The quality of social relationships affects male health in a complex bird society

Claudia A.F. Wascher[1,2,3], Hugo Robles[4], Daniela Canestrari[5] & Vittorio Baglione[1]

[1]Departamento de Ciencias Agro-Forestales, University of Valladolid, Spain

[2]Konrad Lorenz Forschungsstelle, Core Facility University of Vienna, Austria

[3] Animal and Environment Research Group, Department of Life Sciences, Anglia Ruskin University, United Kingdom

[4] Evolutionary Ecology Group (EVECO), Department of Biology, University of Antwerp, Campus Drie Eiken, Universiteitsplen 1, BE-2610, Wilrijk, Belgium.

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

Short title: Social bonds and health in crows

Corresponding author (present address):

Claudia A.F. Wascher: Animal and Environment Research Group, Department of Life Sciences, Anglia Ruskin University, United Kingdom; Phone: ++4369912381419; e-mail: claudia.wascher@gmail.com

Some animal societies, particularly in primate and corvid species, are based on enduring social bonds, based on sophisticated cognitive skills. A key unresolved issue for understanding the evolution of complex sociality and the associated advanced cognition is to uncover the fitness advantages that social relationships convey to individuals. Here, we investigated whether the social environment and the quality of individuals' social relationships in captive groups of carrion crows affect excretion patterns of coccidian oocysts, which have been shown to exert detrimental consequences on bird health. In females, variables relating to the social environment and the quality of individuals' social relationships did not have a strong influence on the occurrence of coccidian oocysts. However, male crows with strong social bonds and with a large number of relatives in their group were less likely to excrete feces containing coccidian oocysts. Thus, our data present evidence that high quality social relationships help male carrion crows to keep endo-parasite burden low, suggesting that the social life might have potential fitness advantages by reducing parasite burden. Ultimately, these advantages might be important in driving the evolution of complex group living.

Significance statement

Uncovering the fitness benefits of close social bonds is a key factor in understanding why close relationships between individuals have evolved in many distantly related taxa, such as mammals and birds. Here, we investigated potential health benefits of close social bonds in carrion crows. Carrion crows live in complex male-biased social groups and possess high cognitive skills that allow managing social relationships. Male crows with strong social bonds and with a large number of relatives in their group were less likely to excrete feces containing coccidian oocysts. Our results show that social bonds might have direct fitness implications in male crows, which ultimately might drive the evolution of complex group living.

Author contributions: C.A.F.W. designed and performed research;

H.R. analyzed data; and C.A.F.W., H.R., D.C. and V.B. wrote the paper.

Key words: social bonds, group size, affiliation, parasites, coccidian oocysts, carrion crows

Introduction

In many animals, the benefits of conspecific aggregations (e.g. protection against predators, increased access to food through shared defense or knowledge of resource locations) can arise in unstructured assemblages, where anonymous individuals show minimal interactions that they can manage with a relatively small brain and unsophisticated cognitive abilities (e.g. fish schools, ungulate grazing herds). However, some animal societies, notably those in some primate species, are based on enduring social bonds and according to the 'social brain hypothesis', the management of these complex relationships requires sophisticated cognition [1].

Currently, the key issue for understanding the emergence of this kind of complex sociality and the associated cognitive skills is to uncover the fitness advantages that bonding conveys to individuals [2]. In spite of much interest, this question is largely unresolved. Research in primates has shown that the quality of social relationships may affect individuals' longevity and reproductive success. The largest body of evidence supporting this hypothesis has been found in humans, where a rich social network and social support yields measurable positive consequences for health [3]. Other primate species show similar patterns. Social relationships help female chacma baboons (*Papio hamadryas ursinus*) cope with stressful events and increase longevity [4], social bonds in male Assamese macaques (*Macaca assamensis*) are directly linked to the number of offspring sired [5], and in Barbary macaques strong social bonds have a stress reducing effect [6]. These studies, together with more limited information on other mammalian species [1, 7], suggest that the human tendency to engage in enduring social bonds may have deep evolutionary roots [8]. To test this fascinating hypothesis, however, we

crucially need to investigate the fitness consequences of social bonds in a larger variety of taxa and types of social organizations [2].

Recent research has shown that advanced sociality associated with sophisticated cognition is not unique to humans and closely related primate species, but can be found in a variety of taxa [9, 10]. Among birds, corvids show complex social relationships, proving a suitable model to investigate the fitness consequences of social bonding. Common ravens (*Corvus corax*), for example, are capable of forming valuable relationships, not only within reproductive pairs but also between short/long-term coalition and alliance partners in their social group [11, 12]. Such bonds are characterized by low levels of aggressive and high levels of affiliative behaviors exchanged in a reciprocal way over extended periods of time [13]. Within such valuable relationships, individuals support each other in agonistic encounters [12, 14] and share information and resources [12, 15, 16], whereas competition dominates in other social contexts [17, 18].

Carrion crows (*Corvus corone*) are also capable of developing enduring non-reproductive social bonds, especially among males, which in some populations can share and defend a territory, and cooperate in rearing a communal brood [19, 20]. Within-groups, linear dominance hierarchies help reduce conflicts and keep the group cohesive [21, 22]. As expected, cognitive skills mirror the social complexity in these species. For example, crows can discriminate between reliable and unreliable conspecifics [23] and show inequity aversion, being able to quantify other individuals' efforts and payoff in comparison with their own in token exchange tasks [24]. Carrion

crows are therefore a suitable model to investigate the fitness correlates of social bonding and, ultimately, the evolution of the social brain [25].

In this study, we investigated whether the social environment and the quality of an individual's social relationships affects health in captive groups of carrion crows that varied in size and composition. In particular, we focused on the pattern of excretion of coccidian oocysts, as a proxy of health in carrion crows. Coccidian protozoans are among the most common endoparasites of birds [26, 27] and are widespread among corvids, including the carrion crows [28–30]; this study, see below. Infections with large numbers of coccidia clinically manifest as 'coccidiosis', causing infections in the intestinal tract [31]. This severely affects individual body condition, longevity and fecundity, by inhibiting the uptake of essential dietary components [32, 33]. The pathogenicity is well documented in poultry [34–36], and evidence for it is further accumulating in wild bird species (e.g. [37, 38]). Coccidia are transmitted via the fecal-oral route. Coccidian oocysts excreted in the feces of host individuals become infectious by undergoing sporogony within 24 hours [35].

In this study, we address three non-mutually exclusive hypotheses: 1. Group size hypothesis: parasite excretion patterns depend on the size of the group and/or the number of related individuals. We expect infections to spread more easily in large groups, although the presence of relatives in the group may counteract the effect of crowding by reducing the occurrence of stressful conflicts and competition [39] that can affect vulnerability to parasite infection. 2. Social bonds hypothesis: parasite excretion patterns 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. 3. Intrinsic factors: parasite excretion rates are explained by an individual's sex and age. We did expect sex differences, because males are more competitive than females within their groups [21] and are probably more exposed to the negative consequences of stress, which is expected to impair their ability to fight against parasites [40]. Also, previous results in wild and captive carrion crows suggest that males are more sensitive to the presence/absence of relatives [41] and therefore are expected to be more likely to show a health response to the composition of their social group compared to females. Age must also be controlled for, as it could affect parasite infection rate, although no specific predictions can be formulated based on the current knowledge of the host species.

Methods

Study subjects and ethics statement

We collected data over four different periods, from November 2008 to January 2009, from January to February 2013, from May to June 2013 and from January to February 2014, from a total of 34 crows, which were housed in a large outdoor aviary (30 x 12 x 6 m) in Northern Spain (Navafria, 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, however, varied due to the death of some individuals and reproduction of breeding pairs, as summarized in Table S1.

Behavioral protocol data

A total of 1075 individual focal protocols have been recorded. Each focal protocol lasted 5 minutes, and all occurring behaviors where recorded. However, for the present study, we focused on frequencies of agonistic behavior (threat, chase flight, and fight) and affiliative behaviors (approach, allopreening and sitting in contact). The identity of the interacting individuals was noted, as well as their role (initiator/receiver). All behavioral protocols (see sample size in Table S1) were recorded on video and analyzed by CW.

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 [4]. A CSI was constructed for five affiliative behaviors as follows: (AIij/AIave + ARij/ARave + CSij/CSave + APIij/APIave + APRij/APRave)/5. AIij represents the mean number of approaches initiated by individual i towards individual j per focal protocol, and AIave is

184 the mean number of approaches initiated by all members of the group per social
185 protocol. Similarly, AR refers to approaches received, CS to contact sit, API to
186 allopreening initiated and APR to allopreening received. Note that we used mean values
187 instead of absolute numbers because the sample of focal protocols varied among
188 individuals (see Table S1). A second CSI for four agonistic behaviors (aggression
189 initiated won, aggression initiated lost, aggression received won, aggression received
190 lost) was calculated as follows: (AIWij/AIWave + AILij/AILave + ARWij/ARWave +
191 ARLij/ARLave)/4. For each period of data collection, we determined the average and
192 maximum affiliative CSI for each dyad. Further, over the entire study period and all
193 observed dyads, we calculated a mean affiliative and aggressive CSI. When an
194 individual fulfilled both conditions of having a higher than average affiliative CSI and
195 lower than average aggressive CSI with another individual, they were considered
196 closely bonded. In each period of data taking we determined the number of group
197 members to which each individual was closely bonded.
198

199 *Parasitological examination*

200 During the entire study period, 399 individual fecal samples were collected, directly
201 after defecation (for a detailed overview see Table S1). Further, from April 2013 to
202 October 2014, 178 fecal samples were collected from 30 different groups belonging to a
203 long term studied population of wild carrion crows [42] in the rural area 'La Sobarriba',
204 Northern Spain (42°37′ N, 5°26′ W). For the purpose of this study, after observing a
205 crow group for up to 30 min, we approached the area where the crows were foraging
206 and looked for fresh fecal samples on the ground. We could assign the samples to a
207 given group but not to individual crows. Sex and age of the wild crows were unknown.

208 Eggs and oocysts of intestinal parasites were searched in fecal samples. In 2008, we
209 used a modified version of the flotation method [43] to examine the
210 occurrence/abundance of parasite products in the fecal samples. Fresh feces (0.1g) were
211 suspended in a 2 ml collecting tube with 1 ml saturated saline. Collection tubes were
212 shaken for 10 seconds and afterwards centrifuged for 5 minutes at 3000 rpm. After
213 centrifugation, the collection tubes were filled with saline solution and a cover slip (18 x
214 18 mm) was positioned onto the tube. The high density of the saline solution causes the
215 parasite eggs and oocysts to float up and be caught on the cover slip [44]. After 10
216 minutes, the cover slip was moved onto an object slide and the parasite eggs and
217 oocysts were identified (by size and shape) and counted. From January 2013 onwards,
218 we used a McMaster counting chamber to examine the occurrence of parasite products
219 in the fecal samples. The entire fecal sample was weighed, then diluted with 3 ml
220 saturated NaCl solution per 0.1 g of feces and thoroughly mixed. Afterwards, the
221 solution was filled into both McMaster counting chambers. After 10 minutes of resting
222 period we counted parasite eggs and oocysts in both chambers and calculated the
223 number of parasite products per 1 ml of feces.

224 We used a binocular with 100-fold and 400-fold amplification to identify parasite
225 products. We found Coccidian oocysts, eggs of several nematode species (*Capillaria*
226 *sp*., *Ascarida sp*., *Syngamus sp. and Heterakis sp., Trichostrongylus tenius*) and cestode
227 eggs to a varying degree. The proportion of positive samples was highest for coccidian
228 oocysts (24.7 %, n = 336), whereas the prevalence of eggs of nematode and cestode
229 species ranged between 1 and 17 %. We therefore restricted our analyses to coccidia,
230 the frequency of which allowed for robust statistical testing. Coccidia are a diverse
231 group of protozoan parasites which frequently infect the avian intestinal tract, causing
232 lesions [45]. Because the abundance of parasite cocciadian oocysts in the feces depends

233 on the stadium of the parasite cycle, which is difficult to control, we analyzed
234 presence/absence instead of absolute numbers.

235

236 *Data analysis*

237 Parasites with different life cycles and virulence may exert diverse and
238 synergetic effects on birds [43]. Exploring the causes and consequences of multiple
239 parasitism exceeded the aims of this study, which focused on the most common
240 infection found in crows at the study place, i.e. coccidia, and that represents a threat for
241 many species of wild birds [46, 32, 47]. Thus, to reduce the environmental noise
242 associated with the presence of multiple parasites, we restricted our analyses to samples
243 infected only by coccidia, i.e. with no indications of other parasitic taxa (nematode
244 eggs, cestodes). Likewise, we considered control ('healthy') samples those that were
245 found free from any of the parasitic taxa described above.

246

247 We used generalized linear mixed models (GLMMs) with binomial error
248 distributions and logit link functions in the package lme4 [48] to examine the variation
249 in the occurrence of coccidian oocysts (presence of oocyst in the feces = 1, absence =
250 0). We used an information-theoretic approach to assess which variables and models
251 best explained the variation in the data [49]. The information-theoretic approach
252 recognizes the uncertainty associated with biological data, and allows calculating
253 model-averaged parameter estimates and standard errors by considering non-exclusive
254 candidate models. Such analytical approach has been shown to be particularly suitable
255 for the comparison of alternative hypotheses – *i.e.* competing models – when multiple
256 variables may depict the data [50, 51], which is the case in our study. We built up and

compared models composed of explanatory variables associated with the three sets of hypotheses that may influence the occurrence of coccidia infection as described in the introduction section. We considered three age categories (first-year, second-year and adult) and assessed the differences by Tukey post-hoc testing in the multcomp package [52]. We conducted separate analyses for each sex because of different expectations regarding the influence of social factors on the occurrence of coccidian oocysts between males and females (see introduction and supplementary materials). Apart from sex, we did not include highly correlated variables (see supplementary materials) simultaneously in the same model to avoid potential spurious results due to multicollinearity. 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. Given the low number of individuals per group for each sex (19 males in 14 groups, 15 females in 12 groups), we did not fit group identity as a random term in the models to avoid redundancy. Overall, we ran two groups of models (16 and 11 models for males and females, respectively) that included combinations of low-correlated explanatory variables as well as the intercept-only models, i.e. the null models. We ranked the models for each candidate group of models according to Akaike's Information Criterion corrected for small sample sizes (AICc) and Akaike model weights [49, 53] by using the MuMIn package [54]. Models with lower AICc values and higher Akaike model weights are better supported by the data, with the sum of all model weights being one [49]. We calculated model-averaged parameter estimates and standard errors for each parameter by considering all candidate models within each group of models. Statistical analyses were performed in R 3.2.2 [55].

281

282 ## Results

283 ***Social bonds and parasitological examination***

284 We observed 57 bonded dyads, 31 of which were male-female dyads (19
285 between related individuals and 12 between unrelated individuals), 18 were male-male
286 (5 between related and 13 between unrelated individuals) and 8 female-female (6
287 related, 2 unrelated). On average, males and females had 1.7 ± 1.71 and 1.64 ± 1.60
288 bonded partners respectively. The mean CSI of related male-female bonds was 2.135 ±
289 0.846 and 3.034 ± 2.165 for unrelated male-female bonds. The mean CSI of male-male
290 bonds was 2.345 ± 0.952 for related and 2.754 ± 1.798 for unrelated individuals. In
291 female-female bonds, the mean CSI was 4.806 ± 1.549 and 1.556 ± 0.101 for related
292 and unrelated partners respectively.

293

294 Overall, 83 out of 336 samples contained coccidian oocysts, whereas 253
295 samples were not infected (i.e., free of parasite products of any of the considered taxa).
296 Coccidian oocysts occurred in 57 of 198 samples in males, and in 26 of 138 samples in
297 females. In the droppings collected from wild carrion crows, 84 out of 178 samples
298 contained coccidian oocysts, showing that coccidia are a common parasite in groups of
299 wild carrion crows.

300

301 ***(a) Occurrence of coccidian oocysts in males***

302 The selection of models that examined the occurrence of coccidian oocysts in
303 males yielded a high-ranking model that accounted for a weight of 0.41 (Table 1). The
304 maximum CSI value and the number of related individuals in the group were included

305 in the best model. Crows with a strong social partner and living with a larger number of
306 related individuals were less likely to contain coccidia (Table 2, Figures 1a and 1b).
307
308 The addition of the factor group size to the model with the maximum CSI value
309 and the number of related individuals did not improve model performance, as indicated
310 by the higher AICc value and the similar log-likelihood value of the second-ranking
311 model compared to the best model (Table 1). Further indication of the low influence of
312 group size on the occurrence of oocysts arises from the fact that the 95% confidence
313 interval of the model-averaged parameter estimate for group size included zero (- 0.187,
314 + 0.433; see Table 2).
315
316 Model averaging results also suggested a tendency for males with fewer
317 affiliated individuals to be more likely to host coccidia compared to males with more
318 affiliated individuals (Table 2). However, the number of affiliated individuals was fitted
319 in models with rather low weights (0.01 - 0.06, Table 1), which suggests a low
320 influence of this variable. Likewise, the average CSI value was fitted in low-ranking
321 models (Table 1) and its model-averaged parameter estimate clearly included zero
322 (Table 2), suggesting low explanatory power.
323
324 The third-ranking model included age as a fixed term (Tables 1 and 2). Post-hoc
325 analyses by Tukey contrasts showed that first-year males were less likely to host
326 coccidia than second-year birds (second-year – first-year: estimate ± SE = 2.44 ± 0.89, z
327 = 2.733, p = 0.016) and adults (first-year – adult: estimate ± SE = - 2.62 ± 0.90, z = -
328 2.896, p = 0.010), whereas no difference was found between the latter two age
329 categories (second-year – adults: estimate ± SE = -0.17 ± 0.55, z = -0.312, p = 0.946).

Although age was highly correlated with the maximum CSI value and the number of related individuals (see Methods section), the addition of these two variables significantly improved the performance of the model based on age (Anova test: AICc = 203.14 vs 208.08 respectively for the model with the three variables and the model with the age only, Chi-squared = 9.172, df = 2, $p = 0.010$). Thus, both the age, the maximum CSI value, and the number of related individuals had a strong influence on the occurrence of coccidian oocysts in males.

The negative relationship between the maximum CSI value and the occurrence of oocysts may be difficult to interpret. On the one hand, it may indicate that birds with a highly affiliated group member are less likely to excrete fecal samples containing coccidian oocysts, but, on the other hand, it may also suggest that only healthy crows are able to maintain strong social bonds. To disentangle the two possibilities, we ran two additional analyses. First, we fitted a binomial GLMM with the maximum CSI value at a given day t as a predictor of the occurrence of coccidian oocysts later in time ($t + n$ days), including individual identity as a random term and two additional explanatory terms, namely the occurrence of parasites at time t and the time elapsed between measuring maximum CSI values and assessing the occurrence of oocysts (n days). Neither of the two latter variables were significant (occurrence of parasites at time t: estimate ± SE = 0.611 ± 0.520, $z = 1.175$, $p = 0.240$; number of days elapsed: estimate ± SE = 0.001 ± 0.004, $z = 0.320$, $p = 0.749$), whereas crows with higher maximum CSI values proved less likely to host coccidia later in life (estimate ± SE = -0.191± 0.077, $z = -2.477$, $p = 0.013$). This significant relationship supports a causal effect of maximum CSI value on the occurrence of the parasites. In a second analysis, we addressed the possibility that infected birds were less able to maintain strong social

355 bonds. In this case, we expected that the presence of oocysts in the fecal samples of a
356 given individual at time *t* would predict a low maximum CSI value later in life (*t* + *n*
357 days). However, a linear mixed-effects model, where individual identity was fitted as
358 random term, showed that the presence of coccidia at time *t* did not significantly reduce
359 the maximum CSI value at time *t* + *n* days (estimate ± SE = -0.104± 0.126, $t = -0.834$, p
360 $= 0.406$), after controlling for the maximum CSI value at *t* (estimate ± SE = 0.981 ±
361 0.018, $t = 55.038$, $p < 0.001$) and the number of days elapsed between assessing the
362 occurrence of oocysts and measuring maximum CSI values (estimate ± SE = -0.005 ±
363 0.001, $t = -4.456$, $p < 0.001$). The results of this second model therefore also supports
364 the conclusion that a strong social bond enhanced resistance against coccidian
365 endoparasites.
366
367 ***(b) Occurrence of coccidian oocysts in females***
368 The selection of models that examined the occurrence of coccidian oocysts in
369 females yielded five high-ranking models that accounted for more model weight than
370 the intercept-only model (Table 1). The best model included age as a fixed term and
371 was approximately 10 times more likely to be the best model than the null model (i.e.,
372 model weights: 0.49 vs 0.05). Post-hoc analysis by Tukey contrasts showed that first-
373 year females were less likely to host coccidia than adult females (first-year – adult:
374 estimate ± SE = - 1.37 ± 0.50, $z = -2.729$, $p = 0.017$), whereas no difference was found
375 between second-year and adults (second-year – adult: estimate ± SE = - 1.27 ± 0.69, z =
376 -1.847, $p = 0.151$), nor between second-year and first-year (second-year – first-year:
377 estimate ± SE = 0.11 ± 0.73, $z = 0.143$, $p = 0.989$).
378

The second-ranking model included group size as an explanatory variable (Table 1). Despite model-averaging analyses suggesting that females in smaller groups tended to be less likely to host coccidia (Table 2), this model had a ΔAICc value of only 1.68 compared to the null model. Moreover, the second-ranking model was only around two times as likely to be the best model as compared to the null model (model weights: 0.11 vs 0.06), suggesting a limited influence of group size on coccidian infection in female crows.

The average and maximum CSI values, as well as the number of affiliated individuals and the number of relatives, were fitted in rather low-ranking models (ΔAICc to the null model < 0.75, Table 1). Examinations of model-averaging parameter estimates confirmed a low influence of these explanatory variables on the occurrence of coccidian oocysts in females (Table 2).

Discussion

In the present study, we have shown that carrion crow males with closely bonded social partners (high CSI scores) proved less likely to excrete coccidian oocysts. The fact that high CSI values predicted low occurrence of coccidia at a later point in time and that, conversely, the presence of oocysts in the feces did not predict the strength of future social bonds, confirms the causal link between the quality of social relationships and reduced occurrence of coccidian oocysts, which can be considered an estimate of health [32, 33].

Health correlates of high quality social ties have been reported in humans (e.g. [56]) and a large body of research has focused on the causal psychological and biological processes that underlie this strong link [3, 57]. Similar evidence has been recently found in non-human primates [4, 5], suggesting that the tendency to form strong social ties may have deep phylogenetic roots [58]. Furthermore, as Silk [2] pointed out, it is important to recognize that social complexity is not limited to primate species. Indeed, coalition formation has been reported in several mammalian and bird species, e.g. African elephants *Loxodonta africanus* [59], spotted hyenas *Crocutta crocutta* [60], bottlenosed dolphins *Tursiops aduncus* [61], ravens [62], and carrion crows [20]. Our study uncovered for the first time, potential health consequences of high quality social relationships in a bird species, showing similarities with primates and suggesting that the direct fitness benefits of strong social bonds may be a key factor that triggers advanced sociality in 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 [63], and formation of long lasting social bonds among distant relatives, most often males, that share all purpose territories and frequently mate polyandrously [19, 20]. 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 [20]. Cooperative breeding, with group members working together to raise the brood, can only arise once stable groups have formed [64]. 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 [65–67]. In other words, to understand why carrion crows form groups we need to understand the fitness 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 [42], but little is known about the fitness advantage of forming long lasting social bonds. We suggest that the health benefits of high quality relationships may be an important factor for establishing stable alliances between males.

Besides the positive effect of strong social bonds, we found that the number of relatives in the group also affected parasite excretion patterns in carrion crows, with individuals living in groups with more related individuals excreting less samples 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 [42]. 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 [69]. However, our results now show that kin living can also accrue immediate direct benefits to carrion crows in terms of improved health, as estimated via parasite product excretion.

Male versus female sociality

In cooperatively breeding carrion crows, group sex ratio is male biased [68]. Within the social groups, conflicts are more likely among males, which form stable linear hierarchies that are much stronger than those of females. This sex difference mirrors the level of competition for resources, such as territory and reproduction, which is higher in males than females [21, 68]. Females of a group also generally gain unrestricted access to food sources, whereas males often interfere with each other and fight [39]. In their groups, males are therefore likely to undergo higher levels of social stress than females. This may explain why the observed benefits of social bonding in carrion crows arise in males but not in females. First year males were also less likely to excrete feces containing coccidian oocysts than second year and adult males. This may also be due to the increasing level of competiveness that males experience when they age and face the challenge of acquiring a territory and breeding position in the population.

Conclusions

Social complexity, associated with high cognitive abilities, has deep phylogenetic roots, being widespread not only among primate species but also in a variety of other mammals and birds. Understanding its evolution, however, is difficult because of our scant knowledge of the fitness consequences of sophisticated social behavior across taxa. We are just starting to fill the gaps, and this study shows a measurable positive health 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, i.e. cooperative breeding, to arise. Importantly, our results parallel previous findings in primate species, suggesting a general pattern in vertebrates for the evolution of sociality.

Acknowledgments

We thank Kurt Kotrschal for feedback and discussion, Jenna Kiddie for editing the manuscript and Friederike Hillemann for help with fecal sample collection. This work was supported by the Spanish Ministry of Economy and Competitiveness, project CGL2011-27260, to VB and a KWA ('kurzfristiges wissenschaftliches Auslandsstipendium') stipend of the University of Vienna to CAFW.

References

1. Dunbar RIM, Shultz S (2007) Evolution in the social brain. Science (80-) 317:1344–1347. doi: 10.1126/science.1145463

2. Silk JB (2007) The adaptive value of sociality in mammalian groups. 539–559. doi: 10.1098/rstb.2006.1994

3. Berkman LF, Glass T (2000) Social integration, social networks, social support, and health. In: Berkman LF, Kawachi I (eds) Soc. Epidemiol. Oxford University Press, Oxford, UK, p 137

4. Silk JB, Beehner JC, Bergman TJ, et al (2010) Female chacma baboons form strong, equitable, and enduring social bonds. Behav Ecol Sociobiol 64:1733–1747. doi: 10.1007/s00265-010-0986-0

5. Schülke O, Bhagavatula J, Vigilant L, Ostner J (2010) Social Bonds Enhance Reproductive Success in Male Macaques. Curr Biol 20:2207–2210. doi: 10.1016/j.cub.2010.10.058

6. Young C, Majolo B, Heistermann M, et al (2014) Responses to social and environmental stress are attenuated by strong male bonds in wild macaques. Proc Natl Acad Sci 111:18195–18200. doi: 10.1073/pnas.1411450111

7. Cameron EZ, Setsaas TH, Linklater WL (2009) Social bonds between unrelated females increase reproductive success in feral horses. Proc Natl Acad Sci U S A 106:13850–3. doi: 10.1073/pnas.0900639106

8. Silk JB, Beehner JC, Bergman TJ, et al (2010) Strong and consistent social bonds enhance the longevity of female baboons. Curr Biol 20:1359–61. doi: 10.1016/j.cub.2010.05.067

9. Shultz S, Dunbar RIM (2010) 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 100:111–123. doi: 10.1111/j.1095-8312.2010.01427.x

10. Pollen AA, Dobberfuhl AP, Scace J, et al (2007) Environmental complexity and social organization sculpt the brain in Lake Tanganyikan cichlid fish. Brain Behav Evol 70:21–39. doi: 10.1159/000101067

11. Heinrich B (2011) Conflict, cooperation, and cognition in the common raven. Adv Study Behav 43:189–237. doi: 10.1016/B978-0-12-380896-7.00004-6

12. Fraser ON, Bugnyar T (2012) Reciprocity of agonistic support in ravens. Anim Behav 83:171–177. doi: 10.1016/j.anbehav.2011.10.023

13. Fraser ON, Bugnyar T (2010) The quality of social relationships in ravens. Anim Behav 79:927–933. doi: 10.1016/j.anbehav.2010.01.008

14. Emery NJ, Seed AM, von Bayern AMP, Clayton NS (2007) Cognitive adaptations of social bonding in birds. Philos Trans R Soc Lond B Biol Sci 362:489–505. doi: 10.1098/rstb.2006.1991

15. Bugnyar T, Kijne M, Kotrschal K (2001) Food calling in ravens: are yells referential signals? Anim Behav 61:949–958. doi: 10.1006/anbe.2000.1668

16. de Kort SR, Emery NJ, Clayton NS (2006) Food sharing in jackdaws, Corvus monedula: what, why and with whom? Anim Behav 72:297–304. doi: 10.1016/j.anbehav.2005.10.016

17. Bugnyar T, Heinrich B (2006) Pilfering ravens, Corvus corax, adjust their behaviour to social context and identity of competitors. Anim Cogn 9:369–376. doi: 10.1007/s10071-006-0035-6

18. Bugnyar T, Heinrich B (2005) Ravens, Corvus corax, differentiate between knowledgeable and ignorant competitors. Proc R Soc B Biol Sci 272:1641–1646. doi: 10.1098/rspb.2005.3144

19. Baglione V, Marcos M, Canestrari D, Ekman JAN (2002) Direct fitness benefits of group living in a complex cooperative society of carrion crows , Corvus corone corone. Anim Behav 64:887–893. doi: 10.1006/anbe.2002.2007

20. Baglione V, Canestrari D, Marcos JM, Ekman J (2003) Kin selection in cooperative

536 alliances of carrion crows. Science (80-) 300:1947–9. doi:
537 10.1126/science.1082429

538 21. Chiarati E, Canestrari D, Vera R, et al (2010) Linear and Stable Dominance
539 Hierarchies in Cooperative Carrion Crows. Ethology 116:346–356. doi:
540 10.1111/j.1439-0310.2010.01741.x

541 22. Chiarati E, Canestrari D, Vera R, Baglione V (2012) Subordinates benefit from
542 exploratory dominants: response to novel food in cooperatively breeding carrion
543 crows. Anim Behav 83:103–109. doi: 10.1016/j.anbehav.2011.10.012

544 23. Wascher CAF, Canestrari D, Baglione V (2015) Carrion crows learn to discriminate
545 between calls of reliable and unreliable conspecifics. Anim Cogn 18:1181–1185.
546 doi: 10.1007/s10071-015-0879-8

547 24. Wascher CAF, Bugnyar T (2013) Behavioral responses to inequity in reward
548 distribution and working effort in crows and ravens. PLoS One 8:e56885.
549 doi:10.1371/journal.pone.0056885.

550 25. Humphrey NK (1976) The social function of intellect. In: Bateson PPG, Hinde RA
551 (eds) Grow. Points Ethol. Cambridge University Press, Cambridge, UK, pp 303–317

552 26. Page CD, Haddad K (1995) Coccidial infections in birds. Semin Avian Exot Pet Med
553 4:138–144.

554 27. López G, Figuerola J, Soriguer R (2007) Time of day, age and feeding habits
555 influence coccidian oocyst shedding in wild passerines. Int J Parasitol 37:559–564.
556 doi: 10.1016/j.ijpara.2006.12.014

557 28. SK P, WK C (1991) Isospora corvi Ray, Shivnani, Oommen and Bhaskaran, 1952
558 from the common house crow (Corvus splendens Vieillot) of Selangor, peninsular
559 Malaysia. Folia Parasitol (Praha) 38:201–207.

560 29. Upton SJ, Langen TA, Wright TF (1995) A new species of Isospora Schneider, 1881
561 (Apicomplexa: Eimeriidae) from the white-throated magpie jay Calocitta formosa
562 (Passeriformes: Corvidae) from Costa Rica. Syst Parasitol 31:195–199. doi:
563 10.1007/BF00009117

564 30. Cawthorn RJ, Wobeser GA (1985) Exogenous and endogenous stages of Isospora
565 brachyrhynchi sp. n.(Protozoa: Eimeriidae) from the American crow Corvus
566 brachyrhynchos Brehm. Can J Zool 63:2639–2645.

567 31. Conway DP, McKenzie ME (2007) Poultry Coccidiosis. Diagonistic Testing and
568 Procedures. Blackwell Scientific Publications, Iowa

569 32. Hõrak P, Saks L, Karu U, et al (2004) How coccidian parasites affect health and
570 appearance of greenfinches. J Anim Ecol 73:935–947. doi: 10.1111/j.0021-
571 8790.2004.00870.x

572 33. Stenkewitz U, Nielsen ÓK, Skírnisson K, Stefánsson G (2016) Host-parasite
573 interactions and population dynamics of rock ptarmigan. PLoS One 11:1–19. doi:
574 10.1371/journal.pone.0165293

575 34. Allen PC (1987) Physiological responses of chicken gut tissue to coccidial infection:
576 Comparative effects of Eimeria acervulina and Eimeria mitis on mucosal mass,
577 carotenoid content, and brush border enzyme activity. Poult Sci 66:1306–1315.

578 35. Allen PC, Fetterer RH (2002) Recent Advances in Biology and Immunobiology of.
579 Cytokine 15:58–65. doi: 10.1128/CMR.15.1.58

580 36. Allen PC, Lydon J, Danforth HD (1997) Effects of components of Artemisia annua on
581 coccidia infections in chickens. Poult Sci 76:1156–1163. doi: 10.1093/ps/76.8.1156

582 37. Brawner WR, Hill GE, Sundermann CA (2000) Effects of coccidial and mycoplasmal
583 infections on carotenoid-based plumage pigmentation in male house finches. Auk
584 117:952–963.

585 38. McGraw KJ, Hill GE (2000) Differential effects of endoparasitism on the expression
586 of carotenoid- and melanin-based ornamental coloration. Proc R Soc B Biol Sci
587 267:1525–1531. doi: 10.1098/rspb.2000.1174

588 39. Chiarati E, Canestrari D, Vila M, et al (2011) Nepotistic access to food resources in
589 cooperatively breeding carrion crows. Behav Ecol Sociobiol 65:1791e1800. doi:
590 10.1007/s00265-011-1187-1

591 40. Schat KA, Skinner MA (2008) Avian immunosuppressive diseases and immune
592 evasion. In: Davison F, Kaspers B, Schat KA (eds) Avian Immunol. Elsevier Academic
593 Press, Oxford, UK, pp 299–322

594 41. Wascher CAF, Heiss RS, Baglione V, Canestrari D (2015) Behavioural responses to
595 olfactory cues in carrion crows. Behav Processes 111:1–5. doi:
596 10.1016/j.beproc.2014.11.009

597 42. Baglione V, Canestrari D (2016) Carrion crows: Family living and helping in a
598 flexible social system. In: Koenig WD, Dickinson JL (eds) Coop. Breed. Vertebr. Stud.
599 Ecol. Evol. Behav. Cambridge University Press, Cambridge, UK, pp 97–114

600 43. Schnieder T, Boch J, Supperer R (2006) Veterinärmedizinische Parasitologie., 6th
601 ed. Parey, Berlin

602 44. Carta LK, Carta DG (2000) Nematode specific gravity profiles and applications to
603 flotation extraction and taxonomy. Nematology 2:201–210.

604 45. Ciganovich EA, Friend M, Franson JC, et al (1999) Intestinal coccidiosis. In: F. Man.
605 Wildl. Dis. USGS, Madison, pp 207–214

606 46. Pap PL, Vagasi CI, Barbos L, Marton A (2013) Chronic coccidian infestation
607 compromises flight feather quality in house sparrows Passer domesticus. Biol J
608 Linn Soc 108:414–428.

609 47. Sepp T, Karu U, Blount JD, et al (2012) Coccidian Infection Causes Oxidative Damage
610 in Greenfinches. PLoS One 7:e36495. doi: 10.1371/journal.pone.0036495

611 48. Pinheiro J, Bates D, DebRoy S, et al (2017) nlme: Linear and Nonlinear Mixed Effects
612 Models. R package version 3.1-130.

613 49. Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a
614 practical information-theoretic approach. Springer, New York

615 50. Stephens P, Buskirk S, Hayward G, Martínez Del Río C (2005) Information theory
616 and hypothesis testing: a call for pluralism. J Appl Ecol 42:4–12.

617 51. Garamszegi L, Calhim S, Dochtermann N, et al (2009) Changing philosophies and
618 tools for statistical inferences in behavioral ecology. Behav Ecol 20:1363–1375.

52. Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biometrical J 50:346–363.

53. Johnson J, Omland K (2004) Model selection in ecology and evolution. Trends Ecol Evol 19:101–108.

54. Bartón K (2014) MuMIn: multi-model inference. R package version 1.12-2,.

55. Team RC (2016) R: a language and environment for statistical computing.

56. Seeman TE (1996) Social ties and health: The benefits of social integration. Ann Epidemiol 6:442–451.

57. Cacioppo JT, Hawkley LC (2009) Perceived social isolation and cognition. Trends Cogn Sci 13:447–454. doi: 10.1016/j.tics.2009.06.005

58. Shultz S, Dunbar R (2010) Bondedness and sociality. Behaviour 147:775–803. doi: 10.1163/000579510X501151

59. Bates LA, Lee PC, Njiraini N, et al (2008) Do elephants show empathy? J Conscious Stud 15:204–225.

60. Holekamp KE, Sakai ST, Lundrigan BL (2007) Social intelligence in the spotted hyena (Crocuta crocuta). Philos Trans R Soc Lond B Biol Sci 362:523–538. doi: 10.1098/rstb.2006.1993

61. Connor RC, Krützen M (2015) Male dolphin alliances in Shark Bay: Changing perspectives in a 30-year study. Anim Behav 103:223–235. doi: 10.1016/j.anbehav.2015.02.019

62. Braun A, Bugnyar T (2012) Social bonds and rank acquisition in raven nonbreeder aggregations. Anim Behav 84:1507–1515. doi: 10.1016/j.anbehav.2012.09.024

63. Baglione V, Marcos JM, Canestrari D (2002) Cooperatively breeding groups of carrion crow (Corvus corone corone) in Northern Spain. Auk 119:790–799.

64. Canestrari D, Marcos J, Baglione V (2005) Effect of parentage and relatedness on the individual contribution to cooperative chick care in carrion crows Corvus corone corone. Behav Ecol Sociobiol 116:422–428. doi: 10.1007/s00265-004-0879-1

65. Ekmann J, Baglione V, Egger S, Griesser M (2001) Delayed dispersal: living under the reign of nepotistic parents. Auk 118:1–10. doi: 10.1642/0004-8038(2001)118[0001:DDLUTR]2.0.CO;2

66. Ekman J, Dickinson JL, Hatchwell BJ, Griesser M (2004) Delayed dispersal. In: Ecol. Evol. Coop. Breed. Birds. Cambridge University Press, Cambridge, UK, pp 35–47

67. Hatchwell B, Komdeur J (2000) Ecological constraints, life history traits and the evolution of cooperative breeding. Anim Behav 59:1079–1086. doi: 10.1006/anbe.2000.1394

68. Baglione V, Marcos JM, Canestrari D, et al (2005) Does year-round territoriality rather than habitat saturation explain delayed natal dispersal and cooperative breeding in the carrion crow? J Anim Ecol 74:842–851. doi: 10.1111/j.1365-2656.2005.00983.x

69. Clutton-Brock T (2002) Breeding Together: Kin Selection and Mutualism in

Cooperative Vertebrates. Science (80-) 296:69–72. doi: 10.1126/science.296.5565.69

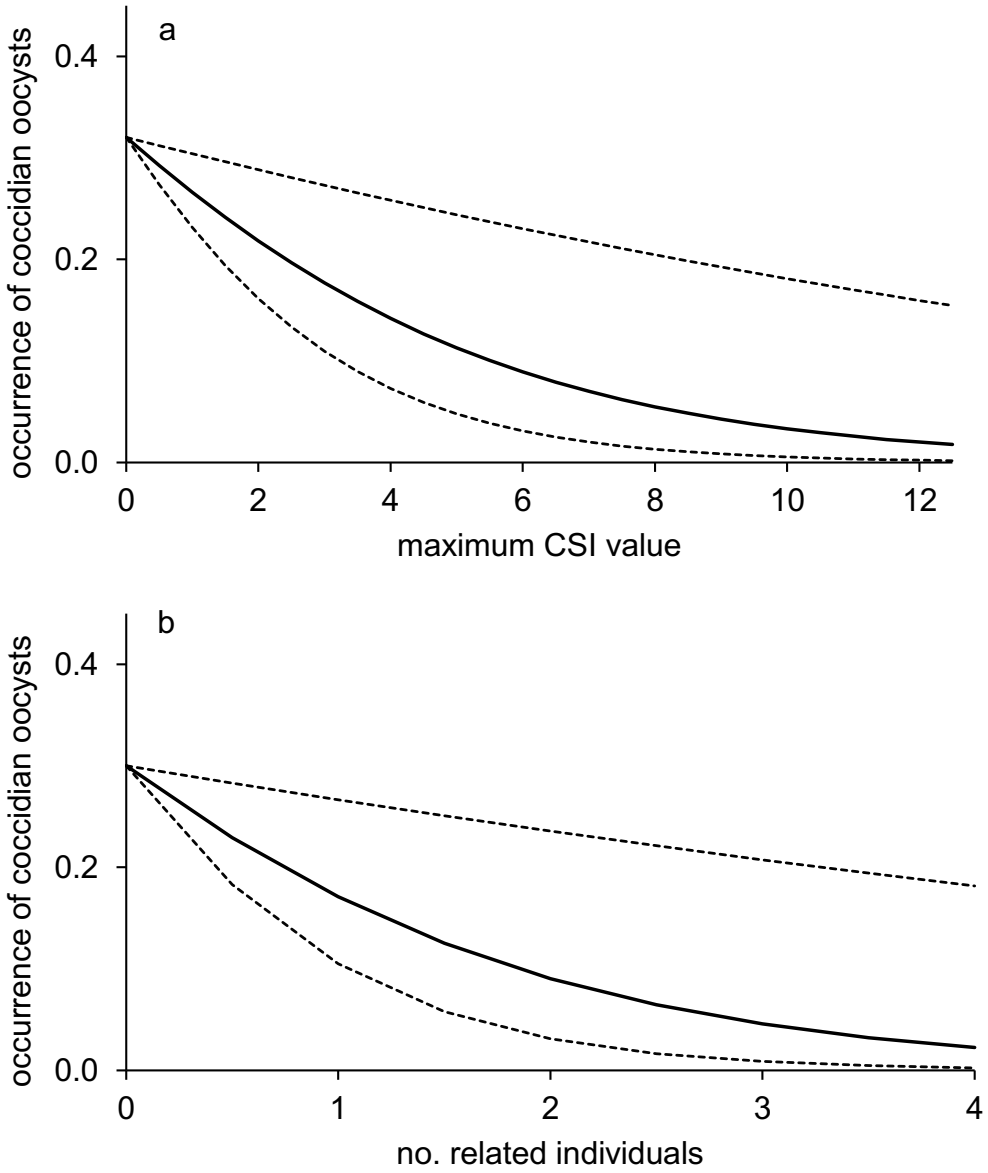

Figure 1: Occurrence of coccidan oocysts in carrion crow droppings. Occurrence probabilities were calculated as the predicted values (solid lines) and 95% CI (dashed lines) from the model-averaged parameter estimates for maximum CSI value (a) and number of related individuals (b).

672 **Table 1.** Model selection of analyses that examined the occurrence of coccidian oocysts
673 in males and females. The occurrence of oocysts was related to variables associated
674 with three sets of hypotheses: the "group structure" hypothesis (group size, number of
675 related individuals), the "social bonds" hypothesis (maximum CSI value, average CSI
676 value, number of affiliated individuals) and the "age" hypothesis. Individual identity
677 was fitted as a random term in all models. LogLik: log-likelihood, df: degrees of
678 freedom, ΔAICc: difference in AICc to the best model. Models are ranked according to
679 their Akaike weight (Weight). N = 198 samples of 19 males and 138 samples of 15
680 females.

Sex	Hypotheses	Models	df	LogLik	AICc	ΔAICc	Weight
males	Group structure + Social bonds	No. related ind., Max. CSI	4	-98.16	204.52	0.00	0.41
	Group structure + Social bonds	No. related ind., Max. CSI, Group size	5	-97.64	205.59	1.08	0.24
	Age	Age	4	-99.94	208.08	3.56	0.07
	Group structure + Social bonds	No. related ind., No. affiliated ind.	4	-100.06	208.32	3.80	0.06
	Age + Social bonds	Age, Average CSI	5	-99.05	208.42	3.90	0.06
	Group structure	No. related ind.	3	-101.64	209.41	4.89	0.04
	Group structure + Social bonds	No. related ind., No. affiliated ind., Group size	5	-99.78	209.88	5.36	0.03
	Social bonds	Max. CSI	3	-102.10	210.33	5.81	0.02
	Social bonds	No. affiliated ind.	3	-102.39	210.90	6.38	0.02
	Group structure	No. related ind., Group size	4	-101.61	211.42	6.91	0.01
	Null model	Intercept-only model	2	-103.99	212.04	7.52	0.01
	Group structure + Social bonds	Group size, Max. CSI	4	-102.01	212.23	7.71	0.01

	Social bonds	Average CSI	3	-103.36	212.84	8.32	0.01
	Group structure + Social bonds	Group size, No. affiliated ind.	4	-102.37	212.94	8.42	0.01
	Group structure	Group size	3	-103.81	213.75	9.24	0.00
	Group structure + Social bonds	Group size, Average CSI	4	-103.08	214.38	9.86	0.00
females	Age	Age	4	-62.22	121.74	0.00	0.49
	Group structure	Group size	3	-64.76	135.69	2.95	0.11
	Group structure	No. related ind.	3	-65.22	136.62	3.88	0.07
	Group structure	Group size, No. related ind.	4	-64.32	136.94	4.20	0.06
	Group structure + Social bonds	Group size, No. affiliated ind.	4	-64.44	137.19	4.45	0.05
	Null model	Intercept-only model	2	-66.64	137.37	4.63	0.05
	Social bonds	No. affiliated ind.	3	-65.71	137.60	4.86	0.04
	Group structure + Social bonds	Group size, Max. CSI	4	-64.67	137.63	4.89	0.04
	Group structure + Social bonds	Average CSI, Group size	4	-64.74	137.79	5.05	0.04
	Social bonds	Max. CSI	3	-66.29	138.77	6.03	0.02
	Social bonds	Average CSI	3	-66.44	139.06	6.32	0.02

689 **Table 2.** Model-averaged parameter estimates and standard errors for analyses that
690 examined the occurrence of coccidian oocysts in males and females. Significant values
691 ($p \leq 0.05$) are highlighted in bold.

Sex	Parameters	Estimate ± SE	*z*	*p*
males	Intercept	0.230 ± 0.837	0.275	0.783
	Group size	0.123 ± 0.158	0.782	0.434
	Number of related individuals	-0.731 ± 0.289	2.529	**0.011**
	Number of affiliated individuals	-0.354 ± 0.205	1.729	0.084
	Maximum CSI value	-0.262 ± 0.095	2.746	**0.006**
	Average CSI value	-0.208 ± 0.170	1.226	0.220
	Age (first-year)	-2.686 ± 0.907	2.961	**0.003**
	Age (second-year)	-0.233 ± 0.562	0.415	0.678
females	Intercept	-0.816 ± 0.448	1.822	0.069
	Group size	-0.167 ± 0.101	1.650	0.099
	Number of related individuals	-0.273 ± 0.232	1.176	0.240
	Number of affiliated individuals	-0.311 ± 0.347	0.895	0.371
	Maximum CSI value	-0.076 ± 0.141	0.537	0.591
	Average CSI value	-0.145 ± 0.487	0.298	0.765
	Age (first-year)	-1.373 ± 0.508	2.704	**0.007**
	Age (second-year)	-1.269 ± 0.693	1.831	0.067

692
693
694