No strings attached:
social bonds, cooperative feeding and neophobia in free-flying common ravens (*Corvus corax*)

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Photo: Peanut standing on a tree stem on a warm day. Credit: Bram van Beek

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1. Abstract

Cooperation occurs regularly in nature and can entail direct fitness benefits but also indirect costs. Individual animals should cooperate when the benefits of such cooperation outweigh the costs, especially if cooperation occurs frequently. Relatedness, group selection and reciprocity can skew the benefits of an interaction towards cooperation. Group-living social animals can therefore often be seen cooperating, as is the case in common ravens (Corvus corax). These birds are monogamous and live in groups outside of the breeding season or when they do not have a partner. Ravens are regarded as cognitively sophisticated birds and are excellent subjects for cooperative problem-solving studies. However, most such studies have been conducted on captive ravens. Here, we wished to investigate how coordinated feeding and problem-solving behaviour are influenced by social bonds in a free-flying population of common ravens. We expected raven dyads with strong social bonds to be present during feeding and to solve a string-pulling task more often together than alone. We measured parameters related to relationship value and reciprocity in 24 raven dyads during the breeding season. In addition, we recorded presence during a daily feeding service to captive wild boars and the raven's interest in a string-pulling task. Although reciprocity parameters showed no significant effect on dyad presence at the feeding, one parameter of relationship quality did show an effect. However, the correlation was negative, suggesting ravens prefer coordinating in dyads with a low relationship quality. Interestingly, no ravens approached our string-pulling setup, most likely due to neophobia. We also conclude neophobia is much stronger in our population than anticipated. Young ravens (less than 6 months old), which are less neophobic, could be habituated to our setup and apparatuses in order to prevent future difficulties studying cooperative problem-solving in wild birds.

2. Introduction

One of Charles Darwin's biggest hurdles while formulating the theory of natural selection was the existence of nonreproductive castes in social insects such as bees and ants (Darwin, 1859). The greater problem being that, according to his theory, "natural selection cannot possibly produce any modification in any one species exclusively for the good of another species" (1859, Ch VI). Not only do individuals in sterile castes vary greatly from other castes in both morphology and behaviour - not to mention variation within the sterile castes - they also showcase altruism. Altruism, or more specifically altruistic cooperation (West et al., 2007), stands in direct contrast to interindividual competition, on which Darwin's theory was built. Bees of all castes cooperate to achieve certain goals, with the main goal being the reproductive success of the queen; the female worker bees don't get to reproduce. Cooperation occurs everywhere in nature and, in fact, directed all major evolutionary transitions (Maynard Smith & Szathmáry, 1995; Buss, 1987; Michod & Roze, 1997; Korb & Heinze, 2016). Altruistic cooperation provides an issue, as is made clear by the famous Prisoner's Dilemma (PD) in game theory. Individuals within the PD have either the choice to cooperate with their partner or betray them. When both individuals cooperate, they yield the highest possible reward *as a duo*. However, when one cooperates but the other betrays, the betrayer yields the highest possible reward *as an individual*. Several versions of the dilemma exist, but none render altruistic cooperation an evolutionary stable strategy, due to the difference in benefits between the individual and the duo (Nowak & Sigmund, 1993; Koeslag, 1997, see also Trivers, 1971; Axelrod & Hamilton, 1981). But if evolution acts only on the level of the individual, how can cooperation like this even exist?

Currently, multiple sound answers to this question are accepted, including Hamilton's famous rule, $r \cdot b > c$ (Hamilton, 1964a,b), which contributed to the theory of kin selection (Maynard Smith, 1964). In the formula, r represents relatedness, b benefits and c costs. Hamilton's rule describes that benefits to one individual can indirectly benefit another, as long as they are related. Darwin himself actually thought of a similar solution, writing "This difficulty, though appearing insuperable, is lessened or, as I believe, disappears when it is remembered that selection may be applied to the family as well as to the individual…" (1859, Ch VII). Records show he realised the importance of kinship as early as 1848 (Dugatkin, 2006). Incidentally, he alludes to another mechanism for the evolution of cooperation, namely that of group selection. Group selection posits that evolution can act on the level of the group, not just that of the individual. Kin selection may favour interindividual cooperation when the individuals are related to each other, which changes the benefits gained in the PD according to $r \cdot b > c$ (Hamilton, 1964a,b; Maynard Smith, 1964; Sachs et al., 2004; Nowak, 2006). Group selection may favour intra-group cooperation when two populations are directly competing with one another: a cooperative group will win over a non-cooperative one in the PD (Maynard Smith, 1964; Nowak, 2006). A third important mechanism is reciprocity: especially when two individuals meet often, they can rely on tit-for-tat mechanisms to ensure mutual cooperation and the highest benefit yield (Trivers, 1971; Axelrod & Hamilton, 1981; Sachs et al., 2004; Nowak, 2006). Cooperation may

also be a by-product of individual, "selfish" selection, as is the case in Mullerian mimicry for example (Sachs et al., 2004). Mullerian mimicry occurs when two poisonous or otherwise well-defended species share warning signals, thereby sharing the burden of educating predators to their mutual benefit (Müller, 1879; Chatelain, 2023). This type of cooperation differs from altruistic cooperation by being mutually beneficial (West et al., 2007). These mechanisms often co-occur and interact (Sachs et al., 2004). In conclusion, cooperation is not only apparent in social, group-living animal species like bees, but also essential for their formation.

Researchers have been studying cooperation not only on a macroevolutionary scale, but also on a smaller scale *in vivo*. One paradigm investigates cooperative feeding behaviour with an apparatus consisting of a string run through solid rings connected to a board (Hirata, 2003). In this loose string-pulling task, two individuals need to move the board by pulling on the string in order to receive a reward that is otherwise out of reach. Pulling on one end of the string (i.e. by one individual) is ineffective: the string will merely move through the rings. Only by pulling on both ends simultaneously can the board be moved forward. This method has been used in apes (e.g. Hirata, 2003; Hirata & Fuwa, 2007), other primates (e.g. Molesti & Majolo, 2016), wolves and dogs (e.g. Range et al., 2019), elephants (Li et al., 2021), parrots (e.g. Bastos et al., 2021) and corvids (e.g. Scheid & Noë, 2009; Asakawa-Haas et al., 2016), among others. The mentioned species are all altricial, social, group-living animals, and most are also cognitively sophisticated, making them excellent subjects to study cooperation. Another aspect these animals have in common is the regular occurrence of cooperative and altruistic behaviour in wild populations (e.g. Dugatkin, 1997; Dugatkin, 2014; Widdig et al., 2000; Boesch & Boesch-Achermann, 2000; Mech & Boitani, 2003; Heaney et al., 2017; Diamond & Bond, 1991; Sukumar, 2003; Marzluff et al., 1996). It is perhaps no surprise that all of them manage to solve the loose string-pulling task and that some even specifically wait for their partner before trying to solve it (Heaney et al., 2017; Li et al., 2021). The aforementioned characteristics are also shared by humans (Dugatkin, 1997; Heinrich & Heinrich, 2006).

Among the species and taxa listed above, corvids, and in particular ravens, have historically been viewed as intelligent, as is demonstrated in the work of Bernd Heinrich (1995a). Heinrich found over 1000 accounts in scientific literature that described ravens as "smart" birds, almost all of which were anecdotal in nature (see also Bugnyar, 2023). Since 1995, many scientific studies on corvid intelligence have emerged and confirmed the validity of such accounts: common ravens (*Corvus corax*) are capable of intricate cognitive feats such as inferential reasoning, perspective taking and planning for the future (Schloegl et al., 2009; Bugnyar et al., 2016; Kabadayi & Osvath, 2017; see also Pika et al., 2020). In fact common ravens manage to reach the final Piagetian stage of sensorimotor development, which had only been observed in great apes before (Jacobs et al., 2019), and already show cognitive skills comparable with adult great apes at the age of 4 months (Pika et al., 2020). This comparability leaves one asking how exactly intelligence evolved in animals.

The evolution of intelligence and large brains have historically been explained by ecological hypotheses but, according to Dunbar & Schultz (2007), most of them fail. In their stead, the social intelligence (or social brain) hypothesis proposed human cognition evolved in order to deal with increased social complexity within populations (Jolly, 1966, Byrne & White, 1988; Dunbar, 1998). However, whereas brain (neocortex) size correlates positively with social group size in humans, the same cannot be said for other mammals and non-mammals. In birds and certain mammals, brain size instead correlates with long-term pairbonds and monogamy, which suggests that dealing with one particular conspecific over time, rather than multiple individuals, might be equally or more cognitively challenging (Dunbar & Schultz, 2007; Emery et al., 2007; see also Braun & Bugnyar, 2012). The strong relation between human brain size and group size supposedly emerged after our species started using its cognitive capabilities to maintain pairbonds to form relationships with individuals who are not reproductive partners (Dunbar & Schultz, 2007). Additionally, in social group-living animals, incohesion in terms of group size and composition could pose cognitive challenges. A high degree of fission-fusion dynamics requires members of such social species to keep track of individuals that are temporarily absent and to regularly update their knowledge on the group composition (Aureli et al., 2008; Bugnyar, 2013). Such dynamics are present in several mammalian and avian species (de Waal & Tyack, 2003; Emery, 2006), including ravens, at least outside of the breeding season (Heinrich, 1989; Marzluff & Angell, 2005, Massen et al., 2014).

This social flexibility is particularly significant for common ravens because, as they are scavengers, they often face challenges related to finding enough food sources and are ecologically flexible (Ratcliffe, 1997). Cooperation and group formation substantially aid in finding and accessing food sources that are otherwise unavailable or unpredictable (Heinrich & Marzluff, 1991; Marzluff & Heinrich, 1991; Bugnyar & Kotrschal, 2002a). Non-breeder groups are often joined by adult pairs that are not breeding or actively raising offspring, supposedly for similar foraging benefits (Braun et al., 2012; see also Bugnyar, 2013). Ravens will occasionally cooperate to distract and take food from dangerous predators (Ratcliffe, 1997, p. 95), for instance by pulling on the tail feathers of vultures feeding at carcasses (Kilham, 1989; see also Bent, 1946). They also regularly recruit conspecifics to feeding sites by emitting a specific call (Heinrich, 1988b, 1994; Heinrich & Marzluff, 1991, 1995; Marzluff et al., 1996; Bugnyar et al., 2001), in order to receive help in acquiring food (Sierro et al., 2020). Ravens thus exhibit a large propensity for engaging in cooperative tasks and for foraging in pairs to obtain food.

Understanding these behaviours in the context of relationship quality (RQ) provides deeper insight into how and why these cooperative interactions occur. According to Cords & Aureli (2000), RQ comprises three separate elements: relationship value, security and compatibility. Relationship value (RV) encompasses direct (fitness) benefits gained from the social bond, such as from cooperative feeding. Relationship security (RS) refers to the

predictability of the pairbond's cohesion, relating to the partner's consistency in behavioural responses. Relationship compatibility (RC) refers to the general disposition of the partners towards each other, which depends on their personality and their social history with each other. Fraser & Bugnyar (2010), similarly to Fraser et al. (2008) in primates, defined behavioural parameters to measure these RQ elements in ravens: contact sitting, allopreening and agonistic support for RV, lack of variation in response to approach over time for RS and lack of aggression, lack of counter-intervention and tolerance to approach for RC.

The loose string-pulling task has so far only been tested in captive common ravens. However, wild-caught ravens that were held captive for over a year were able to solve a *vertical* string-pulling task, where food is attached to a string that is hanging from a perch so that it is out of reach from the ground (Heinrich, 1995a; Heinrich, 2000; see also Heinrich & Bugnyar, 2005). A preliminary study on wild ravens experienced difficulties, as all the individuals avoided the immediate area of the food on strings. Fear of the strings and/or the food on it proved to be a big issue, also in studies on captive ravens (Heinrich, 2000). One article remarks how in hand-reared ravens, isolated individuals were more hesitant to approach vertical strings than individuals in groups (Heinrich, 1995a). Indeed, social context, particularly the presence of conspecifics (siblings), has been shown to significantly increase exploration of novel objects and food in both ravens and crows (Miller et al., 2015). Sex combination, dominance and several other socio-ecological factors also play important roles in novel object exploration (Stöwe et al., 2006; Miller et al., 2022). Once again, this was tested in captive, hand-reared birds. It remains to be seen how different social contexts affect the string-pulling behaviour of wild ravens.

In this study we addressed this by focusing on the social bonds, coordinated foraging as a form of cooperation and string-pulling behaviour in a population of free-flying common ravens (*C. corax*) in Austria during the breeding season. This also helped us investigate how ravens select cooperative partners. We aimed to address the following questions:
1. How does relationship quality affect the presence of common raven dyads at a daily feeding event during the breeding season?
2. How does within-dyad reciprocity affect the presence of common raven dyads at a daily feeding event during the breeding season?
3. How does social context determine participation in a string-pulling task in free-flying common ravens?

Considering what is known about raven relationship quality and string-pulling behaviour, we formulated the following hypotheses and predictions:
1. Relationship quality has an effect on dyad presence at the daily feeding event. We predict that members of raven dyads with a high RV are present together more often than alone at the daily feeding event.

2. Reciprocity has an effect on dyad presence at the daily feeding event. We predict that members of raven dyads with a high degree of reciprocity are present together more often than alone at the daily feeding event.
3. Social context has a significant effect on the raven's approach to and participation in the string-pulling task. We predict that ravens approach and participate in the task more often together with partners than alone. Moreover, dyads with a high RV approach and participate more often than those with a low RV. Lastly, dyads with a high RV tolerate each other more and will thus be able to participate in the task closer together than dyads with a low RV.

In order to answer our questions, we carried out two separate study designs which shall hereafter be referred to as the cooperative feeding study and the string-pulling study.

3. Shared methods of both studies

The two studies were conducted between February 26th and June 3rd 2024 in the Cumberland Wildlife Park Grünau situated 6 km south of Grünau im Almtal in Upper Austria. Here, among the northern Austrian Alps, a population of wild ravens has been monitored by researchers of the university of Vienna since the 1990s. Groups of ravens visit the park year-round, where they forage, socialise and engage in playing behaviour (Drack & Kotrschal, 1995). Most individuals are non-breeders (i.e. either sexually immature or not reproductively active) but roost communally on cliffs on the other side of the river next to which the park is situated. All birds within the population are habituated to humans to some extent (Braun & Bugnyar, 2012), but the main observer (B.v.B.) still invested almost a month of time to ensure the birds were habituated to his presence, allowing him to move between enclosures without causing too much disturbance or too many flight responses. Ethical approval for the study was granted by the university of Vienna (approval number 2024-008).

The free-flying ravens often pillage food given to the captive animals in the park, in particular the wild boars (*Sus scrofa*) which are fed multiple times a day. Staff and students of the Konrad Lorenz Research centre of the university of Vienna regularly provide the morning feeding for the boars, after which a record is taken of the presence (and social interactions) of any marked ravens. A total of 37 marked subjects were spotted over the course of the aforementioned period. No new individuals were marked during the study period.

Between February 26th and May 31st 2024, behavioural data of raven dyads was collected by B.v.B. over the course of 102 observational rounds lasting approximately 60 minutes. In some cases (e.g. help was needed elsewhere or few to no dyads could be found) the observation was extended or cut short (see **Table S2**). Observational rounds took place up to twice per day: in the morning between 0800 and 1100 and in the afternoon between 1300 and 1800. These rounds would involve the observer walking along a specific route through the park, past several

enclosures where the ravens spend the most time. These enclosures housed wolves and bears (shared enclosure), Przewalski's horses, boars and deer (Braun & Bugnyar, 2012; see **Figure 1**). During each round, observational samples of any affiliative interactions between study subjects and their partners were recorded, provided they lasted longer than 20 seconds, and recording was stopped once a sample exceeded 300 seconds. In this way, a total of 188 observational samples were collected, of which 56 were among marked-marked dyads and 132 were among marked-unmarked dyads. Parameters recorded during samples can be divided into three categories: proximity, affiliative contact and self-aggrandising display (SAD), a typical raven display involving increased perceived body size by feather erection, often accompanied by an acoustic signal (e.g. Boeckle et al., 2012). Instances and durations of proximity were recorded, subdivided into ground proximity (≤ 1m from partner), perch proximity (≤ 1m but > 1 body length from partner) and contact sitting (within 1 body length of a partner). Affiliative contact concerned instances and durations of allopreening, requests for allopreening and the partner's response, and instances of affiliative touch. Lastly, SADs can be either affiliative or agonistic, but all instances and durations of SADs were recorded.
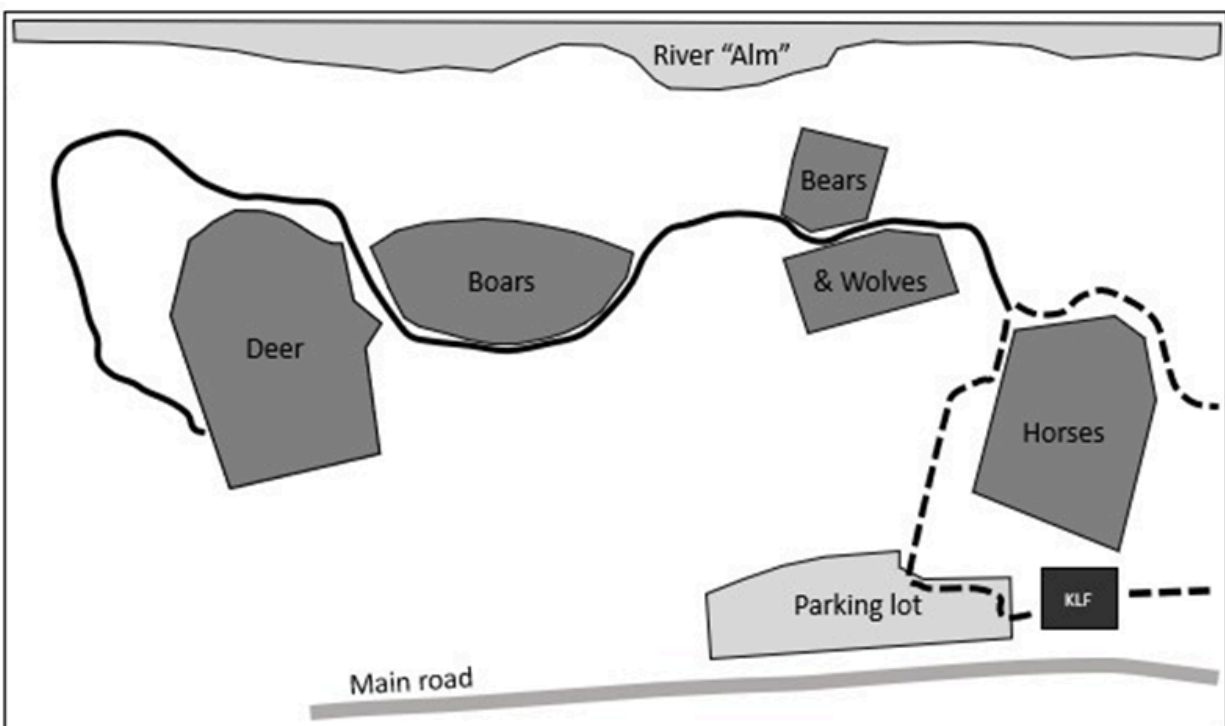

Figure 1. A sketch of the enclosures of interest in the wildpark. The route of the observer is indicated with a thick black line. The dotted lines indicate two separate ways to start/end the route around the horse enclosure.

4. Cooperative feeding study

Behavioural observations

Daily presence of ravens at the morning feeding of the wild boars was recorded for a total of 62 days between March 1st and June 31st, starting between the hours of 0800 and 0900 and

lasting 15 minutes. Presence was documented by calling out the IDs of any ravens that were inside or within 10m of the boar enclosure while recording audio on a smartphone. Additionally, several other factors were noted just before the feeding, including the type of weather, the temperature, the number of people present and the type of food the boars would receive. At the end of the 15 minutes, an estimate for the total number of ravens (both marked and unmarked) was noted as well. When a member of a dyad was spotted at least once during a specific week, we assumed that individual was generally present for the entirety of that week. This gave us a proxy for the general presence of individuals in the park and allowed us to control for absence due to, for instance, parental caretaking or mortality. Our proxy was correct at least 82% of the times an individual was deemed present for the entire week. This was calculated by averaging the ratio of [number of days an individual was seen in week x] to [number of boar feedings in week x] for all individuals that were present at least once in week x (see **Table S3**).

Statistical analysis

Data was analysed using R (4.2.2) and RStudio (2024.04.1+748). In order to better understand abiotic effects on the total raven presence, we created a linear model with food type, temperature and weather type as fixed effects, including interactions. To analyse this model, we ran an ANCOVA from the "car" package (Fox & Weisberg, 2019) and ran post-hoc tests where applicable using the "emmeans" package (Lenth, 2024).

Daily presence at the feeding was used as a binomial response variable, where 1 represents both individuals of a dyad were spotted and 0 represents only one half of the dyad was spotted in the aforementioned 15 minutes. Cases where neither member of a dyad were present were ignored. We only analysed data from periods when both individuals of the dyad were present in the park. In other words, our response variable is a measure of when we expected both individuals of a dyad to be present at the feeding, and whether that was actually the case (1) or only half the dyad was present (0). We considered variables with p-values lower than 0.050 as significant effects. We used a singular model combining fixed effects from both RQ and reciprocity. We ran the model twice; once with all data and once excluding dyads with less than 3 observational samples. Where our original dataset included 24 dyads and 56 samples, the adjusted dataset included just 6 dyads and 33 samples. We wanted to test both, because the dyad sample size of the original dataset is substantial but most dyads only have 1 or 2 samples to their name, which will have skewed the data significantly; many of these dyads have not been observed allopreening.

For our first question concerning RQ, we included one fixed effect: proportion of time spent allopreening (at the dyad level), relative to the total time a dyad was observed. This is a measure of relationship value; behavioural measures of relationship security and compatibility were beyond the scope of this research. Initially, we wished to include the proportion of time

spent in contact sit as a fixed effect, but we were forced to exclude it from the model because of collinearity with the effect of allopreening.

For our second question concerning reciprocity, fixed effects included interindividual differences in durations of allopreening and in occurrences of touches, relative to the dyad total, as well as mutual favouritism. These first two variables ranged from 0, meaning one half of the dyad initiated exactly 50% of the interactions, to 1, meaning one half of the dyad initiated 100% of the interactions. With 'mutual favouritism' we mean dyads in which both individuals were seen most often with the other individual, i.e. there was a bi-directional preference for social interaction with the other half of the dyad, rather than with any individuals outside of the dyad. Again we wished to include another fixed effect, namely the relative interindividual difference in number (rather than duration) of preening bouts, but ultimately had to drop it due to collinearity. For our main questions, we used a generalised linear mixed-effect model (lme4; Bates et al., 2015) with all previously-mentioned fixed effects, without interactions, and a random effect of dyad-ID.

Results

Out of the three abiotic effects we entered into the linear model, two had a significant effect: food type ($p < 0.001$) and temperature ($p = 0.032$). All three factors are represented graphically in **Figure 2**. Our subjects varied both in how many partners they were seen affiliating with outside the boar feeding (mean±se: 2.593 ± 0.321), as well as how affiliative they were (e.g. mean±se of proportion of time spent preening: 0.034 ± 0.010) (see **Figure S1**). We identified a total of 24 marked-marked raven dyads, of which three had mutual favouritism: Kibi & Padma (m-f, breeding pair), Peanut & Walnut (m-m, full siblings) and Foxtrot & Zwiebel (m-f, non-breeding pair) (see **Table S1**).
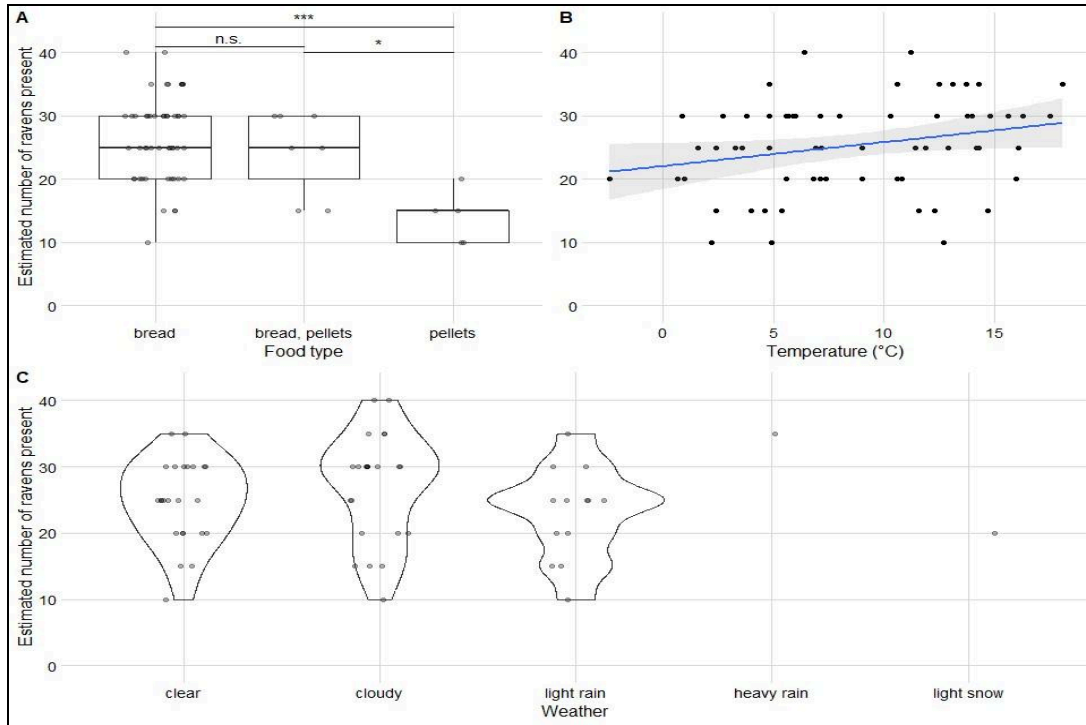
Figure 2. *The effect of several factors on the estimated total number of ravens at the daily feeding. **A:** the effect of food type, separated into three categories; bread, bread and pellets, and pellets. Data is represented with boxplots and with points with 20% jitter. **B:** the effect of temperature. A linear regression line with standard error bars shows the influence of the parameter. **C:** the effect of weather. Data is represented with violin plots and with points with 15% jitter.*

Proportion of time spent preening was the only parameter that had a significant influence on our response variable (df = 288, p = 0.038), but only when all data was included (See **Table 1**). According to the model output, allopreening negatively affects dual presence of dyads at the daily feeding. None of the fixed effects showed a significant influence when we ran the model including dyads with 3 or more samples. **Figures 3** and **4** show dyad presence as a function of all RV and reciprocity parameters.

Table 1. Full model output including estimate, standard error, z-value, p-value and lower and upper 95% confidence intervals. Both the output of the full dataset and adjusted dataset are shown. Stars represent effects below *p* = 0.05.

| Fixed effect	Dataset	Estimate	Std. error	Z value	P value	Lower CI	Upper CI
Proportion of time spent preening	Full	-4.732	2.276	-2.079	0.038*	-9.404	-0.302
Difference in preening time	Full	-0.294	0.618	-0.476	0.634	-1.566	0.961
Difference in no. of touches	Full	-0.916	0.521	-1.760	0.078	-2.099	0.134
Mutual favouritism	Full	0.467	0.315	1.482	0.138	-0.183	1.177
Proportion of time spent preening	Adjusted	-6.438	3.761	-1.712	0.087	-14.29	0.865
Difference in preening time	Adjusted	-0.399	0.644	-0.620	0.535	-1.723	0.916
Difference in no. of touches	Adjusted	-0.944	0.523	-1.804	0.071	-2.146	0.124
Mutual favouritism	Adjusted	0.433	0.321	1.352	0.177	-0.242	1.161
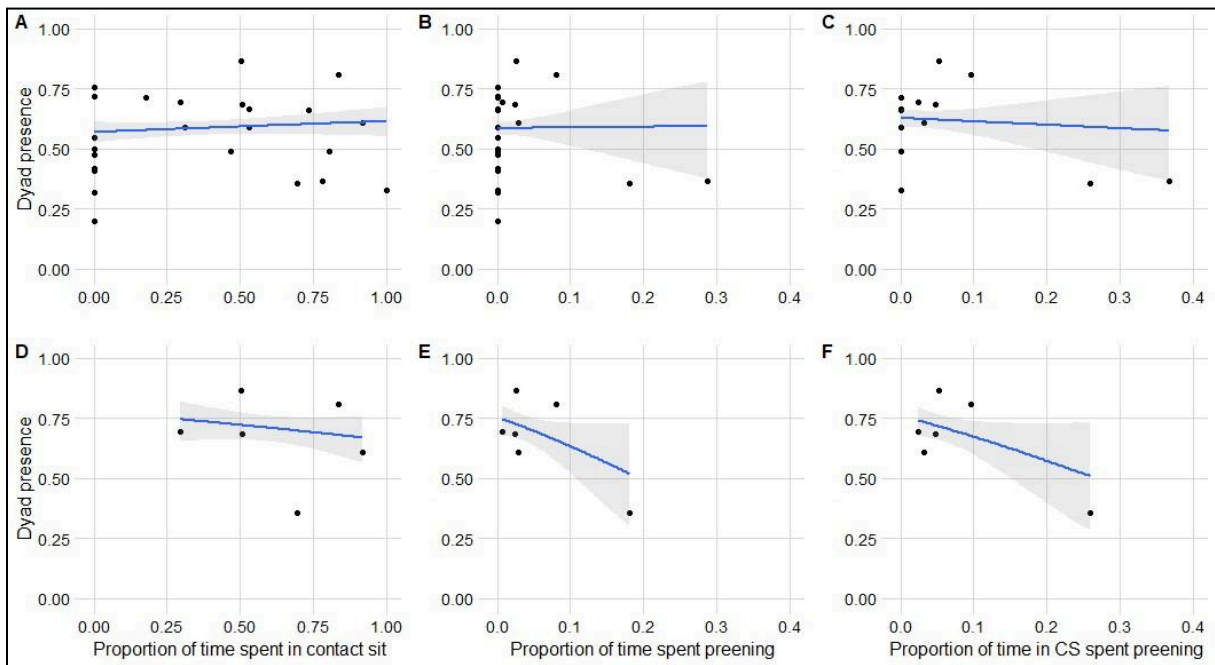
Figure 3. *Dyad presence according to parameters of relationship value for the whole dataset (A-C) and for dyads with 3 or more observational samples (D-F). Presence was averaged per dyad. Regression lines show the best fitting binomial curve through the data plus the standard error. All axes have similar scales for easy interpretation between A-C and D-F.*
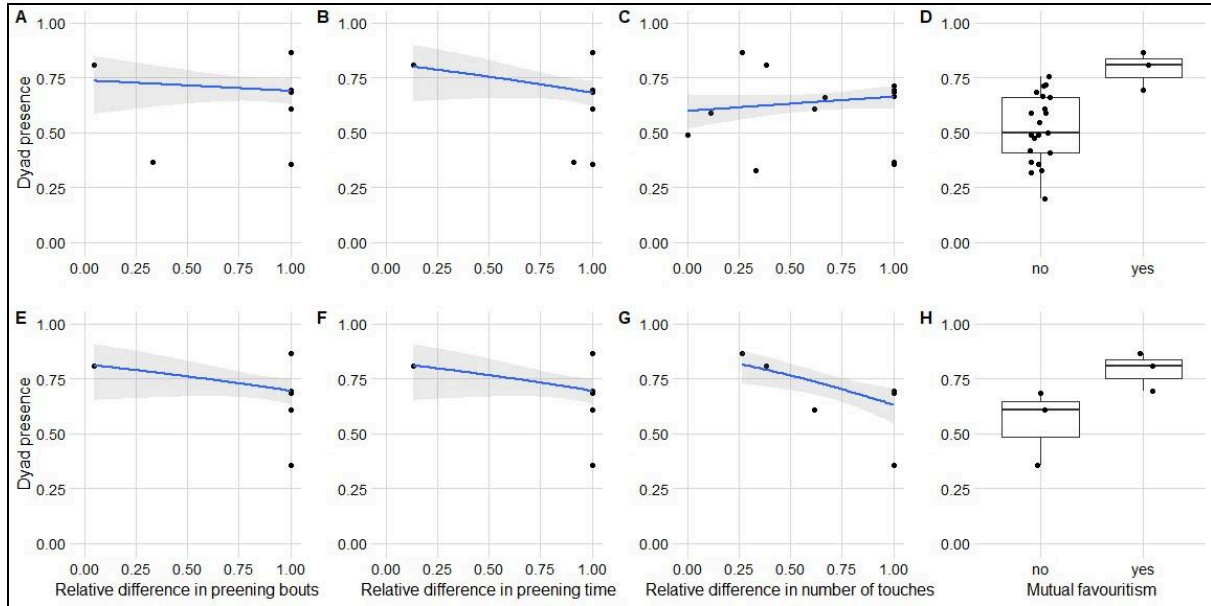
Figure 4. *Dyad presence according to parameters of reciprocity for the whole dataset (A-D) and for dyads with 3 or more observational samples (E-H). Dyad presence was averaged per dyad. Trendlines show the best fitting binomial curve through the data plus the standard error, and is based on the original binomial dyad presence data. All axes have the same scale for easy interpretation between A-D and E-H. Graphs D and H show both boxplots and the raw data with some horizontal jitter.*

5. String-pulling study

Experimental setup

We used two experiments involving 3 mm thick white nylon strings hanging vertically or placed horizontally on the ground. Vertical strings were hung from the fence of the enclosure at a length such that the end of the string was visible, but out of reach for the ravens (60-65 cm long). Horizontal strings were placed in wooden boxes with metal grating such that 65 cm of the string extended outside of them and were therefore accessible. The boxes were previously used for loose string-pulling tasks and still housed such apparatuses for the duration of this study. Each experiment had two identical setups located roughly equidistant from a central observation point at the wild boar enclosure, for a total of four setups (see **Figure 5**) We used two different distances between the strings, because feeding next to a conspecific requires a high level of tolerance, which could be interpreted as cooperation. This tolerance needs to be higher the shorter the distance between the strings. At any point in time one setup had 3 strings 10 cm apart while the other had 3 strings 45 cm apart. For instance, if the left horizontal experiment had strings 45 cm apart, the left vertical experiment would have them 10 cm apart, the right horizontal one would have them 10 cm apart and the right vertical one would have them 45 cm apart. All strings (12 in total) were present at all times to ensure habituation among test subjects, but only one setup was used per day of data collection. Which experiment was baited - horizontal or vertical - and which distance condition was used - 10 or 45 cm - was determined daily semi-randomly: the same combination was not used more than 3 days in a row. Experiments

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were conducted for 1 hour up to twice per day - once in the morning and once in the afternoon - and recorded using Panasonic® HC-V777 video cameras. Three separate treatments were considered with regards to the strings and bait: a training treatment, a control treatment and a test treatment (see **Figure 6**). The training treatment involved bait placed on top of the fence above each respective string for the vertical setups. Horizontal setups had bait simply placed on top of but disconnected from the string ends. The control treatment involved bait placed in the same way as in the training treatment, but attached to the string ends. The test treatment involved bait attached on the string ends, but hanging from the fence (vertical setup) or placed inside of the box (horizontal setup), the idea being that the ravens need to pull on the string in order to reach the food. For bait we used 1-day old chicks, a high-quality food.
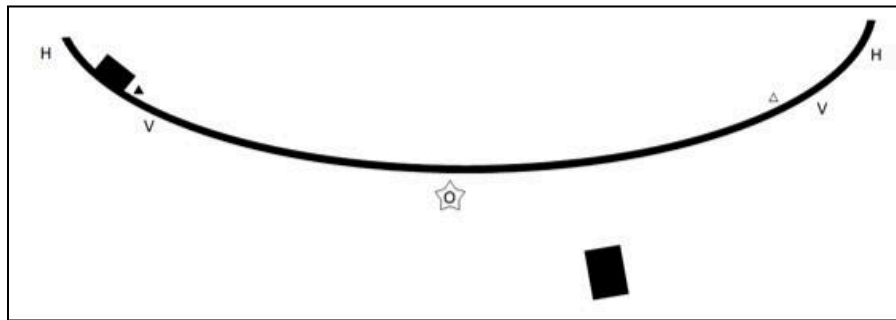

Figure 5. A sketch of the outer fence of the boar enclosure. Black rectangles represent wooden structures of the wildpark. Triangles represent the approximate locations of feeding sites, with the filled triangle being the main site. The white star with an "O" shows the main observation point. Letters indicate the locations of our strings; V for vertical and H for horizontal strings.
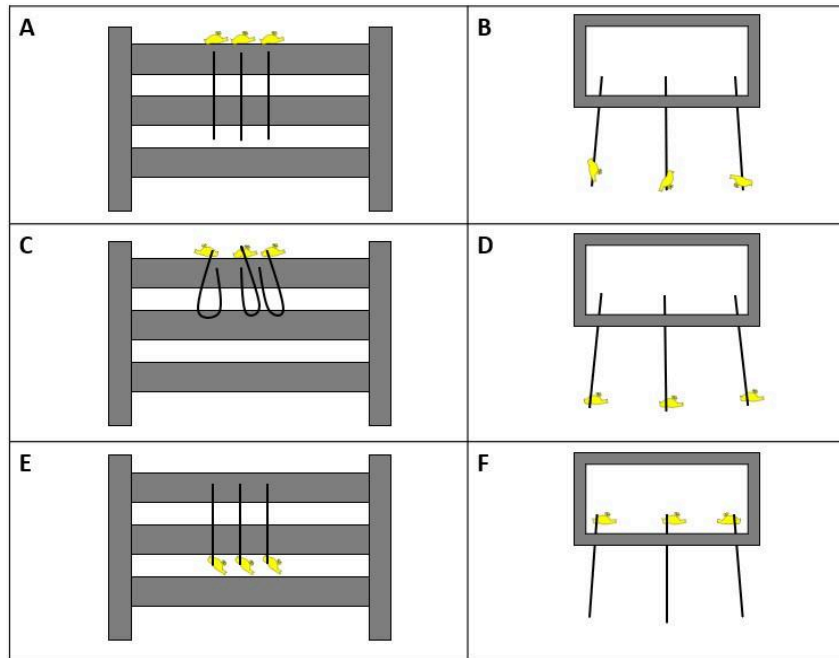
*Figure 6. A sketch of the vertical (A, C, E) and horizontal (B, D, F) string-pulling setups. The vertical setups are shown in a front-facing view of the fence, while the horizontal setups are shown in a top-down view of the apparatuses. The strings are represented by black lines and the bait by yellow bird icons. **A and B:** training condition; where bait was unattached. **C and D:** control condition; where bait was attached but reachable. **E and F:** test condition; where bait was attached and not readily available.*

After 2-3 weeks of the training treatment, no ravens had approached any of our setups, leading us to include an additional experiment without strings. This ground experiment involved three pairs of chicks placed on the ground just beside the path outside of the enclosure, 45 cm apart. This allowed us to control for the neophobic effect of the novel strings, but also to observe the behaviour of secondary subjects in response to a primary subject taking one of the chicks. We could then monitor effects of local enhancement and kleptoparasitic behaviour.

The string and ground experiments were often combined with the observational rounds, during which the setups were left unattended for at least half of the 60 minute duration of the experiments. For the rest of the duration, the observer would be in the vicinity of the setups to personally observe any subjects interacting with them. Over the course of 50 days, a total of 79 experiments (vertical string, horizontal string and ground experiment) were conducted in roughly equal amounts. These experiments took place between March 15th 2024 and June 3rd 2024. Because ravens show colour preferences that vary between individuals (Miller et al., 2016), we decided to change the colours of half of the strings from May 10th onward. Specifically, the white strings of the vertical and horizontal setups of the left side (see **Figure 5**) were swapped out for blue ones.

Despite our efforts to habituate the birds to the strings, no raven participated in our experiments or even came within 1 m of the string setups. On three separate occasions, a single chick was taken from the ground experiment, but only by an unmarked raven/unmarked ravens. On several occasions, the main observer put out pieces of cat food on top of the fence around the boar enclosure at different spots and at different times. The goal being to habituate the birds further to the observer and to get them to land on top of the fence. These occurrences were not explicitly recorded, but usually involved 4-8 pieces of food, 10-15 cm apart, on top of the fence and some additional pieces strewn on the ground. The observer would oftentimes lay out the pieces on the fence individually, one by one, after showing each to any nearby raven(s). For some, the observer stayed with the food (10-20 m away) to observe any nearby birds, while other times the food was left alone. Two of these occasions are of interest:

- On one occasion, three marked birds (Foxtrot, Walnut, Yamaha) were seen approaching the fence, taking some of the food strewn on the ground. Two of them (Foxtrot and Yamaha) then flew to the fence posts on each side of the fence rail and tried, but failed, to reach it from those locations.
- On another occasion, one marked raven (Yamaha) was seen flying to the top fence rail and consequently successfully taking 5 out of 5 pieces of cat food that the experimenter had just placed there.

6. Discussion

Cooperative feeding study

Our data analysis revealed that the proportion of time spent preening has a significant effect on the dyads' presence at the daily feeding event. None of the other parameters entered into the model showed a significant influence. We cannot say with statistical confidence that a dyad's reciprocity has an effect on their presence at a daily feeding event during the breeding season. In addition to the proportion of preening time, mutual favouritism seems, at least visually, to have some effect on dyad presence (see **Figure 4D, 4H**). Boucherie and colleagues (2016) studied different types of social bonds in rooks (*Corvus frugilegus*), identifying three types of bonds: primary, secondary and weak. Primary bonds are those that are the strongest in an individual's social circle for both halves of a dyad and are thus equivalent to what we have dubbed mutual favouritism. The researchers concluded that primary relationships show the highest levels of spatial proximities and affiliations. Reciprocity for proximities and affiliations was similar between primary and secondary relationships, however. According to our findings, primary bonds (i.e. relationships with mutual favouritism) do not necessarily show higher levels of proximity and affiliation compared to secondary and weak bonds. This is likely due to several differences between our study and that of Boucherie and colleagues, including the difference in study subjects (captive rooks versus wild ravens) and the length of the study (several years versus a single breeding season). The classification of corvid social bonds into primary,

secondary and weak bonds provides an excellent proxy for a bird's subjective view of their social circle and could thereby provide an excellent categorical measure of relationship quality.

Previous work conducted outside of the breeding-season found a positive correlation between relationship value and dyad presence (Koskela et al., in progress), whereas we find a negative one. While this is a striking difference between the breeding and non-breeding seasons, it might be a product of breeding pairs prioritising nesting and raising offspring. With one parent on the nest and the other scavenging for food, it is unsurprising to find that strong pairbonds are often not together at the daily feeding. Asakawa-Haas and colleagues (2016) sought to test partner preference in a loose string-pulling task in captive common ravens and found that relationship quality is not a strong factor in decisions of which partner to cooperate with. Rather, tolerance of spatial proximity to close associates or, indeed, avoidance of proximity to not so close associates better predicts the preference for cooperating with friends over non-friends. A number of studies on primates corroborated this finding (Suchak et al., 2014; Molesti & Majolo, 2016). Regardless, Asakawa-Haas et al. find that relationship quality does increase the raven's performance in the task, a conclusion shared by research in other animals before and since their publication (Keeble et al., 2022 Battacharjee et al., 2024). Interestingly, Asakawa-Haas and colleagues used contact sitting, allopreening and allofeeding to determine a dyad's relationship quality, whilst Fraser & Bugnyar only attribute these to relationship value. However, their goal was to discover a proximate driver for cooperation. Most of the experiments used up to that point did not distinguish between partner choice as a byproduct of close proximity or as a result of an actual choice based on relationship quality. In this regard, their conclusion is very solid. This leaves us with the curious suggestion that the negative effect of allopreening found in this research and the positive effect of Koskela et al. combined produce a net-zero effect over the course of a breeding and non-breeding season. The experiments of Asakawa-Haas et al. took place between August 8th 2014 and September 12th 2014, which is after young ravens have fledged. A long-term study on captive and/or wild ravens could pinpoint precisely how relationship quality affects partner choice and cooperation.

Our study was confined to measures of relationship value, whilst relationship quality encompasses two more factors: relationship security and relationship compatibility. Including relationship security and compatibility in our analysis would perhaps have provided more validity to our conclusions, although RV contributes most to relationship quality (35.1% compared to 24.7% for RS and 15.4% for RC, Fraser & Bugnyar, 2010). However, other researchers in the field have also omitted the factors of RS and RC, and found a clear effect of RV on performance in cooperative tasks (e.g. Suchak et al., 2014; Asakawa-Haas et al., 2016; Molesti & Majolo, 2016).

String-pulling study

Our study subjects exhibited an unexpectedly high degree of neophobia. None of our marked subjects approached any of our setups, despite some bolder individuals showing motivation to acquire high-quality food from similar locations. Previous work on string-pulling behaviour in ravens was successfully carried out in captivity and showed a clear effect of social context (Miller et al., 2015; Stöwe et al., 2006; Miller et al., 2022). Wild-caught birds that were kept in captivity for little over a year succeeded in a string-pulling task (Heinrich & Bugnyar, 2005). However, previous efforts outside of the breeding season were also unsuccessful in getting wild ravens to interact with a loose string-pulling task (work by a master student who placed pieces of high-quality meat on the metal prongs of the apparatus in its pulled-out state, so that it was readily accessible for the ravens). The difference between the wild and captive ravens is not a large one, as both groups were highly familiar with anthropomorphic settings at the time of the experiments. Whether a raven is raised in captivity or in the wild has no influence on how likely they are to be present at anthropomorphic feeding sites, according to Jain et al. (2022).

Ravens will often approach both large and small carrion with extreme caution, even when they have been hand-reared (Heinrich, 1988a, 1988b; Heinrich, 1989; Kilham, 1989; Ratcliffe, 1997). Young ravens are quite curious and highly explorative until about 1 month after fledging, after which they become very neophobic (neophobia is a fear of novel objects or situations)(Heinrich, 1988a, 1995b; Heinrich et al., 1995; Miller et al., 2015). Habituating ravens to novel objects can take months (Kijne & Kotrschal, 2002).

An animal's willingness and ability to solve a task depends on several motivational factors or behavioural traits, including neophobia , motor diversity and flexibility (an animal's repertoire of problem-solving behaviours and ability to apply these to novel problems or to obtain new solutions to known problems) and persistence (the motivation and quantifiable time spent resolving a task of an animal) (Lefebvre et al., 2004; Biondi et al., 2010; Hiestand, 2011; Cole et al., 2011; Morrand-Ferron et al., 2011; Thornton & Samson, 2012; Benson-Amram & Holekamp, 2012; Griffin & Guez, 2014; Moretti et al., 2015; Griffin & Diquelou, 2015; Huebner & Fichtel, 2015; Udell, 2015; Borrego & Gaines, 2016). Research shows that where a species or population lands on the spectrum of these traits is determined by socio-ecological factors (Webster & Lefebvre, 2001; Lefebvre et al., 2004; Cauchard et al., 2013; Griffin et al., 2014). For example, birds in stable environments exhibit higher degrees of neophobia and less behavioural flexibility than birds of the same species in dynamic environments (Mettke-Hofmann et al., 2002; Sol et al., 2005; Sol et al., 2011; Kozlovsky et al., 2015). Since the environment of our subjects is, at least ecologically but also to an extent socially, highly stable, it is unsurprising that they exhibit such a high degree of neophobia. Perhaps the biggest difference between wild and captive ravens lies in their neophobia, and a high degree of explorative behaviour is what allowed the wild-caught group to be caught in the first place. The difference might also lie in the familiarity of the food. The captive ravens of the wildlife park

receive chicks regularly, twice every weekend, and have been getting them for several years. As mentioned above, ravens are known to be highly fearful of animal carcasses, especially larger ones (Heinrich, 1988a, 1988b; Heinrich, 1989; Kilham, 1989; Ratcliffe, 1997). They likely evolved this fear-response in order to ensure the animal is dead rather than asleep or ill and still dangerous (Heinrich, 1988a). While our bait was high-quality small animal carcasses, an evolved fear-response would explain the observed behaviours.

Very few birds approached our ground experiment, indicating their neophobia is directed not just towards the strings, but also towards the apparatuses and *general setting*. This indicates that their neophobia carried over from the strings to the general area around the strings. Changing the colour of half of the strings to blue did not increase the raven's motivation to interact with our setups. Some bolder ravens were unafraid of the main observer, as they would only flee after he got closer than ~3 metres, indicating we had clearly achieved habituation towards him. However, the main observer wore the same black coat for most of the three months and noticed that, once it got too warm for him to wear it, it seemed some of the birds were more vigilant of his presence. Regardless, it is surprising the ravens readily accept novel people, but exhibit extreme caution towards novel objects. Again, this can be explained by their ecological circumstances: while their food sources, both in sense of location and in sense of volume, are extremely stable, the people they encounter in the park vary greatly from day to day. It is surprisingly fitting that their neophobia reflects this fact.

Miller et al. (2022) identified socio-ecological correlates of neophobia specifically in several corvid species. While neophobia towards novel *food* had only one correlate (maximum flock size), neophobia towards novel *objects* had four: use of urban environment (versus not), pair versus group sociality, large versus small maximum flock size and moderate versus specialised caching. These factors were determined for the birds on a species-specific level and, out of the ten species tested, ravens showed the largest degree of neophobia, second only to the 'Alala (*Corvus hawaiiensis*).

Conclusion

Our efforts have aided in pinpointing effects of relationship quality and reciprocity on cooperative feeding, as well as identifying issues with using string-pulling experiments in wild ravens. We expected that at least some marked birds would approach our setups. Efforts to eliminate the influence of neophobia are already in motion. Captive-bred young ravens have been habituated to the loose string-pulling apparatus while in captivity and will be released into the wild. These birds will hopefully coax other free-flying subjects – both adults and subadults – to engage with the strings via contagious behaviour. This will allow researchers to thoroughly study cooperative partner choice in wild ravens, possibly long-term.

7. Acknowledgements

8. Bibliography

Asakawa-Haas, K., Schiestl, M., Bugnyar, T. & Massen, J. J. M. (2016). Partner choice in raven (Corvus corax) cooperation. *PLOS ONE*, *11*(6), e0156962.

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., Connor, R., Fiore, A. di, 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. & van Schaik, C. P. (2008). Fission-fusion dynamics, new research frameworks. *Current Anthropology*, *49*(4).

Bastos, A. P. M., Wood, P. M. & Taylor, A. H. (2021). Kea (Nestor notabilis) fail a loose-string connectivity task. *Scientific Reports*, *11*(1), 15492.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software, 67*(1), 1–48.

Benson-Amram, S. & Holekamp, K. E. (2012). Innovative problem solving by wild spotted hyenas. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1744), 4087-4095.

Bent, A. C. (1946). *Life histories of North American jays, crows, and titmice: order Passeriformes*. Smithsonian Institution.

Bhattacharjee, D., Waasdorp, S., Middelburg, E., Sterck, E. H. M. & Massen, J. J. M. (2024). Personality heterophily and friendship as drivers for successful cooperation. *Proceedings. Biological sciences*, *291*(2019), 20232730.

Biondi, L. M., Bó, M. S. & Vassallo, A. I. (2010). Inter-individual and age differences in exploration, neophobia and problem-solving ability in a Neotropical raptor (Milvago chimango). *Animal cognition*, *13*, 701-710.

Boesch, C. & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest: behavioural ecology and evolution*. Oxford University Press, USA.

Borrego, N. & Gaines, M. (2016). Social carnivores outperform asocial carnivores on an innovative problem. *Animal Behaviour*, *114*, 21-26.

Boucherie, P. H., Mariette, M. M., Bret, C. & Dufour, V. (2016). Bonding beyond the pair in a monogamous bird: impact on social structure in adult rooks (Corvus frugilegus). *Behaviour, 153*(8), 897–925.

Braun, A. & Bugnyar, T. (2012). Social bonds and rank acquisition in raven nonbreeder aggregations. *Animal Behaviour*, *84*(6), 1507–1515.

Braun, A., Walsdorff, T., Fraser, O.N. & Bugnyar, T. (2012). Socialized sub-groups in a temporarily-stable raven flock? Journal of Ornithology, 153, 97-104.

Bugnyar, T. (2013). Social cognition in ravens. *Comparative Cognition & Behavior, Reviews, 8*, 1-12.

Bugnyar, T. (2023). Why are ravens smart? Exploring the social intelligence hypothesis. *Journal of Ornithology*, *165*(1), 15–26.

Bugnyar, T., Reber, S. A. & Buckner, C. (2016). Ravens attribute visual access to unseen competitors. *Nature Communications 2015 7:1*, *7*(1), 1–6.

Bugnyar, T., Kijne, M. & Kotrschal, K. (2001). Food calling in ravens: are yells referential signals? *Animal Behaviour*, *61*(5), 949–958.

Bugnyar, T. & Kotrschal, K. (2002). Scrounging tactics in free‑ranging ravens, Corvus corax. *Ethology*, *108*(11), 993-1009.

Buss, L. W. (1987). *The evolution of individuality*. Princeton University Press.

Byrne, R. W. & Whiten, A. (eds) (1988). *Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes and humans*. Clarendon Press, Oxford, UK.

Cauchard, L., Boogert, N. J., Lefebvre, L., Dubois, F. & Doligez, B. (2013). Problem-solving performance is correlated with reproductive success in a wild bird population. *Animal Behaviour*, *85*(1), 19-26.

Chatelain, P., Elias, M., Fontaine, C., Villemant, C., Dajoz, I., & Perrard, A. (2023). Müllerian mimicry among bees and wasps: a review of current knowledge and future avenues of research. *Biological Reviews*, *98*(4), 1310-1328.

Cole, E. F., Cram, D. L. & Quinn, J. L. (2011). Individual variation in spontaneous problem-solving performance among wild great tits. *Animal Behaviour*, *81*(2), 491-498.

Cords, M. & Aureli, F. (2000). Reconciliation and relationship qualities. *In: Natural conflict resolution* (Aureli, F. & de Waal, F. B. M., eds.). University of California Press, 177-198.

Darwin, C. (1859). *The Origin of Species*. Gramercy Books.

De Waal, F. B. M. & Tyack, P. L. (Eds.). (2003). *Animal social complexity: intelligence, culture, and individualized societies*. Harvard University Press.

Diamond, J. & Bond, A. B. (1991). Social behavior and the ontogeny of foraging in the kea (Nestor notabilis). *Ethology*, *88*(2), 128-144.

Drack, G. & Kotrschal, K. 1995. Aktivitätsmuster und Spiel von freilebenden Kolkraben (Corvus corax) im inneren Almtal/Oberösterreich. *Monticula, 7*, 159-174.

Dugatkin, L. A. (1997). *Cooperation among animals: an evolutionary perspective*. Oxford University Press.

Dugatkin, L. A. (2006). *The altruism equation: seven scientists search for the origins of goodness*. Princeton University Press.

Dugatkin, L. A. (2014). *Principles of animal behavior*. University of Chicago Press.

Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology*, *6*(5), 178-190.

Dunbar, R. I. M. & Shultz, S. (2007). Evolution in the social brain. *science*, *317*(5843), 1344-1347.

Emery, N. J. (2006). Cognitive ornithology: the evolution of avian intelligence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *361*(1465), 23-43.

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*, *362*, 489–505.

Fox, J. & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). Sage publications.

Fraser, O. N. & Bugnyar, T. (2010). The quality of social relationships in ravens. *Anim Behav*, *79*(4), 927–933.

Fraser, O. N., Schino, G. & Aureli, F. (2008). Components of relationship quality in chimpanzees. *Ethology*, *114*(9), 834-843.

Griffin, A. S. & Diquelou, M. C. (2015). Innovative problem solving in birds: a cross-species comparison of two highly successful passerines. *Animal Behaviour*, *100*, 84-94.

Griffin, A. S., Diquelou, M. C. & Perea, M. (2014). Innovative problem solving in birds: a key role of motor diversity. *Animal Behaviour*, *92*, 221-227.

Griffin, A. S. & Guez, D. (2014). Innovation and problem solving: a review of common mechanisms. *Behavioural Processes*, *109*, 121-134.

Hamilton, W. D. (1964a). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, *7*(1), 1–16.

Hamilton, W. D. (1964b). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, *7*(1), 17–52.

Heaney, M., Gray, R. D. & Taylor, A. H. (2017). Keas perform similarly to chimpanzees and elephants when solving collaborative tasks. *PloS one*, *12*(2), e0169799.

Heinrich, B. (1988a). Why do ravens fear their food? *The Condor*, *90*(4), 950–952.

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.

Heinrich, B. (1989). *Ravens in winter*. Simon and Schuster.

Heinrich, B. (1994). Does the early common raven get (and show) the meat? *The Auk*, *111*(3), 764–769.

Heinrich, B. (1995a). An experimental investigation of insight in common ravens (Corvus corax). *The Auk*, *112*(4), 994–1003.

Heinrich, B. (1995b). Neophilia and exploration in juvenile common ravens, Corvus corax. *Animal Behaviour*, *50*(3), 695–704.

Heinrich, B. (2000). *Testing insight in ravens. In: The Evolution of Cognition* (Heyes, C. & Huber, L., eds). MIT Press, 289-305.

Heinrich, B. & Bugnyar, T. (2005). Testing problem solving in ravens: string-pulling to reach food. *Ethology*, *111*(10), 962–976.

Heinrich, N. & Heinrich, J. P. (2007). *Why humans cooperate: A cultural and evolutionary explanation*. Oxford University Press.

Heinrich, B. & Marzluff, J.M. (1991). Do common ravens yell because they want to attract others? *Behavioural Ecology and Sociobiology, 28*, 13-21.

Heinrich, B. & Marzluff, J. (1995). Why ravens share. *American Scientist*, *83*(4), 342–349.

Heinrich, B., Marzluff, J. & Adams, W. (1995). Fear and food recognition in naive common ravens. *The Auk*, *112*(2), 499–503.

Hiestand, L. (2011). A comparison of problem-solving and spatial orientation in the wolf (Canis lupus) and dog (Canis familiaris). *Behavior genetics*, *41*, 840-857.

Hirata, S. (2003). Cooperation in chimpanzees. *Hattatsu 95*, 103–111.

Hirata, S. & Fuwa, K. (2007). Chimpanzees (Pan troglodytes) learn to act with other individuals in a cooperative task. *Primates*, *48*, 13-21.

Huebner, F. & Fichtel, C. (2015). Innovation and behavioral flexibility in wild redfronted lemurs (Eulemur rufifrons). *Animal cognition*, *18*, 777-787.

Jacobs, I., Kabadayi, C. & Osvath, M. (2019). The development of sensorimotor cognition in common ravens (Corvus corax) and its comparative evolution. *Animal Behavior and Cognition, 6*(3), 194–212.

Jain, V., Bugnyar, T., Cunningham, S. J., Gallego-Abenza, M., Loretto, M. C. & Sumasgutner, P. (2022). The spatial and temporal exploitation of anthropogenic food sources by common ravens (Corvus corax) in the Alps. *Movement Ecology*, *10*(1), 1–15.

Jolly, A. (1966). Lemur social behavior and primate intelligence: The step from prosimian to monkey intelligence probably took place in a social context. Science, 153(3735), 501-506.

Kabadayi, C. & Osvath, M. (2017). Ravens parallel great apes in flexible planning for tool-use and bartering. *Science*, *357*(6347), 202-204.

Keeble, L., Wallenberg, J. C. & Price, E. E. (2022). The evolution of coordination: a phylogenetic meta-analysis and systematic review. *Royal Society open science*, *9*(4), 201728.

Kilham, L. (1989). *The American Crow and the Common Raven*. Texas A & M University Press.

Kijne, M. & Kotrschal, K. (2002). Neophobia affects choice of food-item size in group-foraging common ravens (Corvus corax). *Acta Ethologica*, *5*(1), 13–18.

Koeslag, J. H. (1997). Sex, the prisoner's dilemma game, and the evolutionary inevitability of cooperation. *Journal of Theoretical Biology*, *189*(1), 53–61.

Korb, J. & Heinze, J. (2016). Major hurdles for the evolution of sociality. *Annual review of entomology*, *61*(1), 297-316.

Kozlovsky, D. Y., Branch, C. L. & Pravosudov, V. V. (2015). Problem-solving ability and response to novelty in mountain chickadees (Poecile gambeli) from different elevations. *Behavioral Ecology and Sociobiology*, *69*, 635-643.

Lenth, R. V. (2024). emmeans: Estimated Marginal Means, aka Least-Squares Means. R Package Version 1.10.3. https://cran.r-project.org/package=emmeans

Lefebvre, Louis, Simon M. Reader, and Daniel Sol. Brains, innovations and evolution in birds and primates. *Brain Behavior and Evolution* 63.4 (2004): 233-246.

Li, L-L., Plotnik, J. M., Xia, S. W., Meaux, E. & Quan, R. C. (2021). Cooperating elephants mitigate competition until the stakes get too high. *PLoS Biology*, *19*(9), e3001391.

Massen, J. J., Pašukonis, A., Schmidt, J., & Bugnyar, T. (2014). Ravens notice dominance reversals among conspecifics within and outside their social group. *Nature communications*, *5*(1), 3679.

Marzluff, J. M. & Angell, T. (2005). *In the company of crows and ravens*. Yale University Press.

Marzluff, J. M. & Heinrich, B. (1991). Foraging by common ravens in the presence and absence of territory holders: an experimental analysis of social foraging. *Animal Behaviour*, *42*(5), 755-770.

Marzluff, J. M., Heinrich, B. & Marzluff, C. S. (1996). Raven roosts are mobile information centres. *Animal Behaviour*, *51*(1), 89-103.

Maynard Smith, J. (1964). Group selection and kin selection. *Nature*, *201*(4924), 1145–1147.

Maynard Smith, J. & Szathmáry, E. (1995). *The major transitions in evolution*. Oxford University Press.

Mech, L. D. & Boitani, L. (eds). (2003). *Wolves: behavior, ecology, and conservation*. University of Chicago Press.

Mettke‑Hofmann, C., Winkler, H. & Leisler, B. (2002). The significance of ecological factors for exploration and neophobia in parrots. *Ethology*, *108*(3), 249-272.

Michod, R. E. & Roze, D. (1997). Transitions in individuality. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *264*(1383), 853-857.

Miller, R., Bugnyar, T., Pölzl, K. & Schwab, C. (2015). Differences in exploration behaviour in common ravens and carrion crows during development and across social context. *Behavioral Ecology and Sociobiology*, *69*(7), 1209–1220.

Miller, R., Lambert, M. L., Frohnwieser, A., Brecht, K. F., Bugnyar, T., Crampton, I., Garcia-Pelegrin, E., Gould, K., Greggor, A. L., Izawa, E. I., Kelly, D. M., Li, Z., Luo, Y., Luong, L. B., Massen, J. J. M., Nieder, A., Reber, S. A., Schiestl, M., Seguchi, A., Seperhi, P., Stevens, J. R., Taylor, A. H., Wang, L., Wolff, L. M., Zhang, Y., Clayton, N. S. (2022). Socio-ecological correlates of neophobia in corvids. *Current Biology*, *32*(1), 74-85.e4.

Miller, R., Schwab, C., & Bugnyar, T. (2016). Explorative innovators and flexible use of social information in common ravens (Corvus corax) and carrion crows (Corvus corone). *Journal of Comparative Psychology*, *130*(4), 328–340.

Molesti, S. & Majolo, B. (2016). Cooperation in wild Barbary macaques: factors affecting free partner choice. *Animal Cognition*, *19*(1), 133–146.

Morand-Ferron, J., Cole, E. F., Rawles, J. E. & Quinn, J. L. (2011). Who are the innovators? A field experiment with 2 passerine species. *Behavioral Ecology*, *22*(6), 1241-1248.

Moretti, L., Hentrup, M., Kotrschal, K. & Range, F. (2015). The influence of relationships on neophobia and exploration in wolves and dogs. *Animal Behaviour*, *107*, 159-173.

Müller, F. (1879). *Ituna* and *Thyridia*: a remarkable case of mimicry in butterflies. *Transactions of the Entomological Society of London* 20–29.

Nowak, M. A. (2006). Five rules for the evolution of cooperation. *Science*, *314*(5805), 1560–1563.

Nowak, M. A. & Sigmund, K. (1993). Chaos and the evolution of cooperation. *Proceedings of the National Academy of Sciences of the United States of America*, *90*(11), 5091–5094.

Pika, S., Sima, M. J., Blum, C. R., Herrmann, E. & Mundry, R. (2020). Ravens parallel great apes in physical and social cognitive skills. *Scientific Reports*, *10*(1), 1–19.

Range, F., Kassis, A., Taborsky, M., Boada, M. & Marshall-Pescini, S. (2019). Wolves and dogs recruit human partners in the cooperative string-pulling task. *Scientific Reports*, *9*(1), 1–10.

Ratcliffe, D. (1997). *The Raven: a Natural History in Britain and Ireland*. A & C Black.

Sachs, J. L., Mueller, U. G., Wilcox, T. P. & Bull, J. J. (2004). The evolution of cooperation. *The Quarterly Review of Biology*, *79*(2), 135–160.

Scheid, C. & Noë, R. (2010). The performance of rooks in a cooperative task depends on their temperament. *Animal Cognition*, *13*(3), 545–553

Schloegl, C., Dierks, A., Gajdon, G. K., Huber, L., Kotrschal, K. & Bugnyar, T. (2009). What you see is what you get? Exclusion performances in ravens and keas. *Plos one*, *4*(8), e6368.

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

Sol, D., Griffin, A. S., Bartomeus, I. & Boyce, H. (2011). Exploring or avoiding novel food resources? The novelty conflict in an invasive bird. *PloS one*, *6*(5), e19535.

Sol, D., Lefebvre, L. & Rodríguez-Teijeiro, J. D. (2005). Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1571), 1433-1441.

Stöwe, M., Bugnyar, T., Loretto, M. C., Schloegl, C., Range, F. & Kotrschal, K. (2006). Novel object exploration in ravens (Corvus corax): effects of social relationships. *Behavioural processes*, *73*(1), 68-75.

Suchak, M., Eppley, T. M., Campbell, M. W. & de Waal, F. B. M. (2014). Ape duos and trios: spontaneous cooperation with free partner choice in chimpanzees. *PeerJ*, *2*, e417.

Sukumar R. (2003). *The living elephants: evolutionary ecology, behavior, and conservation*. New York: Oxford University Press.

Tabachnick, B. G. & Fidell, L. S. (2007). *Using multivariate statistics* (5th ed.). Pearson.

Thornton, A. & Samson, J. (2012). Innovative problem solving in wild meerkats. *Animal Behaviour*, *83*(6), 1459-1468.

Trivers, R. L. (1971). The evolution of reciprocal altruism. *The Quarterly Review of Biology*, *46*(1), 35–57.

Udell, M. A. R. (2015). When dogs look back: inhibition of independent problem-solving behaviour in domestic dogs (Canis lupus familiaris) compared with wolves (Canis lupus). Biology letters, 11(9), 20150489.

Webster, S. J. & Lefebvre, L. (2001). Problem solving and neophobia in a columbiform–passeriform assemblage in Barbados. *Animal Behaviour*, *62*(1), 23-32.

West, S. A., Griffin, A. S., & Gardner, A. (2007). Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology*, *20*(2), 415–432.

Widdig, A., Streich, W. J. & Tembrock, G. (2000). Coalition formation among male Barbary macaques (Macaca sylvanus). *American Journal of Primatology*, *50*(1), 37-51.

9. Supplementary materials

Table S1. Information on each of the 24 marked-marked raven dyads.

| Dyad ID	Individual 1 + ring code	Individual 2 + ring code	Sex combination (respectively)	Relatedness	N. of focals	Total time observed together (s)
BongoClove	Bongo, BG3	Clove, BA7	m-?	0	1	201
BongoUeno	Bongo, BG3	Ueno, VO9	m-?	unknown	1	219
CheyenneHierro	Cheyenne, CN5	Hierro, IE6	f-m	unknown	2	383
CheyenneRaikiri	Cheyenne, CN5	Raikiri, RI6	f-m	unknown	3	576
DoctorWhoGwen	Doctor Who, D0C	Gwen, GW3	?-f	unknown	4	826
DoctorWhoRumble	Doctor Who, D0C	Rumble, RU7	?-?	unknown	1	300
DoctorWhoXmas	Doctor Who, D0C	Xmas, XM5	?-f	unknown	2	496
FoxtrotUber	Foxtrot, OY6	Uber, UB2	m-f	0	1	157
FoxtrotUeno	Foxtrot, OY6	Ueno, VO9	m-m	0	1	300
FoxtrotXmas	Foxtrot, OY6	Xmas, XM5	m-?	0	2	192
FoxtrotYama	Foxtrot, OY6	Yama, YA2	m-f	0	2	546
FoxtrotYamaha	Foxtrot, OY6	Yamaha, VH0	m-f	0.5	1	32
FoxtrotZwiebel	Foxtrot, OY6	Zwiebel, ZW8	m-f	0	3	854
HierroXmas	Hierro, IE6	Xmas, XM5	m-f	unknown	1	269
KibiPadma	Kibi, KB2	Padma, PM0	m-f	unknown	12	2342
PadmaUeno	Padma, PM0	Ueno, VO9	f-m	unknown	1	118
PeanutSpitfire	Peanut, RW2	Spitfire, SK0	m-f	0	1	87
PeanutWalnut	Peanut, RW2	Walnut, WK0	m-m	0.5	8	1254
PeanutYama	Peanut, RW2	Yama, YA2	m-f	unknown	1	300
PeanutYamaha	Peanut, RW2	Yamaha, VH0	m-f	0	2	564
RumbleWalnut	Rumble, RU7	Walnut, WK0	?-m	unknown	1	300
UweYamaha	Uwe, UW3	Yamaha, VH0	?-f	unknown	1	205
WalnutXmas	Walnut, WK0	Xmas, XM5	m-f	0	1	300
WalnutYamaha	Walnut, WK0	Yamaha, VH0	m-f	0	3	509
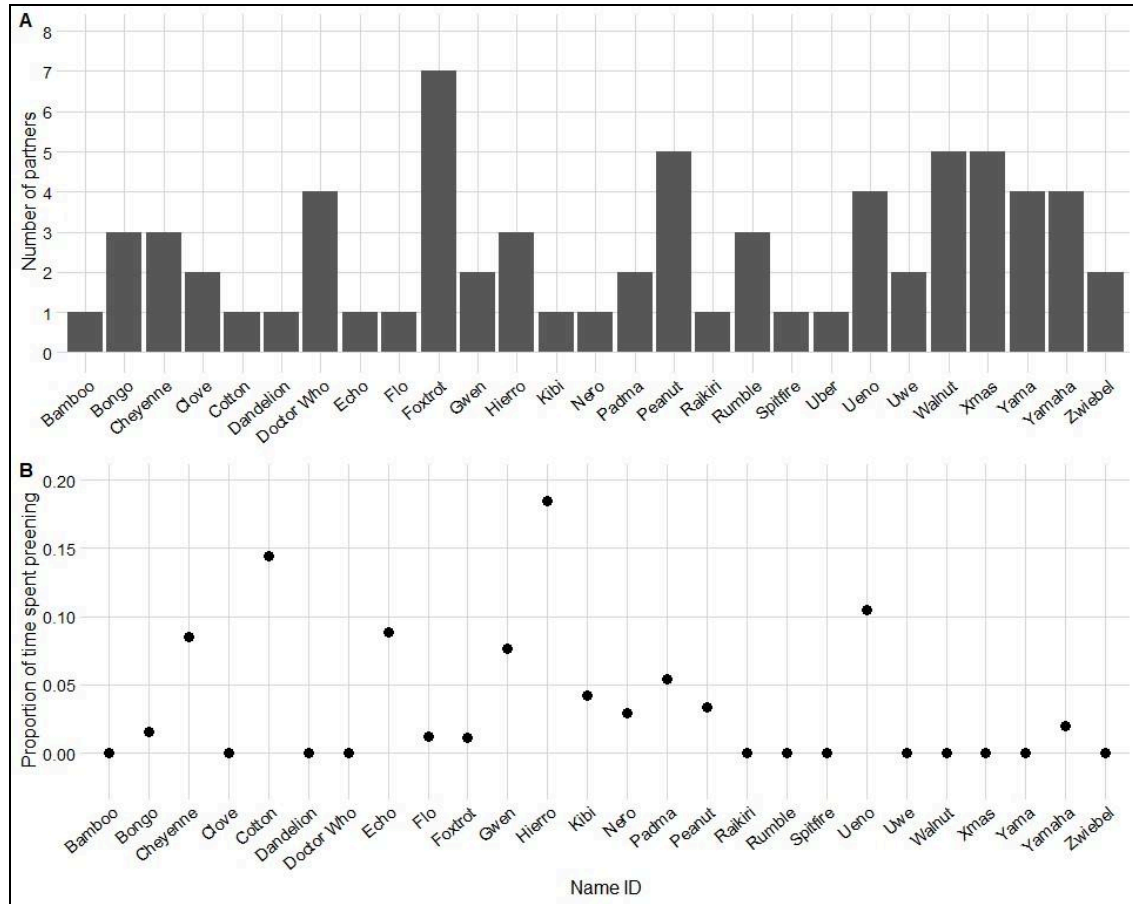
Figure S1. Information on the raven's individual affiliative behaviours, showing the variability within the population. This graph includes several individuals who are missing in Table S1 because they were only seen with unmarked partners. A: The number of partners each individual has been seen with, including unmarked ravens. Actual numbers may be larger due to the fact that multiple unmarked individuals were counted as one. B: the proportion of time each individual has spent preening over the total time they have been observed. Note that one individual is missing compared to A, Uber, because he has not been observed in contact sit with anyone.

Table S2. Information on all the observational rounds that were carried out.

Date of observational round	Morning or afternoon	Duration (minutes)	No. of observational samples
26-02-2024	Afternoon	90	3
27-02-2024	Afternoon	60	2
29-02-2024	Afternoon	60	4
04-03-2024	Morning	60	3
04-03-2024	Afternoon	60	2
05-03-2024	Morning	60	2

05-03-2024	Afternoon	60	3
06-03-2024	Afternoon	60	3
07-03-2024	Morning	60	3
07-03-2024	Afternoon	60	2
08-03-2024	Morning	60	1
11-03-2024	Morning	60	3
11-03-2024	Afternoon	60	1
12-03-2024	Morning	60	3
12-03-2024	Afternoon	60	2
13-03-2024	Afternoon	60	2
14-03-2024	Morning	60	6
14-03-2024	Afternoon	60	3
15-03-2024	Morning	60	1
15-03-2024	Afternoon	60	2
18-03-2024	Morning	60	4
18-03-2024	Afternoon	60	3
19-03-2024	Afternoon	60	1
20-03-2024	Morning	60	6
20-03-2024	Afternoon	60	1
21-03-2024	Morning	60	2
21-03-2024	Afternoon	60	1
22-03-2024	Morning	60	4
22-03-2024	Afternoon	60	2
25-03-2024	Morning	60	3
26-03-2024	Morning	60	3
26-03-2024	Afternoon	60	1
27-03-2024	Morning	60	1
27-03-2024	Afternoon	60	2

28-03-2024	Morning	60	1
29-03-2024	Morning	60	1
29-03-2024	Afternoon	60	3
08-04-2024	Morning	60	4
08-04-2024	Afternoon	60	1
09-04-2024	Morning	60	1
10-04-2024	Morning	60	3
10-04-2024	Afternoon	60	2
11-04-2024	Morning	60	1
12-04-2024	Morning	60	3
12-04-2024	Afternoon	60	1
15-04-2024	Afternoon	60	4
16-04-2024	Morning	60	3
17-04-2024	Morning	60	2
17-04-2024	Afternoon	60	1
19-04-2024	Morning	60	2
19-04-2024	Afternoon	60	2
22-04-2024	Morning	45	1
22-04-2024	Afternoon	45	1
23-04-2024	Morning	60	1
24-04-2024	Morning	60	5
25-04-2024	Afternoon	60	1
26-04-2024	Afternoon	60	2
29-04-2024	Afternoon	60	1
01-05-2024	Morning	60	1
01-05-2024	Afternoon	60	3
02-05-2024	Afternoon	60	2
03-05-2024	Morning	60	5

03-05-2024	Afternoon	60	1
06-05-2024	Morning	50	0
06-05-2024	Afternoon	60	1
07-05-2024	Morning	60	3
08-05-2024	Morning	60	2
08-05-2024	Afternoon	60	4
09-05-2024	Morning	60	1
10-05-2024	Afternoon	60	2
13-05-2024	Morning	60	1
14-05-2024	Afternoon	60	1
15-05-2024	Morning	60	1
15-05-2024	Afternoon	60	3
16-05-2024	Morning	60	1
16-05-2024	Afternoon	60	1
17-05-2024	Morning	60	1
20-05-2025	Morning	60	1
21-05-2024	Afternoon	60	1
22-05-2024	Afternoon	60	1
23-05-2024	Morning	60	1
24-05-2024	Morning	60	2
27-05-2024	Morning	60	3
27-05-2024	Afternoon	60	1
28-05-2024	Afternoon	60	3
29-05-2024	Morning	60	1
29-05-2024	Afternoon	60	1
30-05-2024	Morning	40	3
31-05-2024	Afternoon	60	4

Table S3. Average presence per week of all ravens that were seen at least once

Week	No. of boar feedings that week	Percentage present for the entire week
9	1	100.0%
10	5	66.7%
11	5	72.0%
12	5	68.0%
13	5	80.0%
14	2	83.3%
15	5	82.1%
16	5	80.0%
17	4	87.5%
18	5	90.5%
19	5	87.4%
20	5	86.3%
21	5	80.0%
22	5	90.5%
Total / Average	**62**	**81.8%**