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# Food calling in wild ravens (*Corvus corax*) revisited: Who is addressed?

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## Abstract

Numerous birds and mammals use vocal signals to advertise feeding opportunities but often such signals vary with individual and contextual factors. Non-breeding ravens call at food that is difficult to access, resulting in the attraction of nearby conspecifics. Although callers may benefit from group formation in various ways, we recently found substantial individual variation in food calling. We here explored whether this variation can be partly explained by the social dynamics in raven foraging groups, together with already known effects of age class and sex. Specifically, we expected ravens to respond to the presence or absence of affiliates that could act as cooperative partners in the forthcoming feeding event, that is they should call when other ravens were present but they themselves were alone rather than when they were also in company of an affiliation partner. We observed the vocal behaviour of individually marked wild ravens and, simultaneously, categorized their affiliative behaviour with other ravens in the minutes before experimentally controlled feedings. In line with our prediction, individuals were less likely to produce food-associated calls when they were in close contact with an affiliation partner prior to feeding as compared to when they were alone. Furthermore, sex and age class influenced food calling as females called more often than males and younger birds called more often than adult ravens. In conclusion, these results suggest that ravens attempt to find support from a particular cooperative partner by broadly advertise feeding opportunities via food-associated calls, especially when they have low chances in contest competition due to their age and sex. These findings lend further support to the assumption of raven flocks being structured by social relationships and individual birds flexibly controlling their vocal signalling according to the current flock composition.

**KEYWORDS**

common raven, fission–fusion dynamics, food-associated calls, functional referential signal, individual recognition, recruitment, social foraging

## 1 | INTRODUCTION

Social life brings a number of benefits such as decreased predation risk, but it also implies certain costs like increased competition for resources (Giraldeau & Caraco, 2018; Kappeler & van Schaik, 2002).

These challenges might be mitigated by engaging in long-term differentiated social relationships with other individuals, referred to as social bonds or alliances (Byrne & Bates, 2007). The formation of these long term relationships requires individuals to interact repeatedly (Dunbar, 1998; Shultz & Dunbar, 2010), which is affected by

group cohesion but also group size and the degree of fission–fusion dynamics (Aureli & Schaffner, 2008). Together, these factors contribute to the complexity of the social environment (Byrne & Bates, 2007). It has been proposed that a complex social environment is one of the main driving forces for the evolution of cognition (Ashton, Ridley, Edwards, & Thornton, 2018; Dunbar, 1998; Humphrey, 1976). Complex social structures may also impose a selective pressure on communication favouring large signal repertoires (McComb & Semple, 2005, but see also Manser et al., 2014) and the origin of functionally referential signals (Freeberg, Dunbar, & Ord, 2012; Freeberg & Lucas, 2002; Graw, Hollén, Bousquet, Furrer, & Roux, 2014).

Several species of birds and mammals have been found to produce vocal signals at the encounter of food and thereby advertise its location to conspecifics (Clay & Zuberbühler, 2009; Evans & Evans, 1999; Gros-Louis, 2006; King & Janik, 2015). Here, we refer to such vocal signals as "food-associated calls" (Clay, Smith, & Blumstein, 2012; Heinrich & Marzluff, 1991). Advertising food may lead to competition and can only evolve if the callers have direct or indirect benefits, for example when group formation increases the chance to access food for each individual (by-product mutualism, [Bednekoff, 1997]), or helps close kin (Hamilton, 1964; Smith, 1964), or the information exchange is reciprocated (Trivers, 1971). Like most vocalizations, food-associated calls are embedded in a communication network (Evans & Evans, 1999; King & Janik, 2015; McGregor, 2005; Slocombe et al., 2010) giving rise to audience effects (e.g. Evans & Evans, 1999; Evans & Marler, 1994; King & Janik, 2015). In several cases, receivers attend to the identity and social status of the signaller as well as their shared social relationship, indicating that food calls may convey more information than the mere location of food (Clay et al., 2012). For instance, white-tailed ptarmigan (*Lagopus leucurus*) use food-associated calls to mediate learning of feeding preferences from mothers to offspring (Allen & Clarke, 2005). Food-associated calls in domestic fowl mediate socio-sexual interactions between the male (sender) and females (receivers) and such behaviour has been suggested to increase social prestige in males (Evans & Marler, 1994; Pizzari, 2003; Zahavi, 1995). Chimpanzees (*Pan troglodytes*) and brown capuchin monkeys (*Cebus apella*) seem to direct their food-associated calls to specific high-ranking individuals, perhaps seeking social tolerance or prosperous social alliances (Pollick, Gouzoules, & Waal, 2005; Schel, Machanda, Townsend, Zuberbühler, & Slocombe, 2013). Finally, bottlenose dolphins (*Tursiops truncatus*) produce food-associated vocalizations during social foraging presumably to synchronize and coordinate with certain individuals in the group (King & Janik, 2015).

Like in food calls, there is an increasing body of evidence that individual social cues might influence communication about predators, with social bonds between signallers and receivers playing a key role. For instance, superb fairy wrens (*Malurus cyaneus*) respond preferentially to mobbing calls of their mates or kin over unrelated individuals (Colombelli-Négrel & Evans, 2017). A similar case was found in dwarf mongoose (*Helogale parvula*) where the social relationship between the sender and the receivers influenced the recruitment

following the production of mobbing calls (Kern & Radford, 2016). In crested macaques, Micheletta et al. (2012) found that females attend more to the alarm calls produced by affiliates than by non-affiliates. These examples show the importance of social bonds from the receivers' perspective but there is also evidence that senders may pay attention to their relationships with the audience when signalling. Chimpanzees producing screams while being attacked modify the acoustic structure of their signal if high-ranking individuals are present, especially during cases of severe aggression (Slocombe & Zuberbühler, 2007). Common ravens (*Corvus corax*) adjust their rate of defensive calling during conflicts depending on the audience: victims increase the call rate if they find close kin nearby, while they reduce the number of calls if their aggressor's partner is in the audience (Szipl, Ringler, & Bugnyar, 2018).

In this study, we focused on the possible effects of social context on individual food calling in raven groups. Ravens produce food-associated calls (termed "yells" or "haa" calls) when they encounter food that is defended by territorial pairs (Heinrich, 1988a,1988b) or otherwise dangerous to access for example when co-feeding with wolves (Bugnyar, Kijne, & Kotrschal, 2001; Stahler, Heinrich, & Smith, 2002), and they usually do not approach the food until a group of individuals has formed. Such foraging groups represent temporal gatherings rather than cohesive units leading to a dynamic fission–fusion system, that is individuals form groups, split up and gather again at the same or different site sometimes more than 100 km apart (Loretto et al., 2017). Parker, Waite, Heinrich, and Marzluff (1994) showed that these temporary groups are not cohesive genetic clans. Typically, only some individuals are in company of a close kin during co-feeding with a large number of unrelated individuals. It is thus unlikely that the formation of foraging groups is a strongly kin-selected trait in ravens (Parker et al., 1994); given the low proportion of close kin in foraging groups, it is also unlikely that kin selection is the primary evolutionary mechanism for calling at food. Heinrich (1988a,1988b) proposed that non-breeding ravens gain direct benefits from recruiting others to food. Indeed, by forming a group of about 10 individuals, non-breeders can overpower the food defence of socially dominant territorial breeding pairs (Marzluff & Heinrich, 1991). Furthermore, forming a group may help ravens to overcome their neophobia (Heinrich, 1988a; Marzluff & Heinrich, 1991) and offers scrounging opportunities (Bugnyar & Kotrschal, 2002). Hence, ravens' calling at food has been interpreted as a form of cooperation based on mutualism rather than reciprocal altruism (Bednekoff, 1997; Wright, Berg, De Kort, Khazin, & Maklakov, 2001).

In its original form, the recruitment hypothesis of (Heinrich, 1988a, 1988b) assumes that calling at food attracts any other ravens nearby, that is an "anonymous crowd." However, recent findings show large and consistent inter-individual variation in food calling (Szipl & Bugnyar, 2014) that varies with the birds' age class, sex and residency status. Furthermore, analyses of food-associated calls recorded from free-ranging ravens revealed that these signals carry identity cues (Boeckle, Szipl, & Bugnyar, 2012) and playback experiments on wild ravens showed that birds respond preferentially to calls of familiar than of unfamiliar individuals (Szipl, Boeckle,

Wascher, Spreafico, & Bugnyar, 2015). Taken together, these recent studies strongly suggest that raven foraging groups are not entirely anonymous crowds but structured by different levels of social relationships (Braun, Walsdorff, Fraser, & Bugnyar, 2012; Loretto et al., 2017). Despite the fluid character of non-breeding foraging groups, individuals have been found to meet repeatedly in several foraging sites, spread out over thousands of square kilometres (Loretto et al., 2017); such iterated encounters allow ravens to form and maintain social bonds in non-breeder groups (Braun et al., 2012). Notably, the birds' bonding status influences their dominance rank and access to resources (Braun & Bugnyar, 2012; Braun et al., 2012). This is because, on the one hand, ravens tend to intervene in others' conflicts, providing agonistic support to those individuals with whom they share a valuable relationship (Fraser & Bugnyar, 2010, 2012); on the other hand, they prefer to cooperate with such partners and share food after successful cooperation in experimental settings (Asakawa-Haas, Schiestl, Bugnyar, & Massen, 2016; Massen, Ritter, & Bugnyar, 2015).

Given the identity cues encoded in food-associated calls and the importance of social status in the access to resources, we hypothesized that ravens should make sure that their affiliates are nearby within the foraging flock. We thus expected that ravens should primarily advertise a feeding opportunity through food-associated calls when their affiliate partner(s) is not yet at the feeding site. Hence, we predicted that if ravens had a potential cooperative partner(s) already by their side, they should be less likely to utter food-associated calls. Here, we tested such prediction. We expected that the individuals' immediate social context prior to feeding (i.e. its close proximity to a potential cooperative partner), rather than the overall size of the foraging group, should explain the inter-individual variation in food calling behaviour.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site and raven population

We conducted the study at the Cumberland Wildpark located 5 km south of the village of Grünau im Almtal (47°51'10"N, 13°57'20"E), Upper Austria. Free-ranging non-breeding ravens use the park year-round for foraging and socializing, with numbers ranging from 20 to 50 in summer, and up to 120 in winter (Braun & Bugnyar, 2012; Bugnyar & Kotrschal, 2002). In addition to non-breeding ravens, our study site is also used by some reproductive pairs that hold breeding territories along the valley (Loretto, Reimann, Schuster, Graulich, & Bugnyar, 2016). Breeding individuals can be identified by their behaviour during the breeding season (e.g. carrying nest material, incubating eggs, feeding young) and throughout the year by their status displays and suppression of dominant displays in non-breeding ravens (see Heinrich, 1988b). A group of non-breeder ravens usually scrounge food from the feedings of the captive animals in the park, notably wild boars (*Sus scrofa*), wolves (*Canis lupus*) and bears (*Ursus arctos*). The formation of foraging crowds is characteristic of ravens

during their non-breeding life stage; therefore, our study focused on non-breeders (Braun & Bugnyar, 2012).

In the course of a long-term monitoring programme on ravens, we regularly capture birds at our study site in drop-in traps (Stiehl, 1978) for measuring and marking (see Braun & Bugnyar, 2012, for details). Since the beginning of the current study in 2008, approximately 300 ravens had been marked with individualized patagial wing tags (Caffrey, 2000) and unique colour-coded ring combinations. Sex was determined through the genetic analysis of blood samples and age class was estimated using the colouration of the inner beak and feathers; "subadult" (1–3 years), pinkish inner beak with black spots and "adult" (>3 years), fully black inner beak and black glossy feathers (Heinrich & Marzluff, 1992).

### 2.1.1 | Ethical note

### 2.2 | Set-up and data collection

We collected data during the morning feeding of the wild boars from January to June 2015. We fed the wild boars with 2–4 buckets of chow, bread and vegetables between 8:00 and 9:00 o'clock. We divided the daily observation session in two separate phases: a presentation phase (20 min) and a feeding phase (20 min). During the presentation phase, we placed the food buckets directly in front of the wild boar's enclosure, clearly visible to the animals in the enclosure and to birds in the area. Note that neither the wild boars nor the ravens obtained any food during the presentation phase; the fence prevented the wild boars from reaching the food and the ravens' neophobia prevented them from approaching the buckets (Bugnyar et al., 2001). The ravens gathered around the wild boar enclosure, soaring in the air and/or perching in nearby trees, which offered the opportunity to observe their vocal behaviour and social interactions from close distance (< 50m). At the end of the presentation phase, we placed the food inside the wild boar enclosure initiating the feeding phase, in which the boars could feed and the ravens snatch some pieces of food. The ravens' vocalization during the entire observation session was recorded using a Marantz PMD661 handheld Solid State audio recorder together with a Sennheiser ME 67 directional microphone covered with a foam windshield. Both the microphone and the recording device stood on a tripod at a fixed spot approx. 20–30 m away from the observer's position and pointed towards the centre of the enclosure.

We carried out behavioural observations of individually marked ravens using focal sampling (Altmann, 1974) only during the presentation phase. Due to the fluid character of raven groups, the number of marked ravens present at our study site changed across days. We thus balanced the number of protocols per bird according to their presence patterns (prioritizing birds that showed up from time to time over those that were present every day). Otherwise, we chose focal subjects randomly per observation session. The same individual was only sampled once per day with the help of binoculars and a scope (ZEISS Conquest 10 × 42, Swarovski ATS 65). We chose to make focal protocols of 6 min, since this was approx., the longest time window where it was feasible to track a single individual (personal observation). If the focal subject moved out of sight before the end of the focal protocol, the observation was discarded. Per protocol, we recorded, in real time, the vocal behaviour of the focal subject (whether or not it produced food-associated calls), its social interactions and spatial distance to other ravens (see below) with the help of a digital voice dictaphone (Sony IC recorder ICD-PX312). Note that the proportion of marked individuals at the daily feedings was about 40%; we therefore found focal subjects to interact not only with other marked birds but also with unmarked birds. Since we could not calculate the bonding status between marked and unmarked ravens, we opted for defining the social context before feeding on the basis of spatial proximity and affiliative interactions (agonistic interactions hardly occurred during the presentation phase). A focal bird would be nearby an affiliate raven if it was in close proximity with another individual (<1/2m) and/or engaged in an affiliative interaction (i.e. allopreening, beak touch, joint object manipulation; cf. Massen, Sterck, & De Vos, 2010). Alternatively, it could be alone during the entire focal protocol. It is important to note that ravens engage in affiliative interactions since their first year of age (Loretto, Fraser, & Bugnyar, 2012) and that social grooming in corvids is provided to individuals sharing a valuable relationship (Morales et al., in review). We sampled a total of 26 individual ravens in the course of the study of which we excluded three individuals from our statistical analysis because they were observed less than three times. Our final data set included a total of 163 focal protocols over 126 food presentation events, resulting in 978 min of total observation time (mean ± SE = 7.09 ± 0.59 focal observations per individual). Because previous studies have indicated sex and age class differences in food calling behaviour (Szipl & Bugnyar, 2014), we made sure to have a *similar* number of individuals across sex-age classes: 4 female-subadults, 5 male-subadults, 8 female-adults and 6 male-adults ravens. Furthermore, we focused on those calls that are renowned for their recruitment effect, that is "yells" (Heinrich & Marzluff, 1991) or "haa" calls (Bugnyar et al., 2001), see spectrogram in Figure 1. Some ravens also emit another type of calls (commonly labelled as "who") that clearly differ from yells in respect to their length and timing (Bugnyar et al., 2001); we excluded those calls from the analysis as they likely have a different function (Heinrich & Marzluff, 1991). We measured the daily foraging group size as the average of three separate counts of the number of ravens present during the feeding phase. We counted the ravens during the feeding
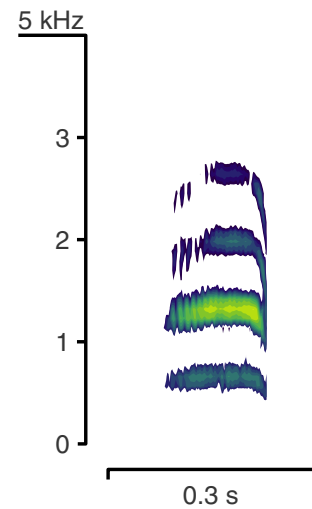


**FIGURE 1** Spectrogram of a "haa" food call, also known as "yells" (Heinrich & Marzluff, 1991)

phase and not during the presentation phase (when we carried out the focal protocols) because, after food delivery, ravens tend to land at the feeding spot almost synchronously, allowing a much more accurate estimate of group size.

## 2.3 | Statistical analysis

All statistical analyses were carried out in R software, version 3.3.1 (R Development Core Team, 2016). To explore how our selected variables explained food calling behaviour, we fitted a Generalized Linear Mixed Model (GLMM). The response variable was the food calling behaviour per focal protocol (calling yes/no). We acknowledge that a binomial approach is less informative than a frequency approach, for example the number of food calls per minute. Unfortunately, linear and generalized linear models perform very poorly as such variable is inherently extremely zero-inflated. Furthermore, carrying out a zero truncated model would extremely skew the data in terms of sex and age (e.g. adult males would nearly be omitted). Henceforth, we fitted a model based on a binomial distribution and used a logit link function in "lme4" package (Bates, 2010). In the explanatory side of the formula, we included social context (presence/absence of potential cooperative partners), group size (number of birds present), age class (adults vs. subadults) and sex (males vs. females). As there is strong evidence from previous research that the effect of age class varies between sexes (Szipl & Bugnyar, 2014), we also included a two-way interaction between sex and age. Finally, we added a random intercept for each individual to control pseudo-replication due to repeated measurements. We standardized all regression predictors of the full model by centreing and dividing by two standard deviations following Gelman (2008), which facilitates the interpretation and direct comparisons of the parameter estimates (Schielzeth, 2010). For model selection and inference, we used an information-theoretic approach (Burnham & Anderson, 2002; Grueber, Nakagawa, Laws, & Jamieson, 2011) and created a set of candidate models

with all possible predictor combinations "MuMIn" package (Barton, 2011). We ranked all models according to their corrected Akaike information criteria (AICc) and calculated the full average model of those models that added up to 0.95 Akaike cumulative weight and were also within a ΔAICc < 7, see Table 1 (Burnham, Anderson, & Huyvaert, 2011). Finally, we calculated $R^2_{GLMM}$ of each of these 7 models (Nakagawa & Schielzeth, 2013).

# 3 | RESULTS

Food calling occurred in 67 out of 163 focal observations (41%) and 14 out of 23 (61%) individuals participated in food calling (see Table 2 and Figure 2). The remaining 9 individuals (39%) never uttered food-associated calls.

The averaged model showed a negative effect of the presence of an affiliating individual (Table 3; Figure 3), that is ravens were less likely to call when they were sitting in close contact with another individual and/or exchanged affiliative behaviours before feeding (Figure 3). Further evidence of the relationship between food calling behaviour and the social context comes from the model averaging process: the relative importance indicates the relevance of a predictor among the models selected to construct the average model. Social context was present in all those models; hence, it had a relative importance of 1 (Table 3). We also found an interesting combined effect of sex and age in food calling behaviour, evidenced in the high relative importance of these two factors and the large effect size, especially in the interaction between them (Table 3; Figure 3). These results indicated that age had a very relevant effect within males, as adults were less likely to call than subadults. In contrast, within females, the effect of age was much less important (Table 3; Figure 3). The effect of group size may be neglected based on its low relative importance and small effect size (Table 3).

# 4 | DISCUSSION

In this study, we addressed possible factors explaining whether or not ravens call at the sight of a potential food source. We showed that, in the presence of food that is difficult to access, ravens were less likely to give food-associated calls if a potential cooperative partner was in close proximity. This supports our prediction that the immediate social context experienced by individuals before feeding affects their propensity to announce that feeding opportunity. Consistent with previous findings, we also found that the birds' sex and age class had an influence on food calling behaviour (Szipl & Bugnyar, 2014). There was a notable difference in males based on age class; subadult males called much more often than adult males, but such difference was not apparent in females as subadult and adult females showed similar calling behaviour. Taken together, our results support the idea that ravens with low chances in contest competition, as is the case for subadult individuals and females (Braun & Bugnyar, 2012; Izawa & Watanabe, 2008), tend to broadly advertise feeding opportunities

via food-associated calls, yet refrain from doing so if they have a potential cooperative partner nearby.

Our study rests on the fact that ravens show high individual variation in food calling (Szipl & Bugnyar, 2014), that is some birds have higher propensity than others to advertise their motivation to feed and thereby the location of food (Bugnyar et al., 2001). Indeed, we found that about 61% of the sampled birds engaged in food calling at least once, and 43% of those did so in >75% of the observations, whereas around 40% of the sampled individuals never called at food. These proportions fit well to those reported in the study by Szipl and Bugnyar (2014), which was conducted at the same study site but on a different sample of free-ranging ravens. The current study also corroborates that sex and age class explains some of the variation in food calling (Szipl et al., 2015). Specifically, we found that females were more likely to call than males, and young males were more likely to call than adult males. Note that these differences do not reflect a biased sampling as we had similar number of observations for both sexes (6.5 ± 1.1 observations per female and 7.6 ± 0.6 observations per male) and for the two age classes (8.7 ± 0.9 observations per subadult and 5.8 ± 0.6 observations per adult). Instead, the observed patterns seem to reflect differences in rank and resource holding potential, respectively, as males are dominant over females and older birds typically outrank younger ones (Braun & Bugnyar, 2012; Heinrich, 2011; Izawa & Watanabe, 2008). Braun & Bugnyar, 2012 showed that individuals with low resource holding potential would benefit from any kind of affiliation during conflicts as opposed to high-rank adult males. In this study, we found that 1) food-associated calls are primarily given by birds that face a high probability of being outcompeted and 2) ravens are less likely to call when a social partner is nearby. Hence, we suggest that food calling increases the chance of joining a cooperative partner at the feeding, as opposed to recruiting an anonymous crowd. Given the social nature of feeding crowds in wild ravens, this interpretation fits to the overall picture derived from Heinrich and Marzluff (1991), that is that food-associated calls are given by non-breeders rather than dominant breeders. Within the non-breeders, however, they found food calling to be positively correlated with dominance rank. Note that the non-breeder group in the study by Heinrich and Marzluff (1991) was formed experimentally and consisted of juvenile birds only. However, our study was conducted on free-ranging birds with a highly dynamic social structure including also adult non-breeders, some of them more than 10 years old, see (Boucherie, Loretto, Massen, & Bugnyar, 2019; Loretto et al., 2017).

In addition to these known effects of sex and age class, we here show for the first time that the social context experienced by ravens right before feeding correlates with the individuals' likelihood to call. If ravens were in close proximity to and/or engaged in affiliative interactions with a conspecific, they called less than if they were alone. It is important to highlight that engaging in affiliative interactions does not necessarily impose any sort of constraint to the time addressed to food calling. Food-associated calls are single, short pulses (Bugnyar et al., 2001; Marzluff & Heinrich, 1991) that could easily be given in a short break of an interaction

| Model | LogLik | ΔAICc | Cum. weight | $R^2_m$ | $R^2_c$ |
|---|---|---|---|---|---|
| ~ social context + age class + sex +age class: sex | −74.203 | 0.00 | 0.542 | 0.47 | 0.72 |
| ~ social context + age class + sex +age class: sex + group size * (Full model) | −74.073 | 1.92 | 0.749 | 0.48 | 0.72 |
| ~ social context + age class + sex | −77.106 | 3.65 | 0.836 | 0.32 | 0.72 |
| ~ social context + age class | −78.890 | 5.09 | 0.879 | 0.19 | 0.68 |
| ~ social context + age class + sex +group size | −77.006 | 5.61 | 0.912 | 0.32 | 0.71 |
| ~ social context + sex | −79.673 | 6.66 | 0.931 | 0.16 | 0.71 |
| ~ social context | −80.810 | 6.83 | 0.949 | 0.06 | 0.68 |
| Null model: ~. | −86.011 | 15.15 | 1 | 0 | 0.63 |

*Full model

**TABLE 1** Model selection of the analysis investigating the variation in food calling behaviour (binomial response: calling yes or no). Final model was the average of a subset of models within a cumulative Akaike weight of > 0.95, presented here from lowest to highest AICc value. LogLik = log-likelihood, ΔAICc = difference of the second-order Akaike's information criterion with the best model, weight = model weight, cum. weight = cumulative model weight, $R^2_m$ = marginal $R^2_{glmm}$, $R^2_c$ = conditional $R^2_{glmm}$

| Age class | Sex | ID | Percentage of observation calling | Mean ± SE food calls per observation (6 min) |
|---|---|---|---|---|
| Subadult | Female | CD8 | 50% | 17.8 ± 11.1 |
| Subadult | Female | HK6 | 75% | 12.4 ± 4.3 |
| Subadult | Female | XT6 | 22% | 0.7 ± 0.6 |
| Subadult | Female | YZ0 | 62% | 10.3 ± 4.0 |
| Subadult | Male | AT53 | 83% | 20.8 ± 7.5 |
| Subadult | Male | HA2 | 91% | 43.1 ± 8.9 |
| Subadult | Male | PB0 | 0% | 0.0 ± 0.0 |
| Subadult | Male | TX6 | 73% | 18.6 ± 5.1 |
| Subadult | Male | VL9 | 0% | 0.0 ± 0.0 |
| Subadult | Male | VM8 | 71% | 10.3 ± 4.8 |
| Adult | Female | AT08 | 78% | 10.2 ± 4.1 |
| Adult | Female | HNT | 75% | 14.0 ± 5.9 |
| Adult | Female | Ht | 0% | 0.0 ± 0.0 |
| Adult | Female | HU6 | 100% | 23.0 ± 9.5 |
| Adult | Female | Ka | 50% | 8.7 ± 5.4 |
| Adult | Female | Mv | 20% | 0.6 ± 0.6 |
| Adult | Female | SV3 | 0% | 0.0 ± 0.0 |
| Adult | Male | AT77 | 14% | 1.1 ± 1.1 |
| Adult | Male | AX3 | 0% | 0.0 ± 0.0 |
| Adult | Male | Fo | 0% | 0.0 ± 0.0 |
| Adult | Male | Mn | 0% | 0.0 ± 0.0 |
| Adult | Male | Pa | 0% | 0.0 ± 0.0 |

**TABLE 2** For each individual the table shows its age class, sex, percentage of observations where the individual uttered at least one food call and the mean number of calls per observation protocol of that individual (±SE)

bout. Indeed, we sometimes observed birds producing these calls while they were engaged in allopreening. Furthermore, our focal protocols lasted for 6 min and the measurements of both categories were binomial, meaning that a single affiliative interaction or a single call within the entire 6 min period was enough to count the observation as "affiliated and called." That ravens reduced food calling in the presence of an affiliation partner fits to the hypothesis that they may regard affiliates as potential cooperative partners in the forthcoming feeding event. Further studies need to test if such affiliation partners indeed provide social support to each other in the subsequent competition for food. What we can already say on the basis of the current data is that the reduced likelihood of food calling is specific to the *individuals'* social context, as the number of ravens present in the area of our study site (that subsequently formed a feeding crowd) had no influence on the individuals' calling behaviour.

Our current findings are consistent with the hypothesis that social relationships between the caller and the receiver are relevant in

**FIGURE 2** Descriptive plot of individuals' food calling behaviour. X-axis represents individuals name codes. Bars attend to the left Y-axis showing the percentage of observations where an individual uttered one or more food calls. Diamonds attend to the right Y-axis representing the mean (±SE) number of food calls per observation for each individual
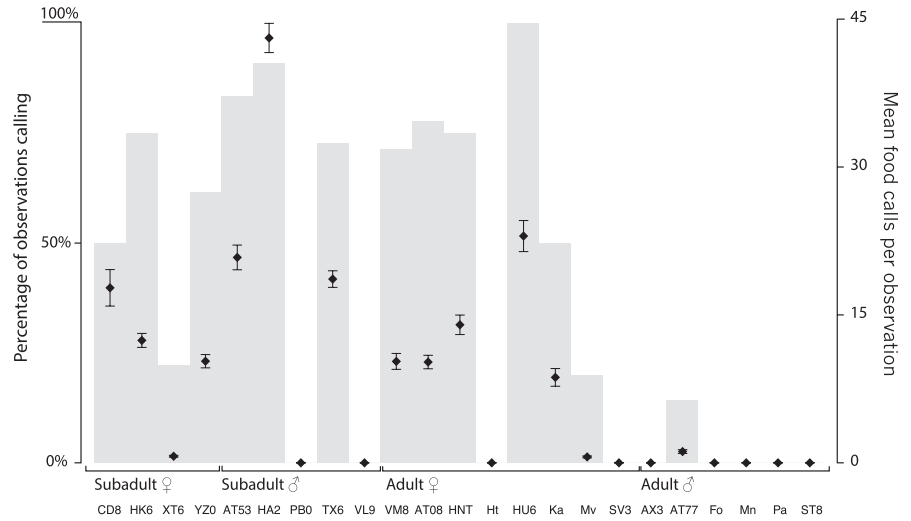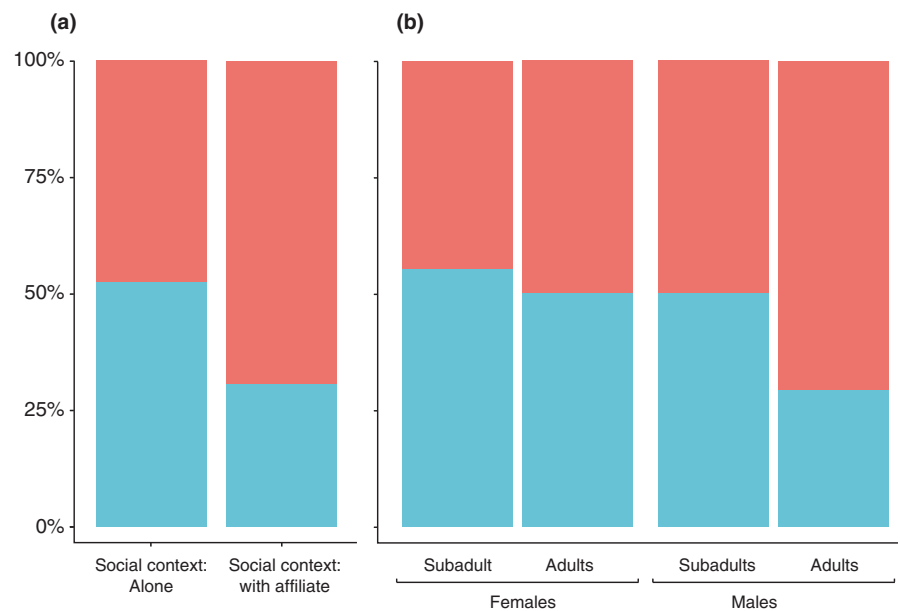
**TABLE 3** Results of the full average model. Given are Logit-transformed estimates and back-transformed estimates and 2.5%–97.5% confident intervals, Rel. Import = relative importance of the fixed effect and No. Mods = number of models containing a fixed effect. The estimate at the intercept is calculated for the following levels in each factor: cooperative partner nearby (*no*), age class (*subadult*), sex (*female*)

| Fixed effects | Logit-transformed model estimates | | | Back-transformed model estimates | | | | |
|---|---|---|---|---|---|---|---|---|
| | Estimate | CI 2.5%–97.5% | | Estimate | CI 2.5%–97.5% | | Rel. Import | No. Mods |
| Intercept | −0.48 | −1.64 | 0.69 | 0.38 | 0.16 | 0.67 | – | – |
| **Affiliate nearby—(*yes*)** | −1.55 | −2.61 | −0.5 | 0.17 | 0.07 | 0.38 | 1 | 7 |
| **Age class—(*adult*)** | −2.75 | −5.04 | −0.69 | 0.06 | 0.01 | 0.33 | 0.96 | 5 |
| **Sex—(*male*)** | −1.82 | −4.02 | 0.12 | 0.14 | 0.02 | 0.53 | 0.94 | 5 |
| **Age class (*adult*): sex (*male*)** | −3.88 | −8.98 | −0.85 | 0.02 | 0.00 | 0.30 | 0.79 | 2 |
| Group size | −0.03 | −0.63 | 0.37 | 0.49 | 0.35 | 0.59 | 0.25 | 2 |

*Note:* Bold type indicates relevant parameters influencing food calling behaviour.

**FIGURE 3** Proportion of focal observations with food calling (blue bars) and without food calling (red bars) grouped by (a) social context and (b) sex and age classes. The plot represents raw data, not model predicted values

the ravens' food call signals. Although we cannot draw firm conclusions on the exact bonding status of focal subjects on the basis of our protocol (that includes interactions with unmarked birds), behaviours

like sitting in close contact and exchanging affiliative interactions typically occur between familiar ravens with a positive relationship only (Fraser & Bugnyar, 2010; Massen et al., 2010; Morales et al., in

review). We know from playback studies that ravens have the capacity to mentally represent relationships (Boeckle & Bugnyar, 2012; Massen, Pašukonis, Schmidt, & Bugnyar, 2014a). Moreover, we know from field studies that ravens make use of their social knowledge in third-party interventions (Massen, Szipl, Spreafico, & Bugnyar, 2014b) and for recruiting social support (Szipl et al., 2018). Given that food-associated calls include individual information (Boeckle et al., 2012; Bugnyar & Kotrschal, 2001; Heinrich & Marzluff, 1991; Szipl et al., 2015) and receivers pay attention to the identity of the sender (Szipl et al., 2015), we expected senders to modify their call activity according to social context. Showing that ravens respond to the presence of an affiliation partner with reduced food calling is an important first step. Future studies have to test if ravens actively recruit such partners by increasing the calling activity when their partner is experimentally removed from the foraging group. We may also expect possible effects of age class, with younger birds having weaker relationships than older ones and therefore being less responsive to social context; adults, in contrast, should modify their calling to recruit specific individuals, that is their bonding partner.

Taken together, like most vocalizations, raven food-associated calls are embedded in a communication network (Bugnyar et al., 2001; Evans & Evans, 1999; King & Janik, 2015; McGregor, 2005; Slocombe et al., 2010), which adds communicative relevance beyond the advertisement of food (Clay et al., 2012). We here show that the social context experienced by individuals prior to feeding, aside of the birds' age class and sex, affects their likelihood of calling. These results raise the possibility that food calling ravens may not only address an "anonymous crowd" but take into account their relationships to potential receivers.

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