

1 **Why preen others? Predictors of allopreening in parrots and corvids and comparisons to**  
2 **grooming in great apes**

3 *Short running title: Allopreening in parrots and corvids*

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56

57 **Abstract**

58           Allogrooming in primates serves not only a hygienic function, but also plays a crucial role  
59 in maintaining strong affiliative bonds between group members, which in turn, underpin the  
60 emergence of cooperative behavior. In contrast, although allopreening occurs in many avian  
61 species, we know little about its social functions. Our study addresses this issue by investigating  
62 allopreening in a broad comparative data set including six corvid and nine parrot species. We  
63 assessed whether rates of allopreening initiations, proportion of time spent allopreening, and the  
64 number of grooming partners in captive group-housed birds were comparable to patterns observed  
65 in captive chimpanzees and bonobos. While parrots and corvids were found to have similar rates  
66 of social grooming to bonobos and chimpanzees, *Pan* species dedicated significantly more time to  
67 social grooming. Animals in larger groups had more grooming partners, but when controlling for  
68 the number of potential partners, birds tended to have fewer grooming interaction partners than  
69 *Pan* species. We then investigated whether allopreening in parrots and corvids was predicted by  
70 behavioral markers of affiliative social bonds (close physical proximity, active feeding, and low  
71 levels of agonistic behavior). Results revealed that providing allopreening to a partner was  
72 significantly predicted by often being in close proximity, but not engagement in active feeding or  
73 agonistic behavior. We examined the region allopreened in a subset of species and found that  
74 preening a partner's head was predicted by both close physical proximity and active feeding, while  
75 body allopreening was only predicted by close physical proximity. Head preening may confer  
76 more hygienic benefits to recipients, and thus may be more selectively provided to valued partners.  
77 Results support the hypothesis that allopreening in corvids and parrots helps maintain social bonds  
78 with an individual's most important social partners, showing some similarities to allogrooming in  
79 primates.

80 *Keywords:* parrots, corvids, primates, allopreening, allogrooming, social bonds, affiliative  
81 relationships

82

### 83 **Introduction**

84 For animals that live in stable social groups, social grooming is one of the most common  
85 forms of affiliative behavior (Dunbar, 1991; Emery et al., 2007; Fraser & Bugnyar 2010; Carter &  
86 Leffer, 2015; Kenny et al., 2017; Kutsukake & Clutton-Brock, 2006; Watts, 2000; Zabel et al.,  
87 1992). Investigations looking into the adaptive value of social grooming (known as allogrooming  
88 in mammals and allopreening in birds) have identified two main categories of potential functions.  
89 One category consists of hygienic benefits (e.g., maintaining good skin/fur/feather condition  
90 through the removal of ectoparasites, dirt, or debris; Akinyi et al., 2013; Brooke, 1985; Clayton et.  
91 al., 2010; Mooring, 1995), while the other identifies social functions (e.g., facilitating the  
92 formation and maintenance of partnerships; di Bitetti, 1997; Gill, 2012; Henazi & Barrett, 1999;  
93 Kenny et al., 2017; Kutsukake & Clutton-Brock, 2006). Note that these benefits are not necessarily  
94 mutually exclusive. Evidence supporting the social function hypothesis has come from a range of  
95 species (e.g., vampire bats, *Desmodus rotundus*, Carter & Leffer, 2015; herb-field mice, *Apodemus*  
96 *microps*, Stopka & Graciasová, 2001; meerkats, *Suricata suricatta*, Kutsukake & Clutton-Brock,  
97 2006; cows, *Bos Taurus*, Val-Laillet et al., 2009), with primate research producing some of the  
98 most compelling evidence.

99 The body of research on primate allogrooming is extensive and suggests that social  
100 grooming likely confers several evolutionary advantages for animals living in socially complex  
101 environments. Although grooming confers an important hygienic benefit to recipients through the  
102 removal of parasites, the time primates dedicate to grooming is better explained by group size than

103 body size, suggesting grooming plays a social function in addition to a hygienic function (Dunbar,  
104 1991). In primates, like in various other species, individuals do not groom others at random, but  
105 are instead selective with whom they provide this service to; individuals are more likely to groom  
106 kin, reproductive partners, and dominant individuals (di Bitetti, 1997; Call et al., 1996; Franz,  
107 1999; Gill, 2012; Gilby & Wrangham, 2008; Ju & Lee, 2016; Koyama et al., 2012; Kutsukake &  
108 Clutton-Brock, 2006; Massen et al. 2012; O'Brien, 1993; Schino, 2001; Silk et al., 2006; Seyfarth,  
109 1977). Allogrooming is also associated with alliance formation and the maintenance of cooperative  
110 alliances (Berghänel et al. 2011; di Bitetti, 1997; Seyfarth & Cheney, 1984; Watts, 2000). Primate  
111 studies also indicate that the fostering of reciprocity may be one of the key advantages derived  
112 from grooming partners (e.g., exchanging grooming for access to food or assistance during  
113 agonistic encounters with others; Barrett et al., 1999; De Waal, 1997; Schino, 2006; Ventura et al.,  
114 2006). Furthermore, there is evidence that allogrooming reduces individual stress and group  
115 tension (e.g., reduction of heart rate, cortisol concentrations, and de-escalating aggressive  
116 interactions; Aureli et al., 1999; Feh & de Mazières, 1993; Schino et al., 1988; Wittig et al., 2008;  
117 Young et al., 2014).

118         Although allopreening has been observed in over 100 avian species and is widespread  
119 among some avian groups, such as Psittaciformes, it has not been found among most birds (Kenny  
120 et al., 2017) and has not attracted the same research effort to understand its function as  
121 allogrooming has in mammals such as primates. The absence of allopreening in large numbers of  
122 avian species indicates that, unlike autopreening (self-preening), it is not vital to the maintenance  
123 of good feather condition, which is necessary for flight. Instead, explanations for the occurrence  
124 of this behavior appear to be found in the social organization of avian species. Previous research,  
125 for instance, has indicated that allopreening is most likely to occur among birds that live in

126 colonies, family groups, or that maintain stable partnerships (Brooke, 1985; Clayton & Emery,  
127 2007; Gill, 2012; Kenny et al., 2017; Lewis et al., 2007; Seibert, 2006). The fact that allopreening  
128 is most commonly found among birds that live in close physical proximity with conspecifics is  
129 consistent with the hygienic function of allopreening, as preening partners would help control  
130 ectoparasitic infestation among group members. This is supported by the fact that ectoparasitic  
131 infestation rates have been found to be higher in gregarious bird species (Boyd, 1951; Poulin, 1991;  
132 Rifkin et al., 2012), and among those species, non-paired birds have been found to have higher  
133 infestation rates than paired birds that regularly allopreen (e.g., Macaroni Penguins, *Eudyptes*  
134 *chrysolophus*, Brooke, 1985). Ectoparasitic infestation rates are also generally higher in the head  
135 and neck regions, as these areas cannot be autopreened (Boyd, 1951; Cox, 2012). While these  
136 findings indicate that allopreening may play a significant role in helping some avian species  
137 maintain good physical condition, there is also evidence it is not the sole function of allopreening.

138         As is the case with primates, there is reason to believe that allopreening may have initially  
139 evolved to serve hygienic functions but became adapted to serve social functions as well. Evidence  
140 supporting this assertion comes from Kenny et al.'s (2017) large-scale comparative study  
141 (including 503 species from 116 avian families), which revealed that allopreening most commonly  
142 occurs among species in which cooperative bi-parental care is necessary for offspring survival.  
143 Their analyses also showed that pair bond stability was predicted by whether allopreening between  
144 partners was known to occur in a species; species that allopreened showed significantly lower  
145 divorce rates between breeding seasons (e.g., species belonging to Procellariiforme and  
146 Psittaciforme orders). The findings from Kenny et al.'s (2017) study, which also included  
147 phylogenetic analyses, suggest that allopreening developed as a facilitator of bond strength for  
148 species whose reproductive strategies require individuals to form stable and cooperative

149 partnerships to successfully rear offspring. Previous research focusing on intra-species variation  
150 in pair bond relationship quality also provides support for this conclusion. Gill (2012), for instance,  
151 found that divorce rates were higher for wren (*Cantorchilus leucotis*) pairs that were not observed  
152 allopreening as compared to those that frequently and consistently preened each other. Similarly,  
153 Spoon et al. (2006; 2007) found that allopreening behavior predicted pair bond stability.  
154 Furthermore, they found that relationship quality (which included allopreening measures) was  
155 predictive of egg production and offspring survival rate, with successful pairs showing more  
156 effective coordination of bi-parental care.

157         Allopreening occurs predominately among mated pairs (though not exclusively, e.g.  
158 Miyazawa et al. in this issue) and appears to play a substantial role in some species' courtship  
159 behavior (Clayton et al., 2010; Erickson, 1973; Forsman & Wight, 1979; Kushlan, 2011). Studies  
160 also indicate that allopreening assists in re-establishing familiarity after periods of separation  
161 (Black, 1996; Erickson, 1973; Kushlan, 2011). Although allopreening appears to be most common  
162 between reproductive partners, allopreening between same-sex pairs is also documented in various  
163 species (e.g., zebra finches, *Taeniopygia guttata*, Tomaszycski & Zatirka, 2014; budgerigars,  
164 *Melopsittacus undulates*, Abbassi & Burley, 2012; large billed crows, *C. macrorhynchos*,  
165 Miyazawa et al. *this issue*; ravens, *Corvus corax*, Fraser & Bugnyar 2010; rooks, *Corvus*  
166 *frugilegus*, Boucherie et al., 2016, Emery et al., 2007). Studies also found evidence of preference  
167 of siblings over non-siblings for preening partners in juvenile birds (Fraser & Bugnyar, 2010;  
168 Garnetzke-Stollmann & Franck, 1991; Ju & Lee, 2016). Furthermore, research on avian species  
169 that demonstrate dominance hierarchies in their social organization indicate that in some species  
170 dominant individuals are more likely to be the recipients of preening from subordinate group  
171 members (e.g., green woodhoopoe, *Phoeniculus purpureus*, Radford & Du Plessis, 2006).

172 Research on a colonial species (common guillemots, *Uria aalge*) also provides evidence that  
173 allopreening serves as a mechanism for the reduction of aggression; between pairs breeding in  
174 close physical proximity, agonistic rates were negatively correlated with allopreening and breeding  
175 success (Lewis et al., 2007). Allopreening has also been found to be predictive of agonistic support.  
176 In a study of captive group-housed ravens, Fraser and Bugnyar (2012) found that individuals were  
177 more likely to provide aid to group members they received preening from, even after controlling  
178 for “symmetry-based reciprocity” (including kin, same sex, same rank).

179         Previous studies on avian allopreening have provided us with pockets of insight into this  
180 seemingly complex behavior. Although preliminary research suggests that allopreening plays an  
181 equally important role in meeting challenges of social life in some avian species as allogrooming  
182 does in primates, the extent to which that is true is not yet fully known. One reason why this is the  
183 case is that investigations which directly compare birds to primates on social grooming measures  
184 are lacking. The vast phylogenetic separation between these taxa and the absence of social  
185 grooming in the majority of bird species suggests that social grooming represents an example of  
186 convergence. Evidence of cognitive complexity in parrots (birds belonging to the Psittaciforme  
187 order) and corvids (birds belonging to the Corvidae family, commonly referred to as the crow  
188 family), which in some cases appears to be comparable to great ape intelligence (Emery & Clayton,  
189 2004; Güntürkün & Bugnyar, 2016; Lambert et al., 2018), also indicates that bird and primate taxa  
190 have experienced convergence in cognitive processes (Emery et al., 2007).

191         Parrots and corvids serve as ideal subjects for investigating the quality and functions of  
192 allopreening. This behavior occurs in a variety of parrot and corvid species and appears to be  
193 particularly widespread among parrots (Kennedy et al., 2017; Seibert, 2006). A common  
194 characteristic of these avian taxa, which they share with many primates, is the presence of stable



195 social bonds, often lasting several years (Clayton & Emery, 2007; Seibert, 2006; Spoon, 2006).  
196 These bonds are maintained throughout and across breeding seasons; in various parrot species, for  
197 instance, pair bonds may remain stable for more than a decade (Forshaw, 2006; Seibert, 2006).  
198 Evidence of complexity is also found in these partnerships. Research on ravens, for example, has  
199 shown that relationship quality is comprised of the same three components that make up many  
200 primate relationships: value (based on allopreening, proximity, agonistic support), compatibility  
201 (based on aggression, counter-intervention, tolerance to approaches), and security (based on  
202 variation in response to approach over time) (Fraser & Bugnyar, 2010; Fraser et al., 2008). Another  
203 important characteristic of parrots and corvids is that they produce altricial young, which have  
204 long developmental periods and require substantial care from parents or reproductive helpers (such  
205 as in cooperative breeders; e.g. Horned and New Caledonian Parakeet (*Eunymphicus cornutus*,  
206 *Cyanoramphus saisseti*), Theuerkauf et al., 2009; Florida scrub-jay (*Aphelocoma coerulescens*),  
207 Clayton & Emery, 2007). The stability of partnerships, and the effectiveness with which partners  
208 coordinate the care they provide to offspring, therefore have substantial fitness implications. This  
209 is supported by Spoon et al.'s (2006; 2007) research demonstrating an association between  
210 behavioral coordination and reproductive success in cockatiels. Effective parrot/corvid partners  
211 not only cooperate in the direct care of young (e.g., providing nourishment to chicks), but also in  
212 the protection of resources (e.g., nest sites; Renton, 2004) and in managing conflicts with  
213 conspecifics (Braun & Bugnyar, 2012; Emery et al., 2007, Fraser & Bugnyar, 2010b).

214 We argue that comparative examinations of social grooming quality in primates and birds,  
215 and its potential associations to social factors, provide a valuable opportunity for deepening our  
216 understanding of conditions that supported the likely convergent evolution of social bonding  
217 behaviors. The present study therefore had two main aims: (i) to offer a preliminary comparison

218 of the social preening behavior in parrots and corvids, and social grooming in chimpanzees and  
219 bonobos, in terms of the time dedicated to social grooming and diversity of social grooming  
220 partners and (ii) to investigate whether social preening is associated with other affiliative social  
221 behaviors and therefore serves as a reliable marker of bond strength in parrots and corvids, as has  
222 previously been found in primates. Although a broad range of avian and primate species would be  
223 ideal for such comparisons, the logistical challenges involved in obtaining directly comparable  
224 measures from a wide variety of species, meant, in line with previous comparisons of cognition  
225 (e.g., Emery & Clayton, 2004), we had to focus our efforts on parrot and corvid species for birds  
226 and chimpanzees and bonobos for primates. Using a large data set, representing nine parrot and  
227 six corvid species, we assess the rate of grooming initiations, the proportion of time spent socially  
228 grooming, and the diversity of grooming partners, in these captive birds and, additionally, in  
229 captive groups of the two *Pan* species (bonobos and chimpanzees). It would be ideal to look at  
230 wild rather than captive animals in these analyses, as the impact of captivity on the behaviors of  
231 different species is unknown. However, as it is only possible to observe the social interactions of  
232 most species of corvids and parrots in the wild at nest or roost sites, which is incomparable to the  
233 full day follows that are possible for *Pan* species, our investigations necessarily had to focus on  
234 captive populations.

235 In order to address our second aim, we investigated potential associations between  
236 allopreening and three additional measures of relationship strength (proximity, active feeding, and  
237 agonistic behavior). We focused on these measures/interactions because they serve as reliable  
238 measures of relationship quality in a variety of species (Boucherie et al., 2016; Bräger et al., 1994;  
239 Dunbar & Shultz, 2010; Fraser & Bugnyar, 2010; Gilby & Wrangham, 2008; Spoon et al., 2006,  
240 2007; Zabel et al., 1992). Maintenance of close physical proximity is widely used to measure

241 relationship stability (Black, 2001; De Kort et al., 2006; Dunbar & Shultz, 2010; Garroway &  
242 Broders, 2007; Gilby & Wrangham, 2008; Emery et al., 2007; Massen et al. 2010; Möller et al.,  
243 2001; Silk et al., 2006; Zabel et al., 1992). Among birds, active feeding may involve either  
244 regurgitation into the mouth of a partner (known as allofeeding, Seibert, 2006) or transferring a  
245 monopolizable food item to a partner's beak. This behavior commonly occurs between parents and  
246 offspring, and between mates during egg incubation, but also occurs outside breeding contexts (De  
247 Kort et al., 2006; Duque & Stevens, 2016; Garnetzke-Stollmann, & Franck, 1991; Pitter &  
248 Christiansen, 1997; Seibert, 2006; Smith, 1980; Spoon, 2006, von Bayern et al., 2007). Frequency  
249 of agonistic interactions among social partners has been identified as indicative of bond strength  
250 (Spoon, 2006). Rook pairs with high levels of affiliative behaviors have been found to show little  
251 to no intrapair aggression (Emery et al., 2007), and Siberian jays (*Perisoreus infaustus*) were more  
252 likely to direct aggression towards non-kin in a foraging context (Sklepkovych, 1997); time spent  
253 in proximity, however, was not controlled for in these studies. Agonistic behavior has also been  
254 used as a measure of behavioral compatibility, which has been found to be predictive of breeding  
255 success (number of eggs laid and chicks reared to independence) and pair bond stability (extra-  
256 pair copulation and divorce rates) in cockatiels (Spoon et al., 2006, 2007).

257         In our study, we also engaged in explorations of mutual allopreening (defined as two birds  
258 simultaneously preening each other) and body region preened. While variation is found among  
259 mammals in the occurrence of mutual allogrooming (e.g., it's highly common in Camargue horses,  
260 *Equus caballus*, but appears to be rare (or absent) in Assamese macaques, *Macaca assamensis*,  
261 Cooper & Bernstein, 2000), it is unclear to what extent it serves as a meaningful indicator of  
262 relationship quality. Studies on chimpanzee mutual allogrooming yielded mixed results in this  
263 regard, with some research suggesting that it serves to strengthen bonds (Fedurek & Dunbar,

264 2009), while other findings indicate that it is used to prolong grooming bouts (Machanda et al.,  
265 2014). By assessing mutual allopreening in birds we may gain some insight regarding its functions.  
266 Similarly, little is currently known about the significance of variation in body region preened.  
267 Although preening of the head and neck areas is relatively common among birds, there is inter-  
268 species variation in how much individuals preen partners' bodies (Seibert, 2006). It is possible that  
269 this variation may be explained by anatomical or social factors. For instance, species that possess  
270 preen (uropygial) glands may be more likely to allopreen the body as the preen gland (dorsally  
271 located at the tail base) secretes oil that must be spread throughout the body during preening. While  
272 most species have preen glands (Elder, 1954), some birds maintain feathers through powder down,  
273 which is secreted throughout the body. Thus, in those species, body preening may have less benefit.  
274 However, inter-species (or intra-species) variation may be better explained by social factors such  
275 as bond strength. For example, as head/neck preening cannot be achieved via autopreening, and  
276 may be more valuable, so it may occur more frequently between dyads with strong bonds or  
277 between kin.

278         We predicted that if social grooming has a social function in addition to a hygienic one in  
279 parrots and corvids, they would show similar social grooming rates to *Pan* species. Based on  
280 previous research suggesting that allopreening most commonly occurs between pair bond partners,  
281 we expected that parrots and corvids would show less widely distributed allopreening, preening  
282 fewer group members than bonobos and chimpanzees. If found, this might result in parrots and  
283 corvids spending less time overall engaged in social grooming than *Pan* species. In terms of  
284 addressing whether allopreening in corvids and parrots served as a marker of social bonds, we  
285 hypothesized that allopreening would be positively predicted by physical proximity and active  
286 feeding (i.e., individuals are more likely to preen partners they choose to maintain close physical

287 contact to and/or actively feed). We also expected results to indicate that individuals are less likely  
288 to direct aggression to group members they preened. Finally, for a subset of species for whom the  
289 data were available, we also investigated inter-species variation in the occurrence of mutual  
290 allopreening (defined as two birds simultaneously preening each other) and body region preened.  
291 Species variation in percentage of allopreening that focused on the head versus the body was  
292 assessed and compared to species' anatomical preening mechanisms (uropygial gland or powder  
293 down) to determine whether they appeared to be associated. Potential associations between  
294 location preened and social factors (proximity, active feeding, agonistic behavior) were also  
295 investigated. These were explorative analyses, and as such, no specific predictions were made.

296

## 297 **Methods**

### 298 **Study groups**

299 The observational data we used for this study were obtained through a collaborative effort. Data  
300 were collected at various sites on captive, group-housed (3+ individuals sharing a single species  
301 enclosure) parrots (nine species,  $N = 99$ ), corvids (six species,  $N = 125$ ), bonobos ( $N = 38$ ), and  
302 chimpanzees ( $N = 56$ ). The majority of groups were mixed-age or consisted entirely of  
303 adults/subadults. Four corvid groups were entirely composed of juvenile birds (one year or  
304 younger at time of observation). Species, number of groups, group size, and group composition  
305 (age and presence of breeding pairs; listed for descriptive purposes, not included in analyses) can  
306 be seen in Table 1. For additional subject details and study site information see Table S1 in  
307 supplementary material.

308

### 309 **Data collection**

310 Observational data on social behaviors were collected using individual focal sampling for three  
311 out of nine *Pan* groups and 14 out of 23 groups of birds; group all-occurrence or scan sampling  
312 was used for six *Pan* groups and nine bird groups (see Table 1). Proximity scan data were collected  
313 using individual focal sampling for 10 bird groups; group focal sampling was used for 11 bird  
314 groups; proximity data were not available for two species (black headed caiques, red shouldered  
315 macaws; see Table 1). Length of observations varied among groups (2 min to 30 min).

316

### 317 **Measures**

318 An overview of the measures used is given here, with more detailed information on definitions  
319 and how measures were extracted across the different groups in the Supplementary methods. We  
320 calculated three different measures of social grooming effort: (i) in two bird species and some *Pan*  
321 groups instantaneous scan samples were recorded (see Table 1), enabling the proportion of scans  
322 where an individual was engaged in social grooming to be calculated; (ii) for some groups, the  
323 duration a focal individual spent engaging in social grooming was available, enabling the  
324 calculation of proportion of time spent allogrooming; and (iii) some groups shared a similar  
325 definition of allogrooming bout, so rate of allogrooming bouts could be calculated for these groups.  
326 For more detailed analysis of allopreening behavior within some bird species, individual  
327 allopreening behaviors were also coded. For individual behaviors, location being preened  
328 (head/neck or body) and focal role (giver, recipient, or mutual) were identified; a change in body  
329 region, focal role, or partner marked the end of one behavior and the start of another. Active  
330 feeding (regurgitation into the mouth (allofeeding) or transfer of a monopolizable food item to the  
331 mouth) and agonistic behavior were recorded for most bird groups using all occurrence sampling.

332 Proximity data was collected using scan sampling for all bird groups and subjects' nearest  
333 neighbors were identified during scans (see Table 1 for additional information on how nearest  
334 neighbors were defined across our groups).

335

### 336 **Data Analysis**

337 We focused our statistical models on data obtained from animals that lived in mixed age or  
338 adult/subadult groups where they had at least two potential grooming partners and more than 120  
339 min (+/- 5%) observation time. As data were not available for all groups for all measures and  
340 variables we conducted analyses on subsets of available data. Thus, not all groups are included in  
341 all analyses, and some analyses have larger sample sizes than others. To address our hypotheses,  
342 we fitted a series of Generalized Linear Mixed Models (Baayen, 2008; GLMM). These differed in  
343 the response variable investigated, the amount of available data, and, hence, also in sample sizes.  
344 To keep type I error rate at the nominal level of 0.05 we included random slopes (Schielzeth &  
345 Forstmeier, 2009; Barr et al., 2013) for combinations of fixed and random effects as applicable.  
346 Whenever a model comprised at least two key test predictors we conducted a full-null model  
347 comparison. Such a full-null model comparison aims to avoid 'cryptic multiple testing' (which is  
348 an issue whenever the number of predictors exceeds one) and reveals the overall significance  
349 associated with the predictors being present in the full but not in the null model (Forstmeier &  
350 Schielzeth, 2011). Below we specify for each model which random slopes we included and which  
351 predictors were dropped from the full model to obtain the null model. We are aware that for most  
352 of the models it would be required to account for the phylogenetic relationships among the species.  
353 However, we are not aware of well-established options allowing us to account for this within the

354 framework of multilevel data (i.e., with repeated observations per species and individual and  
355 multiple social groups per species). Hence, we used GLMMs instead.

356

### 357 Comparison of social grooming in birds and *Pan* species

358 Five GLMMs were conducted to compare different aspects of bird and *Pan* social grooming  
359 (Models 1a-c; 2a-b). For these analyses we considered all grooming interactions the focal animal  
360 was involved in, regardless of its role (recipient or provider). In order to assess whether taxon (bird  
361 or *Pan*) could explain variation in the time dedicated to social grooming, we ran three separate  
362 GLMMs on three different measures of grooming effort:

363

### 364 *Proportion of time dedicated to social grooming in corvids, parrots and Pan species (Models 1a,* 365 *1b and 1c)*

366 To estimate to what extent the proportion of time individuals spent allogrooming (Model 1a) was  
367 influenced by taxon we fitted a GLMM with beta error distribution (Bolker, 2008) and logit link  
368 function. Taxon was included as the key fixed effects predictor, but removed to obtain the null  
369 model. To control for group size (number of potential grooming partners), group size was  
370 included as an additional fixed effects covariate. As random intercept effects we included species  
371 and group. The model was not overdispersed (dispersion parameter: 0.978) and collinearity was  
372 not an issue (maximum Variance Inflation Factor, VIF: 1.043; see below). The sample for this  
373 model consisted of a total of 125 proportions obtained from 14 groups in 11 species.

374 We fitted two further identical models with regard to the predictors but with slightly  
375 varying response variables. In Model 1b the response was the proportion of scans individuals  
376 spent grooming. Neither collinearity (maximum VIF = 1.466) nor overdispersion (dispersion



377 parameter = 0.888) were an issue. However, the random effect of species comprised only four  
378 levels making the assessment of its contribution unreliable. Hence, results for this model should  
379 be treated cautiously. The sample for this model consisted of a total of 94 proportions, obtained  
380 for 11 social groups in four species. In Model 1c the response was the rate of social grooming  
381 initiations (number of social grooming bouts/observation time). Again, Model 1c did not present  
382 an issue with collinearity (maximum VIF = 1.027) and it also was not overdispersed (dispersion  
383 parameter = 0.972). The sample analyzed for this model comprised a total of 175 proportions,  
384 obtained for 18 groups in 14 species. In Model 1b we z-transformed group size to a mean of zero  
385 and a standard deviation of one to ease model convergence.

386

387 *Number of grooming interaction partners in corvids, parrots and Pan species (Models 2a and*  
388 *2b)*

389 We tested whether taxon (bird or *Pan*) could explain variation in the diversity of grooming  
390 partners. As more partners are likely to be identified with increased observation time, we limited  
391 this analysis to the first 240 minutes (+/- 5%) of observation for each animal. Thus, we only  
392 included individuals with at least one grooming event and 240 minutes of observation time in  
393 this analysis, resulting in  $N = 178$ . To test whether the proportion of groupmates individuals  
394 groomed with differed between *Pan* and birds we fitted a GLMM with binomial error structure  
395 and logit link function (McCullagh & Nelder, 1989; Model 2a). The sole fixed effect (besides the  
396 intercept) in this model was taxon with two levels (ape and bird). To avoid pseudo-replication,  
397 we included random intercept effects for species and group ID into the model. The response in  
398 this model was the proportion of groupmates the individuals interacted with. Practically, we  
399 modelled this by using a two-column matrix as the response which comprised the number of

400 groupmates individuals groomed with and did not groom with as the response (Baayen, 2002).  
401 To account for interaction propensities potentially varying among individuals we further  
402 included a random effect of subject ID into this model. We dropped taxon from the full model to  
403 obtain the null model. The model was not overdispersed (dispersion parameter = 0.778).

404 Since we also wanted to explicitly test to what extent the number of interaction partners  
405 per individual depended on number of available interaction partners, we fitted a further model in  
406 which the response was the total number of grooming interaction partners per individual and into  
407 which we included group size as an additional fixed effect (Model 2b). This model was fitted  
408 with a Poisson error structure. We removed the random effect of subject ID from this model, but  
409 we included random slopes of the number of available interaction partners within group ID and  
410 species into this model. Originally, we also included the parameters for the correlations between  
411 random intercepts and slopes into this model, but, since these were both estimated to be  
412 essentially 1 or -1 (being indicative of them being unidentifiable; Matuschek et al., 2017) we  
413 decided to remove them. The model was not overdispersed (dispersion parameter = 0.470), and  
414 collinearity was no issue (maximum VIF = 1.014). We dropped taxon and the number of  
415 potential partners from the fixed effects to obtain the null model. The samples for both models  
416 comprised 178 individuals of 21 groups from 11 species.

417

418 *Is allopreening associated with other affiliative social behaviors in corvids and parrots? (Models*  
419 *3a and 3b)*

420 In order to test whether allopreening in parrots and corvids is positively related to other  
421 affiliative behaviors, such as frequent close proximity and active feeding, and negatively  
422 associated with agonistic interactions we ran two GLMMs. For each group, we looked at each

423 focal bird's dyadic interactions with all other birds in the group. First, due to the differences in  
424 definition of allopreening bouts and sampling methods across our diverse data sets, we  
425 constructed binary categorical variables (Y/N) indicating whether the focal bird had: preened a  
426 partner, actively fed a partner, or directed aggression towards a partner. Dyadic proximity scores  
427 were calculated by dividing the total number of scans the focal bird had with the dyad partner as  
428 their nearest neighbor, by the total number of proximity scans available for the focal bird. In the  
429 first GLMM we investigated what social behaviors were associated with the occurrence of  
430 allopreening within a dyad. Since the response was binary (allopreening absent or present) we  
431 fitted the model with binomial error structure and logit link function. As fixed effects we  
432 included the presence of active feeding (no or yes) and agonistic interactions (no or yes) and also  
433 a dyadic proximity score. As random intercept effects we included the ID of the subject, the  
434 partner, the group, and also species. We included random slopes of agonistic interactions and the  
435 proximity score into all four random effects, and a random slope of active feeding within group  
436 ID and species. Originally, we also included parameters for correlations among random  
437 intercepts and slopes. However, as all of the absolute correlation parameters for partner ID,  
438 group ID, and species were essentially one or unidentifiable ('not a number') we removed them  
439 from the model (log-likelihoods, model with all correlation parameters: -166.43; model with no  
440 correlation parameters: -171.225). The sample for this model comprised a total of 1,222 dyads  
441 (only 86 engaged in preening) from 77 subjects with 90 partners in seven groups from six  
442 species.

443         As there was a large number of birds for which agonistic data were not collected (or  
444 emitters and receivers not identified), we fitted a second GLMM (Model 3b) excluding the  
445 predictor presence of agonistic behaviors, which allowed us to test whether proximity or active

446 feeding affected the likelihood of focal birds preening partners, using a larger sample size. This  
447 was important to test whether patterns identified in Model 3a would generalize to a broader  
448 sample of birds. Model 3b was identical to Model 3a with the exception that it lacked the fixed  
449 effects and random slopes of presence of agonistic interactions. The sample for this model  
450 consisted of a total of 1606 dyads (128 of which engaged in grooming) from 118 subjects with  
451 131 partners in 11 groups from nine species. Furthermore, several of the correlation parameters  
452 among random intercepts and slopes in Model 3b appeared unidentifiable, and we removed them  
453 from the model (log-likelihoods; full model: -240.888; model with only the correlation  
454 parameters within subject left: -245.399).

455         In the data sets for both models we z-transformed the proximity score to a mean of zero  
456 and a standard deviation of one to ease model convergence and we also manually dummy coded  
457 and then centered factors entering random slopes. In both models we included an offset term  
458 (McCullagh & Nelder, 1989) to control for varying dyadic observation times (log of observation  
459 time in hours). In the case of both models, the null model lacked the fixed effects of presence of  
460 active feeding and the dyadic proximity score, and for Model 3a the null model also lacked the  
461 fixed effect of agonistic interactions. Collinearity was no issue in either of the two models  
462 (maximum VIF, Model 3a: 1.352; Model 3b:1.317).

463

#### 464 Does head preening have a special value? (Models 4a and 4b)

465         Lastly, we examined the body part preened to determine whether head/neck preening was  
466 more valuable than body preening and indicative of stronger social bonds within a dyad. For blue  
467 and gold macaws, blue-throated macaws (two groups), great-green macaws (two groups),  
468 common ravens, orange-winged amazon, greater vasa, and New Caledonian crows, data on the

469 body part groomed were available. For these birds, we determined the proportion of preening the  
470 focal birds directed to their partners' heads. To estimate the extent to which different factors  
471 influenced the probability of allopreening another individual's head (Model 4a) and body (Model  
472 4b) we focused on the three species with body part and social data available (blue and gold  
473 macaw, orange winged Amazon, and vasa). We fitted two separate GLMMs with binomial error  
474 structures and logit link functions (originally, we considered using a multinomial model, but  
475 since it was common that in a given dyad preening of the head and the body was observed this  
476 was not a viable option). Both models included the presence of active feeding (no or yes) in a  
477 given dyad and the dyadic proximity score as key fixed effects. To control for their potential  
478 differences, we further included species (factor with levels blue and gold macaw, orange winged  
479 Amazon, and vasa) as a fixed effect. We included random intercept effects for subject ID and  
480 partner ID and a random slope of proximity within both of them. As with the other models we  
481 had originally included parameters for the correlation between random intercept and slope, but,  
482 as these appeared unidentifiable, we removed them from both models. We dropped presence of  
483 active feeding and the dyadic proximity score from the full models to obtain the null models. To  
484 control for observation effort varying among dyads we included it as an offset term (log of  
485 observation hours). Prior to fitting the models, we z-transformed the proximity score to a mean  
486 of zero and a standard deviation of one to ease model convergence. Collinearity was no issue in  
487 either of the two models (maximum squared Generalized VIF, after taking it to the power of  
488  $1/(\text{twice its degrees of freedom})$  (Fox & Monette, 1992), Model 4a: 1.186; Model 4b: 1.186). The  
489 sample for both models comprised a total of 392 dyads of 37 subjects with 45 partners in three  
490 groups from three species. Head preening happened in 45 dyads and body preening in 31 dyads.  
491

492 Mutual grooming

493 We examined relative rates of mutual allopreening on three species for which these data were  
494 available (orange-winged Amazon parrots, blue and gold macaws, and New Caledonian crows).  
495 For this analysis, we only considered dyads that showed instances of allopreening (mutual or  
496 unidirectional). We then assessed the proportion of allopreening that was mutual, and whether  
497 this differed across the three species. The data we used for this assessment differed from the  
498 allopreening bout data we used for the analyses described above. To consider the role of mutual  
499 grooming, we examined the focal bird's role in preening behaviors and used the role to define  
500 three types of grooming event: Give preening event, receive preening event or mutual preening  
501 event. Each preening bout could contain multiple events. We calculated the proportion of mutual  
502 grooming as the total number of mutual allopreening events for each dyad (i.e., number of  
503 mutual allopreening events where A and B were mutually preening each other, with either A or  
504 B being the focal bird) divided by total number of allopreening events involving A and B,  
505 regardless of focal roles. Due to small sample sizes, a Mann Whitney U test was run to determine  
506 whether there were significant differences in mutual allopreening proportion between blue and  
507 gold macaws ( $N = 9$ ) and orange-winged Amazon parrots ( $N = 16$ ) (crows were excluded from  
508 this analysis because they did not demonstrate mutual allopreening). The data lacked  
509 independence due to individuals involved in multiple dyads. Thus, we randomly sampled the  
510 data from dyads 1,000 times such that each individual was present at most once and averaged  
511 results. The number of dyads retained ranged from nine to twelve and the minimum number  
512 dyads per species was four. We then used an exact (Mundry & Fischer, 1998) Mann-Whitney U-  
513 test (Siegel & Castellan, 1988) to compare the proportion of mutual preening between the two  
514 species.

515

516 *Implementation of GLMMs and general considerations*

517 We fitted the GLMMs in R (version 3.6.1; R Core Team, 2019) using the functions glmmTMB  
518 of the identically named package (version 0.2.3; Brooks et al., 2017; models with beta error  
519 distribution) or glmer of the package lme4 (version 1.1-21; Bates et al., 2015; models with other  
520 error distributions). We compared full and null models utilizing likelihood ratio tests (Dobson,  
521 2002), and obtained significance tests of individual fixed effects by dropping them from the  
522 model one at a time and comparing model fits using likelihood ratio tests as well (Barr et al.,  
523 2013). For all models we determined model stability by removing the levels of the random  
524 effects one at a time and then comparing the estimates derived for the respective subsets of data  
525 with those obtained for the complete data set. This revealed Model 1a, 1b, 1c, 2a, and 2b to be of  
526 good and Model 3a, 3b, 4a, and 4b of moderate to poor stability (see results for details). We  
527 determined confidence intervals of model estimates and fitted models using a parametric  
528 bootstrap ( $N = 1,000$ ) implemented with the functions simulate (package glmmTMB; models  
529 with beta error distribution) or bootMer (package lme4; models with other error distribution). We  
530 determined VIF or Generalized VIF (Fox & Monette, 1992) using the function vif of the package  
531 car (version 3.0-3; Fox & Weisberg, 2011), applied to models lacking the random effects. We  
532 report odds ratios which indicate how much the odds of observing a positive response changes  
533 when a predictor increases by one unit.

534

535 **Results**

536 Comparison of social grooming in birds and *Pan* species

537 *Proportion of time dedicated to social grooming in corvids, parrots and *Pan* species (Models 1a,*

538 *1b and 1c)*

539 The results of the three GLMMs showed that while rates of social grooming initiations (total  
540 number of grooming bouts/observation time) in *Pan* species and birds were not significantly  
541 different (Model 1c, Table 2), on average, corvids and parrots devoted a smaller proportion of  
542 their time to social grooming than *Pan* species (total duration of grooming bouts/total  
543 observation time; Model 1a; Table 2; Fig. 1a:). They also tended to socially groom in a smaller  
544 proportion of scans (Model 1b; Table 2; Fig. 1b). Descriptives can be seen in Table 3.

545

546 *Number of grooming interaction partners in corvids, parrots and Pan species (Models 2a and*  
547 *2b)*

548 Individual animals from both taxa groomed a similar proportion of their group members (Model  
549 2a; Table 4; see Table 5 for descriptive statistics). However, when controlling for the number of  
550 potential interaction partners, we found that, first, the number of actual interaction partners  
551 clearly increased with the number of potential partners, and, second, that parrots and corvids  
552 tended to have fewer grooming interaction partners than *Pan* species (Model 2b; Table 4; Fig. 2).  
553 Descriptive statistics for adult and mixed-age groups included in these inferential analyses and  
554 for juvenile groups are indicated in Table 6.

555

556 *Is allopreening associated with other affiliative social behaviors in corvids and parrots? (Models*  
557 *3a and 3b)*

558 Allopreening was influenced by the three test predictors in Model 3a (proximity, presence of  
559 active feeding and agonistic interactions; full null model comparison:  $\chi^2 = 7.61$ ,  $df = 3$ ,  $P =$   
560  $0.055$ ) and also by the two test predictors in Model 3b (proximity and presence of active feeding;  
561  $\chi^2 = 14.04$ ,  $df = 2$ ,  $P = 0.001$ ). When individual predictors within each model were considered,



562 however, both models revealed that only proximity explained a significant amount of variation in  
563 the probability of allopreening to occur. The probability of allopreening being observed in a  
564 given dyad clearly increased with its proximity score (Table 7; Fig. 3). This is unlikely to be  
565 driven by sampling proximity when grooming was occurring (when close proximity is required),  
566 as grooming occupied a very small proportion of the time budget: Four of six species included in  
567 Model 3a and six of nine species included in Model 3b had duration of allopreening data  
568 available; mean percentage of observation time these species spent allopreening was 2.63% and  
569 2.30%, respectively.

570

571 *Does head preening have a special value? (Models 4a and 4b)*

572 We found no obvious association between the occurrence of head preening and the anatomical  
573 preening mechanism (uropygial gland or powder down; Table 8). Across species with data on  
574 region preened ( $N = 7$ ), half or more of preening was directed to partners' heads (Table 8).  
575 GLMMs run on a subset of these species (blue and gold macaw, orange-winged Amazon, greater  
576 vasa) for whom all variables of interest were available, indicated that birds were selective in  
577 whom they directed head preening towards. Both head and body preening were clearly  
578 influenced by at least some of the test predictors in the model (active feeding and proximity; full  
579 versus null model comparisons: head preening:  $\chi^2 = 57.938$ ,  $df = 2$ ,  $p < 0.001$ ; body preening:  $\chi^2$   
580  $= 33.951$ ,  $df = 2$ ,  $p < 0.001$ ). More specifically, head preening was significantly more common in  
581 the orange-winged Amazons compared to the vasas, significantly more common in dyads in  
582 which we observed active feeding, and also significantly more common in dyads with a larger  
583 proximity score (Model 4a; Fig. 4a, b; Table 9). Body preening was not explicitly correlated with

584 the dyadic presence of active feeding and did not differ between species, but it clearly increased  
585 with increased dyadic proximity (Model 4b; Fig. 4c; Table 9).

586

### 587 Mutual allopreening

588 We compared frequency of mutual allopreening in three species for which these data were  
589 available. Of dyads that engaged in allopreening, 89% of blue and gold macaw dyads ( $N = 9$ ) and  
590 31% of orange-winged Amazon dyads ( $N = 16$ ) engaged in mutual allopreening. No crow dyad  
591 ( $N = 2$ ) was observed mutually preening. The average result across the 1,000 random selections  
592 of dyads revealed a significant species effect ( $U = 2.264, P = 0.043$ ), indicating that the  
593 proportion of total allopreening that was mutual was significantly higher in macaws ( $Mdn = .22,$   
594  $N = 8$ ) compared to Amazons ( $Mdn = .02, N = 10$ ). Further statistical testing of whether mutual  
595 preening is a particularly valuable type of grooming, indicative of strong social bonding was not  
596 possible due to the low sample size. However, descriptively, dyads that mutually preened had  
597 higher proximity scores ( $M = .55, SD = .26$ ) compared to dyads that were allopreening partners  
598 but did not mutually preen ( $M = .18, SD = .14$ ).

599

### 600 **Discussion**

601 Although inter-species variation was found in rates of allopreening initiations and proportion of  
602 time invested in this activity, allopreening was observed in all parrot and corvid species in this  
603 study. This is consistent with findings from Kenny et al.'s (2017) comparative analyses, which  
604 indicate that allopreening most commonly occurs in species that engage in bi-parental care of  
605 offspring and show pair bond stability across breeding seasons. These avian partnerships share  
606 key similarities with chimpanzee and bonobo alliances; namely, their cooperative and stable  
607 nature (often persisting across years, Clayton & Emery, 2007; Emery et al., 2007; Forshaw,

608 2006; Seibert, 2006). For *Pan* species and corvids/parrots, the quality and effectiveness of these  
609 partnerships have substantial fitness implications (De Waal, 1995; Hoppe, 1992; Kaburu et al.,  
610 2013; Mitani, 2009; Røskaft, 1983; Spoon, 2006; Spoon et al., 2006, 2007; Wilson et al., 1995).  
611 These similarities, along with associations between social grooming and relationship  
612 quality/stability that previous studies have found (Fraser & Bugnyar, 2010; Gill, 2012; Kenny et  
613 al., 2017; Spoon et al., 2006, 2007), suggest that bond strength may be similarly maintained  
614 through social grooming in parrot/corvid pair bonds and chimpanzee/bonobo alliances. Our  
615 analyses revealed that parrots/corvids and bonobos/chimpanzees initiated social grooming bouts  
616 at similar rates; however, *Pan* species demonstrated significantly higher levels of investment in  
617 social grooming than parrots and corvids in terms of the duration spent engaged in grooming.  
618 *Pan* species also tended to groom with a higher proportion of their group members when  
619 controlling for group size, than corvids and parrots. The implications of these cross-taxon  
620 comparisons are constrained both by the focus on *Pan* species, rather than a wide range of  
621 primate species and the focus on captive animals. Unfortunately, due to a lack of data on wild  
622 parrot and corvid behavior, the effect of captivity on behavior, and particularly social grooming,  
623 cannot be quantified and may therefore be different for each species included in our study. This  
624 may have added noise to our data and/or biased our results. Whilst keeping these caveats in  
625 mind, one potential explanation for the pattern of results we found is that chimpanzees and  
626 bonobos have more affiliative relationships to maintain than parrots and corvids which requires a  
627 greater investment of overall grooming time. This is in line with the suggestion that primates  
628 form strong affiliative bonds with multiple individuals, that are similar in nature to reproductive  
629 pair bonds in other taxa (Dunbar & Shultz, 2007). Maintaining multiple strong affiliative  
630 relationships through social grooming may be more important for *Pan* species than most parrots

631 and corvids due to differences in mating behavior (promiscuous mating vs monogamy; e.g.  
632 Seibert, 2006; Stanford, 1998), the degree of fission-fusion dynamics (time separated from  
633 important social partners is high vs low; e.g. Aureli et al., 2008; Clayton & Emery, 2007;  
634 Boucherie et al., 2019) and the linearity of the dominance hierarchy (the utility of alliances to  
635 climb the hierarchy and to protect from severe physical aggression from higher ranking  
636 individuals is high vs low; e.g. Baker & Aureli, 2000; Terry, 1970). Future research should  
637 include a greater diversity of primate species and investigate whether the proportion of time  
638 investment in grooming per dyadic relationship is similar between taxa, in order to distinguish  
639 between the possibilities that *Pan* species require more time grooming to maintain multiple  
640 relationships or to create stronger bonds than are necessary in birds. In particular, data from  
641 primarily monogamous primates such as gibbons or titi monkeys may be valuable to address this  
642 question.

643         Despite most parrot and corvid species included in our analyses having a monogamous  
644 mating system, approximately half of the birds we observed had two or more preening partners,  
645 with some birds having as many as five in just a 240-minute period of observation. Although  
646 distributed grooming effort might be expected in immature birds, the majority of our groups  
647 (16/24) contained only adult birds, so this was an unexpected finding. Although extra-pair  
648 affiliative relationships have been documented in parrot and corvids, these relationships tend to  
649 be less stable, and relationships between reproductive partners appear to have the greatest fitness  
650 implications (Boucherie et al., 2016; Clayton & Emery, 2007; Garnetzke-Stollmann et al., 1991;  
651 Spoon et al., 2006, 2007). This finding may support a growing body of evidence suggesting that  
652 extra-pair affiliations are much more common among socially monogamous birds than  
653 previously thought (Boucherie et al., 2016; Griffith et al., 2002; Spoon et al., 2002); based on

654 genetic analyses. For instance, it has been estimated that approximately 11% of offspring are the  
655 product of extra-pair copulation in species identified as socially monogamous (Griffith et al.,  
656 2002). Alternatively, aspects of the captive environment may have also contributed to the  
657 provision of grooming to multiple partners observed in our birds, just as it may have done in the  
658 *Pan* species. In the birds, being confined in a cage with other pair bonded animals may also  
659 produce dynamics similar to those found in colonial species, where allopreening occurs between  
660 neighboring pairs with the apparent function of reducing aggression between them (Lewis et al.,  
661 2007), or in large wild aggregations, where grooming of unrelated non-mates can occur  
662 (Harrison, 1965). The persistent close contact with multiple individuals may also increase the  
663 likelihood of assessing other potential mates. As species' behavior may have been affected in a  
664 variety of ways by captivity, it is unclear whether similar patterns as those observed in our study  
665 would be found if social grooming of wild individuals of the same species were investigated.

666         In terms of assessing whether allopreening was associated with other affiliative behaviors,  
667 and may therefore be part of a suite of behaviors used to maintain affiliative relationships with  
668 important social partners, we found support for allopreening being provided selectively within a  
669 group, with focal birds more likely to preen a dyad partner that they were often in close proximity  
670 to. Our findings are consistent with previous studies of captive and wild birds which have provided  
671 substantial evidence indicating that parrots and corvids demonstrate spatial organization and  
672 association patterns that are not random, with individuals showing a high degree of consistency in  
673 with whom they maintain close physical proximity to and interact with (Boucherie et al., 2016;  
674 Emery et al., 2007; Forshaw, 2006; Fraser & Bugnyar, 2010; Garnetzke-Stollmann & Franck,  
675 1991; Pitter & Christiansen, 1997; Seibert & Crowell-Davis, 2001; Seibert, 2006; Spoon et al.,  
676 2006, 2007; Wechsler, 1989). Our findings are also consistent with studies of mammalian species,

677 which identified positive correlations between allogrooming and proximity measures. For  
678 instance, associations between these two factors are widely found in a range of primates (e.g.,  
679 chimpanzees, Langergraber et al., 2009; bonobos, Tokuyama & Furuichi, 2016; gibbons, Palombit,  
680 1996; java monkeys, pigtail macaques, Troisi et al., 1989). Outside the primate order, Sato and  
681 colleagues (1993) found a positive correlation between allogrooming duration while housed and  
682 maintenance of physical proximity while out at pasture in cows. Importantly, the maintenance of  
683 close physical proximity is also predictive of long-term bond stability in a number of species (e.g.,  
684 Black, 2001; Garroway & Broders, 2007; Gilby & Wrangham, 2008; Koski et al. 2012; Massen &  
685 Sterck 2013; Moller, et al., 2001; Silk et al., 2006; Zabel et al., 1992). It seems that parrots and  
686 corvids are selective in whom they maintain close physical proximity to and are more likely to  
687 engage in allopreening with these individuals, who likely represent important social partners.

688         Alternative explanations for our results must, however, be considered. As allopreening  
689 requires close physical proximity, if individuals were preening as a proximity scan was taken, they  
690 would be recorded as nearest neighbors, which might offer a simple explanation for this  
691 relationship. Unfortunately, we were unable to identify and exclude proximity scans taken whilst  
692 birds were preening from our analysis as the behavioral context of the animal at the time of each  
693 scan was not recorded in the majority of our groups. However, we estimate (from study groups  
694 that had duration of allopreening data available in each model) that on average the birds in our  
695 models only spent approximately 2.63% (based on four of six species included in Model 3a) and  
696 2.30% (based on six of nine species included in Model 3b) of their observation time engaged in  
697 preening. It therefore seems unlikely that a sufficient number of proximity scans would have  
698 coincided with preening to be responsible for this effect. It is also possible that the variation in  
699 bird density within an aviary and the proximity criteria used to identify nearest neighbors in each

700 species (see Table 1, Table S1) may have influenced the relationship between proximity and  
701 allopreening. It is thus vital that future studies are conducted, where data collection methods are  
702 agreed in advance with a broad range of species to understand the relationship between proximity  
703 and allopreening in more depth. Future investigations would also benefit from longitudinal  
704 analyses, examining how measures of relationship quality, including proximity, predict variation  
705 in allopreening interactions over time. While cross-sectional correlational analyses such as the  
706 ones we report in the present paper do not allow for the determination of whether associations  
707 between allopreening and social factors are causal in nature, further in-depth investigations would  
708 contribute to our understanding of how allopreening may be used to manage relationships and help  
709 clarify the directionality of associations.

710         We predicted that allopreening would be negatively correlated with agonistic behavior,  
711 however we found no evidence for such a relationship. Subjects were not less likely to preen  
712 individuals they had directed aggression towards than those they had not. While it is not clear why  
713 no such relationship was found, it is possible that parrots and corvids are simply less likely to  
714 directly interact with individuals that they do not have affiliative relationships with, compared to  
715 those they do have affiliative relationships with. If so, there may be less opportunity to enter into  
716 conflicts with individuals outside the pair bond. Additionally, limitations of our analysis may have  
717 reduced our ability to observe a significant correlation between these two factors. Due to  
718 differences in sampling methods and behavioral definitions across our diverse data set, we used  
719 binary measures for social behaviors (e.g., did subjects direct aggression towards partners? Y/N).  
720 Assessing potential associations between social behaviors using categorical variables, as opposed  
721 to rates, for example, may have limited the detection of more subtle variation dyads may have  
722 demonstrated on these social measures. Our analyses were also solely focused on aggressive

723 behavior and preening that was directed to partners by focal birds. It would be valuable to also  
724 investigate whether preening a partner is predicted by being the recipient of aggression emitted by  
725 a partner. If such a relationship were found, it would suggest that allopreening may be used as a  
726 strategy for reducing or avoiding aggression, as has been found in ravens (Fraser & Bugnyar,  
727 2011).

728         In contrast to our predictions, active feeding was not a significant predictor of allopreening  
729 occurrence in either of our main models. There are several reasons that may explain this  
730 unexpected pattern of results. First, this may partly be due to the rare occurrence of active feeding  
731 in our study groups (occurring in just 34 of 1222 dyads in Model 3a and in 57 of 1606 dyads in  
732 Model 3b). It was not observed at all in three of the nine species included in our analyses (Goffin's  
733 cockatoo, orange-winged Amazon, New Caledonian crow). Second, as active feeding, and in  
734 particular allofeeding, has been most widely found to occur between parent and offspring and  
735 between reproductive partners during breeding seasons, our findings may be explained by the fact  
736 that most of the groups included in our analyses did not include breeding pairs (see Table 1). Third,  
737 it is possible that the type of active feeding individuals engage in may have particular significance.  
738 In our study, the behavioral category of active feeding combined the transfer of monopolizable  
739 food items and regurgitation into the mouth. The latter is a more physically intimate act and may  
740 occur in a more affiliative context than the transfer of a food item, which may be more likely to  
741 occur in situations where the donor may be motivated by harassment avoidance (e.g. De Kort et  
742 al., 2006). It is, however, also possible that allofeeding may be more instinctually driven, and may  
743 be triggered by others engaging in submissive or begging behaviors that reliably elicit allofeeding  
744 when performed by juveniles or reproductive partners (Ellis et al., 2009; Wright, 1998). Assessing  
745 whether functional differences exist between these types of active feeding, and between active



746 feeding that occurs within and outside the breeding context, are avenues of research worth pursuing  
747 as they may provide deeper insight into the mechanisms avian species use to manage their social  
748 relationships. Finally, it could also be that allofeeding is selectively performed with the most  
749 valuable partners, and by considering preening of any body region in the main models we may  
750 have overlooked the predictive value of allofeeding. In our analyses focusing on blue-throated  
751 macaws, orange-winged Amazons and vassals (Models 4a; 4b), we found that birds who engaged in  
752 allofeeding were more likely to engage in allopreening of their partner's head, but not their body.  
753 Ectoparasitic infestations tend to be higher in the head since it cannot be autopreened (Boyd, 1951;  
754 Cox, 2012). Thus, head preening, as opposed to body preening, may make a greater contribution  
755 to an individual's fitness due to its hygienic benefits and thus be of higher value and conferred  
756 only on the most valuable partners. It is also possible that individuals may be more willing to  
757 receive head preening from partners they have a strong, valued relationship with, and therefore  
758 trust; allowing a conspecific to preen the head, particularly around the eyes, carries risk of injury  
759 that could negatively affect long-term survival. Taken together it seems that head-preening and  
760 allofeeding may be markers of a strong and valued relationship in parrots and corvids, but future  
761 research needs to confirm this in a wider range of species.

762         In our exploratory investigation of mutual preening, we found significant differences in  
763 how frequently it occurred in the three species for which these data were available. While it was  
764 not observed at all in New Caledonian crows, it was found to occur in blue and gold macaws and  
765 orange-winged Amazons, with macaws showing significantly higher proportions of mutual  
766 preening as compared to Amazons. Although we did not have data on mutual preening for a  
767 sufficient number of groups to carry out an analysis of its potential functions, we found that for  
768 dyads that engaged in allopreening, mean proximity scores were higher for those that mutually

769 preened as compared to those that did not. Future research should investigate this potential  
770 relationship further in a broad number of species, as mutual grooming may be an important  
771 indicator of bond strength. Further investigation is also needed to determine whether inter-species  
772 variation in whether mutual preening occurs or not may be better explained by social factors (e.g.  
773 bond strength) or anatomical differences (e.g., neck length, bill morphology), that may make it  
774 easier for one species to engage in this behavior than another.

775         In conclusion, allopreening seems to serve an important social function in corvids and  
776 parrots. These birds are selective with whom they maintain regular close proximity with and they  
777 are more likely to engage in allopreening with these specific social partners, indicating that both  
778 frequent close physical proximity and allopreening are markers of affiliative social bonds. Head  
779 preening and mutual preening should be investigated in a wider range of species to confirm  
780 whether these types of allopreening are markers of particularly strong and valuable relationships.  
781 Corvids and parrots, in comparison to *Pan* species, tend to socially groom a smaller proportion  
782 of their group members, and this may explain the reduced time birds dedicate to social grooming  
783 compared to chimpanzees and bonobos.

784

## 785 **References**

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1094

1095 **Table 1.**

1096 *Number of individuals, group composition, study duration (number of months data collection*  
 1097 *period consisted of), average observation time/bird (rounded to nearest hr), data collection*  
 1098 *methods for social behaviors and proximity, and distance criteria used to identify nearest neighbor*  
 1099 *during proximity scans for study groups (Parrots/corvids, N = 15 species; Pan species, N = 2).*

1100

Taxa	Species	N	Group composition	Study duration (mos) and hrs of observation /individual	Method for social behavior	Method for proximity	Nearest neighbor criteria
Parrot	<b>Black-headed caique</b>	4	A, NB	2, 3	F	NA	NA
	<b>Blue and gold macaw</b>	12	A, NB	4, 4	F	F	NR
	<b>Blue-throated macaw</b>						
	Group 1	3	A, NB	6, 4	GS	G	DR, physical contact
	Group 2	7	A, NB	8, 4	GS	G	DR, physical contact
	<b>Great green macaw</b>						
	Group 1	3	A, NB	1, 4	GS	G	DR, physical contact
	Group 2	6	A, NB	10, 4	GS	G	DR, physical contact
	<b>Greater vasa</b>	10	MA, BP	7, 6	F	F	NR
	<b>Goffin's cockatoo</b>	14	MA, NB	8, 5	F	G	DR, 40cm
<b>Kea</b>	21	MA, BP	21, 3	F	F	DR, 1m	
<b>Orange-winged Amazon</b>	23	A, NB	5, 4	F	F	NR	



	<b>Red shouldered macaw</b>	<b>4</b>	A, NB	<b>2, 3</b>	<b>F</b>	<b>na</b>	<b>NA</b>
	<b>Azure-winged magpie</b>						
	Group 1	6	A, BP	4, 4	F	F	NR
	Group 2	6	A, NB	5, 6	F	F	NR
	<b>Common raven</b>						
	Group 1	8	A, NB	7, 5	F	F	NR
	Group 2	8	A, NB	7, 5	F	F	NR
Corvid	Group 3	10	J	10, 8	F	F	NU
	<b>Eurasian jay</b>	<b>14</b>	<b>J</b>	<b>6, 15</b>	<b>GA</b>	<b>G</b>	<b>NU</b>
	<b>Jackdaw</b>						
	Group 1	10	A, NB	18, 64	GA	G	DR, within 2 body lengths
	Group 2	15	J	12, 22	GA	G	NU
	<b>New Caledonian crow</b>	<b>3</b>	<b>MA, BP</b>	<b>1, 2</b>	<b>F</b>	<b>F</b>	<b>NR</b>
	<b>Rook</b>						
	Group 1	14	A, BP	21, 24	F	G	NU
	Group 2	9	A, NB	17, 64	GA	G	DR, within 2 body lengths
	Group 3	12	A, NB	18, 62	GA	G	DR, within 2 body lengths
	Group 4	13	J	12, 34	GA	G	NU
	<b>Bonobos</b>						
	Group 1	11	MA	2, 15	F		
Apes	Group 2	13	A	2, 49	GS		
	Group 3	6	A	2, 40	GS		
	Group 4	8	A	3, 32	GS		
	<b>Chimpanzees</b>						
	Group 1	8	MA	1, 10	F		
	Group 2	7	A	2, 51	GS		
	Group 3	17	A	3, 36	GS		

Group 4	6	A	3, 25	GS
Group 5	18	A	12, 51	GS & GA

1101 *Note.* Groups were either composed of adult only (A), mixed-age (MA), or juvenile only (J). For  
1102 birds, groups had either no breeding pairs (NB) or having one or more breeding pairs (BP). Data  
1103 collection methods for social behaviors (allopreening/grooming, agonistic, active feed) consisted  
1104 of individual focal (F), group all-occurrence (GA), or group scan (GS) sampling; for one ape group,  
1105 group all-occurrence data and scan sampling data were available. For birds, data collection  
1106 methods for proximity (nearest neighbor) consisted of individual focal (F) or group (G) scans;  
1107 criteria used for identifying nearest neighbors consisted of distance requirements (DR), where  
1108 individuals would have to be within a certain distance of one another in order to be considered  
1109 nearest neighbors, or no distance requirement (NR), where an individual that was closest in  
1110 physical proximity to a subject was considered the subject's nearest neighbor; minimum distance  
1111 criteria is indicated for groups where a distance requirement was used. NA indicates that proximity  
1112 data were not available, while NU indicates that proximity data were available but not used in  
1113 GLMMs because study groups did not have data on the other factors included in the models or  
1114 because they were juvenile groups and were thus not included in GLMMs. The mean number of  
1115 observation hours/individual is used for groups where observation time varied between  
1116 individuals.

1117

1118

1119

1120 Table 2.

1121 *Results of Models 1a, 1b, and 1c which examined whether taxon could explain variation in time*  
1122 *dedicated to social grooming as measured by proportion of time spent social grooming (1a),*  
1123 *proportion of scans spent social grooming (1b) and rate of social grooming initiations (1c).*  
1124 *Models 1a-c varied in the number of groups of birds and Pan species they included: Model 1a*  
1125 *had 11 bird groups and three Pan groups; Model 1b had four bird groups and seven Pan*  
1126 *groups; Model 1c had 16 bird groups and two Pan groups. The table shows estimates (est.),*  
1127 *together with odds ratios (OR), standard errors (SE), confidence limits (CI), significance tests as*  
1128 *well as minimum and maximum of model estimates obtained when dropping levels of random*  
1129 *effects one at a time).*

Model	Term	est.	OR	SE	lower CI	upper CI	$\chi^2$	df	P	min	Max
1a	Intercept	-2.111	0.121	0.464	-3.084	-1.077			( <sup>1</sup> )	-2.381	-0.970
1a	taxon <sup>(2)</sup>	-1.634	0.195	0.378	-2.423	-0.814	7.813	1	0.005	-2.059	-1.350
1a	gr. Size	0.009	1.009	0.030	-0.056	0.071	0.050	1	0.822	-0.090	0.029
1b	Intercept	-2.027	0.132	0.146	-2.353	-1.726			( <sup>1</sup> )	-2.171	-1.892
1b	taxon <sup>(2)</sup>	-0.722	0.486	0.337	-1.418	-0.044	3.655	1	0.056	-1.001	-0.452
1b	z.gr. size <sup>(3)</sup>	0.063	1.066	0.152	-0.280	0.420				-0.222	0.144

1c	Intercept	-2.417	0.089	0.590	-3.643	-1.287			(1)	-2.641	-2.048
1c	taxon <sup>(2)</sup>	-0.423	0.655	0.552	-1.532	0.724	0.576	1	0.448	-0.612	-0.318
1c	gr. Size	0.002	1.002	0.035	-0.061	0.069	0.003	1	0.954	-0.043	0.029

1130 <sup>(1)</sup> not shown because of having a very limited interpretation

1131 <sup>(2)</sup> dummy coded with ape being the reference category

1132 <sup>(3)</sup> z-transformed to a mean of zero and a standard deviation of one; mean and sd of the original variable  
 1133 were 10.383 and 5.350; no test indicated as the model lacking group size did not converge

1134

1135 **Table 3.**

1136 *Medians (Mdn) and interquartile ranges (IQR) of social grooming rate (Corvids/parrots N = 16*  
 1137 *groups from 12 species; Pan species N = two groups from two species) and proportion of time*  
 1138 *(Corvids/parrots, N = 11 groups from nine species; Pan species N = three groups from two*  
 1139 *species) or scans (Corvids/parrots, N = four groups from two species; Pan species N = seven*  
 1140 *groups from two species) subjects spent socially grooming, for all individuals included in the*  
 1141 *GLMMs comparing birds and Pan species.*

1142

	Birds (Parrots & Corvids)			Apes (Pan species)		
	<i>N</i>	<i>Mdn</i>	<i>IQR</i>	<i>N</i>	<i>Mdn</i>	<i>IQR</i>
Rate of grooming initiations	156	.02	.07	19	.06	.04
Proportion of time spent grooming (Duration)	88	.01	.04	37	.09	.09
Proportion of time spent grooming (Scans)	19	.03	.05	75	.12	.12

1143

1144

1145 Table 4.

1146 *Results of Models 2a and b which examined whether taxon could explain variation in the*  
 1147 *proportion of group members an individual engaged in grooming with. Model 2b controlled for*  
 1148 *group size by including the number of potential partners (nr.partn.) as a fixed factor. Both*  
 1149 *models included data from 13 groups of nine bird species and nine groups of two Pan species.*  
 1150 *Table shows estimates (est.), together with odds ratios (OR), standard errors (SE), confidence*  
 1151 *limits, significance tests as well as minimum and maximum of model estimates obtained when*  
 1152 *dropping levels of random effects one at a time.*

Model	term	est.	OR	SE	lower CI	upper CI	$\chi^2$	df	P	min	max
2a	Intercept	-0.984	0.374	0.333	-1.592	-0.369			(1)	-1.087	-0.874
2a	taxon <sup>(2)</sup>	-0.369	0.691	0.391	-1.104	0.357	0.811	1	0.368	-0.500	-0.258

2b	Intercept	0.245	1.277	0.192	-0.105	0.566			(1)	0.085	0.459
2b	taxon <sup>(2)</sup>	-0.320	0.726	0.137	-0.605	-0.062	3.151	1	0.076	-0.389	-0.237
2b	nr. partn.	0.050	1.051	0.012	0.029	0.073	16.323	1	<0.001	0.032	0.062

1153 <sup>(1)</sup> not shown because of having a very limited interpretation

1154 <sup>(2)</sup> dummy coded with ape being the reference category

1155

1156

1157

1158 **Table 5.**

1159 *Descriptive statistics for number of different grooming partners birds (parrots and corvids: N =*  
 1160 *13 groups from nine species) and apes (N = nine groups from two Pan species) had in 240-*  
 1161 *minute sample of observation time. SD – standard deviation, IQR – inter quartile range*

1162

	Birds	Apes	
	(N= 95 focal animals)	(N= 85 focal animals)	
<i>Mean (SD)</i>	1.78 (1.94)	2.73 (1.69)	1163
<i>Median (IQR)</i>	2 (1)	2 (1)	1164
<i>Range</i>	4 (1 to 5)	8 (1 to 9)	1165

1168

1169

1170 **Table 6.**  
 1171 *Descriptive statistics for species (birds (parrots/corvids), N = 15; apes (Pan), N = 2) and study*  
 1172 *group allopreening/grooming rate, percentage of time or scans spent allopreening/grooming,*  
 1173 *number of unique allopreening/grooming partners, and number of potential partners within the*  
 1174 *captive group.*  
 1175

Family and age groups	Species	Allopreen/groom rate (bouts/min)		% Time spent Allopreening/Grooming		% Scans Allopreening/Grooming		No. of unique partners in first 240 min observation		No. of potential partners
		<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	
			<b>Black-headed caique</b>	<b>.02</b>	<b>.01</b>	<b>0.35</b>	<b>0.45</b>	<b>na</b>	<b>na</b>	
	<b>Blue and gold macaw</b>	<b>.21</b>	<b>.21</b>	<b>6.11</b>	<b>5.43</b>	<b>na</b>	<b>na</b>	<b>1.36</b>	<b>.67</b>	<b>11</b>
	<b>Blue-throated macaw</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>4.00</b>	<b>4.61</b>	<b>1.88</b>	<b>.83</b>	<b>4</b>
Parrot adult and mixed age groups	Group 1	na	na	na	Na	9.44	5.09	1.33	.58	2
	Group 2	na	na	na	Na	1.67	1.44	2.20	.84	6
	<b>Great green macaw</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>3.89</b>	<b>3.89</b>	<b>1.67</b>	<b>.87</b>	<b>3.50</b>
	Group 1	na	na	na	Na	8.33	3.63	1.33	.58	2
	Group 2	na	na	na	Na	1.67	1.05	1.83	.98	5
	<b>Greater vasa</b>	<b>.03</b>	<b>.03</b>	<b>0.11</b>	<b>0.05</b>	<b>na</b>	<b>na</b>	<b>1.88</b>	<b>1.46</b>	<b>9</b>
	<b>Goffin's cockatoo</b>	<b>.03</b>	<b>.03</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>1.55</b>	<b>.93</b>	<b>13</b>
	<b>Kea</b>	<b>.01</b>	<b>.01</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>19.43</b>
	<b>Orange-winged Amazon</b>	<b>.12</b>	<b>.08</b>	<b>2.96</b>	<b>2.05</b>	<b>na</b>	<b>na</b>	<b>2.40</b>	<b>.91</b>	<b>22</b>
	<b>Red shouldered macaw</b>	<b>.23</b>	<b>.07</b>	<b>8.73</b>	<b>3.68</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>3</b>
	<b>Azure-winged magpie</b>	<b>.03</b>	<b>.04</b>	<b>0.26</b>	<b>0.48</b>	<b>na</b>	<b>na</b>	<b>1.43</b>	<b>.53</b>	<b>4.90</b>
	Group 1	.03	.05	0.29	0.68	na	na	1.50	.71	4.80
Group 2	.03	.03	0.18	0.17	na	na	1.40	.55	5	

	<b>Common raven</b>	<b>.07</b>	<b>.05</b>	<b>0.66</b>	<b>0.00</b>	<b>na</b>	<b>na</b>	<b>1.87</b>	<b>.92</b>	<b>7</b>
Corvid adult and mixed age groups	Group 1	.06	.04	0.48	0.00	na	na	2.13	1.13	7
	Group 2	.08	.06	0.87	0.47	na	na	1.86	1.07	7
	<b>Jackdaw</b>	<b>.00</b>	<b>.00</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>9</b>
	<b>New Caledonian crow</b>	<b>.07</b>	<b>.05</b>	<b>1.15</b>	<b>1.18</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>2</b>
	<b>Rook</b>	<b>.02</b>	<b>.03</b>			<b>na</b>	<b>na</b>			<b>10.23</b>
	Group 1	.04	.04	3.18	2.33	na	na	1.36	.51	11.70
	Group 2	.00	.00	na	Na	na	na	na	na	8
	Group 3	.01	.01	na	Na	na	na	na	na	11
	<b>Eurasian jay</b>	<b>.00</b>	<b>.00</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>13</b>
Juvenile corvid groups	<b>Common raven</b>	<b>.05</b>	<b>.04</b>	<b>1.01</b>	<b>.95</b>	<b>na</b>	<b>na</b>			<b>9</b>
	<b>Jackdaw</b>	<b>.03</b>	<b>.01</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>14</b>
	<b>Rooks</b>	<b>.06</b>	<b>.04</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>na</b>	<b>12</b>
	<b>Bonobos</b>									
Apes	Group 1	.06	.03	13.79	5.19	na	na	2.36	1.57	10
	Group 2	na	na	na	na	12.77	7.11	2.00	.82	12
	Group 3	na	na	na	na	6.69	4.56	1.60	.89	5
	Group 4	na	na	na	na	14.02	5.90	2.86	1.22	7
	<b>Chimpanzees</b>									
	Group 1	.07	.03	17.05	7.89	na	na	2.50	1.20	7
	Group 2	na	na	na	na	3.93	2.26	2.20	.45	6
	Group 3	na	na	na	na	17.10	10.67	4.24	2.44	16
	Group 4	na	na	na	na	15.58	7.39	1.60	.55	5
	Group 5	na	na	6.83	0.04	10.12	5.61	2.76	1.35	17

1176 *Note.* Number of potential partners refers to the number of individuals who co-occurred with  
1177 focal animals in observations of that specific group. The mean number of potential allopreening  
1178 partners (calculated across observations) is used for groups where the group size varied due to  
1179 changes in group composition.

1180

1181 **Table 7**

1182 *Results of Models 3a and b which examined if variation in whether or not a dyad engaged in allopreening*  
 1183 *could be explained by other dyadic social behaviours. Model 3a included as fixed factors the proportion*  
 1184 *of time spent in close proximity, the occurrence of active feeding, and the occurrence of agonistic*  
 1185 *interactions. Model 3b only included proximity and active feeding as fixed effects. Models 3a and 3b*  
 1186 *included seven and 11 bird groups, respectively. The table shows estimates (est.), together with odds*  
 1187 *ratios (OR), standard errors (SE), confidence limits, significance tests as well as minimum and maximum*  
 1188 *of model estimates obtained when dropping levels of random effects one at a time.*

Model	term	est.	OR	SE	lower CI	upper CI	$\chi^2$	df	P	min	max
3a	Intercept	-4.966	0.007	0.539	-21.359	-4.435			(1)	-17.679	-4.484
3a	feeding <sup>(2)</sup>	-1.424	0.241	1.321	-14.368	1.295	1.397	1	0.237	-9.630	0.229
3a	agon <sup>(3)</sup>	-0.400	0.670	0.696	-6.751	0.625	0.384	1	0.535	-5.283	0.021
3a	proximity <sup>(4)</sup>	3.825	45.854	1.287	1.682	24.860	6.439	1	0.011	2.319	23.457
3b	Intercept	-6.174	0.002	0.678	-9.830	-5.114			(1)	-6.877	-5.538
3b	feeding <sup>(2)</sup>	0.598	1.818	1.457	-3.325	4.047	0.159	1	0.690	-1.074	1.031
3b	proximity <sup>(4)</sup>	4.000	54.624	0.781	2.629	7.831	13.801	1	0.000	3.024	4.774

1189 <sup>(1)</sup> not shown because of having a very limited interpretation

1190 <sup>(2)</sup> dummy coded with no feeding observed being the reference category

1191 <sup>(3)</sup> dummy coded with no agonistic behaviors observed being the reference category

1192 <sup>(4)</sup> z-transformed to a mean of zero and a standard deviation of one; mean and sd of the original variable  
 1193 were 0.044 and 0.115 (Model 3a) and 0.046 and 0.113 (Model 3b), respectively

1194

1195 **Table 8.**

1196 *Percentage of preening behaviors subjects (N = 7 species) directed to partners that focused on*  
 1197 *preening the head/neck area) and anatomical preening mechanism (G = uropygial gland, P =*  
 1198 *powder down) per species.*

	% head	Mechanism
Blue and gold macaw	55.72	G (Vincze et al., 2013)
Blue-throated macaw	72.50	G (Abramson et al., 1995)
Great-green macaw	50.00	G (Lambert, personal communication)
Greater vasa	50.00	G (Christian, 2000)

Common raven	50.65	G (Montalti & Salibián, 2000)
New Caledonian crow	65.00	G (Montalti & Salibián, 2000) <sup>†</sup>
Orange-winged amazon	76.14	P (Vincze et al., 2013)

1199 *Note.* Percentages for blue-throated and great-green macaws were calculated using scan  
1200 frequency data (number of scans in which A preened B's head divided by total number of scans  
1201 during which A preened B, regardless of region); for all other species, percentages were  
1202 calculated using frequency data obtained via all-occurrence sampling (total frequency of head  
1203 preening given by A to B divided by total frequency of preening given by A to B, regardless of  
1204 region). <sup>†</sup>Montalti and Salibián, (2000) report presence of uropygial glands in species closely  
1205 related to New Caledonian crows (e.g., Carrion crows, *Corvus corone*); a source could not be  
1206 found that reports presence or absence of uropygial glands specifically in New Caledonian  
1207 crows.

1209 **Table 9.**

1210 *Results of Models 4a and b which examined whether variation in the occurrence of head (4a) or*  
1211 *body (4b) preening within a dyad could be explained by the occurrence of active feeding and the*  
1212 *proportion of time in close proximity. Table shows estimates (est.), together with odds ratios*  
1213 *(OR), standard errors (SE), confidence limits, significance tests as well as minimum and*  
1214 *maximum of model estimates obtained when dropping levels of random effects one at a time.*

Model	term	est.	SE	OR	lower CI	upper CI	$\chi^2$	df	P	min	max
4a (H)	Intercept	-5.257	0.978	0.005	-35.132	-4.277			( <sup>1</sup> )	-24.260	-4.887
4a (H)	feeding <sup>(2)</sup>	5.443	1.622	231.176	2.947	45.825	14.769	1	<0.001	4.691	20.312
4a (H)	proximity <sup>(3)</sup>	6.118	1.792	454.134	4.171	50.626	39.580	1	<0.001	5.585	24.705
4a (H)	spec. Amaz.	1.738	1.003	5.686	-2.012	12.425	16.008	2	<0.001	1.375	7.032
4a (H)	Spec. Vasa	-2.485	1.413	0.083	-24.450	1.426				-5.803	-0.746
4a (B)	Intercept	-4.181	0.496	0.015	-45.448	-3.456			( <sup>1</sup> )	-4.684	-3.959
4a (B)	feeding <sup>(2)</sup>	0.981	1.032	2.667	-4.376	16.724	0.836	1	0.361	-3.262	2.463
4a (B)	proximity <sup>(3)</sup>	2.081	0.378	8.011	1.647	29.611	32.790	1	<0.001	1.952	2.415
4a (B)	spec. Amaz.	-1.198	0.776	0.302	-12.124	0.958	2.789	2	0.248	-1.707	-0.934
4a (B)	Spec. Vasa	-0.978	0.701	0.376	-19.852	0.699				-1.563	-0.774

1215 (<sup>1</sup>) not shown because of having a very limited interpretation

1216 (<sup>2</sup>) dummy coded with no feeding observed being the reference category; the large odds ratio arises from  
1217 effects being fairly extreme (see Fig. 4)

1218 (<sup>3</sup>) z-transformed to a mean of zero and a standard deviation of one; mean and sd of the original variable  
1219 were 0.093 and 0.152, respectively; the large odds ratio arises from effects being fairly extreme (see Fig.  
1220 4)



1221 <sup>(4)</sup> dummy coded with Blue and gold macaw being the reference category; the indicated test refers to the  
1222 overall effect of species

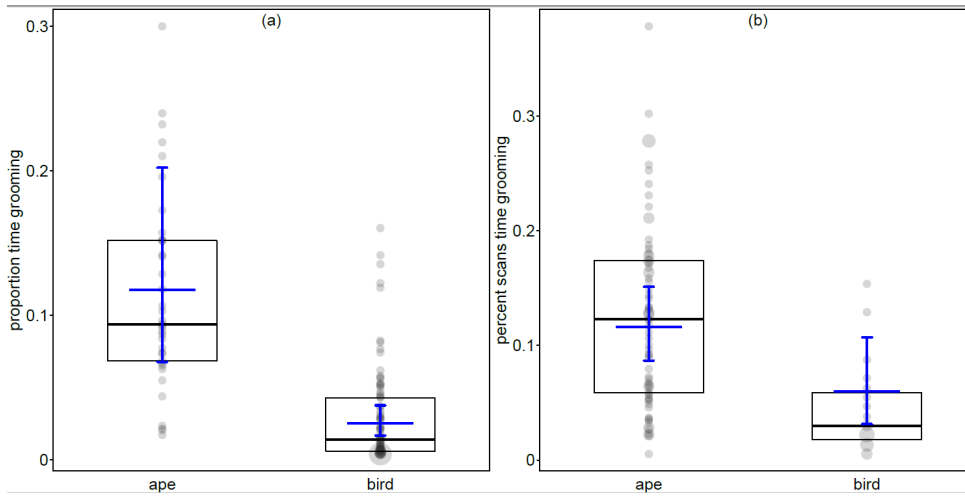
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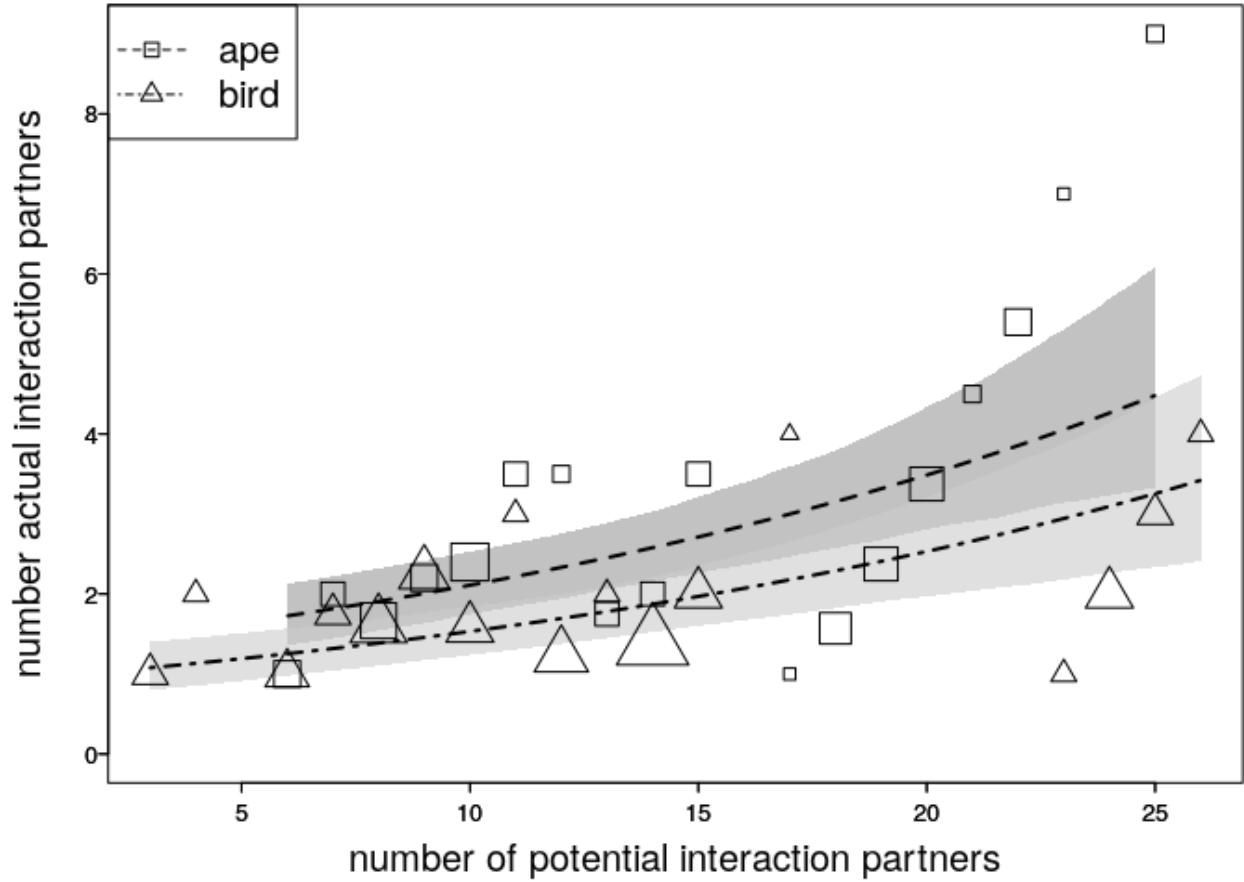
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1227 **Figure legends**



1228  
1229 *Figure 1.* Proportion time (a) and percent scans (b) spent grooming, separately for apes  
1230 (chimpanzees/bonobos) and birds (corvids/parrots). Depicted are the raw data (grey dots), whereby  
1231 the area of the dots is proportionate to the number of observations per value of the response ( $N=1$   
1232 to 9). Thick black horizontal lines and boxes depict medians and quartiles, and the blue vertical  
1233 line with error bars depicts the fitted model and its confidence intervals. Corvids and parrots spent  
1234 a significantly smaller proportion of their time grooming than *Pan* species (a) and also tended to  
1235 spend fewer scans grooming than *Pan* species (b).

1236  
1237

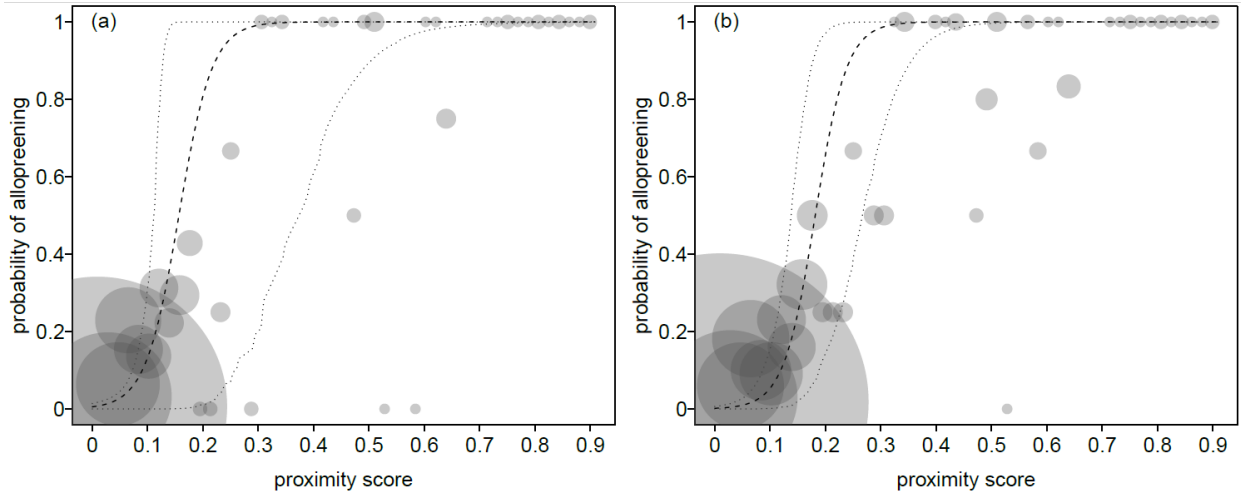


1238

1239 *Figure 2.* Number of grooming interaction partners as a function of the number of potential  
 1240 interaction partners, and separately for birds (corvids/parrots) and apes (chimpanzees/bonobos).  
 1241 Indicated are average numbers of interaction partners per number of potential interaction  
 1242 partners, whereby the area of the dots corresponds to the number of observations per taxon and  
 1243 number of potential interaction partners ( $N = 1$  to 16). The dotted lines depict the fitted model  
 1244 and the shaded areas its confidence interval. As group size increased the number of grooming  
 1245 partners increased and when controlling for group size parrots and corvids tended to have fewer  
 1246 grooming interaction partners than *Pan* species.

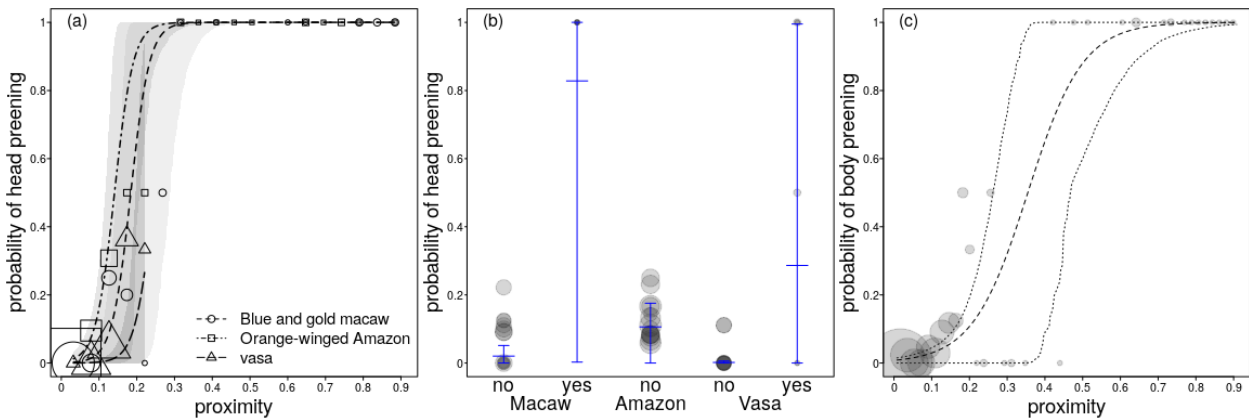
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1249  
 1250 *Figure 3.* Probability of dyadic allopreening to be observed within a given dyad, as a function of  
 1251 their proximity score. (a) illustrates the relationship from Model 3a where proximity, active  
 1252 feeding and agonistic interactions were included as fixed factors ( $N = 77$  individuals from six  
 1253 species) and (b) illustrates the relationship from Model 3b where just proximity and active feeding  
 1254 were included as fixed factors ( $N = 118$  individuals from nine species). Each dot shows the average  
 1255 probability per bin of the proximity score, whereby the area of the dots depicts the number of dyads  
 1256 per dot ( $N = 1$  to 1005). The dashed and dotted lines depict the fitted model and its confidence  
 1257 interval (with all other predictors in the model being at their average and assuming an observation  
 1258 effort of 4 hrs, which roughly equals the average observation effort). The two plots differ in the  
 1259 amount of data used and the additional predictors being present in the model. In both models,  
 1260 allopreening was more likely to occur in dyads that spent a higher proportion of their time in close  
 1261 physical proximity.

1262  
 1263



1264  
 1265  
 1266 *Figure 4.* Probability of head preening (a, b) and body preening (c) as a function of dyadic  
 1267 proximity (a, c) or separately for three species and dyads that exhibited or did not exhibit active  
 1268 feeding (b). Dots in (a) and (c) show the average probability per bin of the dyadic proximity, and  
 1269 dots in (b) depict average probability per individual. The area of the dots is proportionate to the  
 1270 number of dyads per dot (range, a: 1 to 147; b: 1 to 18; c: 1 to 154). The fitted model and its

1271 confidence intervals are depicted by dashed lines and shaded areas (a), vertical blue lines with  
1272 error bars (b), or the dashed and dotted line (c). Head preening (a) and body preening (c) was more  
1273 likely to occur in dyads that spent a high proportion of their time in close proximity and in macaws  
1274 and vasas who exhibited active feeding, head preening was more likely in dyads who also engaged  
1275 in active feeding (b).

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