212, $df=1291$, $t=4.466$, $p\leq 0.001$; non-affiliate - unfamiliar: $\beta=0.290$, S.E.=0.290, $df=1291$, $t=0.116$, $p=0.012$). Interestingly, this component includes formant spacing and harmonicity (Table 2); it has the highest value in calls emitted in response to affiliates and the lowest value in calls emitted in response to unfamiliar individuals (Figure 2). Kinship (GLMM: $F_{1,1288}=7.992$, $p=0.005$) and sex combination (GLMM: $F_{1,1288}=5.509$, $p=0.019$) significantly influenced component 5. Pairwise comparisons revealed

that ravens emit calls with lower component 5 values when calling back to kin affiliates (non-kin – kin: $\beta=-0.194$, S.E.=0.241, df=1288, $t=-2.347$, $p=0.019$) and calls with lower component 5 values when calling back to same sex combinations (same sex – different sex: $\beta=-0.681$, S.E.=0.194, df=1288, $t=-2.827$, $p=0.005$).

Discussion

Ravens separated for up to three years responded differently to playbacks of former group members according to the categorization into affiliated versus non-affiliated individuals and familiar versus unfamiliar birds. This differentiation is expressed in call numbers and call modulation respectively and indicates that ravens possess long-term memory not only for categories based on familiarity ('former group members') but also for the valence of their relationships to them (former affiliates or non-affiliates). Distinctions between familiar and unfamiliar individuals are encoded mainly in the number of calls. The response to relationship valence is reflected in call modulation only (component 5).

Long-term Memory

The ravens' ability to differentiate between familiar and unfamiliar individuals in our experiment exemplifies long-term memory at class-level recognition. These findings are in accordance with studies showing that songbirds remember pair-partners [22], territorial neighbors [3] as well as nesting and feeding sites for an extended time period [23, 24]. However, to our knowledge, this is the first study showing that non-human animals remember the relationship valence of former group members, that is, whether others were affiliates or non-affiliates. Although the results were suggestive, our set-up is not conclusive concerning memory for specific individuals [1]. It could be enough that the birds were

memorizing former group members according to the categories ‘nice/affiliates’ and ‘not nice/non-affiliates’.

The time span tested for memory in our study is comparable to the time ranges known from other social *mammals* (two years in sheep, four years in seals and cotton-top tamarins) [2, 4, 7]. So far long-term memory in birds has been considered as remembering neighbors [3] or places from one breeding season to the next - roughly nine months - [23, 24], whereas long-term memory of social relationships during territorial defense, i.e. wrens (*Troglodytes troglodytes*) [25] and nightingales (*Luscinia megarhynchos*) [26], was considered as remembering individuals over a period of one night. In comparison to those results, our maximum separation of three years appears to be a rather long period; however, it only represents a fraction of a raven’s maximum lifespan of 25-30 years in the wild [27]. Hence, the birds’ ability to remember familiar individuals might well exceed the tested timespan, particularly since the memory persists after the birds have made the transition from non-breeder to breeder status, as was clearly the case in the current study. Tested individuals were aviary birds and thus lived under relatively stable conditions, which might have led to an enhanced memory for relationship valence. Nevertheless, recent field studies suggest that temporarily stable subgroups [20, 28] exist within non-breeder flocks of ravens, providing opportunities for regular encounters. Although our findings are consistent with the idea that the high degree of fission-fusion dynamics found in raven non-breeder flocks may have selected for enhanced memory capacities, further studies should test birds for longer time periods, for the ability to differentiate between a number of different individuals, and for a greater variety of relationship qualities.

An alternative explanation for our results might be that ravens were solely responding to subtle differences in call features of the playback stimuli. This is unlikely because our control birds, which were unfamiliar to all birds, were tested with the same acoustic stimuli as the nine birds that were housed together as non-breeders; however, the control birds did not

discriminate between stimulus categories. Calls used as stimuli possibly represent different dialects and thus group-members of the previous non-breeder flock would only differentiate between same dialect versus different dialect and control birds would not differentiate as all calls are from an unknown dialect. However, this alternative hypothesis for the differentiation between familiar and unfamiliar birds cannot explain why test subjects could discriminate within these supposed dialects, i.e. between affiliates and non-affiliates.

A potential shortcoming of our set-up could be seen in the fact that the affiliate category consisted of kin *and* non-kin whereas the non-affiliate category consisted of non-kin only. However, this distribution reflects the nature of many complex social systems, whereby kin share valuable relations of different kinds and degrees (e.g.: [5, 29, 30]). From an evolutionary point of view this makes sense because of the benefits of indirect/inclusive fitness [31]. Finally, our birds could only be tested in pairs, raising the possibility that the individuals' responses during the test might have been influenced by the behavior of the pair-partners. Note that we applied stimuli with similar relationship valence to both individuals of the pair (Table S3), so that the birds' responses could be enhanced but should not be inhibited or even annihilated by the pair partner.

Call Modulation

Interestingly, the raven's ability to differentiate the relationship valence between familiar birds became evident with a detailed acoustic analysis only. Their response to a previously familiar and non-affiliated individual, as compared to an affiliated one, was characterized by lowering the formant spacing and increasing the chaotic parts of the vocalization. This suggests that ravens exaggerated the impression of body size with former non-affiliates but not with affiliates; with unfamiliar birds, the formant dispersion was the lowest, i.e. they increased their perceived size as compared to affiliates and exaggerated more than to non-affiliates. It previously has been hypothesized that call structure correlates

with social valence in birds and mammals [32] but to our knowledge, this is the first time showing how songbirds use formant dispersion to encode social valence.

In addition to responding to social valence, ravens adjusted call characteristics according to inter- and intra-sex competition, as calls emitted to same-sex stimuli were lower in component 5. Similarly, when calling back to kin affiliates ravens revealed lower values in component 5 than when calling back to non-kin affiliates. Ravens may profit from discriminating kin from non-kin during pair formation and territory defense; as non-breeders, they seem to use this ability for sharing information [19] and providing social support during and after conflicts [17]. Note that about half of the affiliated stimuli played back were from non-kin, indicating that the ravens' differentiation according to relationship valence is not based on kinship relations only.

Numerous studies have demonstrated that animals can differentiate between various categories of vocalizations [6, 32, 33] and encode specific information in temporal and/or spectral call parameters [34, 35]. In our study, an important variable represented in component 5 is the relation of harmonic parts of the call to chaotic parts of the call. During enhanced excitement levels, ravens increase the chaotic parts of the call, as observed in mammalian vocalizations [36]. Notably, call parameters in component 5 may affect the acoustically perceived size of the calling individual [37]. The primary parameter determining formants is the length of the vocal tract [38]. Vocal-tract length correlates in various mammal species with body size [37, 39]. The link between these components should enable calling individuals to manipulate or slightly change the acoustically perceived size. As formant dispersion and vocal tract length seem to be negatively correlated in ravens (own unpubl. data), low loadings in component 5 represent lower formant spacing and thus appear to simulate longer vocal tract sizes. Our results reflect the size exaggeration shown in red and fallow deer [37] and add a biologically meaningful interpretation to the findings of vocal tract resonances in avian vocal production [40, 41]. Even though ravens emitted calls differing in

formant spacing as responses to playback stimuli, we have no evidence yet that the acoustic changes can be perceived. However, formant perception has already been demonstrated in some birds (e.g.: *Grus americana*: [42], speech producing parrots like: *Psittacus erithacus*: [43]) as well as in mammalian species (e.g.: *Cervus elaphus*: [44], *Macaca mulatta*: [45]).

Taken together, we demonstrate that ravens have an extensive memory of former group members and, via call modulation analysis, reveal that they differentiate between affiliates and non-affiliates. Our study provides support for using natural communication and acoustic signals as a tool for addressing cognitive questions (e.g.: [30, 46-48]). Applying this approach to bird species differing in degrees of social complexity seems promising and may expand our understanding of avian cognition and convergent evolution of socio-cognitive skills.

Methods

Subjects and Housing

We used a total of 16 adult ravens housed in male-female pairs in public zoos or at private keepers (see supplementary experimental procedures). Nine of these birds were previously part of a non-breeder group established in 2004 at the Konrad Lorenz Forschungsstelle (KLF) in Grünau, Austria. After reaching sexual maturity, birds were allowed to form breeding pairs; pairs were then transported to their new enclosures and have not heard or seen their former group members since (mean distance between enclosures 170km; min. 18km; max. 389km). At the time of the experiment (October 2009-March 2010), they had been separated for an average of 24 months (min. 8; max 36). We here considered them as previously ‘familiar’ individuals. Importantly, records of the birds’ social behavior were available for the entire period as non-breeders (2004-2007). On the basis of these protocols on agonistic and affiliate interactions, the relationship valence among birds was

calculated and the resulting components were labeled as value, compatibility and security [16]. For the current study, we considered birds with high loadings in these components as affiliates and birds with low loadings as non-affiliates, taking possible effects of kin, sex and age into account (see supplementary information for details; Table S3). Highest loadings were mostly found among siblings [16]. In addition to the nine familiar birds, we used seven individuals, which had not been part of the non-breeder group at KLF. These control birds had no experience with any of the other ravens and thus were considered as ‘unfamiliar’ individuals.

Stimulus Recording and Playback Presentation

For playbacks we used a specific long distance call ‘rab’, a short vocalization with low pitch, few harmonics and amplitude modulation typically used in territorial defense (Figure 1). Stimuli were recorded shortly before the experiment, between March 2008 and October 2009, from ten individuals, housed at seven different locations (see supplemental experimental procedures; Table S3). Recordings of seven individuals were used more than once, depending on the relationship valence among test subjects.

Each raven pair was subjected to two playback sessions, featuring either male or female callers. We focused on behavioral responses of both male and female individuals to every playback. Sessions were conducted in the morning (between 9-11 am) and in the afternoon (between 2-4 pm), respectively, with the order of males and females being counterbalanced across subjects. For those birds (n=9) that had been part of the non-breeder group at KLF, stimuli categories consisted of calls from a familiar raven with which both birds of the pair previously shared an affiliate relationship (*i*) or non-affiliate relationship (*ii*) or from an unfamiliar raven, which they did not know at all (*iii*). Control birds (n=7) that had not been part of the non-breeder group were presented with calls from the same individuals; however, to them, all three callers were unfamiliar. All playback stimuli used per session were roughly matched for the callers’ age and broadcasted at naturally occurring

sound pressure levels. The order of categories was counterbalanced across subjects (for details see supplementary experimental procedures, Figure S1). Stimuli were presented with speakers (Ion Block Rocker (freq. response: 70Hz-50kHz $\pm$ 3dB) connected to a MacBookPro using Quick Time Player Pro (V:7.6.9). All experiments were audio and video recorded (Marantz PMD-660; Sennheiser K6ME66; Sony Handycam DCR-HC23) by two human experimenters, each of whom focused on one member of the tested pair. This enabled us to identify all vocalizations each bird made in response to the stimuli sets presented (when being the focal subject and when being the pair-partner). Note that the responses to both sets of stimuli (own and partner) entered our statistical model.

Playback Analysis

We measured the acoustic features of these calls using custom-built programs in PRAAT 5.2.10 DSP package [49] that automatically logged these variables in an output file. Call parameters measured were: call length, dominant frequency, dominant frequency of the first, second and third part of the call, mean minimum maximum and standard deviation of harmonicity to noise ratio, formant candidates from 1-5, formant dispersal, alpha ration 1000 and 2000, first to third peak frequency of amplitude modulation (for further details see supplemental experimental procedures).

Statistical analysis was conducted using IBM SPSS for Mac 19. To reduce data dimensionality of call parameters we calculated a Principle Component Analyses, using an un-rotated correlation method and setting a minimum eigenvalue of 1.0 for components to be extracted. Differences between reactions to the different stimuli categories were calculated with Type III Generalized Linear Mixed Models (GLMM). To correct for differences between playback individuals, focal individuals and presentation order, we included the nested term (focal(session(call))) and playback individual as a random factor. We used standard model selection procedures [50] for acoustic parameters. For post-hoc tests we used Student's *t*

Statistic with sequential Bonferroni correction for alpha because of repeated pairwise comparisons.

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Tables

Chapter 6 - Table 1. Explained Variance.

Six components with eigenvalues above 1.0 were extracted. Eigenvalues, percent of variance and cumulative percent are shown.

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	3.528	17.640	17.640	3.528	17.640	17.640
2	2.477	12.386	30.026	2.477	12.386	30.026
3	2.356	11.782	41.808	2.356	11.782	41.808
4	1.980	9.902	51.709	1.980	9.902	51.709
5	1.701	8.505	60.214	1.701	8.505	60.214
6	1.263	6.316	66.530	1.263	6.316	66.530

Chapter 6 - Table 2. Component Matrix.

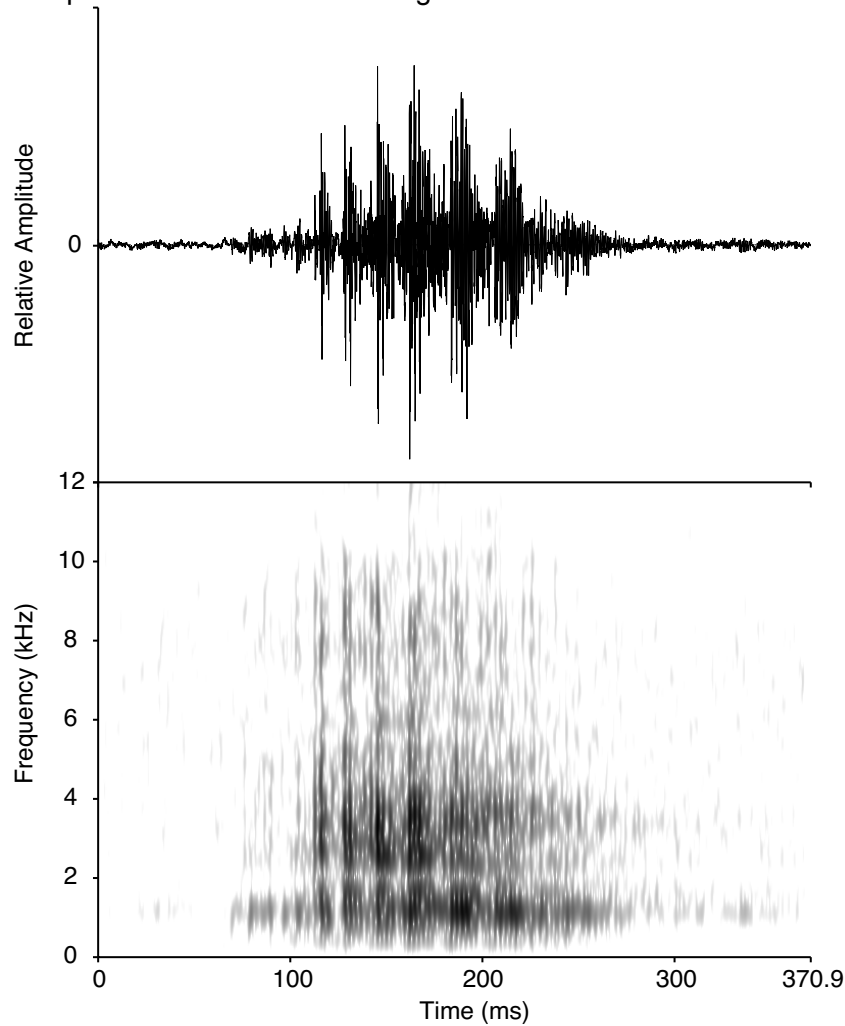
Loadings of the original variables on the different components are shown. Loadings below ± 0.1 are omitted and loadings exceeding 0.4 are highlighted with bold letters.

	Component					
	1	2	3	4	5	6
Call length	.275	.220		.161	-.124	-.580
Mean harmonicity to noise ratio	.369	-.376		.560	-.440	
Minimum HNR				-.212	.345	.642
Maximum HNR		-.247	.115	.286	-.270	-.418
Stdv. HNR	.222	-.483	.173	.435	-.223	.293
Formant 1	-.758			.166		
Formant 2	-.557	-.374	.388		.282	-.240
Formant 3	-.361	-.573	.397	.223	.291	
Formant 4	-.272	-.559	.363	.293	.324	
Formant 5	.474	.107	-.336	.441	.650	-.121
Formant dispersal	.474	.107	-.336	.441	.650	-.121
Dominant frequency	-.568	.290	-.142	.448	-.141	
Dominant frequency of first third	-.398	.416	-.203	.180		
Dominant frequency of second third	-.490	.298	-.126	.348		
Dominant frequency of third third	-.344	.259	-.270			.157
Alpha 1000	.527	-.220	.200	-.509	.176	-.140
Alpha 2000	.640	-.140	-.186	.272	-.267	.266
1 st peak frequency of amplitude modulation	.279	.474	.669	.122		
2 nd peak frequency of amplitude modulation	.261	.510	.725	.176		
3 ^{ed} peak frequency of amplitude modulation	.223	.464	.661	.188		

Figures

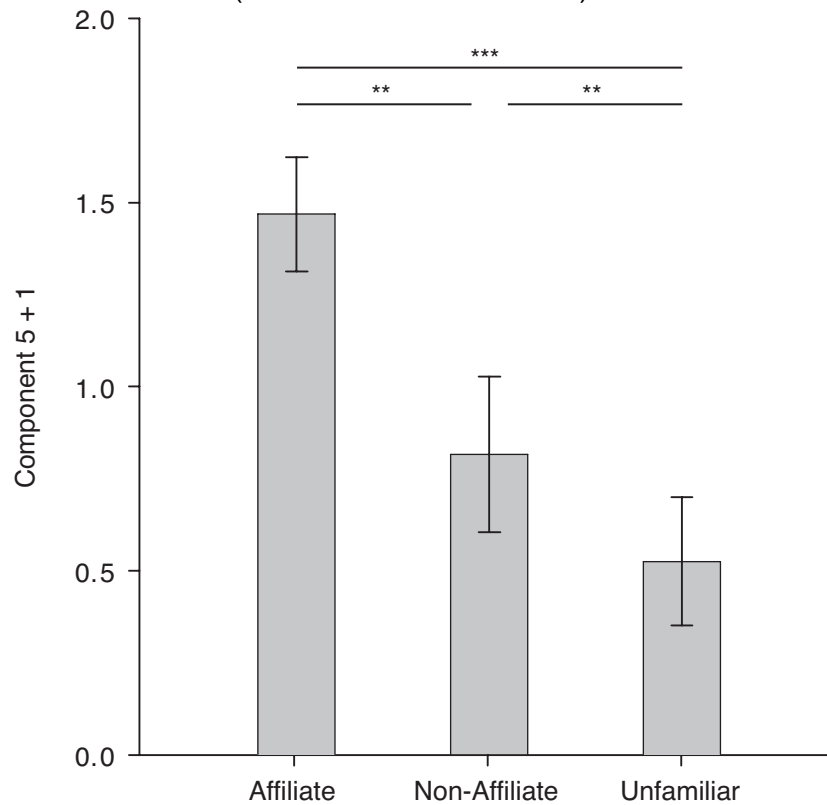
Chapter 6 - Figure 1. Example spectrogram and oscillogram of a stimulus call.

Amplitude modulation is best seen in the oscillogram, low frequency and noisiness in the spectrogram. (spectrogram settings: FFT with Gaussian window shape; windowlength = 0.003 s; dynamic range = 40dB). For details on stimulus presentation and experimental setup see also Table S3 and Figure S1.



Chapter 6 - Figure 2. Differences between playback categories in component 5 of call parameters.

Analysis of call parameters show that they react different to affiliate, non-affiliate and/or unknown ravens (see also Table S1 and S2).



Supplement: Long-term memory for affiliates in ravens

Chapter 6 - Table S1 related to Figure 2. Model Selection.

All components of call parameters were analyzed with the three fixed components kinship, sex relation and affiliation. In all components the full model was also the final model as AICc values were the lowest. Significant relationships are highlighted in bold letters.

	df	F	P
component 1	AICc: 2656.152		
kinship	2	0.858	0.354
sex relation	1	7.770	0.005
affiliation	2	4.118	0.003
component 2	AICc: 3093.280		
kinship	2	0.121	0.728
sex relation	1	0.004	0.947
affiliation	2	3.505	0.030
component 3	AICc: 3297.639		
kinship	2	0.006	0.938
sex relation	1	2.968	0.085
affiliation	2	3.722	0.024
component 4	AICc: 2945.752		
kinship	2	2.191	0.139
sex relation	1	1.182	0.277
affiliation	2	4.956	0.007
component 5	AICc: 3387.972		
kinship	2	7.992	0.005
sex relation	1	5.509	0.019
affiliation	2	12.368	≤0.001
component 6	AICc: 2712.115		
kinship	1	0.153	0.695
sex relation	2	5.654	0.018
affiliation	1	5.330	0.005

Chapter 6 - Table S2 related to Figure 2. Pairwise Comparisons.

Significant results are presented only. All pairwise comparisons were calculated using Student's *t*-Test and sequential Bonferroni correction. Only significant differences are presented.

sex relation	estimated means		β	t	p
	same sex	different sex			
component 1	0.096	0.599	-0.504	-2.788	0.005
component 5	-0.404	0.278	-0.681	-2.827	0.005
component 6	-0.327	0.088	-0.416	-2.378	0.018
kinship	kin	non-kin			
component 5	0.034	-0.160	0.194	2.347	0.019
affiliation	affiliate	non-affiliate	unfamiliar		
component 1	0.694	-0.063	0.412		
non-affiliate vs. unfamiliar			-0.474	-2.641	0.025
component 3	0.509	0.022	-0.179		
affiliate - unfamiliar			0.688	2.703	0.021
component 4	0.125	-0.242	0.301		
non-affiliate - unfamiliar			-0.543	-3.121	0.006
component 5	0.468	-0.184	-0.474		
affiliate - non-affiliate			0.651	2.772	0.011
affiliate - unfamiliar			0.942	4.446	≤0.001
non-affiliate - unfamiliar			0.290	0.116	0.012
component 6	0.255	-0.558	-0.055		
non-affiliate - unfamiliar			-0.503	-2.821	0.015

Supplemental Experimental Procedures

Animal Housing

Experiments were conducted on adult ravens kept in male-female pairs at Alpenzoo Innsbruck, Cumberland Wildpark Grünau, Konrad Lorenz Forschungsstelle, Wildpark Wels, Wildpark Haag, Vogelpark Turnersee (all Austria), Wildlife Enclosure in the National Park Center Lusen (Germany), Wildpark Goldau (Switzerland) and at private keepers in Wolkersdorf and Weidling (all Austria). Table S3 lists the nine birds from the former non-breeder group in Grünau, Austria, their kinship and affiliate relationships as well as their assignment as affiliates and non-affiliates in the playback experiment. Furthermore, Table S3 lists the seven birds used as controls in the playback experiment (i.e. having no experience with the played back ravens). The remaining two pairs have been used for stimuli recording only.

In all but one case, affiliates were characterized by high loadings in value (featuring high rates of allo-preening, contact sitting and help in agonistic support) and compatibility (high tolerance to approaches and low rates of aggression and counter-intervention). The exception was the adult male H, whose relations to subadult birds in the non-breeder group was expressed in tolerance to approach and aggression levels; thus, affiliate dyads with H had a high loading in compatibility only. The relationships of all dyads used in the experiment were stable across the entire period the birds lived together in a social group, i.e. all had high loadings in the security component.

Chapter 6 - Table S3 related to Figure 1. Background information on test subjects.

Ravens (ID, sex) are listed according to pair membership (number 1-10) and current housing. Subjects of pairs 1-5 were part of the non-breeder group at WP Grünau, of which all kin and affiliate relations are listed. For pairs 6-10 relationships are unknown. (Note that the female Mä of pair 5 was also not part of the non-breeder group and consequently no background information is available). The affiliate and non-affiliate same-sex stimuli used in the playback are listed per individual. Each individual was also subjected to the respective stimuli of the pair-partner, and its responses to both sets of stimuli (own and partner) entered our statistical model. We excluded two pairings (H>T, D>Q) in our model because their affiliation to the same-sex playback of the respective partner was neutral. Thus a total of 18 affiliated and 18 non-affiliated pairings were tested. Out of the affiliate combinations, seven were from kin and eleven from non-kin. Birds of pair 6-8 and the female Mä from pair 5 served as controls in the playbacks. Pairs 9,10 have been used for additional stimuli recording.

Pair	ID	Sex	Current Housing	Former Housing	Kinship	Affiliation	Stimulus affiliate	Stimulus non-affiliate
1	I	M	WP Grünau	WP Grünau	Q, T	Q; O, E	Q	L
1	O	F	WP Grünau	WP Grünau	E	E; I, Q	E	D
2	Q	M	NP Bayr. Wald	WP Grünau	I, T	I; O, E	I	P
2	E	F	NP Bayr. Wald	WP Grünau	O	O; I, Q	O	D
3	H	M	KLF	WP Grünau	-	P, Q; D*	Q	L
3	D	F	KLF	WP Grünau	L, P	L, P; T	T	E
4	L	M	Zoo Wels	WP Grünau	D, P	P; D, T	P	I
4	T	F	Zoo Wels	WP Grünau	I, Q	L, P; D	D	E
5	P	M	Wolkersdorf	WP Grünau	D, L	L; D, T	L	Q
5	Mä	F	Wolkersdorf			Control	D**	O**
6	Kä	M	WP Haag			Control		
6	Lu	F	WP Haag			Control		
7	Ru	M	Weidling			Control		
7	Ro	F	Weidling			Control		
8	Pa	M	Zoo Innsbruck			Control		
8	Fl	F	Zoo Innsbruck			Control		
9	Gm	M	WP Goldau					
9	Gf	F	WP Goldau					
10	Km	M	VP Turnersee					
10	Kf	F	VP Turnersee					

*As the only adult, H behaved aggressively to most of the group members; his relationship to these three birds, however, was tolerant and non-aggressive.

**Stimuli for the individual Mä were the female stimuli for P only, as the female Mä was not part of the group.

Vocalizations and Recordings

We differentiated between long distance calls/broadcast vocalizations (a large variety of high amplitude calls) and soft calls/proximal vocalizations (relatively low intensity signals produced in close spatial proximity of conspecifics and used in a variety of communicative

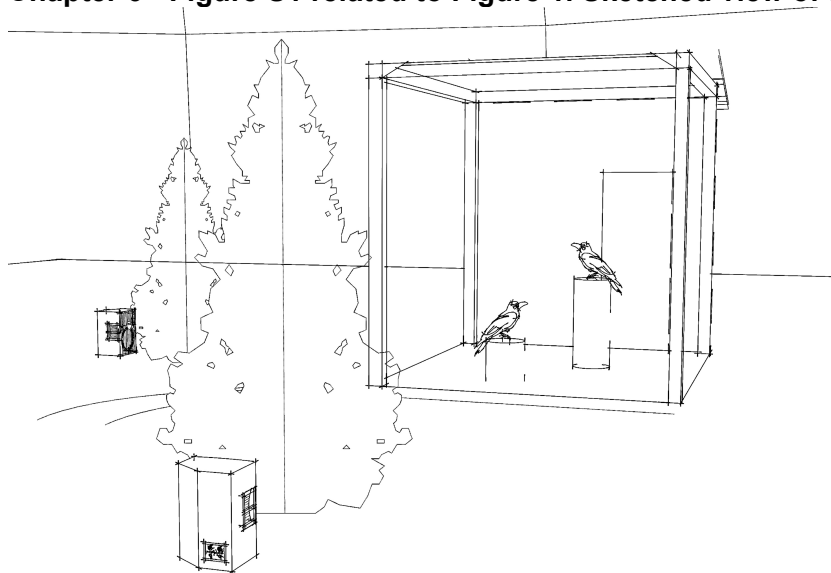
and social contexts) [S1]. The seven locations of stimuli recordings were Cumberland Wildpark Grünau, Konrad Lorenz Forschungsstelle, Vogelpark Turnersee, Wildpark Wels, Wolkersdorf, all Austria; National Park Center Lusen, Germany; Wildpark Goldau, Switzerland.

Playback Presentation and Analysis

A playback session consisted of three blocks; each presenting calls of one of the stimuli categories (i-iii). Per block, a 15-minute baseline without playback was followed by 5 calls of a given category, a 1-minute intermission interval, 5 calls of the same category, a 1-minute interval, and another 5 calls of the same category. Thus, we presented a total of 15 calls per individual, category and block, separated by 15 min pauses.

We conducted two playbacks for each raven pair; one in the morning and one in the afternoon, with either female or male stimuli and counterbalanced combinations between pairs. Two loudspeakers were set up in the vicinity of the aviary ($10\text{m} \pm 3\text{m}$) behind a visual barrier. Each playback block was presented from one side, whereby each successive playback block was played back from the respective other location, so that stimulus block one and three were played back from the same location and two from the other location. The randomization of the playback order for familiarity also resulted in the randomization of familiarity and location combinations, whereby starting location was alternating between morning and afternoon playbacks and was randomized between pairs (Also see Figure S1).

Chapter 6 - Figure S1 related to Figure 1. Sketched view of the playback setup.



Responses were coded during the one-minute intermission intervals and five minutes after the last playback of the session with Solomon coder (V: beta 11.01.22 see [S2]) video analysis software. All emitted calls were counted and categorized as long distance calls and soft calls. As vocal interactions between distant individuals (i.e. our simulated intruder and the focal subject) necessitate a minimum threshold sound pressure level, we focused on long distance calls for further analysis, as long distance calls are obvious response to our stimuli whereas soft-calls in this context are mainly used for within-pair communication.

Acoustic Analysis

The acoustic analysis was performed with PRAAT DSP package 5.2.10 [47]. We used dominant frequency, formants, harmonicity, call length, alpha ratios and frequencies of amplitude modulation as parameters to describe long distance calls of ravens.

To measure call length we extracted the F0 contour of calls using the 'To pitch (cc)' command (time step = 0.01s; minimum and maximum F0 = 300 and 900 Hz). Time-varying numerical representations of the F0 contour were compared with the F0 as visualized on a

spectrogram to test if F0 was tracked correctly. In case of incorrect software tracking the F0 was adjusted using the 'Edit' function. Call length was calculated with begin- and end times of the pitch contour. Due to the considerable influence of amplitude modulation on the perceived and calculated pitch was not employed as measurement value for raven calls.

To quantify the harmonic parts in relation to the chaotic parts of the call, we measured the harmonics-to-noise ratio (HNR), which calculates the relation of the energy in harmonics to the energy in noise in dB (low levels represent main energy in the periodic part). HNR was measured using the 'To Harmonicity (cc)' command in PRAAT (time step = 0.01; minimum pitch (Hz) = 300; silence threshold = 0.1 and periods per window = 1) and Minimum HNR, Maximum HNR and the standard deviation of HNR were obtained.

Dominant frequency was measured of the complete call and the first to third part. As all raven call frequencies were above 100 Hz we applied a stop Hann band filter from 0 Hz to 100 Hz with a 150 Hz smoothing to reduce influences of wind noise on dominant frequency measurements. In a long-term average spectrogram with a 50 Hz bandwidth we extracted frequency values with the 'Get frequency of maximum' command (Minimum and maximum frequency = 100 and 6000).

For the alpha ratios we used the equivalent Hann band filter and applied a long-term average filter (for alpha 1000: bandwidth = 1000 Hz; for alpha 2000: bandwidth = 200). We extracted dB measurements for the first two columns representing the sound pressure level for 0-1000 and 1000-2000 in alpha 1000 and 0-2000 and 2000-4000 in alpha 2000, respectively. Subsequently we calculated the difference between the first and the second frequency range and thus retrieved a relative dB value of the lower frequency in relation to the upper frequency level for both alpha 1000 and alpha 2000.

To obtain amplitude modulation an intensity object was extracted with the 'To Intensity' command (Minimum pitch = 200 Hz; time step = 0.001 s), the dc offset was removed from intensity data by subtracting the mean energy. We used the 'Down to Matrix' command to retrieve numerical representations of the intensity change and created a sound slice on the basis of this matrix. A sine wave with the same length as the original phonated call

$(0.5 + 0.5 \cdot \sin(2 \cdot \pi \cdot x / \text{length of the call} + 3 \cdot \pi / 2))$ was created. The sine wave and the original amplitude were multiplied with the 'Formula' command and a long-term averaged spectrum on the basis of the created sound was conducted. In order to retrieve the frequencies of the amplitude modulation we measured frequencies of the first three peaks.

For formant measurements we used the 'To Formant (burg)' command (time step = 0.025 s; Maximum number of formants = 5; Maximum formant = 6000 Hz; window length = 0.03 s; Pre emphasis = 10 Hz) and extracted mean formant values for f1 to f5. Formant dispersal was calculated applying the equation: $\text{formant dispersal} = (f_4 - f_1) / 3$.

Supplemental References

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- S2. Péter, A. (2011). Solomon Coder (version beta 11.01.22): A simple solution for behavior coding, retrieved from <http://solomoncoder.com/> (Last Viewd 08/2011). Volume 2011.

General Discussion

In this thesis I have been able to show (1) production mechanisms of raven calls, (2) structure of selected vocalizations and (3) the cognitive abilities of raven to differentiate between various call categories. I chose this integrative approach because it may represent a viable and fruitful path to understand signal evolution and function. Based on the combination of morphological studies, along with bioacoustics and cognitive abilities me and my co-authors were able to show various interesting details of raven communicative abilities, which here will be summarized and discussed in short.

We first investigated the structure of the vocal organs in *Corvus corax* in chapter 1 (Boeckle & Bugnyar in submitted). Especially size related features seem to be relevant for the analysis of raven acoustic signals. Formant frequencies that in many species are cues to body size (Charlton, Zhihe & Snyder 2009; Fitch & Fritz 2006; Ghazanfar et al. 2007; Reby & McComb 2003) are also found in ravens (see chapter 1 and 6). Whether the morphological differences between sexes and individuals might not be large enough for clear differentiation between classes and individuals is still to be investigated. However we were able to demonstrate differences within an individual that transmits different levels of motivations (Morton 1977) when calling back to affiliates or non-affiliates in chapter 6 (Boeckle & Bugnyar 2012). We also report that there are correlates of motivational structure and formant dispersal. The flexibility of the vocal tract in ravens from an un-extended to an extended length is low and is about 1.5 cm (see chapter 1). While shortening the VTL by compression is not included in this differences, it seems that also inter-individual differences between individuals, that range from minimum 10 cm to maximum 17 cm measured in an un-extended excised tract, should be perceivable (see chapter 1; Boeckle et al. in prep.).

Similarly differences that transmit sex and age of the caller were found in source related measurements in food calls (chapter 2; Boeckle, Szípl & Bugnyar submitted). Sex differentiations via acoustic analysis do not seem reliable, as predicted by other authors (Fitch & Hauser 2002; Patel, Mulder & Cardoso 2010), probably because slight selection pressures change internal structures correlated with fundamental frequency (Fitch & Hauser 2002) and sexual size differences might be too small to be shown within many birds (Patel et al. 2010). Still differences that might be related to maturing of internal structures and/or increasing motor control with age can be perceived in the source related measurements of food calls (chapter 2; Boeckle et al. submitted).

In addition to size and age differences individual differentiation seems plausible based on the acoustic structure of raven yells (chapter 3; Boeckle, Szípl & Bugnyar 2012). Individual differences are correlated with source-dependent measurements of raven yells and are perceived in a habituation-dishabituation experiment (chapter 3; Boeckle et al. 2012). Especially the balancing for age and sex in our playback study, make it likely that the only difference between presented stimuli are based on individuality. Thus calls of individuals that are unfamiliar to the perceiver, i.e. our focal individual, have to rely on individual differences between the habituation and dishabituation stimuli.

Similarly, raven long distance calls are differentiated by tested individuals based on the acoustic features of the territorial call (chapter 4; Boeckle & Bugnyar in submitted). Whereas in food calls no formant frequencies can be perceived based on the interaction of fundamental frequency and formant dispersal, long distance calls show clear formants (chapter 6; Boeckle & Bugnyar 2012, in submitted). As individuality might be easier to encode in a more complex signal (Pollard & Blumstein 2011) individual differences could be more pronounced than in yells. While the detailed analysis of differences between individuals is still pending, differentiating between two unknown territorial callers is apparent (chapter 4; Boeckle & Bugnyar in submitted). Interestingly, in our playback study (chapter 4; Boeckle &

Bugnyar in submitted) ravens seem to respond more to territorial callers, that call from different places around their territory, while we were unable to find this effect in food yells (chapter 3; Boeckle et al. 2012). Furthermore, while the location of the individual caller seems to be important in one call and not in the other call type, general response did not differ between the two call types (unpublished data). This indicates that any call that does not come from the pair-partner and possibly also not from offspring that is still cared for (study in prep by Weigersdorfer, Boeckle, & Bugnyar) induce high territorial response of the territory holders. Interestingly though especially in territorial playbacks, female stimuli elicited higher territorial calls than male stimuli. Yet it is unclear whether territorial responses are stronger by the male partner than by the female, as effect size might be small and the data set was too small to indicate these differences (chapter 4; Boeckle & Bugnyar in submitted).

In general individual recognition is supposed to be one of the fundamental mechanisms underlying any complex social interaction (Steiger & Müller 2008; Tibbetts & Dale 2007; Tibbetts, Sheehan & Dale 2008). This ability is discussed to be demanding and has so far been discussed only to be fully proven in cross-modal studies (Kondo, Izawa & Watanabe 2012; Proops, McComb & Reby 2009; Townsend, Allen & Manser 2012). On the other hand class level recognition is expected to be less demanding. In both abilities the characteristics that differentiate between the classes (individuality, kinship, familiarity, etc.) might have to be learned. Individual recognition is based on learning the combination between individual characteristics and the specific individual. On the other hand class level recognition might be applied to unknown individuals as soon as the categories are formed and in case the characteristics are constant across individuals, like shown in chapter 2 (Boeckle et al. submitted) in food calls of ravens. A category that might be used when encountering unknown individuals but still is based on individual recognition might be individual differentiation. Thus, perceivers that are ignorant about the identity of the caller, might still be able to differentiate between two unknown individuals as discussed in chapter 3 (Boeckle et al. 2012) and chapter 4 (Boeckle & Bugnyar in submitted). In both chapters focal individuals

have already entered the breeding stage. We expect that also non-breeders at least as subadults have developed the cognitive mechanisms responsible for individual differentiation.

Based on the abilities of acoustic differentiation between callers in ravens, we expect that also other corvid species might have the ability to differentiate between conspecifics. Additionally it might be possible that not only conspecific callers can be differentiated based on the individually distinct call characteristics but also heterospecific callers. This was shown in chapter 5 (Wascher et al. 2012), where results reveal that crows are able to differentiate between familiar and unfamiliar callers of two different species they regularly encounter (Lockie 1956). While differences between the two species (humans and jackdaws) were apparent focal individuals responded differentially via classifying them as familiar or unfamiliar. Human familiar stimuli were collected from care-takers and thus crows responses might be different to familiar individuals of jackdaws that breed and feed in the vicinity.

In addition to the individual differences in call structure and call differentiation we predict that ravens based on their complex social system (e.g. Marzluff 2005) are able to memorize affiliations they had with other individuals over longer periods. The social brain (Dunbar 1992) in combination with fission-fusion systems (Aureli et al. 2008) might require ravens to remember individuals over prolonged periods of time. Especially demanding might be the non-breeder stage, where constant forming of groups and subgroups (Braun et al. 2012; Dall & Wright 2009; Huber 1988; Huber 1991; Wright, Stone & Brown 2003) in combination with large roaming-areas the number of individuals (Heinrich et al. 1994; Huber 1988; Huber 1991). We therefore tested territorial ravens' ability to remember individuals with whom they lived together in a non-breeder flock and with whom they shared different relationships. As predicted, ravens were able to differentiate between familiar and unfamiliar individuals even after a tested maximum time of three years (chapter 6; Boeckle & Bugnyar 2012). In addition to the memory of in-group vs. out-group differentiation, focal individuals

differentially responded to affiliates and non-affiliates. While the differentiation between familiar and unfamiliar is mainly shown in the number of calls given, ravens changed acoustic structure of the responded long distance calls (chapter 6; Boeckle & Bugnyar 2012).

In summary raven acoustic communication that is based on the morphology of vocal organs and neural motor control seems to be highly developed. The observed syringeal structures and vocal tract reported in chapter 1 are typical for songbirds (Boeckle et al. in prep.; Shufeldt 1890) and corvids (Chamberlain et al. 1968; Tsukahara, Aoyama & Sugita 2006; Tsukahara, Yang & Sugita 2008; Tsukahara et al. 2009). The reported ability of recognizing different classes via acoustic communication is in congruence with the highly developed social skills of ravens.

In this thesis I was able to contribute to the increasing body of work that utilizes acoustic communication as an excellent tool to study social cognition in animals (e.g. Seyfarth, Cheney & Marler 1980; Slocombe et al. 2010; Townsend et al. 2012). To my knowledge this work represents one of the first that applies this approach to birds. My work contributes to the understanding of evolutionary forces that shape signal structure as well as the cognitive abilities to use signals. It may also help to better understand convergent evolution of intelligence and eventually the evolution of the extraordinary cognitive abilities of some bird species but also primate species that contain us humans.

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Appendix 1: Additional Co-authored Work on Birds

Grey parrots use inferential reasoning based on acoustic cues alone

Schloegl, C., Schmidt, J., Boeckle, M., Weiß, B. M., & Kotrschal, K. (2012). Grey parrots use inferential reasoning based on acoustic cues alone. *Proceedings Of The Royal Society B-Biological Sciences*, 279(1745), 4135-4142. doi: 10.1098/rspb.2012.1292

Our ability to make logical inferences is considered as one of the cornerstones of human intelligence, fueling investigations of reasoning abilities in non-human animals. Yet, the evidence to date is equivocal, with apes as the prime candidates to possess these skills. For instance, in a two-choice task, apes can identify the location of hidden food if it is indicated by a rattling noise caused by the shaking of a baited container. More importantly, they also use the absence of noise during the shaking of the empty container to infer that this container is not baited. However, since the inaugural report of apes solving this task, to the best of our knowledge, no comparable evidence could be found in any other tested species such as monkeys and dogs. Here, we report the first successful and instantaneous solution of the shaking task through logical inference by a non-ape species, the African grey parrot. Surprisingly, the performance of the birds was sensitive to the shaking movement: they were successful with containers shaken horizontally, but not with vertical shaking resembling parrot head-bobbing. Thus, grey parrots seem to possess ape-like cross-modal reasoning skills, but their reliance on these abilities is influenced by low-level interferences.

Croop calls in Northern Bald Ibis (*Geronticus eremita*) allow for mate recognition of pair partners and encode the affective state of the sender

Szipl, G., Boeckle, M., Werner, S., & Kotrschal, K. (in prep.). Croop calls in Northern Bald Ibis (*Geronticus eremita*) allow for mate recognition of pair partners and encode the affective state of the sender. Planed to submit to Animal Conservation.

The critically endangered Northern Bald Ibis is a socially monogamous and year-round colonial bird with a moderate repertoire of calls. Almost extinct in the wild, little is known about the species acoustic communication and its relevance for social interactions. The 'croop' call, for example, is used during greeting of mates, but also during agonistic encounters, indicating some acoustic differences that can be perceived by the birds. Furthermore, their ability to recognise each other individually by these calls has not yet been proven. We recorded croop calls in in a semi-tame and free-roaming population of Northern Bald Ibis in Austria, and analysed the vocal structure to see which parameters (e.g. call duration, fundamental frequency) differ within different social contexts, sexes and individuals. Additionally we conducted playback experiments to test whether mated pairs would discriminate each other by their greeting croops. Acoustic features showed highly variable temporal and structural parameters. Almost all calls could be classified correctly within different social contexts. Classification results were less clear for sex and individuality within males and females, yielding only low numbers of correctly classified greeting croops. Incubating individuals looked up more often and longer in response to playbacks of the greeting calls of their mate than to other colony members, indicating mate recognition. We show that acoustic parameters of agonistic and greeting croops encode the motivation of the sender and contain features that indicate the expression of affective states. These findings can help improve the chances of this species' recovery in captive and reintroduced populations.^{##}

^{##} This abstract or a similar version of it was submitted as conference and workshop applications. In case of acceptance the abstract might be published in the conference booklet and might be found in the internet.

Appendix 2: Additional Work on Anurans

Call Acoustics Reflect Body Size Across Four Genera of Anurans

Gingras, B., Boeckle, M., Herbst, C. T., & Fitch, W. T. (in press). Call acoustics reflect body size across four genera of anurans. *Journal of Zoology*. doi: 10.1111/j.1469-7998.2012.00973.x. Accepted 7th September 2012.

An inverse relationship between body size and advertisement call frequency has been found in several frog species. However, the generalizability of this relationship across different clades and across a large distribution of species remains underexplored. We investigated this relationship in a large sample of 136 species belonging to four clades of anurans (*Bufo*, *Hylina*, *Leptodactylus* and *Rana*) using semi-automatic, high-throughput analysis software. We employed two measures of call frequency: fundamental frequency (F0) and dominant frequency (DF). The slope of the relationship between male snout-vent length (SVL) and frequency did not differ significantly among the four clades. However, *Rana* call at a significantly lower frequency relative to size than the other clades, and *Bufo* call at a significantly higher frequency relative to size than *Leptodactylus*. Because the relationship between F0 and body size may be more straightforwardly explained by biomechanical constraints, we confirmed that a similar inverse relationship was observed between F0 and SVL. Finally, spectral flatness, an indicator of the tonality of the vocalizations, was found to be inversely correlated with SVL, contradicting an oft-cited prediction that larger animals should have rougher voices. Our results confirm a tight and widespread link between body size and call frequency in anurans, and suggest that laryngeal allometry and vocal fold dimensions in particular are responsible.

Multimodal signaling in the Small Torrent Frog (*Micrixalus saxicola*) in a complex acoustic environment

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Many animals use multimodal (both visual and acoustic) components in courtship signals. The sonic communication of anuran amphibians can be masked by the presence of environmental background noise, and multimodal displays may enhance receiver detection in complex acoustic environments. In the present study we measured sound pressure levels of concurrently calling males of the Small Torrent Frog (*Micrixalus saxicola*), and used acoustic playbacks and an inflatable balloon mimicking a vocal sac to investigate male responses to controlled unimodal (acoustic) and multimodal (acoustic and visual) dynamic stimuli in the frogs' natural habitat. Our results suggest that abiotic noise of the stream does not constrain signal detection, but males are faced with acoustic interference and masking from conspecific chorus noise. Multimodal stimuli elicited greater response from males and triggered significantly more visual signal responses than unimodal stimuli. We suggest that the vocal sac acts as a visual cue and improves detection and discrimination of acoustic signals by making them more salient to receivers amidst complex biotic background noise.^{§§}

^{§§} This abstract or a similar version of it was submitted as conference and workshop applications. In case of acceptance the abstract might be published in the conference booklet and might be found in the internet.

Divergent receiver responses to components of multimodal signals in foot-flagging frog species offer clues to visual signal evolution

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Multimodal communication of acoustic and visual signals serves a vital role in the mating system of anuran amphibians. To understand signal evolution and function in multimodal signal design it is critical to test receiver responses to unimodal signal components versus multimodal composite signals. We investigated two anuran species displaying a conspicuous foot-flagging behavior in addition to or combination with advertisement calls while announcing their signaling sites to conspecifics. To investigate the conspicuousness of the foot-flagging signals we measured and compared spectral reflectance of foot webbings of *Micrixalus saxicola* and *Staurois parvus* using a spectrophotometer. We performed behavioral field experiments using a robotic frog including an extendable leg combined with acoustic playbacks to test receiver responses to acoustic, visual and combined audio-visual stimuli. Our results indicated that the foot webbings of *S. parvus* were almost five times brighter than those of *M. saxicola*. The main response to all experimental stimuli in *S. parvus* was foot flagging, whereas *M. saxicola* responded primarily with calls but never foot flagged. Together these across-species differences suggest that in *S. parvus* foot-flagging behavior is applied as a salient and frequently used communicative signal during agonistic behavior, whereas we propose it constitutes an evolutionary nascent state in ritualization of the current fighting behavior in *M. saxicola*.***

*** This abstract or a similar version of it was submitted as conference and workshop applications. In case of acceptance the abstract might be published in the conference booklet and might be found in the internet.

Abstract

Common ravens (*Corvus corax*) have a complex social system – juveniles and unpaired individuals aggregate in non-breeder flocks whereas paired individuals defend territories. Former studies have shown that ravens have advanced cognitive skills especially in the social and technical domain. Furthermore, ravens flexibly utilize a large repertoire of calls. Yet nobody has tried to use ravens' vocalization as means for testing social knowledge. This cumulative dissertation describes the connection between raven call characteristics, morphometric measurements, and phenotypic characteristics. Furthermore, response variation according to call category presentation as well as ravens ability to utilize social knowledge based on acoustic stimuli are analyzed. Based on the anatomical and morphological studies of the raven we expect variation in the call structure. We explain variances of specific raven vocalizations, namely long distance calls that are mainly used in territorial defense and food associate calls 'yells'. 'Yells' are a common vocalization emitted in food related contexts and attract conspecifics to feeding opportunities. 'Yells' were analyzed according to the variation of sex, age, and individuality. Food calls as well as territorial calls of unknown individuals were played back in a habituation-dishabituation paradigm in order to experimentally study whether ravens are able to use call parameters to differentiate between two unknown individuals within one call-type. Additionally ravens were tested for recognition of former group members in a playback experiment. Results show that calls are highly variable and, among others, contain indicators for sex, age, and individuality. Based on these differences we can show that ravens have the ability to differentially respond to these categories but also between affiliation categories of 'friend', 'foe', and unknown. Further more, we can show that the ability to differentiate between individuals is retained for prolonged periods of time. These capacities indicate that ravens might have a complex social knowledge, an ability long considered to be uniquely found in primates. The studies gathered in this cumulative dissertation are the foundation of future studies on raven vocalizations and their ability to use vocal information in various complex contexts like e.g. third party interactions.

Zusammenfassung

Raben (*Corvus corax*) sind bekannt für ihr komplexes soziales Netzwerk; Juvenile und nicht verpaarte Individuen versammeln sich in Nicht-Brüter-Gruppen, während verpaarte Individuen Territorien verteidigen. Es wurde bereits gezeigt, dass Raben vor allem sozial und technisch hoch entwickelte kognitive Fähigkeiten besitzen. Trotz der Beschreibung des großen Ruf-Repertoires wurde noch nicht versucht, Raben und ihre sozialen Fähigkeiten an Hand bestimmter Rufe zu testen. Diese kumulative Dissertation beschreibt den Zusammenhang von akustischen Eigenschaften der Rufe, morphometrischen Messungen und phänotypischen Merkmalen. Zusätzlich werden Raben auf ihre Fähigkeit, Rufkategorien zu unterscheiden und soziales Wissen zu verwenden, getestet. Basierend auf den morphometrischen Studien, die einen Teil der akustischen Variation begründen, beschreiben wir die Rufcharakteristika von Distanzrufen, die hauptsächlich zur Verteidigung des Territoriums verwendet werden und Futterrufen. Futterrufe („Yells“) sind mit Futter assoziierte Rufe, die Artgenossen zu potentiell gefährlichen Futterressourcen locken. Futterrufe wurden auf ihre Variation auf Grund von Geschlecht, Alter und Individualität des Rufers beschrieben. Beide Rufe wurden in Playbackstudien („Habituation-Dishabituation“) verwendet, um zu zeigen, dass Raben in der Lage sind, zwischen zwei unbekannten Individuen innerhalb eines Ruftyps zu unterscheiden. Zusätzlich wurde zur Erforschung der sozialen Fähigkeiten und des Langzeitgedächtnisses ein Versuch durchgeführt, bei dem ehemalige „Freunde“, „Feinde“ und unbekannte Individuen nach mehreren Jahren Trennung präsentiert wurden. Die in dieser kumulativen Dissertation gesammelten und teilweise bereits in Fachzeitschriften publizierten Arbeiten sind Grundlage für zukünftige Studien, die sich mit Vokalisationen von Raben und deren Fähigkeit, Ruf Typen zu unterscheiden, beschäftigen.

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Publikationen und Manuskripte

Veröffentlichte Publikationen:

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Eingereichte Manuskripte:

- Boeckle, M., & Bugnyar, T. (submitted). Ravens discriminate long distance calls of unknown individuals in a habituation-dishabituation experiment. *Ethology*.
- Boeckle, M., Szípl, G., & Bugnyar, T. (submitted). Indicators of Sender's Age and Sex in Raven Food Calls? *Ibis*.
- Preininger, D., Boeckle, M., Szatecsny, M., & Hödl, W. (submitted). Divergent receiver responses to components of multimodal signals in foot-flagging frog species offer clues to visual signal evolution. *PLoS ONE*, submitted, 1-27.

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Vocal Tract Length and Syringeal Structures of Common Ravens.

Szipl, G., Boeckle, M., Werner, S., & Kotrschal, K. (in prep.). Croop calls in Northern Bald Ibis (*Geronticus eremita*) allow for mate recognition of pair partners and encode the affective state of the sender.

Ich bestätige hiermit, dass ich die Einleitung (General Introduction), die Diskussion (General Discussion), die Zusammenfassung (Abstract) geschrieben habe und bei jedem hier aufgelisteten Manuskript wesentlich beigetragen habe.

Wien, am 11.10.12

MMag. Markus Böckle