Affiliative social relationships but not dominance rank affects endo-parasite product excretion in a cooperatively breeding bird species

Claudia A.F. Wascher[1], Daniela Canestrari[2] & Vittorio Baglione[3]

[1] School of Life Sciences, Anglia Ruskin University, United Kingdom

[2] Unidad Mixta de Investigación en Biodiversidad, Campus de Mieres, University of Oviedo, Spain

[3] Departamento de Biodiversidad y Gestión Ambiental, Universidad de León, Spain

Short title: Social relationships reduce parasite burden in crows

Corresponding author (present address):

Claudia A.F. Wascher: Department of Biology, Anglia Ruskin University, United Kingdom; Phone: ++4369912381419; e-mail: claudia.wascher@gmail.com

Abstract

In group living animals behavioural interactions with conspecifics strongly modulate an individual's physiological stress response. A secure social embedding, with stable social relationships is expected to dampen an individual's stress response which is in turn will affect the immune system and health. Ultimately, positive health effects of stable social bonds may contribute to maintain group living. We investigated whether, in cooperatively breeding carrion crows (*Corvus corone*), the quality of social relationships have measurable effects on patterns of gastrointestinal parasite product excretion. We repeatably collected behavioural data on dyadic social interactions and individual droppings to quantify parasite products, from 34 individuals in a captive population of carrion crows in northern Spain. Individuals with strong social bonds and living with more related individuals in a group, excreted less samples containing coccidian oocysts. Sex, group size, number of social bonds and dominance rank had no significant effect on number of samples containing coccidian oocysts. Also, the likelihood to excrete samples containing nematode eggs was not affected by any of the factors we considered. Our data presents evidence for affiliative social relationships to be linked to coccidian oocyst excretion, indicating that the social environment has strong fitness implications. This suggests that next to humans and other primate species, social relationships may be important in driving the evolution of complex sociality in a larger variety of taxa, including birds.

Key words: carrion crows, coccidian oocysts, dominance rank, group size, parasites, social bonds.

Background

In group living animals the social environment directly affects an individual's physiology and health (1–4). Adverse effects are caused for example by increased competition and aggressive behaviour (5,6), which affect especially low-ranking individuals (7,8). Further, large group sizes increase the exposure to directly transmitted parasites (9,10) and social interaction patterns can also facilitate pathogen transmission (11,12).

Affiliative behaviour and reliable social allies on the other hand, have a stress-reducing effect (13–16). In several mammalian species, stable social bonds have a fitness enhancing effect (17–19). Social relationships in female chacma baboons (*Papio hamadryas ursinus*) help coping with stressful events and increase longevity (20), whereas social bonds in male Assamese macaques (*Macaca assamensis*) and feral horses (*Equus ferus caballus*) are directly linked to the number of offspring sired (18).

In humans, a rich social network and social support yields measurable positive consequences for health (21–27). Recent research, however, has shown that complex sociality associated with the formation of strong, long-lasting social bonds, is not unique to humans and closely related primate species (28,29). This suggests the fascinating hypothesis that positive health effects of social bonds may contribute to maintain stable group living in a large variety of taxa and types of social organizations (30).

Among birds, corvids show complex social relationships. Common ravens (*Corvus corax*), for example, are capable of forming valuable relationships, not only within

reproductive pairs but also with social partners in their groups (31,32). Such bonds are characterized by low levels of aggression and high levels of affiliative behaviours exchanged in a reciprocal way over extended periods of time (33). Within such valuable relationships, individuals support each other in agonistic encounters (32,34) and share information and resources (32,35,36), whereas they typically act competitively with other non-bonded conspecifics (37,38). In the present study we investigated the benefits of social bonds in carrion crows (*Corvus corone*). In most European populations carrion crows form socially monogamous pairs during the breeding season (39,40) whereas in northern Spain crows live in stable social groups of up to nine individuals, consisting of the breeding pair and retained offspring as well as male immigrants (41). Group living in carrion crows is based on kinship (41) and cooperation in nestling provisioning (42) and territory defence (Hillemann, et al. in prep.). Dominant males are more aggressive towards same sex group members compared to females (43) and are less aggressive towards related individuals than to unrelated ones (44). In captive crows, males are more attentive towards non-kin compared to kin individuals (45) and, unlike females, show less avoidance towards the scent of a stressed familiar individual, compared to a stressed unfamiliar one, which might reflect a stronger willingness to provide social support (46).

In this study, we investigated whether the social environment and the quality of an individual's social relationships affects prevalence of gastrointestinal parasites in captive groups of carrion crows that varied in size and composition. In particular, we focused on the pattern of excretion of oocysts of coccidian protozoans and different nematode species, mainly *Syngamus trachea* and *Capillaria* sp.. Coccidian oocysts are among the most common endoparasites of birds (47,48) and are widespread among

corvids, including carrion crows (49–51). Infections with large numbers of coccidia clinically manifest as ‘coccidiosis’, which damages the intestinal tract (52) and severely affects individual body condition, longevity and fecundity by inhibiting the uptake of essential dietary components (53,54). The pathogenicity is well documented in poultry (55–57), and further evidence is accumulating in wild bird species (e.g. 58,59). Coccidia are transmitted via the faecal-oral route, when oocysts undergo sporogony and become infectious (typically within 24 hours after excretion) (56). Similarly, different nematode species are described as regular endo-parasites of different corvid species (60,61). *Syngamus trachea* is usually located in the trachea of birds and can lead to severe respiratory distress and pulmonary lesions (62,63). *Capillaria* sp. infect the intestinal tract and clinical symptoms are weight loss, diarrhoea, regurgitation, anaemia and oral necrotic plaques (64). Different nematode species infect their avian hosts via a direct life cycle, when embryonated eggs are ingested. Nematode eggs have a prepatent period of several weeks (65).

Here we address three hypotheses: 1. Group size hypothesis: parasite product excretion depends on the size of the group, with infections spreading more easily in crowded conditions; 2. Social bonds hypothesis: parasite product excretion depend on the quality of the social relationships that an individual maintains, with individuals with strong social bonds being less likely to be infected than individuals with weak social bonds. The presence of relatives in the group might also show a positive effect by reducing the occurrence of stressful conflicts and competition (44) that can impair the ability to fight against parasites (66). 3. Dominance rank hypothesis: parasite product patterns depend on the position along the hierarchy. Indeed, dominance rank is known to affect individual social stress, weakening the immune system either in subordinates

or dominants, depending the relative allostatic load of social status in the respective species (67). In addition, we expect sex differences, because males are involved in more competitive interactions than females within their groups (43) and are probably more exposed to the negative consequences of social stress.

Results

Social bonds and parasitological examination

We observed 50 bonded dyads (out of 312 dyads), 23 of which were male-female dyads (4 between related individuals and 19 between unrelated individuals), 12 were male-male (7 between related and 5 between unrelated individuals) and 15 female-female (5 related, 10 unrelated). On average, males and females had 1.136 ± 1.206 and 1.315 ± 0.945 bonded partners respectively. Mean CSI between bonded dyads was 2.698 ± 2.182 for male-female dyads, 2.299 ± 1.373 for female-female bonds and 3.035 ± 3.388 for male-male bonds.

Occurrence of coccidian oocysts

Overall, 104 out of 416 samples from captive crows contained coccidian oocysts. Coccidian oocysts occurred in 69 out of 220 samples in males (31 %) and 35 out of 196 samples in females (18 %). The maximum CSI value and the number of related individuals in the group had a significant influence on the occurrence of coccidian oocysts. Crows with a strong affiliative relationship (maximum CSI value: estimate ± SE = -1.25 ± 0.557, z = 2.237, p = 0.025) and living with a larger number of related individuals (estimate ± SE = -1.229 ± 0.467, z = 2.623, p = 0.008) were less likely to excrete samples containing coccidian oocysts (Figures 1 and 2), whereas the size of the group (estimate ± SE = -0.384 ± 0.5, z = 0.765, p = 0.443), number of social bonds (estimate ± SE = 0.723 ± 0.512, z = 1.412, p = 0.157) and dominance rank (estimate ± SE = 0.326 ± 0.463, z = 0.702, p = 0.482) did not have a significant effect. Males showed a weak trend to excrete more samples containing coccidian oocysts compared to females (estimate ± SE = -0.811 ± 0.461, z = 1.753, p = 0.079).

Occurrence of nematode eggs

Overall, 52 out of 416 samples contained nematode eggs. None of the factors investigated significantly affected excretion patterns of nematode eggs (supplementary Table 4), in fact the null model was amongst the best models in the candidate set (Table 1).

Discussion

In the present study, we have shown that carrion crows with closely bonded social partners (high CSI scores) proved less likely to excrete coccidian oocysts, which represent an important threat for health in birds (53,54). Health correlates of high quality social ties have been reported in humans (*e.g*. 76) and a large body of research has focused on the causal psychological and biological processes that underlie this strong link (21,69). Similar evidence has been recently found in non-human primates (18,20), suggesting that the tendency to form strong social ties may have deep phylogenetic roots (70). Social complexity, however, is not limited to primate species. Indeed, coalition formation has been reported in several mammalian and bird species, e.g. African elephants (*Loxodonta africanus)* (71), spotted hyenas (*Crocutta crocutta)* (72), bottlenose dolphins (*Tursiops aduncus)* (73), ravens (74), and carrion crows (41). Our study uncovered, for the first time, that high quality social relationships may reduce the occurrence of parasites, showing immediate positive effects that parallel those of primates (including humans) and suggesting a route towards advanced sociality that may be common to a variety of taxa.

Cooperatively breeding groups of carrion crows form through two different mechanisms, namely delayed dispersal of offspring, which remain in the natal territory with their parents and siblings (75), and formation of long lasting social bonds among distant relatives, most often males, that share all-purpose territories and frequently mate polyandrously (41,76). These bonds typically form when an immigrant male joins an established family group and allies with the same sex resident breeder, to whom it is related (41). Cooperative breeding, with group members working together to raise the brood, can only arise once stable groups have formed (77). Both offspring delayed

dispersal and bonding between adults males are therefore necessary preceding steps that eventually lead to cooperation, which has to be considered a consequence rather than the cause for the formation of the social group (78–80). In other words, to understand why carrion crows, as well as any other bird species, form groups we need to understand the advantages that sociality conveys, independently of the payoff derived from cooperation at the nest. In carrion crows, as well as in many other cooperatively breeding species, the benefits of delayed dispersal for offspring are well studied (81), but little is known about the advantages of forming long lasting social bonds outside the nuclear family. We argue that the health benefits of high-quality relationships extend beyond the bonds between parents and offspring or reproductive partners, and may be associated with a reduction of harmful endo-parasites and may be an important factor for establishing stable relationships in groups.

Besides the positive effect of strong social bonds, we found that the number of relatives in the group also affected parasite product excretion in carrion crows, with individuals living in groups with more related individuals being less likely to excrete droppings containing coccidian oocysts. Sociality is based on kinship in wild cooperatively breeding carrion crows. Offspring remain in the natal territory with their parents for years and more distant relatives are actively recruited to form cooperative alliances with the resident breeders (Baglione et al. 2003). As a result, social groups in cooperatively breeding carrion crow are extended families, comprising members with different degree of relatedness. Indirect fitness benefits are known to be a primary driver of kin-based sociality in many taxa of animals (83). However, our results now show that living with kin can also accrue immediate direct benefits to carrion crows through reduced infection by coccidia.

Increased exposure to parasites and disease transmission is considered as one of the major disadvantages of group living. Group size is usually positively related to parasite burden, which is seen as major selective force in group living animals (10). In our study, group size did not have a significant effect on frequency of samples containing coccidian oocysts. Therefore, contrary to the expectation that probability of pathogen transmission increases with group size, we found group composition, *i.e.* number of related individuals and the quality of social relationships to mediate an individual's parasite product excretion, likely via dampening of the physiological stress response which might suppress an individual's immune system. This is also supported by a recent study in Japanese macaques (*Macaca fuscata*), which shows that individuals with more affiliative social partners to have fewer ectoparasites (84).

We only found effects of social relationships and number of related individuals in coccidia, but not in nematode species. One reason could be that the lower occurrence of nematode eggs compared to coccidian oocysts in the samples (12 % of samples contained nematode eggs and 24 % of samples contained coccidian oocysts) limited the power of our analysis. However, the quicker life cycle of coccidians, with a prepatent period of approximately one week, compared to nematodes, *e.g.* capillaria, with a pre-patent period of 3 - 4 weeks (64) could also play a role, as short-term changes in the immune system, probably in response to suppressive effects of glucocorticoids in response to social interactions, might have stronger effects on coccidia compared to nematodes.

Conclusions

Social complexity has deep phylogenetic roots, being widespread in a wide variety of mammals and birds. Understanding its evolution, however, is difficult because of our scant knowledge of the fitness consequences of sophisticated social behaviour across taxa. We are just starting to fill the gaps, and this study shows a measurable positive effect of the quality of social relationships in a bird species that may trigger social bonding, setting the stage for a complex form of cooperation (cooperative breeding). Importantly, our results parallel previous findings in primate species, suggesting a general pattern in vertebrates for the evolution of sociality.

Methods

Study subjects and ethics statement

We collected data over four different periods (November 2008 - January 2009, January - February 2013, May - June 2013, January - February 2014), from a total of 34 crows (16 females, 18 males), which were housed in a large outdoor aviary (30 x 12 x 6 m) in Northern Spain (Navafría, León, 42°36’33 N 5°26’56 W). The aviary comprised four major compartments (12 x 6 x 3 m) connected through eight smaller testing compartments (3 x 3 x 3 m). The major compartments were equipped with wooden perches, natural vegetation and rocks. An enriched diet consisting of fruit, vegetables, bread, meat and milk products was provided on a daily basis. Water and dry food were available *ad libitum*. Keeping crows in captivity was authorized by Junta de Castilla y León (núcleo zoológico 005074).

Birds were kept in groups that mirrored the social aggregations that naturally occur in the wild: (A) ‘Flock’: three or more juvenile individuals; in 2008 some juveniles

were initially kept in ‘sibling pairs’ and subsequently merged into a juvenile flock; (B) ‘Pairs’: adult male and adult female; in some cases adults were also kept in trios; (C) ‘Cooperative Family’: a reproductive pair with its own already independent offspring. Group composition (supplementary Table 1), however, varied during the course of the study due to the death of some individuals.

Behavioural data

A total of 1045 individual focal observations have been recorded. Each observation lasted 5 minutes, and all occurring behaviours were recorded. For this study, we focused on frequencies of agonistic behaviour (threat, chase flight, and fight) and affiliative behaviours (approach, allopreening and sitting in contact). The identity of the interacting individuals was noted, as well as their role (initiator/receiver). All behavioural observations were recorded on video and analysed by CAFW (supplementary Table 1).

Composite sociality index

For each period of data recording, we calculated a composite sociality index (CSI) for each crow dyad within a group according to Silk et al. 2010 (20). A CSI was constructed from three affiliative behaviours: approach, contact sit and allopreen. Note that we used mean values per observation instead of absolute numbers because the number of focal observations varied among individuals (supplementary Table 1). For each period of data collection, we also calculated for each individual the maximum CSI value among all the dyads that involved that particular bird. Dyads with CSI higher than the average of the entire sample were classified as ‘bonded’, and we counted the number of bonded group members for each individual.

Normalized David's Score

We calculated the success of individuals in agonistic encounters using the corrected normalized David's Score (nDS), which considers the proportion of wins and losses, corrected for the chance occurrence (85). In order to compare individuals between different groups, we calculated the relative difference in nDS among individuals in each group (ΔnDS), with 0 being the most dominant individual (supplementary Table 1).

Parasitological examination

During the entire study period, 441 individual droppings were collected, directly after defecation, so that each sample could be assigned to a particular individual (supplementary Table 1). Samples were examined for eggs and oocysts of intestinal parasites. In 2008, we used a modified version of the flotation method (64) to examine the occurrence of parasite products in the droppings. Fresh droppings (0.1 g) were suspended in a 2 ml collecting tube with 1 ml saturated saline. Collection tubes were shaken for 10 seconds and afterwards centrifuged for 5 minutes at 3000 rpm. After centrifugation, the collection tubes were filled with saline solution and a cover slip (18 x 18 mm) was positioned onto the tube. The high density of the saline solution causes the parasite eggs and oocysts to float up and be caught on the cover slip (86). After 10 minutes, the cover slip was moved onto an object slide and the parasite eggs and oocysts were identified and counted. From January 2013 onwards, we used a McMaster counting chamber to examine the occurrence of parasite products in the droppings. The entire sample was weighed, then diluted with 3 ml saturated NaCl solution per 0.1 g of droppings and thoroughly mixed. Afterwards, the solution was filled into both McMaster counting chambers. After 10 minutes of resting period we identified the parasite eggs and oocysts in both chambers. We used a binocular with 100-fold and

400-fold amplification to identify parasite products. We found Coccidian oocysts, eggs of several nematode species (*Capillaria sp., Ascarida sp., Syngamus sp., Heterakis sp., Trichostrongylus tenius*) and cestode eggs to a varying degree. The proportion of positive samples was highest for coccidian oocysts (24 %, n = 441). Nematode eggs were found in 12 % of samples and cestode eggs where only found in less than 1 % of samples. We therefore limited our statistical analysis to coccidian occysts and nematodes.

Data analysis

We analysed the occurrence (presence/absence) of coccidian oocysts and nematode eggs in the droppings. We used generalized linear mixed models (GLMMs) with binomial error distributions and logit link functions. GLMMs were fitted by maximum likelihood. All models were calculated in R v. 3.0.2 (87) using the glmmADMB package (version 0.7.7; 88). We based our model selection on second-order Akaike's Information Criterion values (AICc; 89). We calculated the difference between the best model and each other possible model (ΔAICc) and ranked the model combinations according to their ΔAICc, which provides an evaluation of the overall strength of each model in the candidate set. Multiple models qualified as the similarly good models, *i.e.* $\Delta AICc \leq 2$ (90,91) and therefore we applied a model averaging approach, which calculates model averaged parameters using the MuMIn package (version 1.15.6). Full statistical models are presented in the supplementary materials (supplementary Table 2 and 4). Maximum CSI value, group size, number of bonds, number of related individuals, normalized David's score (ΔnDS) and sex were included as explanatory variables. Further, we ran a model including two-way interactions between sex and the fixed factors. All interactions were non-significant (supplementary

Table 3 and 5) and subsequently removed from the model (92). For each model, we fitted individual identity as a random term to control for the potential dependence associated with multiple samples from the same individuals.

Author contributions

C.A.F.W. designed the study, collected the data, performed lab identification of parasites and analysed the data; all the authors wrote the paper.

Availability of data and materials

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

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References

1. DeVries AC, Glasper ER, Detillion CE. Social modulation of stress responses. Physiol Behav. 2003;79(3):399–407.
2. Holst D Von. The concept of stress and its relevance for animal behavior. Adv Study Behav. 1998;37:1–131.
3. Hanley KA, Stamps JA. Does corticosterone mediate bidirectional interactions between social behaviour and blood parasites in the juvenile black iguana, Ctenosaura similis? Anim Behav. 2002;63(2):311–22.
4. Sheridan JF, Dobbs C, Brown D, Zwilling B. Psychoneuroimmunology: stress effects on pathogenesis and immunity during infection. Clin Microbiol Rev. 1994;7(2):200–12.
5. Hawley DM, Lindström K, Wikelski M. Experimentally increased social competition compromises humoral immune responses in house finches. Horm Behav. 2006;49(4):417–24.
6. Chester EM, Bonu T, Demas GE. Social defeat differentially affects immune responses in Siberian hamsters (Phodopus sungorus). Physiol Behav. 2010;101(1):53–8.
7. Ungerfeld R, Correa O. Social dominance of female dairy goats influences the dynamics of gastrointestinal parasite eggs. Appl Anim Behav Sci. 2007;105(1):249–53.
8. Zuk M, Kim T, Robinson S, Johnsen T. Parasites influence social rank and morphology, but not mate choice, in female red junglefowl, Gallus gallus. Anim Behav. 1998;56(2):493–9.
9. Loehle C. Social barriers to pathogen transmission in wild animal populations. Ecology. 1995;76(2):326–35.
10. Côté IM, Poulin R. Parasitism and group size in social animals: a meta-analysis. Behav Ecol. 1995;6(2):159.165.
11. Drewe JA. Who infects whom? Social networks and tuberculosis transmission in wild meerkats. Proc R Soc B Biol Sci. 2010;277(1681):633–42.
12. Fouchet D, Verrier D, Ngoubangoye B, Souquiere S, Makuwa M, Kazanji M, et al. Who infects whom? Social networks and tuberculosis transmission in wild meerkats. Proc R Soc B Biol Sci. 2012;279(1742):3426–35.
13. Frigerio D, Weiss B, Dittami J, Kotrschal K. Social allies modulate corticosterone excretion and increase success in agonistic interactions in juvenile hand-raised graylag geese (Anser anser). Can J Zool. 2003;81:1746–54.
14. Stöwe M, Bugnyar T, Schloegl C, Heinrich B, Kotrschal K, Möstl E. Corticosterone excretion patterns and affiliative behavior over development in ravens (Corvus corax). Horm Behav. 2008;53(1):208–16.
15. Sachser N, Dürschlag M, Hirzel D. Social relationships and the management of stress. Psychoneuroendocrinology. 1998;23(8):891–904.
16. Young C, Majolo B, Schülke O, Ostner J. Male social bonds and rank predict supporter selection in cooperative aggression in wild Barbary macaques. Anim Behav; 2014;95:23–32.
17. Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, et al. The benefits of social capital: close social bonds among female baboons enhance offspring survival. Proc Biol Sci. 2009;276(1670):3099–104.
18. Schülke O, Bhagavatula J, Vigilant L, Ostner J. Social bonds enhance reproductive success in male macaques. Curr Biol. 2010;20(24):2207–10.
19. Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, et al. Strong and consistent social bonds enhance the longevity of female baboons.

Curr Biol. 2010;20(15):1359–61.
20. Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, et al. Female chacma baboons form strong, equitable, and enduring social bonds. Behav Ecol Sociobiol. 2010;64(11):1733–47.
21. Berkman LF, Glass T. Social integration, social networks, social support, and health. In: Berkman LF, Kawachi I, editors. Social Epidemiology. Oxford, UK: Oxford University Press; 2000. p. 137.
22. Theorell T, Blomkvist V, Jonsson H, Schulman S, Berntorp E, Stigendal L. Social support and the development of immune function in human immunodeficiency virus infection. Psychosom Med. 1995;57(1):200–12.
23. Kiecolt-Glaser JK, McGuire L, Robles TF, Glaser R. Psychoneuroimmunology: Psychological influences on immune function and health. J Consult Clin Psychol. 2002;70(3):537–47.
24. Cobb S. The role of social relations in health promotion. Psychosom Med. 1976;38(5):300–14.
25. Uchino BN, Cacioppo JT, Kiecolt-Glaser JK. The relationship between social support and physiological processes: a review with emphasis on underlying mechanisms and implications for health. Psychol Bull. 1996;119(3):488–531.
26. Berkman LF. The role of social relations in health promotion. Psychol Bull. 1995;57(3):245–54.
27. Cassel J. The contribution of the social environment to host resistance. Psychosom Med. 1976;104(2):107–23.
28. Shultz S, Dunbar RIM. Social bonds in birds are associated with brain size and contingent on the correlated evolution of life-history and increased parental investment. Biol J Linn Soc. 2010;100(1):111–23.
29. Pollen AA, Dobberfuhl AP, Scace J, Igulu MM, Renn SCP, Shumway CA, et al. Environmental complexity and social organization sculpt the brain in Lake Tanganyikan cichlid fish. Brain Behav Evol. 2007;70(1):21–39.
30. Silk JB. The adaptive value of sociality in mammalian groups. Philos Trans R Soc B. 2007; 362(1480):539–59.
31. Heinrich B. Conflict, cooperation, and cognition in the common raven. Adv Study Behav. 2011;43:189–237.
32. Fraser ON, Bugnyar T. Reciprocity of agonistic support in ravens. Anim Behav. 2012;83(1):171–7.
33. Fraser ON, Bugnyar T. The quality of social relationships in ravens. Anim Behav. 2010;79(4):927–33.
34. Emery NJ, Seed AM, von Bayern AMP, Clayton NS. Cognitive adaptations of social bonding in birds. Philos Trans R Soc B. 2007;362(1480):489–505.
35. Bugnyar T, Kijne M, Kotrschal K. Food calling in ravens: are yells referential signals? Anim Behav. 2001;61(5):949–58.
36. de Kort SR, Emery NJ, Clayton NS. Food sharing in jackdaws, Corvus monedula: what, why and with whom? Anim Behav. 2006;72(2):297–304.
37. Bugnyar T, Heinrich B. Pilfering ravens, Corvus corax, adjust their behaviour to social context and identity of competitors. Anim Cogn. 2006;9(4):369–76.
38. Bugnyar T, Heinrich B. Ravens, Corvus corax, differentiate between knowledgeable and ignorant competitors. Proc R Soc B Biol Sci. 2005;272(1573):1641–6.
39. Glutz von Blotzheim UN. Handbuch der Vögel Mitteleuropas. Glutz von Blotzheim UN, editor. Wiesbaden: Aula-Verlag; 1985.
40. Meide M. Raben- und Nebelkrähe. Magdeburg: Westarp Wissenschaften; 1984.

41. Baglione V, Canestrari D, Marcos JM, Ekman J. Kin selection in cooperative alliances of carrion crows. Science. 2003;300(5627):1947–9.
42. Canestrari D, Chiarati E, Marcos JM, Ekman J, Baglione V. Helpers but not breeders adjust provisioning effort to year-round territory resource availability in carrion crows. Anim Behav. 2008;76(3):943–9.
43. Chiarati E, Canestrari D, Vera R, Marcos JM, Baglione V. Linear and Stable Dominance Hierarchies in Cooperative Carrion Crows. Ethology. 2010;116(4):346–56.
44. Chiarati E, Canestrari D, Vila M, Vera R, Baglione V. Nepotistic access to food resources in cooperatively breeding carrion crows. Behav Ecol Sociobiol. 2011;65:1791-1800.
45. Wascher CAF, Núñez Cebrián C, Valdez JW, Canestrari D, Baglione V. Social factors modulating attention patterns in carrion crows. Behaviour. 2014;151(5):555–72.
46. Wascher CAF, Heiss RS, Baglione V, Canestrari D. Behavioural responses to olfactory cues in carrion crows. Behav Proc. 2015;111:1–5.
47. Page CD, Haddad K. Coccidial infections in birds. Semin Avian Exot Pet Med. 1995;4(3):138–44.
48. López G, Figuerola J, Soriguer R. Time of day, age and feeding habits influence coccidian oocyst shedding in wild passerines. Int J Parasitol. 2007;37(5):559–64.
49. Poon SK, Chew WK. Isospora corvi Ray, Shivnani, Oommen and Bhaskaran, 1952 from the common house crow (Corvus splendens Vieillot) of Selangor, peninsular Malaysia. Folia Parasitol. 1991;38(3):201–7.
50. Upton SJ, Langen TA, Wright TF. A new species of Isospora Schneider, 1881 (Apicomplexa: Eimeriidae) from the white-throated magpie jay Calocitta formosa (Passeriformes: Corvidae) from Costa Rica. Syst Parasitol. 1995;31(3):195–9.
51. Cawthorn RJ, Wobeser GA. Exogenous and endogenous stages of Isospora brachyrhynchi sp. n.(Protozoa: Eimeriidae) from the American crow Corvus brachyrhynchos Brehm. Can J Zool. 1985;63(11):2639–45.
52. Conway DP, McKenzie ME. Poultry Coccidiosis. Diagonistic Testing and Procedures. Iowa: Blackwell Scientific Publications; 2007.
53. Hõrak P, Saks L, Karu U, Ots I, Surai PF, McGraw KJ. How coccidian parasites affect health and appearance of greenfinches. J Anim Ecol. 2004;73(5):935–47.
54. Stenkewitz U, Nielsen ÓK, Skírnisson K, Stefánsson G. Host-parasite interactions and population dynamics of rock ptarmigan. PLoS One. 2016;11(11):1–19.
55. Allen PC. Physiological responses of chicken gut tissue to coccidial infection: Comparative effects of Eimeria acervulina and Eimeria mitis on mucosal mass, carotenoid content, and brush border enzyme activity. Poult Sci. 1987;66(8):1306–15.
56. Allen PC, Fetterer RH. Recent Advances in Biology and Immunobiology of. Cytokine. 2002;15(1):58–65.
57. Allen PC, Lydon J, Danforth HD. Effects of components of Artemisia annua on coccidia infections in chickens. Poult Sci. 1997;76(8):1156–63.
58. Brawner WR, Hill GE, Sundermann CA. Effects of coccidial and mycoplasmal infections on carotenoid-based plumage pigmentation in male house finches. Auk. 2000;117(4):952–63.
59. McGraw KJ, Hill GE. Differential effects of endoparasitism on the expression of carotenoid- and melanin-based ornamental coloration. Proc R Soc B Biol Sci.

2000;267(1452):1525–31.
60. Halajian A, Eslami A, Mobedi I, Amin O, Mariaux J, Mansoori J, et al. Gastrointestinal Helminths of Magpies (Pica pica), Rooks (Corvus frugilegus) and Carrion Crows (Corvus corone) in Mazandaran Province, North of Iran. Iran J Parasitol. 2011;6(2):38–44.
61. Loman J. Reproduction in a Population of the Hooded Crow Corvus cornix. Holarct Ecol. 1980;3:26–35.
62. Nevarez JG, Gamble KC, Aczm D, Tully TN, Avian DA. Syngamus trachea infection in two red-and-yellow barbets (Trachyphonus erythrocephalus). J Avian Med Surg. 2002;16:31–3.
63. Fernando AMA, Stockdale PHG, Remmler O. The route of migration, development, and pathogenesis of syngamus trachea (Montagu, 1811) Chapin 1925, in pheasants. J Parasitol. 1971;57:107–16.
64. Schnieder T, Boch J, Supperer R. Veterinärmedizinische Parasitologie. 6th ed. Schnieder T, Boch J, Supperer R, editors. Berlin: Parey; 2006.
65. Ortlepp RJ. The life-history of Syngamus trachealis (Montagu) v. Siebold, the gape-worm of chickens. J Helminthol. 1923;1(3):119–40.
66. Schat KA, Skinner MA. Avian immunosuppressive diseases and immune evasion. In: Davison F, Kaspers B, Schat KA, editors. Avian Immunology. Oxford, UK: Elsevier Academic Press; 2008. p. 299–322.
67. Goymann W, Wingfield JC. Allostatic load, social status and stress hormones: the costs of social status matter. Anim Behav. 2004;67:591–602.
68. Seeman TE. Social ties and health: The benefits of social integration. Ann Epidemiol. 1996;6(5):442–51.
69. Cacioppo JT, Hawkley LC. Perceived social isolation and cognition. Trends Cogn Sci. 2009;13(10):447–54.
70. Shultz S, Dunbar R. Bondedness and sociality. Behaviour. 2010;147(7):775–803.
71. Bates LA, Lee PC, Njiraini N, Poole JH, Sayialel K, Sayialel S, et al. Do elephants show empathy? J Conscious Stud. 2008;15(10):204–25.
72. Holekamp KE, Sakai ST, Lundrigan BL. Social intelligence in the spotted hyena (Crocuta crocuta). Philos Trans R Soc Lond B. 2007;362(1480):523–38.
73. Connor RC, Krützen M. Male dolphin alliances in Shark Bay: Changing perspectives in a 30-year study. Anim Behav. 2015;103:223–35.
74. Braun A, Bugnyar T. Social bonds and rank acquisition in raven nonbreeder aggregations. Anim Behav. 2012;84(6):1507–15.
75. Baglione V, Marcos JM, Canestrari D. Cooperatively breeding groups of carrion crow (Corvus corone corone) in Northern Spain. Auk. 2002;119(3):790–9.
76. Baglione V, Marcos M, Canestrari D, Ekman JAN. Direct fitness benefits of group living in a complex cooperative society of carrion crows , Corvus corone corone. Anim Behav. 2002;64:887–93.
77. Canestrari D, Marcos J, Baglione V. Effect of parentage and relatedness on the individual contribution to cooperative chick care in carrion crows Corvus corone corone. Behav Ecol Sociobiol. 2005;116(5):422–8.
78. Ekman J, Baglione V, Egger S, Griesser M. Delayed dispersal: living under the reign of nepotistic parents. Auk. 2001;118(1):1–10.
79. Ekman J, Dickinson JL, Hatchwell BJ, Griesser M. Delayed dispersal. In: Ecology and Evolution of Cooperative Breeding in Birds. Cambridge, UK: Cambridge University Press; 2004. p. 35–47.
80. Hatchwell BJB, Komdeur J. Ecological constraints, life history traits and the evolution of cooperative breeding. Anim Behav. 2000;59(6):1079–86.

81. Chiarati E, Canestrari D, Vera R, Baglione V. Subordinates benefit from exploratory dominants: response to novel food in cooperatively breeding carrion crows. Anim Behav. 2012;83(1):103–9.
82. Baglione V, Canestrari D. Carrion crows: Family living and helping in a flexible social system. In: Koenig WD, Dickinson JL, editors. Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution, and Behavior. Cambridge, UK: Cambridge University Press; 2016. p. 97–114.
83. Clutton-Brock T. Breeding Together: Kin Selection and Mutualism in Cooperative Vertebrates. Science. 2002;296(5565):69–72.
84. Duboscq J, Romano V, Sueur C, MacIntosh A. Pick your lousy friends wisely: Network centrality and seasonality interact to predict lice load in Japanese. Sci Rep; 2015; 22095.
85. De Vries H, Stevens JMG, Vervaecke H. Measuring and testing the steepness of dominance hierarchies. Anim Behav. 2006;71(3):585–92.
86. Carta LK, Carta DG. Nematode specific gravity profiles and applications to flotation extraction and taxonomy. Nematology. 2000;2(2):201–10.
87. Team RC. R: a language and environment for statistical computing. [Internet]. Vienna, Austria: R foundation for statistical computing; 2016. Available from: http://www.r-project.org/
88. Skaug H, Fournier D, Nielsen A, Magnusson A, Bolker B. Generalized Linear Mixed Models using AD Model Builder. 2013.
89. Hurvich C, Tsai C, Chih-Ling T. Regression and time series model selection in small samples. Biometrika. 1989;76:297–307.
90. Burnham KP, Anderson DR. Model selection and multimodel inference: a practical information-theoretic approach. New York: Springer; 2002.
91. Burnham KP. Multimodel Inference: Understanding AIC and BIC in Model Selection. Sociol Methods Res. 2004;33(2):261–304.
92. Engqvist L. The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. Anim Behav. 2005;70(4):967–71.

Table 1. Model selection of analyses that examined the occurrence of coccidian oocysts. The occurrence of oocysts was related to variables associated with two hypotheses: the 'group size' hypothesis and the 'social bonds' hypothesis: maximum CSI value (max CSI), number of social bonds (nr bonds), number of related individuals (nr related), normalized David's score (ΔnDS). Individual identity was fitted as a random term in all models. LogLik: log-likelihood, df: degrees of freedom, ΔAICc: difference in AICc to the best model. Models are ranked according to their Akaike weight (Weight). N = 216 samples of 17 males and 200 samples of 16 females.

	Models	df	LogLik	AICc	ΔAICc	Weight
(a) Coccidia	Max CSI, nr bonds, nr related, sex	6	-209.815	431.835	0.00	0.115
	Max CSI, nr related, sex	5	-210.905	431.956	0.12	0.108
	Max CSI, nr bonds, nr related	5	-211.286	432.718	0.882	0.074
	Max CSI, nr related	4	-212.456	433.009	1.173	0.064
	Group size, max CSI, nr bonds, nr related, sex	7	-209.39	433.054	1.219	0.062
	ΔnDS, max CSI, nr bonds, nr related, sex	7	-209.544	433.362	1.527	0.053
	ΔnDS, max CSI, nr related, sex	6	-210.692	433.589	1.754	0.047
(b) Nematodes	ΔnDS, max CSI	4	-131.953	272.003	0	0.067
	Null model	2	-134.043	272.115	0.111	0.063
	ΔnDS	3	-133.048	272.154	0.15	0.062
	Max CSI	3	-133.054	272.166	0.162	0.061
	Max CSI, nr related	4	-133.714	273.525	1.522	0.031
	Nr related	3	-133.742	273.542	1.538	0.031
	Group size	3	-133.841	273.74	1.736	0.028
	ΔnDS, group size, max CSI	5	-131.804	273.754	1.751	0.027
	ΔnDS, group size	4	-132.84	273.777	1.774	0.027
	ΔnDS, max CSI, nr related	5	-131.84	273.826	1.823	0.026
	Group size, max CSI	4	132.909	273.915	1.191	0.025
	ΔnDS, max CSI, sex	5	-131.9	273.946	1.943	0.025

		ΔnDS, sex	4	-132.932	273.961	1.958	0.252
		ΔnDS, max CSI, nr bonds	5	-131.917	273.98	1.977	0.024
		ΔnDS, nr related	4	-132.944	273.985	1.982	0.024

Table 2. Results of model averaged generalized mixed linear model investigating factors affecting patterns of coccidian oocyst excretion. Significant values ($p \leq 0.05$) are highlighted in bold.

Parameters	Estimate ± SE	*z*	*p*	Relative importance
Max CSI	**-1.25 ± 0.557**	**2.237**	**0.025**	**0.82**
Nr related	**-1.229 ± 0.467**	**2.623**	**0.008**	**0.93**
Sex	-0.811 ± 0.461	1.753	0.079	0.59
Nr bonds	0.723 ± 0.512	1.412	0.157	0.51
Group size	-0.384 ± 0.5	0.765	0.443	0.34
ΔnDS	0.326 ± 0.463	0.702	0.482	0.32

Figure 1.
Occurrence of coccidan oocysts in carrion crow droppings in relation to the maximum CSI. Occurrence probabilities were calculated as the predicted values (solid line) and 95% CI (shaded area).

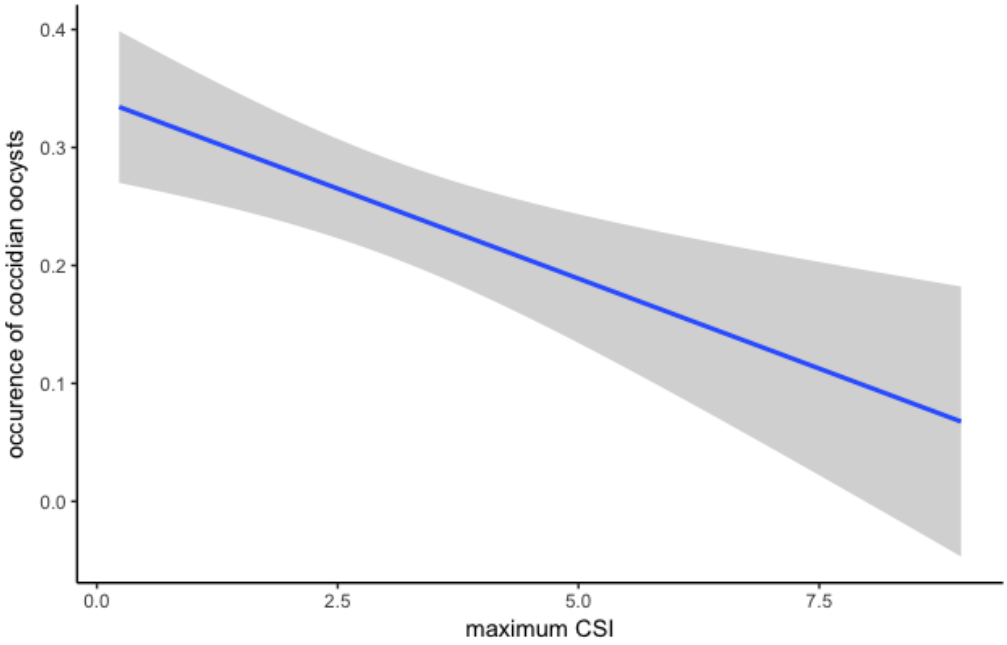
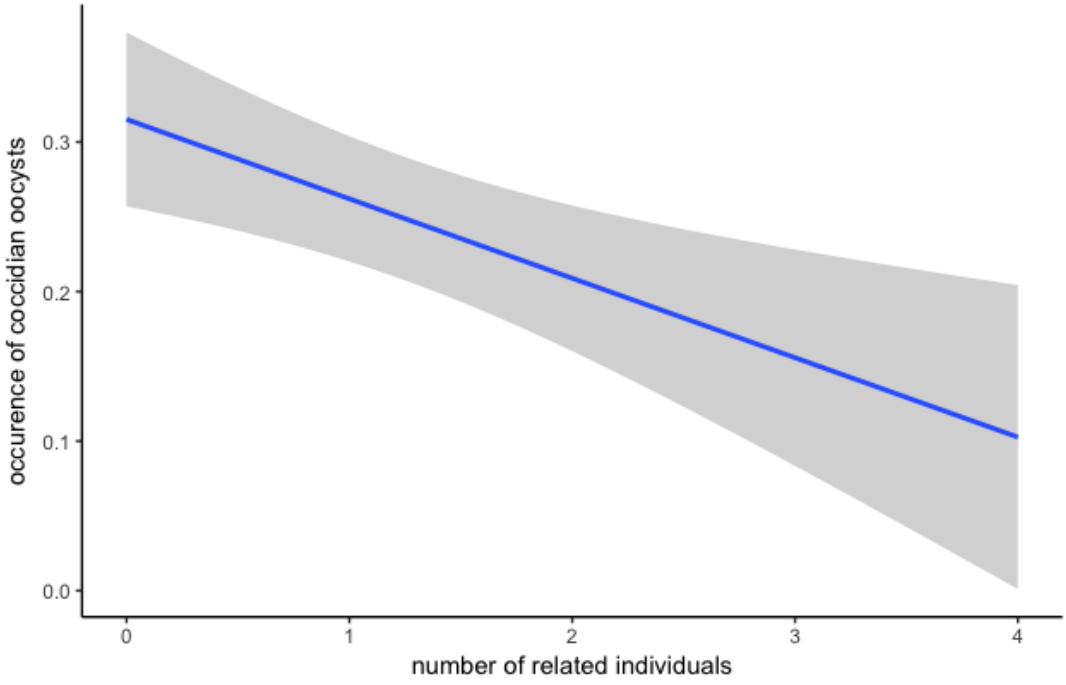
Figure 2.
Occurrence of coccidan oocysts in carrion crow droppings in relation to the number of related individuals in the group. Occurrence probabilities were calculated as the predicted values (solid line) and 95% CI (shaded area).