

Testing the effects of kinship, reciprocity and dominance on prosocial food provisioning in azure-winged magpies (*Cyanopica cyana*), carrion crows (*Corvus corone*) and common ravens (*C. corax*)

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Abstract

Prosocial behaviour (i.e. benefitting others without receiving a direct gain) has long been perceived as an evolutionary puzzle but is nevertheless relatively common among non-human animals. Prosocial food provisioning has recently been documented in several large-brained bird species, such as corvids and parrots. Yet, to date, little is known about which factors influence food provisioning in these species. Here, we investigated whether kinship, reciprocity and dominance affected food provisioning in the group service paradigm in three corvid species, namely azure-winged magpies (*Cyanopica cyana*), carrion crows (*Corvus corone*) and common ravens (*C. corax*). In this paradigm, the subjects are tested in their regular social groups and can choose to make food available to their group members by landing on a simple seesaw apparatus. We found no evidence for an effect of kinship or reciprocity on food provisioning. Contrary to our predictions, the subjects' dominance was not positively correlated with their rate of food provisioning in any species. Among ravens, dominance was instead positively correlated with receiving food. We conclude that preferential provisioning for kin and direct reciprocity might have been impeded by the provider's inability to control who receives the food in the group service paradigm, but that our findings provide another piece of evidence that dominance is a highly important factor in the social interactions of common ravens.

KEYWORDS

comparative research, cooperation, corvid, group service paradigm, prosociality, social relationships

1 | INTRODUCTION

Benefitting others without receiving a direct gain to oneself, also termed prosocial behaviour, was long perceived as an evolutionary

puzzle from the perspective of natural selection theory with its focus on behaviours that increase an individual's own fitness (Darwin, 1859). Marshall-Pescini et al. (2016) define prosocial behaviour as voluntary behaviour that benefits another individual at no

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gain and no or low costs to the actor. They distinguish it from altruism, which typically includes substantial costs for the actor (Marshall-Pescini et al., 2016). Despite the fact that there is no apparent gain for the actor, prosocial behaviour is common among non-human animals and has been experimentally demonstrated in primates (for a review, see Marshall-Pescini et al., 2016), other mammals (e.g. domestic dog, *Canis familiaris*: Quervel-Chaumette et al., 2016; wolf, *Canis lupus*: Dale et al., 2019; brown rat, *Rattus norvegicus*: Bartal et al., 2011; Schweinfurth & Taborsky, 2018; common vampire bat, *Desmodus rotundus*: Carter & Wilkinson, 2013), and several bird species (e.g. azure-winged magpie, *Cyanopica cyana*: Horn et al., 2016, 2020; Massen et al., 2020; pinyon jay, *Gymnorhinus cyanocephalus*: Duque et al., 2018; African grey parrot, *Psittacus erithacus*: Brucks & von Bayern, 2020). This paradox of a ubiquitous behavioural strategy without apparent fitness benefits has thus been at the centre of several evolutionary theories.

The two earliest attempts to explain the evolution of prosocial behaviour (and cooperation in general) were through mechanisms of kin selection (Hamilton, 1964) and reciprocity (Trivers, 1971). Kin selection theory is most easily aligned with natural selection. It postulates that by benefitting related others, the individual's genes are passed on to the next generation, thereby increasing the individual's fitness indirectly (Hamilton, 1964). An individual is therefore expected to show prosocial behaviour preferentially towards kin. Another mechanism, which is applicable to both kin and non-kin, is reciprocal cooperation. According to this theory, it is beneficial to be prosocial towards others who have previously been prosocial towards the individual (Trivers, 1971). Mutually reciprocal acts thus ensure fitness benefits for both individuals. Reciprocity has been documented in several non-human animal species (e.g. brown capuchin monkey, *Cebus apella*: De Waal, 2000; Hattori et al., 2005; brown rat: Rutte & Taborsky, 2007; Schweinfurth & Taborsky, 2018; common vampire bat: Carter & Wilkinson, 2013), although classification might depend strongly on the definition used (i.e. whether the term 'reciprocity' is used only for cognitively demanding calculated reciprocity, or whether it is used to encompass different behavioural strategies that lead to reciprocal outcomes; cf. Carter, 2014; Schweinfurth & Call, 2019a). Researchers have identified three types of reciprocal strategies that differ in their underlying mechanisms and cognitive demands on the individual. Direct reciprocity refers to an individual being selectively prosocial to others, who have previously been prosocial to the individual (Trivers, 1971). Indirect reciprocity refers to an individual being prosocial to others who were observed to be prosocial, irrespective of whether the individual was the recipient of these prosocial acts (Alexander, 1987). And finally, generalised reciprocity refers to a general and non-selective increase in prosocial behaviour after the individual is the recipient of a prosocial act (Boyd & Richerson, 1989). However, one has to consider that the effects of kinship and reciprocity on prosocial behaviour are likely not independent of social context and might therefore be further modulated by socio-relational factors such as dominance relationships between the interacting individuals (cf. Horn et al., 2022).

Dominance hierarchies govern individuals' priority of access to resources in many non-human animal species, with dominant individuals typically receiving more resources than subordinate individuals. If prosocial behaviour follows the same patterns of resource allocation, dominant individuals are expected to be more frequent recipients of prosocial acts than subordinate individuals (e.g. rank-dependent grooming: Seyfarth, 1977; but see Parr et al., 1997). Yet, experimental studies on food provisioning demonstrated that prosocial behaviour is often shown preferentially by dominant individuals on behalf of subordinate individuals (e.g. capuchin monkey: Takimoto et al., 2010; long-tailed macaque, *Macaca fascicularis*: Massen et al., 2010; rhesus macaque, *Macaca mulatta*: Chang et al., 2011). Various underlying mechanisms have been postulated for this phenomenon, such as dominant individuals being more likely to approach the apparatus and less anxious in interactions with others, perceiving a greater chance of later obtaining food after donating it to a subordinate individual, being less in need of food or using prosocial acts to advertise their dominance to others (for a discussion, see Cronin, 2012). The findings summarised above demonstrate that for understanding prosocial behaviour among non-human animals better, it is important to investigate whether and how it is modulated by factors such as kinship, reciprocity and dominance relationships. Additionally, it would be important to extend the number of animal taxa in which prosocial behaviour is investigated.

While early studies on prosocial behaviour have mostly concentrated on non-human primates, large-brained bird species such as corvids and parrots have moved into the focus of social cognition research in the last two decades (Lambert et al., 2019). Most corvids and parrots form long-lasting pair bonds and have a complex social life with distinct dominance relationships among group members. Food sharing between bonded partners as well as food provisioning to dependent offspring by both parents is common (Emery et al., 2007). Systematic observations of food provisioning demonstrated that multiple corvid and parrot species provided food to conspecific group members during free interactions (e.g. cockatiel, *Nymphicus hollandicus*: Liévin-Bazin et al., 2019; Eurasian jackdaw, *Coloeus monedula*: De Kort et al., 2006; rook, *Corvus frugilegus*: Scheid et al., 2008). They also provided food in experimental set-ups, where only one donor bird received food that could be shared with other individuals that were physically separated from the donor bird (azure-winged magpie: Massen et al., 2020; pinyon jay: Duque & Stevens, 2016). Similarly, tool-using Goffin's cockatoos (*Cacatua goffiniana*) were found to provide tools to their group members, if these lacked access to the tools (Laumer et al., 2021). Prosocial choice tasks, where one individual has to choose between two or more options that deliver different reward distributions to the donor and a recipient, however, have so far delivered mixed results in corvids and parrots. Eurasian jackdaws and pinyon jays were found to prefer choices that benefited a recipient (Duque et al., 2018; Schwab et al., 2012), although these choices were dependent on recipient cues or whether the donor received any food themselves, respectively. Common ravens (*Corvus corax*) have so far not shown prosocial behaviour in

such choice tasks (Di Lascio et al., 2012; Lambert et al., 2017). Prosocial behaviour has also been tested in prosocial token tasks, in which the donors are either trained to use tokens to indicate their choice between prosocial or selfish reward distributions or they can simply provide tokens that can be exchanged for food to other individuals. These experiments have so far not revealed substantial prosocial behaviour in most tested corvid and parrot species (e.g. azure-winged magpie and carrion crow, *Corvus corone*: Horn et al., 2022; blue-headed macaw, *Primolius couloni*: Brucks & von Bayern, 2020; common raven: Massen et al., 2015; kea, *Nestor notabilis*: Heaney et al., 2020). Only African grey parrots spontaneously and selectively transferred tokens to recipients in a prosocial token transfer experiment (Brucks & von Bayern, 2020). However, the rarity of prosocial responses in prosocial choice tasks might have in part resulted from the complexities of the task contingencies and a limited understanding on the part of the subjects (cf. Marshall-Pescini et al., 2016). Horn et al. (2020) therefore tested eight corvid species in an experimental setup with simpler contingencies, the so-called the group service paradigm. In this paradigm, the subjects are tested in their regular social groups and can choose to make food available to their group members by landing on a simple seesaw apparatus. The authors found high rates of landing on the apparatus whenever the recipients could actually obtain the food (compared to two control conditions) in azure-winged magpies (see also Horn et al., 2016). There was also substantial and selective prosocial food provisioning by two carrion crows and one New Caledonian crow (*Corvus moneduloides*). Contrastingly, common ravens provided a lot of food in the test condition, but all except one raven landed equally often on the apparatus in the control conditions in which the recipients received no reward. Therefore, it is unclear whether the food provisioning in the raven subjects was motivated by the goal of benefitting the other group members (Horn et al., 2020). In sum, these findings illustrate that there seems to be considerable variation between and within species in the propensity to engage in prosocial behaviour among corvids and parrots. Effects of kinship, reciprocity and dominance might be possible reasons for the within-species variation in individuals' tendency to perform prosocial behaviours.

A small number of studies have examined which factors modulate prosocial behaviour in corvids and parrots. When investigating food sharing during free interactions, Liévin-Bazin et al. (2019) found that cockatiels preferentially co-fed on the same piece of food with siblings and that, among siblings, reciprocally sharing dyads emerged. A similar pattern of reciprocal food sharing was observed in juvenile jackdaws, although kinship and dominance did not affect food transfers in this species (De Kort et al., 2003, 2006). Von Bayern et al. (2007) found that donor-initiated food transfers were common in jackdaws shortly after fledging and argued that they were used to solidify affiliative relationships. Interestingly, rooks displayed different sharing patterns depending on the specific type of food sharing: co-feeding occurred mainly between kin and was reciprocated, whereas active food transfers were rarely reciprocated and were mainly initiated from dominant towards subordinate individuals

(Scheid et al., 2008). This suggests that co-feeding and active food provisioning—specifically donor-initiated active transfers—are cognitively different types of behaviour and might have been subjected to different evolutionary trajectories (De Kort et al., 2006; Scheid et al., 2008). A study using a restricted setup in which the donor bird was separated from a recipient bird showed a similar pattern in pinyon jays: dominant individuals transferred more food pieces than subordinate individuals, but the authors found no evidence for direct or generalised reciprocity (Duque & Stevens, 2016). In a prosocial choice task, jackdaws' choices did not differ depending on whether the recipients were siblings or not (Schwab et al., 2012). The authors did not include measures of dominance and never tested the subjects with reversed donor and recipient roles, so no conclusion about the effects of reciprocity and dominance in this set-up are possible (Schwab et al., 2012). Brucks and von Bayern (2020) investigated reciprocal strategies in a prosocial token transfer task in African grey parrots. More transfers in the preceding session resulted in more transfers in the following session, but independently of the condition: the effect was evident both in the test condition in which recipients were able to exchange the tokens for food and in the control condition in which the recipients were not able to use the tokens (Brucks & von Bayern, 2020). This suggests that the African grey parrots used generalised reciprocity strategies in this experiment, by being more prosocial after being the recipient of a prosocial act without paying attention to the task contingencies. Additionally, dominance might play a role in African grey parrots, as a case study on two birds showed that only the dominant individual was willing to share with a conspecific and to reciprocate choices by human partners, whereas the subordinate individual displayed no prosocial behaviour (Péron et al., 2013). Despite these compelling indications that kinship, reciprocity and dominance shape prosocial behaviour in corvids and parrots, very few studies to date have examined these effects systematically.

Therefore, we investigated whether kinship, reciprocity and dominance affected food provisioning in the group service paradigm in three corvid species, namely azure-winged magpies, carrion crows and common ravens (cf. De Kort et al., 2006 for similar questions in a naturalistic food sharing setting). All three species are highly social (i.e. living and foraging in social groups during at least some stages of their life history; Braun et al., 2012; Komeda et al., 1987; Uhl et al., 2019) but differ in their social systems: azure-winged magpies live in colonies with kin and non-kin (Komeda et al., 1987), while carrion crows and common ravens are highly territorial as adults (Baglione et al., 2002; Boucherie et al., 2019); cooperative breeding, including food provisioning by kin and non-kin helpers, has been documented in azure-winged magpies and carrion crows (Baglione et al., 2002; Ren et al., 2016), but not in common ravens. It is thus interesting to compare the effects of kinship, reciprocity and dominance in these three species. The group service paradigm was originally developed in primates (Burkart et al., 2014), where it has been previously used to test the effects of kinship and dyadic social tolerance on prosocial food provisioning (Bhattacharjee et al., 2023). It has recently been

successfully adapted for birds (Horn et al., 2016). We re-analysed the food provisioning data collected by Horn et al. (2016, 2020) with a focus on provisioning among individual provider/recipient dyads and trial-by-trial provisioning choices of the individual birds. Additionally, we included dominance data collected in the same period. In line with kin selection theory, we predicted that food provisioning would be more frequent among kin than non-kin dyads. If the subjects used direct reciprocity, we expected many dyads with mutual food provisioning. If the subjects instead followed an indirect reciprocity strategy, we predicted that food provisioning and receiving would be correlated. If the birds showed patterns consistent with generalised reciprocity, we expected them to show a higher probability of providing food after they had received food in the preceding trial. Finally, in line with results of previous food provisioning experiments in corvids (Duque & Stevens, 2016; Scheid et al., 2008), parrots (Péron et al., 2013) and non-human primates (e.g. Massen et al., 2010), we predicted that food provisioning would mainly occur from dominant towards subordinate individuals.

2 | METHODS

2.1 | Subjects

We tested captive birds of three corvid species: azure-winged magpies, carrion crows and common ravens. One group of magpies was housed in an outdoor aviary (5×3×3 m) at Haidlhof Research Station, a joint facility of the University of Vienna and the University of Veterinary Medicine Vienna, and the second group was housed in an outdoor aviary (6×3×3 m) at the Animal Care Facility of the Department of Cognitive Biology. The magpies were tested in the group service paradigm in Apr–Nov 2015 and Nov 2015–Apr 2016, respectively. Crows and ravens were housed in aviaries (12×12×5 m and 15×15×5 m, respectively) at Haidlhof Research Station and tested in the group service paradigm in Oct 2015–Apr 2016 and May–Oct 2016, respectively.

One group of magpies consisted of 5 adult birds (3M/2F) and the second of 3 adult birds (1M/2F) and 2 juvenile birds born at our facility (1M/1F). One of the juveniles (M) did not participate in the group service paradigm due to a physical impairment of his feet. All magpies except the juveniles originated from two different zoo populations and none of the birds were hand-raised. Relatedness between the adult birds from the zoo population was unknown. One M/F dyad had formed a pair bond prior to the experiment and had successfully built a nest and raised the juvenile. The group of crows consisted of 6 adult birds (2M/4F). The crows had been obtained from the wild or from private owners and were all hand-raised. By appearance, the crows were either carrion crows or hybrids of carrion and hooded crows, reflecting the hybridisation belt in Europe. The group contained one sibling dyad and one sibling triad. The group of ravens consisted of 6 subadult (2M/4F) and 3 young adult birds (2M/1F). The ravens had been

obtained from different research stations, zoos or private owners as fledglings and were all hand-raised. The group contained three sibling dyads. One sibling dyad had an additional genetic sibling from a previous clutch.

All subjects were housed in large outdoor aviaries. They were tested in their regular social group in their home aviary prior to the first feeding of the day. All subjects had previously participated in various observational and experimental behaviour studies and participated voluntarily in the experiments. Subjects were never food deprived, were being fed an appropriate and varying diet and were in excellent body condition. Water was available ad libitum.

This study followed the Guidelines for the Use of Animals in Research (Animal Behaviour, 2018) in accordance with the institutional guidelines of the University of Vienna and national legislation. All animal care and data collection protocols were approved by the by the ethical board of the behavioural research group of the Faculty of Life Sciences, University of Vienna (permit nos. 2016-008 & 2016-017). After the study ended, subjects remained in captivity at the Haidlhof Research Station and the Animal Care Facility of the Department of Cognitive Biology for further research.

2.2 | Group service paradigm

2.2.1 | Apparatus

We used the same apparatus—adjusted in size and weight—for all three species (Figure 1a). The apparatus consisted of a board outside the aviary and two sticks reaching through the wire mesh into the aviary on one side of the board with a provisioning perch fixed at the end. The apparatus's seesaw mechanism was balanced so that in the starting position the provisioning perch on the inside of the aviary pointed up and the board on the outside pointed down. When a bird landed on the provisioning perch, its weight moved the seesaw down. As soon as the bird left the provisioning perch, the apparatus automatically moved back to its original position. Near the other side of the board, inside the aviary, were sitting perches and branches that were not connected to the apparatus's seesaw mechanism. The apparatus was placed in a central area of the aviary, ensuring that other group members had visual access whenever one or multiple individuals' interacted with the apparatus. High-quality food reward (i.e. mealworms and crickets for the magpies; dry dog food and cheese for the crows and ravens) was used in the experiments.

There were two positions for putting food on the board: one in front of the provisioning perch (position 0) and one on the other side of the board (position 1) out of reach from the provisioning perch (Figure 1b). If food was placed in position 0, a subject could deliver food to itself by landing on the provisioning perch, after which the food slid towards the wire mesh and into reach. If food was placed in position 1 and a bird landed on the provisioning perch, it could not obtain the food itself. However, if the subject stayed on the provisioning perch, it made food available to the group. Crucially, the bird had to stay on the provisioning perch until another bird arrived

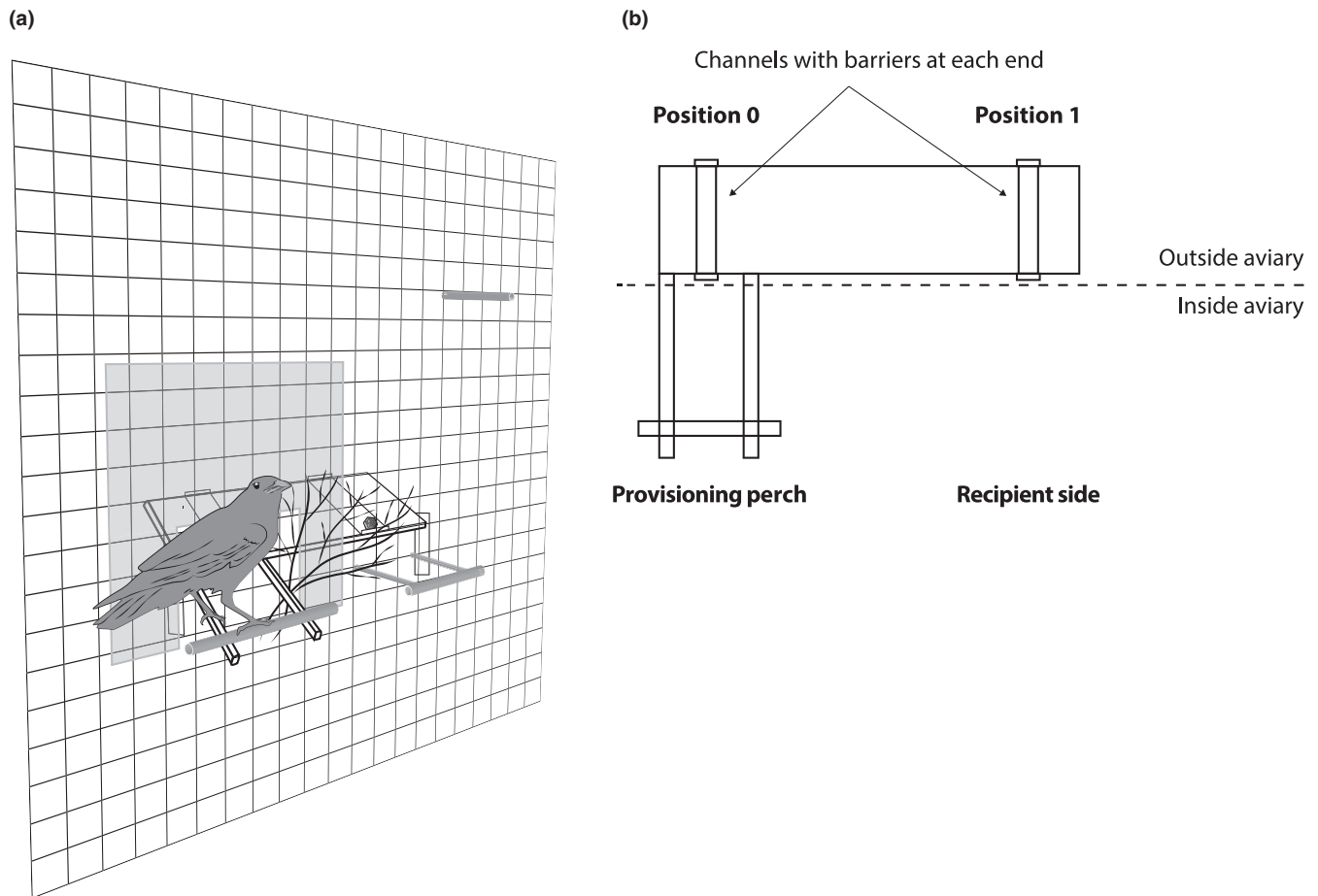


FIGURE 1 Apparatus used in the group service paradigm. (a) Drawing with a bird sitting on the provisioning perch. (b) Bird's-eye view schematics. This figure partly reproduces a figure published in Horn et al. (2020) under a Creative Commons Attribution 4.0 International License.

and took the food in order for successful food provisioning to occur. Positions 0 and 1 were placed so far apart that the subjects could not easily switch from one position to the other (distance: magpies=30cm, crows=60cm, ravens=90cm). Additionally, several branches were fixed in-between the two positions on the inside of the wire mesh, completely removing the opportunity for birds to try and get the rewards themselves and only leaving the option to provide to others.

2.2.2 | Procedure

The group service paradigm experiment consisted of six consecutive phases in a fixed sequence. In phases 0 and I, the birds were habituated to feeding close to and directly from the apparatus, respectively. Phase II was designed to test how even the group members' access was to multiple food pieces that were sequentially provided on the apparatus (these data were not used in the current study). In phase III, the birds were habituated and trained to land on the provisioning perch with food placed in position 0 (for detailed descriptions of these initial phases, see Horn et al., 2016, 2020). In each habituation and training phase (i.e. phases 0, I and III), all animals had

to meet a specific criterion in order for the whole group to proceed to the next phase.

In the crucial prosocial test (phase IV), food was placed in position 1, so that a bird landing on the perch could only make food available to the group, not to itself. Importantly, for successful food provisioning, the bird on the perch had to remain there until another individual arrived in position 1 and could take the food. On alternating days during phase IV, we conducted empty control sessions, which were identical to test sessions except that no food was placed on the apparatus. We conducted 5 prosocial test sessions with food in position 1 and 5 empty control sessions without any food, on alternating days. In the blocked control phase (phase V), access to food in position 1 was blocked with a fine net so that even if a bird landed on the provisioning perch, no other individual could take the food. We again conducted 5 sessions with food in position 1 and 5 sessions without any food (see Horn et al., 2016, 2020).

Each session consisted of a fixed number of trials for each group. Due to the groups' different group sizes, we adjusted the number of trials per session to the number of individuals in the group (i.e. $n_{\text{group}} \times 5$ regular trials). Like this, each individual in each group theoretically had an equal chance to provide and receive food. We

interspersed motivation trials where food was placed in position 0 (the same set-up that we used in training phase III) in the beginning and after every fifth regular trial to ensure that the birds were still motivated to participate in the experiment (i.e. $n_{\text{group}} + 1$ motivation trials). At the start of each trial, the experimenter called the birds' attention and placed or pretended to place food on the board, depending on the condition. The next trial started after a bird obtained the food or after a maximum of 2 min.

For the current analysis, we re-analysed the food provisioning data collected in the prosocial test (phase IV) by Horn et al. (2016, 2020) with a focus on provisioning among individual provider/recipient dyads and trial-by-trial provisioning choices of the individual birds. We used only the prosocial test, as this was the only part of the group service paradigm in which the birds had the opportunity to provide food. Further, we only used the data from the last two sessions (sessions 4 and 5) because by then each bird had had the opportunity to learn about the consequences of operating the apparatus (cf. Horn et al., 2016, 2020). All sessions were video-recorded. For each trial, we scored whether food was provided and the identity of the provider and the recipient.

2.3 | Dominance assessment

Dominance was assessed via food monopolisation experiments conducted during the corresponding time periods of the group service paradigm for each species (magpies: Sept–Dec 2015, crows & ravens: Apr–May 2016). Each group was provided with two large pieces of meat fixed to heavy wooden boards, which represented highly valuable food and were easily monopolised. In the ravens and crows, we conducted two sessions each. In the magpies, there were fewer interactions in each session. Therefore, we conducted five sessions in each group in order to have enough data to assess dominance. We recorded the occurrence and direction of all displacements (i.e. one bird approaches and the other retreats) for 30 min. per monopolisation experiment. For each social group, we then arranged these in a matrix with actors in rows and recipients in columns. We calculated normalised David's scores for each individual, using the formula provided by De Vries et al. (2006; see Appendix S1 for displacement raw data and calculations). Larger normalised David's scores correspond to greater dominance in the social group.

2.4 | Data analysis

Statistical analyses were carried out in R version 4.1.1 (R Core Team, 2021; packages: dplyr, ggplot2, multcomp, parameters, TOSTER). For testing the effect of kinship on food provisioning, we first identified all possible dyads per group ($N=67$ dyads). We did not have any information about the kinship between the magpies in group 1. We thus excluded these dyads from our kinship analysis, resulting in $n=57$ dyads. Each dyad was either categorised as kin (i.e. if the subjects were genetical siblings or parent/offspring;

$n=11$ dyads) or non-kin ($n=46$ dyads). For each dyad, we summed the number of food provisioning instances from both dyad members. We used a Mann–Whitney U-test to compare the number of food provisioning instances between kin and non-kin dyads. We additionally used Fisher's exact test to test whether food provisioning in a dyad (yes vs. no) was dependent on their kinship (kin vs. non-kin). To assess direct reciprocity, we identified all dyads in which both dyad members provided food to each other. We tested for indirect reciprocity with a Spearman rank correlation between the number of instances of providing and receiving food. To assess generalised reciprocity, we conducted a trial-by-trial analysis with all individuals who both provided and received food in the group service paradigm ($n=11$). For each subject in each trial, we first classified whether the subject received food or not. We excluded the last trials of each session since experiences in these trials could not influence subsequent behaviour. We then recorded the number of trials in which each subject either provided or did not provide food, depending on whether they had previously received food or not (Table 2). For each individual, we conducted Fisher's exact test with their respective contingency table. When analysing the effect of dominance, we first calculated a linear model to test whether normalised David's scores differed between the sexes and species and conducted post-hoc tests for species differences (Tukey contrasts). We found that the normalised David's scores differed both between the sexes and between the species (see results below). We therefore calculated Spearman rank correlations between the normalised David's scores and the instances of providing and receiving food, respectively, separately for each species. For all tests, significance levels were set at $p \leq .05$ and marginal effects were reported up to $p = .07$. For non-significant results, we conducted equivalence tests to investigate whether samples were equivalent and relevant effects could be rejected in our sample (cf. Lakens, 2017). Lower and upper equivalence bounds were set to $\Delta_{\text{lower}} = -0.5$ and $\Delta_{\text{upper}} = 0.5$, respectively, for all equivalence tests. We report only the results of the equivalence bound that showed the higher p -value (cf. Lakens, 2017).

3 | RESULTS

3.1 | Kinship

Provisioning occurred in 98% and 96% of the trials in the two magpie groups, respectively, in 62% of the trials in the crows, and in 80% of the trials in the ravens. In each of the groups, most provisioning instances were executed by a small number of providers and received by a small number of recipients (see Table 1 for detailed information about the providers and recipients of food provisioning). There was no significant difference in the likelihood of provisioning to occur between kin and non-kin dyads ($X^2 = 2.45$, $p = .312$) or in the number of food provisioning instances (kin: $n=11$ dyads, $M \pm SD = 4.09 \pm 3.86$; non-kin: $n=46$ dyads, $M \pm SD = 2.43 \pm 4.25$; $U = 326$, $p = .109$; Figure 2). However, the equivalence test revealed that the two groups were not equivalent (TOST Wilcoxon test:

TABLE 1 The matrices show the food provisioning of the individual subjects (rows) to all other group members (columns), the total numbers of providing and receiving food and the overall number of provisioning instances, separately by group.

Provider	Sex	NormDS	Recipient							Total		
Azure-winged magpies (group 1, n=5) – 50 trials												
			Boots	Obi-Wan	Yoda	Mon	Padme					
Boots	M	2.00	—	0	0	0	0			0		
Obi-Wan	M	2.73	16	—	4	1	0			21		
Yoda	M	3.39	1	0	—	0	0			1		
Mon	F	0.30	21	0	6	—	0			27		
Padme	F	1.58	0	0	0	0	—			0		
Total			38	0	10	1	0			49		
Azure-winged magpies (group 2, n=5) – 50 trials												
			Han	Amidala	Chewie	Leia						
Han	M	3.60	—	11	0	21				32		
Amidala	F	1.34	0	—	0	0				0		
Chewie	F	0.89	8	5	—	3				16		
Leia	F	2.36	0	0	0	—				0		
<i>Jabba</i>	<i>M</i>	<i>1.81</i>										
Total			8	16	0	24				48		
Carrion crows (n=6) – 60 trials												
			Saul	Signore	Daisy	Paula	Peppi	Soukie				
Saul	M	3.47	—	0	0	0	0	0		0		
Signore	M	3.75	0	—	0	0	0	0		0		
Daisy	F	1.54	0	0	—	1	0	0		1		
Paula	F	1.24	0	2	7	—	0	1		10		
Peppi	F	2.50	0	0	0	2	—	0		2		
Soukie	F	2.50	0	10	4	10	0	—		24		
Total			0	12	11	13	0	1		37		
Common ravens (n=9) – 90 trials												
			Arthus	George	Laggie	Aramis	Bobby	Martha	Moritz	Munia	Nobel	Total
Arthus	M	5.75	—	0	2	0	0	0	0	0	0	2
George	M	5.81	0	—	0	0	0	0	0	0	0	0
Laggie	M	6.89	0	0	—	0	0	0	0	0	0	0
Aramis	F	4.27	7	0	4	—	2	0	3	0	0	16
Bobby	F	2.56	2	0	0	0	—	0	6	0	0	8
Martha	F	0.90	1	0	5	0	6	—	7	0	0	19
Moritz	F	5.89	3	0	11	0	1	0	—	6	0	21
Munia	F	2.05	0	0	5	0	0	0	1	—	0	6
Nobel	F	1.89	0	0	0	0	0	0	0	0	—	0
Total			13	0	27	0	9	0	17	6	0	72

Note: Sex and normalised David's scores (NormDS) of the providing subjects as well as sample sizes and total number of trials for each group are indicated. Grey background signifies kin dyads. Black frames signify dyads with reciprocal provisioning.

$W_{upper} = 266$, $p = .614$), therefore not supporting the conclusion that the two groups provided food equally.

3.2 | Reciprocity

There were only 2 out of 15 dyads with direct reciprocal provisioning (i.e. each dyad member delivered food to the other at least

once) in the crow group and two out of 36 dyads in the raven group (Table 1). There were no dyads with reciprocal provisioning in the two magpie groups (total: 16 dyads). There was no correlation between providing and receiving food across all subjects ($n = 24$, $\rho = -0.220$, $p = .302$) and the effect was marginally equivalent (TOST correlation: $r_{lower} = -.525$, $p = .068$). When looking at the subjects' provisioning on a trial-by-trial basis, we found that one magpie had a significantly increased likelihood of providing food after receiving

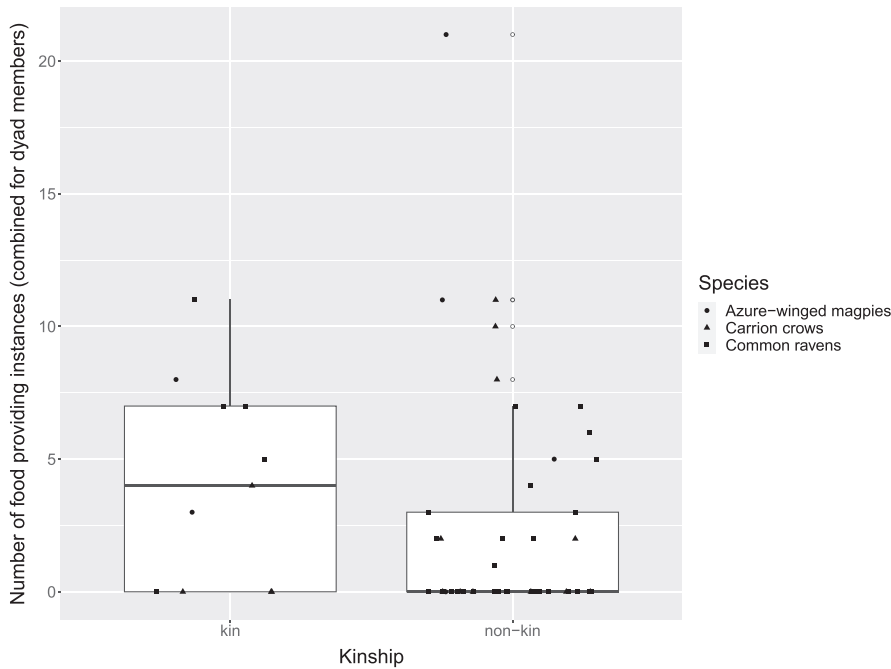


FIGURE 2 Number of food-providing instances among kin and non-kin dyads. The box plots represent the medians (horizontal lines), inter-quartile ranges (boxes) as well as minima and maxima (whiskers). All of the data are represented with dots. Dot shapes indicate the species (circle = azure-winged magpie; triangle = carrion crow; square = common raven). The position of outliers is additionally indicated by empty circles along the centre of the boxplot.

TABLE 2 For all individuals that provided and received food ($n = 11$), this table shows the name, species, sex and number of trials in which they provided or did not provide food, depending on whether they had received food in the preceding trial as well as results from the Fisher's exact test (ns = not significant).

Individual	Species	Sex	After receiving		After not receiving		Fisher's exact test
			Provided YES	Provided NO	Provided YES	Provided NO	
Han	Magpie	M	7	0	24	19	$p = .035$
Yoda	Magpie	M	0	9	1	40	ns
Chewie	Magpie	F	0	0	16	32	ns
Mon	Magpie	F	1	0	27	20	ns
Daisy	Crow	F	0	11	1	46	ns
Paula	Crow	F	1	11	9	37	ns
Soukie	Crow	F	0	1	23	34	ns
Arthus	Raven	M	0	13	2	73	ns
Bobby	Raven	F	0	8	8	72	ns
Moritz	Raven	F	0	16	21	51	$p = .010$
Munia	Raven	F	0	6	6	76	ns

food in the preceding trial, whereas one raven showed the opposite pattern (Table 2). The other subjects' likelihood of providing food was not affected by whether they had or had not received food in the preceding trial.

3.3 | Dominance

In the dominance assessment, there were 115 and 75 displacements in the two magpie groups, respectively (i.e. 4.6 and 3.0 displacements per session per individual, on average). There were 100 displacements in the crows (i.e. 8.3 per session/individual) and 396 displacements in the ravens (i.e. 22 per session/individual). David's

scores differed both between the sexes and between the species (overall regression: $N = 25$, $R^2 = 0.621$, $F(3, 21) = 11.46$, $p \leq .001$; see Table 3 for predictor results). Males had higher scores than females and ravens had higher scores than magpies and marginally higher scores than crows (post-hoc comparisons: raven-magpie, $t = 4.402$, $p < .001$; raven-crow, $t = 2.479$, $p = .054$; magpie-crow, $t = 1.418$, $p = .350$; Figure 3). We therefore looked at the effect of dominance on providing and receiving food for the three species differently.

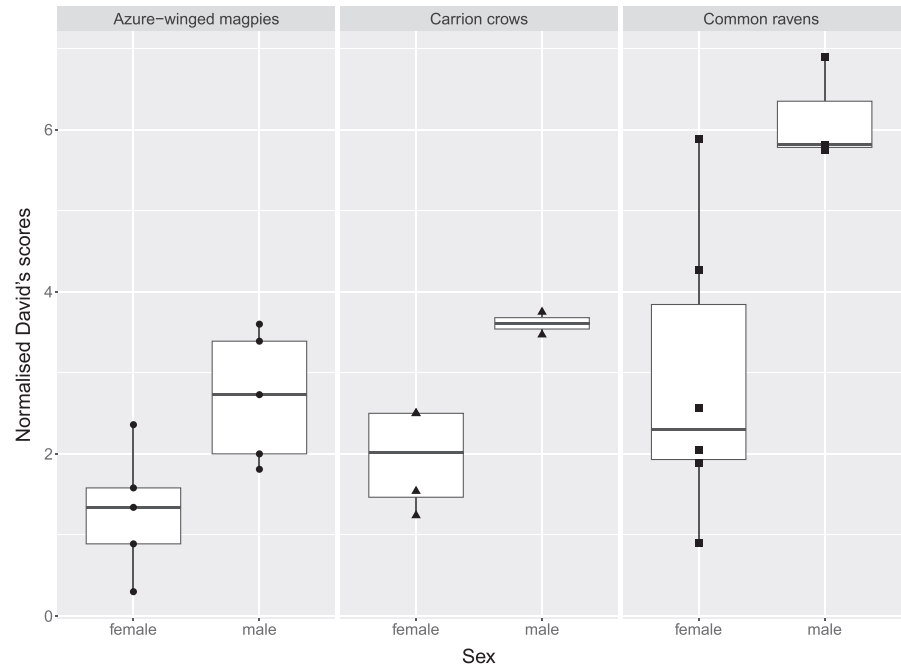
Providing food was not correlated with the individuals' David's scores in any species (magpies: $\rho = 0.174$, $p = .654$, crows: $\rho = -0.647$, $p = .165$, ravens: $\rho = -0.186$, $p = .631$). In ravens, there was a significant positive correlation between the individual's David's score and receiving food in the group service paradigm ($n = 9$, $\rho = 0.670$,

TABLE 3 Results of the general linear model testing the effect of sex and species on the subjects' normalised David's scores.

Parameter	Estimate	SE	CI	t	p	f
(Intercept)	0.95	0.43	[0.05, 1.86]	2.199	.039	–
Sex (male)	2.09	0.48	[1.10, 3.08]	4.396	≤.001	0.96
Species (crow)	0.85	0.60	[-0.40, 2.09]	1.418	.171	0.31
Species (raven)	2.35	0.53	[1.24, 3.46]	4.402	≤.001	0.96

Note: Given are estimates, standard errors (SE), 95% confidence intervals (CI), t-values, p-values and partial Cohen's *f* (*f*) for the intercept and each predictor.

FIGURE 3 Normalised David's scores among female and male subjects, split by species. The box plots represent the medians (horizontal lines), inter-quartile ranges (boxes), as well as minima and maxima (whiskers). All of the data are represented with dots. Dot shapes indicate the species (circle=azure-winged magpie; triangle=carrion crow; square=common raven).



$p = .048$; Figure 4). There was no such correlation in the magpies or crows (magpies: $n = 9$, $\rho = 0.203$, $p = .600$; crows: $n = 6$, $\rho = -0.368$, $p = .473$). The equivalence tests demonstrated non-equivalence for all non-significant effects (TOST correlation: $p > .1$ for all tests).

4 | DISCUSSION

In this study, we investigated the effect of kinship, reciprocity and dominance on food provisioning in the group service paradigm in three corvid species. We found no evidence of an effect of kinship or reciprocity on food provisioning in the tested azure-winged magpies, carrion crows, and common ravens. Contrary to our predictions, the subjects' dominance was not positively correlated with their rate of food provisioning in any species. Among ravens, dominance was instead positively correlated with receiving food.

Given that kinship is particularly relevant for indirect fitness benefits and that kin recognition has been demonstrated in many bird species (see Brecht & Nieder, 2020; Kondo & Watanabe, 2009), we predicted that there would be more frequent food provisioning within kin than non-kin dyads. Corvids typically form strong social bonds among kin (carrion crow: Baglione et al., 2003; common raven: Fraser & Bugnyar, 2010). Many corvid species have been

shown to differentiate between kin and non-kin, for example, by tolerating kin more than non-kin in co-feeding settings (carrion crow: Chiarati et al., 2011) and preferentially supporting kin during agonistic interactions (common raven: Fraser & Bugnyar, 2012). However, we found no significant effect of kinship on food provisioning in our study. Although each of the three groups for which kin relationships were known contained at least two kin dyads, kin dyads were less frequent than non-kin dyads in our sample (kin: $n = 11$ dyads; non-kin: $n = 46$ dyads) and the equivalence test indicated that the kin and non-kin samples were not equivalent. This suggests that further studies with larger sample sizes and more balanced groups might be needed to detect effects of kinship on food provisioning in corvids. Strikingly, however, in a third of the kin dyads in our sample, no single provisioning act occurred, making it unlikely that our non-significant results were only the consequence of the small number of kin dyads. To date, evidence of a positive effect of kinship on prosocial behaviour in corvids has been mixed (De Kort et al., 2006; Scheid et al., 2008; Schwab et al., 2012) and potentially dependent on the specific type of prosocial behaviour (e.g. actively offering food vs. co-feeding; Scheid et al., 2008). In contrast, a recent study using the same experimental set-up and procedures as in the current study and similar sample size, demonstrated a positive effect of kin relations

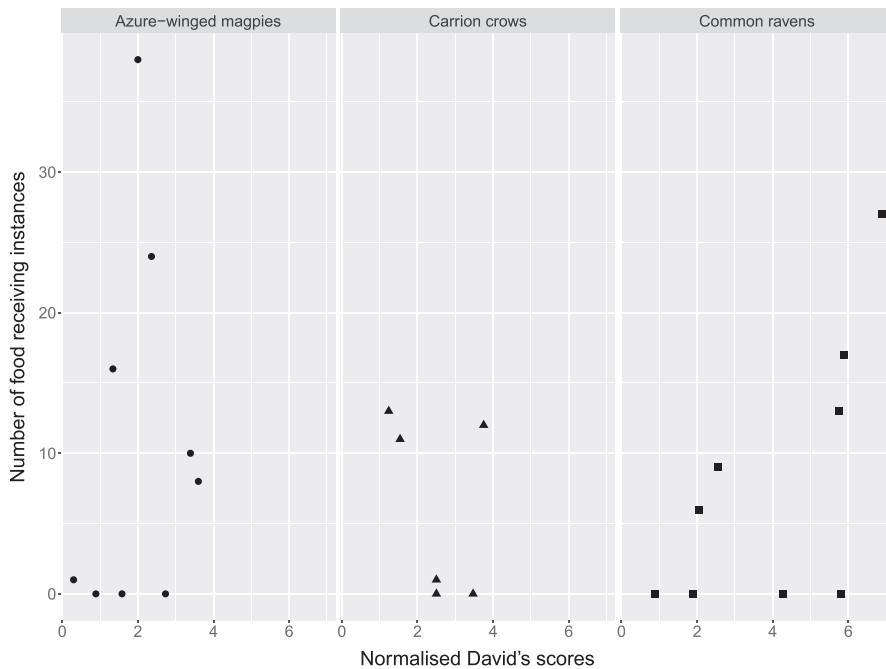


FIGURE 4 Number of receiving instances in relation to normalised David's scores, split by species. All of the data are represented with dots. Dot shapes indicate the species (circle = azure-winged magpie; triangle = carrion crow; square = common raven).

on both the likelihood and the magnitude of prosocial provisioning in Japanese macaques (*Macaca fuscata*; Bhattacharjee et al., 2023). The social organisation of this primate species, however, rests strongly on matrilineal kin relationships, which differs from the more fluid social structure of raven and crow populations (Boucherie et al., 2019; Loretto et al., 2017; Uhl et al., 2019). Azure-winged magpies, in contrast, live in cooperatively breeding groups, which mostly contain kin, but non-kin individuals are also present (Komeda et al., 1987). The interdependency on the group level, which is found in cooperatively breeding species, has been argued to predict high levels of prosocial behaviour among its members, with rather indiscriminate sharing regarding factors such as kinship on the dyadic level (cf. Burkart et al., 2014). But these predictions have never been tested systematically in corvids. Thus, it is evident that more studies are needed to ascertain whether and under which conditions corvids are selectively prosocial towards kin.

We found no evidence for direct reciprocity in our study. There were very few dyads with direct reciprocal provisioning (magpies: none; crows: 2 out of 15 dyads, ravens: 2 out of 36 dyads). Moreover, received food was not equally distributed within the dyads with reciprocal provisioning. In all cases, one dyad member received food only once, whereas the other dyad members received the rest of the food. Cognitively, ravens would fulfil the prerequisites for remembering interactions with specific individuals, as they are capable of recognising conspecifics individually (Boeckle & Bugnyar, 2012) and have been shown to remember the nature of a single reciprocal interaction with a human experimenter for up to 1 month (Müller et al., 2017). One limitation of the group service paradigm, however, is that it is difficult for providers to selectively provide food to specific recipients. They can decide whether or not to land on the provisioning perch when

another individual is already sitting in the receiving location, as well as leave the provisioning perch when a specific individual is approaching. But in agile bird species, such as corvids, unintended recipients might approach the apparatus fast enough to obtain the food. Therefore, reciprocal provisioning on a calculated tit-for-tat basis is not easy to achieve in this paradigm. In two recent studies that were specifically designed to elicit direct reciprocity in azure-winged magpies, carrion crows and common ravens, however, the authors found no direct reciprocity either (with generally low levels of prosocial behaviour; Wascher et al., 2020; Zhang et al., 2022). Other mechanisms such as preferentially approaching the apparatus together with specific individuals would have still allowed for a higher probability of reciprocal provisioning in our study, as has been found in co-feeding during free interactions (De Kort et al., 2006; Liévin-Bazin et al., 2019; Scheid et al., 2008). Reciprocal relationships have in fact been argued to rely on cognitively less demanding mechanisms in comparison to calculated or tit-for-tat reciprocity, described as attitudinal (Brosnan & de Waal, 2002) or emotion-based reciprocity (Massen et al., 2019; Schino & Aureli, 2009). Nevertheless, one can argue that the group service paradigm might be more suitable for eliciting generalised or indirect reciprocity strategies than direct reciprocity. However, when investigating the subjects' behaviour on a trial-by-trial basis, we found that only one magpie had a significantly increased likelihood of providing food after receiving food in the preceding trial. Surprisingly, one raven showed the opposite pattern by having a decreased likelihood of providing food after receiving food. Although such individual results have to be interpreted with caution, the opposite effects make it seem unlikely that generalised reciprocity was the mechanism underlying the food provisioning observed in the current study. Similarly, we found no evidence of indirect reciprocity, since the subjects that

were the most frequent food providers were not the ones that received most food. Contrarily, five subjects that provided food to others never received any food themselves, whereas five individuals that received food never provided any food to others. Two studies found a similar pattern of no direct or generalised reciprocity and only a few dyads with reciprocal food transfers in pinon jays and rooks (Duque & Stevens, 2016; Scheid et al., 2008). Instead, food transfers in both studies were most strongly predicted by dominance, with dominant individuals sharing more food than subordinate individuals.

Contrary to these existing results, we did not find a correlation between the subjects' dominance and their rate of food provisioning in any species. Only in ravens, a different pattern emerged: dominance was positively correlated with receiving food in this species. Despite the fact that dominance has been found to promote food provisioning in some corvid and parrot species (Duque & Stevens, 2016; Péron et al., 2013; Scheid et al., 2008) as well as some non-human primates (Chang et al., 2011; Massen et al., 2010; Takimoto et al., 2010), there are species in which mostly dominant individuals profit from others' prosocial acts. In a study testing targeted helping in chimpanzees, for example, subordinate individuals transferred the tools needed to obtain food to dominant individuals more often than the reverse (Yamamoto et al., 2012). Similarly, ravens are more likely to provide agonistic support to dominant than to subordinate group members (Fraser & Bugnyar, 2012). Therefore, there might be a general tendency to show prosocial behaviour 'up the hierarchy' in common ravens, much like many non-human primate species, who have been found to groom 'up the hierarchy' (cf. Seyfarth, 1977). Alternatively, dominant individuals might have simply been more likely to monopolize the side of the apparatus where food could be received, resulting in a greater likelihood for them to obtain the food (Sima et al., 2016). Further, regarding the non-significant correlations between dominance and food provisioning it is important to note that the equivalence test indicated a lack of equivalence in these statistical tests. Splitting the data by species resulted in very small sample sizes for testing the correlations (magpies: $n=9$; crows: $n=6$; ravens: $n=9$), which was the likely reason for the non-equivalence. Thus, future comparative studies with larger sample sizes are needed to test whether dominance has species-specific effects on prosocial behaviour in corvids.

Despite the many advantages of using the group service paradigm for assessing prosocial behaviour in non-human animals (e.g. being tested in their regular enclosures without the need for potentially stressful separation), one major limitation is that the providing individuals have only limited control over the specific recipients of their prosocial acts. The precise behavioural coordination needed for such targeted provisioning is most likely beyond the scope of a captive group setting in which all subjects are close to the apparatus at the same time and are highly motivated to obtain the food. In a semi-free-ranging group of Japanese macaques, where the subjects had to cover larger distances to approach the group service apparatus, specific individuals were better able to

coordinate their use of the apparatus and particular kin and affiliated dyads emerged in this setup (Bhattacharjee et al., 2023). Nevertheless, for the systematic assessment of reciprocity in corvids, it seems more promising to advance to dyadic testing. Ideally, though, these dyadic paradigms should have simple task contingencies, as cognitively demanding tasks designed to test reciprocity have so far yielded no prosocial behaviour in species that have been prosocial in simpler paradigms (e.g., Horn et al., 2021; Wascher et al., 2020; Zhang et al., 2022). One more limitation of the current study is that we cannot exclude that the subjects that received food in the group service paradigm reciprocated in a different 'currency', such as sharing food outside the experimental context, preening others or providing agonistic support. For example, De Kort et al. (2006) found that donor-initiated food transfers were correlated with later allopreening among jackdaws. Assessing such long-term effects would require observing the interactions within the group for extended periods after the experiment in future studies. In general, a food provisioning experiment might not be the ideal setting to elicit reciprocity. In non-human primates, studies that involved food produced less evidence for reciprocity than studies involving other commodities, most likely because choices in food settings are more strongly affected by loss aversion (see Schweinfurth & Call, 2019b). Regarding the generalisability of the reported findings in line with the STRANGE framework (Webster & Rutz, 2020), we note that we gave each individual enough time to habituate to the apparatus and learn how to use it. Nevertheless, there were nine subjects that never delivered food, of which four birds neither provided nor received food in any of the test or motivation trials. Due to the unrestricted setting in the group service paradigm, it is very difficult to draw conclusions about the motivations of these non-participating birds. Importantly, we only tested captive individuals in the current study and some factors, such as kinship, might be more relevant in the wild than in captive birds. Nevertheless, particularly regarding our findings that dominance increases ravens' likelihood to receive food, we are confident that our results generalise well to non-captive populations, as dominance structure in captive raven groups has been found to be strikingly similar to raven foraging groups in the wild (Boucherie et al., 2022).

In conclusion, our results provide no evidence for the effects of kinship or reciprocity in azure-winged magpies, carrion crows and common ravens. While preferential provisioning for kin and direct reciprocity might have been impeded by the provider's inability to control who receives the food, effects of indirect and generalised reciprocity would have been detectable in the group service paradigm. Moreover, while we did not find that dominance promoted prosocial behaviour in the three tested species, we found another piece of evidence that dominance is a highly important factor in the social interactions of common ravens.

AUTHOR CONTRIBUTIONS

Lisa Horn: Conceptualization (equal); data curation (lead); formal analysis (lead); funding acquisition (supporting); investigation

(lead); supervision (lead); visualization (lead); writing – original draft (lead); writing – review & editing (equal). **Thomas Bugnyar:** Conceptualization (equal); funding acquisition (supporting); resources (lead); writing – review & editing (equal). **Jorg J. M. Massen:** Conceptualization (equal); funding acquisition (lead); resources (supporting); writing – review & editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing financial or other interests.

DATA AVAILABILITY STATEMENT

Raw data are presented directly in the manuscript in Tables 1 and 2. Additional raw data of the dominance assessment are available as Appendix S1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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