universität
wien

DISSERTATION / DOCTORAL THESIS

Titel der Dissertation /Title of the Doctoral Thesis

“Social cognition and fission-fusion dynamics in non-breeder Common ravens (*Corvus corax*)”

verfasst von / submitted by

Lic. Mario Gallego-Abenza

angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of

Doctor of Philosophy (PhD)

Wien, 2022 / Vienna 2022

Studienkennzahl lt. Studienblatt / degree programme code as it appears on the student record sheet:	UA 794 685 437
Dissertationsgebiet lt. Studienblatt / field of study as it appears on the student record sheet:	Biologie
Betreut von / Supervisor:	Univ.-Prof. Mag. Dr. Thomas Bugnyar
Betreut von / Supervisor:	Univ.-Prof. William Tecumseh Sherman Fitch, PhD

(c) Mario Gallego-Abenza

My own suspicion is that the universe is not only

queerer than we suppose, but queerer than we can suppose.

J.B.S. Haldane

Table of contents

Acknowledgments

First, I want to thank the person who trusted me to begin this journey back in 2017, Prof. Dr. Thomas Bugnyar. I have learned more about Ethology and Cognition in a walk with you around the Cumberland Wildpark than I will ever learn from any book. Thank you also for the freedom you have given me to conduct this Thesis and for your understanding when it was needed. I was lucky to work in a place where opinions from any group member counted equally.

I was 9-10 years old when I used to leave some bread on the balcony and hide behind the glass window to observe sparrows coming to feed on it. Similarly, I still don´t know how the captive pair of zebra finches we had at home, managed to breed with that little boy observing them so close for the entire day; now I know that they most likely habituated to a novel stressor: me. My first contact with Academia occurred in 2009 when I joined Dr. Mario León-Ortega during his data collection on the local eagle owl population for his Ph.D. We spent many days and nights in his Suzuki Vitara chasing owls and looking for hints of nocturnal life without being discovered by either the study species or the landowners. Thanks for uncovering for me the wild side of my region and letting me see it through the eyes of an experienced biologist.
There was a moment when I realized that I wanted to do a Ph.D. Imagine an almost 2 meters-tall researcher sitting on the ground using super tiny IR cameras to record nestlings´ behaviors inside breeding nest boxes. This happened in Öland, Sweden, almost 10 years ago, I then conceived another way to conduct science, by exploring animal behavior. He is now a good friend of mine and a current collaborator in science, Prof. Dr. David Wheatcroft. Whenever he sees cool stats results, he can get as excited as when his 5-year-old son finds a new beetle species, that´s the spirit! I also want to thank the Wheatcroft Lab´s members for the kind support and fun times.

This long journey would not have been possible without the help of several Department members. Petra Pesak, Sarah D., Philipp, or Nadja, thanks for being my hands and eyes in Vienna when I was in the Alps. Thanks Petra for giving me the opportunity of talking about anything that concerned me with total privacy and comprehension. Andras and his meticulousness to build things! It was fun to build the releasing aviary with you. My Ph.D. fellows! Paula, Giovanni, Clementine, Raffaela among others, thanks for hosting me when needed in Vienna and for the great times at parties; and my raven people, Lisa-Claire, Christian, Katharina and Palmyre, it was a pleasure to share this experience with all of you, I wish you all the best in your careers and lives.

KLF Leute! Big thanks to all of you! Almost everyone has held a raven for me to take blood, ring or attach a GPS logger. We managed to squeeze ourselves into the old building and run all kinds of projects. The old KLF building and its romanticism. Zivis and Master students, you were a huge help for me on this journey, no matter how crazy my trapping idea was, I always had hands to help on. Who would have told me that I had a gypsy sister in Austria! Ines, thanks for understanding me from the beginning, thanks for making me part of your family, come to visit more often! Verena, thanks for your big help with this annoying office mate, I wish you all the best. Matthias, thanks for teaching me a lot about stats, publication process, GPS tagging and all kinds of support when first arriving at the KLF, I will never forget how discovering Yellowstone next to you guys felt. Petra S., thanks for advising me, ravens are in good hands now. Prof. Sonia K., I will never forget the conversations we had sitting on the wooden bench where Konrad Lorenz himself used to sit in former times! Thanks for the opportunity to be part of the team in Galapagos, I will never forget such a place and experience, I hope it can happen again.

And the last but not least, I want to thank my family. My mum and brother have been and still are my biggest help when I am abroad and need food supplies or even wrap a car door to be shipped abroad because I crushed my car. My brother´s goodness makes him unique, and although we don’t tell much, we love each other a lot. My mum´s organizational skills which can eventually drive me crazy, are also behind her successful thriving in life, as she was able to sometimes financially support a son dreaming of becoming a scientist. I am sure my father would be so proud of me for this new achievement, he was the one holding me up to check nests from serins or blackbirds hidden in orange trees when I was a child. My friends from the neighborhood (ZIP 30012), all the experiences we share since I recall, still make me laugh no matter how far I go. My friends from University, Ana, Mamen, Mara, Punky, Lydia were boosting me with energy to continue this long journey. “Tú sabes una cosa, Marifé, la vida es tan bonita que parece de verdad…” thanks for opening my eyes to the world!

Finally, I would like to highlight the opportunity I had to observe wild ravens so close. The experiences I have lived in the Almtal valley and the ravens will always remain in my mind. Regulus, Honk, Hedda, and Pueblo are only a few of these incredible creatures that taught me so much about their social life in wild conditions.

Zusammenfassung

Zusätzlich zu ökologischen Anforderungen werden Anforderungen des Soziallebens als entscheidender Faktor für die Entwicklung von Intelligenz betrachtet. Das Beobachten von Interaktionen zwischen Gruppenmitgliedern und das Merken ihres Ausgangs kann zu einem vielschichtigen Wissen über Gruppenmitglieder führen und den Tieren dabei helfen, die Intentionen von Artgenossen richtig zu deuten bzw. ihr Verhalten vorherzusagen. Die Fähigkeit soziale Information zu verarbeiten und entsprechende Verhaltensanpassungen vorzunehmen wird als soziale Kompetenz bezeichnet. Es wird angenommen, dass es innerhalb der Mitglieder einer Gruppe zu beträchtlichen Unterschieden betreffend soziales Wissen und sozialer Kompetenz kommen kann, ähnlich wie beim Lernen oder Problemlösen. Solche individuellen Unterschiede könnten erklären, wie sich Tiere im sozialen Umfeld verhalten, wie gut sie eingebunden sind und wie sehr sie auf soziale Information achten. Wenn das soziale Umfeld dynamisch ist und sich durch ein Kommen und Gehen der Individuen auszeichnet, könnten die individuellen Unterschiede im sozialen Wissen und der sozialen Kompetenz mit den demographischen Merkmalen wie die Anzahl der aufgesuchten Gruppen und die Verweildauer in diesen zusammenhängen.

Man weiß von nicht-brütenden Raben, dass sie große individuelle Unterschiede in ihrer Ortsdynamik zeigen, wobei einige Vögel konsistent an einem Ort bleiben („Lokale“), während andere viel herum kommen („Wanderer“). Diese Muster gehen mit unterschiedlichen sozialen Anforderungen einher: Lokale bleiben ständig in derselben Gruppe, während Wanderer immer wieder mit neuen Gruppen konfrontiert sind. Es ist unbekannt, welche Faktoren dafür ausschlaggebend sind, ob Raben zu Lokalen oder Wanderer werden und wie sich das auf ihre Kognition auswirkt. Die vorliegende Arbeit hat zum Ziel mittels Beobachtungs- und experimentellen Ansätzen diese Wissenslücke zu füllen.

Die ersten beiden Kapiteln untersuchen den Einsatz von Kognition bei einer wildlebenden Gruppe von nicht-brütenden Kolkraben in zwei verschiedenen Situationen: i) wenn sie untereinander um Futter konkurrieren (Kapitel 1) und ii) wenn sie anhand von Alarmrufen das Risiko eines Raubfeindangriffs abschätzen (Kapitel 2). In den nächsten beiden Kapiteln wird die Aufmerksamkeit von individuellen wilden Raben (Kapitel 3) bzw. in Gefangenschaft erbrüteter Raben (Kapitel 4) gegenüber sozialer Information experimentell getestet und mit der sozialen Dynamik bzw. frühkindlichen sozialen Erfahrung in Zusammenhang gesetzt. Konkret wird in Kapitel 3 die Hypothese getestet, dass die Aufmerksamkeit gegenüber simulierten Interaktionen von der Ortsdynamik der Raben (Lokale, Wanderer) abhängig ist; in Kapitel 4 wird getestet, ob die Aufmerksamkeit gegenüber sozialen Kategorien variiert und mit frühkindlicher sozialer Erfahrung zusammenhängt.

Zusammengefasst ergeben die Resultate folgendes Bild: währen Erfahrung bzw. soziales Wissen bei Entscheidungsfindungen der Raben klar eine Rolle spielt, zeigen die individuellen Unterschiede in der Orts- und Gruppendynamik keinen messbaren Einfluss. Diese teilweise überraschenden Ergebnisse werden in Hinblick auf jüngste Resultate von anderen Arten betreffend individuelle Unterschiede in sozialer Kognition diskutiert. Zudem wird darüber spekuliert, wie Kognition das Leben von Raben aus sozialer und ökologischer Sicht beeinflussen könnte.

Summary

Aside from ecological demands, living in social groups has been considered as the main force behind the origin of intelligence. Attending to others´ interactions and memorizing the output, may result in sophisticated social knowledge about the group members and it might help individuals to anticipate others´ intentions or behaviours in the future. The ability of social information-processing and posterior adjustment of social behaviours is also known as social competence. Similar to other cognitive abilities such as learning, memory or problem solving that vary across individuals within a group, we could also expect differences in social knowledge and competence across individuals living in the same social group. Such variation may have consequences on how individuals navigate through their social unit, affecting their centrality, connectedness or behavioural responses towards social cues. Moreover, in an `open´ group characterized by fission-fusion dynamics, these pronounced individual differences might correlate with individual demographic traits, e.g., the number of social units and the time spent at each.

Non-breeder raven groups had been described to show high individual variation in the degree of fission-fusion dynamics, whereby individual vagrancy patterns range from “local” (birds spending their lifetime in the same social unit) to “vagrant” (birds spending their lifetime in several social units). Which factors contribute to an individual´s decision to adopt a local or vagrant lifestyle and how this relates to cognition remain poorly known. This thesis aims to shed light on these questions using both observational and experimental approaches on wild and captive-bred ravens.

In the first two chapters, I examine the use of cognition in a wild population of non-breeder common ravens in two different contexts, i) while competing with conspecifics for food sources (Chapter 1) and ii) when assessing the predation risk based on alarming conspecifics (Chapter 2). In the last two chapters, I experimentally test attention responses of individual wild-caught ravens (Chapter 3) and captive-bred juvenile ravens (Chapter 4) and link those to aspects of the birds´ fission-fusion dynamics and early life experience, respectively. Specifically, I hypothesize in Chapter 3 that the ravens´ attentive responses to simulated social interactions are affected by their vagrancy patterns; and in Chapter 4 that early social life influences social competence of socialization strategies.

Taken together, my results provide evidence for the role of experience in the ravens´ decision making but hardly any effects of the large individual variation in vagrancy on cogntion. I discuss the partly unexpected findings of this thesis on individual differences in social cognition in other species and I speculate how cognition shapes common ravens´ life from ecological to social perspectives.

General Introduction

Evolution of cognition and social life

Cognition, broadly defined as information processing (Shettleworth, 1998), allows for flexibly adjusting behaviours to challenges posed by the surrounding world. Depending on the nature of these challenges, several hypotheses have been proposed for explaining the evolution of cognition. Some of these are considered as competing alternatives, whereas others as not mutually exclusive (Ashton, Thornton, et al., 2018; Henke-von der Malsburg et al., 2020; Rosati, 2017) For instance, the cognitive buffer hypothesis points at the variation in the environment as the predictable factor for brain size, authors highlighted the appearance of innovative behaviours in the wild as a proxy for cognition (Byrne & Corp, 2004; Sol, 2009). Other ecological hypotheses put the focus on foraging flexibility, notably challenges associated with spatial variation of food distribution (Milton, 1981) and extracting food (Parker & Gibson, 1977). While the former has been shown to be linked with spatial memory (Healy et al., 2005; Pravosudov & Roth II, 2013), the latter has been associated with tool use (Lefebvre et al., 2002; Reader & Laland, 2002).

In contrast to those ecologically oriented hypotheses, the social intelligence hypothesis (Byrne & Whiten, 1989; Humphrey N K, 1976; Jolly, 1966) and social brain hypothesis (Dunbar, 1998) propose that the challenges of living in a social group impose a sufficient pressure to select for advanced cognitive skills and large brains, respectively. Support for this argument comes from comparative analyses across primates showing that species with larger neocortex ratio live in larger social groups support (Dunbar, 1992; Dunbar & Shultz, 2007). More interestingly, comparative analyses have been also conducted within primate species, resulting in a positive correlation between individuals living in complex groups (understood as group size and the number of maintained relationships) and brain structure, e.g. gray matter density in humans (Kanai et al., 2012) or increased coupling activity in frontal and temporal cortex in macaques (Sallet et al., 2011). Comparisons across species other than primates highlight effects of long-term social relationships, rather than group size, on brain size measures (Dunbar & Shultz, 2007) and cognition (Emery et al., 2007). For instance, bird species forming long-term relationships tend to show greater intellectual abilities than species that do not or have short-term relationships (Emery et al., 2007). On the individual level, studies on Australian magpies and house sparrows also support a link between group size and cognition, as individuals living in bigger groups outperform those from smaller groups in cognitive tasks (Ashton, Ridley, et al., 2018; Liker & Bokony, 2009).

Beyond group size, there are other characteristics to be considered when investigating the number of social relationships that a single individual maintains within its social unit: how much group changes in size and composition over time (Kummer, 1971; Aureli et al., 2008). The so-called fission-fusion dynamics describes the possibility of adjusting groups according to context; for instance, a high degree of fission-fusion dynamics would mean that individuals form large groups at productive food patches but small groups when resources are scarce. The `open´ character of social groups is found in many birds (Silk et al., 2014), bats (Kerth et al., 2006), cetaceans (Connor & Whitehead, 2005), hoofed mammals, such as American Bisons (Fortin et al., 2009) and some primate species (Smuts et al., 1987) fit well to this scheme. From a cognitive point of view, it has been suggested that high degrees of fission-fusion dynamics could be relevant drivers for cognitive development, as dynamically changing social environments may require enhanced memory, inhibition and inference skills (Aureli et al., 2008). Furthermore, a comparative study on primates using a battery of inhibition tasks reveals that species living in a society characterized by fission-fusion dynamics exhibit a better inhibitory control and behavioural flexibility than species with lower degrees, and this effect is not explained by phylogenetic relationships or feeding ecology (Amici et al., 2008). Beyond the cognitive performance in inhibition tasks, little is known about the effects of fission-fusion dynamics on socio-cognitive skills.

Processing social information demands specific cognitive abilities, so-called social competence (Waters & Sroufe, 1983). Apart from the abovementioned correlation between social complexity and cognitive performance, social competence has been also proposed to evolve together with social cognition when evolution pressures rely on the social domain (Varela et al., 2020). Similar to other cognitive abilities such as learning, memory or problem solving that vary across individuals (Boogert et al., 2018), social competence, based on adaptive behavioural flexibility is also expected to strongly vary across individuals living in the same social group. Such variation may have consequences in how individuals navigate through their social unit, affecting their centrality, connectedness or behavioural responses towards social cues (Brandl et al., 2019), and ultimately their fitness (Silk et al., 2003). Developmental, genetic and environmental factors such as stress-related periods during development have been identified as possible sources for the individual differences in social competence (Sachser et al., 2013; Crailsheim et al., 2020). Yet, little is known about how systems characterized by high degrees of fission-fusion dynamics, where individual demographic traits like the number of social units visited and/or the time spent with particular individuals could play an important role in developing and/or expressing social competence.

Taken together, much of the literature on social cognition has focused on interspecific differences, whereby living in complex societies tends to be linked with larger brains and/or advanced cognitive abilities. However, which factors contribute to the social complexity seem to differ among taxonomic groups and species. Among the most prominent factors are group size, the importance of long-term social relationships, and the degree of fission-fusion dynamics. In relation to interspecific comparisons, relatively few studies have investigated which factors influence intraspecific differences in social cognition (but see Ashton, Thornton, et al., 2018; Henke-von der Malsburg et al., 2020; Rosati, 2017). Notably, hardly any study has investigated proposed links between socio-cognitive skills (or social competence) and fission-fusion dynamics within a species.

Common ravens as study species and study site

Fig. 1: Individually marked non-breeding ravens at our study site in the Northen Austrian Alps. ©Mario Gallego-Abenza

Common ravens typically experience two different social stages throughout their life time. As adult breeders, they are socially monogamous and defend a large territory all year round (Rösner & Selva, 2005); as non-breeders, they are vagrant but highly social, regularly forming groups with changing size and composition (Heinrich, 1988; Loretto et al., 2017). Juvenile ravens stay with their parents for an extended period (2-5 months post-fledging) and eventually start joining non-breeder groups, primary for foraging (Heinrich, 1988). Non-breeder groups are composed mainly of immature ravens between their first and fourth year of life (Braun & Bugnyar, 2012; Heinrich, 1989) that may come and go on a daily basis, but also stay together over months and even years. In addition, adults that lack a partner or territory can be also seen in these groups. Raven foraging flocks are thus structured by different age-classes, bonding status and vagrancy patterns (Boucherie et al., 2019). Apart from feeding together, ravens also roost in large groups that might primarily serve as protection against predators but also may serve as information centres regarding ephemeral or scattered food sources (Marzluff et al., 1996). Finally, non-breeding ravens can be also observed socializing in smaller (sub-)groups throughout the day often engaging in affiliative and/or playful interactions (Braun et al., 2012; Heinrich & Smolker, 1998). Affiliative relationships are formed not only between adult pair partners that defend a territory, but also between individuals in non-breeder groups. These pair bond-like relationships are typically found between males and females but sometimes also between members of the same sex and between siblings (Fraser & Bugnyar, 2010). Such relationships seem to function as alliances in conflicts and further enhance the complexity of the `open´ but structured social groups (Braun et al., 2012; Braun & Bugnyar, 2012).

Fig. 2. Affiliated social interaction between a marked (right) and unmarked (left) raven. ©Mario Gallego-Abenza

The socially complex life of ravens fits well to the fact that they have evolved large brains with high neuron densities (Olkowicz et al., 2016) and the general notion that ravens are `smart´ birds (Gwinner, 1964; Marzluff & Angell, 2007). Notably, their reliance on social bonds and the open character of their foraging groups make non-breeder ravens excellent candidates for testing assumptions of social intelligence. Given that ravens regularly join and leave groups, they can be expected to have substantial recognition and memory skills as well as the ability to track own and others´ relationships over time and space. Indeed, playback studies from captivity demonstrate long-term memory of former group members and the relationship valence to them, i.e., birds discriminated whether the played back individuals were former ´friends´ or ´foes´ (Boeckle & Bugnyar, 2012). Likewise, captive ravens remembered over years, which humans might be ´dangerous´ because they were once seen carrying a dead raven (Blum et al., 2020). The existence of third-party knowledge has been shown experimentally in captivity and observationally under wild conditions. Specifically, captive ravens can notice a simulated dominance reversal between group members, even if it concerns those of the neighbouring group (Massen, Pašukonis, et al., 2014). Wild ravens that are victims of aggression adjust their signalling behaviour according to the audience composition, i.e. they increase calling when their own kin is present but decrease calling when the aggressor´s bonding partner is present (Szipl et al., 2018).

Fig. 3: (a) Study site: Cumberland Wildpark, Grünau im Almtal, Upper Austria. (b) Free-ranging Common ravens feeding at the wild boars enclosure. ©Mario Gallego-Abenza

Our study site is allocated in the Northern Austrian Alps, close to the village Grünau im Almtal, where a long-term monitored group of free-ranging ravens snatch food from animal enclosures at a local zoo, Cumberland Wildpark. Group size can range between 15 to 120 ravens at a single feeding site, usually at the wild boars enclosure. Due to the predictability of daily feedings, ravens may simply aggregate at those feeding sites. However, they also actively signal when food becomes available, by eliciting food-associated calls, referred to as “yells” (Heinrich & Marzluff, 1991) or “haa” calls (Bugnyar & Kotrschal, 2001). Food calling attracts conspecifics at natural carcasses and increases the chance of callers to cope with food defence of dominant ravens (Heinrich & Marzluff, 1991). Like at carcasses, most food-associated calls at our study site are given by immature ravens; yet, adults selectively use these calls as well, likely to target their bonded partner when it is not yet visible at the feeding site (Sierro et al., 2020).

Using a trapping/re-sighting method on individually marked ravens allows our team to track the use of our study site across days. Over the course of 14 years, me and former research group members could see highly variable presence/absence patterns between individuals but fairly consistent patterns within individuals, whereby some individuals are absent for long periods of time (up to years) before they show up again and others visiting the feeding sites almost on a daily basis (Braun et al., 2012; Boucherie et al. 2022). Long-term data collection focusses also on individual social behaviour, such as agonistic and affiliative interactions. Observations are possible from close-distance due to the habituation of ravens towards human observers and their recording tools, such as microphones or video cameras which can be placed up to 2 meters of distance to the birds. However, outside our study area we face problems in visually tracking our marked ravens, as flight distances are much larger than at our site (due to a lack of habituation) and the reading distance of marking material. After a pilot phase on 10 ravens (Loretto, Schuster, et al., 2016; Loretto et al., 2017a), we have recently incorporated the tagging with GPS loggers on (most) newly trapped birds (80 in three years). This technique allows us to track individuals with high precision when they leave our study site and to eventually study their fission-fusion dynamics on the large scale. Indeed, first results not only confirm our observations that individuals differ strikingly in their vagrancy (Loretto, Schuster, et al., 2016), but also support our hypothesis of individuals showing different degrees of fission-fusion dynamics, as tagged individuals do encounter each other at same or at different locations and after short or long periods of time (Loretto et al., 2017a).

Fig. 4: Releasing an individually marked wild-caught raven. ©Jakob Guebel

The enormous individual differences in residency/vagrancy of non-breeder ravens at our study site as well as at other foraging sites are poorly understood. Why do some ravens regularly shift between sites, whereas others stay at the same site until reaching adulthood? The availability of food may explain some of their decisions; however, at least in Middle Europe, non-breeding ravens rely heavily on anthropogenic food sources such as garbage dumps or game parks, which are characterized by regular food supply (Loretto, Schuster, et al., 2016). Hence, in addition to food, social factors may play a role; accordingly, ravens would choose to shift between, or stay in, particular foraging groups rather than foraging sites. Life experiences such as difficulties in food acquisition due to high conspecific competition, high rates of perceived risk and/or predation events, or high rates of conflicts about rank/status might be behind the individuals´ decision of leaving a local group. The decision to leave implicates finding a new foraging site and the encountering conspecifics that are likely already part of structured groups. Therefore, individual abilities such as social cognition and competence might be key in shaping the individual population dynamics of non-breeders.

Aims and structure of the thesis

The aims of my thesis is two-fold: i) to improve our knowledge on raven social cognition and social competence, and ii) to examine for the first time how their cognitive skills relate to their dynamic social life (changing group size, composition). I focus mainly on wild ravens, but also use the opportunity to manipulate offspring number, and thus group size during upbringing, in captive-bred ravens. I apply correlative and experimental approaches, ranging from behavioural observations and GPS fixation points to playback experiments under ecologically relevant conditions (in the entire social group) as well as under controlled conditions (on temporary separated single individuals).

My thesis is structured in 4 chapters, all of them referring to a peer-reviewed paper. Two papers are published, one is submitted and one in shortly before submission. In the first two papers, I focus on the use of cognition in a wild population of non-breeders in two different contexts, i) food competition (chapter 1) and ii) predation risk assessment (chapter 2). In the other two papers, I test the attention to conspecific calls in wild-caught ravens (chapter 3) and captive-bred juvenile ravens (chapter 4) and link their responses to their degree of fission-fusion dynamics and the social experiences during upbringing, respectively. I also contributed to another recently published paper entitled "Dominance in a socially dynamic setting: hierarchical structure and conflict dynamics in ravens' foraging groups" listed in the Appendix of this thesis. This paper uses long-term data sets in which I contributed to substantially during my PhD period, and provides an interesting comparative analyses of dominance hierarchies between captive and wild ravens.

In chapter 1, I conducted an observational study on social foraging strategies of wild ravens at the Cumberland Gamepark, Grünau im Almtal, linking individual decisions with presence/absence patterns. Specifically, I tested whether differences in individuals´ presence/absence patterns were reflected in their foraging success and the probability of avoiding kleptoparasitism. Ravens are renowned for their variable scrounging tactics (Bugnyar & Kotrschal, 1997), profiting from the food made available by others either directly via kleptoparasitism or delayed via pilfering caches (Bugnyar & Heinrich, 2006; Heinrich & Pepper, 1998) Throughout 1 year, I video-recorded foraging bouts at the wild boar enclosure and analysed 779 food securing attempts from a total of 46 individually marked ravens. I distinguished two different foraging strategies i) consume the food item at the foraging site or ii) carry the food item away for later consumption. I defined foraging success as i) ravens consuming the food at the foraging site without being harassed by conspecifics and ii) ravens chased by conspecifics. I expected those individuals that spend longer periods of time in our study site to show a greater foraging success compared to individuals that are hardly seen at the study site. I thus modelled individuals´ foraging success for the two feeding strategies to assess the effect of their presence/absence; additionally, I included the parameters age class, sex or winning probability (% of won interactions throughout the entire study period) and decision time (defined as the time since the food was grabbed to the moment when decision to consume or fly off is taken) in the model.

In chapter 2, I used an experimental approach to investigate antipredator responses and threat assessment based on both age class and number of alarming conspecifics. Note that this paper does not examine potential effects of fission-fusion dynamics, but addresses a cognitive aspect of foraging potentially useful under high dynamics: what ravens can make out of alarm calls? Learning what constitutes a threat by observing, or listening to, others´ reactions represents a case of information transmission through social learning (Griffin, 2004; Templeton, 2018). In some species, individuals can also assess the predation risk through (subtle) acoustic differences in calls, referred to as functional reference (Gill & Bierema, 2013). Another way of assessing predation risk is to take into account particular traits of the signaller such as its experience, which usually correlates with age, for instance, when alarm calls of adults are treated as more relevant than those of juveniles, as occurs in Richardson´s ground squirrels (Sloan & Hare, 2008). In addition to individual traits, the number of individuals signalling could also affect the antipredator response, as more callers may indicate a higher threat level (Coomes et al., 2019). Group foraging ravens are highly sensitive to social cues (Heinrich, 1989), including alarm calls (Nácarová et al., 2018). However, overreacting to alarm cues might be costly, particularly when foraging competition is high (see above). I thus hypothesized that ravens should be capable of threat assessment, taking individual attributes (age class) and/or number of callers into account. I exposed foraging ravens to playback of conspecifics alarm calls, manipulating the age class (juveniles versus adults) and the number of individuals that called (one versus two) in a counter-balanced order. For logistical reasons, I conducted the playback experiment in three different seasons (spring, autumn and summer) throughout 2 years (2019 & 2020). From the recorded videos, I measured the i) number of ravens that adopted a vigilance posture (raising the head up) and ii) the number of ravens that flew off from the feeding site within 5 seconds after broadcasting the alarm calls. Taking into account the total number of ravens before the playback, I analysed the proportion of ravens responding to each of the 4 treatments (1 adult caller, 1 juvenile caller, 2 adult callers and 2 juvenile callers). I expected ravens to react stronger towards calls from adults than from juveniles, as the former should have more experience in encountering predators than the latter. Moreover, I expected ravens to discriminate between 1 or more callers and to react stronger in trials were alarm calls were given by two as compared to one caller. I also expected seasonal effects, as i) the predation risk in winter might be higher than in summer and ii) most unexperienced juveniles join the foraging groups for the first time in fall.

In the chapter 3, I combined a playback experiment on individual ravens with observations of their movement patterns using GPS technology. I thus tested here directly for a possible link between how ravens perceive their social environment and their fission-fusion dynamics. In social species, dominance relationships and rank hierarchies typically form on the basis of repeated agonistic interactions between group members (Bernstein, 1981). Moreover, communication can evolve to mainly prevent individuals from physical harassment, whereby context-specific signals can be used by dominant individuals to advertise their strength and by subordinates to signal their submission, e.g. in primates (Chance, 1967). In common ravens, victims of aggression tend to give “defensive calls”, primarily to appease the aggressor (Heinrich et al., 1993) but also to attract potential allies for social support (Szipl et al., 2018a). I hypothesized that these types of interactions should be of particular relevance to newly arriving individuals, which are not yet knowledgeable about the local structure and dominance hierarchy, respectively. Given that non-breeder ravens expressing a high degree of fission-fusion dynamics (“vagrants”) encounter more often new foraging groups than those expressing a low degree of fission-fusion dynamics (“residents”), I predicted the former to pay more attention to vocal interaction than the latter. I used a playback-design experiment to test individual responses of wild-caught ravens towards acoustic social signals of unfamiliar birds (defensive calls given during agonistic interactions, recorded from birds of a captive colony in the east of Austria). Between 2018 and 2020, I carried out playback experiments on 34 newly-caught ravens, while they were singly housed for tagging. I then correlated the birds´ responses to the played back calls with the spatial information obtained through the GPS-loggers in the month after the birds´ release. I defined the degree of fission-fusion dynamics as the number of foraging groups visited in 31 days post-release as well as the mean of daily kilometres travelled and included sex and age-class into the analyses.

In chapter 4, I joined forces with an ongoing program on the development of social competence (manipulating offspring numbers in captive breeding pairs) and experimentally investigated whether the early social environment (upbringing in differently sized families) influences the ravens´ attention to conspecific calls at the time when they integrate into non-breeder groups. Similar to other corvids species, common ravens show an extended upbringing period, where the fledged juveniles spend a few months with their parents before joining the nearby non-breeder groups (Coombs, 1978; Goodwin, 1976). We hypothesized that interacting with siblings during this time period may be key for practising/acquiring social skills (following the logic of studies of fish, rodents, birds and primates, all indicating strong effects of early life experience on the offspring´s behaviour later in life (Branchi & Alleva, 2006; S. Fischer et al., 2015). For three consecutive years, we experimentally manipulated the egg number of several captive breeding pairs, creating families with 2-4 offspring per year. Thus, besides their parents, juveniles could interact with 1-3 siblings in their first 10 weeks post-fledging. Simulating the natural timing of dispersion observed in our study area, we then separated juveniles from their parents and housed them in one of two new aviaries. We thereby formed two non-breeder groups of same-aged peers, creating a first scenario for socialization with unfamiliar, non-related individuals under controlled conditions. Specifically, the two non-breeder groups were of similar size and contained pairs of siblings coming from different families. The two aviaries were located about 1.5 km apart from each other to prevent any vocal contact between the groups. After 5 weeks, I individually tested each of the young ravens in a playback-design experiment for recognition of individuals with different degrees of familiarity. I used food-associated calls, as these calls are known to encode individual signature (Boeckle et al., 2012) and exposed each raven to 3 different caller categories: sibling (individual they grew up and were transferred with into the non-breeder group), a familiar non-sibling (unrelated individual they were housed with in the non-breeder group) and an unknown non-sibling (unrelated individual housed in the other non-breeder group). Assuming that raven juveniles raised in the presence of more than one sibling might have practiced individual identification or social knowledge acquisition better than juveniles raised with one sibling only, I expected ravens to show stronger attentive responses to calls of familiar than unfamiliar conspecifics. Alternatively, our results might align with recent findings on zebra finches, where individuals raised in large broods were later less “choosy” and showed more centrality in the group network than birds from small groups (Brandl et al., 2019). In this case, we could expect ravens from large families to equally respond towards all social categories, showing no preference for calls of familiar individuals.

REFERENCES *(General Introduction)*

Amici, F., Aureli, F., & Call, J. (2008). Fission-Fusion Dynamics, Behavioral Flexibility, and Inhibitory Control in Primates. *Current Biology*, *18*(18), 1415–1419. https://doi.org/10.1016/j.cub.2008.08.020

Aplin, L. M., Firth, J. A., Farine, D. R., Voelkl, B., Crates, R. A., Culina, A., Garroway, C. J., Hinde, C. A., Kidd, L. R., Psorakis, I., Milligan, N. D., Radersma, R., Verhelst, B. L., & Sheldon, B. C. (2015). Consistent individual differences in the social phenotypes of wild great tits, Parus major. *Animal Behaviour*, *108*, 117–127. https://doi.org/10.1016/j.anbehav.2015.07.016

Ashton, B. J., Ridley, A. R., Edwards, E. K., & Thornton, A. (2018). Cognitive performance is linked to group size and affects fitness in Australian magpies. *Nature*, *554*(7692), 364–367. https://doi.org/10.1038/nature25503

Ashton, B. J., Thornton, A., & Ridley, A. R. (2018). An intraspecific appraisal of the social intelligence hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1756), 20170288. https://doi.org/10.1098/rstb.2017.0288

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., Connor, R., Fiore, A. D., Dunbar, R. I. M., Henzi, S. P., Holekamp, K., Korstjens, A. H., Layton, R., Lee, P., Lehmann, J., Manson, J. H., Ramos-Fernandez, G., Strier, K. B., & Schaik, C. P. van. (2008). Fission-Fusion Dynamics. *Current Anthropology*, *49*(4), 627–654. https://doi.org/10.1086/586708

Aureli, F., & Schino, G. (2019). Social complexity from within: How individuals experience the structure and organization of their groups. *Behavioral Ecology and Sociobiology*, *73*(1). https://doi.org/10.1007/s00265-018-2604-5

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bernstein, I. S. (1981). Dominance: The baby and the bathwater. *Behavioral and Brain Sciences*, *4*(3), 419–429.

Blum, C. R., Fitch, W. T., & Bugnyar, T. (2020). Rapid learning and long-term memory for dangerous humans in ravens (Corvus corax). *Frontiers in Psychology*, *11*, 2843.

Boeckle, M., & Bugnyar, T. (2012). Long-term memory for affiliates in ravens. *Current Biology*, *22*(9), 801–806. https://doi.org/10.1016/j.cub.2012.03.023

Boeckle, M., Szipl, G., & Bugnyar, T. (2012). Who wants food? Individual characteristics in raven yells. *Animal Behaviour*, *84*(5), 1123–1130. https://doi.org/10.1016/j.anbehav.2012.08.011

Bonnie, K. E., & Earley, R. L. (2007). Expanding the scope for social information use. *Animal Behaviour*, *74*(2), 171–

181. https://doi.org/10.1016/j.anbehav.2006.12.009

Boogert, N. J., Madden, J. R., Morand-Ferron, J., & Thornton, A. (2018). Measuring and understanding individual differences in cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1756), 20170280. https://doi.org/10.1098/rstb.2017.0280

Borgeaud, C., van de Waal, E., & Bshary, R. (2013). Third-Party Ranks Knowledge in Wild Vervet Monkeys (Chlorocebus aethiops pygerythrus). *PLoS ONE*, *8*(3), e58562. https://doi.org/10.1371/journal.pone.0058562

Boucherie, P. H., Blum, C. R., & Bugnyar, T. (2020). Effect of rearing style on the development of social behaviour in young ravens (Corvus corax). *Ethology*, *00*(March), 1–15. https://doi.org/10.1111/eth.13010

Boucherie, P. H., Gallego-Abenza, M., Massen, J. J. M., & Bugnyar, T. (2022). *Dominance in a socially dynamic setting: Hierarchical structure and conflict dynamics in ravens' foraging groups*. *377*(1845), 12. https://doi.org/10.1098/rstb.2020.0446

Boucherie, P. H., Loretto, M., Massen, J. J. M., & Bugnyar, T. (2019). *Lessons from ravens What constitutes B social complexity ^ and B social intelligence ^ in birds? Lessons from ravens*. *January*.

Branchi, I., & Alleva, E. (2006). Communal nesting, an early social enrichment, increases the adult anxiety-like response and shapes the role of social context in modulating the emotional behavior. *Behavioural Brain Research*, *172*(2), 299–306. https://doi.org/10.1016/j.bbr.2006.05.019

Brandl, H. B., Farine, D. R., Funghi, C., Schuett, W., & Griffith, S. C. (2019). Early-life social environment predicts social network position in wild zebra finches. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1897). https://doi.org/10.1098/rspb.2018.2579

Braun, A., & Bugnyar, T. (2012). Social bonds and rank acquisition in raven nonbreeder aggregations. *Animal Behaviour*, *84*(6), 1507–1515. https://doi.org/10.1016/j.anbehav.2012.09.024

Braun, A., Walsdorff, T., Fraser, O. N., & Bugnyar, T. (2012). Socialized sub-groups in a temporary stable Raven flock? *Journal of Ornithology*, *153*(SUPPL. 1), 97–104. https://doi.org/10.1007/s10336-011-0810-2

Brooks, M. E., Kristensen, K., Benthem, K. J. van, Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., & Bolker, B. M. (2017). GlmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, *9*(2), 378–400.

Bugnyar, T., & Heinrich, B. (2006). Pilfering ravens, Corvus corax, adjust their behaviour to social context and identity of competitors. *Animal Cognition*, *9*(4), 369–376. https://doi.org/10.1007/s10071-006-0035-6

Bugnyar, T., & Kotrschal, K. (1997). *An experimental analysis of social foraging in ravens: Individual tactics,* *scrounging, and deception*. *32*, 497.

Bugnyar, T., & Kotrschal, K. (2001). Movement coordination and signalling in ravens (corvus corax): An experimental field study. *Acta Ethologica*, *3*(2), 101–109. https://doi.org/10.1007/s102110000029

Byrne, R. W., & Corp, N. (2004). Neocortex size predicts deception rate in primates. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(1549), 1693–1699. https://doi.org/10.1098/rspb.2004.2780

Byrne, R. W., & Whiten, A. (1989). *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans (Oxford Science Publications)*. {Oxford University Press, USA}.

Calenge, C. (2006). The package adehabitat for the R software: Tool for the analysis of space and habitat use by animals. *Ecological Modelling*, *197*, 1035.

Cantlon, J. F., & Brannon, E. M. (2006). Shared System for Ordering Small and Large Numbers in Monkeys and Humans. *Psychological Science*, *17*(5), 401–406. https://doi.org/10.1111/j.1467-9280.2006.01719.x

Chance, M. R. A. (1967). Attention Structure as the Basis of Primate Rank Orders. *Man*, *2*(4), 503–518. JSTOR. https://doi.org/10.2307/2799336

Cheney, D. L., & Seyfarth, R. M. (1986). The recognition of social alliances by vervet monkeys. *Animal Behaviour*, *34*(6), 1722–1731. https://doi.org/10.1016/S0003-3472(86)80259-7

Connor, R., Wells, R., Mann, J., & Read, A. J. (2000). *The bottlenose dolphin, Tursiops sp.: Social relationships in a fission-fusion society.* (Whitehead H, pp. 91–126). The University of Chicago Press.

Connor, R., & Whitehead, H. (2005). Alliances II. Rates of encounter during resource utilization: A general model of intrasexual alliance formation in fission–fusion societies. *Animal Behaviour*, *69*(1), 127–132. https://doi.org/10.1016/j.anbehav.2004.02.022

Coombs, F. (1978). *The crows: A study of the corvids of Europe*. BT Batsford Limited.

Coomes, J. R., Mcivor, G. E., Thornton, A., Coomes, J. R., & Thornton, A. (2019). Evidence for individual discrimination and numerical assessment in collective antipredator behaviour in wild jackdaws (Corvus monedula). *Biology Letters*.

Crailsheim, D., Stüger, H. P., Kalcher-Sommersguter, E., & Llorente, M. (2020). Early life experience and alterations of group composition shape the social grooming networks of former pet and entertainment chimpanzees (Pan troglodytes). *PLoS ONE*, *15*(1), 1–26. https://doi.org/10.1371/journal.pone.0226947

Crick, N. R., & Dodge, K. A. (1994). A review and reformulation of social information-processing mechanisms in children’s social adjustment. *Psychological Bulletin*, *115*(1), 74–101. https://doi.org/10.1037/0033-

2909.115.1.74

Dall, S. R. X., Giraldeau, L. A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology and Evolution*, *20*(4), 187–193. https://doi.org/10.1016/j.tree.2005.01.010

Danchin, É., Giraldeau, L.-A., Valone, T. J., & Wagner, R. H. (2004). Public Information: From Nosy Neighbors to Cultural Evolution. *Science*, *305*(5683), 487–491. https://doi.org/10.1126/science.1098254

Delignette-Muller, M. L., & Dutang, C. (2015). fitdistrplus: An R Package for Fitting Distributions. *Journal of Statistical Software*, *64*(4), 1–34. https://doi.org/10.18637/jss.v064.i04

Dunbar, R. I. M. (1992). Neocortex size as a constraint on group size in primates. *Journal of Human Evolution*, *22*(6), 469–493. https://doi.org/10.1016/0047-2484(92)90081-J

Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology: Issues, News, and Reviews*, *6*(5), 178–190. https://doi.org/10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.0.CO;2-8

Dunbar, R. I. M., & Shultz, S. (2007). Evolution in the Social Brain. *Science*, *317*(5843), 1344–1347. https://doi.org/10.1126/science.1145463

Emery, N. J., Seed, A. M., von Bayern, A. M. P., & Clayton, N. S. (2007). Cognitive adaptations of social bonding in birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1480), 489–505. https://doi.org/10.1098/rstb.2006.1991

Farine, D. R., Spencer, K. A., & Boogert, N. J. (2015). Early-life stress triggers juvenile zebra finches to switch social learning strategies. *Current Biology*, *25*(16), 2184–2188. https://doi.org/10.1016/j.cub.2015.06.071

Fischer, J., Farnworth, M. S., Sennhenn-Reulen, H., & Hammerschmidt, K. (2017). Quantifying social complexity. *Animal Behaviour*, *130*, 57–66. https://doi.org/10.1016/J.ANBEHAV.2017.06.003

Fischer, S., Bessert-Nettelbeck, M., Kotrschal, A., & Taborsky, B. (2015). Rearing-group size determines social competence and brain structure in a cooperatively breeding cichlid. *American Naturalist*, *186*(1), 123–140. https://doi.org/10.1086/681636

Fortin, D., Fortin, M.-E., Beyer, H. L., Duchesne, T., Courant, S., & Dancose, K. (2009). Group-size-mediated habitat selection and group fusion–fission dynamics of bison under predation risk. *Ecology*, *90*(9), 2480–2490. https://doi.org/10.1890/08-0345.1

Fraser, O. N., & Bugnyar, T. (2010). The quality of social relationships in ravens. *Animal Behaviour*, *79*(4), 927–933. https://doi.org/10.1016/j.anbehav.2010.01.008

Gill, S. A., & Bierema, A. M.-K. (2013). On the Meaning of Alarm Calls: A Review of Functional Reference in Avian Alarm Calling. *Ethology*, *119*(6), 449–461. https://doi.org/10.1111/eth.12097

Goodwin, D. (1976). *Crows of the World*. Cornell University Press: Ithaca, NY.

Griffin, A. S. (2004). Social learning about predators: A review and prospectus. *Animal Learning & Behavior*, *32*(1), 131–140. https://doi.org/10.3758/BF03196014

Grosenick, L., Clement, T. S., & Fernald, R. D. (2007). Fish can infer social rank by observation alone. *Nature*, *445*(7126), 429–432. https://doi.org/10.1038/nature05511

Gwinner, E. (1964). Untersuchungen über das ausdrucks- und sozialverhalten des kolkraben (Corvus corax). Z. *Tierpsychol*, *21*, 145–178.

Healy, S., Dekort, S., & Clayton, N. (2005). The hippocampus, spatial memory and food hoarding: A puzzle revisited. *Trends in Ecology & Evolution*, *20*(1), 17–22. https://doi.org/10.1016/j.tree.2004.10.006

Heinrich, B. (1988). Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by the raven, Corvus corax. *Behavioral Ecology and Sociobiology*, *23*(3), 141–156. https://doi.org/10.1007/BF00300349

Heinrich, B. (1989). *Ravens in Winter* (Summit Books of Simon & Schuster, Ed.). Vintage Books. https://books.google.at/books?id=YbWtadkEVvUC

Heinrich, B. (1994). Dominance and weight changes in the common raven, Corvus corax. *Animal Behaviour*, *48*(6), 1463–1465. https://doi.org/10.1006/anbe.1994.1384

Heinrich, B., & Marzluff, J. (1992). Age and Mouth Color in Common Ravens. *The Condor*, *94*(2), 549–550. https://doi.org/10.2307/1369233

Heinrich, B., & Marzluff, J. M. (1991). Do common ravens yell because they want to attract others? *Behavioral Ecology and Sociobiology*, *28*(1), 13–21. https://doi.org/10.1007/BF00172134

Heinrich, B., Marzluff, J. M., & Marzluff, C. S. (1993). *Common ravens are attracted by appeasement calls of food discoverers when attacked*. *110*, 247–254.

Heinrich, B., & Pepper, J. W. (1998). Influence of competitors on caching behaviour in the common raven, Corvus corax. *Animal Behaviour*, *56*, 1083–1090.

Heinrich, B., & Smolker, R. (1998). Play in common ravens (Corvus corax). In *Animal play: Evolutionary, comparative, and ecological perspectives.* (pp. 27–44). Cambridge University Press. https://doi.org/10.1017/CBO9780511608575.003

Henke-von der Malsburg, J., Kappeler, P. M., & Fichtel, C. (2020). Linking ecology and cognition: Does ecological specialisation predict cognitive test performance? *Behavioral Ecology and Sociobiology*, *74*(12), 154. https://doi.org/10.1007/s00265-020-02923-z

Hesse, S., & Thünken, T. (2014). Growth and social behavior in a cichlid fish are affected by social rearing environment and kinship. *Naturwissenschaften*, *101*(4), 273–283. https://doi.org/10.1007/s00114-014-1154-6

Hinde, R. A. (1976). Interactions, Relationships and Social Structure. *Man*, *11*(1), 1–17. JSTOR. https://doi.org/10.2307/2800384

Humphrey N K. (1976). The social function of intellect. In *Growing points in ethology* (pp. 303–317). In P. Bateson, & R. A. Hinde (Eds).

Izard, V., & Dehaene, S. (2008). Calibrating the mental number line. *Cognition*, *106*(3), 1221–1247. https://doi.org/10.1016/j.cognition.2007.06.004

Jain, V., Bugnyar, T., Cunningham, Susan J., Gallego-Abenza, M., Loretto, M.-C., & Sumasgutner, Petra. (2022). *The spatial and temporal exploitation of anthropogenic food sources by common ravens (Corvus corax) in the Alps*.

Johnson, C. M., & Karin-D’Arcy, M. R. (2006). Social Attention in Nonhuman Primates: A Behavioral Review. *Aquatic Mammals*, *32*(4), 423–442. https://doi.org/10.1578/AM.32.4.2006.423

Jolly, A. (1966). Lemur social behavior and primate intelligence. *Science (New York, N.Y.)*, *153*(3735), 501—506. https://doi.org/10.1126/science.153.3735.501

Kanai, R., Bahrami, B., Roylance, R., & Rees, G. (2012). Online social network size is reflected in human brain structure. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1732), 1327–1334. https://doi.org/10.1098/rspb.2011.1959

Kerth, G., Ebert, C., & Schmidtke, C. (2006). Group decision making in fission–fusion societies: Evidence from two-field experiments in Bechstein’s bats. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1602), 2785–2790. https://doi.org/10.1098/rspb.2006.3647

Kummer, H. (1971). *Primate Societies*.

Lefebvre, L., Nicolakakis, N., & Boire, D. (2002). Tools and brains in birds. *Behaviour*, *139*(7), 939–973. https://doi.org/10.1163/156853902320387918

Liker, A., & Bokony, V. (2009). Larger groups are more successful in innovative problem solving in house sparrows. *Proceedings of the National Academy of Sciences*, *106*(19), 7893–7898. https://doi.org/10.1073/pnas.0900042106

Loretto, M.-C., Reimann, S., Schuster, R., Graulich, D. M., & Bugnyar, T. (2016). Shared space, individually used: Spatial behaviour of non-breeding ravens (Corvus corax) close to a permanent anthropogenic food source. *Journal of Ornithology*, *157*(2), 439–450. https://doi.org/10.1007/s10336-015-1289-z

Loretto, M.-C., Schuster, R., & Bugnyar, T. (2016). GPS tracking of non-breeding ravens reveals the importance of anthropogenic food sources during their dispersal in the Eastern Alps. *Current Zoology*, *62*(4), 337–344. https://doi.org/10.1093/cz/zow016

Loretto, M.-C., Schuster, R., Itty, C., Marchand, P., Genero, F., & Bugnyar, T. (2017). Fission-fusion dynamics over large distances in raven non-breeders. *Scientific Reports*, *7*(1), 380. https://doi.org/10.1038/s41598-017-00404-4

Marzluff, J. M., & Angell, T. (2007). *In the Company of Crows and Ravens*. Yale University Press.

Marzluff, J. M., Heinrich, B., & Marzluff, C. S. (1996). Raven roosts are mobile information centres. *Animal Behaviour*, *51*(1), 89–103. https://doi.org/10.1006/anbe.1996.0008

Massen, J. J. M., Pašukonis, A., Schmidt, J., & Bugnyar, T. (2014). Ravens notice dominance reversals among conspecifics within and outside their social group. *Nature Communications*, *5*, 3679. https://doi.org/10.1038/ncomms4679

Massen, J. J. M., Szipl, G., Spreafico, M., & Bugnyar, T. (2014). Ravens intervene in others’ bonding attempts. *Current Biology*, *24*(22), 2733–2736. https://doi.org/10.1016/j.cub.2014.09.073

McNelis, N. L., & Boatright-Horowitz, S. L. (1998). Social monitoring in a primate group: The relationship between visual attention and hierarchical ranks. *Animal Cognition*, *1*(1), 65–69. https://doi.org/10.1007/s100710050008

Mikolasch, S., Kotrschal, K., & Schloegl, C. (2013). Transitive inference in jackdaws (Corvus monedula). *Behavioural Processes*, *92*, 113–117. https://doi.org/10.1016/j.beproc.2012.10.017

Milton, K. (1981). Distribution Patterns of Tropical Plant Foods as an Evolutionary Stimulus to Primate Mental Development. *American Anthropologist*, *83*(3), 534–548. https://doi.org/10.1525/aa.1981.83.3.02a00020

Moss, C., & Lee, P. (2011). Female social dynamics: Fidelity and flexibility. In *The Amboseli elephants: A long-term perspective on a long-lived mammal* (pp. 205–223). University of Chicago Press: Chicago, IL, USA.

Nácarová, J., Veselý, P., & Bugnyar, T. (2018). Ravens adjust their antipredatory responses to con- - and specific alarms to the perceived threat. *Ethology*, *May*, 1–8. https://doi.org/10.1111/eth.12764

Olkowicz, S., Kocourek, M., Lučan, R. K., Porteš, M., Fitch, W. T., Herculano-Houzel, S., & Němec, P. (2016). Birds have primate-like numbers of neurons in the forebrain. *Proceedings of the National Academy of Sciences*, *113*(26), 7255–7260. https://doi.org/10.1073/pnas.1517131113

Parker, S. T., & Gibson, K. R. (1977). Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. *Journal of Human Evolution*, *6*(7), 623–641. https://doi.org/10.1016/S0047-2484(77)80135-8

Paz-y-Miño C, G., Bond, A. B., Kamil, A. C., & Balda, R. P. (2004). Pinyon jays use transitive inference to predict social dominance. *Nature*, *430*(7001), 778–781. https://doi.org/10.1038/nature02723

Pravosudov, V. V., & Roth II, T. C. (2013). Cognitive Ecology of Food Hoarding: The Evolution of Spatial Memory and the Hippocampus. *Annual Review of Ecology, Evolution, and Systematics*, *44*(1), 173–193. https://doi.org/10.1146/annurev-ecolsys-110512-135904

Reader, S. M., & Laland, K. N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences*, *99*(7), 4436–4441. https://doi.org/10.1073/pnas.062041299

Rosati, A. G. (2017). Foraging Cognition: Reviving the Ecological Intelligence Hypothesis. *Trends in Cognitive Sciences*, *21*(9), 691–702. https://doi.org/10.1016/j.tics.2017.05.011

Rösner, S., & Selva, N. (2005). Use of the bait-marking method to estimate the territory size of scavenging birds: A case study on ravens Corvus corax. *Wildlife Biology*, *11*(3), 183–191. https://doi.org/10.2981/0909-6396(2005)11[183:UOTBMT]2.0.CO;2

Sachser, N., Kaiser, S., & Hennessy, M. B. (2013). Behavioural profiles are shaped by social experience: When, how and why. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1618), 20120344. https://doi.org/10.1098/rstb.2012.0344

Sallet, J., Mars, R. B., Noonan, M. P., Andersson, J. L., O'Reilly, J. X., Jbabdi, S., Croxson, P. L., Jenkinson, M., Miller, K. L., & Rushworth, M. F. S. (2011). Social Network Size Affects Neural Circuits in Macaques. *Science*, *334*(6056), 697–700. https://doi.org/10.1126/science.1210027

Shettleworth, S. J. (1998). *Cognition, evolution, and behavior.* (pp. xv, 688). Oxford University Press.

Sierro, J., Loretto, M. C., Szipl, G., Massen, J. J. M., & Bugnyar, T. (2020). Food calling in wild ravens (Corvus corax) revisited: Who is addressed? *Ethology*, *126*(2), 257–266. https://doi.org/10.1111/eth.12991

Silk, J. B. (1999). Male bonnet macaques use information about third-party rank relationships to recruit allies. *Animal Behaviour*, *58*(1), 45–51. https://doi.org/10.1006/anbe.1999.1129

Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social Bonds of Female Baboons Enhance Infant Survival. *Science*, *302*(5648), 1231–1234. https://doi.org/10.1126/science.1088580

Silk, M. J., Croft, D. P., Tregenza, T., & Bearhop, S. (2014). The importance of fission-fusion social group dynamics in birds. *Ibis*, *156*(4), 701–715. https://doi.org/10.1111/ibi.12191

Sloan, J. L., & Hare, J. F. (2008). The More the Scarier: Adult Richardson's Ground Squirrels (Spermophilus richardsonii) Assess Response Urgency Via the Number of Alarm Signallers. *Ethology*, *114*(5), 436–443. https://doi.org/10.1111/j.1439-0310.2008.01479.x

Smuts, B., Cheney, D., Seyfarth, R., Wrangham, R., & Struhsaker, T. (1987). *Primate Societies*. Chicago Press.

Sol, D. (2009). Revisiting the cognitive buffer hypothesis for the evolution of large brains. *Biology Letters*, *5*(1), 130–133. https://doi.org/10.1098/rsbl.2008.0621

Szipl, G., Ringler, E., & Bugnyar, T. (2018). Attacked ravens flexibly adjust signalling behaviour according to audience composition. *Proceedings of the Royal Society B*, *285*(June). https://doi.org/10.1098/rspb.2018.0375

Taborsky, B., & Oliveira, R. F. (2012a). Social competence: An evolutionary approach. *Trends in Ecology and Evolution*, *27*(12), 679–688. https://doi.org/10.1016/j.tree.2012.09.003

Taborsky, B., & Oliveira, R. F. (2012b). Social competence: An evolutionary approach. *Trends in Ecology & Evolution*, *27*(12), 679–688. https://doi.org/10.1016/j.tree.2012.09.003

Templeton, C. N. (2018). Animal Communication: Learning by Listening about Danger. *Current Biology*, *28*(16), R892–R894. https://doi.org/10.1016/j.cub.2018.07.039

Tomasello, M., & Call, J. (1997). *Primate cognition*. Oxford Univ. Press. https://pure.mpg.de/pubman/faces/ViewItemOverviewPage.jsp?itemId=item_2260164

Tornick, J. K., Callahan, E. S., & Gibson, B. M. (2015). An investigation of quantity discrimination in Clark's nutcrackers (Nucifraga columbiana). *Journal of Comparative Psychology*, *129*(1), 17–25. https://doi.org/10.1037/a0037863

Varela, S. A. M., Teles, M. C., & Oliveira, R. F. (2020). The correlated evolution of social competence and social cognition. *Functional Ecology*, *34*(2), 332–343. https://doi.org/10.1111/1365-2435.13416

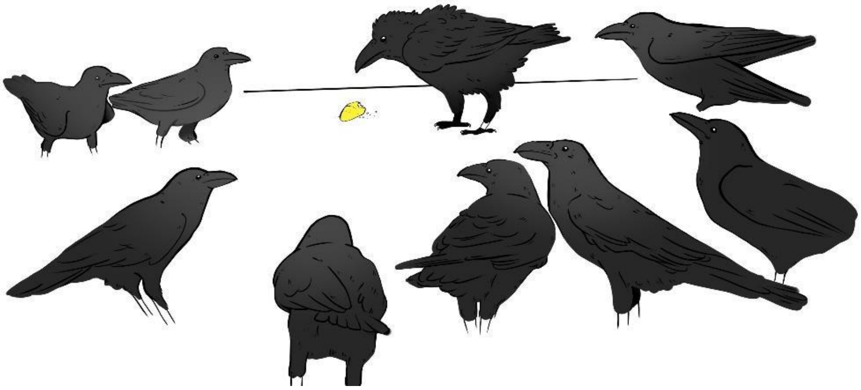
Waters, E., & Sroufe, L. A. (1983). Social competence as a developmental construct. *Developmental Review*, *3*(1), 79–97. https://doi.org/10.1016/0273-2297(83)90010-2

Weiß, B. M., Kehmeier, S., & Schloegl, C. (2010). Transitive inference in free-living greylag geese, Anser anser. *Animal Behaviour*, *79*(6), 1277–1283. https://doi.org/10.1016/j.anbehav.2010.02.029

Chapter 1

Decision time modulates social foraging success in wild common ravens, *Corvus corax*

Mario Gallego-Abenza, Matthias-Claudio Loretto & Thomas Bugnyar



This chapter is published as an article in a peer-review journal

How to cite this article: Gallego-Abenza M, Loretto M-C, Bugnyar T. Decision time modulates social foraging success in wild common ravens, *Corvus corax*. *Ethology*. 2019;00:1–10. https://doi.org/10.1111/eth.12986

Received: 17 July 2019 | Revised: 30 October 2019 | Accepted: 31 October 2019
DOI: 10.1111/eth.12986

RESEARCH PAPER

ethology WILEY

Decision time modulates social foraging success in wildcommon ravens, *Corvus corax*

Mario Gallego-Abenza[1,2] | **Matthias-Claudio Loretto**[1,2,3,4] | **Thomas Bugnyar**[1,2]

[1]Department of Cognitive Biology, University of Vienna, Vienna, Austria

[2]Konrad Lorenz Forschungsstelle, Core Facility for Behaviour and Cognition, University of Vienna, Grünau im Almtal, Austria

[3]Department of Migration, Max Planck Institute of Animal Behavior, Konstanz, Germany

[4]Department of Biology, University of Konstanz, Konstanz, Germany

Correspondence
Mario Gallego-Abenza, University of Vienna - Department of Cognitive Biology, Althanstrasse 14 (UZA1) 1090 Vienna, Wien 1010, Austria.
Email: mario.gallego-abenza@univie.ac.at

Funding information
Austrian Science Fund, Grant/Award Number: P29705

Editor: Jonathan Wright

Abstract

Socialforagingprovidesseveralbenefitsforindividualsbutalsobearsthepotentialcostsof higher competition. In some species, such competition arises through kleptoparasit-ism, that is when an animal takes food which was caught or collected by a member ofits social group. Except in the contextofcaching, few studies have investigated how in-dividuals avoid kleptoparasitism, whichcould be based onphysical strength/dominancebut also cognitive skills. Here, we investigated the foraging success of wild commonravens, *Corvus corax*, experiencing high levels of kleptoparasitism from conspecificswhen snatching food from the daily feedings of captive wild boars in a game park in theAustrian Alps. Success inkeeping thefood depended mainlyontheindividuals' age classand was positively correlated with the time to make a decision in whether to fly off withfood or consume it on site. While the effect of age class suggests that dominant and/orexperiencedindividuals arebetter in avoiding kleptoparasitism, the effect of decisiontime indicates that individuals benefit from applying cognition to such decision-making, independently of age class. We discuss our findings in the context of the ecologicaland social intelligence hypotheses referring to the development of cognitive abilities.We conclude that investigating which factors underline kleptoparasitism avoidance is apromising scenario to test specific predictions derived from these hypotheses.

KEYWORDS

cognition, *Corvus corax*, decision-making, kleptoparasitism, scrounging, social foraging

1 | INTRODUCTION

During foraging, group formation has many advantages for the individuals: conspecifics and/or heterospecifics may provide informa- tion regarding food sources and feeding opportunities (Powell, 1974)or their presence may reduce predation risk (Beauchamp, 2004). However, individuals engaging in group foraging might also experi- ence costs, especially in social species, where group members mightrepresent a source of permanent competition during foraging (Barta & Giraldeau, 1998). This fact leads to potential decline of individual foraging efficiency, especially when food resource becomes limited or group size increases (Goss-Custard & Durell, 1988). To remain efficient, socially foraging individuals typically adjust their behaviour to those of others (Giraldeau & Caraco, 2000). For instance, in star- lings *Sturnus vulgaris*, individuals flexibly use behavioural cues pro- vided by conspecifics for patch assessment, depending on the type of environment in which their foraging takes place (Templeton & Giraldeau, 1995, 1996).

Behavioural plasticity during social foraging is particularly evi- dent when individuals switch between producing food themselves and exploiting the food made available by others (Giraldeau & Caraco, 2000). The latter tactic is termed scrounging (Vickery et al., 1991). Depending on the species' foraging ecology, scrounging can take different forms (Giraldeau & Caraco, 2000), from exploiting a food patch found by others to directly stealing food from others. Hereby, kleptoparasitism commonly refers to those cases where individuals use force, or threat of force, to obtain the food from others (Baglione & Canestrari, 2009), whereas pilfering refers to those cases where food is stolen out of another individual's cache and physical interac- tions between cache owner and thief are avoided (Emery & Clayton,2001; but see Giraldeau & Caraco, 2000 for a slightly different ter- minology). Game theoretical models have been successfully used to understand the conditions under which individuals adopt producer or scrounger roles (Afshar & Giraldeau, 2014; Giraldeau & Caraco, 2000). Comparative analyses of a large set of field reports in birds in-dicate that interspecific kleptoparasitism is associated more closely with cognition than with physical power and aggression: the proba- bility that kleptoparasitism is present in an avian family is positively associated with residual brain size but not with body size; likewise, kleptoparasitic species have larger brains than their hosts (Morand- Ferron, Sol, & Lefebvre, 2007). On the species level, these findings are supported by behavioural observations that explore the cogni- tive mechanisms underlying scrounging and the countermeasures taken against being exploited by others. In some primates species, low-ranking individuals tend to reach feeding sites before high-rank-ing individuals. This "early arrival" tactic has been described in ca- puchin monkeys, *Cebu apella* (Di Bitetti & Janson, 2001), Japanese macaques, *Macaca fuscata* (Belisle & Chapais, 2001) and long-tailedmacaques, *Macaca fascicularis* (Dubuc & Chapais, 2007) and is inter- preted as subordinates applying social knowledge to avoid competi- tion and/or to increase their foraging efficiency. Furthermore, cases of tactical deception, like withholding information and providingfalse information (Byrne & Whiten, 1988a), have been reported pre- dominantly in the context of (avoiding) kleptoparasitism. In primates(Byrne & Whiten, 1988b; Coussi-Korbel, 1994; Hirata & Matsuzawa, 2001; Menzel, 1974), pigs (Held, Mendl, Devereux, & Byrne, 2002) and birds (Bugnyar & Kotrschal, 2004; Flower, Gribble, & Ridley, 2014; Munn, 1986), some individuals (try to) lead conspecifics awayfrom food and/or "cry wolf" in absence of any predator to gain access to food found by others. Such tactics for outwitting competitors are assumed to be cognitively demanding and in line with some of the core hypotheses concerning brain evolution (Byrne, 1997; Byrne & Whiten, 1988b; Dunbar, 2003). Likewise, the interplay between pil- fering and avoidance of cache theft, which has been studied partic- ularly in corvids (Clayton, Dally, & Emery, 2007; Heinrich & Pepper, 1998), can be viewed as a producer-scrounger scenario and has beensuggested as one of the driving forces for the advanced socio-cogni- tive skills of some of these birds (Bugnyar & Kotrschal, 2002a).

Common ravens *Corvus corax* are scavengers, which form tem- porary foraging groups at food bonanzas such as carcasses orkills (Heinrich, 1988) as well as at garbage dumps and game parks (Loretto, Schuster, & Bugnyar, 2016); accordingly, the size and com-position of foraging groups vary across days (Braun, Walsdorff, Fraser, & Bugnyar, 2012; Heinrich, Kaye, Knight, & Schaumburg, 1994). However, ravens also show substantial individual variationin their local preferences and fission-fusion dynamics, respectively, with some birds encountering each other regularly (over up to sev- eral years) at the foraging site or repeatedly at different sites (Loretto et al., 2017). Furthermore, ravens tend to form affiliative social rela-tionships already at the non-breeder state, which resemble primate social bonds (Fraser, Schino, & Aureli, 2008) and function as alli- ances in conflicts (Braun & Bugnyar, 2012; Szipl, Ringler, Spreafico, & Bugnyar, 2017). All these facts indicate that raven foraging groupsare not just aggregations but, at least in part, structured by individual spatial preferences and social relationships.

The foraging behaviour of ravens is highly plastic: individuals may actively attract others via calls to food sources that are diffi-cult to access (Bugnyar & Kotrschal, 2001; Heinrich, 1988), which constitutes a form of cooperation on a mutualistic basis where sig- nallers might benefit from enlarging the foraging group and neutral- ize thus the defence of dominance individuals (Heinrich & Marzluff, 1991). Recruitment can also arise through communal roosting, which serves as information centres for previously encountered food sources (Marzluff, Heinrich, & Marzluff, 1996; Wright, Stone,& Brown, 2003). Aside from these cases of active recruitment, indi- viduals may specialize in exploiting the discoveries of others (Dall & Wright, 2009), opportunistically steal the food acquired from others (Bugnyar & Kotrschal, 2002b) or pilfer the caches made by others (Bugnyar & Kotrschal, 2002a). Raven foraging behaviour can thusbe described as producer-scrounger interactions at different phases during foraging, that is when they search for food, when they try to keep food and when they cache food. Physical strength and dom- inance status may bias individuals in their choices of tactics, spe- cifically in respect to engaging in kleptoparasitism. Note that raven dominance rank depends not only on individual strength but also on age class (adults >juveniles), sex (males >females) and bonding status (bonded >non-bonded; Braun & Bugnyar, 2012). Moreover, due to the frequent changes in group composition, the same birds may be dominant in one foraging situation but not in the other.

Social knowledge and experience may help ravens to negotiate such a dynamic social environment, that is deciding when to exploit others and when to avoid being exploited. Furthermore, cognitive skills, such as decision-making or inhibition control, could allow in- dividuals that are preferred targets of kleptoparasitism to develop countermeasures.

Studies on captive ravens indicate advanced cognition in compe-tition for cached food. While young ravens possess an "innate" moti-vation to store food for later consumption (Gwinner, 1965), they have to learn when and where they place the caches in order to keep themsafe from pilfering (Bugnyar & Kotrschal, 2002a; Bugnyar, Stöwe, & Heinrich, 2007), whereby they may come to comprehend the oth- ers' visual perspective (Bugnyar, 2011; Bugnyar, Reber, & Buckner, 2016). Moreover, ravens have to learn to control their impulse to pil-fer others' caches while the cache owners, or potential competitors, are still present (Bugnyar & Heinrich, 2005, 2006; Bugnyar, Schwab,Schloegl, Kotrschal, & Heinrich, 2007). Aside from caching, ravens have been demonstrated to control their impulsivity in an exchange paradigm, that is instead of consuming an initial food item they later exchange it for one of better quality (Dufour, Wascher, Braun, Miller, & Bugnyar, 2012; Hillemann, Bugnyar, Kotrschal, & Wascher, 2014). Therefore, we could expect prolonged decision time to have some benefits associated with foraging efficiency in wild social birds, in particular in those species with high levels of intra-specific kleptoparasitism.

In the present study, we focused on the foraging success of individually marked ravens snatching food during zoo animal feedings (i.e., applying a producer tactic). We were interested in the factors determining the individuals' foraging success (measured as foraging success rate) based on their capability to elude kleptoparasitism from surrounding conspecifics. We hypothesized that raven foraging success would primarily depend on factors associated with dominance status like age class, sex and winning probability in agonistic interactions. Furthermore, we hypothesized that subordinate ravens would suffer from kleptoparasitism and would, therefore, benefit from exhibiting high levels of behavioural plasticity. The efficiency of subordinate individuals should, in this case, be largely determined by the individuals' experience and cognitive abilities. We thus predicted that the birds' foraging success rate should not only be age class and sex biased, with older ravens being more efficient than younger and males being more efficient that females, but modulated by behavioural plasticity as a result of learning, decision-making and impulsivity control. Specifically, and due to known low survival rate of juveniles (in the first year) compared to subadults (2–3 years old; Webb, 2004), we predicted that subadult ravens should be better in coping with kleptoparasitism than juvenile ravens in terms of judging when it is safe to consume food directly on site or when it is better to carry foodoff. Given the substantial variation in fission-fusion dynamics in our population, we also expected individuals that spend long periods in the study area ("residents") to show high foraging efficiency, as theyshould have a better knowledge of the local social environment thanravens that spend only little time in the study area ("vagrants").

2 | MATERIAL AND METHODS

2.1 | Study species and site

The study took place at Cumberland Wildpark, in Grünau im Almtal, Austria, where common ravens forage at the enclosures of zoo animals all year round in groups of 20–80 birds. These foraging groups are not stable units: while some individuals use the park regularly over several months and even years, others just visit from time to time (Braun et al., 2012; Loretto et al., 2017). The presence and so-cial interactions of these ravens are monitored on a daily basis as part of a long-term programme. For individual identification, birds are caught in drop-in traps and marked with rings and patagial wingtags (Caffrey, 2000). During the marking process, age class is deter-mined based on feather colouration and inner beak colour; birds arethen categorized as juveniles (<1 year old), subadults (1–3 years old) and adults (>3 years old; Heinrich & Marzluff, 1992). Sex is determined via genetic markers from blood samples.

Over the course of the current study, 46 marked ravens used thezoo as a food source; they represented around 50% of the individ- ually identified ravens present at our study site on a daily basis at that time. For data collection, we chose the enclosure of wild boars *Sus scrofa* as the enclosure's landscape allowed an excellent view of the feeding site and its surroundings. Furthermore, compared to thefeedings of large predators like wolves *Canis lupus* and bears *Ursos arctos*, wild boars do not show any aggressive food defence towardsravens (Bugnyar & Kotrschal, 2001; Nácarová, Veselý, & Bugnyar, 2018).

2.2 | Ethical note

Trapping, blood sampling and marking have been carried out under the licence for animal experimentation of the Austrian government (BMWF-66.006/0009-II/3b/2012 and BMBWF-66.006/0015-V/3b/2018). As the study itself was non-invasive and based on behavioural observations only, it was not classified as animal experiment in accordance with the Austrian law (§2. Federal Law Gazette No. 114/ 2012). The monitoring and ringing programmeof the Konrad Lorenz Forschungsstelle is authorized by the Central Administration of Upper Austria.

2.3 | Data collection and analysis

The study was conducted between March 2017 and March 2018.In this one-year period, we video recorded 143 feedings of wild boars using an action camera (GoPro HD Hero 2 and GoPro HDHero 5, attached at the fence of the enclosure, 1.5 m height above the food). From these videos, we reported 779 food retention at- tempts from 46 marked individuals (mean = 16.9 attempts per indi- vidual, range = 1–95). Individual food retention attempts concerned two behavioural tactics: carrying food items away from the feeding site or consuming them directly at the feeding site. In either case, we focused on food items larger than a raven beak's length, since small pieces carried inside the beak or throat pouch are not likelyto be kleptoparasitized. Kleptoparasitic attacks typically result in some food transfer; however, and due to the difficulty of quanti- fying on the video how much food each of the ravens got during/ after harassment, we thus defined success in food retention when ravens managed to carry a food item away or to consume it in front of any conspecific without being chased or harassed, respectively.A recent observational study focussed on caching locations out of our camera's view, reveals that kleptoparasitism hardly occurs and ravens ensure their caches for later consumption (Beck et al.,2019). For each attempt, we measured the time (in seconds) between grab-bing a piece of food and a subsequent decision of either flying off with it or consuming it on site. Further, we measured the distance (in multiples of body length) to the nearest conspecific when grabbing a piece of food and the number of surrounding conspecifics.

In addition to the foraging information scored from the video,we recorded which of the marked individuals were present at our study site every day. Independently to kleptoparasitism events, in- dividual involvement in agonistic interactions was recorded on an*ab libitum* basis via direct observation together with those occurred within the camera's view. We reported a total of 575 dyadic agonis- tic interactions (mean of agonistic interactions per individual = 12.5, range 3–74), in which the "winner" and "loser" were identified by ob-serving how each dyadic agonistic interaction resolved (see Braun & Bugnyar, 2012 for detailed description of agonistic categories). Inter-observer reliability was established by coding agonistic interactions from videos with Dr. Szipl, G. as second observer, and reliability wasexcellent (ICC between 0.997 and 1.0). Since raven non-breeder groups are characterized by high levels of fission-fusion dynamics, not all individuals involved in conflicts were individually marked; we thus calculated the "winning probability" for each marked bird by di- viding the number of won interactions by the total number of agonis-tic interactions being involved and used it as a proxy for dominance rank. A previous study conducted in the same study area showed stability of the dominance measures when looking at repeated in- teractions of individually marked ravens within the same sex, age class and bonding category over 2 years (Braun & Bugnyar, 2012). To obtain a standardized parameter for the individuals' presence at the study site, we calculated the "percentage of days being present at study site," a day-specific value for each individual per feeding protocol based on the percentage of days being present at the studyarea during the 25 days before and 5 days following the day when the feeding attempts were reported.

2.4 | Statistical analysis

We used R software (R Core Development Team, 2014) to run our statistical analyses. We performed generalized linear mixed models using "glmmADMB" package (Fournier et al., 2012), including success of keeping the food in both foraging tactics, "overall foraging success," as response variable (binomial distribution error) and both individual andday as random effects, thus controlling for potential individual differ-ences in being targeted by kleptoparasites (see Table S5). Similarly, we conducted the same modelling approach within each foraging tactic, either flying away with food or consuming it on site. In addition, in order to investigate raven decisions to fly away with food, we includedflying away as response variable (binomial distribution error). Number of ravens, distance to nearest conspecific, decision time (s), percent-age of days being present at study site, winning probability, age classand sex were included as fixed factors in all models. We z-transformed all the continuous predictor variables in the full model. We followed an information-theoretical approach for model selection using "MuMIn package" (Barton, 2019) by calculating all possible models and select-ing the best models within ∆AICc ≤ 6 with respect to the top-rankedmodel (Burnham & Anderson, 2002; Symonds & Moussalli, 2011). Weaveraged these models and obtained model-averaged coefficients fol- lowing Burnham and Anderson (2002). We used R-package "car" (Fox & Weisberg, 2011) to test for collinearity of fixed factors before theywere entered in the full model, with a resulting variance inflation fac-tor <4 for all variables. We discuss the results based on both effect size and relative importance value (0–1) of each predictor, whereby one refers to the highest contribution in explaining the response variable.

3 | RESULTS

3.1 | Descriptive findings

We recorded a total of 779 individual foraging events that were characterized as food retention attempts, that is either carrying food awayor eating it on site: out of those, 272 were made by adults (mean offood retention attempts per individual = 22.6, range = 4–95), 366 by subadults (mean of food retention attempts per individual = 17.4, range = 1–91) and 141 by juveniles (mean of food retention attempts

TABLE 1 Summary of food retention attempts by marked ravens

Age class	Food retention attempts	Carrying food away attempts	Kleptoparasitized carrying food away attempts (%)	Consuming food on site attempts	Kleptoparasitized consuming food on site attempts (%)
Adult (12 ind.)	272	241	46 (**19.09**)	31	22 (**70.97**)
Subadult (17 ind.)	366	266	75 (**28.19**)	100	80 (**80**)
Juvenile (17 ind.)	141	70	28 (**40**)	71	61 (**85.91**)
Sex					
Male (22 ind.)	283	185	45 (**24.32**)	98	73 (**74.49**)
Female (24 ind.)	496	393	104 (**26.46**)	103	90 (**87.38**)

Note: The table shows the percentage of kleptoparasitism occurring for in each foraging tactic (either carrying food away or consuming food on site) by age class and sex.

TABLE 2 Table showing the model-averaged coefficients

	Estimate	Adjusted SE	CI lower limit(2.5%)	CI upper limit(97.5%)	Relative importance
Overall foraging success					
Intercept	1.14	0.29	0.55	1.72	
Age class (Subadult)	−0.72	0.35	−1.41	−0.03	1
Age class (Juvenile)	−2.09	0.44	−2.96	−1.22	1
Distance to conspecific	0.10	0.12	−0.03	0.38	0.59
Decision time (sec)	0.32	0.13	0.07	0.57	1
Number of surrounding ravens	−0.08	0.10	−0.35	0.05	0.52
Sex (male)	0.13	0.27	−0.31	1.02	0.38
Percentage of days being present (0–1)	0.04	0.092	−0.13	0.36	0.36
Winning probability (0–1)	−0.02	0.10	−0.43	0.28	0.28

Note: It shows the coefficients with adjusted standard errors, lower are upper confidence intervals and relative importance values of each fixed factor when modelling the overall foraging success. Factors with a relative importance above 0.6 appear shaded.

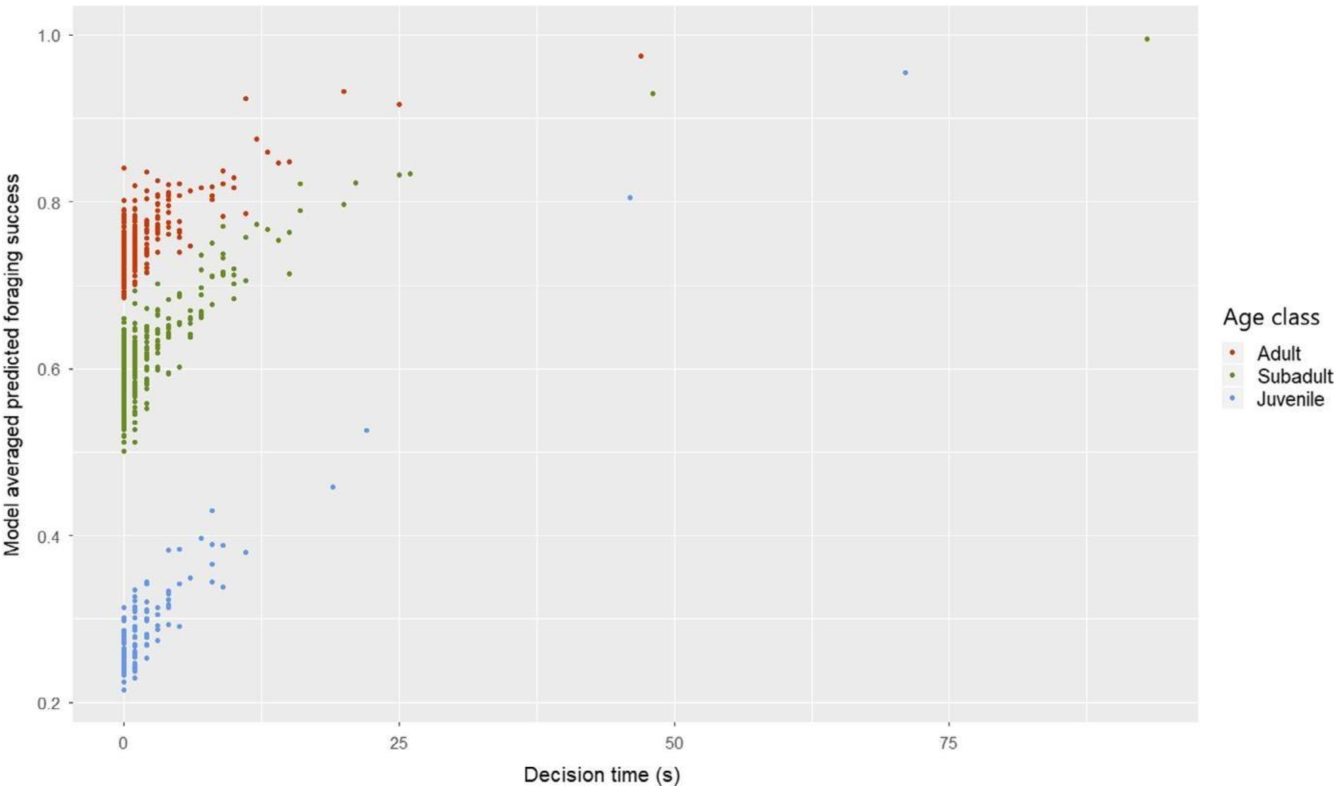


FIGURE 1 Scatterplot of model-averaged predicted foraging success, against the decision time (seconds) coloured by age class. Predicted foraging success positively correlates with decision time in all age classes

per individual = 5.6, range = 1–27). Adults typically attempted to carry food off the site in 241 cases, 89%; subadults attempted on 266 cases, 73%; and juveniles in 70 cases, 50%, Table 1. The two tactics differed inthe likelihood of being kleptoparasitized: attempts to carry food off thesite received less kleptoparasitism (19%–40%, depending on age class) than attempts to feed on site (71%–86%, Table 1). Regarding sex-specific differences in kleptoparasitism occurrence, we found similar valuesin both foraging tactics (24% in males vs. 26% in females when carryingoff food; 74% in males vs. 87% in females when feeding on site, Table 1).

3.2 | Overall foraging success

Both age class and decision time had the highest relative importance explaining foraging success in respect to avoiding kleptoparasitism from surrounding conspecifics (see Table 2 for model coefficients). Subadult and juvenile ravens showed lower foraging success than adults. Regarding the decision time, the time ravens took to make a decision (whether to fly off with food or consume it directly on site) had a positive effect on their foraging success (see Figure 1). The distance to the nearest conspecific when grabbinga food item had a slight positive effect on their foraging success.Sex (male) and percentage of days being present at the study site also had a positive effect on the general foraging success of ravens but their relative importance and effect size were negligible low. As expected, the number of surrounding conspecifics at the moment when food retention was attempted had a negative effect on the foraging success; however, it shows a low effect size. Estimates of the full model before model averaging are available in table S1 of Supplementary material.

3.3 | Consuming food directly on site

When focusing on those cases in which ravens decided to consume the food directly at the feeding site (Table 3), their success of keeping the food was affected mainly by their distance to nearby conspecifics at the time they took the piece of food and the time they took to make a decision (i.e., to stay rather than fly off). In bothcases, these parameters were positively correlated with foraging ef- ficiency. Moreover, social parameters like “winning probability” and “presence” (duration of stay at the study site) became slightly more relevant when consuming food in front of conspecifics. Sex and age class had an effect on foraging success (with old and male individu- als being less harassed than juveniles and females) but their relativeimportance was negligible low. The number of surrounding conspe- cifics did not affect foraging success when consuming food on site. Estimates of full model before model averaging are available in tableS2 of Supplementary material.

3.4 | Decision to carry food away

The ravens’ decision to carry food off the feeding site was positively correlated with the number of surrounding conspecifics (i.e., poten- tial competitors on site; Table 4a). Furthermore, there was a strong effect of age classes: adults and subadults were more likely to carry food away than were juveniles. Apart from these, other fixed fac- tors appeared to not affect relevantly ravens’ decision of carrying offfood. Estimates of full model before model averaging are available in table S3 of Supplementary material.

3.5 | Success at carrying food away

Success in flying off with food meant that ravens carrying food man- aged to avoid being chased by other conspecifics (Table 4b). The number of surrounding conspecifics had a negative effect on suc- cess, as ravens with food were more likely chased when there wasa large number of surrounding conspecifics. There was also a strongeffect of age class, with adults and subadults receiving fewer chasesthan did juveniles. The distance to the nearest neighbour (at the time when a focal raven grabbed the food) was positively correlated with success. Here, we found little effect of decision time, presence atthe study area or winning probability, each of which had both low effect sizes and low relative importance coefficients. However, sex had a clear effect, with males receiving fewer chases than did fe- males. Estimates of full model before model averaging are available in table S4 of Supplementary material.

4 | DISCUSSION

Ravens faced high levels of conspecific kleptoparasitism when snatching food pieces from the feedings of captive wild boars. The success of keeping food depended mainly on the birds’ age class andthe amount of time they took to decide whether to fly off with food or consume it directly on site (Figure 1). When modelling the two tactics (flying off and consuming food on site) separately, we found that adults and subadults had an advantage over juveniles when carrying food away, that is they were less likely chased by others. However, age class did not have such an effect on consumption at- tempts on site; here, the time taken to make a decision (to stay ratherthan fly off) and the timing of grabbing a food piece (measured as distance to nearest conspecific) were the best predictors of keeping food safe from scroungers.

We predicted that age class would strongly affect foraging suc- cess, as adult ravens are known for their high resource holding po- tential and dominance status in comparison with younger ravens (Heinrich, 1989; Marzluff & Heinrich, 1991). Yet, other factors re- lated to dominance, like the birds’ sex and winning probability in con- flicts (Braun & Bugnyar, 2012), had little effect on their success of avoiding kleptoparasitism. Hence, older ravens likely benefited from a combination of both physical strength and experience, particularly when flying off with food. This fits with the age-specific foraging proficiency shown in most of the avian species (Wunderle, 1991).

Aside from age class, the individual attempts to fly off with food were positively correlated with the number of conspecifics around. Note that ravens typically gathered at the wild boar enclosure al- ready before feeding started, reaching their maximum group size at the beginning of the feeding. We may thus interpret the above-men-tioned correlation directionally, that is that birds tried to leave with food more often when the foraging group was larger. However, the individual success in keeping the food when flying off correlated neg- atively with the number of conspecifics around, suggesting that the birds had difficulties in escaping kleptoparasitism when the group was large. Hence, carrying food away without being kleptoparasit- ized represented a challenge for ravens, particularly when they wereyoung and when many conspecifics were around. Ultimately, flying off with food seems to pay off for group foraging ravens (lower klep-toparasitism occurrence, see Table 1), as it allows them to cache foodout of sight of potential competitors (Heinrich & Pepper, 1998) and, despite additional costs in time and energy, to secure several loads of food for later consumption (Heinrich, 1988). However, whether all observed food trips resulted in successful food caching and later

TABLE 3 Table showing the model-averaged coefficients

	Estimate	Adjusted SE	CI lower limit(2.5%)	CI upper limit(97.5%)	Relative importance
Consuming food on site success					
Intercept	−13.28	13.11	−38.97	12.41	
Age class (Subadult)	0.66	4.84	−12.84	15.99	0.42
Age class (Juvenile)	−2.81	6.59	−23.89	10.59	0.42
Distance to conspecific	1.49	1.83	−1.27	5.86	0.65
Decision time (sec)	2.50	2.05	−1.50	6.52	1.00
Number of surrounding ravens	0.003	0.09	−0.62	0.69	0.08
Sex (male)	0.59	0.98	−0.31	3.57	0.36
Percentage of days being present (0–1)	0.81	1.59	−2.16	5.42	0.50
Winning probability (0–1)	0.38	0.60	−0.30	2.11	0.42

Note: It shows the coefficients with adjusted standard errors, lower are upper confidence intervals and relative importance values of each fixed factor when modelling the foraging success in consuming food on site. Factors with a relative importance above 0.6 appear shaded.

TABLE 4 Summary of model-averaged coefficients

	Estimate	Adjusted SE	CI lower limit(2.5%)	CI upper limit(97.5%)	Relative importance
Decision to carry food away					
Intercept	2.23	0.35	1.54	2.93	
Age class (Subadult)	−0.87	0.41	−1.67	−0.07	1
Age class (Juvenile)	−2.44	0.46	−3.35	−1.53	1
Distance to conspecific	−0.01	0.06	−0.26	0.16	0.27
Decision time (sec)	0.02	0.06	−0.11	0.24	0.30
Number of surrounding ravens	0.28	0.12	0.07	0.51	0.99
Sex (male)	−0.10	0.26	−1.03	0.40	0.32
Percentage of days being pre-sent (0–1)	0.0002	0.07	−0.27	0.27	0.25
Winning probability (0–1)	0.01	0.10	−0.34	0.43	0.25
Success at carrying food away					
Intercept	1.55	0.24	1.08	2.02	
Age class (Subadult)	−0.50	0.31	−1.11	0.03	0.93
Age class (Juvenile)	−1.06	0.52	−2.01	−0.27	0.93
Distance to conspecific	0.23	0.18	0.001	0.59	0.77
Decision time (sec)	0.08	0.14	−0.13	0.49	0.45
Number of surrounding ravens	−0.34	0.14	−0.59	−0.09	0.98
Sex (male)	0.24	0.29	−0.10	0.95	0.57
Percentage of days being pre-sent (0–1)	0.03	0.09	−0.17	0.37	0.31
Winning probability (0–1)	−0.05	0.12	−0.47	0.21	0.35

Note: The table shows the coefficients with adjusted standard errors, lower and upper confidence intervals and relative importance values of each fixed factor when modelling a) the ravens' decision to carry off food and b) their foraging success when carrying it.

consumption remains unknown. A similar effect of group size was experimentally shown on coho salmon, *Oncorhynchus kisutch*, whereby, as group size increased, juvenile salmon captured more prey items and ventured closer to the feeder, indicating changes in foraging be-haviour driven by group size variation (Grand & Dill, 1999).

Raven success in saving food for immediate consumption didnot depend on factors related to dominance or group size but on parameters indicative for cognitive processing, that is the distanceto the nearest conspecific when grabbing a piece of food and the time between grabbing a piece of food and making a decision (fly off or consume the food on site). Both parameters correlated positively with success in keeping food, suggesting that the better individuals timed their approach and the longer they waited to decide whether or not to fly off with food, the better they were in avoiding kleptoparasitism on site. In some primate species, flexible timing in feeding has been shown to affect foraging efficiency positively, that is subordinate macaques tend to arrive at the feeding site before than higher-ranked individuals, this is known as early arrival tactic (*Macaca fuscata*: Belisle & Chapais, 2001; *Macaca fascicularis*: Dubuc & Chapais, 2007). Possibly, ravens used their decision time to assess the current situation of competition, that is the amount of aggression and kleptoparasitism in the immediate surrounding. However, what we measured as "decision time" could also reflect the ravens' ability to control their impulse to fly off with food. Thus, our findingsmay support a new avenue for impulse control in ravens shaped by a competitive social foraging scenario. Further studies are needed to distinguish between these alternatives.

Given the substantial spatio-temporal dynamics in our non-breeder population, we also expected individuals that spend long periods in the study area ("residents") to show high foraging success, as they should have a better knowledge of the local social environment than ravens that spend only little time in the study area ("vagrants"). However, our results hardly support this prediction as we found only a weak positive effect of individuals' presence at the study area on their success of consuming food on site (Table 3). A possible explanation for these results is that ravens face similar social challenges at different foraging sites across their home range. GPS-tracking revealed that ravens of our study population in the Austrian Alps make heavy use of anthropogenic food sources, that isfeedings of game and farm animals, garbage dumps and compostingplants (Loretto et al., 2016). At several of those places, they form large groups and potentially face similar levels of competition as at our study site. Avoiding kleptoparasitism would thus be an important skill in their daily life, irrespective of where they forage.

Taken together, our findings support the prediction that foraging ravens show high plasticity in their behaviour. Individuals frequently engaged in producer-scrounger interactions, whereby individuals in possession of food (producers) became the target of kleptoparasitism by conspecifics (scroungers). Beyond the scopeof the producer-scrounger scenario (already described by Bugnyar& Kotrschal, 2002b), our findings shed light on kleptoparasitism avoidance from the producer's perspective, whereby success in keeping the food seemed to depend on the individuals' physical abilities and experience (as indicated by the effect of age class) as well as cognitive skills (as indicated by the effect of decision time). These findings are in line with the "foraging cognition hypothesis" (Byrne, 1997; Parker & Gibson, 1977; Rosati, 2017), which emphasizes the need of food acquisition as one of the main driving forces behind the evolution of cognition. However, the findings also fit the "social intelligence hypothesis" (Humphrey, 1976; Jolly, 1966), as interactions with conspecifics seem to be key for shaping the cognitive abilities employed during social foraging. Further research on the foraging skills of common ravens should test predictions derived from both hypotheses, whereby group size or composition and food accessibility can be experimentally modified. Furthermore, longitudinal studies should investigate the development of behavioural tactics to avoid kleptoparasitism and the cognitive skills identified in this study that presumably underlie these behaviours.

ACKNOWLEDGEMENTS

This study was supported by the Austrian Science Fund (FWF)project P29705, W 1262-B29 and an IP project: IP550002 of the Faculty of Life Sciences, University of Vienna; permanent support is granted by the "Verein der Förderer KLF", the Faculty of Life Sciences, University of Vienna and the VDS CoBeNe, the Vienna Doctoral Scool in Cognition, Behaviour and Neuroscience.M.L. is supported by the European Union's Horizon 2020 research and innovation programme under the Marie Sklodowska-Curie grant agreement No 798091. We thank the team at the CumberlandWildpark Grünau for the excellent cooperation. We further thank our colleagues at the Konrad Lorenz Research Station for discussions and support on site.

CONFLICT OF INTEREST

None.

ORCID

Mario Gallego-Abenza https://orcid.org/0000-0002-4027-5899
Matthias-Claudio Loretto https://orcid.org/0000-0002-1940-3470

REFERENCES

Afshar, M., & Giraldeau, L.-A. (2014). A unified modelling approach for producer–scrounger games in complex ecological conditions. Animal Behaviour, 96, 167–176. https://doi.org/10.1016/j.anbehav.2014.07.022

Baglione, V., & Canestrari, D. (2009). Kleptoparasitism and temporal segregation of sympatric corvids foraging in a refuse dump. The Auk, 126(3), 566–578. https://doi.org/10.1525/auk.2009.08146

Barta, Z., & Giraldeau, L. A. (1998). The effect of dominance hierarchy on the use of alternative foraging tactics: A phenotype-limited producing-scrounging game. Behavioral Ecology and Sociobiology, 42(3), 217–223. https://doi.org/10.1007/s002650050433

Barton, K. (2019). MuMIn: Multi-model inference, version, 1.43.6., 1, 1–75.https://cran.rproject.org/web/packages/MuMIn/index.html

Beauchamp, G. (2004). Reduced flocking by birds on islands with re-laxed predation. Proceedings of the Royal Society B: Biological Sciences, 271(1543), 1039–1042. https://doi.org/10.1098/rspb.2004.2703

Beck, K., Loretto, M.-C., & Bugnyar, T. Effects of site fidelity, group size and age on food caching behaviour of common ravens, Corvus corax. Animal Behaviour, submitted.

Belisle, P., & Chapais, B. (2001). Tolerated co-feeding in relation to degree of kinship in Japanese macaques. Behaviour, 138(4), 487–509. Retrieved from http://www.jstor.org/stable/4535835

Braun, A., & Bugnyar, T. (2012). Social bonds and rank acquisition in raven nonbreeder aggregations. Animal Behaviour, 84(6), 1507–1515. https://doi.org/10.1016/j.anbehav.2012.09.024

Braun, A., Walsdorff, T., Fraser, O. N., & Bugnyar, T. (2012). Socialized subgroups in a temporary stable Raven flock? Journal of Ornithology, 153(Suppl. 1), 97–104. https://doi.org/10.1007/s10336-011-0810-2

Bugnyar, T. (2011). Knower–guesser differentiation in ravens: Others' viewpoints matter. Proceedings of the Royal Society B: Biological Sciences, 278(1705), 634–640. https://doi.org/10.1098/rspb.2010.1514

Bugnyar, T., & Heinrich, B. (2005). Ravens, Corvus corax, differentiate between knowledgeable and ignorant competitors. Proceedings of the Royal Society of London. Series B: Biological Sciences, 272(1573), 1641–1646.

Bugnyar, T., & Heinrich, B. (2006). Pilfering ravens, Corvus corax, ad- just their behaviour to social context and identity of competi- tors. Animal Cognition, 9(4), 369–376. https://doi.org/10.1007/ s10071-006-0035-6

Bugnyar, T., & Kotrschal, K. (2001). Movement coordination and signalling in ravens (corvus corax): An experimental field study. Acta Ethologica, 3(2), 101–109. https://doi.org/10.1007/s102110000029

Bugnyar, T., & Kotrschal, K. (2002a). Observational learning and the raiding of food caches in ravens, Corvus corax: Is it "tactical" deception? Animal Behaviour, 64(2), 185–195. https://doi.org/10.1006/anbe.2002.3056

Bugnyar, T., & Kotrschal, K. (2002b). Scrounging tactics in free-ranging ravens, Corvus corax. Ethology, 108(11), 993–1009. https://doi.org/10.1046/j.1439-0310.2002.00832.x

Bugnyar, T., & Kotrschal, K. (2004). Leading a conspecffic away from food in ravens (Corvus corax)? Animal Cognition, 7(2), 69–76. https://doi.org/10.1007/s10071-003-0189-4

Bugnyar, T., Reber, S. A., & Buckner, C. (2016). Ravens attribute visual access to unseen competitors. Nature Communications, 7(February), 10506. https://doi.org/10.1038/ncomms10506

Bugnyar, T., Schwab, C., Schloegl, C., Kotrschal, K., & Heinrich, B. (2007). Ravens judge competitors through experience with play caching. Current Biology, 17(20), 1804–1808. https://doi.org/10.1016/j.cub.2007.09.048 Bugnyar, T., Stöwe, M., & Heinrich, B. (2007). The ontogeny of caching in ravens, Corvus corax. Animal Behaviour, 74(4), 757–767. https://doi.

org/10.1016/j.anbehav.2006.08.019

Burnham, K. P., & Anderson, D. R. (2002). Model selection and multimodel inference: A practical information-theoretic approach. New York, NY: Springer.

Byrne, R. W. (1997). The technical intelligence hypothesis: An additional evolutionary stimulus to intelligence? In Machiavellian intelligence II: Extensions and evaluations (pp. 289–311). New York, NY: Cambridge University Press. https://doi.org/10.1017/CBO9780511525636.012 Byrne, R. W., & Whiten, A. (1988a). Tactical deception in primates. Behavioral and Brain Sciences, 11(2), 233–244. https://doi.org/

10.1017/s0140525x00049682

Byrne, R. W., & Whiten, A. (1988b). Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans. New York, NY: Oxford University Press.

Caffrey, C. (2000). Marking crows. North American Bird Bander, 26(26), 146–148. Retrieved from https://sora.unm.edu/sites/default/files/journals/nabb/v026n04/p0146-p0150.pdf

Clayton, N. S., Dally, J. M., & Emery, N. J. (2007). Social cognition by food-caching corvids. The western scrub-jay as a natural psychologist. Philosophical Transactions of the Royal Society B: Biological Sciences, 362(1480), 507–522. https://doi.org/10.1098/rstb.2006.1992

Coussi-Korbel, S. (1994). Learning to outwit a competitor in mangabeys (Cercocebus torquatus torquatus). Journal of Comparative Psychology. US: American Psychological Association, 108(2), 164–171. https:// doi.org/10.1037/0735-7036.108.2.164

Dall, S. R. X., & Wright, J. (2009). Rich pickings near large communal roosts favor "gang" foraging by juvenile common ravens, corvus corax. PLoS ONE, 4(2), e4530. https://doi.org/10.1371/journal.pone.0004530

Di Bitetti, M. S., & Janson, C. H. (2001). Social foraging and the finder's share in capuchin monkeys, Cebus apella. Animal Behaviour, 62(1), 47–56. https://doi.org/10.1006/anbe.2000.1730

Dubuc, C., & Chapais, B. (2007). Feeding competition in Macaca fascicularis: An assessment of the early arrival tactic. International Journal of Primatology, 28(2), 357–367. https://doi.org/10.1007/ s10764-007-9118-8

Dufour, V., Wascher, C. A. F., Braun, A., Miller, R., & Bugnyar, T. (2012). Corvids can decide if a future exchange is worth waiting for. Biology Letters, 8(2), 201–204. Retrieved from http://rsbl.royalsocietypublishing.org/content/8/2/201.abstract. https://doi.org/10.1098/rsbl.2011.0726

Dunbar, R. I. M. (2003). The social brain: Mind, language, and society in evolutionary perspective. Annual Review of Anthropology, 32(1), 163–181. https://doi.org/10.1146/annurev.anthro.32.061002.

093158

Emery, N. J., & Clayton, N. S. (2001). Effects of experience and social context on prospective caching strategies by scrub jays. Nature, 414(6862), 443–446. https://doi.org/10.1038/35106560

Flower, T. P., Gribble, M., & Ridley, A. R. (2014). Deception by flexi- ble alarm mimicry in an African bird. Science, 344(6183), 513–516. https://doi.org/10.1126/science.1249723

Fournier, D. A., Skaug, H. J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M. N, Sibert, J. (2012). AD Model Builder: Using auto- matic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software, 27(2), 233–249. https://doi.org/10.1080/10556788.2011.597854

Fox, J., & Weisberg, S. (2011). An R companion to applied regression (Second). Thousand Oaks, CA: Sage. Retrieved from http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

Fraser, O. N., Schino, G., & Aureli, F. (2008). Components of relation- ship quality in chimpanzees. Ethology, 114(9), 834–843. https://doi.org/10.1111/j.1439-0310.2008.01527.x

Giraldeau, L. A., Caraco, T. (2000). Social foraging theory. Ecology (vol. 82). Princeton, NJ: Princeton University Press. https://doi.org/10.2307/2680211

Goss-Custard, J. D., & Durell, S. (1988). The effect of dominance and feeding method on the intake rates of oystercatchers, Haematopus ostralegus, feeding on mussels. The Journal of Animal Ecology, 57(3), 827. https://doi.org/10.2307/5095

Grand, T. C., & Dill, L. M. (1999). The effect of group size on the foraging behaviour of juvenile Coho salmon: Reduction of predation risk or increased competition? Animal Behaviour, 58(2), 443–451. https://doi.org/10.1006/anbe.1999.1174

Gwinner, E. (1965). U¨ ber den Einfluß des Hungers und andere Faktoren auf die Versteck-Aktivita¨ t des Kolkraben (Corvus corax). Vogelwarte, 23, 1–4.

Heinrich, B. (1988). Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by the raven, Corvus corax. Behavioral Ecology and Sociobiology, 23(3), 141–156. https://doi.org/10.1007/BF00300349

Heinrich, B. (1989). Ravens in winter. New York, NY: Vintage Books. Retrieved from https://books.google.at/books?xml:id=YbWtadkEVvUC

Heinrich, B., Kaye, D., Knight, T., & Schaumburg, K. (1994). Dispersal and association among common ravens. The Condor, 96(2), 545–551. https://doi.org/10.2307/1369334

Heinrich, B., & Marzluff, J. M. (1991). Do common ravens yell because they want to attract others? Behavioral Ecology and Sociobiology, 28(1), 13–21. https://doi.org/10.1007/BF00172134

Heinrich, B., & Marzluff, J. (1992). Age and mouth color in common ravens. The Condor, 94(2), 549–550. https://doi.org/10.1242/jeb.089763 Heinrich, B., & Pepper, J. W. (1998). Influence of competitors on caching behaviour in the common raven, Corvus corax. Animal Behaviour, 56, 1083–1090. https://doi.org/10.1006/anbe.1998.0906

Held, S., Mendl, M., Devereux, C., & Byrne, R. W. (2002). Foraging pigs alter their behaviour in response to exploitation. Animal Behaviour, 64(2), 157–165. https://doi.org/10.1006/anbe.2002.3044

Hillemann, F., Bugnyar, T., Kotrschal, K., & Wascher, C. A. F. (2014). Waiting for better, not for more: Corvids respond to quality in two delay maintenance tasks. Animal Behaviour, 90, 1–10. https://doi.org/10.1016/j.anbehav.2014.01.007

Hirata, S., & Matsuzawa, T. (2001). Tactics to obtain a hidden food item in chimpanzee pairs (Pan troglodytes). Animal Cognition, 4(3), 285–295. https://doi.org/10.1007/s100710100096

Humphrey, N. (1976). The social function of intellect. In P. P. G. Bateson & R. A. Hinde (Eds.), Growing Points in Ethology (pp. 303–317). Cambridge, UK: Cambridge University Press.

Jolly, A. (1966). Lemur social behavior and primate intelligence. Science, 153(3735), 501–506. https://doi.org/10.1126/science.153.3735.501 Loretto, M.-C., Schuster, R., & Bugnyar, T. (2016). GPS tracking of non-breeding ravens reveals the importance of anthropogenic food sources during their dispersal in the Eastern Alps. Current Zoology,

62(4), 337–344. https://doi.org/10.1093/cz/zow016

Loretto, M.-C., Schuster, R., Itty, C., Marchand, P., Genero, F., & Bugnyar,

T. (2017). Fission-fusion dynamics over large distances in raven non-breeders. Scientific Reports, 7(1), 380. https://doi.org/10.1038/s41598-017-00404-4

Marzluff, J. M., & Heinrich, B. (1991). Foraging by common ravens in the presence and absence of territory holders: An experimental analy- sis of social foraging. Animal Behaviour, 42(5), 755–770. https://doi.org/10.1016/S0003-3472(05)80121-6

Marzluff, J. M., Heinrich, B., & Marzluff, C. S. (1996). Raven roosts are mobile information centres. Animal Behaviour, 51(1), 89–103. https://doi.org/10.1006/anbe.2000.1579

Menzel, E. W. (1974). Chapter 3 - a group of young chimpanzees in a one-acre field: Leadership and communication. In A. M. Schrier, & F. Stollnitz (Eds.), Behaviour of nonhuman primates, Vol. 5 (pp. 83–153). San Diego, CA: Academic Press. https://doi.org/10.1016/ B978-0-12-629105-6.50009-2

Morand-Ferron, J., Sol, D., & Lefebvre, L. (2007). Food stealing in birds: Brain or brawn? Animal Behaviour, 74(6), 1725–1734. https://doi.org/10.1016/j.anbehav.2007.04.031

Munn, C. A. (1986). Birds that 'cry wolf'. Nature, 319(6049), 143–145. https://doi.org/10.1038/319143a0

Nácarová, J., Veselý, P., & Bugnyar, T. (2018). Ravens adjust their anti-predatory responses to con- and specific alarms to the perceived threat. Ethology, 124, 1–8. https://doi.org/10.1111/eth.12764

Parker, S. T., & Gibson, K. R. (1977). Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. Journal of Human Evolution, 6(7), 623–641. https://doi.org/10.1016/S0047-2484(77)80135-8

Powell, G. V. N. (1974). Experimental analysis of the social value of flocking by starlings (Sturnus vulgaris) in relation to predation and foraging. Animal Behaviour, 22(2), 501–505. https://doi.org/10.1016/S0003-3472(74)80049-7

R Core Development Team (2014). R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Rosati, A. G. (2017). Foraging cognition: Reviving the ecological intelligence hypothesis. Trends in Cognitive Sciences, 21(9), 691–702. https://doi.org/10.1016/j.tics.2017.05.011

Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in be- havioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology, 65(1), 13–21. https://doi.org/10.1007/ s00265-010-1037-6

Szipl, G., Ringler, E., Spreafico, M., & Bugnyar, T. (2017). Calls during agonistic interactions vary with arousal and raise audience attention in ravens. Frontiers in Zoology, 14(1), 1–13. https://doi.org/10.1186/s12983-017-0244-7

Templeton, J. J., & Giraldeau, L. A. (1995). Patch assessment in foraging flocks of european starlings: Evidence for the use of public informa- tion. Behavioral Ecology, 6(1), 65–72. https://doi.org/10.1093/behec

o/6.1.65

Templeton, J. J., & Giraldeau, L. A. (1996). Vicarious sampling: The use of personal and public information by starlings foraging in a simple patchy environment. Behavioral Ecology and Sociobiology, 38, 105– 114. https://doi.org/10.1007/s002650050223

Vickery, W. L., Giraldeau, L. -A., Templeton, J. J., Kramer, D. L., & Chapman, C. A. (1991). Producers, scroungers and group foraging. The American naturalist, 137(6), 847–863.

Webb, W. C. (2004). Common raven juvenile survival in a human-augmented landscape, (February 2014). https://doi.org/10.1650/7443

Wright, J., Stone, R. E., & Brown, N. (2003). Communal roost as structured information centre in the rave, Corvus corax. Journal of Animal Ecology, 72(6), 1003–1014. https://doi. org/10.1046/j.1365-2656.2003.00771.x

Wunderle, J. M. J. (1991). Age-specific foraging proficiency in birds.

Current Ornithology, 8, 273–324. Retrieved from 10017456741/en/

SUPPORTING INFORMATION

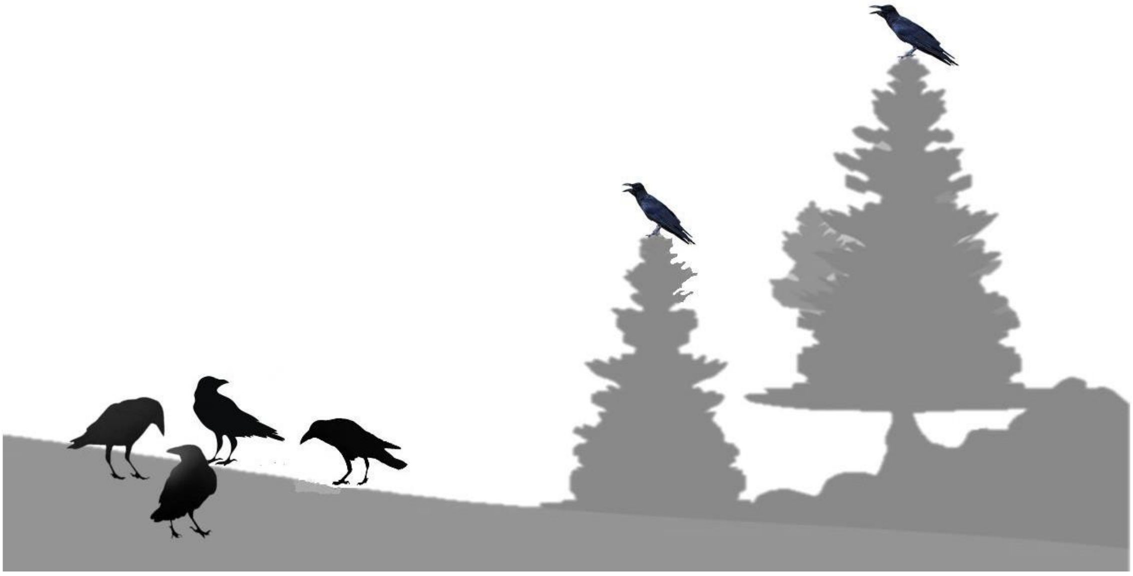
Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Gallego-Abenza M, Loretto M-C, Bugnyar T. Decision time modulates social foraging success in wild common ravens, *Corvus corax*. *Ethology*. 2019;00:1–10. https://doi.org/10.1111/eth.12986

Chapter 2

Who is crying wolf? Seasonal effect on antipredator response to age-specific alarm calls in common ravens, *Corvus corax*

Mario Gallego-Abenza, Christian R. Blum and Thomas Bugnyar



This chapter is published as an article in a peer-review journal

How to cite this article: Gallego-Abenza, M., Blum, C. R., & Bugnyar, T. (2021). Who is crying wolf? Seasonaleffect on antipredator response to age-specific alarm calls in common ravens, Corvus corax. *Learning & behavior*, *49*(1), 159–167. https://doi.org/10.3758/s13420-020-00455-0

Learning & Behavior
https://doi.org/10.3758/s13420-020-00455-0

Who is crying wolf? Seasonal effect on antipredator response to age-specific alarm calls in common ravens, *Corvus corax*

Mario Gallego-Abenza[1,2] • Christian R. Blum[1] • Thomas Bugnyar[1,2]

Accepted: 7 December 2020

Abstract

Communication about threats including those posed by the presence of predators occurs mainly through acoustic signals called alarm calls. The comprehension of these calls by receivers and their rapid antipredator response are crucial in terms of survival. However, to avoid overreaction, individuals should evaluate whether or not an antipredator response is needed by paying attention to who is calling. For instance, we could expect adults to be more experienced with predator encounters than juveniles and thus elicit stronger antipredator responses in others when alarming. Similarly, we could expect a stronger response to alarmcalls when more than one individual is calling. To test these assumptions, we applied a playback experiment to wild ravens, inwhich we manipulated the age class (adult or juvenile) and the number (one or two) of the callers. Our results revealed a seasonaleffect of age class but no effect of number of callers. Specifically, the ravens responded with stronger antipredator behaviour(vigilance posture) towards alarm calls from adults as compared to juveniles in summer and autumn, but not in spring. We discuss alternative interpretations for this unexpected seasonal pattern and argue for more studies on call-based communication in birds tounderstand what type of information is relevant under which conditions.

Keywords Discrimination · Perception · Communication · Antipredator behaviour

Introduction

Birds are famous for their vocalization. Song learning, for instance, has been intensively studied over the last decades (Catchpole & Slater, 2008) and is fairly well understood from a behavioural and neurobiological perspective (Bolhuis & Gahr, 2006), making it an excellent model for human speech (Bolhuis, Okanoya, & Scharff, 2010). In comparison to the vast literature on song learning, bird calls have received limited attention (Marler, 2004), and studies on the cognitive skills underlying the production and usage of bird calls are rare. In respect to the latter, research on a single grey parrot, ‘Alex’, has become famous: using English words for communicating with human trainers, Alex not only labelled objects, but responded to questions probing his knowledge (e.g. of relational concepts like same/different) and expressed intentions via requests (Pepperberg, 1999). While Alex’s skills are impressive in many ways, sparking debates on various conceptual and methodological levels (Pepperberg, 1983, 1990, 2008), his apparent understanding and intentional use of communicative signals with humans raises the question of what predispositions these skills might be based upon? Why would a grey parrot like Alex need a sophisticated neuro-cognitive machinery allowing him to copy sounds, attach meaning to it, form concepts, and use them in interaction with others? Twenty-five years of research on grey parrots´ life support the idea of evolutionary pressures underpinning complex communicative and cognitive capacities (Pepperberg, 2002). It has been argued that parrots need such abilities in daily social life (Pepperberg, 1999), which in the case of Alex, happened to be the human setting. But what challenges could parrots, or other birds, face under ecologically relevant situations that require communication other than song, i.e. that they should ‘talk’ about?

Obvious candidates are live-threatening events, like predator encounters, that can occur to wild animals at any time. Using communication may help individuals to detect predators (Smith, 1965; Zuberbühler, Noë, & Seyfarth, 1997) andassess the type or level of threat (Seyfarth, Cheney, & Marler, 1980), and, as a consequence, respond with appropriate

---

* Mario Gallego-Abenza
mario.gallego-abenza@univie.ac.at

[1] Department of Behavioural and Cognitive Biology, University of Vienna, Vienna, Austria

[2] Konrad Lorenz Forschungsstelle, Core Facility for Behaviour and Cognition, University of Vienna, Grünau im Almtal, Austria

behaviours such as escaping, hiding or repealing an attack (Botham et al., 2008; Kotler, Blaustein, & Brown, 1992; Lohrey, Clark, Gordon, & Uetz, 2009). Potential victims may also gather forces and drive the predator away from thearea (Foster & Treherne, 1981). While acoustic signals givenin the presence of predators are commonly referred to as alarmcalls (Hauser, 1996), the behaviour associated with driving the predator away is known as mobbing or collective anti-predator behaviour (Curio, 1978; Graw & Manser, 2007).

Like many mammals, birds tend to give different alarm calls to specific events in the environment, like the occurrence of ground or areal predators (Evans, Evans, & Marler, 1993). Avian alarm calls are thus a prime candidate for investigating information content about external reference (Gill & Bierema, 2013). Experiments revealed that in some species, alarm calls denote different types of predator classes that require different response strategies (Kalb, Anger, & Randler, 2019; Suzuki, 2012, 2014), which fulfil the criteria of functional reference (Evans et al., 1993; Rendall, Owren, & Ryan, 2009); in other species, however, the calls denote the urgency level to respond (Leavesley & Magrath, 2005), and thus likely represent differences in arousal states (Blumstein & Récapet, 2009). Typically, alarm calls have a strong genetic component in respect to production, but are relatively flexible in respect to usage (Fichtel & Van Schaik, 2006; Townsend, Rasmussen, Clutton-Brock, & Manser, 2012). Senders may thus fine-tune the use of alarm calls, for example to denote a specific predator type or behaviour (Griesser, 2008; Suzuki, Wheatcroft, & Griesser, 2016), and/or adjust their signalling to the audience, for example call more when kin or mating partners are present(e.g. Shields, 1984). On the receiver side, getting accurate information about predators and learning to respond appropriately to alarm calls are of high survival value (Griesser, 2013). Receivers may readily learn about alarm calls even across species, as demonstrated in the mobbing flocks of mixed-species communities of songbirds (Magrath, Pitcher, & Gardner, 2009; Wheatcroft, Gallego-Abenza, & Qvarnström, 2016).

Like most vocalizations, alarm calls also contain informa-tion about the sender, such as its sex, age class, kin or indi-vidual identity (Blumstein & Munos, 2005). Receivers of alarm calls may thus not only respond to the type of threat/ level of urgency encoded in the calls but take the senders’ features and/or identities into account when engaging in anti-predator behaviour (Hare, 1998; Hare & Atkins, 2001). Surprisingly few studies have tested the receivers’ responsesto such sender-specific characteristics in birds (with the exception of kin in nepotistic alarm calling and/or mobbing,

e.g. Griesser & Ekman, 2004, 2005). Experiments on Pied flycatchers (*Ficedula hypoleuca*) showed that they do not automatically respond to any alarm calls of their territory neighbours with predator mobbing but selectively help those neighbours to mob a predator, who had helped them before (Krams, Krama, Igaune, & Mänd, 2008; Wheatcroft & Price, 2008). The reciprocal pattern indicates that the birds acquire some form of knowledge and/or attribute about their neighbours through previous predator encounters. Recent experiments on jackdaws (*Corvus monedula*) revealed that birds respond stronger with collective anti-predator behaviour to the play back alarm calls of colony members as compared to non-colony members, indicating that receivers discriminate between familiar and unfamiliar birds (Woods, Kings, McIvor,& Thornton, 2018). Furthermore, the number of callers had a similar positive effect on the probability to engage in collective antipredator behaviour, indicating that receivers take into account whether the alarm calls were elicited by a single or a few birds and hence the intensity of the response (Coomes, Mcivor, Thornton, Coomes, & Thornton, 2019). Such assessment capability by receivers was also documented in small mammals, precisely in adult Richardson´s ground squirrels (Sloan & Hare, 2008). When confronted with alarm calls from conspecifics and closely related heterospecifics during foraging, carrion crows tended to respond to any alarm calls (Bílá, Beránková, Veselý, Bugnyar, & Schwab, 2017), whereas ravens adjusted their antipredator behaviour depending on the perceived risk (whether or not they snatched food from predators; Nácarová, Veselý, & Bugnyar, 2018) and the familiarity of the calling species (Davidkova, Veselý, Syrova, Nacarovà, & Bugnyar, 2020).

In the present study, we followed the logic of the studies on jackdaws (Coomes et al., 2019) and investigated whether common ravens are attentive to sender-specific characteristics in alarm calls. Unlike jackdaws, adult ravens defend large territories (Scarpignato & George, 2011) and thus do not form colonies during breeding. However, non-breeding ravens tend to form large groups, usually near food sources (Heinrich, 1989; Loretto, Schuster, & Bugnyar, 2016). These groups are composed mainly of immature individuals (juveniles intheir first year, subadults in their second or third year; making up about 20% and 60% of a group, respectively) but also ofadult birds (older than 3 years, often having no partner and/orno territory; typically about 20% of a group) (Braun & Bugnyar, 2012; Heinrich, 1989). Apart from age-class, ravenforaging groups are structured by social relationships (social bonds based on reciprocal exchange of affiliative interactions; Braun & Bugnyar 2012) and kinship (Szipl, Ringler, & Bugnyar, 2018; but see Parker, Waite, Heinrich, & Marzluff,1994). Yet, the foraging groups have an open character, with individuals coming and going on a regular basis (Heinrich, 1989). How long birds stay at a site/in a given group variesextensively from a few days to years; hence, individuals canmeet rarely, regularly or frequently at the same or different sites (Loretto et al., 2017). Taken together, the socially struc-tured but fluid nature of raven foraging groups constitutes a promising scenario for studying what individuals know about others and which features they attend to (Boucherie, Loretto, Massen, & Bugnyar, 2019). With respect to alarm calls, we could expect adults to be more reliable in terms of threat perception than young individuals, due to the adults' previous life-experience encountering different types of threats. Furthermore, we could expect not only the number of callers but also the identity of the callers to be critical for the receivers' decision to engage in antipredator behaviour.

Here we focussed on two of the identified factors, age class(as a proxy for experience) and number and callers (as a proxyfor threat intensity), while controlling for the callers' identity (always unfamiliar). We exposed groups of free-ranging ravens during foraging to playbacks of a standardized number of alarm calls given either by a single juvenile, two juveniles, a single adult or two adults. We predicted ravens to show stronger responses when listening to adult individuals as compared to juveniles and when listening to two different individuals alarming as compared to one individual.

Material and methods

Study site and study species

This study was conducted at the Cumberland Wildpark, a zoo in the Austrian Alps (N 47°48.421′, E 13°57.032′), where groupsof common ravens snatch food from animal enclosures. These ravens are the focus of a long-term monitoring program (startedin 2007), during which more than 300 birds have been markedwith rings and wing tags for individual identification. The size ofthe daily foraging groups in the park ranges between 20 and 80 individuals. The groups are composed mostly of non-breeders in the first years of life (juveniles and subadults, < 4 years old) but also adults that do not hold a territory and/or visit this group in the non-breeding period opportunistically; they continuously change in composition with noticeable individual differencesin terms of how long ravens stay and/or leave (Braun & Bugnyar, 2012; Loretto et al., 2017). We focused on the wild boar enclosure for our experiment, as this enclosure allows a good view of the foraging ravens, the wild boars themselvesdo not represent a risk for the ravens, and the ravens are knownfor responding well to playbacks of heterospecific and conspe-cific calls at this location (Nácarová et al., 2018). A total of 48trials were conducted in three different seasons, starting in spring2019 (17 January 2019-7 May 2019), followed by autumn (25 September 2019-18 December 2019) and finishing in summer 2020 (25 May 2020-18 July 2020), with two non-testing periods of approximately4 and7 months between seasons.

Playback stimuli

We used alarm calls that were recorded from captive ravens at Haidlhof Research Station, which is located in the east of Austria, about 200 km away from our field site in the Alps. While our marked wild ravens may roam over larger areas (Loretto et al., 2017), they have never been observed near Haidlhof.

Ravens at Haidlhof were housed in a social group structured by age class (juveniles, subadults and adults) simulating thewild conditions. In an experimental study, these ravens were exposed to a human carrying a dead raven resulting in intense mobbing behaviour and alarm calling (Blum, Fitch, & Bugnyar, 2020). We used these calls from that experiment because: (1) these captive ravens were unfamiliar to the wild ravens in Grünau, and (2) we could identify callers at the individual level. The known identity of callers allowed us to compose the four different treatments: single caller versus two callers from either juvenile or adult age class, thus creating 16 different broadcasting files (four per each treatment) to be broadcast in randomized order within and among each season, conducting 16 trials per season, 48 trials in total. Testing days were separated from each other by 4.3 days on average (range 2-18) to avoid habituation. Sex was also known and controlled within a treatment composition, generating a similar number of broadcasting files of each sex. Each treatment was composed using four calls, where the third and fourth calls occurred after3 s of silence interval and could correspond to either the sameor a different individual (see Fig. 1). We equalized all calls´ amplitude in the composed files to be broadcast using Audacity software (https://www.audacityteam.org/). Alarm calls were played back in .wav format using a digital music player (Musrun k188) connected to a loudspeaker (JBL xtreme, frequency response 70-20,000 Hz). All calls were standardized to an identical volume of 73 dB measured at 2m of distance (Sound Level Meter RadioShack, model 3300099, A-weighting, fast response).

Behavioural responses

Playbacks were conducted during the feedings of wild boars, i.e. while the wild ravens were foraging. The same experimenter (MGA) conducted all trials to avoid a potential effectof experimenter identity (MGA has been studying the ravensat this location for than 2 years: hence, the ravens were well habituated to his presence from the beginning of the experiment). Ravens´ responses were filmed using two GoPro Hero5 cameras from fixed positions at 2 m and 5 m of distance tothe foraging site. We measured the total number of ravens present in the camera´s field of view. In addition, we scoredwhether ravens in the video were flying off from the foragingplace or adopted a vigilance posture for 5 s right after broad-casting the alarm calls. We defined vigilance posture as being when ravens raised up their heads, elongating their necks, and directed their gaze repeatedly towards sky, while switchingbetween eyes, following studies on antipredator behaviours conducted in other avian species (Fernández-Juricic, 2012; Guillemain, Duncan, & Fritz, 2001).

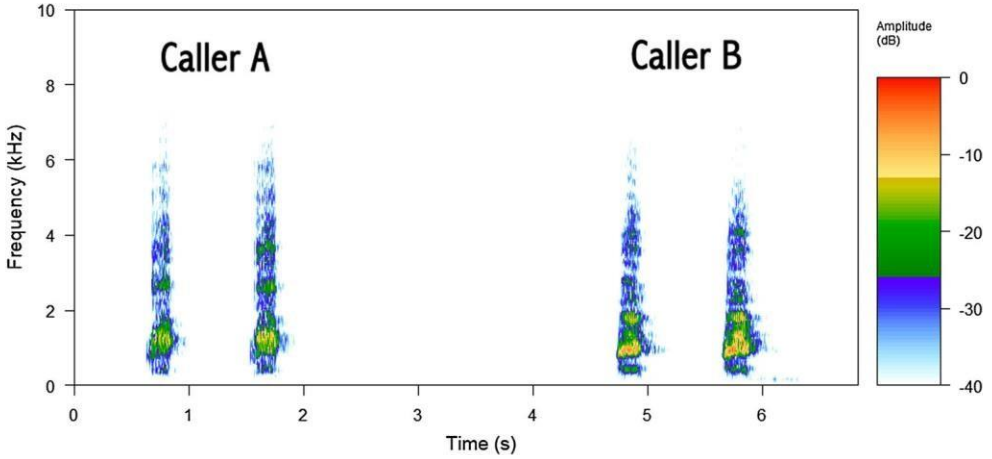


Fig. 1 Spectrogram of a single playback stimulus. In this case, two different adult individuals were broadcast

Statistical analyses

We conducted our statistical analyses in R software (v. 3.6.1., R Development Core Team 2014). For modelling the two response variables: `vigilance posture´ and `flying off´, we used the function glmer in the package `lme4´ (Bates, Mächler, Bolker, & Walker, 2015). Due to an inconstant number of total ravens across testing days, we used the command `cbind´ with-in the model formula to control for it, thus modelling the proportion of ravens showing any of the two behavioural responses (`vigilance posture´ and `flying off´) with a binomial error distribution. To answer the question whether ravens responded differently depending on the `treatment´ (single adult, two adults, single juvenile or two juveniles) being exposed to, we used `season´ as random factor, together with `broadcasting file´, controlling for potential seasonal effects. When testing the effect of `season´ on ravens´ response, we included it as fixed factor and ´broadcasting file´ remained as unique random factor. When using `age class´ or `calling composition´ (one or two callers), trials were clumped together according to these predictors. Model selection through both AICc and weight comparison was conducted using the function `model.sel´, ´ MuMIn´ package (Barton, 2019). The best model explaining `vigilance posture´ response contained the interaction between `age class´ and `season´, in order to examine significant differences within each season, we conducted a post hoc Tukey contrast test using `emmeans´ package (Searle, Speed, & Milliken, 1980) to calculate differences in estimated marginal means and P values.

Results

Ravens responded to played back alarm calls by adopting `vigilance posture´, in 46 out of 48 trials (95.8%), whereas a `flying off´ response occurred in only 12 out of 48 trials (25%). For both behavioural response variables, the model containing `treatment´ as unique explanatory predictor did not result in a significant difference between the four playback conditions (single adult, two adults, single juvenile, two juveniles). However, model selection indicated that for `vigilance posture´ the model containing the interaction between `season´ and `age class´ was the best model (lower AICc and higher weight; see Tables 1 and 2). `Age class´ independently affected ravens´ vigilance response, where ravens were less responsive to juvenile compared to adult callers (Estimate = -0.777, SE = 0.342, Z = -2.272, P = 0.023). Similarly, we found that `season´ had an effect on the ravens´ vigilance posture response to any played-back alarm call´s composition, whereby higher vigilance posture values occurred in summer (Estimate = 0.563, SE = 0.259, Z = 2.172, P = 0.029). Additionally, the interaction between the two abovementioned factors revealed age-specific responses depending on the season. The post hoc Tukey contrasttest revealed that stronger responses to adult as com- pared to juvenile callers occurred in summer and au- tumn, but not in spring (Fig. 2).

A similar procedure with model selection was followed to estimate how `season´ and `age class´ affected the `flying off´

Table 1 Model selection with model candidates to explain the vigilance posture response ordered by AICc and weight

Explanatory variables	df	logLik	ΔAICc	Weight
Age class x Season	7	-128.26	0	0.651
Season	4	-133.01	1.81	0.263
Age class	3	-136.15	5.52	0.041
Null model	2	-138.03	7.00	0.020
Season x number of callers (1 or 2)	7	-132.15	7.78	0.013
Number of callers (1 or 2)	3	-137.91	9.05	0.007
Treatment	5	-135.96	10.03	0.004
Season x Treatment	13	-126.93	17.24	0.000

Table 2 Summary of the generalized mixed model containing the interaction effect of `season´ and `age class´ in the vigilance posture response to broadcasted alarm calls of conspecifics in different seasons

Parameter	Estimate	SE	Z value	P
Intercept	-0.633484	0.231475	-2.737	0.00621 **
Season *Summer*	0.562793	0.259168	2.172	0.02989 *
Season *Spring*	-0.401102	0.289806	-1.384	0.16635
Age class *Juvenile*	-0.776795	0.341911	-2.272	0.02309 *
Season *Summer* x Age class *Juvenile*	-0.002671	0.387085	-0.007	0.99450
Season *Spring* x Age class *Juvenile*	0.895711	0.401529	2.231	0.02570 *

response. In this case, the model containing the interaction between `season´ and `treatment´ was classified as the best model (Supplementary Table 1). However, neither of those had a significant effect (separately or in interaction) on ´flying off´ response (Supplementary Table 2).

Discussion

We tested whether wild ravens respond to two types of information possibly encoded in conspecifics alarm calls, i.e. the age class of the caller, and whether calls are given by one or more individuals. Playbacks of alarm calls elicited a stronger vigilance response when given by adults as compared to juveniles in two out of three seasons (in summer and autumn, not in spring). The number of calling individuals, however, did not lead to a significant difference in the ravens´ antipredator responses.

That ravens respond more strongly to alarm calls of adults rather than juveniles meets our expectation and supports the assumption that receivers can extract information about the age class of alarm callers. That this effect is dependent on season was not expected, however, and may be explained in different ways. On the one hand, ravens might have responded less to alarm calls given by juveniles in summer and autumn because at that time juveniles are very young and likely lack experience with predators and/or may easily give alarm callsto any disturbing situation. Hence, juveniles might be perceived as less reliable in alarm calling than adults. Similar findings have been described in some studies on mammals (Ramakrishnan & Coss, 2000; Seyfarth & Cheney, 1986), whereas other studies reported no effect of age class (Swan& Hare, 2008) or even the opposite (Blumstein & Daniel, 2004). On the other hand, ravens might be particularly recep-tive to alarm calls in spring, when local low temperatures allow them to scavenge on carcasses, putting them into in- creased contact with predators, and their survival rates are lowest (Webb, Boarman, & Rotenberry, 2004). Hence, in the season with a high likelihood of dangerous predator en-counters, they might respond to any alarm calls, irrespective

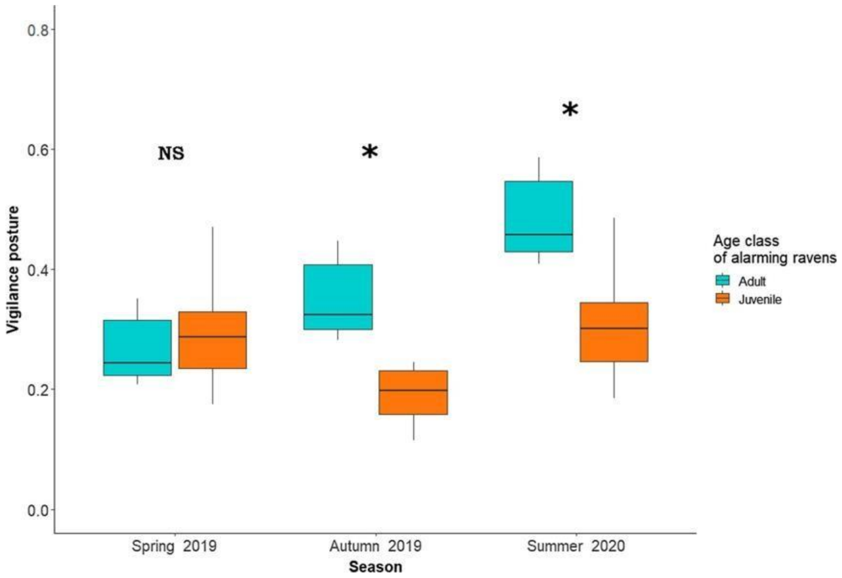


Fig. 2 This plot shows the significant differences (post hoc Tukey contrast test, using “emmeans” package) found in the proportion of ravens responding towards adult and juvenile alarming conspecifics in the three tested seasons

of the caller´s age class. Similar patterns of seasonal variation in antipredator behaviour have been described for other spe-cies (Shedd, 1982; Uchida, Suzuki, Shimamoto, Yanagawa, & Koizumi, 2016). Interestingly, the temporal pattern of our results renders either interpretation unlikely (Fig. 2). Receivers did not increase their response to juvenile alarm calls across the year, as would be expected with increasing experience of young birds or with increased threat levels after the first winter; conversely, they decreased their response toalarm calls of adults across the seasons, showing the lowestresponse rates in spring. This pattern suggests that ravens treatalarm calls of adults particularly seriously during summer and autumn, i.e. the period when families with young ravens are around. Alternatively, the pattern could be interpreted as resulting from reduced attention towards alarm calls of adultsduring cold periods (winter-spring). Although ravens face se-vere foraging competition in winter (Heinrich, 1989) and may divide their attention between gaining access to food (B. Heinrich & Marzluff, 1995), fending off conspecific kleptoparasitism and cache pilferage (Bugnyar & Kotrschal,2002; Gallego-Abenza, Loretto, & Bugnyar, 2020; Heinrich& Pepper, 1998), there are hardly any indications that compe- tition for food affects their antipredator behaviour, at least not at our study site (Nácarová et al., 2018). Finally, the temporal pattern found might be considered an artefact of our testing.Note that the order of playback presentation (first in spring 2019, then in autumn 2019, and then in summer 2020) makes it unlikely that our results are due to an order effect or habit-uation. Moreover, the played-back individuals were unfamil-iar to the tested ravens, indicating that receivers can extractage-class information from any conspecific alarm calls, which is perfectly in line with the ecological relevance of alarm calls (Gill & Bierema, 2013) and the structure of raven foraging groups with moderate to high fission-fusion dynamics (Braun,Walsdorff, Fraser, & Bugnyar, 2012).

Contrary to our expectation and to recent findings in jack-daws (Coomes et al., 2019), we could not find any effect of thenumber of played-back individuals on ravens’ antipredator behaviour. Our failure to detect a numerical discrimination through alarm calls may be due to the salience of the chosenstimuli. For instance, while we used one or two callers, the study on jackdaws used one, three or five callers; it is known that animals, including birds, have more difficulties in discriminating one versus two in comparison to one versus larger numbers (Tornick, Callahan, & Gibson, 2015). In a study conducted on mammals, more precisely on Richardson´s Ground Squirrels, only adult receivers showed enhanced antipredator responsiveness to two versus one alarm caller, even though juvenile receivers discriminate among individual callers, suggesting a developmental shift in the parameters employed to assess the veracity of any threat (Sloan & Hare, 2008). Alternatively, the ravens might have a problem in picking up on the individual information in the calls. We already know that some ravens’ calls like food-associated calls (`haa´) and territory calls (`rab´) contain strong individual signatures, which the birds respond to in habituation-dishabituation experiments (Boeckle, Szipl, & Bugnyar, 2012); in other calls, like those given in agonistic interactions, individual information is less evident in comparison to affective information (Szipl, Ringler, Spreafico, & Bugnyar, 2017). Possibly, thisis similar with alarm calls. A proper acoustical analysis and further playback experiments are needed to investigate this question.

Taken together, our study contributes to our understanding of what type of information birds may pick up when hearingalarm calls. While most studies on alarm calls have focused on functional reference about predators (Evans et al., 1993; Griesser, 2008; Suzuki, 2011, 2014), relatively few studies have experimentally tested for other types of information, like familiarity of caller/group membership (Griesser & Ekman, 2004, 2005; Woods et al., 2018), number of callers and callers´ age class (Coomes et al., 2019; this study). The findings reveal that birds respond selectively to different features that appear to be ecologically relevant, like the seasonal effect of responding to adults in this study. What is yet unknown is how much birds make use of individual information encoded in alarm calls, as several results could be explained by (refined) class-level discrimination (Tibbetts & Dale, 2007). In this respect, studies on behavioural deception are interesting, as there are multiple reports of individual callers becoming unreliable when repeatedly giving false alarms (Flower, Gribble,& Ridley, 2014; Munn, 1986). Experimental approaches manipulating the reliability of alarm callers could be a promising future step.

Coming back to our original question about what birds `talk about´, the information content in alarm calls certainly encompasses only one of many aspects in avian communication. Yet, these studies support the notion that examining the socio-cognitive underpinnings of call-based communicationin birds is a promising endeavour (Lambert, Jacobs, Osvath,& Von Bayern, 2019). If we eventually manage to examinethe information content (such as individual attributes, motiva- tions, affective states, functional reference to external events) of various calls individuals of a species respond to, we mayend up with a relatively complex picture on the receiver side,just as Pepperberg´s pioneering Alex studies defined the realmof be possibility on the production side.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.3758/s13420-020-00455-0.

Acknowledgements The present study was funded by the Austrian Science Fund (FWF) project P29705 and an IP project IP550002 of the Faculty of Life Sciences, University of Vienna; permanent support is granted by the ‘Verein der Förderer KLF’ and the Faculty of Life Sciences, University of Vienna. CB was supported by the uni:docs stipend of University of Vienna. We thank our colleagues Dr. Petra

Sumasgutner and Dr. Mauricio Nicolas Adreani for their help in the statistical analyses and Noelia Abenza for her kind help editing figures. We also thank the Cumberland Wildpark Grünau for the excellent cooperation while conducting this study.

Funding Open Access funding provided by University of Vienna.

Data Availability The data and materials for the experiments will be available upon publication.

References

Barton, K. (2019). MuMIn: Multi-Model Inference. Retrieved from https://cran.r-project.org/package=MuMIn

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67(1). https://doi.org/10.18637/jss.v067.i01

Bílá, K., Beránková, J., Veselý, P., Bugnyar, T., & Schwab, C. (2017). Responses of urban crows to con- and hetero-specific alarm calls in predator and non-predator zoo enclosures. Animal Cognition, 20(1), 43–51. https://doi.org/10.1007/s10071-016-1047-5

Blum, C. R., Fitch, W. T., & Bugnyar, T. (2020). Rapid learning and long-term memory for dangerous humans in ravens (Corvus corax). Frontiers in Psychology, 11, 2843.

Blumstein, D. T., & Daniel, J. C. (2004). Yellow-bellied marmots discriminate between the alarm calls of individuals and are more responsive to calls from juveniles. Animal Behaviour, 68(6), 1257–1265. https://doi.org/10.1016/j.anbehav.2003.12.024

Blumstein, D. T., & Munos, O. (2005). Individual, age and sex-specific information is contained in yellow-bellied marmot alarm calls. Animal Behaviour, 69, 353–361. https://doi.org/10.1016/j.anbehav.2004.10.001

Blumstein, D. T., & Récapet, C. (2009). The sound of arousal: The addition of novel non-linearities increases responsiveness in marmot alarm calls. Ethology, 115(11), 1074–1081. https://doi.org/10.1111/ j.1439-0310.2009.01691.x

Boeckle, M., Szipl, G., & Bugnyar, T. (2012). Who wants food? Individual characteristics in raven yells. Animal Behaviour, 84(5), 1123–1130. https://doi.org/10.1016/j.anbehav.2012.08.011

Bolhuis, J. J., & Gahr, M. (2006). Neural mechanisms of birdsong memory. Nature Reviews Neuroscience, 7(5), 347–357. https://doi.org/10.1038/nrn1904

Bolhuis, J. J., Okanoya, K., & Scharff, C. (2010). Twitter evolution: Converging mechanisms in birdsong and human speech. Nature Reviews Neuroscience, 11(11), 747–759. https://doi.org/10.1038/nrn2931

Botham, M. S., Hayward, R. K., Morrell, L. J., Croft, D. P., Ward, J. R., Ramnarine, I., & Krause, J. (2008). Risk-sensitive antipredator behavior in the Trinidadian Guppy, Poecilia reticulata. Ecology, 89(11), 3174–3185. https://doi.org/10.1890/07-0490.1

Boucherie, P. H., Loretto, M., Massen, J. J. M., & Bugnyar, T. (2019). Lessons from ravens What constitutes “social complexity” and “social intelligence” in birds ? Lessons from ravens. Behavioral Ecology and Sociobiology, (January).

Braun, A., & Bugnyar, T. (2012). Social bonds and rank acquisition in raven nonbreeder aggregations. Animal Behaviour, 84(6), 1507–1515. https://doi.org/10.1016/j.anbehav.2012.09.024

Braun, A., Walsdorff, T., Fraser, O. N., & Bugnyar, T. (2012). Socialized sub-groups in a temporary stable raven flock? Journal of Ornithology, 153(1), 97–104. Retrieved from https://doi.org/10.1007/s10336-011-0810-2

Bugnyar, T., & Kotrschal, K. (2002). Scrounging tactics in free-ranging ravens, Corvus corax. Ethology, 108(11), 993–1009. https://doi.org/ 10.1046/j.1439-0310.2002.00832.x

Catchpole, C. K., & Slater, P. J. B. (2008). Bird Song Biological Themes and Variations. Cambridge University Press. https://doi.org/10.1017/CBO9781107415324.004

Coomes, J. R., Mcivor, G. E., Thornton, A., Coomes, J. R., & Thornton, A. (2019). Evidence for individual discrimination and numerical assessment in collective antipredator behaviour in wild jackdaws (Corvus monedula). Biology Letters.

Curio, E. (1978). The Adaptive Significance of Avian Mobbing: I. Teleonomic Hypotheses and Predictions. Zeitschrift Für Tierpsychologie, 48(2). https://doi.org/10.1111/j.1439-0310.1978.tb00254.x

Davidkova, M., Veselý, P., Syrova, M., Nacarovà, J., & Bugnyar, T. (2020). Ravens respond to unfamiliar corvid alarm calls. Journal of Ornithology, Accepted for publication.

Evans, C. S., Evans, L., & Marler, P. (1993). On the meaning of alarm calls: functional reference in an avian vocal system. Animal Behaviour. https://doi.org/10.1006/anbe.1993.1158

Fernández-Juricic, E. (2012). Sensory basis of vigilance behavior in birds: Synthesis and future prospects. Behavioural Processes, 89(2), 143–152. https://doi.org/10.1016/j.beproc.2011.10.006

Fichtel, C., & Van Schaik, C. P. (2006). Semantic differences in sifaka (Propithecus verreauxi) alarm calls: A reflection of genetic or cultural variants? Ethology, 112(9), 839–849. https://doi.org/10.1111/j. 1439-0310.2006.01239.x

Flower, T. P., Gribble, M., & Ridley, A. R. (2014). Deception by Flexible Alarm Mimicry in an African Bird. Science, 344(6183), 513 LP–516. https://doi.org/10.1126/science.1249723

Foster, W. A., & Treherne, J. E. (1981). Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. Nature, 293(5832), 466–467. https://doi.org/10.1038/293466a0

Gallego-Abenza, M., Loretto, M.-C., & Bugnyar, T. (2020). Decision time modulates social foraging success in wild common ravens , Corvus corax. Ethology, (126), 413–422. https://doi.org/10.1111/eth.12986

Gill, S. A., & Bierema, A. M. K. (2013). On the Meaning of Alarm Calls: A Review of Functional Reference in Avian Alarm Calling. Ethology, 119(6), 449–461. https://doi.org/10.1111/eth.12097

Graw, B., & Manser, M. B. (2007). The function of mobbing in cooperative meerkats. Animal Behaviour, 74(3). https://doi.org/10.1016/j.anbehav.2006.11.021

Griesser, M. (2008). Referential Calls Signal Predator Behavior in a Group-Living Bird Species. Current Biology, 18(1), 69–73. https://doi.org/10.1016/j.cub.2007.11.069

Griesser, M. (2013). Do warning calls boost survival of signal recipients? Evidence from a field experiment in a group-living bird species. Frontiers in Zoology, 10(1), 1. https://doi.org/10.1186/1742-9994-10-49

Griesser, M., & Ekman, J. (2004). Nepotistic alarm calling in the Siberian jay, Perisoreus infaustus. Animal Behaviour, 67(5), 933–939. https://doi.org/10.1016/j.anbehav.2003.09.005

Griesser, M., & Ekman, J. (2005). Nepotistic mobbing behaviour in the Siberian jay, Perisoreus infaustus. Animal Behaviour, 69(2), 345– 352. https://doi.org/10.1016/j.anbehav.2004.05.013

Guillemain, M., Duncan, P., & Fritz, H. (2001). Switching to a feeding method that obstructs vision increases head-up vigilance in dabbling ducks. Journal of Avian Biology, 32(4), 345–350. https://doi.org/10. 1111/j.0908-8857.2001.320409.x

Hare, J. F. (1998). Juvenile Richardson's ground squirrels, Spermophilus richardsonii, discriminate among individual alarm callers. Animal Behaviour, 55(2), 451—460. https://doi.org/10.1006/anbe.1997.

0613

Hare, J. F., & Atkins, B. A. (2001). The squirrel that cried wolf: Reliability detection by juvenile Richardson's ground squirrels (Spermophilus richardsonii). Behavioral Ecology and Sociobiology, 51(1), 108–112. https://doi.org/10.1007/ s002650100414

Hauser, M. D. (1996). The evolution of communication. The MIT Press.

Cambridge, MA, US: The MIT Press.

Heinrich, B., & Marzluff, J. (1995). Why ravens share. American Scientist, 83(4), 342–349. Retrieved December 16, 2020, from http://www.jstor.org/stable/29775481

Heinrich, B., & Pepper, J. W. (1998). Influence of competitors on caching behaviour in the common raven, Corvus corax. Animal Behaviour, 56(5), 1083–1090. https://doi.org/10.1006/anbe.1998.0906

Heinrich, Bernd. (1989). Ravens in Winter. (Summit Books of Simon & Schuster, Ed.) (New York). Vintage Books. Retrieved from https:// books.google.at/books?id=YbWtadkEVvUC

Kalb, N., Anger, F., & Randler, C. (2019). Subtle variations in mobbing calls are predator-specific in great tits (Parus major). Scientific Reports, 9(1), 1–7. https://doi.org/10.1038/s41598-019-43087-9

Kotler, B. P., Blaustein, L., & Brown, J. S. (1992). Predator facilitation: the combined effect of snakes and owls on the foraging behavior of gerbils. Annales Zoologici Fennici.

Krams, I., Krama, T., Igaune, K., & Mänd, R. (2008). Experimental evidence of reciprocal altruism in the pied flycatcher. Behavioral Ecology and Sociobiology, 62(4), 599–605. https://doi.org/10. 1007/s00265-007-0484-1

Lambert, M. L., Jacobs, I., Osvath, M., & Von Bayern, A. M. P. (2019). Birds of a feather? Parrot and corvid cognition compared. Behaviour, 156(5–8), 505–594. https://doi.org/10.1163/1568539X

- 00003527

Leavesley, A. J., & Magrath, R. D. (2005). Communicating about danger: Urgency alarm calling in a bird. Animal Behaviour, 70(2), 365–373. https://doi.org/10.1016/j.anbehav.2004.10.017

Lohrey, A. K., Clark, D. L., Gordon, S. D., & Uetz, G. W. (2009). Antipredator responses of wolf spiders (Araneae: Lycosidae) to sen- sory cues representing an avian predator. Animal Behaviour, 77(4), 813–821. https://doi.org/10.1016/j.anbehav.2008.12.025

Loretto, M.-C., Schuster, R., & Bugnyar, T. (2016). GPS tracking of non- breeding ravens reveals the importance of anthropogenic food sources during their dispersal in the Eastern Alps. Current Zoology, 62(4), 337–344. https://doi.org/10.1093/cz/zow016

Loretto, M.-C., Schuster, R., Itty, C., Marchand, P., Genero, F., & Bugnyar, T. (2017). Fission-fusion dynamics over large distances in raven non-breeders. Scientific Reports, 7(1), 380. Retrieved from https://doi.org/10.1038/s41598-017-00404-4

Magrath, R. D., Pitcher, B. J., & Gardner, J. L. (2009). Recognition of other species' aerial alarm calls: speaking the same language or learning another? Proceedings. Biological Sciences / The Royal Society, 276(February), 769–774. https://doi.org/10.1098/rspb. 2008.1368

Marler, P. (2004). Bird Calls: Their Potential for Behavioral Neurobiology. Annals of the New York Academy of Sciences, 1016(1), 31–44. https://doi.org/10.1196/annals.1298.034

Munn, C. A. (1986). Birds that 'cry wolf.' Nature, 319(6049), 143–145. https://doi.org/10.1038/319143a0

Nácarová, J., Veselý, P., & Bugnyar, T. (2018). Ravens adjust their antipredatory responses to con- and specific alarms to the perceived threat. Ethology, (May), 1–8. https://doi.org/10.1111/eth.12764

Parker, P. G., Waite, T. A., Heinrich, B., & Marzluff, J. M. (1994). Do common ravens share ephemeral food resources with kin? DNA fingerprinting evidence. Animal Behaviour, 48(5), 1085–1093. https://doi.org/10.1006/anbe.1994.1342

Pepperberg, I. M. (1983). Cognition in the African Grey parrot: Preliminary evidence for auditory/vocal comprehension of the class concept. Animal Learning & Behavior, 11(2), 179–185. https://doi. org/10.3758/BF03199646

Pepperberg, I. M. (1990). Cognition in an African gray parrot (Psittacus erithacus): Further evidence for comprehension of categories and labels. Journal of Comparative Psychology, 104(1), 41–52. https:// doi.org/10.1037/0735-7036.104.1.41

Pepperberg, I. M. (1999). The Alex Studies. Harvard University Press. https://doi.org/10.2307/j.ctvk12qc1

Pepperberg, I. M. (2002). Cognitive and communicative abilities of grey parrots. Current Directions in Psychological Science, 11(3), 83–87. https://doi.org/10.1111/1467-8721.00174

Pepperberg, I. M. (2008). Peer-reviewed parrot studies speak for themselves, as he did. Nature, 456(7219), 166. https://doi.org/10.1038/ 456166a

R Development Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Ramakrishnan, U., & Coss, R. G. (2000). Age differences in the responses to adult and juvenile alarm calls by bonnet macaques (Macaca radiata). Ethology, 106(2), 131–144. https://doi.org/10. 1046/j.1439-0310.2000.00501.x

Rendall, D., Owren, M. J., & Ryan, M. J. (2009). What do animal signals mean? Animal Behaviour, 78(2), 233–240. https://doi.org/10.1016/ j.anbehav.2009.06.007

Scarpignato, A. L., & George, T. L. (2011). Home range and habitat use of breeding common ravens in Redwood National and State Parks. Searle, S. R., Speed, F. M., & Milliken, G. A. (1980). Population Marginal Means in the Linear Model: An Alternative to Least

Squares Means. The American Statistician, 34(4), 216–221. https://doi.org/10.1080/00031305.1980.10483031

Seyfarth, R. M., & Cheney, D. L. (1986). Vocal development in vervet monkeys. Animal Behaviour, 34(6), 1640–1658. https://doi.org/10. 1016/S0003-3472(86)80252-4

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Vervet monkey alarm calls: Semantic communication in a free-ranging primate. Animal Behaviour, 28(4), 1070–1094. https://doi.org/10.1016/ S0003-3472(80)80097-2

Shedd, D. (1982). Seasonal Variation and Function of Mobbing and Related Antipredator Behaviors of the American Robin (Turdus migratorius). The Auk: Ornithological Advances, 99(2), 342–346. https://doi.org/10.1093/auk/99.2.342

Shields, W. M. (1984). Barn swallow mobbing: Self-defence, collateral kin defence, group defence, or parental care? Animal Behaviour, 32(1), 132–148. https://doi.org/10.1016/S0003-3472(84)80331-0

Sloan, J. L., & Hare, J. F. (2008). The More the Scarier: Adult Richardson's Ground Squirrels (Spermophilus richardsonii) Assess Response Urgency Via the Number of Alarm Signallers. Ethology, 114(5), 436–443. https://doi.org/10.1111/j.1439-0310.2008.01479.

Smith, J. M. (1965). The evolution of alarm calls. The American Naturalist, 99(904), 59–63. Retrieved from http://www.jstor.org/ stable/2459256

Suzuki, T. N. (2011). Parental alarm calls warn nestlings about different predatory threats. Current Biology, 21(1), R15–R16. https://doi.org/ 10.1016/j.cub.2010.11.027

Suzuki, T. N. (2012). Referential mobbing calls elicit different predator-searching behaviours in Japanese great tits. Animal Behaviour, 84(1), 53– 57. https://doi.org/10.1016/j.anbehav.2012.03.030

Suzuki, T. N. (2014). Communication about predator type by a bird using discrete, graded and combinatorial variation in alarm calls. Animal Behaviour, 87, 59–65. https://doi.org/10.1016/j.anbehav.2013.10.009

Suzuki, T. N., Wheatcroft, D., & Griesser, M. (2016). Experimental evidence for compositional syntax in bird calls. Nature Communications, 7, 1–7. https://doi.org/10.1038/ncomms10986

Swan, D. C., & Hare, J. F. (2008). Signaler and Receiver Ages Do Not Affect Responses to Richardson's Ground Squirrel Alarm Calls. Journal of Mammalogy, 89(4), 889–894. https://doi.org/10.1644/07-mamm-a-228.1

Szipl, G., Ringler, E., & Bugnyar, T. (2018). Attacked ravens flexibly adjust signalling behaviour according to audience composition. Proceedings of the Royal Society B, 285(June). https://doi.org/10.1098/rspb.2018.0375

Szipl, G., Ringler, E., Spreafico, M., & Bugnyar, T. (2017). Calls during agonistic interactions vary with arousal and raise audience attention in ravens. Frontiers in Zoology, 14(1). https://doi.org/10.1186/ s12983-017-0244-7

Tibbetts, E. A., & Dale, J. (2007). Individual recognition: it is good to be different. Trends in Ecology and Evolution, 22(10), 529–537. https://doi.org/10.1016/j.tree.2007.09.001

Tornick, J. K., Callahan, E. S., & Gibson, B. M. (2015). An investigation of quantity discrimination in Clark's nutcrackers (Nucifraga columbiana). Journal of Comparative Psychology. Tornick, Jan K.: Department of Psychology, University of New Hampshire, 10 Library Way, Durham, NH, US, 03824, j.tornick@unh.edu: American Psychological Association. https://doi.org/10.1037/ a0037863

Townsend, S. W., Rasmussen, M., Clutton-Brock, T., & Manser, M. B. (2012). Flexible alarm calling in meerkats: The role of the social environment and predation urgency. Behavioral Ecology, 23(6), 1360–1364. https://doi.org/10.1093/beheco/ars129

Uchida, K., Suzuki, K., Shimamoto, T., Yanagawa, H., & Koizumi, I. (2016). Seasonal variation of flight initiation distance in Eurasian red squirrels in urban versus rural habitat. Journal of Zoology, 298(3), 225–231. https://doi.org/10.1111/jzo.12306

Webb, W. C., Boarman, W. I., & Rotenberry, J. T. (2004). Common Raven Juvenile Survival in a Human-Augmented Landscape. The Condor, 106(3), 517–528. https://doi.org/10.1093/condor/106.3.517

Wheatcroft, D., Gallego-Abenza, M., & Qvarnström, A. (2016). Species replacement reduces community participation in avian antipredator groups. Behavioral Ecology, 00, arw074. https://doi.org/10.1093/beheco/arw074

Wheatcroft, D., & Price, T. D. (2008). Reciprocal cooperation in avian mobbing: playing nice pays. Trends in Ecology and Evolution, 23(8), 416–419. https://doi.org/10.1016/j.tree.2008.04.011

Woods, R. D., Kings, M., McIvor, G. E., & Thornton, A. (2018). Caller characteristics influence recruitment to collective anti-predator events in jackdaws. Scientific Reports, 8(1), 1–8. https://doi.org/10.1038/s41598-018-25793-y

Zuberbühler, K., Noë, R., & Seyfarth, R. M. (1997). Diana monkey long-distance calls: Messages for conspecifics and predators. Animal Behaviour, 53(3), 589–604. https://doi.org/10.1006/anbe.1996.0334

Chapter 3

Individual movement dynamics do not correlate with attentive responses towards acoustic social cues in common ravens, *Corvus corax*

This chapter is in preparation to be submitted in a peer-reviewed journal

Abstract

In hierarchical groups, individuals use social information regarding hierarchy in order to thrive by either competing or cooperating with different group members. Such information acquisition can be acquired by either interacting with group members or from observing others´ interactions, i.e. using the so-called transitive inference. The latter form prevents from physical harassment but it may require finer-tuned cognitive abilities to process the interaction outcome and mentally represent a hierarchy. As a result of phenotypic variation, inter-individual differences in social information acquisition can raise within a social group. Such differences might reflect individual connectedness within the group or individual dynamics when living in open groups. Non-breeder common ravens form foraging groups characterized by fission-fusion dynamics where they socialize and establish dominance hierarchies despite the open character of the groups. When housed in separate groups, ravens are capable to notice rank reversal of neighbouring group, indicating fine-tuned socio-cognitive skills. In this study, we investigated the attentive responses of wild ravens towards acoustic cues mimicking a conspecific social interaction and territorial calls given mostly by dominant individuals. Since highly vagrant individuals encounter a larger number of unfamiliar conspecifics differing in rank status across different foraging groups. We predicted to show a greater attentive responses to acoustic social cues, in particular defensive calls. We used GPS transmitters to assess individual vagrancy pattern by measuring averaged daily distance and number of visited groups during the first month post-release period. Interestingly, no correlation was found between the two variables, we discuss alternative reasons that could help to understand our results. To the best of our knowledge, little is known about what triggers individual decisions to show high vagrant patterns in common ravens. Future studies should address what causes individual decisions to leave a social group and get integrated in another.

Introduction

As suggested by the social intelligent hypothesis, being part of a structured social group demands fine-tuned socio-cognitive abilities to monitor conspecifics´ identities and track their relationships (Byrne & Whiten, 1989; Humphrey, 1976). A hierarchical society is maintained by dyadic interactions between its members and the valence of these interactions´ outcomes (dominant and subordinate identities) (Hinde, 1976). Each group member can acquire such social information directly, by getting involved in an agonistic interaction with one or several group members or indirectly, by attending others´ interactions (Dall et al., 2005). The latter form is referred to as using bystander information and linked to the concept of eavesdropping (Bonnie & Earley, 2007; Danchin et al., 2004). Compared to direct information acquisition through individual trial-and-error learning, using bystander information may save time and avoid potential injuries; however, it may require the cognitive abilities to make inferences about others´ relationships based on indirect evidence. There is cumulating evidence that various taxonomic groups are capable of transitively inferring rank relationships, i.e. using bystander information to predict own rank (Grosenick et al., 2007; Mikolasch et al., 2013; Paz-y-Miño C et al., 2004; Weiß et al., 2010) and understanding third-party relationships, i.e. representation of others´ (rank) relationships (Borgeaud et al., 2013; Cheney & Seyfarth, 1986; Massen, Pašukonis, et al., 2014; Silk, 1999).

The complexity of a species´ social group may foster the development of inter-individual variation in socio-cognitive abilities (Aureli & Schino, 2019; Fischer et al., 2017), whereby distinct phenotypes may arise due to individually distinct genetic, developmental and/or environmental processes. As a result, individuals may vary in their social competence, as well as their predisposition to interact with others (Taborsky & Oliveira, 2012). A key component of social complexity is the number of potential interaction partners, which is typically reflected in group size (Dunbar, 1992; Dunbar & Shultz, 2007) but also in the spatio-temporal dynamics of group composition (Aureli et al., 2008). In systems with regular sub-groups formation (fission-fusion dynamics, Kummer, 1971), the group members´ decisions to stay in their (sub)group or join others ultimately determine the level of group cohesion (Aureli & Schino, 2019). Little is known about what determines these decisions on an individual basis. One possibility is that the decision is associated with the individuals´ socio-cognitive abilities and the way they interpret their social environment. Hints in this direction come from field studies on non-human primates that investigated social monitoring patterns, focusing on the subjects´ attentive responses such as gaze following or head orientation (see review Johnson & Karin-D'Arcy, 2006; McNelis & Boatright-Horowitz, 1998). To the best of our knowledge, no experimental studies has investigated i) whether such differentiated attention patterns to social cues can be found in a system with high degrees of fission-fusion dynamics and ii) whether it is correlated with individual movement dynamics.

The social life of common ravens features a fluid dynamic system, particularly in the non-breeder state. After fledging, young ravens remain in the parental territory for several weeks until they join non-breeder groups, primary for foraging reasons (Heinrich, 1988). At foraging sites, juveniles come to interact with non-related conspecifics of several age classes: adults (> 4 y.o.), subadults (1-3 y.o.) and juveniles (< 1 y.o.). The open character of these groups, where both composition and size change over time, does not hinder individuals from forming social bonds and establishing a hierarchy (Boucherie et al., 2022; Braun & Bugnyar, 2012). Moreover, although individuals differ substantially in vagrancy, they may repeatedly encounter each other at particular foraging sites (Loretto et al., 2017). Playback experiments in captivity (Boeckle & Bugnyar, 2012; Massen, Pašukonis, et al., 2014) and observations of third-party interventions in the field (Massen, Szipl, et al., 2014) indicate that ravens´ social behaviour may be based on sophisticated social knowledge, i.e. birds recognize and remember their relationship valence to group members and are capable of representing third-party relationships. However, these studies have been conducted on ravens that were confronted with a limited number of individuals (captivity) or with the same free-ranging individuals over time (i.e. wild birds with a preference for a particular foraging site). Little is known about social information use when ravens encounter unfamiliar individuals at different foraging sites, as it is typical for young and/or highly vagrant birds. The lack of experimental evidence that determines whether the distinct phenotypes regarding presence patterns correlates with socio-cognitive abilities in the wild makes non-breeder common ravens a suitable candidate to investigate such correlation.

Here we tested the attention of wild ravens to simulated encounters with unfamiliar conspecifics in a playback design. We used two distinct and well-described calls for playbacks: defensive calls and territorial calls. Defensive calls are given by the victim of aggression during an agonistic interaction and primarily serve to appease the aggressor (Heinrich et al., 1993; Szipl et al., 2018); hence, these calls might be used from bystander ravens as a source of information to assess dominance relationships and aspects of the current hierarchy in a given foraging group. Territorial calls, on the other hand, are typically given by settled pair-bonded individuals defending a territory and likely function to regulate distances between neighbours and fend off trespassing non-breeders in search for food; these calls might thus be used by receivers to decide which places to avoid. In a second step, we examined how much our test subjects varied in their degree of vagrancy, i.e. how many foraging sites they visited within the following month post-release. We hypothesized that highly vagrant ravens would be more used to encounter unfamiliar individual in foraging groups and thus should more readily pick up on social cues provided in the played back calls than local ravens that regularly meet at the same time and rarely encounter unfamiliar birds. More specifically, we predicted vagrant birds to pay attention to defensive calls, as those might give an indication of the dominance status of unfamiliar birds. Local ravens, in contrast, may pay more attention to territorial calls, as those might indicate a potentially new territory owner within a foraging site.

Materials and methods

Subjects and playback experiments

This survey was part of the long-term data collection conducted on a non-breeder raven population located in the Austrian Alps. Since 2007, our team has been catching and marking ravens for individual identification. Tagged birds are subjected to observations at the Cumberland Wildpark, where ravens snatch food from wild boars and wolves enclosures in a varying number of 15 (summer) to 120 individuals (winter). Apart from marking, we genetically determine sex and estimate age class based on blood analysis and mouth and feather coloration (Heinrich, 1994; Heinrich & Marzluff, 1992). On a daily basis, we collect data on individuals´ presence at the foraging sites as well as their agonistic and affiliate interactions during and outside foraging. Based on these data, we could show that sexually immature ravens exchange affiliative interactions with non-kin peers of same and different sex; individuals present at our study site may thus form social bonds (Braun & Bugnyar, 2012). With the help of GPS transmitters, we could also show that our ravens encounter former group members at different foraging sites, even over a relatively large spatial scale (Loretto et al., 2017).

Between September 2018 and December 2019, we trapped 30 newly marked and 4 captive-bred released ravens in our study site (Table 1). After the marking procedure and equipped with GPS-tags, each bird was transferred to an experimental aviary (2 m3) (Figure 1) where it stayed overnight before it got tested with the playback stimuli on the following morning. Experimental aviaries were located outdoor in a non-public area of the Cumberland Wildpark, Grünau im Almtal, Austria. Ravens were provided with food and water ad libitum. The playback files were composed of: two territorial calls and two defensive calls. To ensure unfamiliarity with the stimuli, territorial calls were downloaded through an open-access database of avian vocalizations (www.xenocanto.com; XC310460, XC322755, XC197025, Netherlands; XC374527, XC289859, XC449092, Sweden) whereas defensive calls came from 4 different individuals from a captive group of ravens located at c.a. 200 km from the study site in the Alps and from two wild ravens from a foraging group of non-breeders in Italy; 190 km apart from our study site. Each tested individual was exposed to the two call types separated by 15-minutes silence gap and at identical volume; 64 dB at 2 m, calibrated using a digital sound level meter (RadioShack model 3300099, A weighting). The order of the treatment was randomized across tested individuals. The experimental aviary had two parallel perches, perpendicular to the back wall which was blinded using a plastic sheet with two peepholes (2 cm2). Broadcasting sounds came always from behind the blinded side and ravens could use the peepholes to look through. The experimenter mounted a GoPro camera on a fix-positioned tripod right before the experiment.

Response to playback was scored as the total duration of looks towards the blind wall (measured as total duration when the bird looks at the sound source pointing it with their bill) during the first minute right after playing back the calls. We also scored the same behaviours during the minute prior to playing occurred, named "baseline" measurements. In order to model the response, we used delta values for each behaviour, calculated by subtracting the baseline to the response measurements. Videos were coded with Solomon Coder beta 11.07.04 (Copyright by András Péter; http://solomoncoder.com) by MGA.

Vagrancy analysis

Ravens we tagged with a backpack-style, solar-powered GPS-transmitters (OrniTrack-25, Ornitela UAB, Lithuania; https://www.ornitela.com/25g-transmitter), these weighed 25g and never exceeded 3% of the bird´s bodyweight. We assessed the vagrancy pattern of each bird over the following 31 days after being tested and released. First, we subsampled the GPS points to every 3 hours to get a similar number of GPS fixes per individual and day. Distance between fixed positions was calculated and averaged per day. Then, we calculated average of mean daily travelled distance to describe the vagrancy pattern. Kernel area was also calculated for each raven using the function "kernelUD" (95% estimation) within the R package `adehabitatHR´ (Calenge, 2006), and in addition, we plotted each individual´s track on Google Earth to visually identify and count all distinct foraging groups (separated by at least 10 km) that were visited by each subject. We used the Shannon Index as a proxy for revisiting different foraging groups. The Shannon index, normally used for biodiversity estimations, results from the combination of number of individuals encountered in each found species at a certain location. Instead, we included the number of days spent at each of the visited foraging group, resulting in an individual value ranging between 0 and 1, similar to the biodiversity assessment for each studied location.

Statistical analyses

We used the statistical software R (R Core Team, 2017) to conduct the analyses. We used the function `lmer´ contained in the package "lme4" (Bates et al., 2015). Delta values for each behaviour were calculated by subtracting the 1 min-baseline to the 1 min-response period. In order to reduce the number of explanatory variables containing vagrancy information, we conducted a correlation test which showed high correlation between variables. Thus, we only used "Mean daily distance" and "Shannon Index" as explanatory variables. Regarding behavioural responses, we modelled "Head towards the speaker" being a so-called variable response: "Attention". Since the variable "Attention" (continuous) did not commit the parametric parameters, we transformed into a discrete variable by simply multiplying by 10. We did run the function "descdist" within the package `fitdistrplus´ (Delignette-Muller & Dutang, 2015) to estimate the better distribution of the new variable, resulting in "negative bimomial". We used the function "glmmTMB" to run the models, family "nbinom2", package `glmmTMB´ (Brooks et al., 2017). The full model contained “age class”, “treatment”, “mean of daily travelled distance” and “Shannon index” as fixed effects, whereas “individual” and “playback file” were included as random factors.

Table 1. Table containing information regarding sex, age-class and origin of the tested ravens. Season in which they were tested is also provided.

Individual	Sex	Age class	Season	Origin
Napoleon	Female	Juvenile	Winter	Wild-caught
Escher	Female	Juvenile	Winter	Wild-caught
Reese	Female	Subadult	Autumn	Wild-caught
Coqui	Female	Adult	Autumn	Wild-caught
Unesco	Female	Juvenile	Autumn	Wild-caught
Clove	Male	Subadult	Autumn	Captive-bred released
Hickory	Female	Juvenile	Autumn	Captive-bred released
Rollo	Male	Subadult	Autumn	Captive-bred released
Hektor	Female	Adult	Autumn	Wild-caught
Jojoba	Female	Juvenile	Autumn	Wild-caught
Loco	Female	Juvenile	Autumn	Wild-caught
Dessert	Female	Juvenile	Spring	Wild-caught
Default	Female	Juvenile	Autumn	Wild-caught
Clara	Female	Juvenile	Autumn	Wild-caught
Cava	Male	Juvenile	Autumn	Wild-caught
Caspian	Male	Juvenile	Autumn	Wild-caught
Bababa	Male	Juvenile	Autumn	Wild-caught
Fabio	Female	Juvenile	Autumn	Wild-caught
Lava	Female	Juvenile	Winter	Wild-caught
Verena	Female	Juvenile	Winter	Wild-caught
Tweety	Female	Juvenile	Winter	Wild-caught
Uber	Female	Subadult	Spring	Wild-caught
Farewell	Male	Juvenile	Autumn	Wild-caught
Gwen	Female	Juvenile	Autumn	Wild-caught
Archaox	Female	Subadult	Spring	Wild-caught
Junior	Female	Juvenile	Autumn	Wild-caught
Gizla	Female	Subadult	Spring	Wild-caught
Taco	Male	Subadult	Spring	Wild-caught
Mumbo	Male	Juvenile	Winter	Wild-caught
Etienne	Male	Juvenile	Autumn	Wild-caught
Lbujcia	Male	Juvenile	Spring	Wild-caught

Alfonds	Male	Juvenile	Spring	Wild-caught
Aj	Male	Juvenile	Winter	Wild-caught
Dandelion	Female	Subadult	Summer	Captive-bred released

Results

Results revealed positive delta measurements for attention in 47% of the tested ravens. Regarding vagrancy patterns, we found a strong inter-individual variation in both mean of daily travelled distance (range=0.17-103km, mean=19.78km) and number of foraging groups visited (range=1-5, mean=2.4 foraging sites). However, based on our model results we could not confirm our hypothesis that individual vagrancy values (either daily travelled distance or Shannon Index) and has an effect on the attentive responses observed to the played back calls. Interactions with either sex or age class were neither relevant to explain ravens´ attention responses. Although in the full model Shannon index seemed to almost significantly affect "attention", the comparison against null model (ΔAIC > 6) invalided any consideration of significance.

Table 2. Summary of the terms included in the full model explaining the number of seconds (discrete) devoted to look at the side where sounds came from.

Response	Explanatory	Estimate	SE	Z value	P
Attention	Intercept	4.68	0.37	12.43	< 2e-16***
	Treatment (territorial calls)	-0.13	0.15	-0.89	0.37
	Mean daily distance	-0.002	0.003	-0.62	0.54
	Age class (Juvenile)	-0.1	0.36	-0.27	0.78
	Age class (Subadult)	0.20	0.39	0.52	0.60
	Shannon Index	0.16	0.09	1.75	0.08

Table 3. Model comparison results.

	AIC	ΔAIC
Null model	747.0	
Full model	755.2	8.18

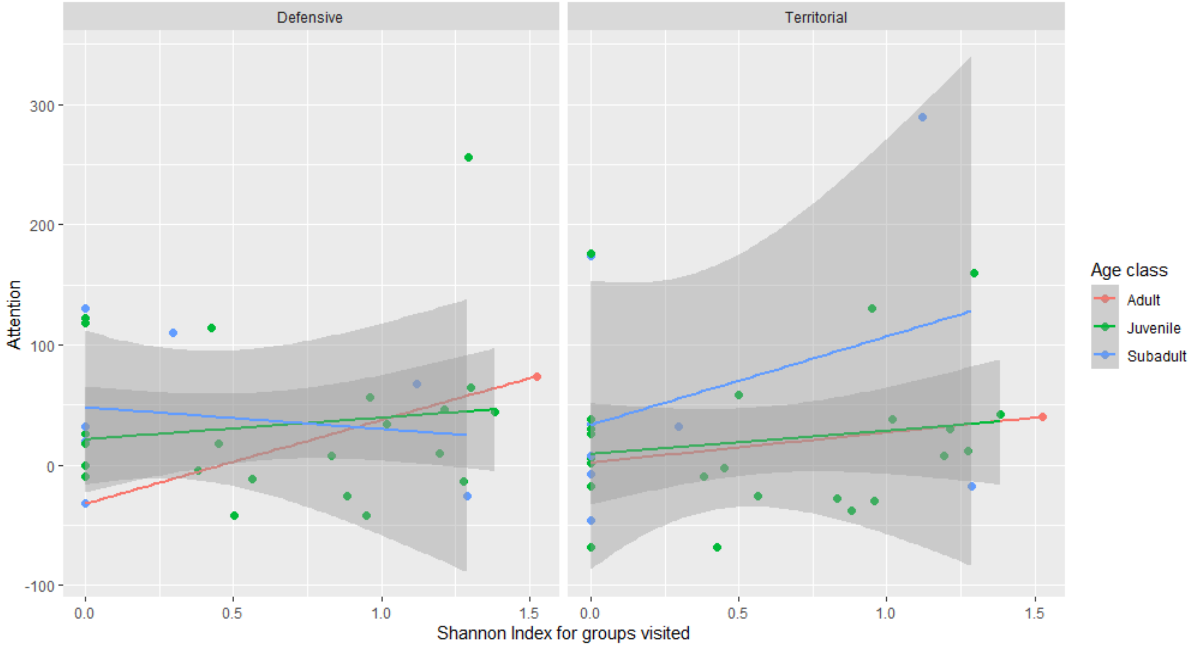


Fig. 2. Attentive responses of ravens using raw data towards the two distinct call types. We can see the Shannon Index as explanatory variable and responses are grouped by different age classes.

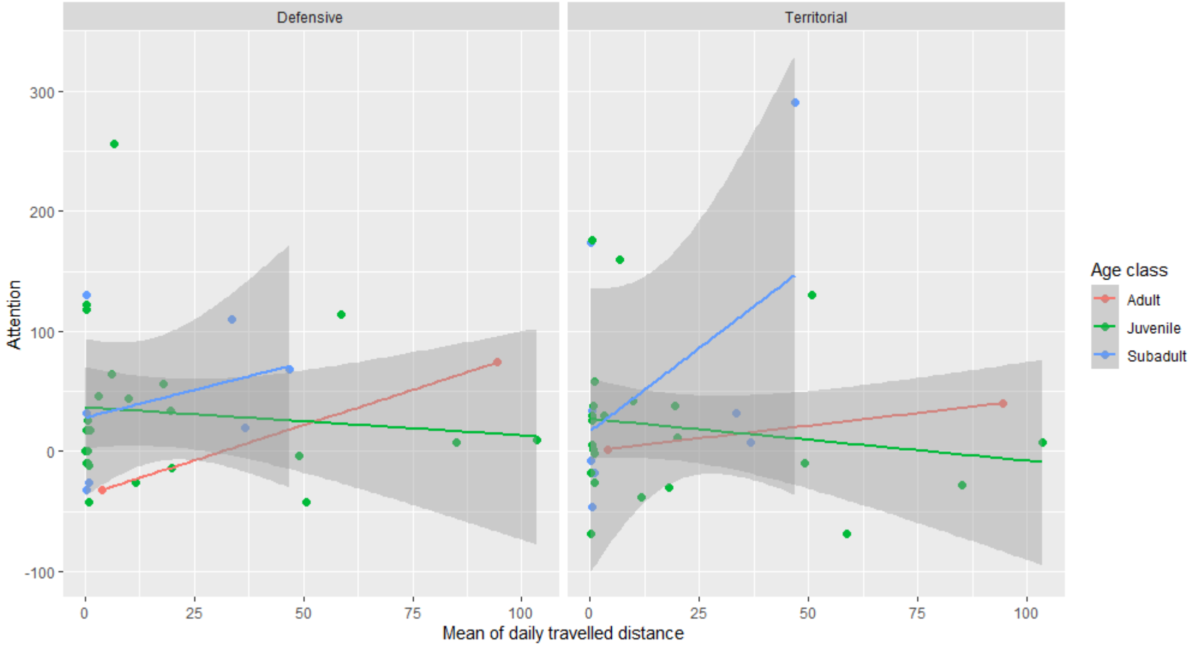


Fig. 3. Attentive responses of ravens using raw data towards the two distinct call types. Here, the mean of daily travelled distance is included as explanatory variable and responses are grouped by different age classes.

Discussion

In this study, we investigated the attentive responses of wild ravens towards played back calls signalling either the outcome of agonistic interactions (defensive calls) or the presence of dominant individuals (territorial calls). We then correlated the ravens´ responses to playbacks with their spatial movements in the following month, testing the predictions that i) ravens with extended vagrancy patterns were more attentive towards playbacks than those ravens that remained in the local foraging group and/or that ii) ravens with extended vagrancy patterns were specifically attentive to defensive calls, whereas local ravens were more attentive to territorial calls. The underlying hypothesis for these predictions was that highly vagrant individuals would be more used to encounter unfamiliar individuals in foraging groups and thus should more readily pick up on social information provided in the played back calls than local ravens that regularly meet at the same site and rarely encounter unfamiliar birds. However, our findings did not support these predictions.

What could be the reason for our negative results? First of all, we had a skewed sample size, as about two thirds of tested individuals (25 out of 34) were juveniles in their first year. This might have coincided with limited social experiences at the time of testing, i.e. most ravens simply had too little time to learn about their social environment and/or figure out the salience of different social cues. In fact, as most of the test subjects (30 out of 34) were individually marked right before testing, we were naïve about their previous social experience like how long they have been part of the local non-breeder group and whether or not they have close kin in this group. It is well known that individuals´ social behaviours are affected by the individuals´ early social environment such as family composition or group size at upbringing not only in ravens (Boucherie et al., 2020), but also in other birds (Farine et al., 2015), mammals (Branchi & Alleva, 2006; Sachser et al., 2013) and fish (Hesse & Thünken, 2014). Hence, it is likely that adding some information about the ravens´ social background would have enhanced the quality of our models. For getting such information, we would have had to mark ravens in the nest. However, this is not feasible in the Northen Alps, where ravens breed exclusively at hard to access cliffs. Nevertheless, in a parallel study we tested captive juvenile ravens with known upbringing history (raised by parents with one or more siblings) with playbacks of different social categories (sibling, familiar and unfamiliar non-kin). Similar to the present study, those young ravens did respond to played back calls but also had some problems in discriminating social categories (Gallego-Abenza et al. subm.). Taken together, these studies indicate that while our playback set-up seems to work, we need to take the socio-cognitive development within the ravens´ first year into account.

Another methodological point concerns the calculation of vagrancy patterns as proxy for fission-fusion dynamics. Notably, little is known about the minimum time period to estimate the individual vagrancy pattern of ravens. A smaller sample size of ravens (21 individuals) equipped with VHF transmitters provided enough evidence for inter-individual difference in space use at a fine scale after 12 months maximum of data collection (Loretto, Reimann, et al., 2016). Due to technical reasons, we fixed 31 days as data collection period because the uncertainty of GPS logger lifespan. For instance, three of the GPS loggers stopped sending fixes shortly after a month, whereas others stopped working approximately two months after being applied onto ravens. Our spatial analyses match the expectation of inter-individual pattern of anthropogenic food sources use. Such information had been extracted from a larger sample size of

81 ravens throughout a period of 2.75 years (Jain et al., 2022). This study used an average of 286 tracking days per individual and revealed a strong seasonal effect on vagrancy pattern, with ravens showing smaller ranging movements in spring and summer. In the present study, potential seasonal effect was not possible to assess due to our low sample size and short tracking period. Indeed, the season in which a raven was tested and released for GPS tracking might have influenced our spatial analyses. We thus claim for a further study in which long-term vagrancy pattern can be applied to explain attention responses to social cues using a substantially larger sample size.

Taking together, the current findings did not match our predictions, where we hypothesized that vagrant individuals would show higher level of attention to social interactions. This might suggest that either socio-cognitive abilities of ravens may not be reflected in attentive responses or that we failed in estimating vagrancy pattern underestimating the needed period. Further studies are needed to shed light on what triggers ravens´ decisions to either move across groups or stay in the single group during such extended immature period of life, including sometimes their adulthood.

REFERENCES

Amici, F., Aureli, F., & Call, J. (2008). Fission-Fusion Dynamics, Behavioral Flexibility, and Inhibitory Control in Primates. *Current Biology*, *18*(18), 1415–1419. https://doi.org/10.1016/j.cub.2008.08.020

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., Connor, R., Fiore, A. D., Dunbar, R. I. M., Henzi, S. P., Holekamp, K., Korstjens, A. H., Layton, R., Lee, P., Lehmann, J., Manson, J. H., Ramos-Fernandez, G., Strier, K. B., & Schaik, C. P. van. (2008). Fission-Fusion Dynamics. *Current Anthropology*, *49*(4), 627–654. https://doi.org/10.1086/586708

Aureli, F., & Schino, G. (2019). Social complexity from within: How individuals experience the structure and organization of their groups. *Behavioral Ecology and Sociobiology*, *73*(1). https://doi.org/10.1007/s00265-018-2604-5

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bernstein, I. S. (1981). Dominance: The baby and the bathwater. *Behavioral and Brain Sciences*, *4*(3), 419–429.

Boeckle, M., & Bugnyar, T. (2012). Long-term memory for affiliates in ravens. *Current Biology*, *22*(9), 801–806. https://doi.org/10.1016/j.cub.2012.03.023

Boeckle, M., Szipl, G., & Bugnyar, T. (2012). Who wants food? Individual characteristics in raven yells. *Animal Behaviour*, *84*(5), 1123–1130. https://doi.org/10.1016/j.anbehav.2012.08.011

Bonnie, K. E., & Earley, R. L. (2007). Expanding the scope for social information use. *Animal Behaviour*, *74*(2), 171–181. https://doi.org/10.1016/j.anbehav.2006.12.009

Boogert, N. J., Madden, J. R., Morand-Ferron, J., & Thornton, A. (2018). Measuring and understanding individual differences in cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1756), 20170280. https://doi.org/10.1098/rstb.2017.0280

Borgeaud, C., van de Waal, E., & Bshary, R. (2013). Third-Party Ranks Knowledge in Wild Vervet Monkeys (Chlorocebus aethiops pygerythrus). *PLoS ONE*, *8*(3), e58562. https://doi.org/10.1371/journal.pone.0058562

Boucherie, P. H., Blum, C. R., & Bugnyar, T. (2020). Effect of rearing style on the development of social behaviour in young ravens (Corvus corax). *Ethology*, *00*(March), 1–15. https://doi.org/10.1111/eth.13010

Boucherie, P. H., Gallego-Abenza, M., Massen, J. J. M., & Bugnyar, T. (2022). *Dominance in a socially dynamic setting: Hierarchical structure and conflict dynamics in ravens' foraging groups*. *377*(1845), 12. https://doi.org/10.1098/rstb.2020.0446

Boucherie, P. H., Loretto, M., Massen, J. J. M., & Bugnyar, T. (2019). *Lessons from ravens What constitutes social complexity and social intelligence in birds? Lessons from ravens*. *January*.

Branchi, I., & Alleva, E. (2006). Communal nesting, an early social enrichment, increases the adult anxiety-like response and shapes the role of social context in modulating the emotional behavior. *Behavioural Brain Research*, *172*(2), 299–306. https://doi.org/10.1016/j.bbr.2006.05.019

Braun, A., & Bugnyar, T. (2012). Social bonds and rank acquisition in raven nonbreeder aggregations. *Animal Behaviour*, *84*(6), 1507–1515. https://doi.org/10.1016/j.anbehav.2012.09.024

Braun, A., Walsdorff, T., Fraser, O. N., & Bugnyar, T. (2012). Socialized sub-groups in a temporary stable Raven flock? *Journal of Ornithology*, *153*(SUPPL. 1), 97–104. https://doi.org/10.1007/s10336-011-0810-2

Brooks, M. E., Kristensen, K., Benthem, K. J. van, Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., & Bolker, B. M. (2017). GlmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, *9*(2), 378–400.

Bugnyar, T., & Heinrich, B. (2006). Pilfering ravens, Corvus corax, adjust their behaviour to social context and identity of competitors. *Animal Cognition*, *9*(4), 369–376. https://doi.org/10.1007/s10071-006-0035-6

Bugnyar, T., & Kotrschal, K. (1997). *An experimental analysis of social foraging in ravens: Individual tactics, scrounging, and deception*. *32*, 497.

Bugnyar, T., & Kotrschal, K. (2001). Movement coordination and signalling in ravens (corvus corax): An experimental field study. *Acta Ethologica*, *3*(2), 101–109. https://doi.org/10.1007/s102110000029

Byrne, R. W., & Corp, N. (2004). Neocortex size predicts deception rate in primates. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(1549), 1693–1699. https://doi.org/10.1098/rspb.2004.2780

Byrne, R. W., & Whiten, A. (1989). *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans (Oxford Science Publications)*. {Oxford University Press, USA}.

Calenge, C. (2006). The package adehabitat for the R software: Tool for the analysis of space and habitat use by animals. *Ecological Modelling*, *197*, 1035.

Chance, M. R. A. (1967). Attention Structure as the Basis of Primate Rank Orders. *Man*, *2*(4), 503–518. JSTOR. https://doi.org/10.2307/2799336

Cheney, D. L., & Seyfarth, R. M. (1986). The recognition of social alliances by vervet monkeys. *Animal Behaviour*, *34*(6), 1722–1731. https://doi.org/10.1016/S0003-3472(86)80259-7

Connor, R., Wells, R., Mann, J., & Read, A. J. (2000). *The bottlenose dolphin, Tursiops sp.: Social relationships in a fission-fusion society.* (Whitehead H, pp. 91–126). The University of Chicago Press.

Connor, R., & Whitehead, H. (2005). Alliances II. Rates of encounter during resource utilization: A general model of intrasexual alliance formation in fission–fusion societies. *Animal Behaviour*, *69*(1), 127–132. https://doi.org/10.1016/j.anbehav.2004.02.022

Coombs, F. (1978). *The crows: A study of the corvids of Europe*. BT Batsford Limited.

Crailsheim, D., Stüger, H. P., Kalcher-Sommersguter, E., & Llorente, M. (2020). Early life experience and alterations of group composition shape the social grooming networks of former pet and entertainment chimpanzees (Pan troglodytes). *PLoS ONE*, *15*(1), 1–26. https://doi.org/10.1371/journal.pone.0226947

Crick, N. R., & Dodge, K. A. (1994). A review and reformulation of social information-processing mechanisms in children’s social adjustment. *Psychological Bulletin*, *115*(1), 74–101. https://doi.org/10.1037/0033-2909.115.1.74

Dall, S. R. X., Giraldeau, L. A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology and Evolution*, *20*(4), 187–193. https://doi.org/10.1016/j.tree.2005.01.010

Danchin, É., Giraldeau, L.-A., Valone, T. J., & Wagner, R. H. (2004). Public Information: From Nosy Neighbors to Cultural Evolution. *Science*, *305*(5683), 487–491. https://doi.org/10.1126/science.1098254

Delignette-Muller, M. L., & Dutang, C. (2015). fitdistrplus: An R Package for Fitting Distributions. *Journal of Statistical Software*, *64*(4), 1–34. https://doi.org/10.18637/jss.v064.i04

Dunbar, R. I. M. (1992). Neocortex size as a constraint on group size in primates. *Journal of Human Evolution*, *22*(6), 469–493. https://doi.org/10.1016/0047-2484(92)90081-J

Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology: Issues, News, and Reviews*, *6*(5), 178–190. https://doi.org/10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.0.CO;2-8

Dunbar, R. I. M., & Shultz, S. (2007). Evolution in the Social Brain. *Science*, *317*(5843), 1344–1347. https://doi.org/10.1126/science.1145463

Farine, D. R., Spencer, K. A., & Boogert, N. J. (2015). Early-life stress triggers juvenile zebra finches to switch social learning strategies. *Current Biology*, *25*(16), 2184–2188. https://doi.org/10.1016/j.cub.2015.06.071

Fischer, J., Farnworth, M. S., Sennhenn-Reulen, H., & Hammerschmidt, K. (2017). Quantifying social complexity. *Animal Behaviour*, *130*, 57–66. https://doi.org/10.1016/J.ANBEHAV.2017.06.003

Fraser, O. N., & Bugnyar, T. (2010). The quality of social relationships in ravens. *Animal Behaviour*, *79*(4), 927–933. https://doi.org/10.1016/j.anbehav.2010.01.008

Grosenick, L., Clement, T. S., & Fernald, R. D. (2007). Fish can infer social rank by observation alone. *Nature*, *445*(7126), 429–432. https://doi.org/10.1038/nature05511

Gwinner, E. (1964). Untersuchungen über das ausdrucks- und sozialverhalten des kolkraben (Corvus corax). Z. *Tierpsychol*, *21*, 145–178.

Healy, S., Dekort, S., & Clayton, N. (2005). The hippocampus, spatial memory and food hoarding: A puzzle revisited. *Trends in Ecology & Evolution*, *20*(1), 17–22. https://doi.org/10.1016/j.tree.2004.10.006

Heinrich, B. (1988). Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by the raven, Corvus corax. *Behavioral Ecology and Sociobiology*, *23*(3), 141–156. https://doi.org/10.1007/BF00300349

Heinrich, B. (1989). *Ravens in Winter* (Summit Books of Simon & Schuster, Ed.). Vintage Books. https://books.google.at/books?id=YbWtadkEVvUC

Heinrich, B. (1994). Dominance and weight changes in the common raven, Corvus corax. *Animal Behaviour*, *48*(6), 1463–1465. https://doi.org/10.1006/anbe.1994.1384

Heinrich, B., & Marzluff, J. (1992). Age and Mouth Color in Common Ravens. *The Condor*, *94*(2), 549–550. https://doi.org/10.2307/1369233

Heinrich, B., & Marzluff, J. M. (1991). Do common ravens yell because they want to attract others? *Behavioral Ecology and Sociobiology*, *28*(1), 13–21. https://doi.org/10.1007/BF00172134

Heinrich, B., Marzluff, J. M., & Marzluff, C. S. (1993). *Common ravens are attracted by appeasement calls of food discoverers when attacked*. *110*, 247–254.

Heinrich, B., & Pepper, J. W. (1998). Influence of competitors on caching behaviour in the common raven, Corvus corax. *Animal Behaviour, 56*, 1083–1090.

Hesse, S., & Thünken, T. (2014). Growth and social behavior in a cichlid fish are affected by social rearing environment and kinship. Naturwissenschaften, 101(4), 273–283. https://doi.org/10.1007/s00114-014-1154-6

Hinde, R. A. (1976). Interactions, Relationships and Social Structure. Man, 11(1), 1–17. JSTOR. https://doi.org/10.2307/2800384

Humphrey, N. (1976). The social function of intellect. *Growing Points in Ethology, 1970*, 303 317.

Jain, V., Bugnyar, T., Cunningham, Susan J., Gallego-Abenza, M., Loretto, M.-C., & Sumasgutner, Petra. (2022). The spatial and temporal exploitation of anthropogenic food sources by common ravens (Corvus corax) in the Alps. *Submitted*

Johnson, C. M., & Karin-D'Arcy, M. R. (2006). Social Attention in Nonhuman Primates: A Behavioral Review. *Aquatic Mammals*, *32*(4), 423–442. https://doi.org/10.1578/AM.32.4.2006.423

Jolly, A. (1966). Lemur social behavior and primate intelligence. *Science (New York, N.Y.), 153*(3735), 501—506. https://doi.org/10.1126/science.153.3735.501

Kanai, R., Bahrami, B., Roylance, R., & Rees, G. (2012). Online social network size is reflected in human brain structure. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1732), 1327–1334. https://doi.org/10.1098/rspb.2011.1959

Kerth, G., Ebert, C., & Schmidtke, C. (2006). Group decision making in fission–fusion societies: Evidence from two-field experiments in Bechstein's bats. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1602), 2785–2790. https://doi.org/10.1098/rspb.2006.3647

Kummer, H. (1971). *Primate Societies*.

Lefebvre, L., Nicolakakis, N., & Boire, D. (2002). Tools and brains in birds. *Behaviour*, *139*(7), 939–973. https://doi.org/10.1163/156853902320387918

Liker, A., & Bokony, V. (2009). Larger groups are more successful in innovative problem solving in house sparrows. *Proceedings of the National Academy of Sciences*, *106*(19), 7893–7898. https://doi.org/10.1073/pnas.0900042106

Loretto, M.-C., Reimann, S., Schuster, R., Graulich, D. M., & Bugnyar, T. (2016). Shared space, individually used: Spatial behaviour of non-breeding ravens (Corvus corax) close to a permanent anthropogenic food source. *Journal of Ornithology*, *157*(2), 439–450. https://doi.org/10.1007/s10336-015-1289-z

Loretto, M.-C., Schuster, R., & Bugnyar, T. (2016). GPS tracking of non-breeding ravens reveals the importance of anthropogenic food sources during their dispersal in the Eastern Alps. *Current Zoology*, *62*(4), 337–344. https://doi.org/10.1093/cz/zow016

Loretto, M.-C., Schuster, R., Itty, C., Marchand, P., Genero, F., & Bugnyar, T. (2017). Fission-fusion dynamics over large distances in raven non-breeders. *Scientific Reports*, *7*(1), 380. https://doi.org/10.1038/s41598-017-00404-4

Marzluff, J. M., & Angell, T. (2007). *In the Company of Crows and Ravens*. Yale University Press.

Marzluff, J. M., Heinrich, B., & Marzluff, C. S. (1996). Raven roosts are mobile information centres. *Animal Behaviour*, *51*(1), 89–103. https://doi.org/10.1006/anbe.1996.0008

Massen, J. J. M., Pašukonis, A., Schmidt, J., & Bugnyar, T. (2014). Ravens notice dominance reversals among conspecifics within and outside their social group. *Nature Communications*, *5*, 3679. https://doi.org/10.1038/ncomms4679

Massen, J. J. M., Szipl, G., Spreafico, M., & Bugnyar, T. (2014). Ravens intervene in others' bonding attempts. *Current Biology*, *24*(22), 2733–2736. https://doi.org/10.1016/j.cub.2014.09.073

McNelis, N. L., & Boatright-Horowitz, S. L. (1998). Social monitoring in a primate group: The relationship between visual attention and hierarchical ranks. *Animal Cognition*, *1*(1), 65–69. https://doi.org/10.1007/s100710050008

Mikolasch, S., Kotrschal, K., & Schloegl, C. (2013). Transitive inference in jackdaws (Corvus monedula). *Behavioural Processes*, *92*, 113–117. https://doi.org/10.1016/j.beproc.2012.10.017

Milton, K. (1981). Distribution Patterns of Tropical Plant Foods as an Evolutionary Stimulus to Primate Mental Development. *American Anthropologist*, *83*(3), 534–548. https://doi.org/10.1525/aa.1981.83.3.02a00020

Moss, C., & Lee, P. (2011). Female social dynamics: Fidelity and flexibility. In *The Amboseli elephants: A long-term perspective on a long-lived mammal* (pp. 205–223). University of Chicago Press: Chicago, IL, USA.

Paz-y-Miño C, G., Bond, A. B., Kamil, A. C., & Balda, R. P. (2004). Pinyon jays use transitive inference to predict social dominance. *Nature*, *430*(7001), 778–781. https://doi.org/10.1038/nature02723

R Core Team. (2017). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing. https://www.R-project.org/

Sachser, N., Kaiser, S., & Hennessy, M. B. (2013). Behavioural profiles are shaped by social experience: When, how and why. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1618), 20120344. https://doi.org/10.1098/rstb.2012.0344

Silk, J. B. (1999). Male bonnet macaques use information about third-party rank relationships to recruit allies. *Animal*

Behaviour, *58*(1), 45–51. https://doi.org/10.1006/anbe.1999.1129

Silk, M. J., Croft, D. P., Tregenza, T., & Bearhop, S. (2014). The importance of fission-fusion social group dynamics in birds. *Ibis*, *156*(4), 701–715. https://doi.org/10.1111/ibi.12191

Szipl, G., Ringler, E., & Bugnyar, T. (2018). Attacked ravens flexibly adjust signalling behaviour according to audience composition. *Proceedings of the Royal Society B*, *285*(June). https://doi.org/10.1098/rspb.2018.0375

Taborsky, B., & Oliveira, R. F. (2012). Social competence: An evolutionary approach. *Trends in Ecology and Evolution*, *27*(12), 679–688. https://doi.org/10.1016/j.tree.2012.09.003

Weiß, B. M., Kehmeier, S., & Schloegl, C. (2010). Transitive inference in free-living greylag geese, Anser anser. *Animal Behaviour*, *79*(6), 1277–1283. https://doi.org/10.1016/j.anbehav.2010.02.029

Chapter 4

Early social environment affects attention to social cues in juveniles Common ravens, *Corvus corax*

This chapter was accepted for publication in Royal Society Open Science on May 12th, 2022.

Abstract

Social competence i.e., defined as the ability to adjust the expression of social behaviour to the available social information, is known to be influenced by early-life conditions. Brood size might be one of the factors determining such early conditions, particularly in species with extended parental care. We here tested in ravens, whether growing up in families of different sizes affects the chicks' responsiveness to social information. We experimentally manipulated the brood size of 20 captive raven families, creating either small or large families. Simulating dispersal, juveniles were separated from their parents and temporarily housed in one of two captive non-breeder groups. After five weeks of socialization, each raven was individually tested in a playback setting with food-associated calls from three social categories: sibling, familiar unrelated raven they were housed with, and unfamiliar unrelated raven from the other non-breeder aviary. We found that individuals reared in small families were more attentive than birds from large families, in particular towards the familiar unrelated peer. These results indicate that variation in family size during upbringing can affect how juvenile ravens value social information. Whether the observed attention patterns translate into behavioural preferences under daily life conditions remains to be tested in future studies.

Keywords: Early-social environment, brood size, attention response, Common ravens

Introduction

The social intelligence hypothesis posits that species living in complex social systems should evolve cognitive abilities to cope with the challenges derived from social life, like the formation and maintenance of differentiated social relationships and extended social networks (Byrne & Whiten, 1989; Humphrey, 1976; Jolly, 1966). Within a given species (or population), individuals are expected to vary in their ability to deal with and respond to social information, which is commonly referred to as 'social competence'. Following Oliveira (2009), social competence can be defined as an individual ability to adjust and optimize the expression of its social behaviours according to the surrounding social information. As such, social competence can be viewed as an adaptive trait that varies between individuals because of heritable phenotypic differences, but also in response to differences in environmental conditions (Taborsky & Oliveira, 2012).

It is well known that epigenetic factors in early-life such as rearing conditions, quantity and quality of parental care, and presence or absence of peers – subsumed under the term social experience – can alter ontogenetic pathways and shape individual life history trajectories (Sachser et al., 2011; Taborsky et al., 2012; Taborsky & Oliveira, 2012). Notably, social deprivations or stress experienced during upbringing can have detrimental consequences on the development of individual social behaviour. For instance, socially deprived and/or stressed individuals tend to engage in fewer relationships, show a lower propensity to gregariousness, increased aggressiveness, a reduced acquisition of social knowledge, and/or less elaborated strategies to access resources. Such effects have been described across taxa i.e., in humans (Bick & Nelson, 2016; Tottenham, 2014), non-human primates (Anderson & Mason, 1978; Bastian et al., 2003; Levine & Mody, 2003), rodents (Ros-Simó & Valverde, 2012; Sachser et al., 1994; Tóth et al., 2008), birds (Boogert et al., 2014; Farine et al., 2015) and fish (Arnold & Taborsky, 2010; Hesse & Thünken, 2014). Note that low social competence might arise from difficulties in detecting the social information (i.e., reduced social responsiveness) or from inappropriate response to this information (Taborsky & Oliveira, 2013).

Compared to the wealth of deprivation studies, where key social partners such as mothers or care givers are lacking, relatively few studies have experimentally investigated effects of natural group size variation during upbringing e.g., due to different number of offspring (for species showing bi-parental care) or helpers (for species engaging in cooperative breeding). A recent study on wild zebra finches (Brandl et al., 2019) showed that being reared in enlarged broods results in less choosy and more central individuals in associations networks and a greater gregariousness during foraging. On the mechanistic level, these patterns were explained with increased sibling competition and thus increased stress in enlarged broods (Brandl et al., 2019), as predicted by the developmental stress hypothesis (Boogert et al., 2014). Originally formulated in the context of song learning (Buchanan, 2011; Nowicki et al., 1998, 2002), and then applied to social learning and social behaviour in general (Boogert et al., 2014; Farine et al., 2015), the developmental stress hypothesis states that competition for resources during upbringing results in increased stress which affects the development of individuals´ brain structures and behavioural choices later in life.

Besides stress increment, large groups in early life might also represent enriched social environments and potentially foster the development of socio-cognitive skills, positively affecting social competence later in life. In line with this assumption, cooperative breeding cichlids that were raised in larger groups later expressed more adequate social behaviours during hierarchy formation than those raised in small groups, thereby increasing their chances to be tolerated on dominants´ territories and their survival (Fischer et al., 2015). Communal rearing in mice (i.e., mothers rearing their pups in a single nest, which is a typical feature under field conditions) as compared to the standard laboratory condition (i.e., single mother with pups) was also found to affect the offspring´s social responsiveness and the adequacy of expressed social behaviour to context. Specifically, male mice reared in communal nest showed a quicker establishment of hierarchy and acquisition of a dominance status (Branchi et al., 2006); increased selectivity when display aggressiveness (D'Andrea et al., 2007), and increased anxiety-like behaviour but only when being socially isolated (Branchi & Alleva, 2006). In female mice, however, communal rearing seems to diminish responsiveness to social cues, with reduced reaction to novelty (Gracceva et al., 2009a). This suggests that an enriched social environment might not always potentiate social competences and mediate them differently across sexes. Overall, these findings on birds, fish and rodents strongly support the (hardly tested) assumption that the natural range of variation in early-life experience, like small or large broods in birds, can be sufficient to affect individuals´ social competences, and in particular responsiveness to social information, later in life. What is yet unclear, however, is what guides the individuals´ decision, i.e. do offspring from large broods have difficulties-in detecting social information, or do they value social information differently than birds from small broods?

Common ravens, *Corvus corax*, are long-term monogamous birds, renowned for their elaborated socio-cognitive skills (Heinrich, 1999; Massen et al., 2020). Pairs defend territories for breeding and show an extended period of bi-parental care (Coombs, 1978; Goodwin, 1976). After dispersal (3-6 months after fledging), juveniles join non-breeder groups that tend to form for foraging, socializing and roosting (Heinrich, 1989; Wright et al., 2003). Non-breeder groups show an open composition, with moderate to high degrees of fission-fusion dynamics (Loretto et al., 2017); yet, they are structured by social relationships (Braun & Bugnyar, 2012) and individual preferences for particular sites (Dall & Wright, 2009; Loretto et al., 2016). During the non-breeder stage, ravens profit from others in finding and/or accessing food (Heinrich & Marzluff, 1991; Sierro et al., 2020) and predator protection (Gallego-Abenza et al., 2021); however, they also face high competition for resources and partners (Bugnyar & Kotrschal, 2002). Hence, living in these groups likely depicts socio-cognitive demanding situations. This assumption has been supported by observational and experimental findings in wild and captive ravens, showing flexible behavioural responses about: e.g., when to call at food (Szipl et al., 2015), with whom to cooperate (Asakawa-Haas et al., 2016), when to intervene in conflicts and whom to join (Szipl et al., 2018), when to engage in post-conflict affiliation (Fraser & Bugnyar, 2010, 2011), and when to disrupt others´ bonding attempts (Massen et al., 2014). All these manoeuvers likely rest on paying selective attention to social information, categorization of group members and/or recognition and memory of individuals and their social relationships, as demonstrated in playback experiments on subadult and adult ravens (Boeckle & Bugnyar, 2012; Massen et al., 2014). Considering the complexity of the non-breeder stage, we would expect ravens to develop such competences early in life. Specifically, juveniles might already start learning to recognize and to remember individuals and their social relations while growing up in their family. Family size in ravens naturally ranges from three to seven individuals (two parents and one to five chicks). This offers an ideal opportunity to test whether growing up with a varying number of siblings affects the development of individual social competence, later in life. As the competition for parental resources as well as the social information available to young ravens likely increases with sibling number, birds from small and large families should vary in their responsiveness to social information at dispersal, when they leave their family and start interacting with other peers. The adequacy of response could be expressed in whether or not they orient towards the stimuli of interest (detection) and/or in varying the duration of attention according to the social category (value).

We here experimentally tested the effect of brood size variation on juvenile ravens´ ability to discriminate between calls from same-aged peers of different social categories in the early non-breeder state. Simulating the natural breeding dynamics and brood size variation of ravens, we manipulated brood size of captive breeding pairs over three consecutive years, creating seven small families (with two chicks) and six large families (four with three chicks and two with four chicks) in a cross-design. After fledging in early May, juvenile ravens stayed in their families until mid-July. They were transferred into one of the two non-breeder aviaries, where they formed two similar-sized groups of same aged peers. After 5 weeks of socialization in those non-breeder groups, we tested birds individually in a playback design with calls from a sibling (with whom they grew up and were transferred with into the non-breeder group), a familiar non-sibling (unrelated individual they were housed in a captive non-breeder group) and an unknown non-sibling (unrelated individual housed in the other non-breeder group, never encountered). Following Brandl et al. (2019), we hypothesized that ravens brought up in large families experienced more sibling competition and thus increased developmental stress as compared to ravens brought up in small families. We thus expected ravens from large families to be less choosy/more open in with whom to interact, which should result in similar responses to the different played back calls, irrespective of the social category. We also reasoned that ravens brought up in large families learn to divide their attention between more partners, whereas ravens brought up in small families had their attention focused on a single sibling. Accordingly, we expected ravens from small families to show more selective responses to calls from individuals they know, notably their sibling and potentially also a familiar peer they have recently been housed with. An alternative hypothesis would be that experience with different siblings could give birds from large families an advantage in detecting social information; in this case, we would predict birds from large families to be more skilled in differentiating between callers of different social categories than birds from small families. Taken together, we expected the offspring from large and small broods to value social information differently.

Material and Methods

Study subjects and housing

We worked with 28 juvenile ravens from 13 captive families throughout three consecutive breeding seasons (2018-2020). Families were generated from nine captive breeding pairs (Supplementary table 1). All families were housed separately from each other at Haidlhof Research Station (four pairs), Konrad Lorenz Research Center (four pairs) and Zoo Vienna (one pair) in spacious aviaries (80-120 m^2). See Supplementary table 1 for more details on families´ composition and location. Since families were housed in separated aviaries, offspring from different families never met or interacted in the family phase. Throughout the consecutive breeding seasons, we manipulated the brood size by removing and/or replacing eggs to create same sized clutches of four eggs, from which either all four (large family) or only two eggs were fertile (small family). Which pair received a large or small brood treatment was randomly allocated in the first year and then changed across years following a cross-design (e.g., pairs with a large brood in year one were treated as a small brood in year two). In some cases, the actual offspring number per pair deviated from our egg manipulation. Typically because an egg did not hatch or a chick died in the first days, resulting in an uneven number of siblings (one juvenile: small family, three juveniles: large family). All juveniles were marked with coloured rings for individual identification before fledging.

Juvenile ravens were raised from hatching (late March-early April) to 10 ± 1 weeks post fledging (early May) by their parents (family phase). In mid-July of each year, all chicks were taken out from their parents´ aviary on the same day and transferred to one of the two non-breeder aviaries of the Konrad Lorenz Research Center, in the area of the Cumberland Wildpark Grünau. Captive non-breeder groups ranged in size between six to nine individuals. To compose each group, we control for sibling number, transferring maximum two siblings from the same family per group. As a result: single juvenile from one-juvenile-families (small) were transferred alone in one group; siblings from two-juveniles-families (small) were transferred together in the same group; siblings from three-juveniles-families (large) were split in one and two chicks in each group; while siblings from four-juveniles-families (large) were split in two dyads of two in each group. Note that we excluded single juveniles with no sibling in their non-breeder group from the study, resulting in a total of 28 subjects (13 from small families; 8 females and 3 males and 15 from large families; 6

females and 9 males, Supplementary Table 1). The two non-breeder aviaries were of similar size (60 m^2) and equipped similarly with natural ground cover (gravel, sand, grass), wooden perches, shallow pools for bathing and roofs for sun and rain protection. They were located 1.5 km apart, separated by dense forest areas, preventing birds of the two peer groups from being in any visual or acoustic contact. Juveniles in both groups were fed twice a day with a mixture of pellets, meat, vegetables and fruits and they had *ad libitum* access to water. The ravens stayed in the non-breeder groups for a total of six weeks, before being released in the wild by beginning of September. In the week before release, juveniles were individually taken out from their group for being measured, blood sample and marked with rings from the Austrian Ornithological Center and coloured wing tag, and equipped with a GPS logger. We scheduled our playback experiment in the same week to make use of the birds´ separation from the group for this marking procedure.

Experimental setting

After being measured and marked, juveniles were transferred to an experimental aviary (2 m^3), which was temporally set-up in a remote woodland part of the park, more than two km away from any keeping aviaries. In the experimental aviary, the test subject was provided with food and water *ab libitum* and it remained undisturbed by humans for about 20 hours, including overnight, before playback experiments were conducted. Then the playback was conducted. The experimental aviary was equipped with two perches positioned at the same height (1.5 meter above ground), both were perpendicular to a back wall which was covered by an opaque plastic sheet. Broadcasting stimuli came from a loudspeaker located behind the opaque back wall in two meters distance to the aviary. On the opposite side, a GoPro Hero 7 was mounted on a tripod for video recording of the subject´s behaviour.

Acoustic recordings and playback experiments

We used food-associated calls known for their individual signature (Boeckle et al., 2012; Sierro et al., 2020). Calls were recorded in the last week of the family phase prior juveniles´ transfer to the non-breeder groups. Standing outside the aviary, we individually identified juveniles by their coloured rings and recorded their calls using a shot-gun microphone (Sennheiser ME-67) plugged into a Tascam DR-100mkII voice recorder (wav. Format, 44.1 kHz, 16bit-rate).

During the playback experiment, each subject was exposed to two consecutive calls (separated by 0.3 seconds) from each of the three social categories: sibling (related individual with whom the subject was brought up and then housed in the non-breeder group), familiar individual (a random unrelated individual with whom the subject was housed in the non-breeder group) and unknown individual (a random unrelated individual from the other non-breeder group, never encountered by the subject). Note that for unknown individuals, calls were collected from a different family coming either from a different or same research station. However, since families were housed in single aviaries, these juveniles had never met and thus interacted. The broadcasting order for caller categories was randomized across tested subjects and a six-minutes silence pause occurred between the exposure to each category of call. Two of the 28 subjects receive two unknown and one familiar unrelated calls (instead of one call of each type) due to missing recordings from their sibling. All calls´ amplitude was standardized using Audacity software (https://www.audacityteam.org/) to match an identical broadcasting volume of 67 dB measured at two-meters of distance (Sound Level Meter RadioShack, model 3300099, A-weighting, fast response). Calls were played back in .wav format using a digital music player (Musrun k188) connected to a loudspeaker (JBL xtreme, frequency response 70 – 20000 Hz) and loudspeaker was placed in a blind side of the experimental aviary, being this the opposite site to where the camera recorded subjects´ behaviours.

Behaviour responses and video coding

From the video recordings, we coded the subjects´ behaviour in the minute before the stimulus was played (baseline phase) and in the minute right after the stimulus was played (test phase). Videos were coded using the free software Solomon Coder (https://solomon.andraspeter.com/). Specifically, we scored the number and duration of orientation responses towards the opaque wall (`looks´: lateral head position, facing with their beak in the direction of the loudspeaker). It results in two behaviour measurements: “Duration of head turns (sec)” and “Number of looks”. The majority of videos sequences were coded by a single coder (I.M., 82%), who was blind to the hypothesis and the caller´s identities. About 20% were coded by MGA (inter-observer reliability between the two coders: Cohen´s kappa, K = 0.904, $p < 0.001$; R package “irr”; (Gamer et al., 2019)). We used delta values as response variable in our statistical analyses by subtracting the measurements (frequencies and durations) of the one-minute baseline phase from those of the one-minute test phase.

Statistical analysis

We investigated how brood size affected raven´s attentiveness to callers from different social categories. To do so, we ran a linear and a generalised linear mixed effect models, respectively using the i) “Duration of head turns” and ii) “Number of looks” as response variables using the functions *lmer* and *glmer* (Poisson error distribution, *log link* function) within R package `lme4´, respectively (Bates et al., 2015). In both models, we included “Brood size” (categorical: small, large), “Caller class” (categorical: sibling, familiar, unknown), “Sex” of the subject (categorical: male, female), and the two interactions between “Brood size : Caller class” and “Sex : Caller class” as fixed factors. “Subject” nested within “Family identity” were included as random factors. To test for the overall significance of each interaction, we ran full-reduced model comparisons, between the above-mentioned full model and reduced models (lacking each interaction). We also ran a full-null model comparison between the full model and the null model lacking all fixed factors (but including the random factors). For model comparisons we used the *anova* R test function and reported AIC, degree of freedom, Chi^2 and p values to assess significance of the interaction. For “Caller class”, we ran post hoc comparisons applying Tukey´s contrasts (*glht* function, “multcomp” R package) (Hothorn et al., 2008). We also ran post-hoc comparisons for the interaction terms “Brood size : Caller class” and “Sex : Caller class” using the functions `emmeans; pairwise comparison´ and `contrast´ within the “emmeans” R package (Lenth, 2021) to assess estimated marginal means and report associated p-values. For the linear model, the normality of the residuals was confirmed using the Shapiro-Wilk normality test (function *shapiro.test*, “stats” R package). All our statistical analyses were conducted in R software, version 4.1.1. (R Core Team, 2017), with a significance threshold set at $\alpha = 0.05$.

Ethics approval

The playback study on individually separated ravens was performed under the license for animal experimentation of the Austrian government (BMBWF-66.006/0015-V/3b/2018). Raven breeding pairs are kept according to the guidelines and permissions of the federal states Lower and Upper Austria; the offspring’s free-flight is licensed by the BH Gmunden (BHGMN-2018-87893/10-BUT).

Results

The full-reduced and full-null model comparisons supported the inclusion of both interactions (Caller class : Brood size and Caller class : Sex) in the full model to explain `Duration of head turns´, see Table 1b. As a result, the individual rearing background (Brood size) had an effect on juveniles´ attention responses, however, this effect was mediated by the caller class, with a greater difference between large and small families for calls of familiar individuals (Fig. 1, Table 1). Specifically, emmeans contrasts based on the full model revealed that small-family-juveniles looked significantly longer in the direction of the loudspeaker than large-family-juveniles when broadcasting familiar calls; while this difference was not significant for other caller classes (see contrasts in Table 1d). Interestingly, no significant differences were found when comparing `Duration of head turns´ between caller class categories within each rearing group (small and large brood size, see Table 1e). Although non-significant, the sex appeared to a lesser extent, to influence responsiveness for certain caller class (see overall significance of the interaction term and post-hoc comparisons in Supplementary Table 3). Descriptively, females seemed to look longer in the direction of the loudspeaker than males when broadcasting familiar calls (see Supplementary Figure 1). We found no significant effect of the tested predictors (“Brood size”, “Caller class”, “Sex”, “Brood size : Caller class”, and “Sex : Caller class”) on the “Number of looks” (see Supplementary Table 2 and Supplementary Figures 1,2).

Table 1. a) Summary of the linear mixed model results containing the interactions “Brood size:Caller class” and “Sex:Caller class” to explain the attentive response (Duration of head turns) of juvenile ravens. b) Full-reduced and Full-Null model comparisons using the ANOVA test, we reported the degree of freedom, AIC, χ2 and P-values. c) Post-hoc comparison using Tukey contrast comparison for “Caller class”. d) Post-hoc comparisons of estimated means between “Brood size” for each “Caller class”, using emmeans package. e) Post hoc comparisons of estimated means between “Caller class” for each “Brood size”, using emmeans package.

a)

Full model	**Estimate ± SE**	**CI**	**t value**	**p-value**
Intercept	6.18 ± 4.07	-1.93 – 14.29	1.52	0.133
Caller class (*sibling*)	-2.89 ± 5.51	-13.87 – 8.08	-0.53	0.601
Caller class (*unknown*)	0.01 ± 5.42	-10.78 – 10.81	0	0.998
Brood size (*small*)	11.21 ± 4.51	2.23 – 20.19	2.49	**0.015**
Sex (male)	-8.21 ± 4.51	-17.19 – 0.77	-1.82	0.073
Caller class (*sibling*) * Brood size (*small*)	-5.73 ± 6.2	-18.09 – 6.63	-0.92	0.359
Caller class (*unknown*) * Brood size (*small*)	-16.34 ±5.94	-28.17 – -4.50	-2.75	**0.008**
Caller class (*sibling*) * Sex (*male*)	4.69 ± 6.17	-7.61 – 16.99	0.76	0.449
Caller class (*unknown*) * Sex (*male*)	13.89±5.94	2.04 – 25.74	2.34	**0.022**

b)

Full to Reduced & Null models comparison, ANOVA test		
Full model	Caller class * Brood size + Caller class * Sex	AIC = 675.90
Reduced model	Caller class + Brood size + Caller class * Sex	AIC = 679.32, Chisq = 7.43, Df = 2, P-value = 0.02439
Reduced model	Caller class * Brood size + Caller class + Sex	AIC = 677.15, Chisq = 5.25, Df = 2, P-value = 0.072
Null model		AIC = 676.81, Chisq = 16.91, Df = 8, P-value = 0.03105

c)

Multiple Comparisons of Means: Tukey Contrasts			
	Estimate ± SE	**z value**	**p-value**
Sibling – Familiar non-sibling	-2.895 ± 5.50	-0.526	0.859
Unknown – Familiar non-sibling	0.01 ± 5.41	0.002	1
Unknown – Sibling	2.91 ± 5.47	0.531	0.856

d)

Emmeans contrasts	**Estimate ± SE**	**df**	**t ratio**	**p-value**
Caller class = Familiar non-sibling				
Brood size (large - small)	-11.21 ± 4.93	84.5	-2.276	**0.025**
Caller class = Sibling				
Brood size (large - small)	-5.48 ± 5.15	85.3	-1.065	0.29
Caller class = Unknown				
Brood size (large - small)	5.13 ± 4.83	81	1.062	0.29

e)

Emmeans contrasts	**Estimate ± SE**	**df**	**t ratio**	**p-value**
Brood size = Large				
Familiar non-sibling – Sibling	0.549 ± 4.36	62.5	0.126	0.9913
Familiar non-sibling – unknown	-6.958 ± 4.36	62.5	-1.598	0.2542
Sibling – unknown	-7.507 ± 4.36	62.6	-1.723	0.2049
Brood size = Small				
Familiar non-sibling – Sibling	6.277 ± 4.89	65.2	1.283	0.4098
Familiar non-sibling – unknown	9.377 ± 4.51	64.2	2.081	0.1019
Sibling – unknown	3.100 ± 4.85	71.0	0.640	0.7988

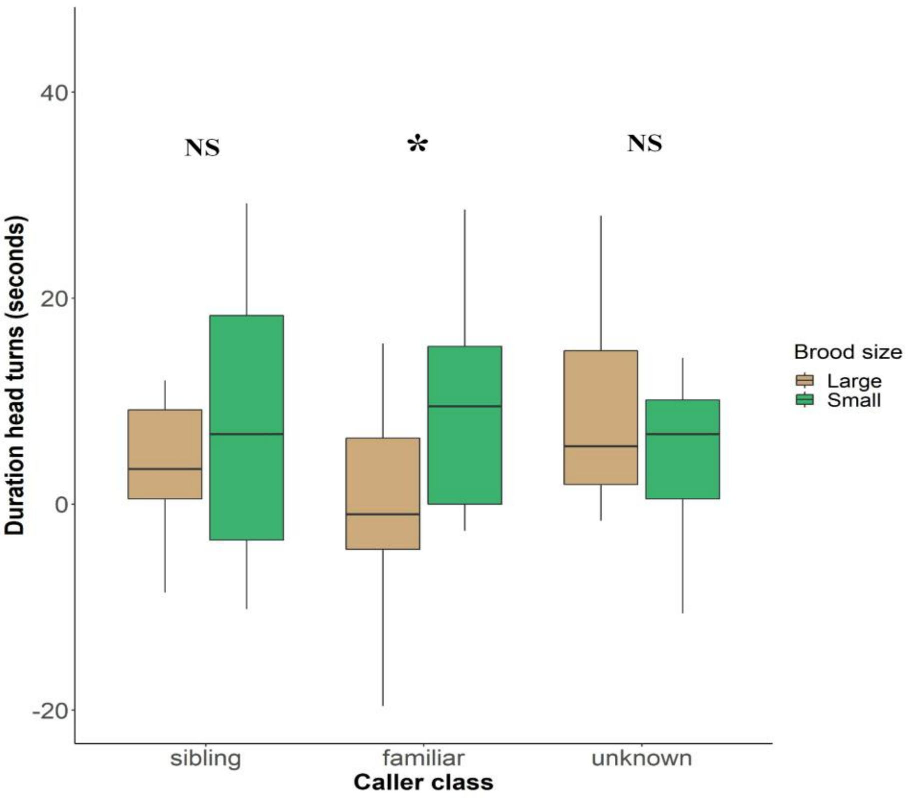


Figure 1. Attention responses of tested subjects towards the three different caller categories. The figure shows the Δ values (response - baseline) of "Duration of head turns" in seconds, towards the three social categories and colored by "Brood size". The resulting significance from GLMM and *post-hoc* analysis is indicated as * when $P < 0.05$.

Discussion

In the present study, we tested the responsiveness of juvenile ravens from small or large families to social information provided in food-associated calls. We experimentally show that, irrespective of their rearing history, juvenile ravens respond to playbacks of food calls of same-aged peers at the time of dispersal (about five months of age). We also show that family size has an effect on the birds´ responsiveness, but only for a certain type of social category i.e., for familiar individuals they have been housed with, in the previous five weeks (non-breeder stage). Indeed, while family size did not seem to affect juvenile´s responsiveness to calls from a sibling (they have also been housed with) or an unknown individual (they have never encountered before), juveniles reared in small families paid longer attention to acoustic cues from familiar individuals than juveniles reared in large families. These results hint in the direction that differences in upbringing affects the social competence of ravens at dispersal, as birds from small and large families seem to value social information differently.

Our findings are partly in line with the developmental stress hypothesis (Boogert et al., 2014; Brandl et al., 2019), predicting that individuals from large families should be less choosy in with whom to interact. In line with this prediction, ravens from large families were equally attentive to the played back calls, irrespective of the callers´ social category. However, ravens from small families showed the same pattern; contrary to our prediction, they were neither selective among the caller categories nor more focus on their sibling (see Table 1e). Possibly, ravens at that early age cannot yet fully pick up on the social information encoded in food calls, making it difficult for them to discriminate between played back callers. That the tested birds have not yet developed their full cognitive capacity is supported by behavioural studies on the ontogeny of food caching (Bugnyar et al., 2007) and gaze following (Schloegl et al., 2007), indicating a cognitive step in the ravens´ development at the end of their first summer (September/October), which might go together with becoming more selective to social cues (Loretto et al., 2012). Our study was scheduled to match the situation of wild ravens at our field site (family phase till early summer, local dispersal and meeting of same-aged peers in summer, integration into non-breeder population in late summer/early fall). Accordingly, the playbacks were carried out in late August, which might have been too early. We do not know of any other study testing for social discrimination in juvenile ravens, or other corvids at a comparable age, and further studies during this sensitive period would be required to better understand possible developmental effects.

Aside the cognitive development, it is well known that young ravens are generally attracted to raven calls (Heinrich, 1988, 1994). Particularly food calls from same-aged conspecifics might be highly salient to them, as those indicate the opportunity to join others at food (Heinrich, 1988) and, potentially, to socialize with them after feeding (Braun et al., 2012). A genuine interest in same-aged peers could thus explain the similar levels of attention shown to callers of different social categories in our experiment. This salience argument would also help explaining our main finding on the effect of upbringing i.e., that birds from small families generally attended more to playbacks of food-associated calls than birds from large families. Possibly, ravens coming from small families were more interested in meeting same-aged peers as compared to ravens from large families. Indeed, ravens start to form affiliative relationships already in their first fall (Loretto et al., 2012), when they face the challenge of integrating into non-breeder groups (Boucherie et al., 2019). Siblings are preferred partners at that stage, providing social support during and post-conflict (Fraser & Bugnyar, 2010). It is conceivable that birds from small families should be more interested in enlarging their social network than birds from large families, who can already rely on support from several siblings.

It must be noted that even though we do find different attention responses of ravens raised in small and large families, and hence an effect of our brood size manipulation (see Table 1d), we do not yet know what specifically has caused this effect in early life, differences in the parents´ behaviour (e.g., feeding rates) or differences in the offspring´s behaviour (e.g., aggression rates). Interestingly, ravens from small and large families differed strongest in the response to calls from familiar non-siblings, indicating that unrelated but familiar individuals were more salient to ravens from small families compared to ravens from large families. We found no noticeable difference between small vs. large families for other types of calls, and this result held even when differentiating unknown callers coming from different vs. from the same research site who might have had some acoustical (but no visual and physical) contact during upbringing (see Supplementary Figure 4).

Coming back to the developmental stress hypothesis, similarly as described for song learning (Nowicki et al., 1998; Soma et al., 2006), it is plausible that more acute stress experienced during upbringing in large families could have affected the development of certain brain areas of large-family-juveniles and potentially resulted in lower preferences for attending to social information later as juveniles. Although we have not analysed stress level of our study subjects, we could recently show that parental care investment varies with brood size, whereby chicks in large families receive significantly less care (feeding and affiliations) than chicks raised in small families, which might increase stress (Ersoy et al., 2021). In this respect, our results could align with those on zebra finches, which showed different social learning strategies depending on the levels of developmental stress induced during upbringing (Boogert et al., 2014; Farine et al., 2015). Additionally, large-family-juveniles could have experienced a stress-related phenomenon due to separation from other siblings, since no more than two siblings were transferred into the same non-breeder groups. While we do know that separation and re-union events can induce stress-related behaviours and hormonal responses, these typically last no longer than a few days (Stocker et al., 2016). Future studies need to investigate in more details the mechanisms underlying the long-lasting effects of varying offspring number at upbringing and the first peer group formation, on the development of ravens´ social competences.

Finally, although non-significant, our analyses also suggest that upbringing conditions might affect ravens of both sexes differently, which would fit to the findings in domestic mice (Branchi et al., 2006; D'Andrea et al., 2007; Gracceva et al., 2009). Indeed, while the effect of upbringing was particularly salient for familiar calls, we also see descriptively, that females tended to be more attentive to these calls than males. Note that males and females were equally represented in the dataset for both family sizes. Future studies should thus aim to consider the possibility of differential early social environment effects in the two sexes.

Taken together, our findings support the assumption that offspring from small families come to value social information differently than birds from large families. In contrast, having experience with different number of siblings did not result in any apparent advantage for large-family-juveniles over small-family-juveniles in detecting information encoded in calls, at least not in our playback experiment. This could be different in alternative test settings, when birds are required to interact with one another, for instance in a separation-reunion setting (see Stocker et al., 2016). Future studies should attempt testing both, the response to acoustic cues and the willingness to interact with the caller. Furthermore, our findings need to be corroborated in older birds, also tested under ecologically relevant conditions (Brandl et al., 2019). Indeed, we plan to track our study subjects under free-flight conditions until adulthood (i.e., four years), which should allow us to investigate how the environment experienced during upbringing shapes the ravens´ social behaviour, association patterns, and network positions at different stages or their life as non-breeders and, eventually, their social competence as adults.

Acknowledgements

The study was funded by the Austrian Science Fund (FWF), projects P29705 and P33960. MGA was additionally supported by the DK program Cognition & Communication (W1262) and the VDS CoBeNe, the Vienna Doctoral School in Cognition, Behaviour and Neuroscience. We thank the Cumberland Wildpark and the Verein der Förderer KLF for their permanent support, and Felix Steinmauer, Max Stiebi and Ines Mayer for their help in constructing aviaries, feeding and transferring ravens to experimental aviaries.

Supplementary table 1. Non-breeder group composition including detailed sibling and family identities and whether juveniles took part in this study.

Year	**Group**	**Family**	**Family**	**Brood**	**Target juveniles**	**Sex**	**Tested**

		identity	Location	size			
2018	Group_1	Tom_Hei	Cumberland WP	Small	Apollo	Female	Yes
2018	Group_1	Tom_Hei	Cumberland WP	Small	Arthemis	Male	Yes
2018	Group_1	Bob_Lag	Haidlhof	Large	Coal	Female	Yes
2018	Group_1	Bob_Lag	Haidlhof	Large	Ila	Male	Yes
2018	Group_1	Astr_Hor	Haidlhof	Large	Diana	Female	Yes
2018	Group_1	Astr_Hor	Haidlhof	Large	Minerva	Male	Yes
2018	Group_1	Joe_Roc	Haidlhof	Small	Jolly	Male	Yes
2018	Group_1	Joe_Roc	Haidlhof	Small	Twinkle	Female	Yes
2018	Group_2	Astr_Hor	Haidlhof	Large	Bacchus	Male	Yes
2018	Group_2	Astr_Hor	Haidlhof	Large	Neptune	Female	Yes
2018	Group_2	Ruf_Mun	Haidlhof	Small	Gusgus	Male	Yes
2018	Group_2	Ruf_Mun	Haidlhof	Small	Mufasa	Female	Yes
2018	Group_2	Bob_Lag	Haidlhof		Draggy		No
2018	Group_2	Bob_Lag	Haidlhof	Large	Talisker	Male	Yes
2019	Group_1	Art_Mart	Cumberland WP	Small	Summer	Female	Yes
2019	Group_1	Art_Mart	Cumberland WP	Small	Winter	Female	Yes
2019	Group_1	Ge_Nobel	Haidlhof	Small	Hazel	Female	Yes
2019	Group_1	Ge_Nobel	Haidlhof	Small	Hickory	Female	Yes
2019	Group_1	Joe_Roc	Haidlhof		Othello		No
2019	Group_1	Mat_Lel	Cumberland WP		Kallisto		No
2019	Group_1	Tom_Hei	Cumberland WP	Large	Genghis	Male	Yes
2019	Group_1	Tom_Hei	Cumberland WP	Large	Xerxes	Male	Yes
2019	Group_2	Tom_Hei	Cumberland WP		Cleo		No
2019	Group_2	Mat_Lel	Cumberland WP	Large	Io	Female	Yes
2019	Group_2	Mat_Lel	Cumberland WP	Large	Ganymed	Female	Yes
2019	Group_2	Ruf_Mun	Vienna Zoo		Toma		No
2019	Group_2	Astr_Hor	Haidlhof		Sansa		No
2019	Group_2	Joe_Roc	Haidlhof	Large	Julliet	Female	Yes
2019	Group_2	Joe_Roc	Haidlhof	Large	Hamlet	Male	Yes
2020	Group_1	Art_Mart	Cumberland WP	Large	Cumulus	Male	Yes
2020	Group_1	Art_Mart	Cumberland WP	Large	Nimbus	Male	Yes
2020	Group_1	Ge_Nobel	Haidlhof		Maple		No
2020	Group_1	Ge_Nobel	Haidlhof		Oak		No
2020	Group_1	Tom_Hei	Cumberland WP		Tango		No
2020	Group_1	Joe_Roc	Haidlhof	Small	Ebony	Male	Yes
2020	Group_1	Joe_Roc	Haidlhof		Inky		No
2020	Group_1	Ruf_Mun	Vienna Zoo		Shiba		No
2020	Group_1	Ruf_Mun	Vienna Zoo		Ueno		No
2020	Group_2	Mat_Lel	Cumberland WP		Watson-Moriarty		No
2020	Group_2	Mat_Lel	Cumberland WP		Sherlock		No
2020	Group_2	Pau_Ara	Haidlhof	Small	Eragon	Male	Yes
2020	Group_2	Pau_Ara	Haidlhof	Small	Saphira	Male	Yes
2020	Group_2	Astr_Hor	Haidlhof		Nyx		No
2020	Group_2	Art_Mart	Cumberland WP		Cirrus		No
2020	Group_2	Ruf_Mun	Vienna Zoo		Asakusa		No
2020	Group_2	Ruf_Mun	Vienna Zoo		Ginza		No

Supplementary Table 2. a) Summary of the generalized linear mixed model results containing the interactions “Brood size : Caller class” and “Sex : Caller class” to explain the `Number of looks´ of juvenile ravens.
b) Full-reduced and Full-Null model comparisons using the ANOVA test, reporting the degree of freedom, AIC,

χ2 and P-values.

Full model	**Estimate ± SE**	**CI**	**t value**	**p-value**
Intercept	1.59 ± 0.15	1.29 – 1.89	10.37	<0.001
Caller class (*sibling*)	0.13 ± 0.21	-0.29 – 0.54	0.60	0.551
Caller class (*unknown*)	-0.00 ± 0.21	-0.42 – 0.42	-0.00	0.997
Brood size (*small*)	0.17 ± 0.16	-0.15 – 0.50	1.07	0.286
Sex (male)	0.04 ± 0.16	-0.28 – 0.36	0.24	0.810
Caller class (*sibling*) * Brood size (*small*)	0.03 ± 0.23	-0.42 – 0.48	0.13	0.898
Caller class (*unknown*) * Brood size (*small*)	0.05 ± 0.22	-0.39 – 0.49	0.21	0.833
Caller class (*sibling*) * Sex (*male*)	-0.06 ± 0.23	-0.51 – 0.39	-0.27	0.790
Caller class (*unknown*) * Sex (*male*)	0.11 ± 0.22	-0.33 – 0.54	0.47	0.639

Full to Reduced & Null models comparison, ANOVA test		
Full model	Caller class * Brood size + Caller class * Sex	AIC = 376.65
Reduced model	Caller class + Brood size + Caller class * Sex	AIC = 372.70, Chisq = 0.045, Df = 2, P-value = 0.9777
Reduced model	Caller class * Brood size + Caller class + Sex	AIC = 373.23, Chisq = 0.5793, Df = 2, P-value = 0.7485
Null model		AIC = 367.15, Chisq = 6.4992, Df = 8, P-value = 0.5915

Supplementary Table 3. Summary of Post-hoc contrast tests using the full model explaining the “Duration of head turns” of a) estimated means between “Caller class” for each `Sex´ and b) estimated means between “Sex” for each “Caller class”, using emmeans package.

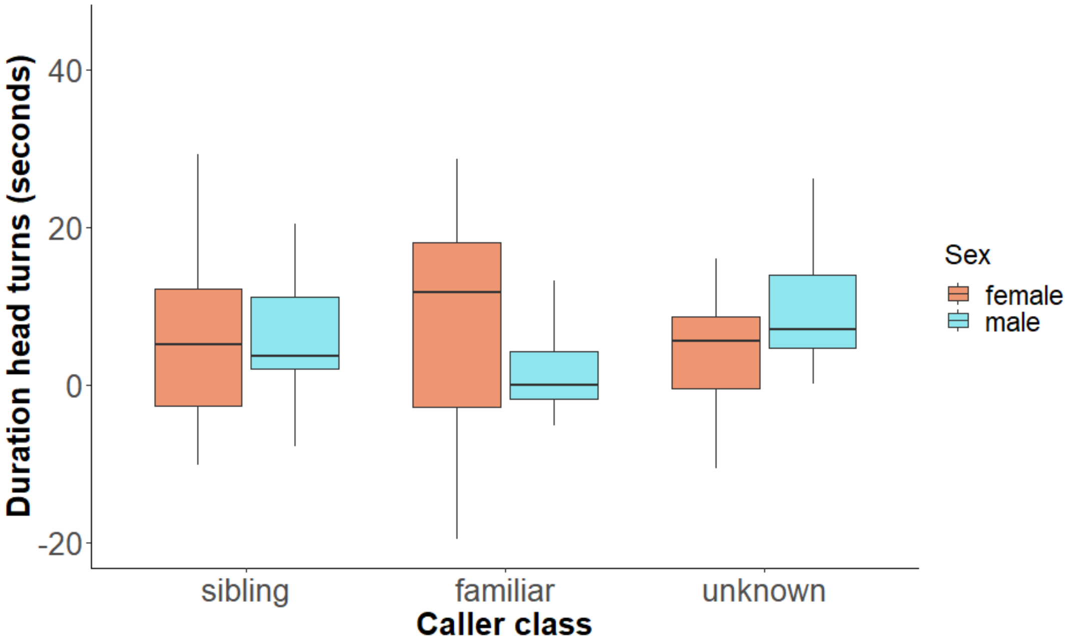
a)

Contrasts	**Estimate ± SE**	**df**	**t ratio**	**p value**
Sex = Female				
Familiar – Sibling	5.76 ± 4.75	63.7	1.213	0.4497
Familiar – unknown	8.15 ± 4.57	63.4	1.783	0.1833
Sibling – unknown	2.39 ± 4.71	66.7	0.508	0.8677
Sex = Male				
Familiar – Sibling	1.07 ± 4.48	64.0	0.238	0.9692
Familiar – unknown	-5.73 ± 4.29	63.5	-1.337	0.3800
Sibling – unknown	-6.80 ± 4.45	67.4	-1.529	0.2840

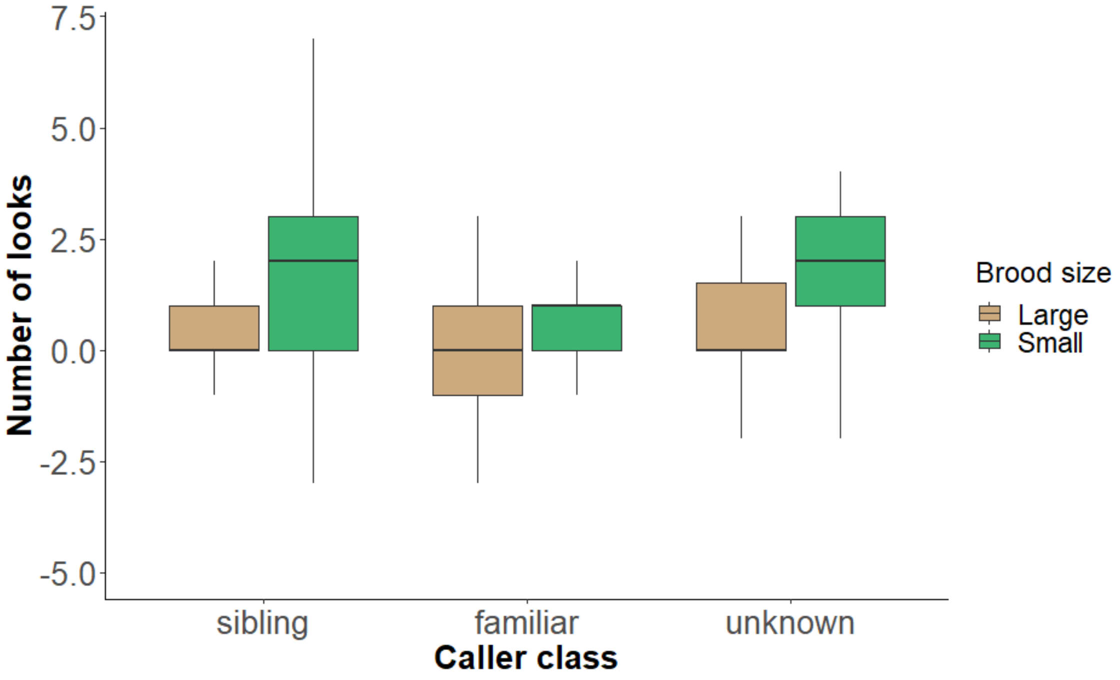
b)

Contrasts	**Estimate ± SE**	**df**	**t ratio**	**p value**
Caller class = Familiar non-sibling				
Sex	-8.21 ± 4.85	91.3	-1.692	0.0940
Caller class = Sibling				
Sex	-3.52 ± 5.04	92.3	-0.697	0.4873
Caller class = Unknown				
Sex	5.68 ± 4.72	87.6	1.203	0.2323

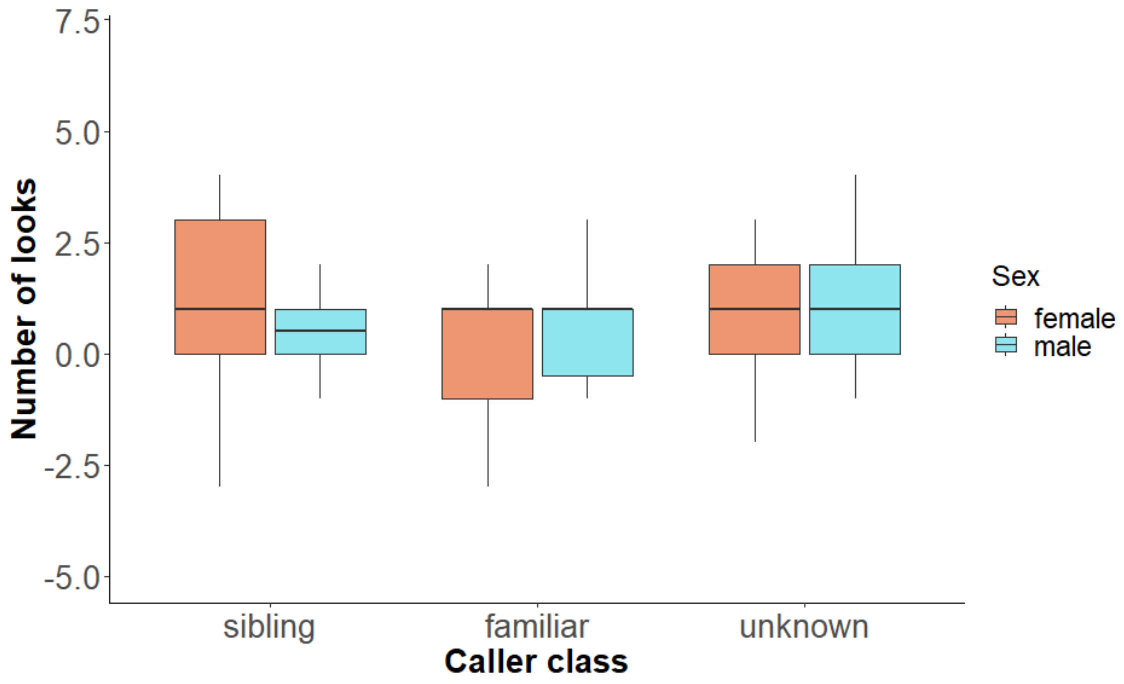
Supplementary Fig. 1. Attention responses of tested individuals toward the three different caller class categories. The figure shows the Δ values (response - baseline) of “Duration of head turns” in seconds, towards the three social categories and colored by “Sex”. The resulting significance from GLMM and *post-hoc* analysis is indicated as * when $P < 0.05$.



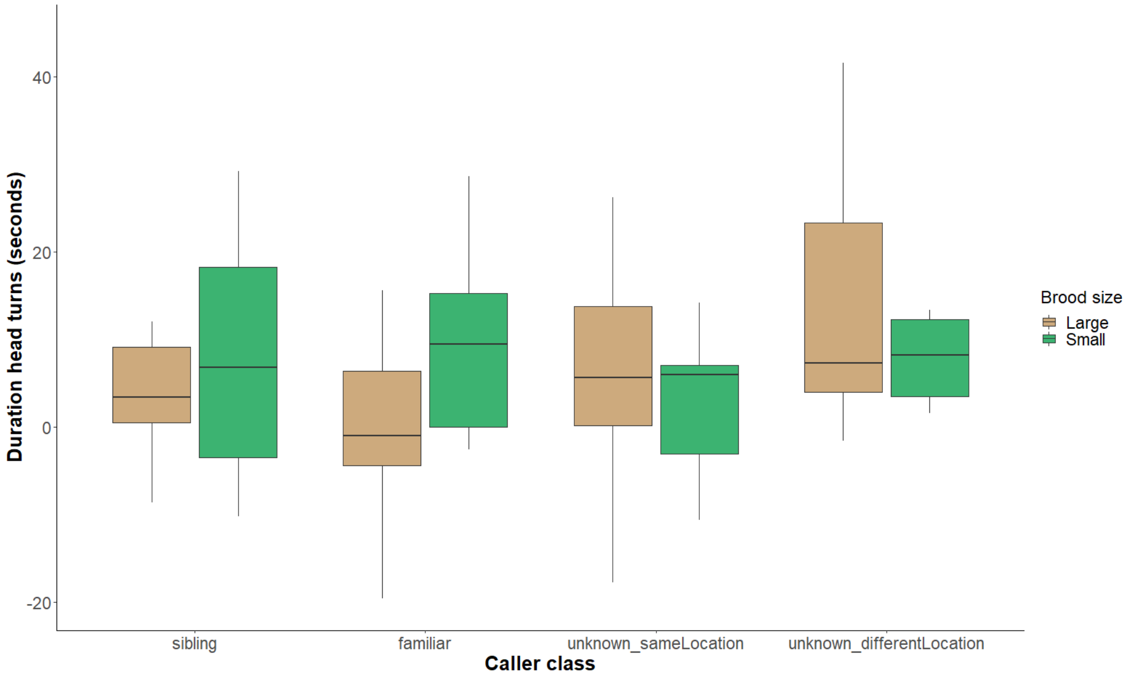
Supplementary Fig. 2. `Number of looks´ toward the three different caller class categories coloured by `Family size´.



Supplementary Fig. 3. `Number of looks´ toward the three different caller class categories colored by `Sex´.



Supplementary figure 4. `Duration of head turns´ of subjects splitting up the “unknown” social category according to the recording location of the calls, from the same vs- a different upbringing location (research station).



REFERENCES

Anderson, C. O., & Mason, W. A. (1978). Competitive social strategies in groups of deprived and experienced rhesus monkeys. *Developmental Psychobiology*, *11*(4), 289–299. https://doi.org/10.1002/dev.420110402

Arnold, C., & Taborsky, B. (2010). Social experience in early ontogeny has lasting effects on social skills in cooperatively breeding cichlids. *Animal Behaviour*, *79*(3), 621–630. https://doi.org/10.1016/j.anbehav.2009.12.008

Asakawa-Haas, K., Schiestl, M., Bugnyar, T., & Massen, J. J. M. (2016). Partner choice in raven (corvus corax) cooperation. *PLoS ONE*, *11*(6). https://doi.org/10.1371/journal.pone.0156962

Bastian, M. L., Sponberg, A. C., Suomi, S. J., & Higley, J. D. (2003). Long-term effects of infant rearing condition on the acquisition of dominance rank in juvenile and adult rhesus macaques (Macaca mulatta). *Developmental Psychobiology*, *42*(1), 44–51. https://doi.org/10.1002/dev.10091

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Bick, J., & Nelson, C. A. (2016). Early adverse experiences and the developing brain. *Neuropsychopharmacology*, *41*(1), 177–196. https://doi.org/10.1038/npp.2015.252

Boeckle, M., & Bugnyar, T. (2012). Long-term memory for affiliates in ravens. *Current Biology*, *22*(9), 801–806. https://doi.org/10.1016/j.cub.2012.03.023

Boeckle, M., Szipl, G., & Bugnyar, T. (2012). Who wants food? Individual characteristics in raven yells. *Animal Behaviour*, *84*(5), 1123–1130. https://doi.org/10.1016/j.anbehav.2012.08.011

Boogert, N. J., Farine, D. R., & Spencer, K. A. (2014). Developmental stress predicts social network position. *Biology Letters*, *10*(10), 1–5. https://doi.org/10.1098/rsbl.2014.0561

Boucherie, P. H., Loretto, M.-C., Massen, J. J. M., & Bugnyar, T. (2019). What constitutes “social complexity” and “social intelligence” in birds? Lessons from ravens. *Behavioral Ecology and Sociobiology*, *73*(1), 12. https://doi.org/10.1007/s00265-018-2607-2

Branchi, I., D’Andrea, I., Fiore, M., Di Fausto, V., Aloe, L., & Alleva, E. (2006). Early Social Enrichment Shapes Social Behavior and Nerve Growth Factor and Brain-Derived Neurotrophic Factor Levels in the Adult Mouse Brain. *Biological Psychiatry*, *60*(7), 690–696. https://doi.org/10.1016/j.biopsych.2006.01.005

Brandl, H. B., Farine, D. R., Funghi, C., Schuett, W., & Griffith, S. C. (2019). Early-life social environment predicts social network position in wild zebra finches. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1897). https://doi.org/10.1098/rspb.2018.2579

Braun, A., & Bugnyar, T. (2012). Social bonds and rank acquisition in raven nonbreeder aggregations. *Animal Behaviour*, *84*(6), 1507–1515. https://doi.org/10.1016/j.anbehav.2012.09.024

Braun, A., Walsdorff, T., Fraser, O. N., & Bugnyar, T. (2012). Socialized sub-groups in a temporary stable Raven flock? *Journal of Ornithology*, *153*(SUPPL. 1), 97–104. https://doi.org/10.1007/s10336-011-0810-2

Buchanan, K. L. (2011). The developmental stress hypothesis: A special case of the evolution of condition-dependent sexual traits. *Behavioral Ecology*, *22*(1), 12–13. https://doi.org/10.1093/beheco/arq083

Bugnyar, T., & Kotrschal, K. (2002). Scrounging tactics in free-ranging ravens, Corvus corax. *Ethology*, *108*(11), 993–1009. https://doi.org/10.1046/j.1439-0310.2002.00832.x

Bugnyar, T., Stöwe, M., & Heinrich, B. (2007). The ontogeny of caching in ravens, Corvus corax. *Animal Behaviour*, *74*(4), 757–767. https://doi.org/10.1016/j.anbehav.2006.08.019

Byrne, R. W., & Whiten, A. (1989). *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans (Oxford Science Publications)*. {Oxford University Press, USA}.

Coombs, F. (1978). *The crows: A study of the corvids of Europe*. BT Batsford Limited.

Dall, S. R. X., & Wright, J. (2009). Rich pickings near large communal roosts favor ‘gang’ foraging by juvenile common ravens, corvus corax. *PLoS ONE*, *4*(2). https://doi.org/10.1371/journal.pone.0004530

D’Andrea, I., Alleva, E., & Branchi, I. (2007). Communal nesting, an early social enrichment, affects social competences but not learning and memory abilities at adulthood. *Behavioural Brain Research*, *183*(1), 60–66. https://doi.org/10.1016/j.bbr.2007.05.029

Ersoy, S., Maag, N., Boehly, T., Boucherie, P. H., & Bugnyar, T. (2021). Sex-specific parental care during postfledging in common ravens. *Animal Behaviour*, *181*, 95–103. https://doi.org/10.1016/j.anbehav.2021.09.004

Farine, D. R., Spencer, K. A., & Boogert, N. J. (2015). Early-life stress triggers juvenile zebra finches to switch social learning strategies. *Current Biology*, *25*(16), 2184–2188. https://doi.org/10.1016/j.cub.2015.06.071

Fischer, S., Bessert-Nettelbeck, M., Kotrschal, A., & Taborsky, B. (2015). Rearing-group size determines social competence and brain structure in a cooperatively breeding cichlid. *American Naturalist*, *186*(1), 123–140. https://doi.org/10.1086/681636

Fraser, O. N., & Bugnyar, T. (2010). Do Ravens Show Consolation? Responses to Distressed Others. *PLoS ONE*, *5*(5). https://doi.org/10.1371/journal.pone.0010605

Fraser, O. N., & Bugnyar, T. (2011). Ravens reconcile after aggressive conflicts with valuable partners. *PLoS ONE*, *6*(3). https://doi.org/10.1371/journal.pone.0018118

Gallego-Abenza, M., Blum, C. R., & Bugnyar, T. (2021). Who is crying wolf? Seasonal effect on antipredator response to age-specific alarm calls in common ravens, Corvus corax. *Learning and Behavior, 49*, 159–167. https://doi.org/10.3758/s13420-020-00455-0

Gamer, M., Lemon, J., & Singh, I. F. P. (2019). *irr: Various Coefficients of Interrater Reliability and Agreement*. https://CRAN.R-project.org/package=irr

Goodwin, D. (1976). *Crows of the World*. Cornell University Press: Ithaca, NY.

Gracceva, G., Venerosi, A., Santucci, D., Calamandrei, G., & Ricceri, L. (2009a). Early social enrichment affects responsiveness to different social cues in female mice. *Behavioural Brain Research*, *196*(2), 304–309. https://doi.org/10.1016/j.bbr.2008.09.023

Gracceva, G., Venerosi, A., Santucci, D., Calamandrei, G., & Ricceri, L. (2009b). Early social enrichment affects responsiveness to different social cues in female mice. *Behavioural Brain Research*, *196*(2), 304–309. https://doi.org/10.1016/j.bbr.2008.09.023

Heinrich, B. (1988). Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by the raven, Corvus corax. *Behavioral Ecology and Sociobiology*, *23*(3), 141–156. https://doi.org/10.1007/BF00300349

Heinrich, B. (1989). *Ravens in Winter* (Summit Books of Simon & Schuster, Ed.; New York). Vintage Books.

Heinrich, B. (1994). Does the Early Common Raven Get (and Show) the Meat? *Auk*, *111*, 764–769. https://doi.org/10.2307/4088489

Heinrich, B. (1999). Planning to facilitate caching: Possible suet cutting by a common raven. *The Wilson Bulletin*, *I*(2), 276–278.

Heinrich, B., & Marzluff, J. M. (1991). Do common ravens yell because they want to attract others? *Behavioral Ecology and Sociobiology*, *28*(1), 13–21. https://doi.org/10.1007/BF00172134

Hesse, S., & Thünken, T. (2014). Growth and social behavior in a cichlid fish are affected by social rearing environment and kinship. *Naturwissenschaften*, *101*(4), 273–283. https://doi.org/10.1007/s00114-014-1154-6

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous Inference in General Parametric Models. *Biometrical Journal*, *50*(3), 346–363.

Humphrey, N. (1976). The social function of intellect. *Growing Points in Ethology*, *1970*, 303 317.

Jolly, A. (1966). Lemur social behavior and primate intelligence. *Science (New York, N.Y.)*, *153*(3735), 501—506. https://doi.org/10.1126/science.153.3735.501

Lenth, R. V. (2021). *emmeans: Estimated Marginal Means, aka Least-Squares Means*. https://CRAN.R-project.org/package=emmeans

Levine, S., & Mody, T. (2003). The long-term psychobiological consequences of intermittent postnatal separation in the squirrel monkey. *Neuroscience and Biobehavioral Reviews*, *27*(1–2), 83–89. https://doi.org/10.1016/S0149-7634(03)00011-3

Loretto, M.-C., Fraser, O. N., & Bugnyar, T. (2012). Ontogeny of Social Relations and Coalition Formation in Common Ravens (Corvus corax). *International Journal of Comparative Psychology*, *25*(3), 180–194. https://doi.org/10.5811/westjem.2011.5.6700

Loretto, M.-C., Schuster, R., & Bugnyar, T. (2016). GPS tracking of non-breeding ravens reveals the importance of anthropogenic food sources during their dispersal in the Eastern Alps. *Current Zoology*, *62*(4), 337–344. https://doi.org/10.1093/cz/zow016

Loretto, M.-C., Schuster, R., Itty, C., Marchand, P., Genero, F., & Bugnyar, T. (2017). Fission-fusion dynamics over large distances in raven non-breeders. *Scientific Reports*, *7*(1), 380.

Massen, J. J. M., Pašukonis, A., Schmidt, J., & Bugnyar, T. (2014). Ravens notice dominance reversals among conspecifics within and outside their social group. *Nature Communications*, *5*, 3679. https://doi.org/10.1038/ncomms4679

Massen, J. J. M., Szipl, G., Spreafico, M., & Bugnyar, T. (2014). Ravens intervene in others' bonding attempts. *Current Biology*, *24*(22), 2733–2736. https://doi.org/10.1016/j.cub.2014.09.073

Massen, J., Schaake, W., & Bugnyar, T. (2020). *A comparison of cooperative cognition in corvids, chimpanzees, and other animals.* (pp. 368–390).

Nowicki, S., Peters, S., & Podos, J. (1998). Song learning, early nutrition and sexual selection in Songbirds. *American Zoologist*, *38*(1), 179–190. https://doi.org/10.1093/icb/38.1.179

Nowicki, S., Searcy, W. A., & Peters, S. (2002). Brain development, song learning and mate choice in birds: A review and experimental test of the 'nutritional stress hypothesis'. *Journal of Comparative Physiology A:*

Neuroethology, Sensory, Neural, and Behavioral Physiology, *188*(11–12), 1003–1014. https://doi.org/10.1007/s00359-002-0361-3

Oliveira, R. F. (2009). Social behavior in context: Hormonal modulation of behavioral plasticity and social competence. *Integrative and Comparative Biology*, *49*(4), 423–440. https://doi.org/10.1093/icb/icp055

R Core Team. (2017). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing. https://www.R-project.org/

Ros-Simó, C., & Valverde, O. (2012). Early-life social experiences in mice affect emotional behaviour and hypothalamic-pituitary-adrenal axis function. *Pharmacology Biochemistry and Behavior*, *102*(3), 434–441. https://doi.org/10.1016/j.pbb.2012.06.001

Sachser, N., Hennessy, M. B., & Kaiser, S. (2011). Adaptive modulation of behavioural profiles by social stress during early phases of life and adolescence. *Neuroscience & Biobehavioral Reviews*, *35*(7), 1518–1533. https://doi.org/10.1016/j.neubiorev.2010.09.002

Sachser, N., Lick, C., & Stanzel, K. (1994). The environment, hormones, and aggressive behaviour: A 5-year-study in guinea pigs. *Psychoneuroendocrinology*, *19*(5), 697–707. https://doi.org/10.1016/0306-4530(94)90051-5

Schloegl, C., Kotrschal, K., & Bugnyar, T. (2007). Gaze following in common ravens, Corvus corax: Ontogeny and habituation. *Animal Behaviour*, *74*, 769–778. https://doi.org/10.1016/j.anbehav.2006.08.017

Sierro, J., Loretto, M. C., Szipl, G., Massen, J. J. M., & Bugnyar, T. (2020). Food calling in wild ravens (Corvus corax) revisited: Who is addressed? *Ethology*, *126*(2), 257–266. https://doi.org/10.1111/eth.12991

Soma, M., Takahasi, M., Ikebuchi, M., Yamada, H., Suzuki, M., Hasegawa, T., & Okanoya, K. (2006). Early Rearing Conditions Affect the Development of Body Size and Song in Bengalese Finches. *Ethology*, *112*(11), 1071–1078. https://doi.org/10.1111/j.1439-0310.2006.01263.x

Stocker, M., Munteanu, A., St??we, M., Schwab, C., Palme, R., & Bugnyar, T. (2016). Loner or socializer? Ravens' adrenocortical response to individual separation depends on social integration. *Hormones and Behavior*, *78*(February), 194–199. https://doi.org/10.1016/j.yhbeh.2015.11.009

Szipl, G., Boeckle, M., Wascher, C. a F., Spreafico, M., & Bugnyar, T. (2015). With whom to dine? Ravens' responses to food-associated calls depend on individual characteristics of the caller. *Animal Behaviour*, *99*, 33–42. https://doi.org/10.1016/j.anbehav.2014.10.015

Szipl, G., Ringler, E., & Bugnyar, T. (2018). Attacked ravens flexibly adjust signalling behaviour according to audience composition. *Proceedings of the Royal Society B*, *285*(June). https://doi.org/10.1098/rspb.2018.0375

Taborsky, B., Arnold, C., Junker, J., & Tschopp, A. (2012). The early social environment affects social competence in a cooperative breeder. *Animal Behaviour*, *83*(4), 1067–1074. https://doi.org/10.1016/j.anbehav.2012.01.037

Taborsky, B., & Oliveira, R. F. (2012). Social competence: An evolutionary approach. *Trends in Ecology and Evolution*, *27*(12), 679–688. https://doi.org/10.1016/j.tree.2012.09.003

Taborsky, B., & Oliveira, R. F. (2013). Social competence vs responsiveness: Similar but not same. A reply to Wolf and McNamara. *Trends in Ecology & Evolution*, *28*(5), 254–255. https://doi.org/10.1016/j.tree.2013.02.005

Tóth, M., Halász, J., Mikics, É., Barsy, B., & Haller, J. (2008). Early social deprivation induces disturbed social communication and violent aggression in adulthood. In *Behavioral Neuroscience* (Vol. 122, Issue 4, pp. 849–854). American Psychological Association. https://doi.org/10.1037/0735-7044.122.4.849

Tottenham, N. (2014). The Importance of Early Experiences for Neuro-affective Development. In *The Neurobiology of Childhood* (pp. 109–129). Springer Berlin Heidelberg. https://doi.org/10.1007/7854

Wright, J., Stone, R. E., & Brown, N. (2003). Communal roost as structured information centre in the raven, Corvus corax. *Journal of Animal Ecology*, *72*(6), 1003–1014. https://doi.org/10.1046/j.1365-2656.2003.00771.x

General Discussion

Thesis overview

Along this thesis, I focused on aspects of social cognition and communication in free-ranging ravens, as well as at to which extent their presence at our study site (and the likelihood of meeting each other) had any effect on their social and communicative decisions. In this thesis, I combined observational and experimental approaches, including clutch size manipulation of captive-bred ravens and GPS-logger fixes to measure individual vagrancy pattern of wild-caught ravens. Furthermore, I investigated the attentive responses of individual ravens to played back calls of different value, testing possible effects of early-social environment (brood size at upbringing, familiarity to non-kin after leaving parents) and possible links to the phenotypic variation in individual vagrancy (how much birds were moving between foraging groups). Applying cognition was demonstrated to have positive consequences in wild ravens during social foraging in i) avoiding kleptoparasitism and ii) assessing threat through alarm callers´ traits. Whereas no correlation was found between attentive behaviour to social cues and phenotypic variation in vagrancy, such attention response was partly explained by early-social environment, as little variation in brood size and familiarity to non-kin affected the birds´ responses to played back calls.

Social cognition in common ravens non-breeder groups

The working hypotheses of the four chapters that compile this thesis were embedded in the social intelligence hypothesis (Byrne & Whiten, 1989; Dunbar, 1998). Under this framework, individuals that repeatedly interact with group members should show more sophisticated social knowledge and competence than those individuals that interact only occasionally. Such knowledge/competence gained through social interactions should provide benefits in terms of avoiding conflicts and coping with competition for resources.

In Chapter 1, I tested this assumption during ravens´ group foraging at the feedings of wild boars in the Cumberland Wildpark. Contrary to my expectation, the time being present at our study area (as a proxy for repeated encounters) did not have a clear effect on the ravens´ foraging success. Specifically, the percentage of days that individual ravens spent foraging with others did not correlate with their foraging success in avoiding kleptoparasitism. Interestingly, our recent analysis of long-term data on agonistic interactions at foraging (Appendix Chapter) revealed that ravens consistently established a dominance hierarchy despite of the open composition of the foraging groups (Boucherie et al., 2022), i.e. how much ravens were present/absent at our site hardly affected the hierarchy. The exception were juveniles (<1 year old) that did suffer aggressions during integration and re-integration periods. The apparent lack of vagrancy effects in older ravens indicates that ravens are skilled enough to keep track of others and maintain a hierarchy under a changing social environment. Even though these findings were unexpected, they fit to the advanced inference skills reported for captive ravens (Massen, Pašukonis, et al., 2014) and corvids in general (e.g. transitive inference: Mikolasch et al., 2013; Paz-y-Miño C et al., 2004). Unfortunately, the study in chapter 1 was conceived before the analysis of the long-term dominance hierarchy. With our current knowledge, my initial prediction for the potential effect of individual presence patterns on social foraging success would have been restricted to juveniles; the assumption of an effect of age and experience, respectively, has been supported, however. Indeed, when ravens attempted to carry food away, their success in keeping the food was age-depended (with adults doing best and subadults doing better than juveniles), which aligned well with the findings of the long-term dominance study (where juveniles received more aggressions than subadults and adults). Notably the results for subadults indicate that having experience with foraging competition might help ravens to choose the right moment to leave with food. Their decisions could be based on the audience composition (presence/absence of dominants or bonding partners) and/or the temporary distraction of potential competitors, supporting my initial assumption that social cognition plays a role in foraging.

The open character of raven foraging groups could also affect the information transmission across groups. For instance, ravens from local groups may be confronted with unfamiliar birds visiting their groups and giving alarm calls. In Chapter 2, I experimentally staged such a scenario with a playback design and investigated whether ravens at our study site would take into account the age-class and the number of unfamiliar individuals uttering alarm calls. Concerning age class, the results (almost) aligned with my prediction: in two out of three seasons (summer and autumn but not in spring) ravens responded stronger to alarm calls from adults compared to those from juveniles. This indicates that ravens can flexibly adapt their antipredator responses based on the callers´ individual traits such as age and (potentially) life experience. However, the ravens did not meet my second prediction as they did not show a stronger response when the alarm calls were uttered by two distinct same-aged individuals as compared to a single caller. The latter findings stand in contrast to those of jackdaws (*Corvus monedula*), which in a similar playback experiment were capable to discriminate between different number of callers (Coomes et al., 2019). However, the ravens in my study were exposed to a lower intra-individual variation (1 vs 2 callers) than the jackdaws (1 vs 5 callers), possibly affecting their capability for numerical discrimination. Indeed, it is well known that quantity discrimination follows Weber-Fechner´s law; hence, for most animals, large difference are easier to discriminate than small ones (Cantlon & Brannon, 2006; Izard & Dehaene, 2008; Tornick et al., 2015). Further studies need to take a closer look into the cognitive abilities to extract encoded information of callers´ traits.

In Chapters 3 and 4, I investigated attentive responses towards social cues of ravens in a playback design, but unlike in the previous Chapter 2, here I tested birds in individual isolation. The chapters differ in their research question and the background of the study subjects: in Chapter 3, wild-caught ravens were exposed to calls simulating agonistic interactions and territorial encounters, whereas in Chapter 4, captive-bred ravens with known upbringing histories were exposed to acoustical variation in food-associated calls. In Chapter 3, I investigated whether ravens that more frequently encounter different foraging groups (high vagrancy) would show a differentiated response to the played back calls than ravens that tend to stay in a local group. Contrary to my predictions, the ravens´ attentive responses towards acoustic social cues, did not correlate with their vagrancy pattern obtained through GPS-logger information in the month post-release. Among other aspects, I potentially underestimated the amount of days needed to calculate the individuals´ vagrancy profiles (as a proxy for fission-fusion dynamics). A further aspect to consider was that most of the tested ravens were juveniles (within their first year) with not fully developed and/or little practiced social skills. Unfortunately, we hardly had any information regarding individual life-history of the wild-caught ravens. It is known from numerous social species that early-social environment may influence the animals´ social skills later in life (Branchi & Alleva, 2006; S. Fischer et al., 2015). Therefore, in the chapter 4, I focused on one aspect of early-social environment in ravens, the number of siblings they were reared with (by manipulating the brood sizes of our captive colony over consecutive years in a cross-design). Once the ravens left their parents, I investigated whether growing up with one or more siblings had an effect on their birds´ responses to social information encoded in food calls.

Indeed, juveniles reared in the presence of a single sibling showed stronger responses to social cues than juveniles reared with two or three siblings and this difference was most pronounced with calls from familiar non-kin. These findings indicate that early social environment may play a role in socialization strategies, particularly at the time when ravens leave their parent´s territory and join non-breeder groups.

Conclusion

Overall, this thesis provides insights into three different aspects of the social life of common ravens. First, during foraging, ravens profit from aspects of cognition: they may use personal experience and social information to avoid kleptoparasitism (chapter 1) and to avoid overreaction when unexperienced individuals alert for predators (chapter 2). Second, contrary to our initial expectations, our measurements on individual vagrancy patterns did not have the expected effect on foraging success (Chapter 1) or attentive responses to social cues (Chapter 3). Moreover, our analysis of agonistic interactions across years in two different time periods (2008-10 and 2017-19) revealed that beside the fluid character of raven foraging groups, a steep and transitive dominance hierarchy is established (Appendix chapter). Taken together, these findings leave me to question whether I have overestimated the important of fission-fusion dynamics on the ravens´ socio-cognitive skills. Alternatively, our measures for proxis of fission-fusion dynamics were not appropriate to detect possible effects. For instance, vagrancy analyses based on one month might not be sufficient to show differences in foraging success or attention-driven behaviours to social cues. Third, the brood size manipulation in our captive breeding colony revealed that subtle differences in sibling number can affect how ravens process social information later in life (Chapter 4). Further studies are needed to understand the extent to which early social environment might shape individuals´ socio-cognitive skills and thus could contribute to the substantial individual variation in vagrancy during non-breeding period. Possibly such findings could be extrapolated to other social species with high degree of fission-fusion dynamics, such as bottlenose dolphins (Connor et al., 2000), African elephants (Moss & Lee, 2011) or bats (Kerth et al., 2006). Even though those mammals typically give birth to one offspring at a time, variation in communal rearing could be a factor comparable to the variation in brood size as studied in the present thesis.

REFERENCES (General Discussion)

Amici, F., Aureli, F., & Call, J. (2008). Fission-Fusion Dynamics, Behavioral Flexibility, and Inhibitory Control in Primates. *Current Biology*, *18*(18), 1415–1419. https://doi.org/10.1016/j.cub.2008.08.020

Aplin, L. M., Firth, J. A., Farine, D. R., Voelkl, B., Crates, R. A., Culina, A., Garroway, C. J., Hinde, C. A., Kidd, L. R., Psorakis, I., Milligan, N. D., Radersma, R., Verhelst, B. L., & Sheldon, B. C. (2015). Consistent individual differences in the social phenotypes of wild great tits, Parus major. *Animal Behaviour*, *108*, 117–127. https://doi.org/10.1016/j.anbehav.2015.07.016

Ashton, B. J., Ridley, A. R., Edwards, E. K., & Thornton, A. (2018). Cognitive performance is linked to group size and affects fitness in Australian magpies. *Nature*, *554*(7692), 364–367. https://doi.org/10.1038/nature25503

Ashton, B. J., Thornton, A., & Ridley, A. R. (2018). An intraspecific appraisal of the social intelligence hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1756), 20170288. https://doi.org/10.1098/rstb.2017.0288

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., Connor, R., Fiore, A. D., Dunbar, R. I. M., Henzi, S. P., Holekamp, K., Korstjens, A. H., Layton, R., Lee, P., Lehmann, J., Manson, J. H., Ramos-Fernandez, G., Strier, K. B., & Schaik, C. P. van. (2008). Fission-Fusion Dynamics. *Current Anthropology*, *49*(4), 627–654. https://doi.org/10.1086/586708

Aureli, F., & Schino, G. (2019). Social complexity from within: How individuals experience the structure and organization of their groups. *Behavioral Ecology and Sociobiology*, *73*(1). https://doi.org/10.1007/s00265-018-2604-5

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bernstein, I. S. (1981). Dominance: The baby and the bathwater. *Behavioral and Brain Sciences*, *4*(3), 419–429.

Blum, C. R., Fitch, W. T., & Bugnyar, T. (2020). Rapid learning and long-term memory for dangerous humans in ravens (Corvus corax). *Frontiers in Psychology*, *11*, 2843.

Boeckle, M., & Bugnyar, T. (2012). Long-term memory for affiliates in ravens. *Current Biology*, *22*(9), 801–806. https://doi.org/10.1016/j.cub.2012.03.023

Boeckle, M., Szipl, G., & Bugnyar, T. (2012). Who wants food? Individual characteristics in raven yells. *Animal*

Behaviour, *84*(5), 1123–1130. https://doi.org/10.1016/j.anbehav.2012.08.011

Bonnie, K. E., & Earley, R. L. (2007). Expanding the scope for social information use. *Animal Behaviour*, *74*(2), 171–181. https://doi.org/10.1016/j.anbehav.2006.12.009

Boogert, N. J., Madden, J. R., Morand-Ferron, J., & Thornton, A. (2018). Measuring and understanding individual differences in cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1756), 20170280. https://doi.org/10.1098/rstb.2017.0280

Borgeaud, C., van de Waal, E., & Bshary, R. (2013). Third-Party Ranks Knowledge in Wild Vervet Monkeys (Chlorocebus aethiops pygerythrus). *PLoS ONE*, *8*(3), e58562. https://doi.org/10.1371/journal.pone.0058562

Boucherie, P. H., Blum, C. R., & Bugnyar, T. (2020). Effect of rearing style on the development of social behaviour in young ravens (Corvus corax). *Ethology*, *00*(March), 1–15. https://doi.org/10.1111/eth.13010

Boucherie, P. H., Gallego-Abenza, M., Massen, J. J. M., & Bugnyar, T. (2022). *Dominance in a socially dynamic setting: Hierarchical structure and conflict dynamics in ravens' foraging groups*. *377*(1845), 12. https://doi.org/10.1098/rstb.2020.0446

Boucherie, P. H., Loretto, M., Massen, J. J. M., & Bugnyar, T. (2019). *Lessons from ravens What constitutes B social complexity ^ and B social intelligence ^ in birds? Lessons from ravens*. *January*.

Branchi, I., & Alleva, E. (2006). Communal nesting, an early social enrichment, increases the adult anxiety-like response and shapes the role of social context in modulating the emotional behavior. *Behavioural Brain Research*, *172*(2), 299–306. https://doi.org/10.1016/j.bbr.2006.05.019

Brandl, H. B., Farine, D. R., Funghi, C., Schuett, W., & Griffith, S. C. (2019). Early-life social environment predicts social network position in wild zebra finches. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1897). https://doi.org/10.1098/rspb.2018.2579

Braun, A., & Bugnyar, T. (2012). Social bonds and rank acquisition in raven nonbreeder aggregations. *Animal Behaviour*, *84*(6), 1507–1515. https://doi.org/10.1016/j.anbehav.2012.09.024

Braun, A., Walsdorff, T., Fraser, O. N., & Bugnyar, T. (2012a). Socialized sub-groups in a temporary stable Raven flock? *Journal of Ornithology*, *153*(SUPPL. 1), 97–104. https://doi.org/10.1007/s10336-011-0810-2

Braun, A., Walsdorff, T., Fraser, O. N., & Bugnyar, T. (2012b). Socialized sub-groups in a temporary stable Raven flock? *Journal of Ornithology*, *153*(SUPPL. 1), 97–104. https://doi.org/10.1007/s10336-011-0810-2

Brooks, M. E., Kristensen, K., Benthem, K. J. van, Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., & Bolker, B. M. (2017). GlmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated

Generalized Linear Mixed Modeling. *The R Journal*, *9*(2), 378–400.

Bugnyar, T., & Heinrich, B. (2006). Pilfering ravens, Corvus corax, adjust their behaviour to social context and identity of competitors. *Animal Cognition*, *9*(4), 369–376. https://doi.org/10.1007/s10071-006-0035-6

Bugnyar, T., & Kotrschal, K. (1997). *An experimental analysis of social foraging in ravens: Individual tactics, scrounging, and deception*. *32*, 497.

Bugnyar, T., & Kotrschal, K. (2001). Movement coordination and signalling in ravens (corvus corax): An experimental field study. *Acta Ethologica*, *3*(2), 101–109. https://doi.org/10.1007/s102110000029

Byrne, R. W., & Corp, N. (2004). Neocortex size predicts deception rate in primates. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(1549), 1693–1699. https://doi.org/10.1098/rspb.2004.2780

Byrne, R. W., & Whiten, A. (1989). *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans (Oxford Science Publications)*. {Oxford University Press, USA}.

Calenge, C. (2006). The package adehabitat for the R software: Tool for the analysis of space and habitat use by animals. *Ecological Modelling*, *197*, 1035.

Cantlon, J. F., & Brannon, E. M. (2006). Shared System for Ordering Small and Large Numbers in Monkeys and Humans. *Psychological Science*, *17*(5), 401–406. https://doi.org/10.1111/j.1467-9280.2006.01719.x

Chance, M. R. A. (1967). Attention Structure as the Basis of Primate Rank Orders. *Man*, *2*(4), 503–518. JSTOR. https://doi.org/10.2307/2799336

Cheney, D. L., & Seyfarth, R. M. (1986). The recognition of social alliances by vervet monkeys. *Animal Behaviour*, *34*(6), 1722–1731. https://doi.org/10.1016/S0003-3472(86)80259-7

Connor, R., Wells, R., Mann, J., & Read, A. J. (2000). *The bottlenose dolphin, Tursiops sp.: Social relationships in a fission-fusion society.* (Whitehead H, pp. 91–126). The University of Chicago Press.

Connor, R., & Whitehead, H. (2005). Alliances II. Rates of encounter during resource utilization: A general model of intrasexual alliance formation in fission–fusion societies. *Animal Behaviour*, *69*(1), 127–132. https://doi.org/10.1016/j.anbehav.2004.02.022

Coombs, F. (1978). *The crows: A study of the corvids of Europe*. BT Batsford Limited.

Coomes, J. R., Mcivor, G. E., Thornton, A., Coomes, J. R., & Thornton, A. (2019). Evidence for individual discrimination and numerical assessment in collective antipredator behaviour in wild jackdaws (Corvus monedula). *Biology Letters*.

Crailsheim, D., Stüger, H. P., Kalcher-Sommersguter, E., & Llorente, M. (2020). Early life experience and alterations of group composition shape the social grooming networks of former pet and entertainment chimpanzees (Pan troglodytes). *PLoS ONE*, *15*(1), 1–26. https://doi.org/10.1371/journal.pone.0226947

Crick, N. R., & Dodge, K. A. (1994). A review and reformulation of social information-processing mechanisms in children's social adjustment. *Psychological Bulletin*, *115*(1), 74–101. https://doi.org/10.1037/0033-2909.115.1.74

Dall, S. R. X., Giraldeau, L. A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology and Evolution*, *20*(4), 187–193. https://doi.org/10.1016/j.tree.2005.01.010

Danchin, É., Giraldeau, L.-A., Valone, T. J., & Wagner, R. H. (2004). Public Information: From Nosy Neighbors to Cultural Evolution. *Science*, *305*(5683), 487–491. https://doi.org/10.1126/science.1098254

Delignette-Muller, M. L., & Dutang, C. (2015). fitdistrplus: An R Package for Fitting Distributions. *Journal of Statistical Software*, *64*(4), 1–34. https://doi.org/10.18637/jss.v064.i04

Dunbar, R. I. M. (1992). Neocortex size as a constraint on group size in primates. *Journal of Human Evolution*, *22*(6), 469–493. https://doi.org/10.1016/0047-2484(92)90081-J

Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology: Issues, News, and Reviews*, *6*(5), 178–190. https://doi.org/10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.0.CO;2-8

Dunbar, R. I. M., & Shultz, S. (2007). Evolution in the Social Brain. *Science*, *317*(5843), 1344–1347. https://doi.org/10.1126/science.1145463

Emery, N. J., Seed, A. M., von Bayern, A. M. P., & Clayton, N. S. (2007). Cognitive adaptations of social bonding in birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1480), 489–505. https://doi.org/10.1098/rstb.2006.1991

Farine, D. R., Spencer, K. A., & Boogert, N. J. (2015). Early-life stress triggers juvenile zebra finches to switch social learning strategies. *Current Biology*, *25*(16), 2184–2188. https://doi.org/10.1016/j.cub.2015.06.071

Fischer, J., Farnworth, M. S., Sennhenn-Reulen, H., & Hammerschmidt, K. (2017). Quantifying social complexity. *Animal Behaviour*, *130*, 57–66. https://doi.org/10.1016/J.ANBEHAV.2017.06.003

Fischer, S., Bessert-Nettelbeck, M., Kotrschal, A., & Taborsky, B. (2015). Rearing-group size determines social competence and brain structure in a cooperatively breeding cichlid. *American Naturalist*, *186*(1), 123–140. https://doi.org/10.1086/681636

Fortin, D., Fortin, M.-E., Beyer, H. L., Duchesne, T., Courant, S., & Dancose, K. (2009). Group-size-mediated habitat selection and group fusion–fission dynamics of bison under predation risk. *Ecology*, *90*(9), 2480–2490. https://doi.org/10.1890/08-0345.1

Fraser, O. N., & Bugnyar, T. (2010). The quality of social relationships in ravens. *Animal Behaviour*, *79*(4), 927–933. https://doi.org/10.1016/j.anbehav.2010.01.008

Gill, S. A., & Bierema, A. M.-K. (2013). On the Meaning of Alarm Calls: A Review of Functional Reference in Avian Alarm Calling. *Ethology*, *119*(6), 449–461. https://doi.org/10.1111/eth.12097

Goodwin, D. (1976). *Crows of the World*. Cornell University Press: Ithaca, NY.

Griffin, A. S. (2004). Social learning about predators: A review and prospectus. *Animal Learning & Behavior*, *32*(1), 131–140. https://doi.org/10.3758/BF03196014

Grosenick, L., Clement, T. S., & Fernald, R. D. (2007). Fish can infer social rank by observation alone. *Nature*, *445*(7126), 429–432. https://doi.org/10.1038/nature05511

Gwinner, E. (1964). Untersuchungen über das ausdrucks- und sozialverhalten des kolkraben (Corvus corax). Z. *Tierpsychol*, *21*, 145–178.

Healy, S., Dekort, S., & Clayton, N. (2005). The hippocampus, spatial memory and food hoarding: A puzzle revisited. *Trends in Ecology & Evolution*, *20*(1), 17–22. https://doi.org/10.1016/j.tree.2004.10.006

Heinrich, B. (1988a). Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by the raven, Corvus corax. *Behavioral Ecology and Sociobiology*, *23*(3), 141–156. https://doi.org/10.1007/BF00300349

Heinrich, B. (1988b). Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by the raven, Corvus corax. *Behavioral Ecology and Sociobiology*, *23*(3), 141–156. https://doi.org/10.1007/BF00300349

Heinrich, B. (1989). *Ravens in Winter* (Summit Books of Simon & Schuster, Ed.). Vintage Books. https://books.google.at/books?id=YbWtadkEVvUC

Heinrich, B. (1994). Dominance and weight changes in the common raven, Corvus corax. *Animal Behaviour*, *48*(6), 1463–1465. https://doi.org/10.1006/anbe.1994.1384

Heinrich, B., & Marzluff, J. (1992). Age and Mouth Color in Common Ravens. *The Condor*, *94*(2), 549–550. https://doi.org/10.2307/1369233

Heinrich, B., & Marzluff, J. M. (1991). Do common ravens yell because they want to attract others? *Behavioral Ecology and Sociobiology*, *28*(1), 13–21. https://doi.org/10.1007/BF00172134

Heinrich, B., Marzluff, J. M., & Marzluff, C. S. (1993). *Common ravens are attracted by appeasement calls of food discoverers when attacked*. *110*, 247–254.

Heinrich, B., & Pepper, J. W. (1998). Influence of competitors on caching behaviour in the common raven, Corvus corax. *Animal Behaviour*, *56*, 1083–1090.

Heinrich, B., & Smolker, R. (1998). Play in common ravens (Corvus corax). In *Animal play: Evolutionary, comparative, and ecological perspectives.* (pp. 27–44). Cambridge University Press. https://doi.org/10.1017/CBO9780511608575.003

Henke-von der Malsburg, J., Kappeler, P. M., & Fichtel, C. (2020). Linking ecology and cognition: Does ecological specialisation predict cognitive test performance? *Behavioral Ecology and Sociobiology*, *74*(12), 154. https://doi.org/10.1007/s00265-020-02923-z

Hesse, S., & Thünken, T. (2014). Growth and social behavior in a cichlid fish are affected by social rearing environment and kinship. *Naturwissenschaften*, *101*(4), 273–283. https://doi.org/10.1007/s00114-014-1154-6

Hinde, R. A. (1976). Interactions, Relationships and Social Structure. *Man*, *11*(1), 1–17. JSTOR. https://doi.org/10.2307/2800384

Humphrey, N. (1976). The social function of intellect. *Growing Points in Ethology*, *1970*, 303 317.

Humphrey N K. (1976). The social function of intellect. In *Growing points in ethology* (pp. 303–317). In P. Bateson, & R. A. Hinde (Eds).

Izard, V., & Dehaene, S. (2008). Calibrating the mental number line. *Cognition*, *106*(3), 1221–1247. https://doi.org/10.1016/j.cognition.2007.06.004

Jain, V., Bugnyar, T., Cunningham, Susan J., Gallego-Abenza, M., Loretto, M.-C., & Sumasgutner, Petra. (2022). *The spatial and temporal exploitation of anthropogenic food sources by common ravens (Corvus corax) in the Alps*.

Johnson, C. M., & Karin-D'Arcy, M. R. (2006). Social Attention in Nonhuman Primates: A Behavioral Review. *Aquatic Mammals*, *32*(4), 423–442. https://doi.org/10.1578/AM.32.4.2006.423

Jolly, A. (1966). Lemur social behavior and primate intelligence. *Science (New York, N.Y.)*, *153*(3735), 501—506. https://doi.org/10.1126/science.153.3735.501

Kanai, R., Bahrami, B., Roylance, R., & Rees, G. (2012). Online social network size is reflected in human brain structure. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1732), 1327–1334. https://doi.org/10.1098/rspb.2011.1959

Kerth, G., Ebert, C., & Schmidtke, C. (2006). Group decision making in fission–fusion societies: Evidence from two-field experiments in Bechstein's bats. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1602), 2785–2790. https://doi.org/10.1098/rspb.2006.3647

Kummer, H. (1971). *Primate Societies*.

Lefebvre, L., Nicolakakis, N., & Boire, D. (2002). Tools and brains in birds. *Behaviour*, *139*(7), 939–973. https://doi.org/10.1163/156853902320387918

Liker, A., & Bokony, V. (2009). Larger groups are more successful in innovative problem solving in house sparrows. *Proceedings of the National Academy of Sciences*, *106*(19), 7893–7898. https://doi.org/10.1073/pnas.0900042106

Loretto, M.-C., Reimann, S., Schuster, R., Graulich, D. M., & Bugnyar, T. (2016). Shared space, individually used: Spatial behaviour of non-breeding ravens (Corvus corax) close to a permanent anthropogenic food source. *Journal of Ornithology*, *157*(2), 439–450. https://doi.org/10.1007/s10336-015-1289-z

Loretto, M.-C., Schuster, R., & Bugnyar, T. (2016). GPS tracking of non-breeding ravens reveals the importance of anthropogenic food sources during their dispersal in the Eastern Alps. *Current Zoology*, *62*(4), 337–344. https://doi.org/10.1093/cz/zow016

Loretto, M.-C., Schuster, R., Itty, C., Marchand, P., Genero, F., & Bugnyar, T. (2017a). Fission-fusion dynamics over large distances in raven non-breeders. *Scientific Reports*, *7*(1), 380. https://doi.org/10.1038/s41598-017-00404-4

Loretto, M.-C., Schuster, R., Itty, C., Marchand, P., Genero, F., & Bugnyar, T. (2017b). Fission-fusion dynamics over large distances in raven non-breeders. *Scientific Reports*, *7*(1), 380.

Marzluff, J. M., & Angell, T. (2007). *In the Company of Crows and Ravens*. Yale University Press.

Marzluff, J. M., Heinrich, B., & Marzluff, C. S. (1996). Raven roosts are mobile information centres. *Animal Behaviour*, *51*(1), 89–103. https://doi.org/10.1006/anbe.1996.0008

Massen, J. J. M., Pašukonis, A., Schmidt, J., & Bugnyar, T. (2014). Ravens notice dominance reversals among conspecifics within and outside their social group. *Nature Communications*, *5*, 3679. https://doi.org/10.1038/ncomms4679

Massen, J. J. M., Szipl, G., Spreafico, M., & Bugnyar, T. (2014). Ravens intervene in others' bonding attempts. *Current Biology*, *24*(22), 2733–2736. https://doi.org/10.1016/j.cub.2014.09.073

McNelis, N. L., & Boatright-Horowitz, S. L. (1998). Social monitoring in a primate group: The relationship between visual attention and hierarchical ranks. *Animal Cognition*, *1*(1), 65–69. https://doi.org/10.1007/s100710050008

Mikolasch, S., Kotrschal, K., & Schloegl, C. (2013). Transitive inference in jackdaws (Corvus monedula). *Behavioural*

Processes, *92*, 113–117. https://doi.org/10.1016/j.beproc.2012.10.017

Milton, K. (1981). Distribution Patterns of Tropical Plant Foods as an Evolutionary Stimulus to Primate Mental Development. *American Anthropologist*, *83*(3), 534–548. https://doi.org/10.1525/aa.1981.83.3.02a00020

Moss, C., & Lee, P. (2011). Female social dynamics: Fidelity and flexibility. In *The Amboseli elephants: A long-term perspective on a long-lived mammal* (pp. 205–223). University of Chicago Press: Chicago, IL, USA.

Nácarová, J., Veselý, P., & Bugnyar, T. (2018). Ravens adjust their antipredatory responses to con- - and specific alarms to the perceived threat. *Ethology*, *May*, 1–8. https://doi.org/10.1111/eth.12764

Olkowicz, S., Kocourek, M., Lučan, R. K., Porteš, M., Fitch, W. T., Herculano-Houzel, S., & Němec, P. (2016). Birds have primate-like numbers of neurons in the forebrain. *Proceedings of the National Academy of Sciences*, *113*(26), 7255–7260. https://doi.org/10.1073/pnas.1517131113

Parker, S. T., & Gibson, K. R. (1977). Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. *Journal of Human Evolution*, *6*(7), 623–641. https://doi.org/10.1016/S0047-2484(77)80135-8

Paz-y-Miño C, G., Bond, A. B., Kamil, A. C., & Balda, R. P. (2004). Pinyon jays use transitive inference to predict social dominance. *Nature*, *430*(7001), 778–781. https://doi.org/10.1038/nature02723

Pravosudov, V. V., & Roth II, T. C. (2013). Cognitive Ecology of Food Hoarding: The Evolution of Spatial Memory and the Hippocampus. *Annual Review of Ecology, Evolution, and Systematics*, *44*(1), 173–193. https://doi.org/10.1146/annurev-ecolsys-110512-135904

R Core Team. (2017). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing. https://www.R-project.org/

Reader, S. M., & Laland, K. N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences*, *99*(7), 4436–4441. https://doi.org/10.1073/pnas.062041299

Rosati, A. G. (2017a). Foraging Cognition: Reviving the Ecological Intelligence Hypothesis. *Trends in Cognitive Sciences*, *21*(9), 691–702. https://doi.org/10.1016/j.tics.2017.05.011

Rosati, A. G. (2017b). Foraging Cognition: Reviving the Ecological Intelligence Hypothesis. *Trends in Cognitive Sciences*, *21*(9), 691–702. https://doi.org/10.1016/j.tics.2017.05.011

Rösner, S., & Selva, N. (2005). Use of the bait-marking method to estimate the territory size of scavenging birds: A case study on ravens Corvus corax. *Wildlife Biology*, *11*(3), 183–191. https://doi.org/10.2981/0909-6396(2005)11[183:UOTBMT]2.0.CO;2

Sachser, N., Kaiser, S., & Hennessy, M. B. (2013). Behavioural profiles are shaped by social experience: When, how and why. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1618), 20120344. https://doi.org/10.1098/rstb.2012.0344

Sallet, J., Mars, R. B., Noonan, M. P., Andersson, J. L., O'Reilly, J. X., Jbabdi, S., Croxson, P. L., Jenkinson, M., Miller, K. L., & Rushworth, M. F. S. (2011). Social Network Size Affects Neural Circuits in Macaques. *Science*, *334*(6056), 697–700. https://doi.org/10.1126/science.1210027

Shettleworth, S. J. (1998). *Cognition, evolution, and behavior.* (pp. xv, 688). Oxford University Press.

Sierro, J., Loretto, M. C., Szipl, G., Massen, J. J. M., & Bugnyar, T. (2020). Food calling in wild ravens (Corvus corax) revisited: Who is addressed? *Ethology*, *126*(2), 257–266. https://doi.org/10.1111/eth.12991

Silk, J. B. (1999). Male bonnet macaques use information about third-party rank relationships to recruit allies. *Animal Behaviour*, *58*(1), 45–51. https://doi.org/10.1006/anbe.1999.1129

Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social Bonds of Female Baboons Enhance Infant Survival. *Science*, *302*(5648), 1231–1234. https://doi.org/10.1126/science.1088580

Silk, M. J., Croft, D. P., Tregenza, T., & Bearhop, S. (2014). The importance of fission-fusion social group dynamics in birds. *Ibis*, *156*(4), 701–715. https://doi.org/10.1111/ibi.12191

Sloan, J. L., & Hare, J. F. (2008). The More the Scarier: Adult Richardson's Ground Squirrels (Spermophilus richardsonii) Assess Response Urgency Via the Number of Alarm Signallers. *Ethology*, *114*(5), 436–443. https://doi.org/10.1111/j.1439-0310.2008.01479.x

Smuts, B., Cheney, D., Seyfarth, R., Wrangham, R., & Struhsaker, T. (1987). *Primate Societies*. Chicago Press.

Sol, D. (2009). Revisiting the cognitive buffer hypothesis for the evolution of large brains. *Biology Letters*, *5*(1), 130–133. https://doi.org/10.1098/rsbl.2008.0621

Szipl, G., Ringler, E., & Bugnyar, T. (2018a). Attacked ravens flexibly adjust signalling behaviour according to audience composition. *Proceedings of the Royal Society B*, *285*(June). https://doi.org/10.1098/rspb.2018.0375

Szipl, G., Ringler, E., & Bugnyar, T. (2018b). Attacked ravens flexibly adjust signalling behaviour according to audience composition. *Proceedings of the Royal Society B*, *285*(June). https://doi.org/10.1098/rspb.2018.0375

Taborsky, B., & Oliveira, R. F. (2012a). Social competence: An evolutionary approach. *Trends in Ecology and Evolution*, *27*(12), 679–688. https://doi.org/10.1016/j.tree.2012.09.003

Taborsky, B., & Oliveira, R. F. (2012b). Social competence: An evolutionary approach. *Trends in Ecology & Evolution*, *27*(12), 679–688. https://doi.org/10.1016/j.tree.2012.09.003

Templeton, C. N. (2018). Animal Communication: Learning by Listening about Danger. *Current Biology*, *28*(16), R892–R894. https://doi.org/10.1016/j.cub.2018.07.039

Tomasello, M., & Call, J. (1997). *Primate cognition*. Oxford Univ. Press. https://pure.mpg.de/pubman/faces/ViewItemOverviewPage.jsp?itemId=item_2260164

Tornick, J. K., Callahan, E. S., & Gibson, B. M. (2015). An investigation of quantity discrimination in Clark's nutcrackers (Nucifraga columbiana). *Journal of Comparative Psychology*, *129*(1), 17–25. https://doi.org/10.1037/a0037863

Varela, S. A. M., Teles, M. C., & Oliveira, R. F. (2020). The correlated evolution of social competence and social cognition. *Functional Ecology*, *34*(2), 332–343. https://doi.org/10.1111/1365-2435.13416

Waters, E., & Sroufe, L. A. (1983a). Social competence as a developmental construct. *Developmental Review*, *3*(1), 79–97. https://doi.org/10.1016/0273-2297(83)90010-2

Waters, E., & Sroufe, L. A. (1983b). Social competence as a developmental construct. *Developmental Review*, *3*(1), 79–97. https://doi.org/10.1016/0273-2297(83)90010-2

Weiß, B. M., Kehmeier, S., & Schloegl, C. (2010). Transitive inference in free-living greylag geese, Anser anser. *Animal Behaviour*, *79*(6), 1277–1283. https://doi.org/10.1016/j.anbehav.2010.02.029

Appendix Chapter

Dominance in a socially dynamic setting: hierarchical structure and conflict dynamics in ravens´ foraging groups.

Palmyre H. Boucherie, Mario Gallego-Abenza, Jorg. M. Massen and Thomas Bugnyar

How to cite this article: Boucherie PH, Gallego-Abenza M, Massen JJM, Bugnyar T. 2022. Dominance in a socially dynamic setting: hierarchical structure and conflict dynamics in ravens' foraging groups. Phil. Trans. R. Soc. B 377: 20200446. https://doi.org/10.1098/rstb.2020.0446

PHILOSOPHICAL
TRANSACTIONS B

royalsocietypublishing.org/journal/rstb

Dominance in a socially dynamic setting: hierarchical structure and conflict dynamics in ravens' foraging groups

Palmyre H. Boucherie[1], Mario Gallego-Abenza[1,2], Jorg J. M. Massen[3] and Thomas Bugnyar[1,2]

[1]Department of Behavioural and Cognitive Biology, and [2]Konrad Lorenz Forschungsstelle, Core Facility for Behaviour and Cognition, University of Vienna, Vienna, Austria
[3]Animal Behaviour and Cognition, Department of Biology, Utrecht University, Utrecht, The Netherlands

PHB, 0000-0002-3238-7479; MG-A, 0000-0002-4027-5899; JJMM, 0000-0002-1630-9606; TB, 0000-0002-6072-9667

Dominance hierarchies typically emerge in systems where group members regularly encounter and compete for resources. In birds, the 'open' and dynamic structure of foraging groups may prevent the emergence of structured hierarchies, although this assumption have hardly been tested. We report on agonistic data for ravens *Corvus corax*, collected over two 18-month periods for 183 marked individuals of a wild (fluid) population and 51 birds from six captive (stable) groups. We show that the dominance structure (steep and transitive) in wild foraging groups is strikingly similar to that found in captivity. In the wild, we found that higher ranks are mainly occupied by males, older and more aggressive individuals that also tend to receive fewer aggressions. Exploring the mechanisms sustaining the wild dominance structure, we confirmed that males are more aggressive than females and, with age, tend to receive fewer aggressions than females. Males that are about to leave the foraging groups for some months are less aggressive than newcomers or locals, while newcomers are specifically targeted by aggressions in their first year (as juveniles). Taken together, our results indicate that the socially dynamic conditions ravens face during foraging do not hinder, but provide opportunities for, using (advanced) social cognition.

This article is part of the theme issue 'The centennial of the pecking order: current state and future prospects for the study of dominance hierarchies'.

Research

Cite this article: Boucherie PH, Gallego-Abenza M, Massen JJM, Bugnyar T. 2022 Dominance in a socially dynamic setting: hierarchical structure and conflict dynamics in ravens' foraging groups. *Phil. Trans. R. Soc. B* 377: 20200446.
https://doi.org/10.1098/rstb.2020.0446

Received: 16 July 2021
Accepted: 30 November 2021

One contribution of 19 to a theme issue 'The centennial of the pecking order: current state and future prospects for the study of dominance hierarchies'.

Subject Areas:
behaviour, cognition

Keywords:
dominance structure, fission–fusion dynamic, elo-rating, cognition

Author for correspondence:
Palmyre H. Boucherie
e-mail: palmyre.boucherie@univie.ac.at

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.5764097.

1. Introduction

Competition for resources and reproduction is a key challenge for animals, and in particular gregarious species [1]. The establishment of dominance hierarchies can (partly) alleviate the costs of competition by regulating and mitigating conflicts [2]. Many social species form dominance relationships as a direct outcome of repeated agonistic interactions, depicting asymmetries in opponents' winning abilities [2]. Functionally, dominance relationships regulate the priority of access to resources [3] and social interactions [4], and can affect individuals' physiology and fitness [5]. The organization, or structure, of dominance relationships defines the hierarchy [6], according to which individuals can be ranked from the most dominant(s) to the most subordinate(s), as described in the seminal paper on pecking order by Schjelderup-Ebbe [7].

While dominance relationship is a relative and dyadic measure (not a property of individuals), dominance rank refers to an individual's position in the hierarchy [2]. Across species, animals rely on a range of mechanisms to establish and maintain dominance relationships and the associated rank structure [8], varying in complexity. Individuals can, for instance, base their decisions on

THE ROYAL SOCIETY
PUBLISHING

whether to aggress or submit to a conspecific on the physical appearance of the opponent (e.g. sex, age, body condition [9]) and/or spatial association patterns (close associations are typical for affiliates that could act as allies in conflicts). Coupled with good learning and memory skills, these decision rules could evolve into rule-of-thumb strategies like 'aggress those that are physically inferior to you' or 'aggress those that have not been seen in spatial association lately'. These cognitively simple strategies could become particularly efficient with additional rules like 'keep on aggressing former victims' or 'redirect aggression to bystanders' (i.e. serial and redirected aggressions). Such behavioural patterns might be used selectively according to context, resulting in a flexible adjustment to social situations [10].

In some species, we can also expect animals to individually recognize conspecifics and memorize their own dominance/submission status relative to them. In the latter case, individuals may additionally come to mentally represent the dominance order and infer their own and others' positions, based on transitivity [11]. Both cognitive building blocks, individual recognition and transitive inference, have been successfully demonstrated in experimental studies across taxonomic orders, e.g. paper wasps ([12]; see also [13]), primates, birds and fish [14,15]. In such systems, rank-related aggression strategies may thus emerge, such as individuals directing aggression towards opponents of similar competitive ability, likely to maintain their rank, resulting in a close-competitor strategy [16,17].

Finally, in societies structured by different types of affiliated relationships, ranks may become dependent on the assistance/presence of individuals like kin, partners or friends [18]. Such species are hypothesized to develop a third-party understanding, i.e. they represent not only their own relationships but also the relationships between others [19]. There is unequivocal experimental evidence for third- party understanding in non-human primates [20,21], and various observations have indicated a strategical use of this knowledge, i.e. planning alliances or preventing others from gaining rank [22]. Similar observations exist in some other taxonomic groups (e.g. hyenas [23], horses [24], corvids [25], geese [26]), but experimental tests for third-party understanding in species other than primates are rare and results are mixed [27-30]. In species expressing high degrees of fission-fusion dynamics, it may become difficult for individuals to keep track of their own and others' relationships [31]. Having the opportunity to leave and join other (sub-)groups might also promote conflict avoidance and dispersive strategies over those of conflict resolution [31]. In comparison with when group composition is stable, highly dynamic social conditions might thus render the emergence and maintenance of structured hierarchies less likely [31,32]. Empirical studies on how dominance hierarchies work under high fission-fusion dynamics are scarce, however (but see [32,33]; see also [34], on the dynamics of dominance).

Common ravens, *Corvus corax*, are an interesting model species to study dominance under 'complex' dynamic social conditions: on one hand their foraging groups are characterized by moderate to high fission-fusion dynamics, on the other hand they are structured by age, breeding status and differentiated relationships. Foraging ravens tend to aggregate on ephemeral but rich and monopolizable food sources (e.g. carcasses, anthropogenic food sources like garbage dumps or game parks [35]), forming 'open' groups with individuals joining and leaving within and across days [36]. While ravens show high levels of mobility and flexibility in exploiting food sources, they may also develop preferences for particular foraging sites, resulting in almost daily visits to those sites [37]. Despite high degrees of fission-fusion dynamics, subsets of individuals may thus more regularly meet than others at certain locations [38,39]. At our study site, most birds in a foraging group are non-breeders i.e. sexually immature (±70%), or adult but lacking a partner and/or territory (±25%), while territorial breeders are in the minority (±5%) [40]. Ravens are long-term socially monogamous: pair partners stay together over several years, often for life; they form a close affiliative relationship and jointly defend a territory for breeding [35]. Interestingly, pair-bond-like relationships can also be found in non-breeders, typically among males and females (sometimes future mated partners) but also among same-sex partners, often kin (e.g. siblings) or familiar individuals [41-43]. These relationships resemble pair-bonds in the nature and frequency of their association and affiliation patterns [41-43]. Pair partners like non-breeder affiliates often act as allies in conflicts, typically when foraging [37,44,45].

We analysed 12 datasets of agonistic interactions collected within a monitoring programme on wild and captive ravens in the course of 12 years. In a first step (objective 1), we examined the structure and certainty of the dominance rank hierarchies under dynamic social conditions in the wild and compared them with the relatively stable social conditions in captivity. Specifically, we used two datasets of 18 months on a total of 183 individually marked ravens belonging to a wild population in the northern Austrian Alps, and 10 datasets from our captive colony of 51 ravens housed in six social groups ranging from 6 to 11 individuals. We tested the assumption that the constraints posed by fission-fusion dynamics (difficulties in track-keeping of relationships, opportunity for dispersive conflict avoidance) should result in a dominance structure different from that found in captivity. Previously, Braun & Bugnyar [37] argued that physical appearance (sex and age) and/or spatial associations (as typical for bonded birds) may serve as reliable cues for ravens to broadly categorize individuals into being 'dominant' or 'subordinate' under dynamic free-flight conditions. They more specifically proposed that individuals could follow the rules-of-thumb that: males dominate females (owing to their weight, around 1250 g for males versus 1100 g for females; see also [41]), older birds dominate younger birds (owing to their weight and/or experience) and bonded birds dominate non-bonded birds (owing to social support). They further argued that birds of similar physical appearance and/or bonding status might develop dominance rank hierarchies within their social category. We thus tested the hypothesis that structured hierarchies do not form in raven foraging groups at the whole group level but mayexist within categories of similar individuals (e.g. of a certain sex or age), resulting in a step-wise pattern in the hierarchy. The findings from the wild should differ from those in captivity, where we expected to find structured (steep and transitive) hierarchies at the whole group level [28,44,46] owing to stable social conditions and limited conflict avoidance options. After establishing the hierarchy structure in the wild, we investigated patterns sustaining ranks, considering in particular conflict dynamics (i.e. how much the individuals initiate and receive aggressions) along with individuals' age and sex. In line with the theory [37,41], we expected older males and more aggressive individuals to dominate the hierarchy.

In a second step (objective 2), we examined how these conflict dynamics were affected by the open and dynamic nature of ravens' foraging groups, notably by the high variation in how often and how long individuals are present/absent at the foraging site. Firstly, we expected ravens with long presence (locals) to initiate more and receive fewer aggressions than non-local birds (e.g. 'newcomers' or individuals that have left the local group for months), as the local dominance structure should be particularly salient for ravens that frequently visit the site. Returning birds could actively try to reintegrate into the dominance structure (and eventually regain their previous rank) and could be specifically targeted by local birds with similar social status. This pattern might be most pronounced in adult males, as we expected them to dominate females and younger birds in the hierarchy. Males might also be more aggressive than females since they are physically stronger, whereas females might be more often victims of aggressions. We used our two wild datasets to test these predictions.

2. Methods

(a) General methods

(i) Field conditions and sampling methods of wild ravens

In the course of our long-term monitoring programme (established in 2007) of a wild raven population in the northern Austrian Alps, we caught more than 400 birds (mean: 27 per year) with drop-in traps [47]. Caught birds were measured, blood-sampled for sex and kinship analysis, and marked with a combination of coloured rings and wing tags for individual identification (electronic supplementary material, S1). Age was determined via the colour of the tongue and oral cavity, which changes from pink to black with maturation [48] (electronic supplementary material, S1). As the ravens' socio-cognitive development is strongest in the first 2 years [46], we considered the following age classes: juvenile (1-12 months), subadult year 2 (13-24 months), subadult year 3 (25-36 months) and adult (more than 36 months). Adults range between 1 and 14 years old in this foraging group. From 61% of the marked juveniles we have records exceeding the first summer, on average for 4.1 years per bird. From 76% of the subadults and 90% of the adults, we have records over consecutive years, on average for 4.1 and 5.1 years.

We studied ravens in the area of the Cumberland Wildpark (latitude: 47.807° N, longitude: 13.950° E), an Alpine Zoo with hiking paths and enclosures of native animals situated in the river valley of Grünau im Almtal. Ravens use the park for foraging in the enclosures when the park's animals are fed [49]. Their foraging groups are composed primarily of non-breeders and typically range from 20 to 80 birds, whereof about 50% can be identified individually. Since 2007, we have recorded almost daily the identity and social interactions (agonistic and affiliatory; collected ad libitum during 30 min observation sessions) of the marked ravens present during the morning feedings of wild boars (*Sus scrofa*), brown bears (*Ursus arctos*) and wolves (*Canis lupus*). Age structure and sex ratio within foraging groups have been fairly constant over years (around 30% juvenile, 40% subadult, 30% adult; the male : female ratio per age class varies between years, but stays around 40 : 60%). Yet, we can see a large variation in how often and how regularly individuals join the feedings (ranging from a few days per year to more than 300 days per year; [37]).

(ii) Wild study periods

We analysed two 18-month datasets compiling agonistic and affiliative data on two distinct wild foraging groups. The first dataset (Wild1) includes 89 marked individuals, sampled between September 2008 and February 2010 by one observer; and the second (Wild2) includes 100 individuals sampled between September 2017 and February 2019 by a team of field assistants. Of the 189 individuals present in the two datasets, 3% were present in both; we thus worked with a total of 183 independent individuals. See electronic supplementary material, S2 for further details on dataset characteristics, sampling methods and sample sizes.

(iii) Housing conditions, sampling methods and study periods of captive ravens

We analysed 10 captive datasets, collected from six groups (ranging from 6 to 11 individuals), all housed in large outdoor aviaries (160-240 m²) at the Haidlhof Research Station (Bad Vöslau, Austria) and at the Cumberland Wildpark. Groups were all composed of non-breeders (i.e. sexually immature birds in their first years) but differed in respect of the birds' origin and upbringing (parent- or hand-raised). While some captive individuals were involved in affiliative relationships (typically with one to three birds), some had no affiliative interactions, which compares well with the situation found in the wild [50]. Across groups, data were collected using either 30 min ad libitum sampling in food monopolization experiments (three datasets), 5 min focal sampling (five datasets), or 30 min ad libitum sampling in a neutral context (two datasets). In the two latter cases, data were collected from January to June for four datasets and from July to December for the three others (electronic supplementary material, table S2).

(b) Methods, objective 1: dominance hierarchies

(i) Datasets and conflict definition

Analyses were run separately on the two wild and 10 captive datasets. For the wild datasets, we selected individuals that were seen in more than 10% of all observation sessions (Wild1: 52 marked ravens, 275 sessions; Wild2: 50 marked ravens, 386 sessions). Analyses of sampling effort and data sparseness of all datasets, wild and captive, indicated sufficient sampling to ensure a reliable estimation of the hierarchy (see electronic supplementary material, S3). We used directed-decided conflicts, defined by an initial aggression (for which the identities of the aggressor and the victim are known), and a clear outcome i.e. the victim leaves/retreats from, or submits to, the aggressor (detailed ethogram in electronic supplementary material, S4).

(ii) Dominance hierarchy structure

We used the randomized elo-rating method developed by Sánchez-Tójar and colleagues to infer the hierarchy and evaluate its steepness and uncertainty (R package aniDom v. 0.1.5; [51,52]; see also [53]). Like other elo-rating methods, the randomized elo-rating works on winner-loser sequences, but replicates the initial sequence n times, randomizing the order of conflicts (replications were set to 1000). Mean individual ranks and 95% confidence intervals are then inferred from the 1000 individual elo-scores. We evaluated the hierarchy steepness from the visualization of the 'shape' of the hierarchy, plotting the probability for a dominant to win a conflict, according to the rank difference with its opponent. In very steep hierarchies, this probability quickly increases to 1, while in flat or unpredictable hierarchies, it would remain close to 0.5 (random) [51]. We quantified the uncertainty of the inferred hierarchy by two means: the repeatability of the individual elo-ratings across randomizations (function 'estimate_uncertainty_by_repeatability') and the correlation score between the two inferred hierarchies when splitting the dataset into two halves (function 'estimate_uncertainty_by_splitting'). Repeatability scores above 0.65 and 0.9 suggest intermediate to very high levels of steepness and a low uncertainty of the inferred hierarchy, respectively. The same logic applies for correlation scores above 0.5 and 0.9, respectively [51]. We evaluated the triangle transitivity as a measure of the orderliness of the dominance structure using the package 'com- pete' v. 0.1 (function 'ttri_test', [54]), following the algorithm and code described by Shizuka & McDonald [55]. In transitive hierarchies, if A dominates B and B dominates C, then A domi- nates C. The function returns a scaled index of triangle transitivity (ttri) which evaluates the tendency of triadic relation- ships to be ordered, i.e. transitive [55]. This metric ranges from 0 when the proportion of transitive triangle in a network is not different from random (proportion evaluated as 0.75), and 1 when all triangles are transitive [55]. The associated p-value evaluates whether the tested empirical dataset is more ordered (i.e. proportion of transitive triads) than expected by chance.

(iii) Daily affiliation ratio and vagrant–resident index

The daily ratio of affiliation was computed to approximate individual bonding status (higher ratio indicating paired individuals and/or individuals with one or several affiliated partners). We did so by dividing the total frequency of affiliations an individual initiated and received by the number of feeding events at which it was present, for each 18-month study period. Affiliations included: contact-sit, allopreening, body contact, allofeeding, co-feeding, co-manipulations, object transfer and play (detailed ethogram in electronic supplementary material, S4). We also computed a vagrant-resident index, as the ratio between the total number of feeding events at which a bird was present and the total number of feeding events at which for each study period. This index ranged from 0 for highly vagrant birds to 1 for highly resident birds.

(iv) Rank predictors

We finally investigated how rank (evaluated over an 18-month period) was affected by individuals' sex, age range (see detailed categories below), daily affiliation ratio (covariate), vagrant-resident index (covariate), and the daily ratio of initiated (covariate) and received aggressions (covariate) over the study period. Ranks varied from 1 to *N* (number of individual) in each period, and were inferred for each individual from its mean elo-scores across the 1000 randomizations. Age ranges over the 18-month study period, respectively, corresponded to individ- uals that hatched: during the study period, 1-10 months old (age range 1); the year before, 5-22 months old (1-2); 2 years before, 17-34 months old (2-3); 3 years before, 29-46 months (3-4); or more (adults). We ran a linear mixed model (LMM, function 'lmer', lme4 R package v. 1.1.27.1, [56]), adding the dataset identity (Wild1, Wild2) as a random intercept in the model. We applied Satterthwaite's approximation of degrees of freedom to compute the *p*-values (function 'tab_model' option 'p.val' = 'satterthwaite' in R package sjPlot v. 2.8.9.1; [57]).

(c) Methods, objective 2: conflict dynamics in groups with changing composition

With this second objective, we further examined the conflict dynamics underlying the wild dominance structure (i.e. initiated and received aggressions). Analyses were performed on a monthly basis to include individuals' temporal variations in presence at the foraging site. Therefore, the daily affiliation ratio and vagrant-resident index were this time computed per month.

(i) Datasets

We focused on the two 18-month wild datasets (Wild1 and Wild2). We worked on initiated and received aggressions for which the identity of the aggressor and/or victim was known, respectively (detailed ethogram in electronic supplementary material, S4).

(ii) Presence dynamics and data subset

On a monthly basis, we evaluated individuals' presence status, whereby a bird was scored as 'present' if it had been seen in at least 10% of the monthly observation sessions (feeding events). We subsequently categorized individuals' presence dynamics, differentiating periods of 'arriving' (i.e. first two months of presence, after at least two months of absence), 'staying local' (i.e. present after at least two months and for at least two more months) and 'before leaving' (i.e. last two months of presence, before at least two months of absence; full details on the procedure in electronic supplementary material, S5). We worked with a total of 53 (Wild1: 275 sessions) and 64 (Wild2: 386 sessions) marked ravens, for which the monthly presence dynamics were known (in total: 82 arriving, 794 local and 115 leaving individuals).

(iii) Statistical analyses

We investigated how the monthly frequency of initiated (model 1) or received (model 2) aggressions was affected by individuals' sex, age class (juvenile, subadult year 2, subadult year 3, adult), daily affiliation ratio (covariate) and presence dynamics (arriving, before leaving, staying local). Since we worked with count response variables i.e. behavioural frequencies, the vagrant-resident index (covariate) was simply used this time as a measure of the proportion of time in the study to control for varying observational effort across individuals. We also considered the interactions between: sex and presence dynamic, age and presence dynamic, sex and age, and sex and daily affiliation ratio. We ran two generalized linear mixed models (GLMMs) using a negative binomial distribution and log-link function (function 'glmer.nb', lme4 R package v. 1.1.27.1), to account for the over-dispersed distribution of our dependent variables. To account for pseudo-replication and repeated measures across individuals and time periods we added the individual identity and the year and month when the data were collected as random intercepts in the models. See electronic supplementary material, S6 for general information on statistics and data visualization.

3. Results

(a) Objective 1: dominance hierarchies

(i) Dominance structure

We found steep and rather steep dominance structures for both the captive and the wild datasets (see groups summary in electronic supplementary material, table S2). In captivity the probability for a dominant to win a conflict very quickly increased above 0.9 for higher rank differences between the two opponents, and above 0.8 in the wild (figure 1: C1.*a* and C2.*a*, Wild1.*a* and Wild2.*a*; electronic supplementary material, S7 for a complete results overview of all captive datasets). For all datasets, the repeatability scores across randomizations were above 0.8 in captivity (ranging from 0.81 to 1.00 across groups; electronic supplementary material, S3), and equal to 0.93 (Wild1) and 0.91 (Wild2) in the wild. The correlation scores between the two inferred hierarchies (when splitting each dataset into two halves) were above 0.74 in captivity (ranging from 0.74 to 0.97 across groups), and 0.76 (Wild1) and 0.75 (Wild2) in the wild. Together, these scores indicate intermediate to very high steepness and a low uncertainty of the inferred hierarchies in both captive and wild data sets. Finally, the triangle transitivity indices were above 0.91 for all captive datasets expect one (ranging from 0.91 to 1.00 across groups, except C7: 0.60; electronic supplementary material, S3), and equal to 0.96 (Wild1) and 0.82 (Wild2) in the wild, indicating highly transitive hierarchies. Top rank positions were occupied by males in

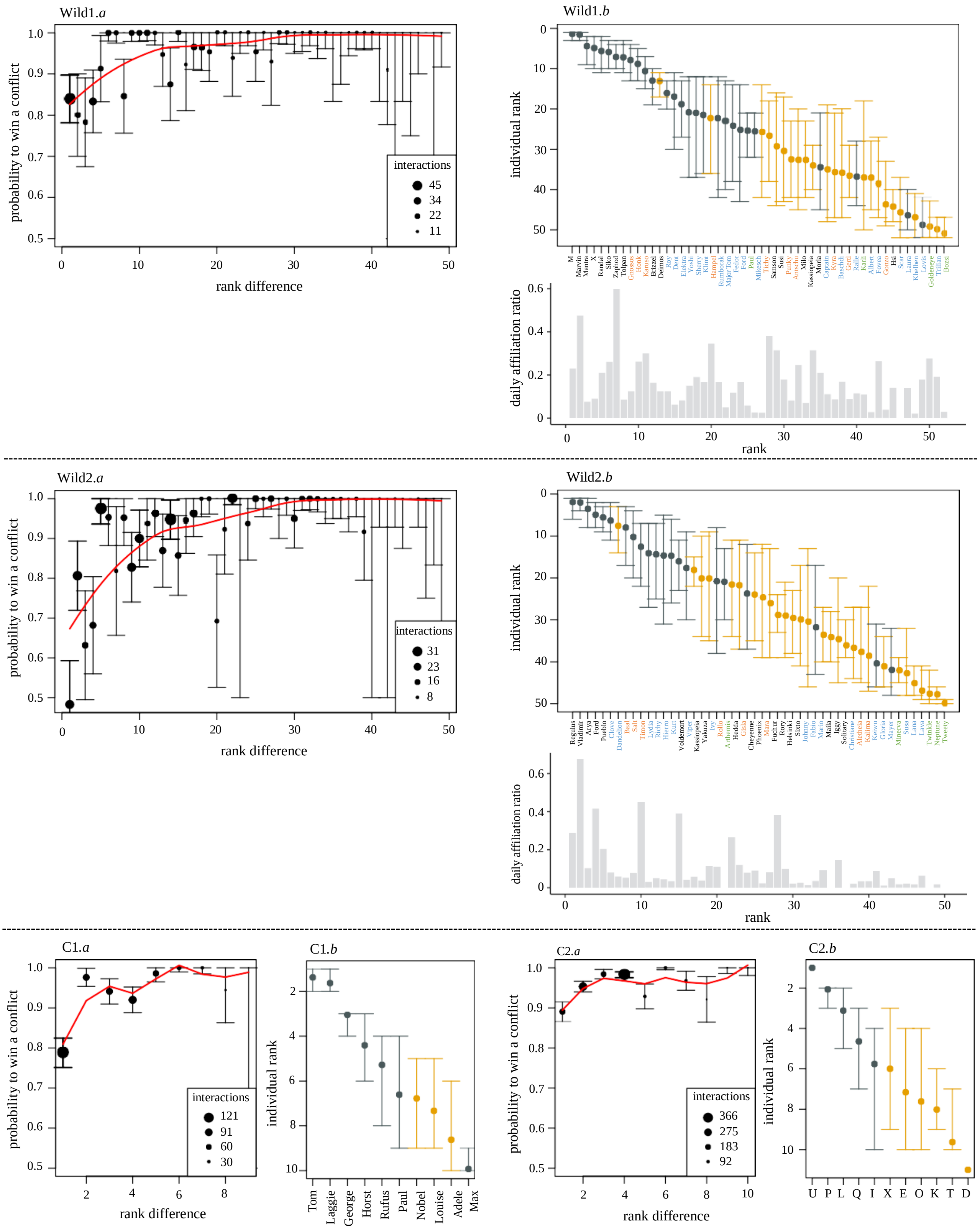


Figure 1. Shape of the hierarchy (*a*) and individuals' dominance rank (*b*) for the two wild (Wild1, Wild2) and two captive datasets (C1 and C2; see all 10 captive datasets in electronic supplementary material, S7). The shape of the hierarchy plots the probability (from 0 to 1) for a dominant to win a conflict with respect to the rank difference with its opponent; point size is function of the number of interactions available in the dataset for each rank difference. Dominance ranks are ordered from top (upper left) to bottom; points represent individuals' mean rank (inferred from the individual elo-scores) and whiskers the 95% confidence interval across the 1000 randomizations; they are coloured in grey for males and yellow for females. In the two wild populations, individuals' names (on the *x*-axis) are coloured according to their age range over the study period: green for age range 1; blue for 1–2; orange for 2–3. Individuals of the 3–4 age range and adults are coloured in black. Individuals' daily affiliation ratio (computed over the whole study period) is shown below their respective dominance ranks and is computed as the total sum of affiliations initiated and received for the whole study period, divided by the total number of feeding events when individuals were present. Age range is not depicted for the captive groups, as group members typically hatched in the same year.

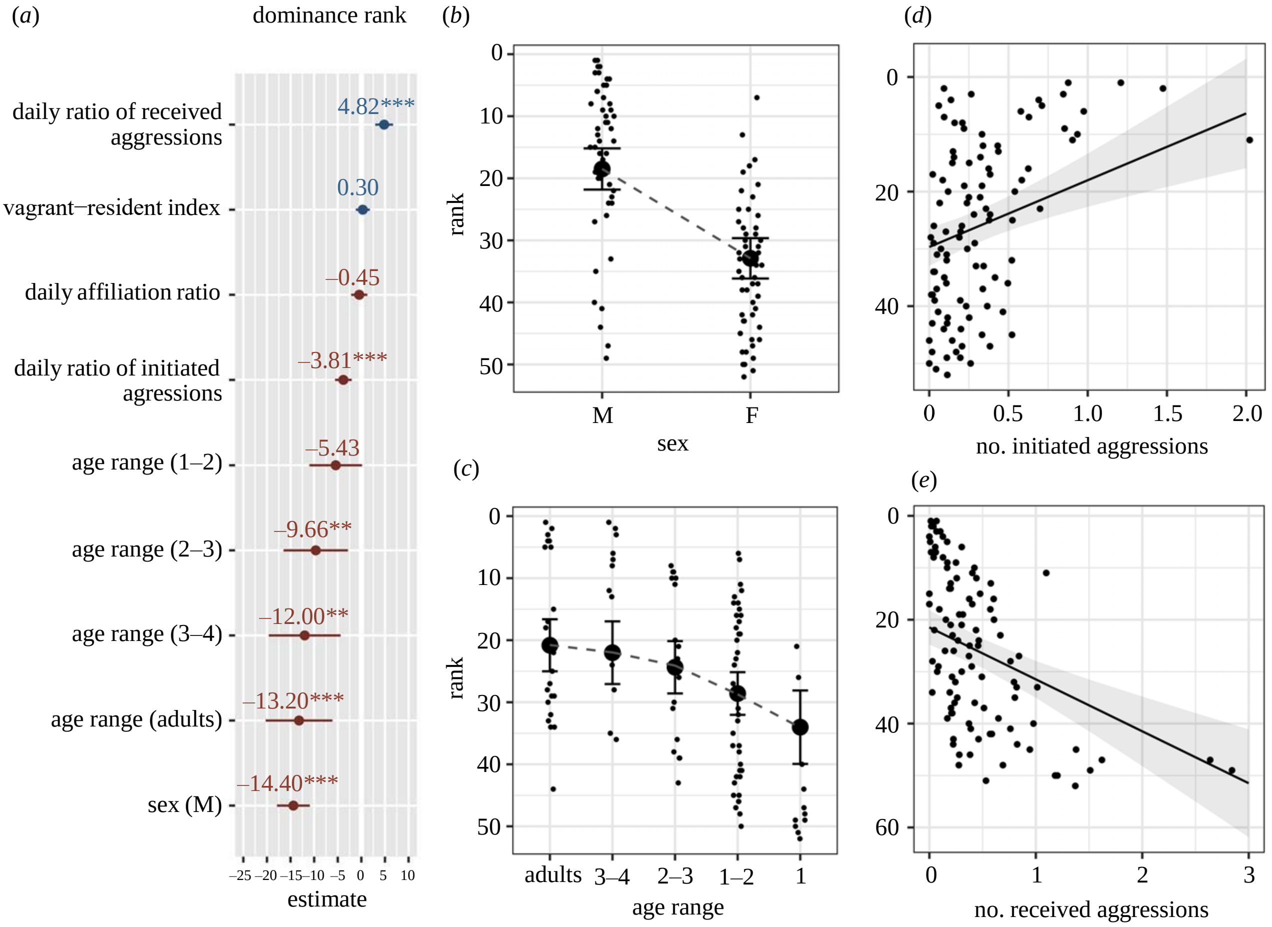


Figure 2. (*a*) Estimates forest plots of the linear mixed model investigating individual rank, together with the associated effects of (*b*) individuals' sex, (*c*) age range, (*d*) daily ratio of initiated aggressions, and (*e*) daily ratio of received aggressions over the study period on individual rank (predicted values), generated with the 'ggeffect' function in R package ggeffects [58]. Reference levels for the categorical predictors in the forest plot are respectively: sex (F, female), age range (1). Full model output in electronic supplementary material, S8. Asterisks indicate the level of statistical significance: ***, <0.001; **, <0.01; *, ≤0.05. In (*b*) to (*e*) the *y*-axis is reversed to show top ranks at the top of the graph and match figure 1. Error bars in (*b*,*c*) and shaded area in (*d* ,*e*), respectively, represent 95% confidence intervals around the estimated marginal means and the marginal effect regression lines. (Online version in colour.)

both captive and wild datasets. But in several of the captive groups and in the two wild datasets, some females were also seen in the top half of the hierarchy (i.e. from the most dominant to the average rank; figure 1: C1.*b* and C2.*b*, Wild1.*b* and Wild2.*b*; electronic supplementary material, S7 for a complete results overview of all captive datasets).

(ii) Rank predictors

Analysing ranks estimated for 102 individuals over two 18-month periods (with two individuals present in both periods), we found that rank was mainly affected by the sex and age of the individual, with males and older individuals, respectively, occupying significantly higher ranks than females and younger birds (estimates forest plot in figure 2*a*, see also figure 2*b*,*c*, full model output in electronic supplementary material, S8). To a lesser extent, individual aggressiveness and received aggressions were also found significant, with high-rank individuals initiating significantly more aggressions while they tended to be less often the target of aggressions than low-rank individuals (figure 2*a*,*d*,*e*, electronic supplementary material, S8).

(b) Objective 2: conflict dynamics in groups with changing composition

(i) Initiated aggressions

Analysing a total of 4048 initiated aggressions over two 18-month periods for 117 marked individuals (with two individuals present in both periods), we found significant effects of sex, the interaction between sex and presence dynamics, and to a lesser extent the daily affiliation ratio (estimates forest plot in figure 3*a*; full model output in electronic supplementary material, S9). While males generally initiated more conflicts than females (figure 4*a*), the difference between sexes was particularly marked for local and 'arriving' (newcomers, or birds arriving after having been away from our foraging groups for two months or longer; figure 4*a*). To a lesser extent, individuals' aggressiveness tended to increase with increasing daily affiliation ratio, for all sexes and age classes (figure 4*b*). Note that individuals' aggressiveness significantly increased with increased vagrant-resident index; however, this is mainly explained by the proportion of time in the study accounted by this predictor (figure 3*a*; electronic supplementary material, S9).

(ii) Received aggressions

Analysing a total of 3847 received aggressions revealed significant effects of age class, the interaction between sex and age class, and to a lesser extent the interaction between age and presence dynamics (estimates forest plot in figure 3*b*; full model output in electronic supplementary material, S9). The amount of aggressions received decreased with age, whereby juveniles (1 year old) received more aggressions than older individuals (figure 5*a*,*b*). Except in juveniles,

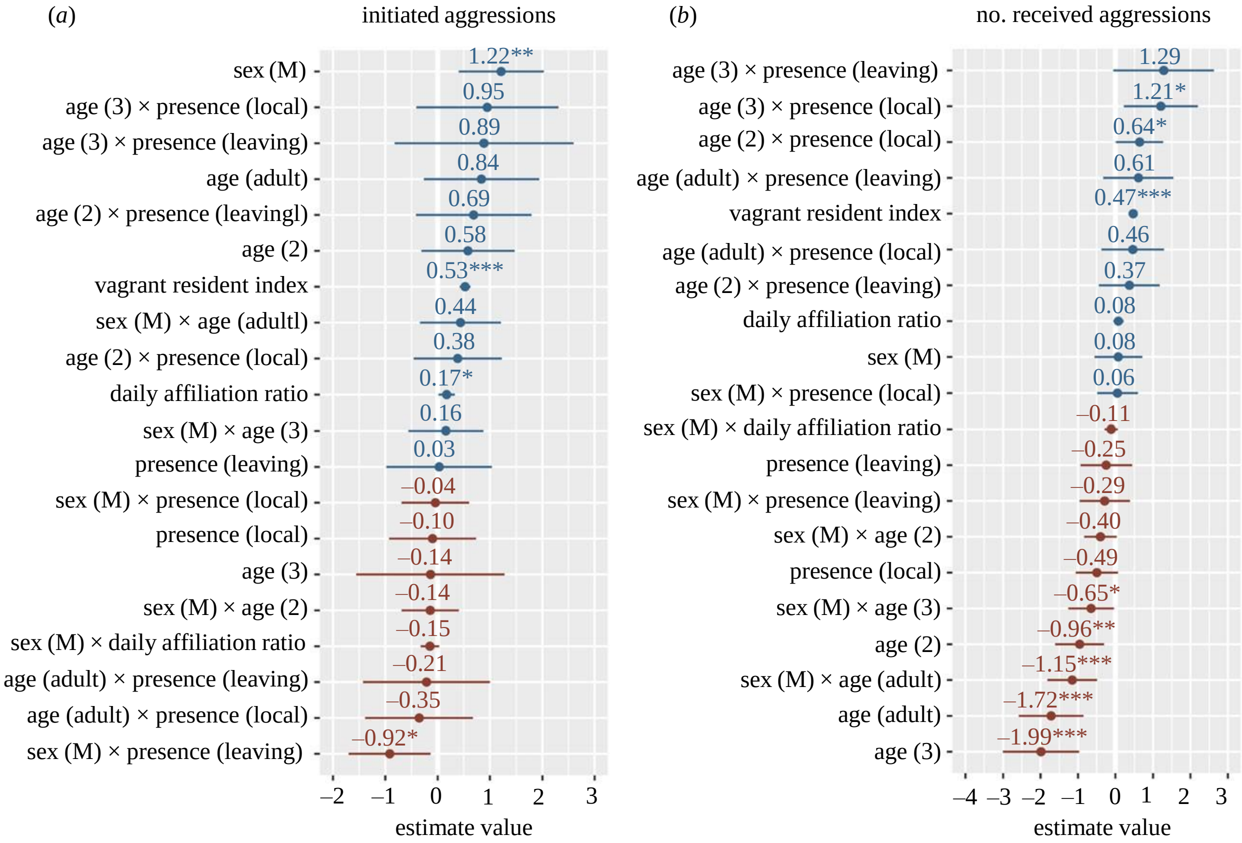


Figure 3. Estimates forest plots of the two generalized linear mixed models investigating monthly rates of (*a*) initiated and (*b*) received aggressions. Reference level for the categorical predictors are respectively: sex (F, female), age (1), presence dynamic (arriving). Asterisks indicate the level of statistical significance: ***, <0.001; **, <0.01; *, ≤0.05. Full model output in electronic supplementary material, S9. (Online version in colour.)

males tend to receive fewer aggressions than females (figure 5*a*). The effect of presence dynamics differed in age classes: while juveniles received the most aggressions in the first two months after 'arriving' (i.e. when integrating with the foraging group for the first time, or after having been away for more than two months), 3-year-old subadults tended to receive slightly fewer aggressions in that period, while the presence dynamics did not affect the amount of aggressions received by adults and 2-year-old subadults (figure 5*b*). Note that the frequency of received aggressions significantly increased with increased vagrant-resident index; however, this is again mainly explained by the proportion of time in the study accounted by this predictor (figure 3*b*; electronic supplementary material, S9).

4. Discussion

(a) Dominance hierarchies

Our findings show that raven groups are structured by a steep and transitive dominance hierarchy, irrespective of the dynamic nature of foraging groups in the wild, and irrespective of the group composition, sampling methods and raising style (parent- or hand-raised) in captivity. Against our hypothesis, the picture obtained from wild ravens falls within the range seen in captivity. For all datasets, captive and wild, the repeatability and correlation scores were well above the theoretical thresholds, indicating low uncertainty—thus a robust assessment—of each inferred hierarchy. We found the same results in the wild in two distinct periods that were 7 years apart and in which only 3% of the identified birds remained the same. This suggests that such a steep and transitive dominance structure is a characteristic feature of wild raven foraging groups, at least under the conditions faced in Middle Europe [59]. Our results are in line with, at that time relatively speculative, interpretations from observations at garbage dumps in Switzerland [40]; how well they fit to ravens in areas with few anthropogenic food sources remains to be tested.

Our robust finding of a structured dominance hierarchy, not only in captivity but also under dynamic conditions in the wild, fits with the competitive nature of socially foraging ravens [35,41], and is in line with primate socio-ecological models [60-63]. Ravens' food competition is mainly characterized by contest competition, which in opposition to scramble competition occurs when a defensible (clumped) food resource can be monopolized by some individuals. Following primate socio-ecological models, species experiencing contest competition are more likely to establish strong linear hierarchies ([60-63]; but see in elephants [64,65] and vampire bats [66]). These models, however, were primarily established to explain the sociality of females, which in most primate species live in stable cohesive groups.

In less cohesive species, fission-fusion dynamics are often interpreted as a strategy to alleviate the costs of foraging competition ([67]; but see also [68,69] for the mitigating effect of predation pressure and travel costs [70] on grouping patterns). Fission-fusion dynamics typically allow dispersive conflict management and reduce scramble competition and/or the intensity of contest competition [31,62,71,72]. Ultimately, this might limit the likelihood for steep and linear dominance structures to develop [31,73,74]. Primates species expressing

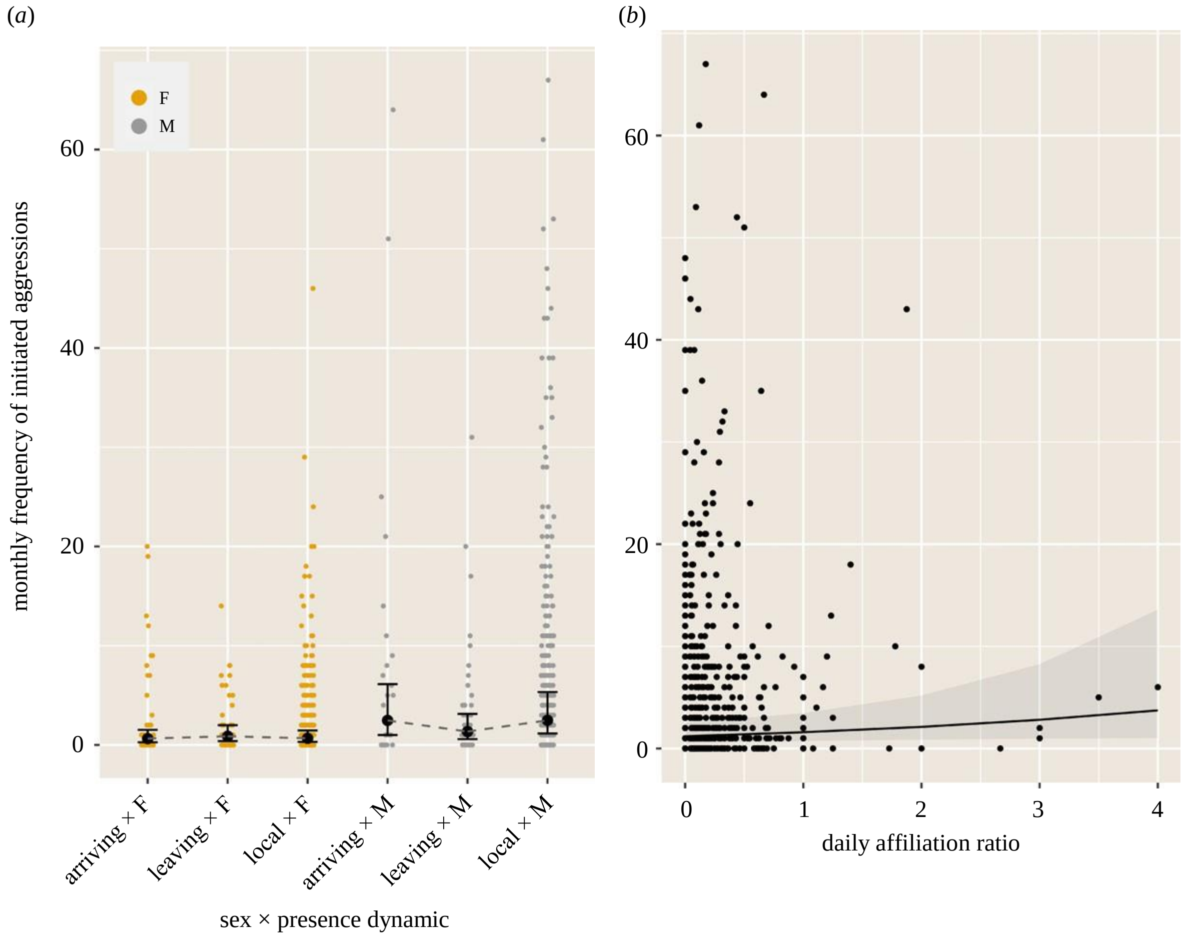


Figure 4. Modelled effects of (*a*) individuals' sex in interaction with the presence dynamic (arriving, leaving, local), and (*b*) daily affiliation ratio on individuals' monthly frequency of initiated aggressions (predicted count values), generated with the 'ggeffect' function in R package ggeffects [58]. Error bars in (*a*) and shaded area in (*b*), respectively, represent 95% confidence intervals around the estimated marginal means and the marginal effect regression line. (Online version in colour.)

a high degree of fission-fusion dynamics indeed tend to show low numbers of intra-group aggressions and little evidence or mixed results regarding the emergence of linear and steep hierarchies (spider monkeys [71,75,76], chimpanzees [22,77], hamadryas baboons [78]; but see [72,79,80]). However, linear hierarchies can be found in other fission-fusion societies, typically characterized by a high degree of relationship differentiation (e.g. spotted hyenas [81], elephants [64,65]). In the case of ravens, groups that form at rich and defensible food sources lead to severe contest competition [35,82], which might foster the development of dominance structures. Additionally, if fission allows conflicts to be reduced, fusion events and increased party size on the contrary might increase conflicts, in particular at high-quality food sources and among members of different communities [72]. Future studies should thus aim to compare intra-group (here emerging communities) and inter-group aggressions in ravens, together with the dynamics of fission and fusion events.

(b) Ranks and conflict dynamics in changing group composition

In line with theory [37,41], our analyses show that rank was mainly affected by sex and age, with males and older individuals occupying higher ranks in the hierarchy. On top of these individual attributes, higher ranks were also associated with higher initiated frequencies and lower received frequencies of aggressions. Corroborating these results, our analyses of conflict dynamics confirm that males were more active than females in initiating conflicts (see also [37]), and thus higher ranked. Also in line with rank predictors, older birds tended to receive fewer aggressions, males in particular, which received fewer aggressions than females from the second year on.

Interestingly, our findings also confirm that, in addition to ravens' sex and age class, aspects of their fission-fusion dynamics can explain how strongly they engaged in conflicts. Specifically, we looked at the presence dynamics. In line with our hypothesis, we found 'arriving' and 'local' males to initiate higher rates of aggressions compared with 'leaving' males, which showed similar rates to females irrespective of their presence dynamic. We also found 'arriving' birds to receive high levels of aggressions, but only when juveniles. This latter finding also suggests that young ravens face the challenge of (re)integrating into local foraging groups, whereas older birds do not seem to have this problem any more.

Finally, we found the vagrant-resident index to positively correlate with the frequencies of initiated and received aggressions. This was expected since in this particular analysis fitting behavioural frequencies (objective 2), the index was basically a measure of the proportion of time in study (i.e. how often the bird was observed). But we also found that the vagrant-resident index had no effect when tested as a predictor of rank (objective 1). This indicates that the dominance status in

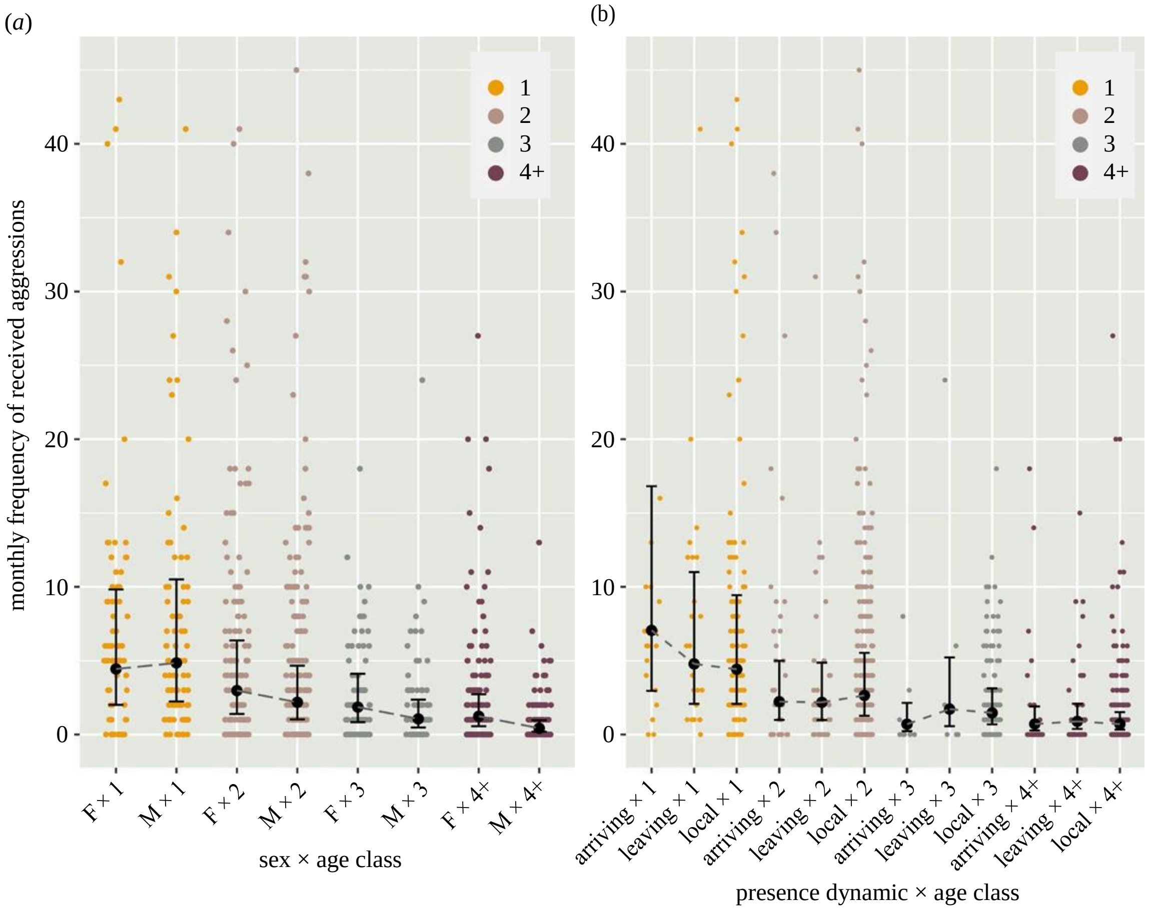


Figure 5. Modelled effects of the interaction between individuals' (*a*) sex and age class (1, 2, 3, 4+ i.e. adult), and (*b*) age and presence dynamic (arriving, leaving, local) on individuals' monthly frequency of received aggressions (predicted count values), generated with the 'ggeffect' function in R package ggeffects [58]. Error bars in (*a*) and shaded area in (*b*), respectively, represent 95% confidence intervals around the estimated marginal means. (Online version in colour.)

this foraging community is independent from the frequency of visits to our specific study site. However, it does not necessarily mean that dominance status is independent from how often individuals meet with others. Indeed, ravens likely rely on multiple sites to forage, e.g. other anthropogenic food sources. It is thus likely that birds that encounter each other in our foraging site also meet in other locations [38]. Future studies will aim to investigate multiple neighbouring foraging sites to detect communities of individuals that meet more often than others, and analyse whether dominance rank is bound to a specific geographical location or a community of individuals.

(c) Implications for cognition

Our surprising findings on dominance hierarchies suggest that wild ravens can cope with and keep track of a relatively large number of conspecifics on an individual basis, when competing for food resources. At our study site, the feedings of zoo animals serve as a strong attractor (more than 90% of all ravens present per day are seen at those feedings), but foraging bouts at enclosures are short (boars: 15-25 min, bears/wolves: 5-15 min) owing to inter- and intra-specific competition. Per foraging bout, an individual raven is confronted with 20-80 conspecifics. The identity of those may change over weeks as about 50% of ravens visit the feedings only from time to time (seen in fewer than 20% of observations), while about 40% are seen regularly (at 20-60% of observation sessions) and about 10% frequently (at more than 60% of observation sessions). Hence, even when daily foraging groups are small, the number of individuals encountered within a period of 1.5 years is relatively large. The inferred hierarchies in our population included around 50 marked birds per period, which were seen at least 10% of the time at the feedings. The fact that on average only half of the birds in the local foraging groups are marked suggests that ravens foraging at our study site might be able to deal with up to 100 conspecifics. Such estimates compare well with the extensive memory skills for conspecifics found in elephants [83], sheep [84] and dolphins [85], and are in line with the hypothesis that high degrees of fission-fusion dynamics may lead to improved memory skills [31].

Surprisingly, the daily affiliative ratio (amount of affiliations initiated and received) did not seem to predict individual rank or how much they received aggressions. However, besides individuals' attributes (sex and age) and presence dynamics, we found that, to a lesser extent, birds' affiliative status also explains how much they initiate aggressions. Birds with a higher daily affiliation ratio (thus with more numerous or stronger potential allies) tended to initiate more aggressions than birds with a lower ratio. This corroborates that after sex and age, bonding status is another predictor for the outcome of dyadic conflicts in ravens [37], although it might not have a strong impact on rank. It also fits previous findings that older bonded ravens tend to intervene in affiliations between younger ravens (potentially in the process of forming a new strong bond), and doing so might prevent them from becoming future competitors [29].

Additionally, whenever a raven is engaged in a social bond (mated partner and/or affiliate) its chances of winning a fight, increase dramatically, while increasing bond strength further increases the likelihood of winning a fight with or without the presence of the partner [37]. Note, that we used the daily ratio of affiliations to approximate bonding status (i.e. type and number of relationships). If it may be reliably assessed for wild populations (with all identities known, and every single interaction tracked down), we could expect to find a more significant impact on rank and agonistic patterns, in particular for territorial breeders (in the minority in foraging groups, thus for which the effect might have been diluted using the affiliation ratio).

Our results pose the question of categorization of ranks, and whether ravens might categorize dominance ranks based on sex, age class and eventually bonding status [37]. Individuals would then only need to remember the actual ranks and rank differences of individuals within their own category (e.g. male/adult and eventually bonded). Such a cognitive ‘strategy’ would, however, predict a step-wise pattern in the dominance hierarchy, where the steps demarcate different sex, age classes and bonding categories, and linear rank orders within each step. Instead, we find in both wild populations one overall steep and transitive hierarchy, encompassing all sexes and age classes. This suggests that using individual attributes and behavioural heuristics alone does not suffice. Furthermore, experimental results from simulated (playback) encounters indicate that captive ravens are capable of mentally representing others’ rank relationships [28]. Captive ravens even respond to simulated rank changes from adjacent aviaries, indicating that they can infer third-party relationships by observations only, i.e. without being able to compare ranks with their own rank position [28]. As the bonding status of ravens, and especially of subadult ravens without a territory, can be volatile [37,86], any heuristics would further need regular updating. To that effect, ravens may use transitive inference, as has been experimentally demonstrated in closely related pinyon jays [14]. Future studies on third-party interactions in a dynamic setting should aim to further our understanding of the strategical use of third-party knowledge in this species and its consequence on the dominance structure(s).

5. Conclusion

To conclude, our results indicate that in the wild, ravens can form and maintain dominance relationships with a large number of conspecifics despite the open and dynamic nature of their foraging groups. These relationships are the backbone of a steep and transitive hierarchy, which encompasses all sexes and age classes. Although the fission-fusion dynamic in this species might alleviate the costs of competition, via the adjustment of parties' size and composition, it does not seem to prevent the establishment of a complex social structure, apparently resilient to constant demographic changes. On the contrary, ravens seem to be able to fine-tune their behaviour to their presence dynamics. In line with ravens’ renowned cognitive skills, this suggests that the high unpredictability and variability of their social environment do not hinder them from using their skills but, instead, open up opportunities for advanced socio-cognitive mechanisms.

Ethics. Wild ravens were trapped, blood-sampled and marked according to the procedure described in Braun & Bugnyar [37] and with licences from the Commission for Animal Experimentation of the Austrian Government (BMWF-66.006/0010-11/10b/2009, BMWF-66.006/0009-II/3b/2012, BMBWF-66.006/0015-V/3b/2018). The monitoring and ringing programme of the Konrad Lorenz Research Center is authorized by the Central Administration of Upper Austria. The studies themselves were non-invasive, purely observational, and thus not classified as animal experiments in accordance with the Austrian law (Federal Law Gazette no. 114/2012, article 1, §2).

Data accessibility. The processed datasets and R code supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. P.H.B.: Conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; M.G.-A.: resources, writing—review and editing; J.J.M.M.: conceptualization, investigation, methodology, writing—original draft, writing—review and editing; T.B.: conceptualization, funding acquisition, investigation, methodology, project administration, supervision, writing—original draft, writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

Funding. The studies were funded by FWF projects Y366-B17, P29705, P33960 to T.B. and M1351-B17, P26806 to J.J.M.M.

Acknowledgements. We thank the teams of the Konrad Lorenz Research Center and the Haidlhof Research Station for their assistance and the logistical support. Specifically, we thank Anna Braun, Christiane Steinbacher, Ines Mayer and Fabio Ribelli for contributing to the field data and marking of ravens, all students who were involved in taking and coding focal videos, and the animal carers. We are grateful for the excellent collaboration with the Cumberland Wildpark Grünau and the permanent support by the ‘Verein der Förderer KLF’. We would also like to thank two thoughtful reviewers for their very valuable comments and suggestions.

References

1. Wrangham RW. 1980 An ecological model of female-bonded primate groups. *Behaviour* 75, 262–300. (doi:10.1163/156853980X00447)
2. Bernstein IS. 1981 Dominance: the baby and the bathwater. *Behav. Brain Sci.* 4, 419–429. (doi:10.1017/S0140525X00009614)
3. Barrette C, Vandal D. 1986 Social rank, dominance, antler size, and access to food in snow-bound wild woodland caribou. *Behaviour* 97, 118–146. (doi:10.1163/156853986X00342)
4. Smith JE, Memenis SK, Holekamp KE. 2007 Rank-related partner choice in the fission–fusion society of the spotted hyena (*Crocuta crocuta*). *Behav. Ecol. Sociobiol.* 61, 753–765. (doi:10.1007/s00265-006-0305-y)
5. Schubert KA, Mennill DJ, Ramsay SM, Otter KA, Boag PT, Ratcliffe LM. 2007 Variation in social rank acquisition influences lifetime reproductive success in black-capped chickadees. *Biol. J. Linn. Soc.* 90, 85–95. (doi:10.1111/j.1095-8312.2007.00713.x)
6. Hinde RA. 1976 Interactions, relationships and social structure. *Man* 11, 1–17. (doi:10.2307/2800384)
7. Schjelderup-Ebbe T. 1922 Beiträge zur sozialpsychologie des Haushuhns [Contributions to the social psychology of the domestic chicken]. *Z. Psychol.* 88, 225–252. [In German.]
8. Tibbetts EA, Pardo-Sanchez J, Weise C. 2022 The establishment and maintenance of dominance hierarchies. *Phil. Trans. R. Soc. B* 377, 20200450. (doi:10.1098/rstb.2020.0450)

9. Henningsen JP, Irschick DJ. 2012 An experimental test of the effect of signal size and performance capacity on dominance in the green anole lizard. *Funct. Ecol.* 26, 3–10. (doi:10.1111/j.1365-2435.2011.01893.x)
10. Barrett L, Henzi P, Kendall D. 2007 Social brains, simple minds: does social complexity really require cognitive complexity? *Phil. Trans. R. Soc. B* 362, 561–575. (doi:10.1098/rstb.2006.1995)
11. Chase ID. 1982 Dynamics of hierarchy formation: the sequential development of dominance relationships. *Behaviour* 80, 218–240. (doi:10.1163/156853982X00364)
12. Tibbetts EA. 2002 Visual signals of individual identity in the wasp *Polistes fuscatus*. *Proc. R. Soc. Lond. B* 269, 1423–1428. (doi:10.1098/rspb.2002.2031)
13. Shimoji H, Dobata S. 2022 The build-up of dominance hierarchies in eusocial insects. *Phil. Trans. R. Soc. B* 377, 20200437. (doi:10.1098/rstb.2020.0437)
14. Paz-y-Mino GC, Bond AB, Kamil AC, Balda RP. 2004 Pinyon jays use transitive inference to predict social dominance. *Nature* 430, 778–781. (doi:10.1038/nature02723)
15. Grosenick L, Clement TS, Fernald RD. 2007 Fish can infer social rank by observation alone. *Nature* 445, 429–432. (doi:10.1038/nature05511)
16. Dehnen T, Papageorgiou D, Nyaguthii B, Cherono W, Penndorf J, Boogert N, Farine D. 2021 Costs dictate strategic investment in dominance interactions. *Phil. Trans. R. Soc. B* 377, 20200447. (doi:10.1098/rstb.2020.0447)
17. Hobson EA, Mønster D, DeDeo S. 2021 Aggression heuristics underlie animal dominance hierarchies and provide evidence of group-level social information. *Proc. Natl Acad. Sci. USA* 118, e2022912118. (doi:10.1073/pnas.2022912118)
18. de Waal FBM, Harcourt A. 1992 Coalitions and alliances: a history of ethological research. In *Coalitions and alliances in humans and other animals* (eds FBM de Waal, A Harcourt), pp. 1–19. Oxford, UK: Oxford University Press.
19. Cheney DL, Seyfarth RM, Silk JB. 1995 The responses of female baboons (*Papio cynocephalus ursinus*) to anomalous social interactions: evidence for causal reasoning? *J. Comp. Psychol.* 109, 134–141. (doi:10.1037/0735-7036.109.2.134)
20. Bergman TJ, Beehner JC, Cheney DL, Seyfarth RM. 2003 Hierarchical classification by-rank and kinship in baboons. *Science* 302, 1234–1236. (doi:10.1126/science.1087513)
21. Borgeaud C, van de Waal E, Bshary R. 2013 Third-party ranks knowledge in wild vervet monkeys (*Chlorocebus aethiops pygerythrus*). *PLoS ONE* 8, 8–11. (doi:10.1371/journal.pone.0058562)
22. De Waal F. 2007 *Chimpanzee politics: power and sex among apes*. Baltimore, MD: Johns Hopkins University Press.
23. Engh AL, Siebert ER, Greenberg DA, Holekamp KE. 2005 Patterns of alliance formation and postconflict aggression indicate spotted hyaenas recognize third-party relationships. *Anim. Behav.* 69, 209–217. (doi:10.1016/j.anbehav.2004.04.013)
24. Schneider G, Krueger K. 2012 Third-party interventions keep social partners from exchanging affiliative interactions with others. *Anim. Behav.* 83, 377–387. (doi:10.1016/j.anbehav.2011.11.007)
25. Emery NJ, Seed AM, von Bayern AMP, Clayton NS. 2007 Cognitive adaptations of social bonding in birds. *Phil. Trans. R. Soc. B* 362, 489–505. (doi:10.1098/rstb.2006.1991)
26. Wascher CAF, Scheiber IBR, Kotrschal K. 2008 Heart rate modulation in bystanding geese watching social and non-social events. *Proc. R. Soc. B* 275, 1653–1659. (doi:10.1098/rspb.2008.0146)
27. Holekamp KE, Sakai ST, Lundrigan BL. 2007 Social intelligence in the spotted hyena (*Crocuta crocuta*). *Phil. Trans. R. Soc. B* 362, 523–538. (doi:10.1098/rstb.2006.1993)
28. Massen JJM, Pašukonis A, Schmidt J, Bugnyar T. 2014 Ravens notice dominance reversals among conspecifics within and outside their social group. *Nat. Commun.* 5, 3679. (doi:10.1038/ncomms4679)
29. Massen JJM, Szipl G, Spreafico M, Bugnyar T. 2014 Ravens intervene in others' bonding attempts. *Curr. Biol.* 24, 2733–2736. (doi:10.1016/j.cub.2014.09.073)
30. Lee VE, McIvor GE, Thornton A. 2019 Testing relationship recognition in wild jackdaws (*Corvus monedula*). *Scient. Rep.* 9, 6710. (doi:10.1038/s41598-019-43247-x)
31. Aureli F *et al.* 2008 Fission-fusion dynamics. New research frameworks. *Curr. Anthropol.* 49, 627–654. (doi:10.1086/586708)
32. de Silva S, Schmid V, Wittemyer G. 2017 Fission–fusion processes weaken dominance networks of female Asian elephants in a productive habitat. *Behav. Ecol.* 28, 243–252. (doi:10.1093/beheco/arw153)
33. Vullioud C, Davidian E, Wachter B, Rousset F, Courtiol A, Höner OP. 2019 Social support drives female dominance in the spotted hyaena. *Nat. Ecol. Evol.* 3, 71–76. (doi:10.1038/s41559-018-0718-9)
34. Strauss ED, Shizuka D. 2022 The dynamics of dominance: open questions, challenges and solutions. *Phil. Trans. R. Soc. B* 377, 20200445. (doi:10.1098/rstb.2020.0445)
35. Heinrich B. 1989 *Ravens in winter*. New York, NY: Simon & Schuster.
36. Marzluff JM, Heinrich B. 1991 Foraging by common ravens in the presence and absence of territory holders: an experimental analysis of social foraging. *Anim. Behav.* 42, 755–770. (doi:10.1016/S0003-3472(05)80121-6)
37. Braun A, Bugnyar T. 2012 Social bonds and rank acquisition in raven nonbreeder aggregations. *Anim. Behav.* 84, 1507–1515. (doi:10.1016/j.anbehav.2012.09.024)
38. Loretto MC, Schuster R, Itty C, Marchand P, Genero F, Bugnyar T. 2017 Fission-fusion dynamics over large distances in raven non-breeders. *Scient. Rep.* 7, 380. (doi:10.1038/s41598-017-00404-4)
39. Dall SRX, Wright J. 2009 Rich pickings near large communal roosts favor 'gang' foraging by juvenile common ravens, *Corvus corax*. *PLoS ONE* 4, e4530. (doi:10.1371/journal.pone.0004530)
40. Huber B. 1991 Bildung, Alterszusammensetzung und Sozialstruktur von Gruppen nichtbrütender Kolkraben (*Corvus corax* L.) [Formation, age composition and social structure of groups of non-breeding common ravens (*Corvus corax* L.)]. *Metel. Schr. Natursch.* 2, 45–59. [In German.]
41. Gwinner E. 1964 Untersuchungen über das Ausdrucks- und Sozialverhalten des Kolkraben (*Corvus corax corax* L.) [Investigations on the expression and social behaviour of the common raven (*Corvus corax corax* L.). *Z. Tierpsychol.* 21, 657–748. (doi:10.1111/j.1439-0310.1964.tb01212.x) [In German.]
42. Fraser ON, Bugnyar T. 2010 The quality of social relationships in ravens. *Anim. Behav.* 79, 927–933. (doi:10.1016/j.anbehav.2010.01.008)
43. Boucherie PH, Blum C, Bugnyar T. 2020 Effect of rearing style on the development of social behaviour in young ravens (*Corvus corax*). *Ethology* 126, 595–609. (doi:10.1111/eth.13010)
44. Fraser ON, Bugnyar T. 2012 Reciprocity of agonistic support in ravens. *Anim. Behav.* 83, 171–177. (doi:10.1016/j.anbehav.2011.10.023)
45. Szipl G, Ringler E, Bugnyar T. 2018 Attacked ravens flexibly adjust signalling behaviour according to audience composition. *Proc. R. Soc. B* 285, 20180375. (doi:/10.1098/rspb.2018.0375)
46. Loretto M-C, Fraser ON, Bugnyar T. 2012 Ontogeny of social relations and coalition formation in common ravens (*Corvus corax*). *Int. J. Comp. Psychol.* 25, 180–194.
47. Stiehl RB. 1978 Aspects of the ecology of the common raven in Harney Basin, Oregon. PhD thesis, Portland State University.
48. Heinrich B, Marzluff J. 1994 Age and mouth color in common ravens. *Condor* 94, 549–550. (doi:10.2307/1369233)
49. Drack G, Kotrschal K. 1995 Aktivitätsmuster und Spiel von freilebenden Kolkraben *Corvus corax* im inneren Almtal/Oberösterreich [Activity patterns and play of free-living common raven *Corvus corax* in the inner Almtal/Upper Austria]. *Monticula* 7, 159–174. [In German with English abstract.]
50. Braun A, Walsdorff T, Fraser ON, Bugnyar T. 2012 Socialized sub-groups in a temporary stable raven flock? *J. Ornithol.* 153, 97–104. (doi:10.1007/s10336-011-0810-2)
51. Sánchez-Tójar A, Schroeder J, Farine DR. 2018 A practical guide for inferring reliable dominance hierarchies and estimating their uncertainty. *J. Anim. Ecol.* 87, 594–608. (doi:10.1111/1365-2656.12776)
52. Farine DR, Sanchez-Tojar A. 2021 *aniDom: inferring dominance hierarchies and estimating uncertainty. R package version 0.1.5*. See https://CRAN.R-project.org/package=aniDom.

53. McCowan B, Vandeleest J, Balasubramaniam K, Hsieh F, Nathman A, Beisner B. 2022 Measuring dominance certainty and assessing its impact on individual and societal health in a nonhuman primate model: a network approach. Phil. Trans. R. Soc. B 377, 20200438. (doi:10.1098/rstb.2020.0438)
54. Curley JP. 2016 compete: Analyzing social hierarchies: R package version 0.1. See https://cran. r-project.org/web/packages/compete/index.html.
55. Shizuka D, McDonald DB. 2012 A social network perspective on measurements of dominance hierarchies. Anim. Behav. 83, 925-934. (doi:10. 1016/j.anbehav.2012.01.011)
56. Bates D, Mächler M, Bolker B, Walker S. 2015 Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1-48. (doi:10.18637/jss.v067.i01)
57. Lüdecke D. 2018 sjPlot: Data visualization for statistics in social science. R package version 2.8.9.1. See https://CRAN.R-project.org/package=sjPlot.
58. Lüdecke D. 2018 ggeffects: Tidy data frames of marginal effects from regression models. J. Open Source Softw. 3, 772. (doi:10.21105/joss.00772)
59. Loretto MC, Reimann S, Schuster R, Graulich DM, Bugnyar T. 2016 Shared space, individually used: spatial behaviour of non-breeding ravens (Corvus corax) close to a permanent anthropogenic food source. J. Ornithol. 157, 439-450. (doi:10.1007/ s10336-015-1289-z)
60. Wrangham RW. 1980 An ecological model of female-bonded primate groups. Behaviour 75, 262-300. (doi:10.1163/156853980X00447)
61. Isbell L, Young T. 2002 Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. Behaviour 139, 177-202. (doi:10.1163/ 156853902760102645)
62. Isbell LA. 1991 Contest and scramble competition: patterns of female aggression and ranging behavior among primates. Behav. Ecol. 2, 143-155. (doi:10. 1093/beheco/2.2.143)
63. Sterck EHM, Watts DP, van Schaik CP. 1997 The evolution of female social relationships in nonhuman primates. Behav. Ecol. Sociobiol. 41, 291-309. (doi:10.1007/s002650050390)
64. Archie EA, Morrison TA, Foley CAH, Moss CJ, Alberts SC. 2006 Dominance rank relationships among wild female African elephants, Loxodonta africana. Anim. Behav. 71, 117-127. (doi:10.1016/j.anbehav.2005.03.023)
65. Wittemyer G, Getz WM. 2007 Hierarchical dominance structure and social organization in African elephants, Loxodonta africana. Anim. Behav. 73, 671-681. (doi:10.1016/j.anbehav.2006.10.008)
66. Crisp RJ, Brent LJN, Carter GG. 2021 Social dominance and cooperation in female vampire bats. R. Soc. Open Sci. 8, 210266. (doi:10.1098/rsos. 210266)
67. Chapman CA, Wrangham RW, Chapman LJ. 1995 Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. Behav. Ecol. Sociobiol. 36, 59-70. (doi:10.1007/BF00175729)
68. Heithaus MR, Dill LM. 2002 Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology 83,
69. 480-491. (doi:10.1890/0012-9658(2002)083[0480: FAATSP]2.0.CO;2)
70. Rubenstein DI, Sundaresan SR, Fischhoff IR, Tantipathananandh C, Berger-Wolf TY. 2015 Similar but different: dynamic social network analysis highlights fundamental differences between the fission-fusion societies of two equid species, the onager and Grevy's zebra. PLoS ONE 10, e0138645. (doi:10.1371/journal.pone.013864)
71. Lehmann J, Korstjens AH, Dunbar RIM. 2007 Fission- fusion social systems as a strategy for coping with ecological constraints: a primate case. Evol. Ecol. 21, 613-634. (doi:10.1007/s10682-006-9141-9)
72. Asensio N, Korstjens AH, Schaffner CM, Aureli F. 2008 Intragroup aggression, fission-fusion dynamics and feeding competition in spider monkeys. Behaviour 145, 983-1001. (doi:10.1163/ 156853908784089234)
73. Aureli F, Schaffner CM. 2007 Aggression and conflict management at fusion in spider monkeys. Biol. Lett. 3, 147-149. (doi:10.1098/rsbl.2007.0041)
74. Preuschoft S, van Schaik CP. 2000 Dominance and communication: conflict management in various social settings. In Natural conflict resolution (eds
75. F Aureli, FBM de Waal), pp. 77-105. Berkeley, CA: University of California Press.
76. Flack JC. 2012 Multiple time-scales and the developmental dynamics of social systems. Phil. Trans. R. Soc. B 367, 1802-1810. (doi:10.1098/rstb. 2011.0214)
77. Izawa K, Kimura K, Nieto AS. 1979 Grouping of the wild spider monkey. Primates 20, 503-512. (doi:10. 1007/BF02373432)