



With whom to dine? Ravens' responses to food-associated calls depend on individual characteristics of the caller



Georgine Szípl ^{a, b, *}, Markus Boeckle ^{a, b, c}, Claudia A. F. Wascher ^{b, d}, Michela Spreafico ^a, Thomas Bugnyar ^{a, b}

^a Department of Cognitive Biology, University of Vienna, Vienna, Austria

^b Konrad Lorenz Forschungsstelle, Core Facility, University of Vienna, Gruenau im Almtal, Austria

^c Department for Psychotherapy and Biopsychosocial Health, Danube University Krems, Krems, Austria

^d Departamento de Ciencias Agro-Forestales, University of Valladolid, Valladolid, Spain

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Upon discovering food, common ravens, *Corvus corax*, produce far-reaching 'haa' calls or yells, which are individually distinct and signal food availability to conspecifics. Here, we investigated whether ravens respond differently to 'haa' calls of known and unknown individuals. In a paired playback design, we tested responses to 'haa' call sequences in a group containing individually marked free-ranging ravens. We simultaneously played call sequences of a male and a female raven in two different locations and varied familiarity (known or unknown to the local group). Ravens responded strongest to dyads containing familiar females, performing more scan flights above and by perching in trees near the respective speaker. Acoustic analysis of the calls used as stimuli showed no sex-, age- or familiarity-specific acoustic cues, but highly significant classification results at the individual level. Taken together, our findings indicate that ravens respond to individual characteristics in 'haa' calls, and choose whom to approach for feeding, i.e. join social allies and avoid dominant conspecifics. This is the first study to investigate responses to 'haa' calls under natural conditions in a wild population containing individually marked ravens.

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Vocalizations produced during foraging can serve various functions, for example contact calls to maintain cohesion within groups (Mahurin & Freeberg, 2009; Oda, 1996), alarm calls given by sentinels during group foraging to warn co-feeding conspecifics about danger (Manser, 1999; McGowan & Woolfenden, 1989; Wright, Berg, De Kort, Khazin, & Maklakov, 2001), and appeasement calls uttered during agonistic interactions over food to appease aggressors (Heinrich, Marzluff, & Marzluff, 1993). But acoustic signals may also be directly associated with food, indicating its location and quality (Bugnyar, Kijne, & Kotrschal, 2001; Dittus, 1984; Evans & Evans, 1999; Gros-Louis, 2006) or individual food preference (Clay & Zuberbühler, 2009; Elgar, 1986; Elowson, Tannenbaum, & Snowdon, 1991; Slocombe & Zuberbühler, 2006). Irrespective of their primary function, these different call types possibly provide receivers with cues about food availability, and attract them to feeding sites. Calls directly associated with external stimuli, such as food or predators, are termed 'functionally

referential signals' because animals hearing these signals can respond to the referred stimulus even without seeing the actual stimulus that elicited the signal (Evans, 1997; Evans & Evans, 2007; Macedonia & Evans, 1993; Marler, Evans, & Hauser, 1992).

Recognition at the individual or class level is favoured by selection whenever it is beneficial for the signaller to be detected, and for the receiver to discriminate appropriately (Johnstone, 1997; Steiger & Müller, 2008; Tibbetts & Dale, 2007). As the benefits of signallers are not necessarily in accordance with the benefits of receivers, and, furthermore, may vary with the context, it is essential to take both context and party perspective into account when studying recognition (Tibbetts & Dale, 2007). Being individually distinct when signalling food may benefit the sender because specific individuals such as social allies may be attracted (Caine, Addington, & Windfelder, 1995). Signallers can thereby manipulate group size and composition, which can result in decreased feeding competition (Chapman & Lefebvre, 1990). Receivers could also benefit from recognizing calling individuals by assessing who is already present at the feeding site, and thus possibly predict the likelihood of competition occurring as well as receiving social support (Sharpe, Hill, & Cherry, 2013).

* Correspondence: G. Szípl, Department of Cognitive Biology, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria.

E-mail address: georgine.szípl@gmail.com (G. Szípl).

In ravens, three types of food-associated calls have been reported: the long 'chii' call uttered by juvenile ravens (Heinrich & Marzluff, 1991), the short 'who' call that dominant ravens utter when landing at feeding sites and the long 'haa' call or yell (Bugnyar et al., 2001; Heinrich & Marzluff, 1991). Most of the literature on food calls in ravens refers to the latter, the 'haa' call. This call type is uttered by ravens when they see food they cannot access because it is monopolized by dominant conspecifics or predators (Heinrich, 1988). Ravens are highly attracted by 'haa' calls of others, as previously shown in a playback study that suggests these calls may function as assembly or recruitment signals (Heinrich, 1988). Moreover, owing to their distinct morphology and context specificity, 'haa' calls have been hypothesized to be functionally referential (Bugnyar et al., 2001), that is, ravens hearing these calls may associate feeding opportunities with them.

A recent study revealed that 'haa' calls contain individually distinct features and that captive ravens were capable of discriminating between calls of two unknown individuals on the basis of these features (Boeckle, Szípl, & Bugnyar, 2012). Whether wild ravens use individual information in 'haa' calls in their daily lives remains untested. On the one hand, calling for an assembly at food sources could be beneficial for the sender because greater numbers of ravens might be needed to overcome monopolization by dominants (Marzluff & Heinrich, 1991), or because kin or affiliates could be among the attracted conspecifics (Braun & Bugnyar, 2012). On the other hand, differentiating between callers would allow receivers to decide whether or not to join a foraging group. These potential benefits have so far been ignored in ravens, probably because of their social organization: adult raven pairs that manage to establish a territory become breeders and defend their territories year-round (Heinrich, 1989), whereas nonbreeding birds are vagrant and tend to form relatively open groups that change in size and composition depending on the foraging situation (Heinrich, 1988). Owing to these high levels of fission–fusion dynamics in nonbreeder groups and the ephemerality of food sources in the wild, reciprocity and kin selection have been considered less important when explaining recruitment to feeding sites via 'haa' calls (Heinrich & Marzluff, 1991). However, long-term studies on a population of individually marked ravens in the Austrian Alps revealed that nonbreeder groups are structured by different types of social relationships, challenging the assumption of raven flocks being anonymous aggregations (Braun, Walsdorff, Fraser, & Bugnyar, 2012). Moreover, huge individual differences in vagrancy were found, with some nonbreeders being identified as local or resident to this particular valley, and others showing gradual degrees of vagrancy, visiting the valley regularly or only infrequently (Braun & Bugnyar, 2012).

Here, we tested for the recruiting function of 'haa' calls in the wild. Given the differences in group composition and vagrancy found in our study population, we focused on the ravens' ability to respond to food-associated calls of specific individuals and/or a particular class of individuals, respectively, by conducting simultaneous two-choice playback experiments. In each playback session, sequences of 'haa' calls of a male and female raven were presented simultaneously from two different locations, whereby the played-back individuals varied in the degree of familiarity to the local ravens. Different sex combinations were chosen because observations of individually marked ravens showed that females tend to call more often than males (Szípl & Bugnyar, 2014). Likewise, testing for familiarity was inspired by the observation that local nonbreeders tend to call more often than vagrant birds that only infrequently visit the study site (Szípl & Bugnyar, 2014). The playback should thus simulate a possible scenario in the birds' daily lives, that is, when they hear food-associated calls of individuals they may have repeatedly met before or of strangers that are new to

this area. If receivers are able to discriminate between familiar and unfamiliar individuals on the basis of their 'haa' calls, they should respond to the played-back stimuli selectively, that is, approach the speaker playing back calls of familiar birds; alternatively, they could prefer to approach the speaker playing back unfamiliar birds. If ravens can discriminate familiar individuals on the basis of their regularly occurring calling activity, they should primarily approach the loudspeakers playing back 'haa' calls of familiar females, as females tend to produce most of the 'haa' calling before daily morning feedings. If they generally respond to sex, however, they should show a preference for the loudspeaker playing back 'haa' calls of females, irrespective of their familiarity status. As many of the birds in the study area are individually marked and subject to long-term observations, we were able to study possible effects of social knowledge (gained through repeated agonistic and affiliative interactions) on the birds' response to the playbacks. Specifically, we expected that receivers should respond to the individual stimuli selectively, that is, approach played-back calls of kin and affiliates, and avoid the speaker playing calls of opponents and birds of higher rank, respectively.

METHODS

Study Site and Subjects

The study was conducted from February to October 2012 in the Cumberland Wildpark, a local zoo in the Northern Austrian Alps close to the village of Gruenau im Almtal (47°48'N, 13°57'E). The park attracts free-ranging ravens that forage and scrounge food from zoo animals year-round. Ravens at this site have been captured and marked in the course of long-term studies (Braun & Bugnyar, 2012; Braun et al., 2012). For this, ravens were caught in drop-in traps (Engel & Young, 1989). Traps were equipped with perches and ad libitum food and water and were checked hourly. Trapped ravens were weighed, measured (e.g. length of tarsus and beak) and ringed with an individual combination of colour rings and a metal ring containing a unique code from the German bird ringing station (Vogelwarte Radolfzell). During this standardized marking procedure, which was performed in less than 30 min by trained personnel, 50–200 µl of blood was taken from the alar vein for sexing and analysis of relatedness (for further details see Braun & Bugnyar, 2012). Age class (juvenile, subadult and adult) was estimated by the colour of the inner beak, as this changes from pink (juvenile) to black (adult) with increasing age (Heinrich & Marzluff, 1992). Frequent resightings and behavioural observations of marked birds suggest that handling and marking had no negative effects and did not elicit suspicious behaviour. Retrapping of approximately 50% of the marked ravens enabled check-ups and showed no indications of injuries (see also Boeckle et al., 2012; Braun & Bugnyar, 2012).

At the time of the study, about 200 ravens had been marked individually. Owing to the high fission–fusion dynamics that characterize ravens' social organization, the size and the composition of the population present in the valley vary over time (Braun & Bugnyar, 2012; Braun et al., 2012). The presence of marked birds was monitored during daily morning feedings (0700–0900 hours) at the enclosures of bears, *Ursus arctos*, wolves, *Canis lupus*, and wild boars, *Sus scrofa*. These enclosures were selected because ravens constantly used them and because they featured relatively open areas with a limited number of trees, allowing a good overview for human observers. The ravens were well habituated to human observers and experimental equipment (e.g. cameras, microphones) at these locations while they scrounged food from the zoo animals. Based on the amount of time spent in the valley, individual ravens were categorized according to their degree of

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