1 **Association between social factors and gastrointestinal parasite product excretion in a**

2 **group of non-cooperatively breeding carrion crows**

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24      **Abstract**

25          In group-living animals the social environment is thought to affect the probability of

26      parasite transmission. Here, I investigate relationships between social behavior and

27      gastrointestinal parasite product excretion in the carrion crow (*Corvus corone*). Individuals

28      from a population of non-cooperatively breeding carrion crows excreted less samples

29      containing coccidian oocysts when kept in larger groups (8 or 9 individuals) compared to

30      those individuals kept in smaller groups (2 or 3 individuals). Lower-ranking individuals

31      excreted more samples containing parasite oocysts compared to higher-ranking individuals.

32      The strength of affiliative relationships and number of related individuals in the group did

33      not relate to the proportion of droppings containing coccidian oocysts. The present results

34      confirm an association between social environment and parasite excretion patterns in

35      carrion crows, but the patterns described in the present study differ from previously

36      published data derived from a group of cooperatively breeding crows. This illustrates that

37      differences between the social systems of carrion crows might result in different

38      associations between the social environment and parasite product excretion patterns.

39

40      **Significance statement**

41      One major cost of group living is increased susceptibility to parasites. Not all individuals are

42      affected by this in the same way. A better understanding of the relationship between social

43      behavior and parasite burden can help to better understand evolution of group living. I

44      investigate associations between dominance rank, affiliative relationships, group size and

45      gastrointestinal parasite product excretion in a group of captive carrion crows. Lower-

46      ranking individuals excreted more samples containing parasite oocysts compared to higher-

47    ranking individuals, confirming an association between social relationships and parasite

48    excretion patterns.

49

50    *Key words:* affiliation, aggression, parasites, coccidian oocysts, nematodes, carrion crows

51

## Introduction

Increased parasite transmission is considered a major cost of group living (Alexander 1974). Recently it has been suggested that certain aspects of group living confer benefits that reduce the costs of parasite infection (Ezenwa et al. 2016). Such benefits include social immunization, microbially-mediated resistance and socially mediated tolerance (Ezenwa et al. 2016). This means that under certain conditions group living could be advantageous rather than costly in terms of parasite infection.

Initially, group size has been hypothesized to be positively associated with parasite infection risk (Côté and Poulin 1995; Loehle 1995), whereas recent research hints towards the possibility of group size being a weak predictor of parasite infection risk (Rifkin et al. 2012) or negatively associated with parasite intensities (Patterson and Ruckstuhl 2013). Instead, behavior of animals in social groups, for example frequency of social interactions and connectedness, affects infection rates among group members (Rimbach et al. 2015; Balasubramaniam et al. 2019; Habig et al. 2019). Next to social interactions (Duboscq et al. 2016; Romano et al. 2016; VanderWaal et al. 2016), physiological processes that allow for increased parasite replication or survival in the host can significantly affect an individual's susceptibility to parasites. For example, social behavior can significantly affect an individual's physiological stress response (Wascher et al. 2009; Wittig et al. 2015), which can affect the immune system and make individuals more susceptible to parasite infections (Apanius 1998; Akinyi et al. 2019). Otherwise, parasitic infections affect an individual's ability to engage in social behavior (Sheridan et al. 1994; von Holst 1998; Hanley and Stamps 2002; DeVries et al. 2003; Klein 2003; Lopes et al. 2016). Behavioral effects on an individual's physiology and immune system range from relatively short-term, as in the effect on disease susceptibility

76    (McEwen et al. 1997), to long-term, as in the effects on reproductive outcome (Buchholz

77    1995; Marzal et al. 2005; Hillegass et al. 2010) and have serious impacts on host longevity

78    (Rousset et al. 1996; Archie et al. 2014).

79

80    The social environment can either facilitate or inhibit susceptibility and exposure to

81    parasitism. Adverse effects of the social environment on health and susceptibility to

82    parasites may be caused, for example, by increased competition and aggressive behavior

83    (Azpiroz et al. 2003; Hawley et al. 2006; Chester et al. 2010). In meerkats, receiving but not

84    initiating aggressive interactions was positively correlated with increased susceptibility of

85    tuberculosis infection (Drewe 2010). Social status also affects an individual's risk to be

86    infected with parasites. A recent meta-analysis shows dominant individuals facing a higher

87    parasite risk compared to subordinate individuals. This effect is mediated by social system

88    (linear versus egalitarian hierarchies) and mating effort (Habig et al. 2018). In baboons

89    (*Papio cynocephalus*), high-ranking males were less likely to become ill, and they recovered

90    more quickly than low-ranking males (Archie et al. 2012).

91

92    Affiliative social interactions have been found to be associated with both increased and

93    reduced risk of parasite infection. In rhesus macaques, *Macaca mulatta*, allo-grooming

94    mediated transmission of *Escherichia coli* and central individuals in the social network could

95    be considered 'super-spreaders' (Balasubramaniam et al. 2019). In Cape ground squirrels,

96    *Xerus inauris,* increased durations of allo-grooming were associated with lower counts of

97    ectoparasites (Hillegass et al. 2008). In northern bald ibis (*Geronticus eremita*) initiating

98    more affiliative interactions was associated with lower excretion of parasite products

99    (Puehringer-Sturmayr et al. 2018), potentially by having a stress-reducing effect, which in

100    turn might positively affect an individual's immune system (Sachser et al. 1998; Frigerio et al.

101    2003; Stöwe et al. 2008; Young et al. 2014; Müller-Klein et al. 2019). In a captive population

102    of cooperatively breeding carrion crows, individuals with strong affiliative relationships

103    excreted less samples containing coccidian oocysts (Wascher et al. 2019).

104

105        In the present study, I investigate associations between social behavior and

106    gastrointestinal parasite burden in the carrion crow, *Corvus coro*ne. Corvids express high

107    variability in their social organization depending on life history and ecological factors. Within

108    species, the social organization might vary between different life history stages, seasons or

109    populations. For example, in most European populations, carrion crows form socially

110    monogamous pairs during the breeding season and large flocks during the rest of the year

111    (Meide 1984; Glutz von Blotzheim 1985), whereas in northern Spain, crows live in stable

112    social groups of up to nine individuals, consisting of the breeding pair and retained offspring

113    as well as immigrants, which are in most cases male individuals (Baglione et al. 2003). Group

114    living in carrion crows is linked to a higher level of cooperation, for example, in nestling

115    provisioning (Baglione et al. 2005). Within their social groups, corvids establish valuable

116    social relationships, characterized by spatial proximity, high levels of tolerance, relatively low

117    frequencies of aggressive interactions and relatively high frequencies of affiliative behaviors

118    (Fraser and Bugnyar 2010; Heinrich 2011). Within such valuable relationships, individuals

119    support one another in agonistic encounters (Emery et al. 2007; Fraser and Bugnyar 2012)

120    and share information and resources (Bugnyar et al. 2001; de Kort et al. 2003). Monogamous

121    pair-bonds in corvids are characterized by complex social interactions that demand a high

122    level of cooperation, coordination and affiliation between the paired individuals, which may

123    explain, in turn, the evolution of advanced cognitive skills ('relationship intelligence': Emery

124   et al. 2007; Wascher et al. 2018). Corvids usually establish linear dominance hierarchies

125   (Izawa and Watanabe 2008). In a previous study on a cooperatively breeding population of

126   captive carrion crows, individuals with strong affiliative bonds excreted a smaller proportion

127   of samples containing coccidian oocysts as did individuals living in larger groups (Wascher et

128   al. 2019).

129

130      Here, I investigate the association between aspects of the social environment of non-

131   cooperatively breeding captive carrion crows (strength of affiliative relationships, dominance

132   hierarchy, and group structure) and fecal egg count. Fecal egg counts provide a reliable

133   estimate of parasite infection rates (Seivwright et al. 2004; Daş et al. 2011). Further, I

134   compare the results of the present study with the previously published data in Wascher et

135   al. (2019). I expect a positive social environment, such as engaging in strong affiliative

136   relationships, to reduce excretion of parasite eggs and oocysts. In the previous study,

137   individual position in the dominance hierarchy was not correlated with eggs and oocysts

138   excretion patterns and I expect to confirm these results. Lastly, I investigate the association

139   between group size (i.e., pairs or trios versus flocks of eight or nine individuals) and parasite

140   product excretion. Parasite transmission may be expected to be facilitated by an increase in

141   group size, however, in line with Wascher et al. (2019), I expect to find a negative

142   association between group size and the number of parasite eggs and oocysts excreted by

143   individuals.

144

**Methods**

*Study subjects and ethics statement*

I collected the data for this study in four phases, between 2008-2010 and between 2012-2015 from a population of captive carrion crows housed in large outdoor aviaries at the Konrad Lorenz research station (KLF), Grünau, Upper Austria (47°51'02 N 13°57'44 E). I observed 21 individuals (10 males and 11 females), kept in different group formations, such as groups of eight or nine individuals and pairs or trios. Due to the long-term character of the present study, individual birds were opportunistically moved between different compartments and group compositions due to age, reproduction, group expansion or the death of individual birds (Table 1). Aviaries were approximately 20-45 $m^2$ and were equipped with wooden perches, natural vegetation and rocks. At the start of the study (2008), groups were kept in the large aviary (45 $m^2$) and then consecutively moved into smaller compartments when separated into pairs and trio. In January 2012, all birds were moved into same sized compartments (20 $m^2$). An enriched diet consisting of fruit, vegetables, bread, meat and milk products was provided on a daily basis. Water was available *ad libitum* for both drinking and bathing. This study complied with Austrian and local government guidelines. Individuals remain captivity housed in the Cumberland game park and the KLF (under the license AT00009917), before and after completion of the present study. Data collection was entirely non-invasive, and no further animal experimental license was required (http://www.ris.bka.gv.at/GeltendeFassung.wxe?Abfrage = Bundesnormen&Gesetzesnummer = 10010558).


*Behavioral data*

I conducted a total of 899 individual focal observations. Each observation lasted five minutes, and I recorded all occurring behaviors. For this study, I focused on the frequencies

170    of agonistic behavior (threat, chase flight, and fight) and affiliative behaviors (allopreen and

171    contact sit). I recorded the identity, role (initiator/receiver) of interacting individuals and the

172    outcome of the agonistic interaction (winner/loser), with the loser of an agonistic interaction

173    defined as the individual that retreated.

174

175    *Composite sociality index*

176    For each phase of data collection, I calculated a composite sociality index (CSI) for each

177    crow dyad within a group according to Silk et al. (2010). I included two affiliative behaviors,

178    namely contact sitting and allopreening, to calculate the CSI. Following Archie et al. (2014) I

179    corrected for different observational effort between individuals by regressing CSI against the

180    number of observations per individual. The residuals from the regression presented the

181    'corrected CSI' (will be referred to as CSI from here onwards). The higher the CSI of a dyad,

182    as compared with the frequency of the affiliative interactions observed within that dyad's

183    group, the stronger the affiliative bond between the two individuals in that dyad. For

184    statistical analysis, I used the maximum CSI among all dyads for each individual, which

185    reflected their strongest affiliative relationship within the group. For descriptive purposes, I

186    classified dyads as 'bonded' when they displayed a higher CSI than the average of the entire

187    sample and lower rates of aggression than the average of the entire group.

188

189    *Elo-rating*

190    I calculated the relative success levels of individuals in agonistic encounters as an Elo-

191    rating in the R package '*aniDom*' (version 0.1.4; Sánchez-Tójar et al. 2018). Elo-rating allows

192    to track dynamic changes in rank over the different phases of data collection. Each individual

193    was rated based on the outcome of each discrete interaction (winner / loser) and the

194 (predicted) probability of that outcome occurring (Neumann et al. 2011). Similar to above, I

195 calculated a 'corrected Elo-rating' to correct for different observational effort between

196 individuals by regressing Elo-rating against the number of observations per individual. The

197 residuals from the regression presented the 'corrected Elo-rating' (will be referred to as Elo-

198 rating from here onwards).

199

200 *Parasitological examination*

201     During the entire study period, I collected a total of 559 individual droppings directly after

202 defecation (for a detailed overview see Table 1). I determined individual gastrointestinal

203 parasite load from droppings. From 2008 until November 2011, I used a modified version of

204 the flotation method (Schnieder et al. 2006). I suspended the fresh droppings (0.1 g) in a 2

205 ml collection tube with 1 ml saturated saline. I shook collection tubes for 10 seconds and

206 afterwards centrifuged for 5 minutes at 3000 rpm. After centrifugation, I filled the collection

207 tubes with saline solution and positioned a cover slip (18 x 18 mm) onto the tube. The high

208 density of the saline solution causes the parasite eggs and oocysts to float up and be caught

209 on the cover slip (Carta and Carta 2000). After 10 minutes, I moved the cover slip onto an

210 object slide and identified and counted the parasite eggs and oocysts (by size and shape).

211 From December 2011 onwards, I used a McMaster counting chamber. I weighted the entire

212 dropping, then diluted with 3 ml saturated NaCl solution per 0.1 g of dropping and mixed

213 thoroughly. Afterwards, I poured the solution into both compartments of the McMaster

214 counting chambers. After a 10-minute resting period, I counted the number of parasite eggs

215 and oocysts in each compartment and calculated the number of parasite products per 1 ml

216 of dropping.

217

218    I used a compound microscope with 100-fold and 400-fold amplification for parasite

219    examination to identify coccidian oocysts, several nematode species (*Capillaria* sp., *Ascarida*

220    sp., *Syngamus* sp. and *Heterakis* sp., *Trichostrongylus tenius*) and cestodes to a varying

221    degree (Table 2). I used presence versus absence of parasite eggs and oocysts for further

222    analysis, which allowed a direct comparison between the two applied methods of droppings

223    examination (flotation versus McMaster). As only nine samples contained cestodes, I

224    conducted no further statistical analysis on this parasite group.

225

226    *Data analysis*

227    All data was analysed by CAFW. During behavioral data collection the author was

228    blind to the outcome of parasitological examination and vice versa. I analyzed factors

229    affecting the proportion of droppings containing coccidian oocysts and nematode eggs in

230    crows using the *glmer* function in R (version 3.5.3; R Core Team 2019) in the *lme4* package

231    (version 1.1-19; Bates et al. 2015). In two models, the number of samples containing

232    nematode eggs or coccidian oocysts for each period of data collection was the response

233    term. I calculated GLMMs with binomial error distribution and a two-vector response

234    variable comprising the number of infected and non-infected samples for each individual in

235    each phase. I employed various model diagnostics to confirm model validity (visual

236    inspection of the distribution of residuals, Q-Q plots, residuals plotted against fitted values),

237    none of which suggested violation of the model's assumptions. To assess multicollinearity

238    between fixed factors, I calculated variance inflation factors (VIFs) using the *vif* function in

239    the package *car* (version 3.0-6; Fox and Weisberg 2011). VIFs for all models were below 1.6,

240    indicating that there was no issue with multicollinearity (Zuur et al. 2009). Strength of

241    affiliative relationships (CSI value), social structure (pair/trio or group), number of related

242 individuals, sex and Elo-rating were included as explanatory variables. For each model, I

243 fitted individual identity as a random term to control for the potential dependence

244 associated with multiple samples from the same individuals. The statistical significance level

245 was adjusted to $P \leq 0.025$ following Bonferroni, to account for multiple testing of coccidia

246 oocysts and nematode eggs. In addition to the main analysis, I compared the results based

247 on the present dataset (collected from a non-cooperatively breeding population of captive

248 carrion crows) with those based on a previously published data (from a cooperatively

249 breeding population) (Wascher et al. 2019). Data collection and analysis (for example

250 calculation of CSI and Elo-rating scores) were comparable in both studies. In order to

251 investigate potential differences in social structure between the two populations, I

252 compared the number of social relationships applying a GLMM with Poisson error

253 distribution, as well as CSI value and Elo-rating applying two general linear models (GLMs)

254 with Gaussian error distribution. Population was included as explanatory variable, individual

255 identity was fitted as a random term in each model and I calculated models in the *lme4*

256 package.

257

258 *Data availability statement*

259      The datasets generated and/or analysed during the current study are available in the

260 Open Science Framework repository, https://osf.io/3ytpf/.

261

262

263 **Results**

264 *Social relationships*

265       I observed 30 bonded dyads (out of 213 dyads in total), of which 19 were male-

266 female dyads (five between related individuals and 14 between unrelated individuals). Six

267 dyads were male-male dyads (all between unrelated individuals) and five female-female

268 dyads (all between unrelated individuals). On average (± SD), males and females had 2.125

269 (± 1.642) and 1.625 (± 1.505) bonded partners, respectively. The mean CSI (± SD) between

270 bonded dyads was 2.467 (± 2.165) for male-female, 2.258 (± 1.744) for female-female and

271 3.911 (± 2.062) for male-male bonds. Neither the number of social bonds, the CSI value or

272 Elo-rating differed between the cooperatively breeding and non-cooperatively breeding

273 populations of crows (number of social bonds: estimate ± SE = -0.157 ± 0.363, z = -0.433, P =

274 0.664; CSI: estimate ± SE = -0.154 ± 0.748, z = -0.206, P = 0.836; Elo-rating: estimate ± SE = -

275 9.733 ± 54.373, z = -0.179, P = 0.857).

276

277 ***Occurrence of coccidian oocysts and nematode eggs***

278       243 samples from 18 individuals contained coccidian oocysts (43 % compared to 31 %

279 in the Spanish population of cooperatively breeding crows). Crows kept in groups of eight or

280 nine individuals excreted less samples containing coccidian oocysts compared to crows kept

281 in pairs or trios (estimate ± SE = 0.986 ± 0.276, z = 3.564, P < 0.001, Fig. 1). Higher ranking

282 individuals excreted fewer samples containing coccidian oocysts than lower ranking

283 individuals (estimate ± SE = -0 ± 0, z = -2.167, P = 0.03, Fig. 2). However, the number of

284 samples containing coccidian oocysts was not related to number of related individuals in the

285 group, CSI (after Bonferroni correction) and sex (Table 3a).

286

287        Overall, 172 samples, collected from 14 individuals contained nematode eggs (31 %

288    compared to 9 % in the Spanish population of cooperatively breeding crows). None of the

289    factors investigated significantly affected excretion patterns of nematode eggs (Table 3b).

290

291

**Discussion**

In this study, individuals from a population of non-cooperatively breeding carrion crows excreted less samples containing coccidian oocysts when kept in larger groups (8 or 9 individuals) compared to those individuals kept in smaller groups (2 or 3 individuals). Further, lower-ranking individuals excreted more samples containing parasite oocysts compared to higher-ranking individuals. A similar association between group-size and parasite excretion patterns was found in a population of cooperatively breeding carrion crows (Wascher et al. 2019). However, other patterns in the present study did not replicate previous findings. In a group of cooperatively breeding crows, the proportion of samples containing coccidian oocysts was negatively correlated with the strength of affiliative social relationships, but dominance hierarchy did not affect parasite excretion patterns (Wascher et al. 2019).

The present study suggests that variation in the social system within a species can result in differences in parasite product excretion patterns. Here, in a population of non-cooperatively breeding carrion crows, subordinate individuals excreted more samples containing coccidian oocysts. In contrast, no such association was found in a population of cooperatively-breeding carrion crows (Wascher et al. 2019). In a way this is surprising, as dominance is a mechanism to suppress reproduction in subordinate individuals in some cooperatively breeding mammalian species (Creel et al. 1992; Young et al. 2006) and I would have expected an effect of rank position on parasite excretion patterns in the cooperatively breeding population of carrion crows, but not in the non-cooperatively breeding group. On the other hand, avian cooperatively breeding societies have often been described as highly tolerant, especially towards related individuals (Baglione et al. 2003; Dickinson et al. 2009),

316 which could explain the present results. The relationship between social rank, glucocorticoid

317 excretion and immune function is a complex one and can depend on factors like mating

318 system, costs of rank acquisition and maintenance, or social stability (Goymann and

319 Wingfield 2004; Cavigelli and Chaudhry 2012; Beehner and Bergman 2017; Habig et al.

320 2018). Further, the relationship between glucocorticoids and parasite burden might not be

321 linear, and only high levels of physiological stress might influence parasite infection (Romeo

322 et al. 2020). In two recent meta-analyses on several vertebrate taxa, dominant individuals

323 exhibited higher parasite burden compared to subordinates, especially in linear versus

324 egalitarian hierarchies and in mating systems where dominance rank predicts mating effort

325 (Habig and Archie 2015; Habig et al. 2018). This is in contrast to the results of the present

326 study. Carrion crows also can be considered to form linear and stable hierarchies (Chiarati et

327 al. 2010), with dominant individuals gaining priority of access to resources such as food

328 (Chiarati et al. 2011). In Siberian hamsters, *Phodopus sungorus*, social defeat affects immune

329 function (Chester et al. 2010). Similar to the results in the present study, subordinate

330 individuals display a higher parasite burden in a variety of species (Guenons, *Cercopithecus*

331 *mitis*: Foerster et al. 2015; mice, *Mus musculus*: Rau 1983; plain zebra, *Equus* quagga:

332 Fugazzola and Stancampiano 2012). Higher levels of parasite excretion in subordinate

333 individuals might reflect higher exposure to psychosocial stressors compared to dominant

334 individuals (Levy et al. 2020).

335

336      I did not find an effect of sex on parasite excretion patterns. Differences in parasite

337 burden between the sexes are mostly mediated by endocrine-immune interactions (Zuk and

338 McKean 1996; Klein 2004). For example, high levels of testosterone are expected to be

339 positively correlated with high parasite burden (Hudman et al. 2000; Decristophoris et al.

340     2007). Related to this, males are usually expected to have higher levels of endoparasites

341     compared to females. However, this pattern does not hold in all species. Similar to the

342     present study in carrion crows, a relationship between sex and parasite excretion was

343     missing, for example, in red-fronted lemurs, *Eulemur fulvus rufus* (Clough et al. 2010), brown

344     mouse lemur, *Microcebus rufus* (Rafalinirina et al. 2019), and four species of songbirds

345     (Granthon and Williams 2017). Data for the present study was collected throughout the year

346     in non-reproductively active birds, hence sex-steroid levels are expected to be generally low

347     (Soma 2006; Hau et al. 2008), and therefore both sexes might have been similarly

348     susceptible to parasite infection in the studied population.

349

350         Increased exposure to parasites and disease transmission is considered as one of the

351     major disadvantages of group living. Group size is usually positively related to parasite

352     burden, which is seen as a major selective force in group living animals (Côté and Poulin

353     1995; Rifkin et al. 2012; Patterson and Ruckstuhl 2013). Similar to a previous study in captive

354     cooperatively breeding carrion crows, individuals in the present study excreted less samples

355     containing coccidian oocysts when living in larger groups. A limitation of the present study is

356     the fact that I only used two categories of group size (2-3 and 8-9 individuals). Individuals

357     were grouped together in these categories opportunistically. Juvenile crows in the wild form

358     'non-breeder flocks' (Meide 1984; Glutz von Blotzheim 1985), usually larger than 8-9

359     individuals, however group sizes at the study site needed to be kept small in order for them

360     to be manageable. It had to be considered that groups size and parasite load are associated

361     in a non-linear manner, which could not be assessed in the present study (Hopkins et al.

362     2020). Infection by parasites in group living animals can be caused by different mechanisms.

363     For example, parasites can be transmitted directly during social interactions, hence

364    individuals engaging more socially are at greater risk of infection. Parasite infection can also

365    be related to physiological processes, which allow parasites increased replication or survival

366    in the host, for example, a compromised immune system, mediated by the physiological

367    stress response (Muehlenbein and Watts 2010). Unfortunately, in the present study I have

368    not measured individual stress levels and therefore cannot verify an association between

369    parasite excretion patterns and levels of stress. The relationships between the physiological

370    stress response, the immune system, and susceptibility to parasites are quite complex. A

371    recent meta-analysis of 110 records from 65 studies in mammalian hosts from experimental

372    and observational studies generally indicated a positive relationship between glucocorticoids

373    and parasite burden (Defolie et al. 2020), however, overall results about the relationship are

374    complex. Future studies investigating the direct link between social behavior, physiological

375    stress response and parasite excretion patterns would be desirable.

376

377        In contrast to Wascher et al. (2019), strengths of affiliative social relationships were

378    not associated with the proportion of samples containing coccidian oocysts. Neither the

379    strength nor the number of affiliative relationships differed significantly between the subject

380    populations in these studies. Therefore, it does not seem that populations show a general

381    behavioral difference in affiliative relationships within groups. In cooperatively breeding

382    crows, individuals with strong affiliative relationships excreted less samples containing

383    coccidian oocysts (Wascher et al. 2019), which could reflect a stress reducing and immune

384    system enhancing function of affiliative social relationships. Strong relationships between

385    pair-partners, between kin, and also between non-paired and unrelated individuals play a

386    significant role in the social life of corvids, and have been hypothesized to be an important

387    driver in the evolution of cognition (Emery et al. 2007). I expected to find, but was unable to

388    confirm in the present study, that the nature of an individual's social relationships would

389    affect their health and physiology. This is especially interesting as dominance rank was

390    negatively correlated with the proportion of samples excreted containing coccidian oocysts.

391    Aggressive social interactions have previously been shown to be among the most potent

392    stressors (Wascher et al. 2008) and position in the hierarchy is related to stress (Creel 2001)

393    and immunodepression (Barnard et al. 1998) in a number of species. Social relationships

394    have been suggested to mitigate the effects of aggression onto the physiological stress

395    response (Sachser et al. 1998) and therefore I would have expected to find an effect of

396    strength of affiliative relationships on parasite product excretion in carrion crows.

397

398         In the present study, the excretion of coccidian oocysts but not excretion of

399    nematode eggs was found to be related to social factors. These results replicated those of

400    Wascher et al. (2019) and may be related to differences between these parasite species in

401    their lifecycles. Coccidian oocysts have a shorter prepatent period compared to nematode

402    eggs (Edgar 1955; French and Zachary 1994). This could potentially make them more

403    sensitive to short-term changes in stress levels and immune system. This is supported by a

404    study in carrion crows, showing coccidian oocysts, but not nematode eggs to significantly

405    increase in the first week after a major stressor (Spreafico et al. 2012). In graylag geese,

406    excretion of coccidian oocysts, but not nematode eggs are significantly increased in the first

407    week after social isolation (Ludwig et al. 2017).

408

409         In summary, more droppings containing coccidian oocysts were excreted by individuals

410    kept in pairs and trios compared to groups of eight or nine individuals. Strength of affiliative

411    social relationships did not correlate with parasite product excretion; however, subordinate

412    individuals excreted more samples containing coccidian oocysts compared to dominant

413    individuals. The present results illustrate differences in the social system in carrion crows

414    also resulting in different associations between social environment and parasite product

415    excretion.

416

434
435    ***Informed consent***


436    Not applicable.

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701 Figure Captions
702
703 **Fig. 1**
704 Percentage of samples containing coccidian oocysts in carrion crow droppings in relation to
705 the group structure. Box plots show the median, the interquartile range from the 25th to the
706 75th percentiles. The upper whisker is the maximum value of the data that is within 1.5
707 times the interquartile range over the 75th percentile. The lower whisker is the minimum
708 value of the data that is within 1.5 times the interquartile range under the 25th percentile.
709
710
711 **Fig. 2**
712 Percentage of samples containing coccidian oocysts in carrion crow droppings in relation to
713 individual Elo-ratings
714

715 **Table 1** List of all focal individuals and information about population, sex (F = female, M = male), age (year of hatching; if not known, individuals
716 are classified as adult), group (group composition: family, flock, pair, trio), phases of data taking during which the individual was recorded (G08:
717 March to May, November to December 2008; G09: September to December 2009; G10: January to June 2010; G12: January to July 2012; G15:
718 May to July 2015), number of droppings and behavioral focal observations collected, maximum composite sociality index (CSI) and Elo-rating
719 (corrected for observational effort)
720

| | Sex | Age | Group | Phase | Droppings | Observations | Maximum CSI | Elo-rating |
|---|---|---|---|---|---|---|---|---|
| **Baerbel** | F | 2012 | Pair | G15 | 6 | 4 | 0.2 | 0 |
| **Baerchen** | M | 2008 | Group | G09 | 10 | 31 | 0.851 | -415.963 |
| | | | Pair | G10 | 7 | 34 | -0.654 | -95.607 |
| | | | | G12 | 40 | 24 | -3.493 | -121.425 |
| | | | | G15 | 10 | 4 | 4.613 | -170.479 |
| **Franz** | M | 2007 | Group | G08 | 8 | 48 | 6.046 | -373.713 |
| | | | Pair | G09 | 4 | 30 | -2.34 | -591.204 |
| | | | | G10 | 4 | 3 | -4.189 | -575.713 |
| | | | | G12 | 34 | 24 | -1.195 | -593.785 |
| **Fritz** | M | 2008 | Group | G09 | 2 | 9 | 3.018 | 140.418 |
| **Gabi** | F | 2007 | Group | G08 | 6 | 39 | -5.234 | 42.354 |
| | | | | G09 | 14 | 28 | -1.093 | 248.54 |
| | | | Pair | G10 | 4 | 27 | -3.841 | 192.931 |
| | | | Trio | G10 | 2 | 4 | -3.841 | 192.931 |
| | | | Trio | G12 | 43 | 24 | -3.493 | 178.891 |
| **Gertrude** | F | 2011 | Pair | G12 | 33 | 24 | 0.871 | -169.628 |
| **Hitchcock** | M | 2007 | Group | G08 | 2 | 48 | 3.259 | 220.656 |
| | | | | G09 | 4 | 22 | 5.691 | 300.681 |
| **Hugo** | M | 1989 | Group | G08 | 2 | 33 | 7.385 | -27.644 |
| | | | | G09 | 9 | 27 | -3.001 | -118.429 |
| | | | Trio | G10 | 5 | 5 | -0.706 | -203.628 |
| **Klaus** | M | 2009 | Group | G08 | 13 | 10 | 0.384 | 350.719 |

| | | | | G09 | 5 | 14 | -1.483 | 359.999 |
|---|---|---|---|---|---|---|---|---|
| | | | Trio | G12 | 33 | 25 | -2.518 | 377.277 |
| **Mate** | M | 2008 | Group | G09 | 2 | 45 | -0.018 | -144.222 |
| **Munin** | F | 2014 | Trio | G15 | 13 | 6 | -1.296 | -140.388 |
| **Olaf** | F | adult | Pair | G12 | 2 | 4 | -1.17 | -6.211 |
| **Peter** | F | 2007 | Group | G08 | 3 | 52 | 7.564 | 344.312 |
| | | | | G09 | 10 | 56 | -0.911 | -0.31 |
| | | | Pair | G10 | 6 | 33 | -4.538 | -408.302 |
| | | | | G12 | 48 | 24 | -3.493 | -431.538 |
| | | | | G15 | 11 | 7 | 2.578 | -476.962 |
| **Pinky** | F | 2008 | Group | G08 | 7 | 10 | 5.287 | 393.195 |
| **Resa** | F | 2009 | Trio | G12 | 35 | 24 | -3.493 | 126.195 |
| **Ronja** | F | 2008 | Group | G08 | 2 | 8 | 0.75 | 211.466 |
| **Ruediger** | M | adult | Pair | G12 | 2 | 4 | -1.17 | -6.211 |
| **Sissi** | F | 2008 | Group | G08 | 2 | 9 | 3.018 | 228.64 |
| **Toeffel** | F | 2008 | Group | G08 | 3 | 20 | 1.741 | -103.002 |
| | | | | G09 | 8 | 37 | 17.919 | 39.523 |
| | | | Pair | G12 | 38 | 23 | -1.195 | 3.378 |
| **Walter** | M | 2011 | Pair | G12 | 37 | 24 | -1.311 | 260.476 |
| | | | | G15 | 7 | 6 | -1.296 | 216.679 |
| **Willi** | M | 2012 | Trio | G15 | 7 | 5 | -1.179 | 135.711 |

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724    **Table 2** Number of samples containing and not containing different parasite products

|  | Number of samples containing | Number of samples not containing | Total number of samples |
|---|---|---|---|
| nematode eggs | 387 | 172 | 559 |
| coccidian oocysts | 316 | 243 | 559 |
| cestodes | 9 | 550 | 559 |

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726 **Table 3** Results of the generalized mixed linear model investigating factors affecting patterns
727 of coccidian oocyst and nematode egg excretion. Models investigate effects of group
728 structure, number of related individuals (Nr related), strength of affiliative relationships
729 (CSI), sex and dominance hierarchy (Elo-rating) on presence or absence of (a) coccidian
730 oocysts and (b) nematode eggs in the sample. Significant values ($p \leq 0.05$) are highlighted in
731 bold

|  | | Parameters | Estimate ± SE | *z* | *p* |
|---|---|---|---|---|---|
| (a) Coccidia | | **Intercept** | **-1.115 ± 0.283** | **-3.929** | **<0.001** |
| | | **Group structure** | **0.99 ± 0.291** | **3.401** | **<0.001** |
| | | Nr related | -1.12 ± 0.633 | -1.768 | 0.077 |
| | | CSI | 0.073 ± 0.036 | 1.997 | 0.045 |
| | | **Elo-rating** | **-0 ± 0** | **-2.49** | **0.012** |
| | | Sex | -0.077 ± 0.181 | -0.424 | 0.67 |
| (b) Nematodes | | **Intercept** | **-1.155 ± 0.475** | **-2.433** | **0.014** |
| | | Group structure | 0.337 ± 0.331 | 1.017 | 0.308 |
| | | Nr related | -1.169 ± 0.631 | -1.852 | 0.063 |
| | | CSI | 0.035 ± 0.044 | 0.799 | 0.423 |
| | | Elo-rating | 0 ± 0 | 0.853 | 0.393 |
| | | Sex | -0.215 ± 0.548 | -0.393 | 0.693 |

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