






Third-party interventions of common ravens, *Corvus corax*

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The social intelligence hypothesis suggests that cognitive capacities evolved because of selection pressures related to increasing social complexity. For instance, social animals may need to monitor the relationships of others and intervene in them if that is ultimately beneficial to themselves. Traditionally, such third-party interactions are studied by examining coalitionary support during conflicts. However, growing evidence shows that some animals also intervene in others' positive social interactions. To aid our understanding of the patterns of such interventions in the wild, we examined third-party interventions in both positive and negative interactions in a population of individually marked wild ravens. Although we found that interventions in negative interactions were more frequently observed than those in positive interactions in this wild population, both were relatively common and, in fact, occurred in almost exact proportions relative to the number of such interactions (~10% of ad libitum interactions in both cases). Interventions were mostly active (compared to mere approaches) and aggressive. However, the mode of intervention varied across interactions. In positive interactions, interventions were mostly impartial, whereas in negative interactions, interventions were not, targeting one of the two partners. Neutral or policing interventions in negative interactions were rare. More than half of negative interventions reflected coalitionary support for the aggressor and a quarter for the victim. Furthermore, the likelihood of initiating an intervention and being the target of an intervention varied according to age, sex, rank, residency status and affiliation index. Taken together, our results provide a complete overview of third-party interventions in wild ravens and suggest that ravens use these interventions selectively and potentially even strategically. Future comparative studies may allow investigations into whether the necessity of such social strategies may have been a selection pressure regarding intelligence in animals.

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The social intelligence hypothesis assumes that complex cognitive capacities have evolved in parallel with increasingly complex social organizations (Dunbar, 1998; Humphrey, 1976) and that this increased cognition allows individuals within a group to outcompete each other through direct competitive strategies (Machiavellian intelligence hypothesis: Byrne & Whiten, 1988) and through collaborative strategies (Vygotskian intelligence hypothesis: Moll & Tomasello, 2007). To map the complexity of sociality in a group, social behaviour has been described at four levels that build on each other and increase in complexity: the behaviour itself, the interaction between actor and receiver, the relationships of actors and receivers and the (resulting) social organisation (Hinde, 1976).

Whereas the first two levels can be observed by researchers, the latter two are inferred from data patterns concerning the first two levels. Quantifying social relationships and the social structure of your study species has proven to be a powerful tool in analyses of animal behaviour; however, the fact that we can deduce such social relationships and social structure does not necessarily imply that the animals themselves can do this too. To study the extent of the social intelligence hypothesis, it is paramount that we investigate such knowledge in our study species.

Several studies that used playback experiments that mimic rank reversals in the group have shown for a few species that they do have expectations and thus some sort of knowledge about the rank and/or kin relations of others (e.g. chacma baboons, *Papio ursinus*, Bergman et al., 2003; Cheney et al., 1995; vervet monkeys, *Chlorocebus aethiops pygerythrus*, Borgeaud et al., 2013; ravens, *Corvus corax*, Massen, Pašukonis, et al., 2014; Massen, Szípl, et al., 2014; acorn woodpeckers, *Melanerpes formicivorus*, Pardo et al., 2020).

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Another powerful tool for investigating animals' understanding of third-party relationships is the analysis of behaviours and interactions that involve third parties (Massen & Mielke, 2021). For example, Slocombe and Zuberbühler (2007) demonstrated that chimpanzees, *Pan troglodytes*, exaggerate their (fear) screams when their audience consists of at least one individual that outranks their attacker. Similarly, raven victims increase their defensive call rates when there are relatives in the audience yet reduce their defensive call rate if the attacker has a bonding partner in the audience (Szipl et al., 2018). Moreover, in a previous study, we showed that ravens intervene specifically in the affiliative interactions of ravens that are trying to establish social bonds, suggesting that they try to prevent them from building strong alliances (Massen, Szipl, et al., 2014). Similar patterns of interventions in grooming were found in chimpanzees and sooty mangabeys, *Cercocebus atys* (Mielke et al., 2017), mandrills, *Mandrillus sphinx* (Schino & Lasio, 2018), rhesus macaques, *Macaca mulatta* (Mielke et al., 2021) and horses, *Equus caballus* (Schneider & Krueger, 2012).

Traditionally, the focus of investigations on such third-party interactions has been on interventions in agonistic encounters of others. Mostly, but not exclusively (Flack et al., 2006; for impartial interventions aka policing), in this situation, the third party supports one of the former opponents and they thereby form a coalition against the other former opponent (Harcourt & de Waal, 1992). Such within-group coalitions have now been described for a range of mammalian species (reviewed in Smith et al., 2010) and in several bird species (Bewick's swans, *Cygnus bewickii*: Scott, 1980; jackdaws, *Corvus monedula*: Wechsler, 1988; greylag geese, *Anser anser*: Scheiber et al., 2005; rooks, *Corvus frugilegus*: Emery et al., 2007; ravens, Fraser & Bugnyar, 2012). However, to truly investigate these third-party interventions, we need to focus more on the underlying patterns (see Bissonnette et al., 2015) and expand our view to not only include third-party interventions in agonistic interactions but also in affiliative (see de Waal, 1982; Massen, Szipl, et al., 2014; Mielke et al., 2017, 2021; Mondragón-Ceballos, 2001; Schino & Lasio, 2018; Schneider & Krueger, 2012; VanDierendonck et al., 2009) or other interactions.

Therefore, we studied third-party interventions in positive (affiliations and close proximity) and negative interactions (aggression, defensive fight postures, displacements, kleptoparasitism and agonistic displays) in a population of wild ravens. Ravens are relatively long-lived (<30 years) birds of the corvid family that, before they acquire and maintain a territory, can spend several years of their (sub) adult life in large social groups (Heinrich, 1989) that are characterized by intense spatial and temporal fission–fusion dynamics (Boucherie et al., 2019; Loretto et al., 2017). These groups are also characterized by steep and transitive dominance structures, in which dominance ranks are modulated by the sex, age and aggressiveness of each bird (Boucherie et al., 2022). Within these groups, ravens form social bonds that resemble those of primates (Fraser & Bugnyar, 2010). Notably, they depend on these social bonds for rank acquisition; that is, the likelihood of winning a fight increases for bonded birds and with the strength of the bond (Braun & Bugnyar, 2012). In addition, experimental studies have shown that ravens can coordinate their actions in a cooperative setup (Massen et al., 2015, 2020), which would be a prerequisite for coalition formation, and that they preferentially cooperate with individuals with whom they have a close social bond (Asakawa-Haas et al., 2016; Massen et al., 2015). Importantly, ravens exhibit various third-party interactions such as interventions in agonistic interactions (Loretto et al., 2012; Fraser & Bugnyar, 2012; this study) and interventions in affiliative interactions (Massen, Szipl, et al., 2014). However, note that the data on interventions in agonistic interactions so far describe the patterns among a limited number of captive birds that were, by definition, restricted in the size,

composition and dynamics of their group and thus of possible interaction partners, and all these factors do seem to play important roles in the patterning of third-party interventions in agonistic interactions (Borgeaud & Bshary, 2015; Kaburu & Newton-Fisher, 2015; Silk et al., 2004) and in the social lives of ravens in the wild in general (Boucherie et al., 2019, 2022; Braun & Bugnyar, 2012; Loretto et al., 2017; Massen, Szipl, et al., 2014; Szipl et al., 2018). Given these limitations, proper analyses of the patterns of third-party interventions in agonistic interactions observed in the wild are required. Moreover, to obtain a more general picture of the third-party interactions of wild ravens, a comparison of previously described patterns of affiliative interactions with those of agonistic interactions in the wild is required.

Here, we first investigated how often each type of intervention happens (i.e. interventions in positive versus negative interactions) and by means of what behaviour (with targeted affiliation, targeted aggression, neutral approach and dual-targeted aggression) the birds perform these interventions. In doing so, we also investigated whether interventions in the population are partial or not (i.e. whether the intervener targets a specific individual), and if partial, who was targeted and how. Specifically with regard to interventions in negative interactions, we can thereby distinguish coalitions from 'policing' (i.e. impartial interventions: Flack et al., 2006; von Rohr et al., 2012), and if these are partial, we can distinguish whether there is victim support or support for the aggressor. Second, we studied which individual characteristics (sex, age, affiliative status or dominance rank) may predict whether birds initiate such an intervention or become the target of an intervention.

Based on findings from captivity, we expected that wild ravens would not randomly intervene but would adjust their mode of intervention to the type of interaction targeted. In addition, we expected that younger, visiting, 'solitary' and/or female ravens would be targeted most often, and conversely that older, local, bonded and/or male ravens would intervene most, because of their better resource-holding potential and status. These interventions may help them to obtain and maintain their status and resource-holding potential (Boucherie et al., 2022; Braun & Bugnyar, 2012; Massen, Szipl, et al., 2014; Noë, 1994). Given that raven populations are very flexible and thus do not really benefit from increased stability due to policing, we expected that the majority of third-party interventions in negative interactions would be partial and thus constitute coalitions (Harcourt & de Waal, 1992). We further expected the majority of these partial interventions to be opportunistic all-down aggressor support (Noë, 1994; Pandit & van Schaik, 2003; van Schaik et al., 2004).

METHODS

Study Site and Population

We conducted this study in Cumberland Wildpark, located in a valley in the Austrian Alps, close to the town of Grünau im Almtal, between September 2011 and March 2012. The park is used for foraging by a population of free-ranging ravens that scrounge food from captive animals such as wolves, bears and wild boars. Our raven population has been the focus of a long-term monitoring programme since November 2007. We consistently habituated ravens to human observers at five locations in the park (i.e. the enclosures of Przewalski's horses, wolves, bears, wild boars and red deer). This allowed us to observe the ravens from close distances (± 5 m).

At the time of the observations for this study, over 200 ravens had been captured and marked individually with coloured wing tags and leg bands (for further details see Braun & Bugnyar, 2012). During marking, age (juveniles in year 1, subadults in year 2 and adults of 3+ years) was estimated based on beak and throat

coloration (Heinrich & Marzluff, 1992), and sex was later determined via analyses of blood samples taken during the marking (Braun & Bugnyar, 2012).

Behavioural Observations and Presence Data

Observer

Data on all third-party interventions were collected by a trained research assistant (RA), Michela Spreafico. Additionally, video recordings of approximately 15% of all observations regarding interventions in positive interactions were made using a Canon HF-11 HD camcorder (Canon Inc., Japan). These videos were recoded by an additional RA, Georgine Szpl, to check for interobserver reliability. Agreement on the identity of the birds involved and their specific roles, whether something was a true intervention, the nature and mode of the interaction was 100% (see Massen, Szpl, et al., 2014).

Behavioural observations

Data were sampled in the areas around three enclosures: the wild boars' (approximately 59.5% of the data), the bears' (27%) and the wolves' (13.5%), which the ravens frequented throughout the day. We chose these sites as observation sites because they have been identified as hotspots where the ravens in the valley 'socialize' (Braun et al., 2012; Loretto et al., 2016). Using a voice recorder and binoculars, the RA recorded all occurrences of positive and negative interactions (see Table S1 for full ethogram) of individually marked birds using behavioural sampling methods (Martin & Bateson, 1993). However, when a third individual intervened in a dyadic interaction between two ravens, methods switched to focal observations and the RA coded the identity of the intervening bird, the identity of the other two birds and all behaviours (i.e. initial interaction[s] and intervention).

Presence data

Since 2007, the identity of marked ravens has been recorded almost daily, from the enclosure of the wild boars, during the morning feeding of the animals (between 0700 and 0900 hours). This allows a systematic evaluation of the presence of ravens in the valley at the same time and location each day, which is used to compute several indices such as the daily affiliation ratio or the vagrant–resident index (see below).

Evaluation of observation bias

The challenge of such data collection in the wild lies in the size of the scanned area and the simultaneity of interactions. Note that the feeding sites of the wild boars, bears and wolves are all relatively open and surrounded by a few trees and fences. Hence, we observed fairly well the interactions among the ravens when they were gathering at those sites. Yet, we likely faced a bias towards birds that remained in the vicinity after feeding compared with those that left the sites shortly after feeding. To ensure balanced sampling of those birds staying in the vicinity, the RA followed a systematic protocol when patrolling between sites. It is also possible that we might have overlooked less conspicuous interactions, such as interventions in affiliations, compared with interventions in agonistic interactions (as conflicts are often accompanied by loud appeasement calls; Heinrich et al., 1993). However, we paid special attention to those 'less conspicuous' interventions (see video recordings above) and, indeed, we found a similar proportion of interventions in positive and negative interactions (10%, see Results). This indicates that interventions involving agonistic behaviours may not have been inflated in our data set, in comparison to less conspicuous behaviour such as mere approaches or affiliations.

Previous analyses

Note that some (~one-third) of these data (i.e. interventions in affiliative interactions) were published in a previous paper (Massen, Szpl, et al., 2014). We feel it is important to keep these data here as they allow the comparison between interventions in positive and negative interactions; moreover, here we analysed these data differently using more sophisticated statistical models (see analyses), and using a more sophisticated measure of bondedness (see below), while adding dominance rank as a predictor, as well as incorporating the effect of a novel individual attribute that has proven important in subsequent studies on raven sociality (e.g. Boucherie et al., 2022), that is, the vagrant–resident index (see below).

Subjects' Selection Criteria for Statistical Analyses

For the analyses, we selected marked ravens that were present at least 10% of all feeding observation sessions at the wild boars' enclosure over the study period (144 observation sessions in 6 months; minimum set to 15 sessions). However, we did not use a more conservative threshold to avoid under-sampling/oversampling rare/regular visitors of the feeding site, respectively. The selection was made on a minimum presence in the valley, and not on the expression of third-party behaviours, to ensure that individuals included in the analyses were seen fairly frequently to allow a reliable assessment of their patterns of interaction. The selection being based on the individuals' presence, subjects included in our analyses may thus have initiated/received no third-party interventions during that time ('real zero'; i.e. individuals that were present but did not perform the behaviour, rather than individuals that were not present of which we do not know whether they did or did not show the behaviour).

Following these selection criteria, a total of 64 wild ravens were included in the analysis of the hierarchy (see below), and 61 in the models (38 females, 23 males; age 1 year, 2 years, 3 years and adult (>3 years): 15, 8, 6 and 32 individuals, respectively), due to missing information on the attributes of two individuals, and an extreme value for the daily affiliation ratio of a third individual.

Evaluation of Potential Sample Bias

In this section, we aim to discuss the STRANGENess of our tested sample following the guidelines of the STRANGE framework, and their implication for the generalizability of our results (Webster & Rutz, 2020).

Social background

All study subjects were free ranging, from a wild population of ravens, showing typical grouping dynamic and party composition for the species. Indeed, ravens are known to exhibit a high degree of fission–fusion dynamics (Aureli et al., 2008), which we also reported in our study population (Loretto et al., 2017). Because of these fission–fusion dynamics, party size and demographic composition (with regard to sex, age and status) may vary greatly across context and location (Loretto et al., 2017; see also Aureli et al., 2008 for a theoretical overview of fission–fusion dynamics). However, the composition of the observed foraging group between the end of September 2011 and March 2012, which can be evaluated on a daily basis at the wild boars' enclosure using the presence data, was balanced with regard to sex (average daily female:male ratio over the studied period, 6:4) and age class (average daily proportions of 1-year-old, 2-year-old, 3-year-old and adult ravens: 19%, 9.5%, 12.5% and 59%, respectively), and resembles what can be observed in other wild populations (Huber, 1991). To evaluate group composition, we considered daily all marked ravens present

during feeding, including individuals that were not included in the analyses (with a presence over the whole period < 10%). At the time of the study, between 50 and 80 ravens attended the morning feedings each day, and just over half of these ravens were marked each day (minimum: 0; maximum 56; average: 36).

Trappability and self-selection

Marked ravens were trapped using drop-in traps baited with meat (Stiehl, 1978). The advantage of this trapping technique is that it constitutes a relatively calm procedure (ravens get in by themselves but cannot get out), which does not cause any excitement in the surrounding ravens (i.e. we get hardly any scolding, etc.). However, the disadvantage of this technique is that it may bias the sampling to bold and/or young birds. Note that about 30% of the tagged ravens revisit the traps, indicating that they are 'bold' enough to trade off access to valuable food over the experience of being caught and tagged. Furthermore, we tended to catch primarily ravens in their first year, indicating that inexperienced individuals have a higher propensity to enter traps. Note that this type of catching bias eventually turns in our favour because we can follow most birds from their first year of life over the years (maximum 15 years so far). Note that trapped ravens attract other, potentially less bold, ravens to also enter the trap, resulting in a less biased sample overall. Nevertheless, this potential sampling bias needs to be taken into account when considering the generalizability of our results.

Rearing history

All individuals originated from the wild (61), except three, which originated from captivity. These three birds hatched in 2009 in Alpenzoo Innsbruck and at a private owner, respectively; they were raised by their parents to fledging, transferred to Grünau, and were introduced into free flight in their first autumn. By the time of the current study, the ravens had been fully integrated into the local wild raven population. They were not involved in any experiments during their time in captivity.

Acclimatization and habituation

Trapping and handling procedures may induce high levels of stress in the following hours/days. However, 71% of the tested individuals were trapped and marked more than 6 months before the study period and 11% within 6 months before the study started. For most tested individuals, we can thus rule out behavioural changes induced by the trapping and handling procedures. For the remaining individuals trapped and marked during the study period (18%), all except one were caught in the first 2 weeks of the study. Even if a trapped individual's behaviour is affected by the procedure, it can be expected to stabilize and normalize after a few days, so that the effect is diluted over the 6 months of data collection.

As a result of our long-term monitoring programme and because of the specific location of our study site (in a wildlife park open to the public), we can expect all ravens from our study to be habituated to the daily presence of humans (visitors or scientists), ruling out an effect of the observer on their behaviour. Reviewing other studies on wild populations, we found that ravens at various sites throughout the world also regularly use anthropogenic food sources (Ho et al., 2023; Jain et al., 2022; Loretto et al., 2017). Thus, although the daily presence of humans may be increased in our population, it suggests that ravens in other populations may also be regularly exposed to human presence. Additionally, it suggests that the foraging behaviour of our population, scrounging food from the park's captive animals, does not deviate from that of others, such sites indeed being regular and natural meeting points for wild ravens.

Natural changes in responsiveness

Data were collected outside (September to January, 54% of the data) and during the breeding season (February and March, 46%) to grasp seasonal variations in behaviour. Therefore, we believe the results from our data collection are generalizable to other months. The impact of individuals' attributes and life stages on their behavioural response is explicitly the focus of this study. For this reason, our sample encompasses individuals of all developmental stages, sex and social status. In detail, the study included both sexes (38 females and 23 males), all age classes (1 year, 2 years, 3 years and adult: 15, 8, 6 and 32 individuals, respectively), varying affiliative status (from a total absence to regular affiliations with other partners) and varying social ranks. Note that the relative proportions across sexes and age classes of our tested sample match the composition of the foraging group (see above). All 61 individuals included in the analyses were ranked according to one another and thus had varying ranks between 1 and 64 (three individuals included in the dominance rank estimation were dropped out from the main analyses; see details below). Table S2 presents a full report on the tested subjects' attributes.

Genetic make-up

We have no reason to suspect the genetic make-up of our tested sample to have biased the studied behaviours in comparison to other wild populations.

Experience

All subjects were free-ranging individuals, with, to our knowledge, no prior experience, such as participation in experiments, that may have affected their behavioural response in the present study.

Nature of Initial Interaction and Mode of Interventions

For the nature of the initial interaction 'In What', we differentiated positive and negative interactions. Positive interactions included affiliations (allofeeding, allopreening, begging, body contact, co-feeding, co-manipulation, contact-sit, joint self-aggrandizing displays and invite allopreening) and close proximity (approaches, follow and walk together). Negative interactions included direct aggression (chase, peck, pull wing and threat), fight (i.e. severe aggression that initially is undecided and consequently escalates), defensive postures and screams, displacements (i.e. responses to aggression), kleptoparasitism (steal and stealing attempts) and agonistic displays (self-aggrandizing display).

For the mode of intervention 'How', we differentiated targeted affiliation, targeted aggression, neutral approach and dual-targeted aggression. In a targeted intervention, the intervener clearly targets one of the two original interacting partners, whereas it targets both in dual-targeted aggression. Note that we only found one case of dual-targeted affiliation (an object offer) directed towards two birds engaged in a positive interaction (joint self-aggrandizing displays). Dual-targeted affiliations were thus not considered in the models. For neutral approaches, we did not distinguish target versus dual-targeted cases because they were less clear to disentangle. Each mode of intervention was associated with the following behaviours: (1) targeted affiliations (allofeeding, body contact, co-feeding, contact-sit, joint self-aggrandizing displays and invite allopreening); (2) targeted and dual-targeted aggressions (direct aggression, fight, displacements and agonistic displays) and neutral approaches (approach and follow).

A detailed description of these behaviours and their occurrence in the different interactions observed (In What, How) is presented in Table S1 (see also Gwinner, 1964).

Estimation of the Hierarchy and Individual Dominance Ranks

We estimated the dominance rank of 64 free-flight ravens present in the valley during the study period (end of September 2011 to March 2012). To do so, we generated a winner–loser sequence from a total of 704 directed and decided conflicts, that is, approach and/or aggression, followed by the retreat and/or submission of the victim (with or without physical contact and/or vocalizations). In detail, conflicts included the following: displace, chase, threat or a peck followed by retreat. A detailed ethogram is presented in [Table S1](#). As a first step, we verified that our sample ensured a reliable estimation of the hierarchy, following the procedure of [Sánchez-Tójar et al. \(2018\)](#). Our sampling effort, that is, the ratio of interactions per individual ($704/64 = 11$), was within the recommended ratio (10–20 interactions per individual; [Sánchez-Tójar et al., 2018](#)). Note that the number of conflicts per individual ranged from 1 to 87. We then evaluated our data sparseness, by estimating the proportion of known dyads, that is, that interacted at least once. Theoretically, the number of conflicts typically follows a Poisson distribution, with a few dyads generating most conflicts, but the majority of them only a few. By comparing the observed proportion of known dyads in our sample (observed mean: 0.2) to the expected proportion under a Poisson distribution, we found that the proportion was within the 'poisson simulated range' (theoretical mean: 0.24; theoretical quantiles 2.5%–97.5%: 0.19–0.29).

We then used the randomized Elo-rating method to infer the hierarchy of the population subset (R package *aniDom* v.0.1.5; [Farine & Sanchez-Tojar, 2021](#)). With this method, the initial winner–loser sequence is replicated n times, and the order of conflicts is randomized at each replication (set to 1000). We can then infer for each individual a mean rank with a 95% confidence interval from the 1000 replications ([Fig. S1](#)). Using the 1000 individual Elo-scores, we estimated the steepness of the hierarchy by plotting the probability of a dominant winning a conflict according to the opponents' rank difference (high steepness, with a probability quickly increasing above 0.9; [Fig. S1](#)). We also evaluated the certainty of the inferred hierarchy by repeatability of the individual scores across randomizations (function 'estimate_uncertainty_by_repeatability' in R package *aniDom*, mean score = 0.89), and the degree of correlation of the hierarchy if inferred twice on two halves of the data set (function 'estimate_uncertainty_by_splitting', mean score = 0.63, and 2.5%–97.5% quantiles = 0.50–0.75). The scores obtained confirm a high certainty and steepness of the hierarchy ([Sánchez-Tójar et al., 2018](#)).

Daily Affiliation Ratio and Vagrant–Resident Index

To estimate individuals' affiliative/bonding status, we computed a daily affiliation ratio by dividing the total frequency of affiliations initiated and received by the number of feeding events during which the individual was present. Affiliations considered included the following: allofeeding, allopreening, body contact, co-feeding, co-manipulation, contact-sit and joint self-aggrandizing displays. Higher ratios indicate paired individuals and/or individuals with one or more affiliated partners. In contrast to our earlier analyses on the interventions of positive interactions only ([Massen, Szpil, et al., 2014](#)), where we used broad categories based on rather artificial cutoff points (see [Braun & Bugnyar, 2012](#)), here we opted to use a continuous variable with regard to bondedness based on indices that capture more of the natural variation in bondedness.

To evaluate individuals' presence in the valley during the study period, we computed a vagrant–resident index by dividing the total number of feeding events at which a bird was present by the total number of feeding events conducted over the study period. The vagrant–resident index ranges from 0 to 1 for highly vagrant

and highly resident birds, respectively. The vagrant–resident index, as a measure of the proportion of time in the study, served in all models as a control for varying observational efforts across individuals.

Statistics

We investigated how the individual frequencies of initiated interventions, as interveners (model 1) and received interventions, as targets (model 2) were affected by the nature of the initial interaction ('In What': positive and negative); the mode of the intervention ('How': targeted affiliation, targeted aggression, neutral approach and dual-targeted aggression); individual's sex (male and female); age class (1 year, 2 years, 3 years, adult); vagrant–resident index (covariate); daily affiliation ratio (covariate) and rank (covariate). We also added to the target model (2), as a covariate, the individual sum of interactions in which each individual was involved (either positive or negative depending on the data set structure and the 'In.What' predictor), recorded ad libitum over the study period. We tested whether individuals that were more often spotted interacting with others were also more 'exposed' to intervention. Additionally, we considered the interaction of the factors 'In What' and 'How' together, and their interaction with all individual attributes ('sex', 'age class', 'daily affiliation ratio' and 'rank'), in order to investigate: (1) which type of interventions were more frequent in the population ('In What' * 'How') and (2) the effect of individuals' attributes on their propensity to intervene/receive certain interactions ('In What' * individuals' attributes) or to intervene in a certain way ('How' * individuals' attributes). Note that the interaction between 'How' * 'age class' generated convergence issues likely due to overparameterization and was thus not included in the models. Finally, we added individual identity as a random factor (intercept) in our model to account for repeated measures per individual and all applicable random slopes (for factors 'In What' and 'How') to maintain type I error rates at a nominal level of 5% ([Barr et al., 2013](#); [Schielzeth & Forstmeier, 2009](#)).

The two models were run using generalized linear mixed models with a Poisson distribution and log link function (GLMM; function 'glmmTMB' in R package *glmmTMB* v.1.1.7; [Brooks et al., 2017](#)). If multiple targets or interveners were reported, each intervener/target was considered individually in the model, and the characteristics of the intervention were duplicated. For this reason, the interaction 'In What' * 'How' is discussed and visualized from the intervener perspective (model 1) and not the target (model 2). Indeed, although the same pattern and model effect are expected in both models because they both investigate the same pool of interventions, only from two different perspectives (the target versus the intervener), the number of dual-targeted interventions is inflated in model 2 because all targets are analysed separately.

In all models, covariates were systematically rescaled/standardized (rescale function in R). We ensured that our models were not overdispersed and zero-inflated, and we performed residual diagnostics using the DHARMA package ([Hartig, 2022](#)). We determined variance inflation factors using the *check_collinearity* function of R-package *performance* ([Lüdtke et al., 2021](#)). To evaluate the statistical significance of the overall model, we compared each model to a null model lacking the entire set of tested predictors ([Dobson, 2002](#)). We also ran full-reduced model comparisons to evaluate the overall statistical significance of the interaction terms, with the reduced model containing all tested predictors except the interaction of interest. Full-null and full-reduced model comparisons were run using the likelihood ratio test: R function 'anova', with argument 'test' set to 'Chisq'. Forest plots were created using the *sjplot* R package (function 'plot_models') and marginal effects plots were created using the R packages *ggeffects* (function

'ggeffect'; Lüdecke, 2018) and the R package ggplot2 (Wickham et al., 2016). The ggeffects R package was used to obtain the 95% confidence intervals around the estimated marginal means (for factors) and the marginal effect regression lines (for covariates), adjusted for all remaining predictors in the model. All statistics were performed using RStudio 2022.07.0 software with a significance threshold set at $\alpha = 0.05$.

Ethical Note

This study was exempted from the Austrian Animal Experiments Act (§ 2, Federal Law Gazette No. 114/2012) as it was observational. Trapping, marking and blood-sampling of free-ranging ravens were performed with a licence from the Austrian Government (BMWF-66.006/0010-11/10b/2009 and -66006/0019-WF/II/3b/2014). Ravens were caught in drop-in traps (Stiehl, 1978) at Cumberland Wildpark following the procedure described by Braun and Bugnyar (2012). Traps were equipped with perches and were positioned in shady areas next to the enclosures where the ravens forage. They were regularly checked during the day so that the time that the ravens spent in captivity was reduced to a minimum. Trapped birds were photographed, weighed and measured; age class (juveniles, subadults and adults) was determined by mouth and feather colour (Heinrich & Marzluff, 1992) and 50–200 μ l of blood were collected from the alar vein to analyse sex and genetic relatedness. Birds were marked with a patagial wing tag (Caffrey, 2000), an individual combination of colour rings and a numbered metal ring of Vogelwarte Radolfzell on the legs. Typically, the entire procedure lasted not longer than 15 min, and the newly tagged birds could be observed at feedings sites/close to the trapping site on the next day.

RESULTS

Frequency of Initiated Interventions as Intervener

Of the 4353 observed interactions considered in the analyses (2966 negative, 1387 positive), we observed a total of 417 intervention events ('In What': 281 in a negative interaction; 136 in a positive interaction; Fig. 1). Thus, interventions occurred in approximately the same number of positive and negative interactions (~10%).

Regarding the patterns of interventions, we found a significant interaction between the nature of the initial interaction ('In What') and the mode of intervention ('How') on the frequency of interventions (Fig. 2a, Table S3). In a population in which most interventions were active (with affiliation or aggression compared to mere approaches), the mode of intervention was dependent on the nature of the initial interaction. Most interventions in negative interactions were partial, that is, targeted interventions, with particularly high rates of targeted aggression compared with all other modes of intervention. However, in positive interactions, ravens relied more equally on all modes of intervention, although they tended to intervene aggressively more often, that is, using targeted aggression and dual-targeted aggression. Finally, where neutral approaches were shown in equivalent proportions in both positive and negative interactions, targeted affiliations were very rarely observed in positive interactions (Fig. 3a, Fig. 1). As a reminder, dual-targeted affiliations were never seen in negative interactions and only once in a positive interaction and thus were not included in the models (Fig. 1).

Regarding the effect of individuals' attributes on their propensity to initiate interventions, we found a significant effect of age class, sex and daily affiliation ratio, both in interaction with the mode of intervention (Fig. 2a, Table S3). Irrespective of the nature of the interaction, juvenile ravens (1 year old) tended to intervene less

often than older ravens, particularly subadults, that is, 2 and 3 years old (Fig. 3b). Female ravens seemed to rely on all modes of intervention but only slightly more often on targeted aggression and neutral approaches. However, males mainly relied on aggressive interventions, that is, either targeted or dual-targeted aggression, and less often on targeted affiliations compared to females (Fig. 3c). Furthermore, ravens with a higher affiliative status intervened more often than those with a low affiliative status when intervening actively, that is, with affiliation or aggression compared to mere approaches (Fig. 4a). We also found a significant positive effect of the ravens' vagrant–resident index, which is likely explained by the proportion of time in the study accounted for by this predictor.

Frequency of Received Interventions as Targets

Regarding the effect of individuals' attributes on their propensity to receive interventions, we found a significant effect of the sum of ad libitum interactions, individual daily affiliation ratio in interaction with the mode of intervention, and age class in interaction with the nature of the initial interaction (Fig. 2b, Table S4). Ravens with higher rates of interactions (positive and negative) were more likely to experience interventions, although the size of the effect was rather low (Fig. 2b). Ravens with a higher affiliative status were more often targeted than ravens with a low affiliative status, when receiving targeted interventions, that is, targeted aggression or affiliation (Fig. 4b). Juvenile and second-year subadult ravens were rarely targeted by interventions when engaged in positive rather than negative interactions, whereas third-year subadult and adult ravens were equally targeted by interventions in both types of interactions (Fig. 4c). We again found a significant positive effect of the vagrant–resident index, which was likely explained by the proportion of time in the study per bird accounted for by this predictor.

Descriptively, in positive interactions, targeted interventions did not seem to favour one particular partner over the two initial partners, that is, the partner receiving or initiating the affiliation; in negative interactions; however, targeted interventions tended to favour the aggressor rather than the victim (e.g. through the aggression of the victim or affiliation of the aggressor; Fig. 1).

DISCUSSION

Here we have provided a detailed analysis of third-party interventions in wild ravens. We showed that interventions occur as often in negative as in positive interactions (9.5% versus 9.8% of interactions recorded ad libitum) and either type of intervention was mostly active and typically featured aggressive behaviour. Nevertheless, the mode of intervention varied with the nature of the interaction. In negative interactions, interventions were mostly partial (mostly targeted aggressions but also affiliations), whereas in positive interactions, the intervention mode was more diverse, although mainly aggressive towards either one or both partners (targeted aggression and dual-targeted aggressions), followed by neutral approaches. Targeted affiliation occurred in negative interactions, but very rarely in positive interactions, and in both negative and positive interactions there was hardly any report of dual-targeted affiliation. Descriptively, targeted interventions in positive interactions did not seem to be in favour of a specific partner (receiving or giving the affiliation), whereas in negative interactions, interventions tended to be in favour of the aggressor (59%) rather than the victim (26%). Regarding individuals' attributes, older ravens and, in particular, subadults (2 and 3 years of age) intervened more often than juveniles (1 year old) in negative and positive interactions, and young ravens (juvenile and 2 year



Figure 1. Percentage of interventions according to the nature of the initial interaction intervened (In What: positive versus negative), mode of intervention (How: targeted affiliation, targeted aggression, neutral approach, dual-targeted affiliation, dual-targeted aggression) and identity of the target (i.e. initiator, receiver, both partners). The percentages were computed over 417 intervention events. NA stands for nonapplicable as it refers to table combinations that cannot exist, and p refers to partner.

olds) were more often targeted by interventions when engaged in negative than in positive interactions, whereas older ravens were equally targeted by interventions in both types of interactions. All ravens mostly intervened with targeted aggression, but females relied more on all types of interventions (and notably also intervened with targeted affiliation) than males which almost only intervened with aggression (targeted and dual-targeted). Ravens

with a high affiliative status initiated more active interventions than those with a low affiliative status (with either aggression or affiliation), but they also tended to receive interventions more often when they were specifically targeted (with either aggression or affiliation). We found no effect of dominance rank on the likelihood of initiating or receiving interventions. Finally, the ravens' interaction count (recorded ad libitum) only had a slight positive effect

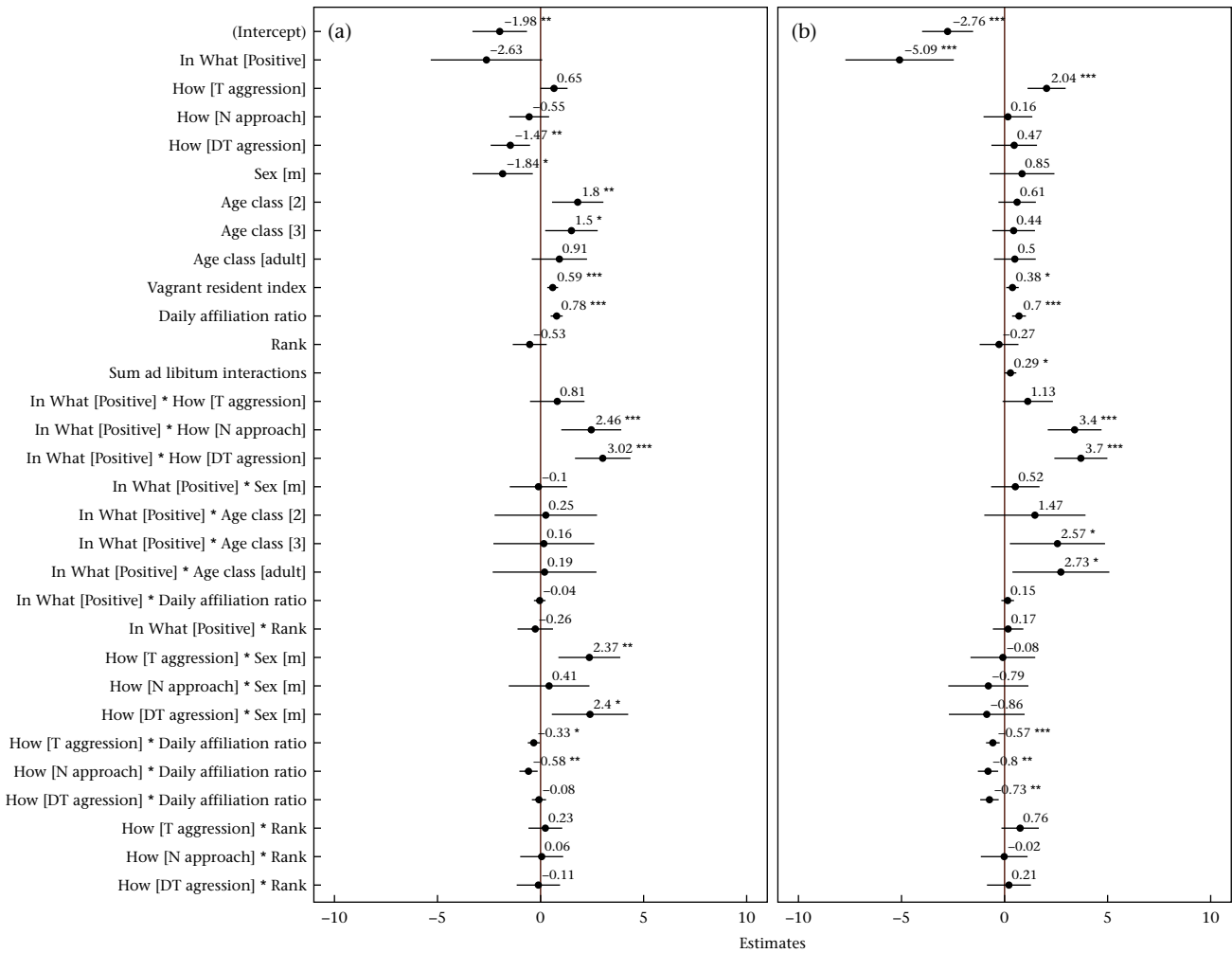


Figure 2. Forest plots for the generalized linear mixed models investigating (a) individual frequencies of initiated interventions, as the intervener; and (b) individual frequencies of received interventions as target. Reference levels for the categorical predictors are, respectively: 'In What' (Negative), 'How' (Targeted affiliation), 'Sex' (f) and 'Age class' (1). See the full model outputs in [Tables S3 and S4](#). * $P \leq 0.05$; ** $P < 0.01$; *** $P < 0.001$.

on their propensity to receive an intervention, aside from the other significant predictors discussed above, including the nature of the interaction and individual attributes, suggesting that interventions do not simply target individuals because they are more active than others. Taken together, these findings fit the picture derived from captive studies ([Fraser & Bugnyar, 2012](#); [Loretto et al., 2012](#)) and support the assumption that ravens selectively and strategically use third-party interventions.

Interventions and Interaction Type

Across species, interventions in conflicts are (much) more often reported than those in affiliations (cf. [Bissonnette et al., 2015](#); [Massen & Mielke, 2021](#); [Smith et al., 2010](#)). This bias might reflect differences in the relevance of the type of intervention but could also be constrained by the conspicuous nature of conflicts: unlike affiliations, conflicts tend to be noisy, attracting the attention of not only conspecifics but also human observers. Furthermore, conflicts are often associated with appeasement calls by the victim that may serve a recruitment function (e.g. ravens: [Szipl et al., 2018](#); chimpanzees: [Slocombe & Zuberbühler, 2007](#)). However, in this study, interventions in negative interactions were roughly as frequent as those in positive interactions (about 10%, relative to the total number of observed interactions ad libitum). This indicates that

observation biases with regard to the nature of the data may have been well mitigated in our protocol and that interventions in either type of interactions happened often enough (in absolute and relative terms) that they might be of relevance to the social status and/or dominance structure of wild ravens (see [Massen, Szipl, et al., 2014](#)).

Irrespective of the interaction type, positive or negative, most interventions were of an agonistic nature, that is, the intervener attacked, threatened or displaced one or both of the interacting individuals. These patterns fit well the literature on third-party interventions in nonhuman animals (e.g. [Emery et al., 2007](#); [Fraser & Bugnyar, 2012](#); [Maffezzini et al., 2023](#); [Scheiber et al., 2005](#); [Scott, 1980](#); [Smith et al., 2010](#); [Wechsler, 1988](#)), including a few studies on interventions in affiliations ([de Waal, 1982](#); [Massen, Szipl, et al., 2014](#); [Mielke et al., 2017, 2021](#); [Mondragón-Ceballos, 2001](#); [Schino & Lasio, 2018](#); [Schneider & Krueger, 2012](#); [VanDierendonck et al., 2009](#)) that are interpreted as separating competitors and stopping them from affiliating. Interestingly, interventions in negative interactions could also feature affiliative interactions towards one individual but never towards both interacting partners, thus supporting either the aggressor (majority of cases) or the victim. In contrast, we hardly ever observed any affiliation following interventions in others' positive interactions; however, the interveners could just approach and watch others

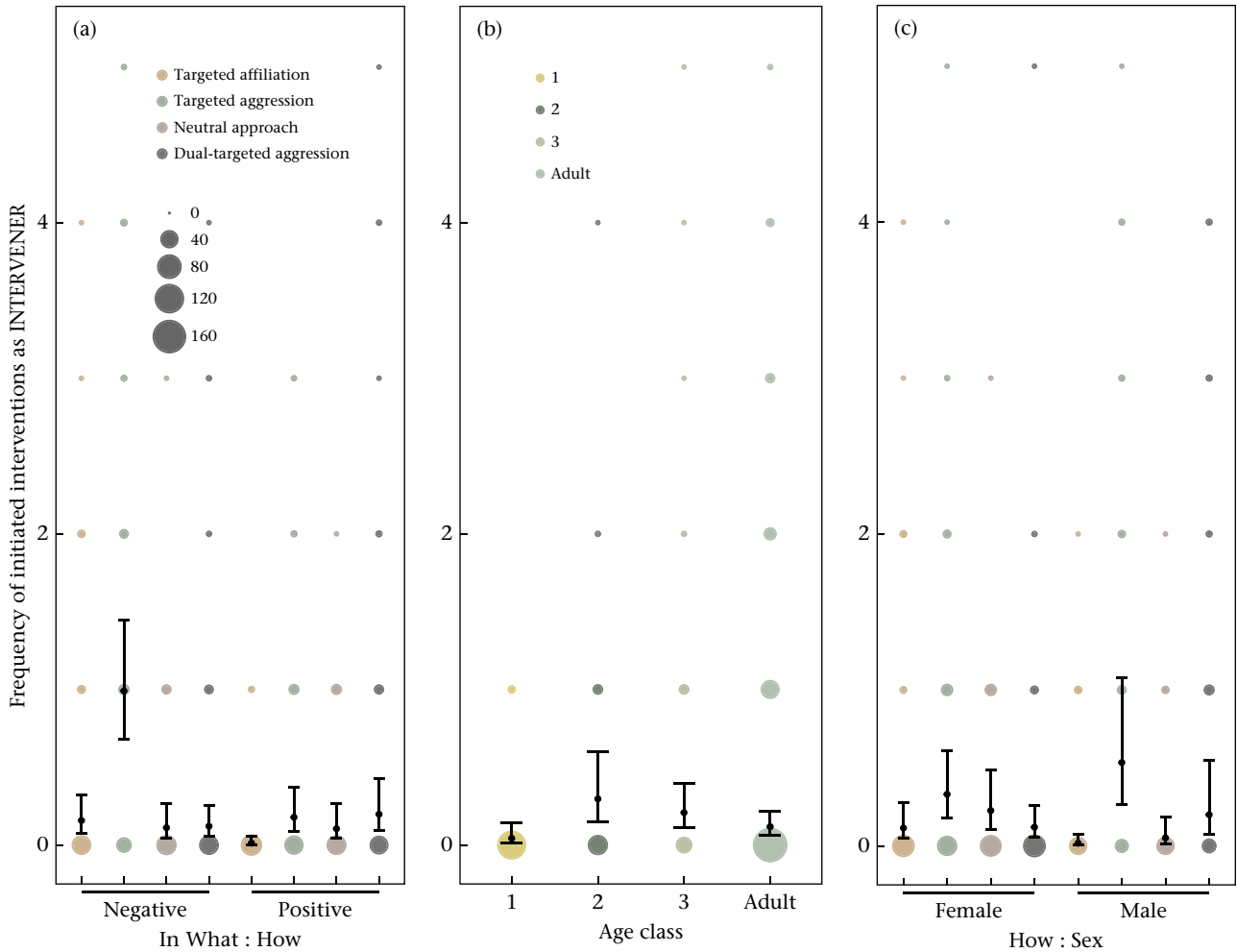


Figure 3. Modelled effects of (a) nature of the initial interaction ('In What': Negative, Positive) in interaction with the mode of intervention ('How': Targeted affiliation, Targeted aggression, Neutral approach and Dual-targeted aggression), (b) individual age class and (c) sex in interaction with the mode of intervention ('How': Targeted affiliation, Targeted aggression, Neutral approach and Dual-targeted aggression) on individual frequencies of initiated interventions, as intervener (model 1; Fig. 2a). Effect plots were generated using the R packages *ggeffects* ('*predict_response*' function) and *ggplot2*. The raw data are shown together with error bars representing the 95% confidence intervals around the estimated marginal means (black dots). The size of the dot area is proportional to the number of observations and thus indicates the sample size of each data point. To focus on the main patterns in the data, the Y axis was zoomed in using the *coord_cartesian* function in *ggplot2*. Consequently, a few extreme data points with a frequency of received interventions greater than five are not visible in this plot, but the overall trends and patterns remain unaffected. The omitted points include those with coordinates such as (In What, How, Sex, Age class; y): (Negative, Targeted aggression, male, Adult; 6), (Positive, Dual-targeted aggression, Male, Adult; 7), (Negative, Targeted aggression, Male, 3; 7), (Negative, Targeted aggression, Male, Adult; 8), (Positive, Dual-targeted aggression, Male, Adult; 8), (Negative, Targeted affiliation, Female, Adult; 9), (Negative, Targeted aggression, Male, Adult; 9), (Negative, Targeted aggression, Male, Adult; 9).

affiliating from close by, without initiating a separation attempt. These subtle interventions may allow (young) ravens to gather information about others' relationships (Massen, Szpl, et al., 2014) or they may simply refrain from aggression because of their low status and dominance rank. The few cases in which we did witness affiliation as a method of intervening in positive interactions were, like affiliation as a measure to intervene in negative interactions, never directed at both interacting individuals and always specific to either of the interaction partners. This suggests a clear partner choice that is potentially based on a thorough understanding of the social relationships within the population (Boucherie et al., 2019; 2022; Massen, Pašukonis, et al., 2014, Massen, Szpl, et al., 2014).

Factors Affecting Interventions

As expected, we found that individual characteristics like age, sex, affiliative status and residency/vagrancy affected the likelihood of becoming involved in interventions, both as targets and interveners. Focusing on the age effect on becoming the target of

interventions, it is interesting that young ravens in their first and second year received mainly interventions in negative interactions, whereas older ravens received interventions in negative and positive interactions. Possibly, this pattern just reflects the relative frequency of agonistic and affiliative interactions across life stages, with younger birds engaging mainly in conflicts and, in most cases, were not yet established in a (territorial) pair bond via affiliative interactions. However, ravens already engage in affiliative interactions in their first year (Loretto et al., 2012), and they show fairly similar rates of affiliation and comparable numbers of affiliation partners in their second year as do adult birds (Bugnyar, n.d). Hence, it is unlikely that young ravens will provide insufficient opportunities for being targeted; more likely, they will not be of particular interest to interveners at this stage. Indeed, ravens' interventions in affiliative interactions have been interpreted as preventing others from forming bonds and alliances in conflicts, respectively (Massen, Szpl, et al., 2014), and this might become particularly relevant when birds reach sexual maturity. Focusing on the intervener side, we also observed an effect of age, irrespective of

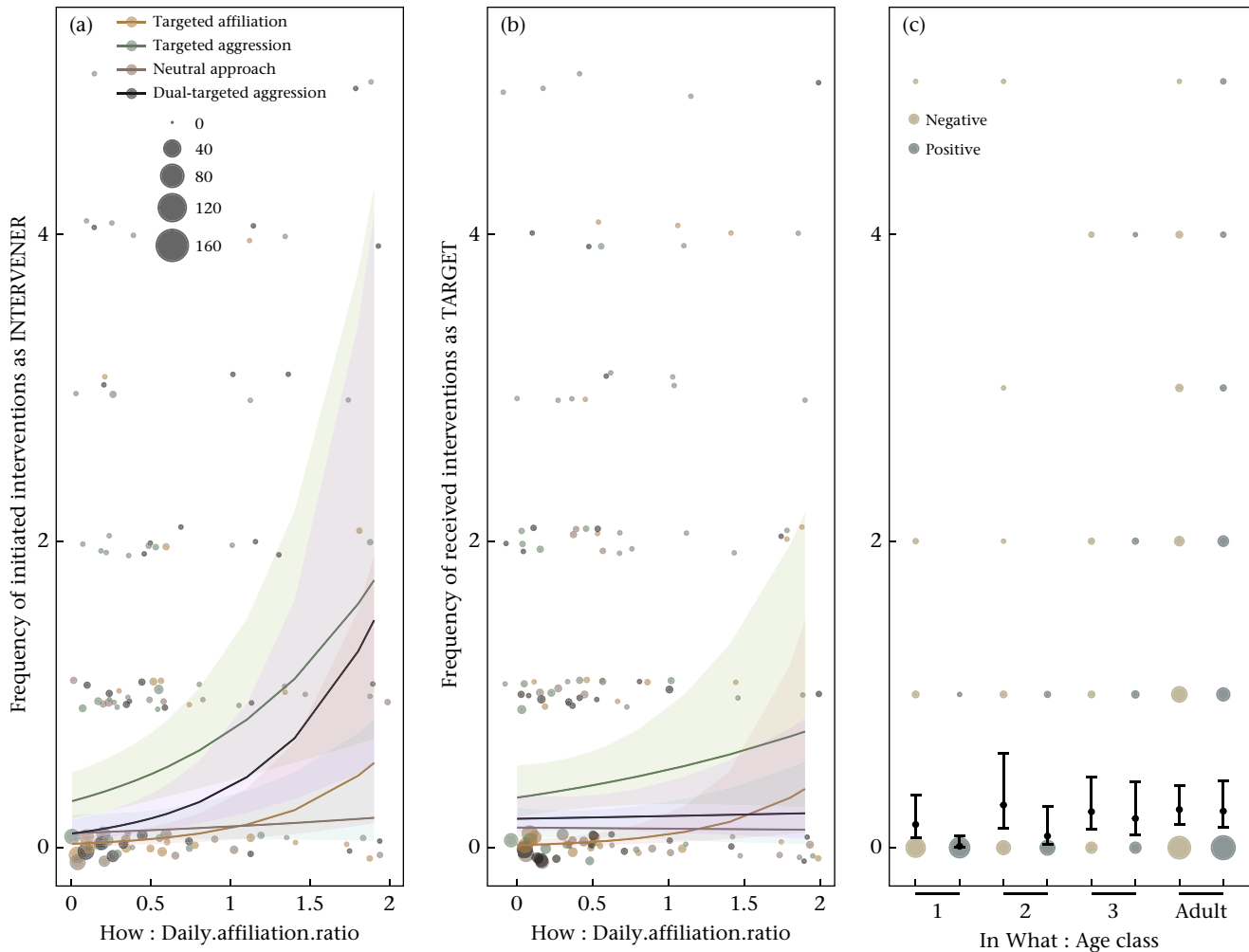


Figure 4. Modelled effects of (a) daily affiliation ratio in interaction with the mode of intervention ('How': Targeted affiliation, Targeted aggression, Neutral approach and Dual-targeted aggression) on individual frequencies of initiated interventions, as intervener (model 1; Fig. 2a), together with the modelled effects of (b) daily affiliation ratio in interaction with the mode of intervention, and (c) individual age class in interaction with the nature of the initial interaction ('In What': Negative and Positive), on individual frequencies of received interventions, as target (model 2; Fig. 2b). Effect plots were generated using the R packages `ggeffects` ('`predict_response`' function) and `ggplot2`. The raw data are shown together with the shaded area (a, b) and error bars (c) representing the 95% confidence intervals around the marginal effect regression lines and the estimated marginal means (black dots). The size of the dot area is proportional to the number of observations and thus indicates the sample size of each data point. A slight jitter (horizontal in Fig. 4a; vertical in Fig. 4b and c) was applied to all plots in `ggplot2` to better visualize data points. To focus on the main patterns within the data, the Y axis was zoomed in using the `coord_cartesian` function in `ggplot2`. Consequently, a few extreme data points with a frequency of received interventions greater than five are not visible in this plot, but the overall trends and patterns remain unaffected. Omitted points include those with coordinates such as (In What, How, Daily affiliation ratio, Age class; y): (Positive, Dual-targeted aggression, 0.5, Adult; 6), (Positive, Dual-targeted aggression, 0.5, Adult; 6), (Negative, Targeted aggression, 0.7, Adult; 6), (Negative, Targeted aggression, 0.3, 1; 9), (Negative, Targeted affiliation, 1.9, Adult; 10).

whether birds intervened in positive or negative interactions. Here, the age effect is mostly linked to the fact that ravens in their first year almost never intervened in interactions, in contrast to older birds, which likely reflect improved fighting ability and higher positions in the hierarchy (see Smith et al., 2010); however, the clear-cut difference between birds in their first and second year is surprising and requires further investigation.

Given that male ravens are generally more active in conflicts than females and that males are generally dominant over females (Boucherie et al., 2022), it is interesting that both sexes intervened in others' interactions in equivalent shares. However, it seems that females used an alternative strategy and notably also intervened with targeted affiliation, whereas males generally intervened only with aggression. This suggests that although males may dominate the hierarchy and have a higher resource-holding potential, females can and do actively manoeuvre in the network of relationships.

Ravens with high affiliative status initiated more active interventions (with aggression or affiliation) but also tended to

receive 'targeted' interventions more often than ravens with low affiliative status, the latter in contrast to our predictions. However, this suggests again that ravens may not intervene randomly but rather target specific individuals, such as individuals with higher affiliative status. This may also be due to differences in opportunity; with increasing affiliation, an individual is involved in more social interactions in general and thus may become the target of an intervention more easily than an individual with less affiliation. Similarly, these individuals may witness more social interactions in which they can intervene. This potentially suggests that the number and/or quality of ravens' relationship(s) in the group increases their social competence and enables them to interfere more in others' relationships. Post hoc analyses of the potential correlation between an individual bird's tendency to intervene in others' interactions and their tendency to receive intervention also revealed a slight positive interaction (Kendal's tau = 0.37, $z = 8.92$, $P < 0.001$). However, if we consider only those individuals that were involved in at least one or three interventions (as intervener or

target), this relationship becomes increasingly negative ($\tau = -0.15$ and -0.39 , $P < 0.05$ and <0.001 , respectively; see Supplementary material: correlations between interventions made and being the target of interventions for details), suggesting that individuals that are more likely to intervene are slightly less likely to be targeted, which would again be according to our predictions.

However, we did not find an effect of rank on the propensity of ravens to intervene in social interactions between others. This was in contrast to our predictions and to earlier findings in primates as follows: (1) when considering interventions in negative interactions, high-ranked individuals (see Bissonnette et al., 2015; von Rohr et al., 2012) tend to be more successful in intervening conflicts than low-ranked individuals and (2) when considering interventions in positive interactions, for example, in rhesus macaques (Mielke et al., 2021), higher-ranking individuals were more likely to intervene in the positive interactions of others successfully. Possibly, our data set did not include sufficient variation for rank to properly assess its effect. Indeed, because rank uniquely identified individuals in this study, it essentially acted as a proxy for individuals, which may make it difficult for the model to estimate the rank effect independently from other individual level predictors. We also speculate that this may be explained by potential differences in the identity of the interaction partners involved in these interactions, their affiliation status and their relative rank position with regard to the intervener. Therefore, future studies should also include the identity of the original interacting partners and their affiliation status, if possible.

Concerning the effect of residency/vagrancy status, resident individuals were more often engaged in third-party interactions than vagrants, both as targets and as interveners, with the former in contrast to our predictions. This pattern implies that social interactions and subsequent interventions are more important for local birds that meet regularly than for vagrant birds that just pass by from time to time. However, the pattern could also simply be a side-effect of our protocol, as the chance of documenting third-party interventions increases with observation time, and vagrant birds per definition spend less time at our study site than residents. Experimental studies are needed to disentangle the effects of time from the effects of vagrancy.

Who is Targeted: One or Both Interaction Partners?

Irrespective of the nature of the initial interaction, most interventions were active (with affiliation or aggression). Considering active interventions, although in most cases of intervened positive interactions, the intervention was aggressive and both initial partners were targeted, the majority of interventions in conflicts (negative interactions) were partial, that is, the intervener was aggressive or affiliative towards either the victim or the initial aggressor. These patterns are in line with the assumption that interventions in positive interactions primarily serve to interrupt an ongoing interaction (Massen & Mielke, 2021), whereas interventions in conflicts constitute coalitions and alliances (Bissonnette et al., 2015; Harcourt & de Waal, 1992). The majority of the partial interventions in negative interactions fit the predictions that raven interventions feature opportunistic all-down aggressor support (59%), either by affiliating with the aggressor or by attacking the victim (Noë, 1994; van Schaik et al., 2004; Pandit & van Schaik, 2003). Still, in 26% of the cases, interveners affiliated with the victim or attacked the aggressor, and hence per definition, supported the victim. Such a constellation could be expected when one partner of a strong social bond is attacked by another individual and thus would be in need of support (Bissonnette et al., 2015). Previous studies on captive and wild ravens have found high-quality relationships between victims and interveners when the

latter provided victim support (Braun & Bugnyar, 2012; Fraser & Bugnyar, 2010, 2012; Szípl et al., 2018). Joint self-aggrandizing displays from interveners with victims, which we observed in this study, further support the idea that bonded ravens act as alliance partners in conflicts. The consequence of such interventions might be that the supported bird's rank becomes dependent on the help of its partner, resulting in bonded ravens being close in rank (see Lorenz, 1931). Dependent ranks due to social support are typical for kin-bonded societies (e.g. matriline in old-world primates, social carnivores, cetaceans; Cheney & Seyfarth, 1990; 2007; Holekamp et al., 2007; Whitehead, 2008), as well as for long-term monogamous species (e.g. greylag geese: Scheiber et al., 2005). Hence, the expectation of support for alliance formation in bonded ravens fits well with the overall scenario. An alternative but hardly tested, interpretation of 'victim support' is that the intervener might try to prevent the aggressor from gaining any benefits from winning conflicts, for example, by reversing a possible winner effect to a loser effect (Hsu & Wolf, 2001). Such a scenario has been discussed for Japanese macaques, *Macaca fuscata* (Prud'homme & Chapais, 1996; Schino et al., 2007), notably when interveners and original aggressors are close in rank or might become close in rank in the future when regarding juvenile interveners (Schino et al., 2007). In such a scenario, interveners would not selectively help particular individuals (as predicted by alliance formation) but distribute their support among various victims. Hence, support would have little effect on victims' ranks but might stabilize the rank relationship between intervener and aggressor. Thus, future studies should address the likelihood of victim support depending on the identity of the intervener-supported partner dyad. Finally, we observed only a few instances in which no party was supported in conflict (8% of police and 7% of neutral interventions). These results support the hypothesis that raven groups are very flexible and thus do not benefit from increased stability due to policing (cf. Flack et al., 2006; von Rohr et al., 2012).

From a cognitive point of view, coalitionary support of aggressors can be explained by relatively simple rules of thumb (Bissonnette et al., 2014; Gigerenzer et al., 1999; Hemelrijk & Puga-Gonzalez, 2012). However, supporting victims of aggression requires some understanding of relationships: 'who is your partner' in case of alliances (Tomasello & Call, 1997; but see Massen et al., 2019 for a 'lower level' explanation) and 'who is close to you in rank' when targeting aggressors to prevent them from winning conflicts (Prud'homme & Chapais, 1996; Schino et al., 2007). Victim support also raises the possibility that interveners can make strategic decisions in helping others in conflicts, which would fit into their capacities for making decisions based on their own and others' relationships (Massen, Szípl, et al., 2014; Szípl et al., 2018).

Conclusion

Third-party interventions in agonistic and affiliative interactions can be observed relatively frequently not only in captive but also in wild ravens. The behaviours shown and most effects of age, sex and bonding status fit nicely with the patterns described for other mammalian and avian species with complex social structures. Moreover, some of our results, like the different age effects in becoming targets of interventions in affiliations and conflicts, may indicate a strategic use of interventions. To truly show whether these interventions are strategic would require analyses that not only consider the demographic features of the intervener and the target of the intervention but also the demographic features of the third individual involved and how these demographics line up relative to each other. Unfortunately, the resolution of our data from the wild, in which many of the actors in these triadic interactions are often unknown, rendered such analyses impossible.

Therefore, further studies are required to experimentally test predictions of the social intelligence hypothesis, for example, the proposed functions of interventions being one of the following: (1) opportunistic coalition formation to gain in rank and/or prevent others from winning conflicts, (2) alliance formation in bonded individuals to prevent the partner from losing a fight and/or maintain one's status and (3) interventions in others' affiliations to prevent them from forming close bonds and thus alliances, as was suggested in an earlier study of our laboratory (Massen, Pašukonis, et al., 2014). Therefore, we hope that our study motivates others to investigate the third-party interactions of their study species in more detail, focusing on affiliative and agonistic interactions as well as affiliative and aggressive modes of intervention, which, through comparison, would allow a more detailed investigation of the social selection pressures that may have caused the evolution of intelligence in species with a complex social life.

Author Contributions

Jorg J.M. Massen: Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Palmyre Boucherie:** Conceptualization, Data curation, Formal analysis, Methodology, Project administration, Visualization, Writing – review & editing. **Thomas Bugnyar:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Data Availability

All data and code are available as Supplementary material.

Declaration of Interest

The authors declare they have no conflicts of interest.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2024.10.018>.

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