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   The social environment strongly affects the physiological stress response in group

26 living animals, which in turn can affect the immune system and increase susceptibility to

27 parasites. Here, I investigate relationships between social behavior and gastrointestinal

28 parasite product excretion in the carrion crow (*Corvus corone*). Individuals from a population

29 of non-cooperatively breeding carrion crows excreted less samples containing coccidian

30 oocysts when kept in larger groups (8 or 9 individuals) compared to those individuals kept in

31 smaller groups (2 or 3 individuals). Lower-ranking individuals excreted more samples

32 containing parasite oocysts compared to higher-ranking individuals. The strength of

33 affiliative relationships and number of related individuals in the group did not relate to the

34 proportion of droppings containing coccidian oocysts. The present results confirm an

35 association between social environment and parasite excretion patterns in carrion crows,

36 but the patterns described in the present study differ from previously published data

37 derived from a group of cooperatively breeding crows. This illustrates that differences

38 between the social systems of carrion crows might result in different associations between

39 the social environment and parasite product excretion patterns.

40

41 **Significance statement**

42 One major cost of group living is an increase in susceptibility to parasites, however not all

43 group living animals are affected by this in the same way. A better understanding how social

44 behavior is associated with parasite burden can help to better understand evolution of

45 group living. This study attempts to investigate associations between dominance rank,

46 affiliative relationships as well as groups size and gastrointestinal parasite product excretion

47 in a group of captive carrion crows. Lower-ranking individuals excreted more samples

48   containing parasite oocysts compared to higher-ranking individuals, confirming an

49   association between social relationships within the groups (for example dominance rank)

50   and parasite excretion patterns.

51

52   *Key words:* social relationships, affiliation, aggression, parasites, coccidian oocysts,

53   nematodes, carrion crows

54

55   **Introduction**

56   Increased parasite burden is considered a major cost of group living (Alexander 1974).

57   Initially group size has been hypothesized to be positively associated with parasite infection

58   risk (Cote and Poulin 1995; Loehle 1995), whereas recent research hints towards the

59   possibility of group size being a weak predictor of parasite infection risk (Rifkin et al. 2012)

60   or negatively associated with parasite intensities (Patterson and Ruckstuhl 2013). Instead,

61   behavior of animals in social groups for example frequency of social interactions and

62   connectedness affects infection rates among group members (Rimbach et al. 2015;

63   Balasubramaniam et al. 2019; Habig et al. 2019). Next to social interactions (Duboscq et al.

64   2016; Romano et al. 2016; VanderWaal et al. 2016), physiological processes that allow for

65   increased parasite replication or survival in the host can significantly affect an individual's

66   susceptibility to parasites. For example, social behavior can significantly affect an individual's

67   physiological stress response (Wascher et al. 2009; Wittig et al. 2015), which can affect the

68   immune system and make individuals more susceptible to parasite infections (Apanius 1998;

69   Akinyi et al. 2019). Otherwise, parasitic infections affect an individual's ability to engage in

70   social behavior (Sheridan et al. 1994; von Holst 1998; Hanley and Stamps 2002; DeVries et al.

71   2003; Klein 2003; Lopes et al. 2016). Behavioral effects on an individual's physiology and

72   immune system range from relatively short-term, as in the effect on disease susceptibility

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

74   1995; Marzal et al. 2005; Hillegass et al. 2010) and have serious impacts on host longevity

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

76

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

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

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

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

81   initiating aggressive interactions was positively correlated with increased susceptibility of

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

83   infected with parasites. A recent meta-analysis shows dominant individuals to suffer a higher

84   risk to be infected compared to subordinate individuals and this effect to be mediated by

85   social system (linear versus egalitarian hierarchies) and mating effort (Habig et al. 2018). In

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

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

88

89   Affiliative social interactions hold a risk of increased disease and parasite transmission.

90   In rhesus macaques, *Macaca mulatta*, allo-grooming mediated transmission of *Escherichia*

91   *coli* and central individuals in the social network could be considered 'super-spreaders'

92   (Balasubramaniam et al. 2019). In Cape ground squirrels, *Xerus inauris,* increased durations

93   of allo-grooming was associated with lower counts of ectoparasites (Hillegass et al. 2008).

94   Affiliative behaviors also affect physiological processes which might affect the immune

95   system, for example they have a stress-reducing effect (Sachser et al. 1998; Frigerio et al.

96   2003; Stöwe et al. 2008; Young et al. 2014; Müller-Klein et al. 2019) and might positively

97   affect an individual's immune system. In a captive population of cooperatively breeding

98   carrion crows, individuals with strong affiliative relationships excreted less samples

99   containing coccidian oocysts (Wascher et al. 2019).

100

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

116   share information and resources (Bugnyar et al. 2001; de Kort et al. 2003). Affiliative

117   relationships, are preferably formed with kin, but also non-kin individuals, in which case,

118   long-term monogamous pair-bonds may ultimately develop (Loretto et al. 2012).

119   Monogamous pair-bonds in corvids are characterized by complex social interactions, that

120   demand a high level of cooperation, coordination and affiliation between the paired

121   individuals, which may explain, in turn, the evolution of advanced cognitive skills

122   ('relationship intelligence': Emery et al. 2007; Wascher et al. 2018). Social relationships,

123   facilitate individuals in gaining access to resources, for example food or territories, and

124   individuals in social relationships are more likely to win agonistic encounter through

125   coalitional support (Bugnyar 2013). Outside such valuable social relationships corvids act

126   more competitively (Bugnyar and Heinrich 2005; Bugnyar and Heinrich 2006) and usually

127   establish linear dominance hierarchies (Izawa and Watanabe 2008). In a previous study on a

128   cooperatively breeding population of captive carrion crows, strength of affiliative social

129   relationships, and group size but not dominance rank or sex correlated with excretion of

130   gastrointestinal parasite eggs and oocysts. Individuals with strong affiliative bonds excreted

131   a smaller proportion of samples containing coccidian oocysts as did individuals living in

132   larger groups (Wascher et al. 2019).

133

134   In the present study, I investigate the association between aspects of the social

135   environment of non-cooperatively breeding captive carrion crows (strength of affiliative

136   relationships, dominance hierarchy, and group structure) and fecal egg count. Fecal egg

137   counts provide a reliable estimate of parasite infection rates (Seivwright et al. 2004; Daş et

138   al. 2011). Further, I compare the results of the present study with the previously published

139   data in Wascher et al. (2019). I expect a positive social environment, such as engaging in

140   strong affiliative relationships, to reduce excretion of parasite eggs and oocysts. In the

141   previous study, individual position in the dominance hierarchy was not correlated with eggs

142   and oocysts excretion patterns. In the present study, I expect to confirm these results. Lastly,

143   I investigate the association between group size (*i.e.* pairs or trios versus flocks of eight or

144   nine individuals) and parasite product excretion. Parasite transmission may be expected to

145   be facilitated by an increase in group size, however, in line with Wascher et al. (2019), I

146   expect to find a negative association between group size and the number of parasite eggs

147   and oocysts excreted by individuals.

148

149 **Methods**

150 *Study subjects and ethics statement*

151   I collected the data for this study in four phases, between 2008-2010 and between 2012-

152 2015 from a population of captive carrion crows housed in large outdoor aviaries at the

153 Konrad Lorenz research station (KLF), Grünau, Upper Austria (47°51'02 N 13°57'44 E). I

154 observed 21 individuals (10 males and 11 females), kept in different group formations, such

155 as groups of eight or nine individuals and pairs or trios. Due to the long-term character of

156 the present study, individual birds were opportunistically moved between different

157 compartments and group compositions due to age, reproduction, group expansion or the

158 death of individual birds (Table 1). Aviaries were approximately 20-45 m^2 and were equipped

159 with wooden perches, natural vegetation and rocks. At the start of the study in 2008 groups

160 have been kept in the large aviary (45 m^2) and were consecutively moved into smaller

161 compartments when separated into pairs and trios. In January 2012, all birds were moved

162 into same sized compartments (20 m^2). An enriched diet consisting of fruit, vegetables,

163 bread, meat and milk products was provided on a daily basis. Water was available *ad libitum*

164 for both drinking and bathing. This study complied with Austrian and local government

165 guidelines. Individuals remain captivity housed in the Cumberland game park and the KLF

166 (under the license AT00009917), before and after completion of the present study.

167

168 *Behavioral data*

169   I conducted a total of 899 individual focal observations. Each observation lasted five

170 minutes, and I recorded all occurring behaviors. For this study, I focused on the frequencies

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

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

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

174   defined as the individual that retreated.

175

176   *Composite sociality index*

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

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

179   namely contact sitting and allopreening, to calculate the CSI. The higher the CSI of a dyad, as

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

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

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

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

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

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

186

187   *Elo-rating*

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

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

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

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

192   (predicted) probability of that outcome occurring (Neumann et al. 2011).

193

194   *Parasitological examination*

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

196   defecation (for a detailed overview see table 1). I determined individual gastrointestinal

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

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

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

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

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

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

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

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

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

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

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

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

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

210   of dropping.

211

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

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

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

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

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

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

218   conducted no further statistical analysis on this parasite group.

219

220

221   *Data analysis*

222   I analyzed factors affecting the proportion of droppings containing coccidian oocysts

223   and nematode eggs in crows using the *glmer* function in R (version 3.5.3; R Core Team 2019)

224   in the *lme4* package (version 1.1-19; Bates et al. 2015). In two models, the number of

225   samples containing nematode eggs or coccidian oocysts for each period of data collection

226   was the response term. I calculated GLMMs with binomial error distribution and a two-

227   vector response variable comprising the number of infected and non-infected samples for

228   each individual in each phase. I employed various model diagnostics to confirm model

229   validity (visual inspection of the distribution of residuals, Q-Q plots, residuals plotted against

230   fitted values), none of which suggested violation of the model's assumptions. To assess

231   multicollinearity between fixed factors, I calculated variance inflation factors (VIFs) using the

232   *vif* function in the package *car* (version 3.0-6; Fox and Weisberg 2011). VIFs for all models

233   were below 1.6, indicating that there was no issue with multicollinearity (Zuur et al. 2009).

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

235   of related individuals, sex and Elo-rating were included as explanatory variables. For each

236   model, I fitted individual identity as a random term to control for the potential dependence

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

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

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

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

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

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

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

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

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

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

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

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

249   package.

250

251 **Results**

252 *Social relationships*

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

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

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

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

257 (± 1.642) and 1.625 (± 1.505) bonded partners, respectively. The mean CSI (± SD) between

258 bonded dyads was 4.122 (± 2.612) for male-female, 2.561 (± 1.154) for female-female and

259 3.911 (± 2.062) for male-male bonds. Neither the number of social bonds, the CSI value or

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

261 populations of crows (number of social bonds: estimate ± SE = -0.085 ± 0.361, z = -0.235, P =

262 0.813; CSI: estimate ± SE = -0.582 ± 0.767, z = -0.758, P = 0.448; Elo-rating: estimate ± SE =

263 0.001 ± 0.001, z = 1.113, P = 0.265).

264

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

266   243 samples from 18 individuals contained coccidian oocysts (43 % compared to 31 %

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

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

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

270 individuals excreted fewer samples containing coccidian oocysts than lower ranking

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

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

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

274

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

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

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

278

279

280 **Discussion**

281   In this study, individuals from a population of non-cooperatively breeding carrion

282 crows excreted less samples containing coccidian oocysts when kept in larger groups (8 or 9

283 individuals) compared to those individuals kept in smaller groups (2 or 3 individuals).

284 Further, lower-ranking individuals excreted more samples containing parasite oocysts

285 compared to higher-ranking individuals. A similar association between group-size and

286 parasite excretion patterns was found in a population of cooperatively breeding carrion

287 crows (Wascher et al. 2019). However, other patterns in the present study contrast did not

288 replicate previous findings. In a group of cooperatively breeding crows, the proportion of

289 samples containing coccidian oocysts was negatively correlated with the strength of

290 affiliative social relationships, but dominance hierarchy did not affect parasite excretion

291 patterns (Wascher et al. 2019).

292

293   The present study suggests that variation in the social system within a species can

294 result in differences in parasite product excretion patterns. Here, in a population of non-

295 cooperatively breeding carrion crows, subordinate individuals excreted more samples

296 containing coccidian oocysts. In contrast, no such association was found in a population of

297 cooperatively-breeding carrion crows (Wascher et al. 2019). In a way this is surprising, as

298 dominance is a mechanism to suppress reproduction in subordinate individuals in some

299 cooperatively breeding mammalian species (Creel et al. 1992; Young et al. 2006) and

300 therefore I would have expected an effect of rank position onto parasite excretion patterns

301 in the cooperatively breeding population of carrion crows, but not in the non-cooperatively

302 breeding group. On the other hand, avian cooperatively breeding societies have often been

303 described highly tolerant, especially towards related individuals (Baglione et al. 2003;

304   Dickinson et al. 2009), which could explain the presented results. The relationship between

305   social rank, glucocorticoid excretion and immune function is a complex one and can depend

306   on factors like mating system, costs of rank acquisition and maintenance, or social stability

307   (Goymann and Wingfield 2004; Cavigelli and Chaudhry 2012; Beehner and Bergman 2017;

308   Habig et al. 2018). Further, the relationship between glucocorticoids and parasite burden

309   might not be linear, and only high levels of physiological stress might influence parasite

310   infection (Romeo et al. 2020). In two recent meta-analysis on several vertebrate taxa,

311   dominant individuals exhibited higher parasite burden compared to subordinates, especially

312   in linear versus egalitarian hierarchies and in mating systems where dominance rank predicts

313   mating effort (Habig and Archie 2015; Habig et al. 2018). This is in contrast to the results of

314   the present study. Carrion crows also can be considered to form linear and stable hierarchies

315   (Chiarati et al. 2010), with dominant individuals gaining priority access to resources such as

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

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

318   subordinate individuals display a higher parasite burden in a variety of species (Guenons,

319   Cercopithecus mitis: (Foerster et al. 2015). Higher levels of parasite excretion in subordinate

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

321   individuals (Levy et al. 2020).

322

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

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

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

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

327   2007). Related to this, males are usually expected to have higher levels of endoparasites

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

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

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

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

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

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

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

335   susceptibly to parasite infection in the studied population.

336

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

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

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

340   1995; Rifkin et al. 2012; Patterson and Ruckstuhl 2013). Similar to a previous study in captive

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

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

343   the fact that I only used limited number of different group sizes (2-3 and 8-9 individuals).

344   Individuals were grouped together in these categories opportunistically. Juvenile crows in

345   the wild form 'non-breeder flocks' (Meide 1984; Glutz von Blotzheim 1985), usually larger

346   than 8-9 individuals, however group sizes at the study site needed to be keep small in order

347   for them to be manageable. As adults, individuals typically form male-female pairs, and this

348   was the preferred social unit size I tried to achieve. Due to reasons of animal management, I

349   temporarily had to keep crows as trios, when I did not have additional individuals available

350   to form pairs. At all times I monitored groups of crows and in cases were levels of aggression

351   increased between individuals, groups have been separated into smaller groups. It had to be

352   considered that groups size and parasite load are associated in a non-linear manner, which

353   could not be assessed in the present study (Hopkins et al. 2020). Infection by parasites in

354   group living animals can be caused by different mechanisms. For example, parasites can be

355   transmitted directly during social interactions, hence individuals engaging more socially are

356   at greater risk to be infected. Parasite infection can also be related to physiological

357   processes, which allow parasites increased replication or survival in the host, for example a

358   compromised immune system, mediated by the physiological stress response (Muehlenbein

359   and Watts 2010). Unfortunately, in the present study I have not measured individual stress

360   levels and therefore cannot verify an association between parasite excretion patterns and

361   levels of stress. The relationship between the physiological stress response and the immune

362   system and related to this susceptibility to parasites is complex. A recent meta-analysis in

363   110 records from 65 studies in mammalian hosts from experimental and observational

364   studies generally indicated a positive relationship between glucocorticoids and parasite

365   burden (Defolie et al. 2020), however overall results about the relationship are complex. For

366   example, in male chimpanzees, *Pan troglodytes schweinfurthii,* intestinal parasite prevalence

367   and richness is positively associated with individual stress levels (Muehlenbein and Watts

368   2010). In chickens, *Gallus domesticus*, increased corticosterone levels were associated with

369   increased numbers of coccidia oocysts and the length of the excretion period (Graat 1996)

370   and in baboons, *Papio cynocephalus*, infection with helminths was associated with higher

371   glucocorticoid levels (Akinyi et al. 2019). Other studies report a lack of correlation between

372   physiological measures of stress and parasite burden, for example in male black grouse,

373   *Tetrao tetrix* (Sokół and Koziatek-Sadłowska 2020) and Blue-crowned manakins, *Lepidothrix*

374   *coronata*, (Bosholn et al. 2020) individual corticosterone levels were not correlated with

375   parasite infection. Future studies investigating the direct link between social behavior,

376   physiological stress response and parasite excretion patterns would be desirable.

377

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

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

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

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

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

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

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

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

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

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

388   driver in the evolution of cognition (Emery et al. 2007). Social relationships in common

389   ravens have been shown to facilitate access to resources (Braun and Bugnyar 2012) and

390   cooperation (Fraser and Bugnyar 2012). Following conflicts, common ravens reconcile and

391   consolidate valuable relationships, therefore mitigating potential costs of disrupted

392   relationships (Fraser and Bugnyar 2010b; Fraser and Bugnyar 2011). Based on these previous

393   findings, it can be assumed that strong affiliative relationships hold significant benefits for

394   corvids. Therefore, I expected to find, but was unable to confirm in the present study, that

395   the nature of an individual's social relationships would affect their health and physiology.

396   This is especially interesting as dominance rank was negatively correlated with the

397   proportion of samples excreted containing coccidian oocysts. Aggressive social interactions

398   have previously been shown to be among the most potent stressors (Wascher et al. 2008)

399   and position in the hierarchy is related to stress (Creel 2001) and immunodepression

400   (Barnard et al. 1998) in a number of species. Social relationships have been suggested to

401   mitigate the effects of aggression onto the physiological stress response (Sachser et al. 1998)

402   and therefore I would have expected to find an effect of strength of affiliative relationships

403   on parasite product excretion in carrion crows.

404

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

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

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

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

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

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

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

412   increase in the first week after a major stressor (Spreafico et al. 2012) and in graylag geese

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

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

415

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

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

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

419   individuals excreted more samples containing coccidian oocysts compared to dominant

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

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

422   excretion.

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426

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435

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691 **Table 1:** List of all focal individuals and information about population, sex (F = female, M = male), age (year of hatching; if not known, individuals
692 are classified as adult), group (group composition: family, flock, pair, trio), phases of data taking during which the individual was recorded (G08:
693 March to May, November to December 2008; G09: September to December 2009; G10: January to June 2010; G12: January to July 2012; G15:
694 May to July 2015), number of droppings and behavioral focal observations collected, maximum composite sociality index (CSI) and Elo-rating.
695

	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	5.156	-515.459
			Pair	G10	7	34	4	-166.849
				G12	40	24	0	-166.849
				G15	10	4	5.9	-166.849
Franz	M	2007	Group	G08	8	48	1.152	-636.627
			Pair	G09	4	30	0	-636.627
				G10	4	3	0	-636.627
				G12	34	24	2.181	-636.627
Fritz	M	2008	Group	G09	2	9	4.769	133.72
Gabi	F	2007	Group	G08	6	39	0	-41.797
				G09	14	28	2.863	192.788
			Pair	G10	4	27	0	139.761
			Trio	G10	2	4	0	139.761
			Trio	G12	43	24	0	133.466
Gertrude	F	2011	Pair	G12	33	24	4.363	-215.052
Hitchcock	M	2007	Group	G08	2	48	9.538	113.269
				G09	4	22	8.95	260.420
Hugo	M	1989	Group	G08	2	33	11.923	-96.304
				G09	9	27	1.536	-187.089
			Trio	G10	5	5	0	-187.089
Klaus	M	2009	Group	G08	13	10	0.384	350.719
				G09	5	14	0	403.747
			Trio	G12	33	25	1.09	329.27

Name	Sex	Year	Type	Code				
Mate	M	2008	Group	G09	2	45	5.913	-243.863
Munin	F	2014	Trio	G15	13	6	0.1	-139.34
Olaf	F	adult	Pair	G12	2	4	0	0
Peter	F	2007	Group	G08	3	52	14.307	226.598
				G09	10	56	6.297	-128.351
			Pair	G10	6	33	0	-476.962
				G12	48	24	0	-476.962
				G15	11	7	2.578	-476.962
Pinky	F	2008	Group	G08	7	10	7.153	383.915
Resa	F	2009	Trio	G12	35	24	0	80.771
Ronja	F	2008	Group	G08	2	8	2.384	207.35
Ruediger	M	adult	Pair	G12	2	4	0	0
Sissi	F	2008	Group	G08	2	9	0.973	221.942
Toeffel	F	2008	Group	G08	3	20	4.769	-138.099
				G09	8	37	22.92	-39.464
			Pair	G12	38	23	2.181	-39.464
Walter	M	2011	Pair	G12	37	24	1.885	215.052
				G15	7	6	0.1	217.726
Willi	M	2012	Trio	G15	7	5	0.1	139.34

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699   **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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705 **Table 3.** Results of the generalized mixed linear model investigating factors affecting
706 patterns of coccidian oocyst and nematode egg excretion. Models investigate effects of
707 group structure, number of related individuals (Nr related), strength of affiliative
708 relationships (CSI), sex and dominance hierarchy (Elo-rating) on presence or absence of (a)
709 coccidian oocysts and (b) nematode eggs in the sample. Significant values ($p \leq 0.05$) are
710 highlighted in bold.

	Parameters	Estimate ± SE	z	p
(a) Coccidia	**Intercept**	**-1.28 ± 0.302**	**-4.229**	**<0.001**
	Group structure	**0.986 ± 0.276**	**3.564**	**<0.001**
	Nr related	-1.134 ± 0.632	-1.794	0.072
	CSI	0.072 ± 0.032	2.209	0.027
	Elo-rating	**-0 ± 0**	**-2.167**	**0.03**
	Sex	-0.007 ± 0.183	-0.038	0.969
(b) Nematodes	**Intercept**	**-1.181 ± 0.506**	**-2.333**	**<0.001**
	Group structure	-0.169 ± 0.318	0.53	0.595
	Nr related	-0.964 ± 0.619	-1.556	0.119
	CSI	-0.001 ± 0.044	-0.039	0.968
	Elo-rating	0 ± 0	0.053	0.957
	Sex	0.043 ± 0.587	0.073	0.941

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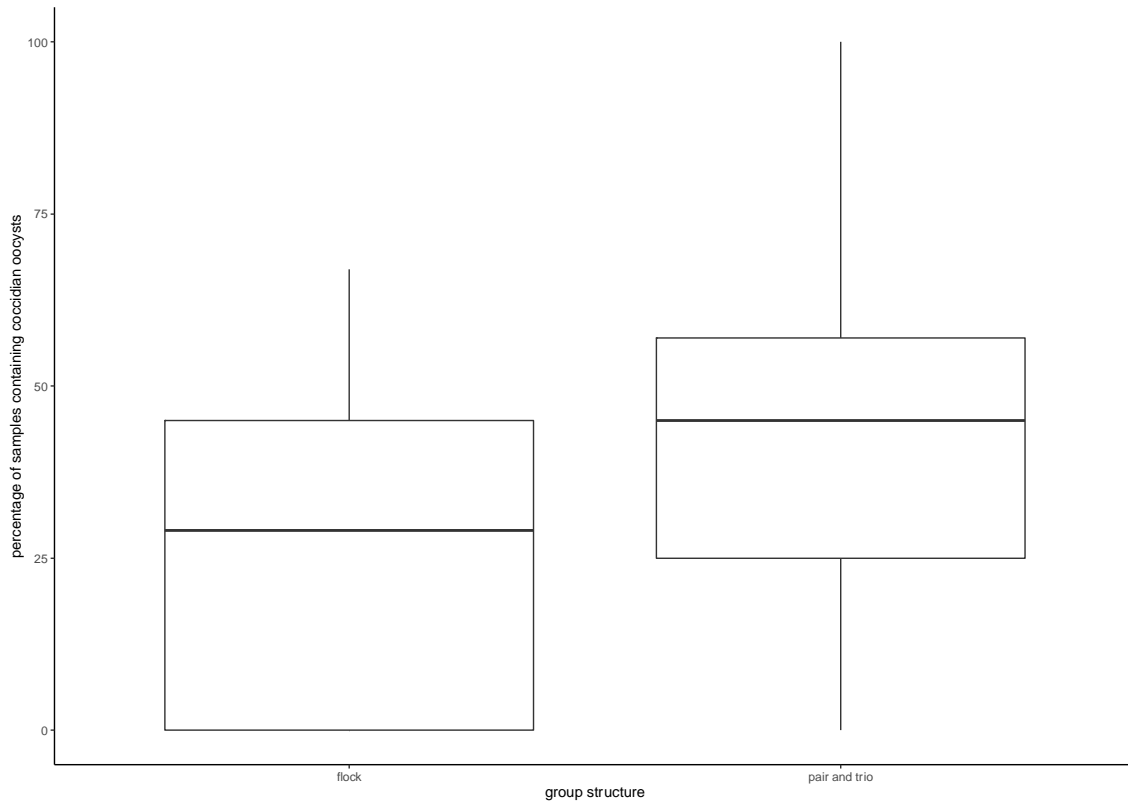
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739 **Figure 1.**
740 Percentage of samples containing coccidian oocysts in carrion crow droppings in relation to
741 the group structure. Box plots show the median and the interquartile range from the 25th to
742 the 75th percentiles.
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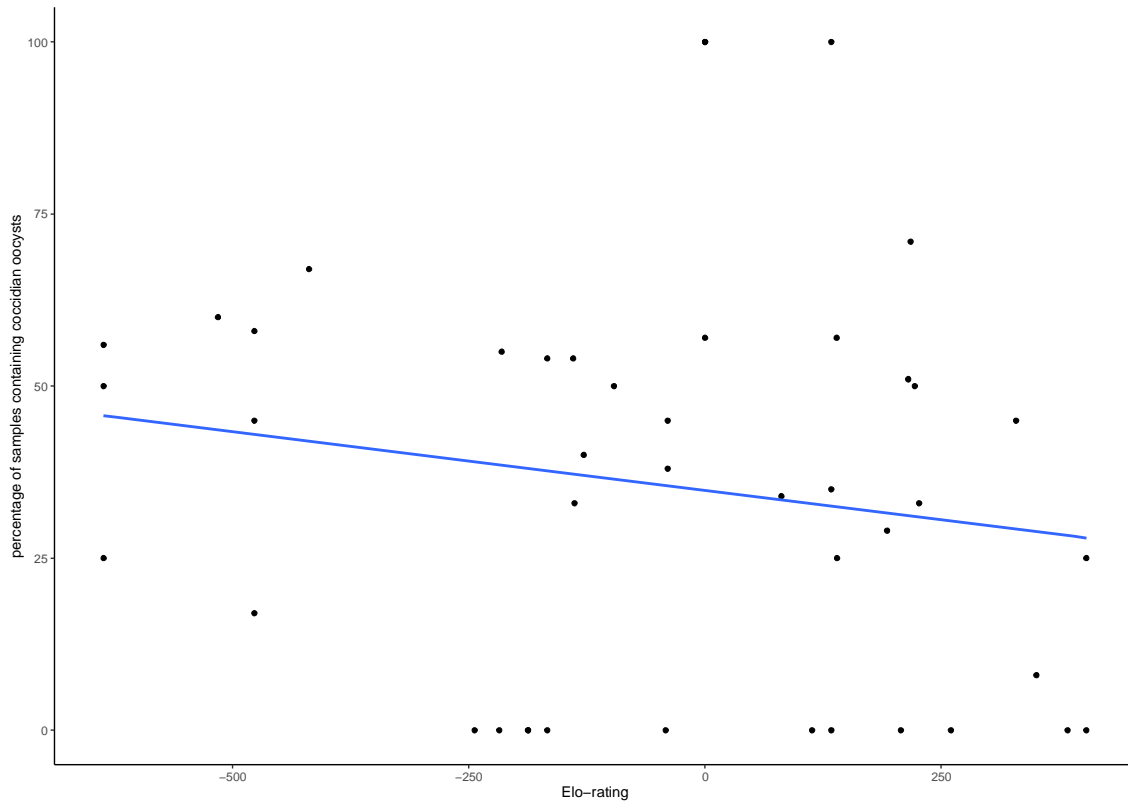761
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767 **Figure 2.**
768 Percentage of samples containing coccidian oocysts in carrion crow droppings in relation to
769 individual Elo-ratings.
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