MASTERARBEIT | MASTER'S THESIS

Titel | Title

Social network development in carrion and hooded crows.

verfasst von | submitted by

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

Master of Science (MSc)

Wien | Vienna, 2025

Studienkennzahl lt. Studienblatt | Degree programme code as it appears on the student record sheet:	UA 066 878
Studienrichtung lt. Studienblatt | Degree programme as it appears on the student record sheet:	Masterstudium Verhaltens-, Neuro- und Kognitionsbiologie
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Abstract

Living in social groups offers advantages such as predator protection and enhanced foraging opportunities. However, navigating social relationships can be cognitively demanding, particularly in unstable social environments characterized by fission-fusion dynamics (i.e., changes in group size and composition over time). In social species, individuals often have preferred social partners, such as kin, and form various kinds of relationships, but little is known about how social relationships develop.

To investigate how sex, kinship and temporal factors influence the social ontogeny of highly social carrion and hooded crows, I observed the social behaviors of a group of six juvenile crows for 12 weeks post-fledging.

Mixed-sex dyads maintained closer spatial proximity and showed a trend toward stronger active affiliative relationships (e.g., co-feeding, co-manipulation) than female-female dyads. However, inactive affiliative relationships (e.g., allopreening) were not influenced by sex. Genetic relatedness did not significantly influence spatial association patterns or affiliative relationship strength. Over time, spatial associations became more polarized, potentially suggesting an initial phase of broad social interactions followed by selective bonding. These findings shed light on the social development of carrion and hooded crows and contribute to our understanding of avian social evolution.

1 Introduction

Living in social groups offers numerous advantages, such as increased protection from predators and enhanced foraging opportunities (Rubenstein, 1978). However, successfully navigating social relationships can be cognitively demanding, as individuals must track social partners, their interactions, and the dynamics of the group. Therefore, the social intelligence hypothesis proposes that the evolution of complex social systems and advanced cognition go hand in hand (Humphrey, 1976; Dunbar & Shultz, 2007). Studying animal social systems is therefore particularly valuable for understanding the evolution of social cognition and behavior.

1.1 Bird social systems

Birds, and especially large-brained and long-lived species, such as parrots or corvids, are excellent models for studying both social complexity and cognition (Boucherie *et al*., 2019; Bugnyar, 2024). Longer lifespans, and thus slower life histories, often go hand in hand with larger brains (Jiménez-Ortega *et al.*, 2020), which provides both the temporal and cognitive prerequisites for forming complex and stable social relationships (Emery *et al.,* 2007). In line with this, many bird species live in complex social environments characterized by fission-fusion dynamics, where group composition and size changes frequently, often multiple times a day (Silk *et al*., 2014). Despite these unstable social environments, social relationships in birds are not random. Individuals form stable long-term relationships, but also flexibly adjust partnerships, for example based on returns from social foraging interactions (rooks, *Corvus frugilegus*: Boucherie *et al*., 2017; parrots, *Cacatua galerita*: Aplin *et al*., 2021; zebra finches, *Taeniopygia guttata*: Brandl *et al*., 2021; jackdaws, *Corvus monedula*: Kings *et al*., 2023). Additionally, individuals of social species often form various types of relationships, including mating pairs, family, foraging partnerships and dominance relationships (Krause & Ruxton, 2002). While the pair bond is the primary social unit in many monogamous species, many birds also form strong social ties beyond mating pairs (Boucherie

et al., 2016). This raises two fundamental questions in the study of avian social systems: (1) Who forms social ties with whom, and why? And (2) How do these ties develop and change over time?

1.1.1 Who forms social bonds with whom, and why?

One major factor influencing social bond formation is kinship. Research in juvenile ravens (*Corvus corax*) found that they form stronger affiliative relationships with siblings (Loretto *et al*., 2015; Boucherie *et al*., 2020), and sulphur-crested cockatoos (*Cacatua galerita*) actively prefer associating with kin even when controlling for passive spatial overlap (Penndorf *et al*., 2023). Another important factor is sex, with evidence from ravens indicating that male-male and mixed-sex dyads tend to form stronger affiliative bonds than female-female dyads (Boucherie *et al*., 2020). Additional influences on social relationships include personality and individual condition. For instance, proactive great tits (*Parus major*) form more, but weaker, associations than reactive individuals (Aplin *et al*., 2013), and the number of coalition partners in female eider ducks (*Somateria mollissima*) is influenced by body condition, breeding experience and personality (Öst *et al*., 2015).

1.1.2 How do social bonds develop and change over time?

In addition to social and individual factors, early-life social environments also shape social behavior later in life. For example, juvenile ravens from smaller families show increased attentiveness to social calls, highlighting how developmental conditions influence later social behavior (Gallego-Abenza *et al*., 2022). Additionally, previous research in juvenile ravens suggests that social relationships become more stable over time: Loretto *et al*. (2015) found an increase in affiliative interactions and a decrease in aggression at around 4-5 months post-fledging. Furthermore, third-party interventions became increasingly directed toward close social partners. This time period corresponds with the establishment of linear

dominance hierarchies and the stage when wild ravens typically integrate into nonbreeding flocks (Niethammer *et al*., 1993).

1.1.3 Carrion and hodded crow social systems

Existing research on corvid social relationships and their development has predominantly focused on common ravens and rooks (e.g.: Loretto *et al*., 2015; Kulahci *et al*., 2016; Boucherie *et al*., 2017, 2020), while little is known about other corvid species. By extending the research focus to include other species we can uncover both general principles and species-specific adaptions in social behavior and thereby deepen our understanding of avian sociality, its evolution (Downing *et al*., 2020) as well as its connection to cognition (social intelligence hypothesis; Humphrey, 1976; Dunbar & Shultz, 2007; Bugnyar, 2024).

Carrion and hooded crows are suitable study species for this endeavor for various reasons. Although, overall, the social organization of carrion and hooded crows seems comparable to that of ravens (Uhl *et al*., 2019), in contrast to ravens, crows inhabit more urban environments (Goodwin & Gillmor, 1986), and show slightly faster development than ravens (Snow *et al*., 1998). Additinally, previous research found differences in exploratory behavior during development: While both crows' and ravens' neophobia in resonse to novel objects and people increased with age, crows consistently interacted less with novel people (Miller *et al*., 2015, 2016).

Carrion crows and hooded crows are currently considered two distinct species (Glandt, 2016). They are, however, part of the same palearctic superspecies (Bauer & Baumann, 2012), with two stable hybrid zones, one of which runs through central Europe (De Knijff, 2014). Hence, for the purpose of this thesis, I will refer to them as "crows".

Crows inhabit diverse habitats across Eurasia (Snow *et al*., 1998). European populations form socially monogamous pairs, and during the breeding season social organization varies depending on environmental factors, such as nest site availability and population density: Some crow populations form loose colonies and share their home range

with neighbors whereas others have well defended breeding territories (Baglione *et al*., 2005). Young crows join nonbreeding flocks about 4-5 weeks after fledging and remain in these groups until establishing their own territories, often several years later. After the breeding season, most adult crows also join flocks characterized by fission-fusion dynamics before returning to their home territories in late autumn and winter (Baglione & Canestrari, 2016).

1.2 The present study

However, little is known about the early social development in crows. Therefore, by investigating spatial association patterns and social interactions early in development, the present study aims to address the following research question: How do the sex composition of dyads, genetic relatedness and temporal dynamics influence spatial association patterns and affiliative relationships between juvenile crows? In line with research on ravens (Boucherie *et al.,* 2020), I expect to find closer spatial associations and stronger affiliative relationships between 1) male-male and mixed sex dyads compared to female-female dyads and between 2) genetic siblings compared to unrelated individuals. Additionally, I expect 3) affiliative relationships to become stronger in later observation periods, which has also been found in ravens (Loretto *et al*., 2015).

2 Methods

2.1 Study site and subjects

The study sample consists of six hooded and carrion (*Corvus cornix* and *Corvus corone*) crow chicks. All crows were acquired from three wild nests in Lower Austria (see Figure 1 and Table S1 for details on individuals). Five individuals (three females and two males) were collected at an estimated age of 10-14 days on May 1st 2024 and a sixth individual (male) close to fledling age on May 16th 2024. The first five nestlings were then hand-reared at Haidlhof Research Station near Bad Vöslau until fledging at 25 to 29 days of age. They were individually marked for identification (initially by coloring their nails, later by coloured leg rings). During the hand-rearing period, the nestlings were housed in two artificial nests indoors and in the same room. The nest properties were manipulated for a different experiment. One nest's inside was lined with paper and contained two genetic siblings. Another nest contained natural materials, such as sticks, straw and feathers, and consisted of two related siblings as well as one unrelated social sibling from the other wild nest (Table S1). In the same room, three other crows that are not part of this study were hand-reared in one additional nest. The crows were hand-fed every two hours from 6 am to 10 pm with a varied diet containing a mixture of ground fruit muesli, day-old chicks, mealworms, fruit, vegetables, feed lime, Korvimin, and fennel tea. They were weighed daily and if the weight gain rate was not as expected, we additionally provided Zophobas larvae.

After fledging, they were ringed and moved to an outside aviary at Haidlhof Research Station as a group, together with the sixth individual. Food and water were provided *ad libitum*. Their daily diet consisted of fruit muesli, seeds, fresh fruits or vegetables, and meat, with adjustments throughout the week including day-old chicks, eggs, and supplements such as Korvimin, feed lime, garlic powder, and herb blends.

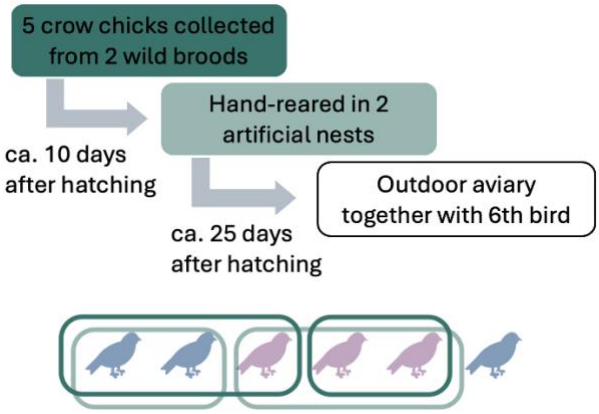

Figure 1: Rearing history, relatedness and sex of the individuals.

Chicks originating from the same wild nests are genetically related ("genetic siblings"), indicated by the dark green box and circles. Nest composition during hand-rearing, that is "social sibling" status, is indicated by the light green box and circles. Blue bird icons, male; pink bird icons, female.

2.2 Data collection

Data for this study was collected between May 20th and August 9th, divided into three four-week periods (P1, P2 and P3). One of the birds died during period 3, on July 24th. Data collection sessions were performed three times a week (on Mondays, Wednesdays and Fridays) and twice a day (am and pm). Am recordings were conducted between 9 am and 12 pm, pm recordings between 12 pm and 3:30 pm. During each data collection session, all group members were systematically observed, in a random order, using 5-min individual focal sampling (Altmann, 1974). Additionally, at the beginning and at the end of each session, all individuals were observed simultaneously in 5-min *ad libitum* samplings. Furthermore, at the beginning of each sampling, scan samplings were performed in which we estimated the distance between the focal bird and all other birds. Videos were recorded with a video camera from outside of the aviaries. For the purpose of this thesis, half of the focal samplings were used for analyses, ensuring that the ratio of am and pm recordings alternated weekly and did not exceed 1:2. This resulted in a total of 208 focal protocols and 362 scan samplings.

2.3 Data coding

All videos were coded using Loopy (http://loopb.io, Loopbio GmbH, Vienna, Austria). The estimated distances from the scan samplings were coded as a categorical variable in meters with the following levels: 0-0.2, 0.2-0.5, 0.5-1, 2, 3, 4, 5, 6, 7, 8. Behaviors recorded during the focal protocols included affiliative behaviors, such as spatial proximities, co-actions, and allo-preening, as well as agonistic behaviors, such as stealing from or pecking another bird. See Table 1 for detailed information on the grouping and definition of all behaviors.

Table 1: Behavioral ethogram used for coding videos

A) Affiliative behaviors

Behavior	Definition
	Inactive behaviors
Contact sit	Two birds are within 0-10 cm of each other, in reaching distance (close enough to enter in body contact within one step), at perch.
Perch proximity	Two birds are within 10-100 cm of each other, at perch.
Allo-preening	One bird touches or runs its beak through the feathers of another bird.
Touch	One bird touches another one's body.
	Active behaviors
Ground proximity	Two birds are within 0-100 cm of each other, on the ground.
Co-feed	Two birds eat the same food piece, or distinct food pieces within reaching distance (i.e., 0-50 cm).
Co-manipulate	Two birds manipulate the same or different item(s) within reaching distance (0-100cm).
Watch	One bird is in proximity or contact with another one and observes it handling a piece of food or an object without any attempt to get it.

B) Agonistic behaviors

Behavior	Definition
Steal	An individual steals/tries to steal an item from another bird and the transfer is initiated by the individual stealing the item.
Supplant	One bird enters in contact with another bird – who retreats or moves away 1 meter or more within 1-2 sec – and takes its position. Typically, during a supplant, one bird takes the exact position of another, forcing it to move and change it initial position. With or without vocalization of the emitter/receiver, and with or without direct physical contact between the two birds.
Pull feathers	One bird pulls the feather of another bird with its beak.
Peck	One bird pecks another one with its beak. Pecking implies physical contact.

To ensure inter observer reliability, the coder (Sara Binder) was trained on a set of videos previously coded by a single coder who served as a reference. The coder had to reach at least 90% of concordance with the coding of reference before starting. Additionally, as inter observer reliability test, 14 videos, which equals 73% of the dataset were re-coded by Valentine Comin and intra class correlation (ICC) scores were calculated separately for duration (ICC =0.92) and frequency (ICC=0.96) using the R package IRR (version 0.84.1;

Gamer *et al*., 2005) in R (version: 4.3.1; R Core Team, 2023). The test terms were set to model=”twoway” and type= “agreement”, according to Koo and Li (2016).

The final dataset consisted of a total of 977 spatial associations from scan samplings, 677 active affiliative interactions, 797 inactive affiliative interactions and 94 agonistic interactions. The behavioral frequencies by dyad sex composition and relatedness can be found in Figure 2.

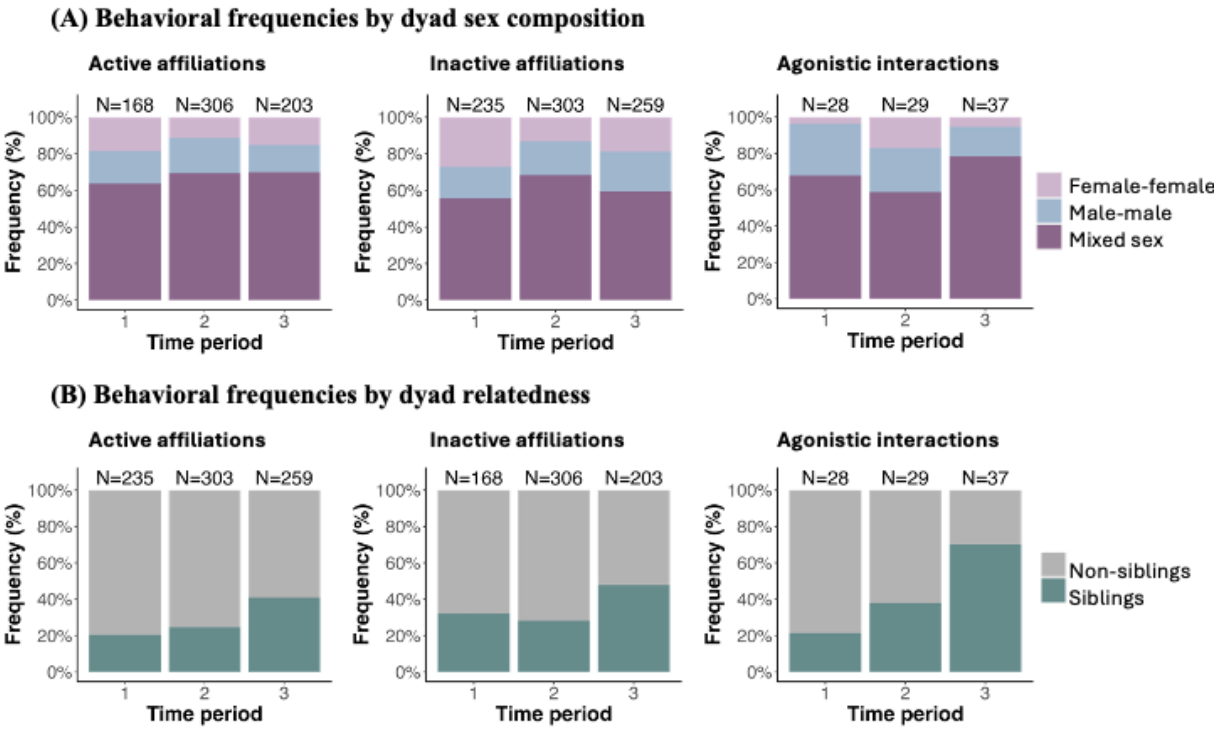

Figure 2: Behavioral frequencies by dyad sex composition and relatedness

Percentages of behavioral frequencies (y-axis) and absolute frequencies (above each bar) for each time period (x-axis) and interaction category are shown for (A) dyad sex composition and (B) dyad relatedness.

2.4 Data analysis

2.4.1 Affiliative relationship strength

To evaluate the relative strength of affiliative relationships in each time period (P1 – P3), I used dyadic undirected sociality indices (see below for a detailed explanation) based on Silk *et al*. (2006) and applied to ravens by Boucherie *et al*. (2020). The affiliative behaviors

were grouped into active and inactive behaviors and two separate sociality indices were computed. The decision to pool behaviors was based on visual inspection of the data and inter-behavior correlations (see Figure S1), following guidelines on pooling behavioral data (van der Marel *et al*., 2021). I found that some affiliative behaviors correlated negatively with each other. For example, perch proximity and ground proximity showed a slight negative correlation, which suggests that pooling all affiliative behaviors into a single measure, as done by Boucherie *et al*. (2020), might not be appropriate for this dataset. Instead, the behaviors appeared to form two distinct clusters, which aligned roughly with a theoretical distinction between inactive affiliative behaviors (e.g., perch proximity, preening, touching) and active affiliative behaviors (e.g., ground proximity, co-feeding, co-manipulation). The distinction may reflect different types of partnerships, such as foraging partnerships (birds feeding and manipulating objects together) versus affiliative/resting partnerships (birds resting or preening together). Therefore, I categorized the behaviors into two separate measures:

The *active* sociality index included ground proximity (GP), co-feed (CF), co-manipulate (CM), and watch (WA) and was calculated as follows:

$$SI\_active_{ij,x} = \frac{\frac{GP_{ij,x}}{GP_x} + \frac{CF_{ij,x}}{CF_x} + \frac{CM_{ij,x}}{CM_x} + \frac{WA_{ij,x}}{WA_x}}{4}$$

with $GP_{ij,x}$ the dyadic frequency of ground proximity for the dyad *ij*, in the period *x*, divided by GP_x the mean frequency of ground proximity for all potential dyads in the group, in period *x* (and similarly for CF, CM and WA). The denominator is fixed and refers to the number of variables. The value of the sociality index increases with the strength of the relationship and a value of 1 means that the frequency of interactions between the dyad *ij* is equal to the group mean.

The inactive sociality index included contact sit (CS), perch proximity (PP), allo-preening (AP) and touch (TO) and was computed as follows:

$$SI\_inactive_{ij,x} = \frac{\frac{CS_{ij,x}}{CS_x} + \frac{PP_{ij,x}}{PP_x} + \frac{AP_{ij,x}}{AP_x} + \frac{TO_{ij,x}}{TO_x}}{4}$$

To account for the death of one bird during period 3, sociality indices for dyads including this bird were calculated by dividing dyadic behavior frequencies by the group mean up until the bird's death, rather than the total mean for the entire period.

2.4.2 Statistical analyses

2.4.2.1 Spatial associations

To investigate spatial association patterns between crows, I used a cumulative link model (CLM; model 1) using the ordinal package (version 12.4.1, Christensen, 2023) in R. The CLM was chosen as it allows for the analysis of ordinal distance categories without assuming equal spacing between them, making it more appropriate given the uneven intervals in the dataset. The initial model included the distance data collected from scan sampling observations as the outcome variable, as well as the following fixed effects: (i) sex composition (female-female vs. male-male vs. mixed sex dyads), (ii) social kinship (non-kin vs. kin), (iii) genetic kinship (non-kin vs. kin), (iv) time period (P1 vs. P2 vs. P3) and (v) the sum of agonistic interactions. To check for multicollinearity, variance inflation factors (VIFs) were calculated using the "vif()" function of the R package car (version 3.1-3; Fox & Weisberg, 2019). VIF values of 1 indicate no multicollinearity while values above 1 indicate correlations with other predictors. Due to high VIF values ($VIF_{social\ kinship} = 5.72$; $VIF_{sex} = 2.30$), social kinship was removed from the model. The proportional odds assumption was tested using the function "nominal_test()" of the R package ordinal (Christensen, 2023), which indicated a violation for time period. To address this, I fitted a partial proportional odds model, relaxing the proportional odds assumption for this predictor while maintaining it for the others. The initial model also included a random effect for dyad, which had to be removed in order to allow relaxing the proportional odds assumption for the time period predictor.

Before doing so, I calculated how much variance was explained by the random effect by applying the function "VarCorr()" of the R package lme4 (version 1.1-34; Bates *et al*., 2015) to the initial model and found the random effect to not contribute much to the model, indicating that relaxing the proportional odds assumption for the time period predictor was more important than the random effect for dyad. Thus, the final model formula included distance as response variable and the fixed effects sex and genetic sibling with an additional fixed effect predictor time period for which the proportional odds assumption was relaxed.

2.4.2.2 Affiliative relationship strength and agonistic interactions

To investigate relationship strength between crows, I constructed two generalized linear models (GLMs) with Gamma distribution and log link function, one with active sociality index (model 2), and one with inactive sociality index (model 3) as response variable. The same fixed effects were included as in the spatial association model (sex composition, time period and genetic kinship), with the addition of the frequency of agonistic interactions. The initial models also included dyad as a random effect to account for repeated measures, which led to singular fit issues, suggesting that the random intercept variance was close to zero and indicating overparameterization. Therefore, the models were simplified by removing the random effect for dyad, and the final models included active or inactive sociality index as response variables and sex, genetic sibling, time period and the sum of agonistic interactions as fixed effects.

For all models, full models were compared to null models lacking the test predictors. Comparson was performed using likelihood ratio tests (LRTs) with the anova() function of the car package (Fox & Weisberg, 2019) in R. I also tested the significanve of entire individual predictors by running a drop1 analysis (removing one predictor at a time and comparing it to the full model). Significant categorical fixed effects with more than two levels were then explored with post-hoc tests (emmeans package in R; Lenth, 2024), using a Tukey multiple testing correction. All code used for analysis is provided in the supplement.

3 Results

3.1 Who forms ties with whom, and why: Sex composition and genetic relatedness

3.1.1 Spatial associations

To test wether the sex compisiton of dyads and genetic kinship influenced spatial association patterns between birds, I used a culumative link mixed model (model 1). The full model perfomed significantly better than the null model ($\chi^2 = 88.7$, df = 21, $p < 0.001$). I found that the sex composition of dyads had a significant effect on the distance between birds ($\chi^2 = 6.09$, df = 2, p = 0.048; Figure 3A). Post-hoc comparisons revealed that the distance between mixed-sex dyads was significantly smaller than between female-female dyads (Estimate= 0.347±0.331, SE = 0.141, p = 0.037) while no significant differences were found between female-female and male-male dyads (Estimate = 0.285±0.422, SE = 0.180, p = 0.254) or male-male and mixed dyads (Estimate = 0.062±0.356, SE = 0.152, p = 0.911). Genetic kinship did not influence spatial association patterns ($\chi^2 = 1.04$, df = 1, p = 0.308; Figure 4A).

3.1.2 Affiliative relationship strength and agonistic interactions

To test wether the sex composition of dyads and genetic relatedness affect active and inactive affiliative relationship strength, respectively, I used two generalized linear models.

3.1.2.1 Active affiliative relationship strength

The full model (model 2) perfomed significantly better than the null model ($\chi^2 = 6.399$, df = 5, p = 0.008). I found that the sex composition of dyads had a significant effect on active affiliative relationship strength ($\chi^2 = 6.730$, df = 2, p = 0.035; Figure 3B). Post-hoc comparisons revealed that mixed-sex dyads had a non-significant trend towards stronger active affiliative relationships than female-female dyads (Estimate = -0.587±0.616, SE = 0.253, p = 0.064). No significant differences were found between female-female and male-male dyads (Estimate = -0.124±0.741, SE = 0.304, p = 0.9128) or male-male and mixed dyads

(Estimate = -0.463±0.602, SE = 0.247, p = 0.160). Genetic kinship (χ^2 = 2.215, df = 1, p = 0.137; Figure 4B) did not influence active affiliative relationship strength, and the sum of agonistic interactions ($\chi^2(1)$ = 3.115, p = 0.078) was marginally not significant, suggesting a non-signifcant trend where individuals with more agonistic interactions also had stronger active affiliative relationships.

3.1.2.2 Inactive affiliative relationship strength

The full model (model 3) did not perform significantly better than the null model (χ^2= 0.868, df = 5, p = 0.952), suggesting that neither sex (Figure 3C) nor genetic relatedness (Figure 4C) influenced inactive affiliative relationship strength.

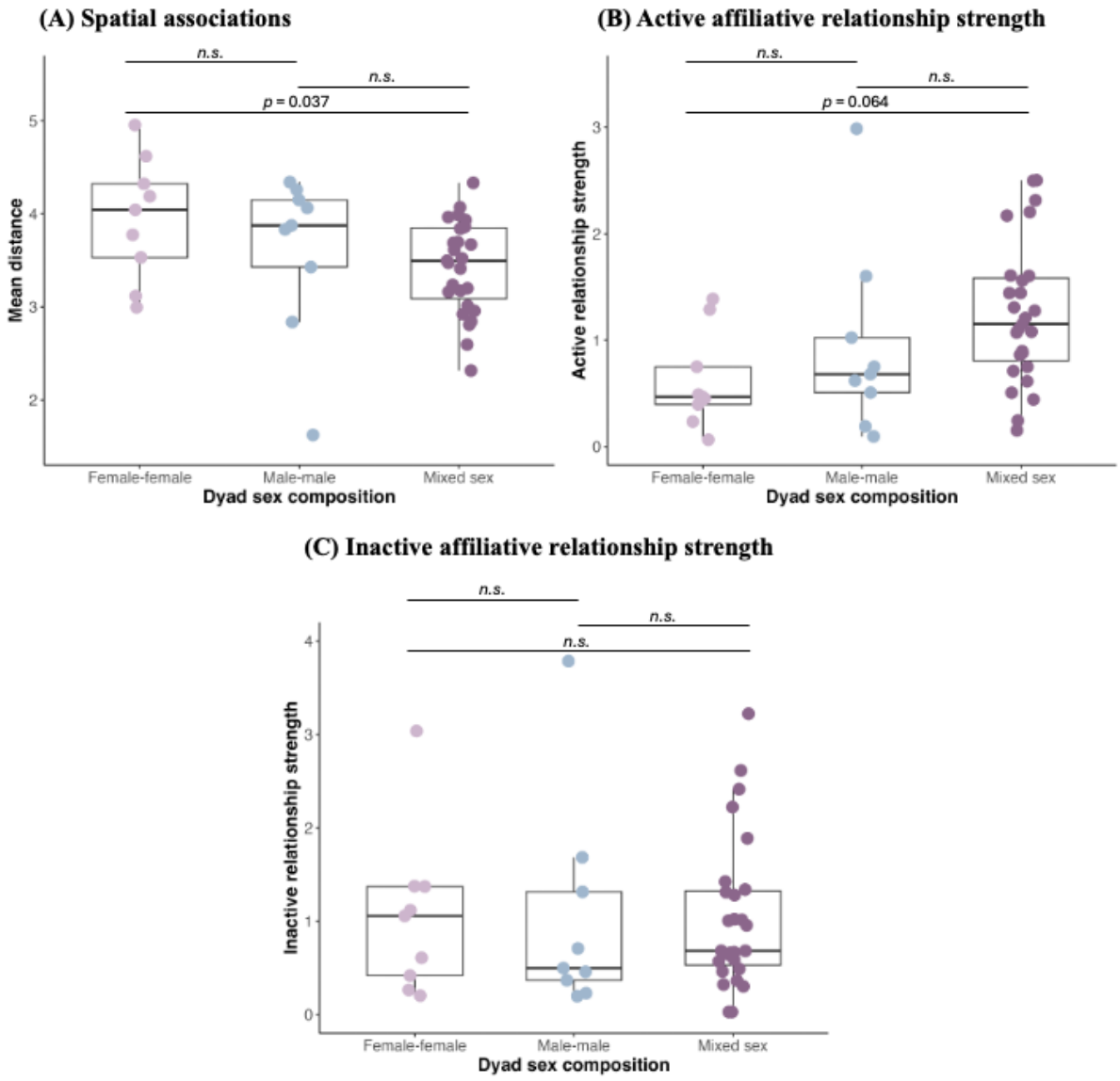

Figure 3: Smaller distances and trend towards stroger active, but not inactive, affiliative relationships in male-male dyads compared to female-female dyads

Dot color represents dyad sex composition (blue, male-male; pink, female-female; purple, mixed sex). Note that in (A), results are visualized using mean distances for each dyad and time period, but statistical analysis was performed with all collected absolute distances. n.s., not significant.

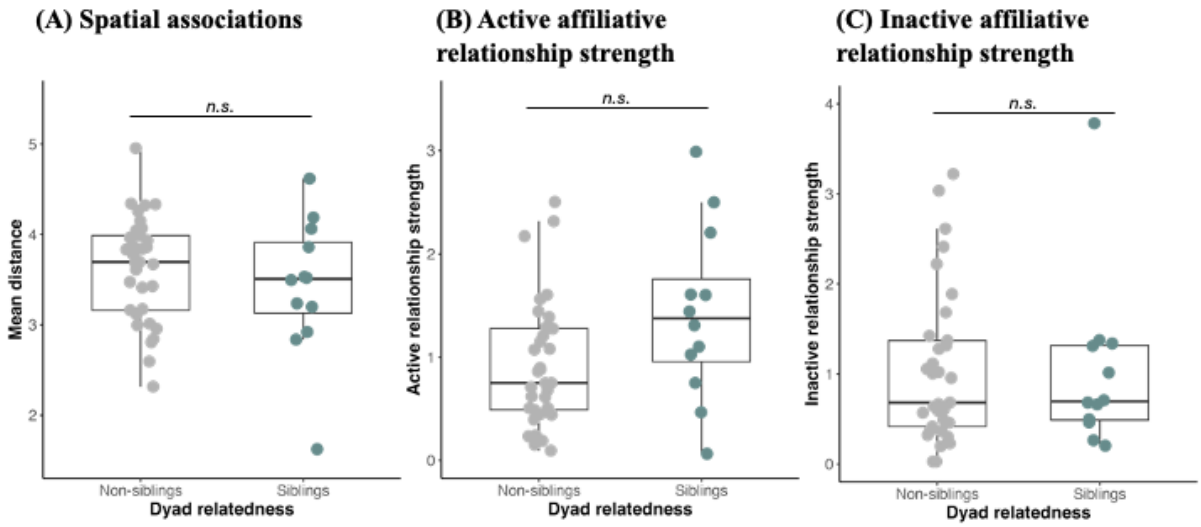

Figure 4: Genetic relatedness did not influence spatial association patterns, active or inactive affiliative relationship strength.

Dot color represents genetic relatedness (grey, unrelated; dark green, genetically related). Note that in (A), results are visualized using mean distances for each dyad and time period, but statistical analysis was performed with all collected absolute distances. n.s., not significant.

3.2 How do ties change over time: Time period

3.2.1 Spatial association patterns

The time period had a significant effect on the spatial association patterns between birds (model 1; see Table S2 and Figure 5A): In the first time period (P1), crows exhibited a high probability of being within medium distances (i.e. 2-5 meters) of others, whereas in the second and third time period, spatial associations became more polarized, with birds being more likely to either be very close or very far from each other.

3.2.2 Affiliative relationship strength

However, active (model 2; $\chi^2 = 0.041$, df = 2, p = 0.840; Figure 5B) and inactive (model 3; $\chi^2 = 0.868$, df = 5, p = 0.952; Figure 5C) relationship strength did not change over time.

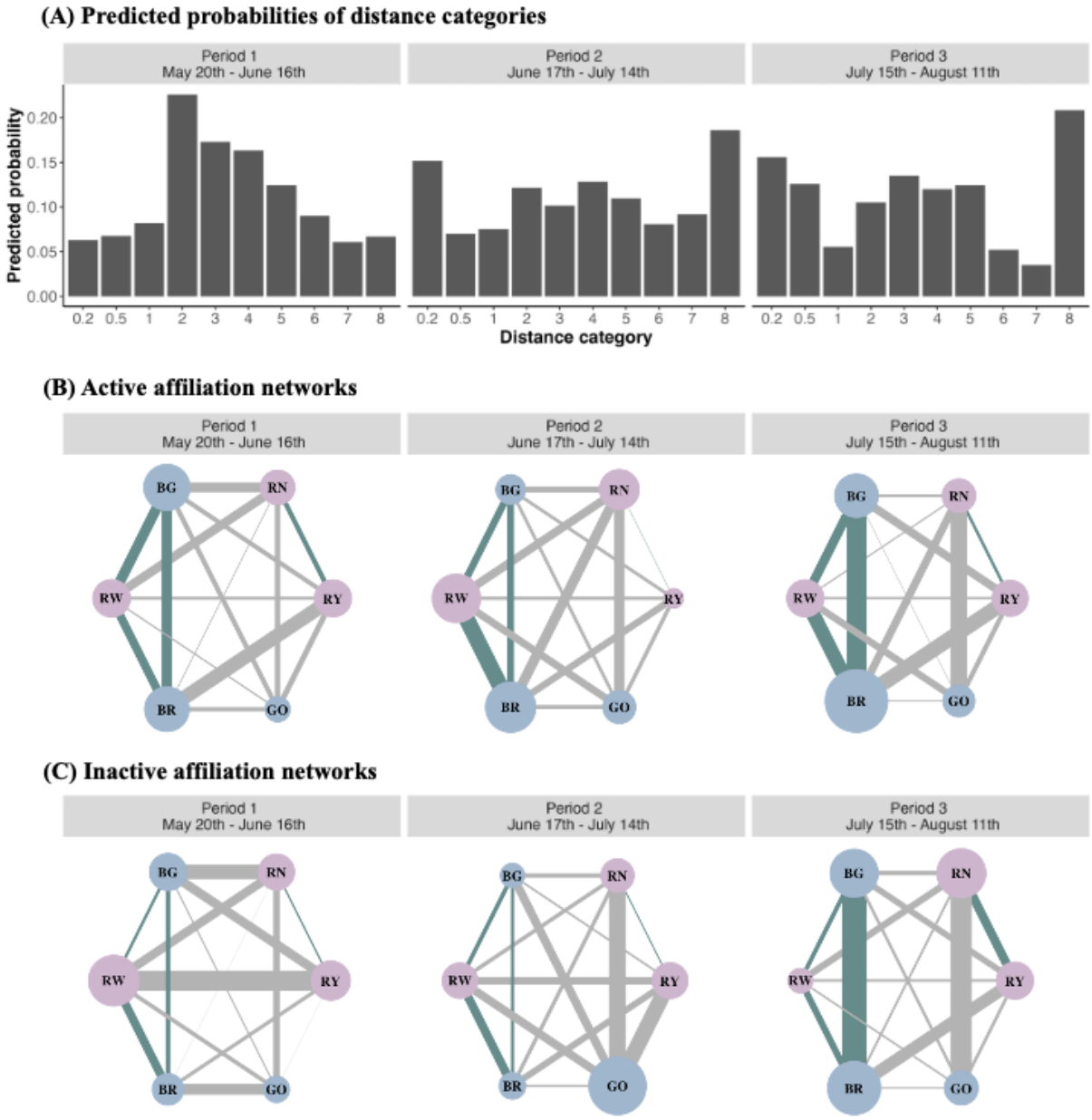

Figure 5: Temporal changes in spatial association patterns, but not in active and inactive affiliative relationship strength

The predicted probabilities of the respective distance categories were extracted from the CLM and visualized in (A). In the network graphs (B and C), individuals (nodes) are represented by circles and sex is represented by circle color (blue, male; pink, female). Line thickness (edge weight) is proportional to relationships trength (i.e. thicker lines represent stronger affiliative relationships) and line color represents genetic relatedness (grey, unrelated; dark green, genetically related). The size of circles is proportional to an individual's weighted degree, that is the sum of relationship strengths or edge weights connected to the individual.

4 Discussion

This study investigated the early social development of carrion and hooded crows, focusing on the effects of sex composition, genetic relatedness, and temporal dynamics on spatial associations and affiliative behaviors. I found that mixed-sex dyads exhibited closer spatial proximity and a trend toward stronger active affiliative relationships compared to female-female dyads, though no differences were observed in inactive affiliative behaviors. Contrary to expectations, genetic relatedness did not significantly influence spatial association patterns or affiliative relationship strength. Over time, spatial associations became more polarized, potentially suggesting an initial phase of broad social interactions followed by selective bonding.

The results indicate that mixed-sex dyads maintained closer spatial associations than female-female dyads. Additionally, I found a trend suggesting that mixed-sex dyads may have stronger active affiliative relationships than female-female dyads, but no sex effect could be found for inactive affiliative relationships. These findings align with research on juvenile ravens, where mixed-sex dyads were also found to form stronger affiliative bonds than female-female dyads (Boucherie *et al*., 2020). One possible interpretation is that early-life mixed-sex associations facilitate pair bond formation later in life. Given that crows are monogamous and form long-term pair bonds (Baglione *et al*., 2005), spending time in close proximity and engaging in affiliative behaviors with the opposite sex during early life could provide social experience necessary for future partnerships.

The lack of a sex effect for inactive affiliative relationships is particularly noteworthy because previous studies (e.g. Boucherie *et al*., 2020) did not differentiate between active and inactive relationship strength. Inactive affiliative behaviors, including perch proximity and allopreening, are behaviors more characteristic of pair bonds and longer-term social relationships (e.g. allo-preening: Kenny *et al*., 2017). Therefore, the absence of sex-based differences in inactive affiliation suggests that pair bond formation may not be strongly

influenced by sex composition at this stage or that these behaviors develop later when pair formation becomes more relevant. On the other hand, active affiliative interactions, such as co-feeding and co-manipulation of objects, are closely tied to immediate benefits in foraging efficiency. These behaviors likely serve as cooperative strategies that enhance access to resources, which could explain why mixed-sex dyads showed higher tendencies toward active affiliation (Miller *et al*., 2014). Therefore, since in many corvid species, including hooded and carrion crows, males typically outrank females (Marzlufi & Heinrich, 1991; Izawa & Watanabe, 2008; Chiarati *et al*., 2010), mixed-sex coalitions might be particularily valuable for females.

Contrary to my expectations, genetic relatedness did not significantly influence spatial associations or affiliative relationship strength. Previous studies on ravens found that siblings tended to maintain stronger affiliative relationships than non-siblings (Loretto *et al*., 2015, Boucherie *et al*., 2020). One possible reason for the discrepancy is that the number of individuals used in this study was not sufficient for the effect of kinship to reach significance.

The temporal dynamics of spatial associations suggest that social organization changes over time. In the first month, crows exhibited a high probability of being within 2-5 meters of others, whereas in the second month, spatial associations became more polarized, with birds being more likely to either be very close or very far from each other. By the third month, this pattern became even more pronounced. This suggests that early on, individuals interacted more evenly across the group before forming stronger bonds with select partners while distancing themselves from others. Note, however, that these results should be interpreted carefully since the proportional odds assumption was relaxed for the time period predictor.

Several limitations should be considered when interpreting the findings. First, while the crows had access to enrichment and conspecifics during their development, being reared by humans and habituated to experimental procedures makes it challenging to generalize their behavior to wild populations. Furthermore, the relatively small sample size may have limited

the ability to detect effects. Additionally, collinearity between sex and social kinship (i.e. being hand reared in the same nest) prohibited the inclusion of social kinship in the analysis, which makes is impossible to differentiate between genetic siblings reared together (social *and* genetic kin) and genetic siblings hand reared in different nests. Future studies would thus profit from a larger and more balanced sample as well as longer observation periods in order to disentangle the effects of genetic relatedness and early-life proximity on later affiliative relationships.

5 Conclusion

This study provides insights into the early social development of carrion and hooded crows, particularly regarding sex-based differences, the role of kinship, and temporal dynamics in spatial associations and affiliative relationships. The smaller distances and trend towards stronger active affiliative relationships observed in mixed-sex dyads suggest that early-life interactions may facilitate cooperative foraging or even serve as a precursor for future pair bonding. Spatial association patterns became more polarized over time, while affiliative interactions were not influenced by spatial dynamics. The absence of kinship effects and the divergence between active and inactive relationship strength highlight the complexity of social development in these species.

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7 Supplementary material

Table S1: Overview of individuals.

Individual	Hatched (estimated date)	Arrived at HH (age in days)	Moved out (age in days)	Nest type	Sex	Siblings	
						Genetic	Social
BR	21.04.24	10	25	natural	m	BG, RW	BG
BG	21.04.24	10	25	natural	m	BR, WR	BR
RW	21.04.24	10	25	paper	f	BG, BR	RY, RN
RY	17.04.24	14	29	paper	f	RN	RW, RN
RN	17.04.24	14	29	paper	f	RY	RW, RY
GO	04.2024	unknown	unknown	none	m	none	none

HH, Haidlhof Research station. m, male; f, female.

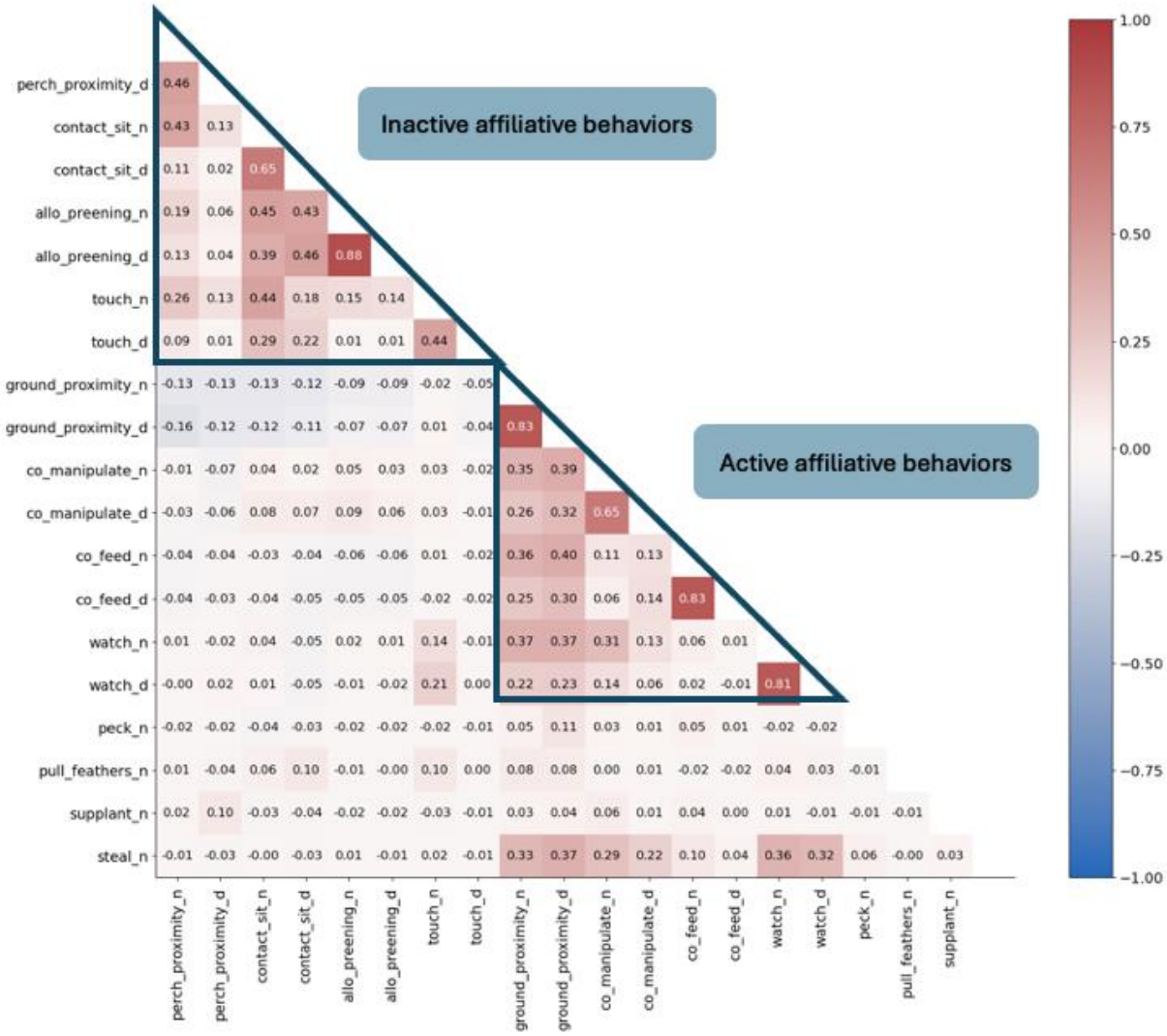

Figure S1: Correlation matrix of recorded behaviors

Based on inter-behavior correlations, I decided to pool behaviors into three categories: Inactive affiliative behaviors, active affiliative behaviors, and agonistic behaviors. Correlation coefficients were calculated for both frequencies (suffix "_n") and durations (suffix "_d"). Correlations between frequencies and durations of the same behavior were relatively high, and thus only frequencies were used to calculate relationship strength, following Boucherie *et al*. (2020).

Table S2: CLM results for time period

CLM results for time period

	Estimate	SE	z	p
0.2|0.5.(Intercept)	-3.178	0.265	-12.009	<0.001***
0.5|1.(Intercept)	-2.369	0.206	-11.486	<0.001***
1|2.(Intercept)	-1.781	0.181	-9.824	<0.001***
2|3.(Intercept)	-0.72	0.16	-4.49	<0.001***
3|4.(Intercept)	-0.022	0.158	-0.14	0.889
4|5.(Intercept)	0.653	0.165	3.958	<0.001***
5|6.(Intercept)	1.277	0.181	7.047	<0.001***
6|7.(Intercept)	1.917	0.211	9.066	<0.001***
7|8.(Intercept)	2.634	0.268	9.846	<0.001***
0.2|0.5.P2	0.984	0.284	3.463	0.001**
0.5|1.P2	0.642	0.216	2.976	0.003**
1|2.P2	0.448	0.183	2.452	0.014*
2|3.P2	-0.081	0.155	-0.523	0.601
3|4.P2	-0.369	0.152	-2.429	0.015*
4|5.P2	-0.526	0.161	-3.258	0.001**
5|6.P2	-0.694	0.183	-3.785	<0.001***
6|7.P2	-0.961	0.22	-4.376	<0.001***
7|8.P2	-1.159	0.286	-4.057	<0.001***
0.2|0.5.P3	1.018	0.295	3.448	0.001**
0.5|1.P3	0.961	0.219	4.385	<0.001***
1|2.P3	0.635	0.191	3.331	0.001**
2|3.P3	0.017	0.165	0.1	0.92
3|4.P3	-0.137	0.163	-0.844	0.399
4|5.P3	-0.33	0.174	-1.889	0.059
5|6.P3	-0.409	0.201	-2.039	0.041*
6|7.P3	-0.785	0.236	-3.334	0.001**
7|8.P3	-1.3	0.293	-4.446	<0.001***

The CLM estimates the probability of two individuals being observed less than a certain distance category apart. The cumulative probabilities are then compared for each time period. For example, row 1, 0.2|0.5.(Intercept), compares the probabilities of two birds being observed less than 0.2 m and less than 0.5 m apart during time period 1 (i.e. the intercept). P2, time period 2, P3, time period 3.

***p<0.001, **p<0.01, *p<0.05

Abstarct (German)

Leben in sozialen Gruppen bietet Vorteile wie Schutz vor Raubtieren und verbesserte Nahrungsbeschaffung. Doch das Navigieren sozialer Beziehungen kann kognitiv anspruchsvoll sein, insbesondere in instabilen sozialen Umgebungen mit Fission-Fusion-Dynamiken (d. h. Veränderungen in Gruppengröße und -zusammensetzung über die Zeit). Individuen sozialer Arten haben oft bevorzugte Sozialpartner, wie Verwandte, und bilden verschiedene Arten von Beziehungen, aber es ist wenig darüber bekannt, wie sich soziale Beziehungen entwickeln.

Um zu untersuchen, wie Geschlecht, Verwandtschaft und Zeit die soziale Entwicklung hochsozialer Nebel- und Rabenkrähen beeinflussen, beobachtete ich das Sozialverhalten einer Gruppe von sechs jungen Krähen über einen Zeitraum von 12 Wochen nach dem Flüggewerden.

Gemischtgeschlechtliche Dyaden hielten sich in kleinerer räumlicher Nähe auf und zeigten eine Tendenz zu stärkeren aktiven affiliativen Beziehungen (z. B. gemeinsames Fressen, gemeinsame Objektmanipulation) als rein weibliche Dyaden. Inaktive affiliative Beziehungen (z. B. gegenseitige Gefiederpflege) wurden jedoch nicht vom Geschlecht beeinflusst. Genetische Verwandtschaft hatte keinen signifikanten Einfluss auf räumliche Nähe oder die Stärke affiliativer Beziehungen. Mit der Zeit wurden räumliche Assoziationen zunehmend polarisiert, was möglicherweise auf eine anfängliche Phase breiter sozialer Interaktionen gefolgt von selektiven Bindungen hindeutet.

Diese Ergebnisse liefern neue Erkenntnisse zur sozialen Entwicklung von Nebel- und Rabenkrähen und tragen zu einem besseren Verständnis der Evolution sozialer Strukturen bei Vögeln bei.