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

Short running title: Allopreening in parrots and corvids

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Abstract

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

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

Introduction

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

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

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

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

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

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

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

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

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

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

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

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

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

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

In order to address our second aim, we investigated potential associations between allopreening and three additional measures of relationship strength (proximity, active feeding, and agonistic behavior). We focused on these measures/interactions because they serve as reliable measures of relationship quality in a variety of species (Boucherie et al., 2016; Bräger et al., 1994; Dunbar & Shultz, 2010; Fraser & Bugnyar, 2010; Gilby & Wrangham, 2008; Spoon et al., 2006, 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,

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

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

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

Methods

Study groups

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

Data collection

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

Measures

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

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

Data Analysis

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

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

Comparison of social grooming in birds and *Pan* species

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

*Proportion of time dedicated to social grooming in corvids, parrots and P*an *species (Models 1a, 1b and 1c)*

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Lastly, we examined the body part preened to determine whether head/neck preening was more valuable than body preening and indicative of stronger social bonds within a dyad. For blue and gold macaws, blue-throated macaws (two groups), great-green macaws (two groups), 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/(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

Mutual grooming

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

Implementation of GLMMs and general considerations

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

Results

Comparison of social grooming in birds and *Pan* species

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

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

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

We found no obvious association between the occurrence of head preening and the anatomical preening mechanism (uropygial gland or powder down; Table 8). Across species with data on region preened ($N = 7$), half or more of preening was directed to partners' heads (Table 8). GLMMs run on a subset of these species (blue and gold macaw, orange-winged Amazon, greater vasa) for whom all variables of interest were available, indicated that birds were selective in whom they directed head preening towards. Both head and body preening were clearly influenced by at least some of the test predictors in the model (active feeding and proximity; full versus null model comparisons: head preening: $\chi^2 = 57.938$, df = 2, $p < 0.001$; body preening: $\chi^2 = 33.951$, df = 2, $p < 0.001$). More specifically, head preening was significantly more common in the orange-winged Amazons compared to the vasas, significantly more common in dyads in which we observed active feeding, and also significantly more common in dyads with a larger 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

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

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

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

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

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Table 1.

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

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

	Red shouldered macaw	**4**	A, NB	**2, 3**	**F**	**na**	**NA**
	Azure-winged magpie						
	Group 1	6	A, BP	4, 4	F	F	NR
	Group 2	6	A, NB	5, 6	F	F	NR
	Common raven						
	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
	Eurasian jay	**14**	**J**	**6, 15**	**GA**	**G**	**NU**
	Jackdaw						
	Group 1	10	A, NB	18, 64	GA	G	DR, within 2 body lengths
	Group 2	15	J	12, 22	GA	G	NU
	New Caledonian crow	**3**	**MA, BP**	**1, 2**	**F**	**F**	**NR**
	Rook						
	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
	Bonobos						
	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		
	Chimpanzees						
	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

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

Table 2.

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

Model	Term	est.	OR	SE	lower Cl	upper Cl	χ^2	df	P	min	Max
1a	Intercept	-2.111	0.121	0.464	-3.084	-1.077			(1)	-2.381	-0.970
1a	taxon(2)	-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			(1)	-2.171	-1.892
1b	taxon(2)	-0.722	0.486	0.337	-1.418	-0.044	3.655	1	0.056	-1.001	-0.452
1b	z.gr. size(3)	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[2]	-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

[1] not shown because of having a very limited interpretation

[2] dummy coded with ape being the reference category

[3] z-transformed to a mean of zero and a standard deviation of one; mean and sd of the original variable were 10.383 and 5.350; no test indicated as the model lacking group size did not converge

Table 3.

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

	Birds (Parrots & Corvids)			Apes (*Pan* species)		
	N	*Mdn*	*IQR*	*N*	*Mdn*	*IQR*
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

Table 4.

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

Model	term	est.	OR	SE	lower Cl	upper Cl	χ^2	df	P	min	max
2a	Intercept	-0.984	0.374	0.333	-1.592	-0.369			[1]	-1.087	-0.874
2a	taxon[2]	-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[2]	-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

[1] not shown because of having a very limited interpretation

[2] dummy coded with ape being the reference category

Table 5.

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

	Birds (*N*= 95 focal animals)	Apes (*N* = 85 focal animals)
Mean (SD)	1.78 (1.94)	2.73 (1.69)
Median (IQR)	2 (1)	2 (1)
Range	4 (1 to 5)	8 (1 to 9)

Table 6.

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

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
		M	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	
Parrot adult and mixed age groups	**Black-headed caique**	**.02**	**.01**	**0.35**	**0.45**	**na**	**na**	**na**	**na**	**3**
	Blue and gold macaw	**.21**	**.21**	**6.11**	**5.43**	**na**	**na**	**1.36**	**.67**	**11**
	Blue-throated macaw	**na**	**na**	**na**	**na**	**4.00**	**4.61**	**1.88**	**.83**	**4**
	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
	Great green macaw	**na**	**na**	**na**	**na**	**3.89**	**3.89**	**1.67**	**.87**	**3.50**
	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
	Greater vasa	**.03**	**.03**	**0.11**	**0.05**	**na**	**na**	**1.88**	**1.46**	**9**
	Goffin's cockatoo	**.03**	**.03**	**na**	**na**	**na**	**na**	**1.55**	**.93**	**13**
	Kea	**.01**	**.01**	**na**	**na**	**na**	**na**	**na**	**na**	**19.43**
	Orange-winged Amazon	**.12**	**.08**	**2.96**	**2.05**	**na**	**na**	**2.40**	**.91**	**22**
	Red shouldered macaw	**.23**	**.07**	**8.73**	**3.68**	**na**	**na**	**na**	**na**	**3**
	Azure-winged magpie	**.03**	**.04**	**0.26**	**0.48**	**na**	**na**	**1.43**	**.53**	**4.90**
	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

Corvid adult and mixed age groups	**Common raven**	**.07**	**.05**	**0.66**	**0.00**	**na**	**na**	**1.87**	**.92**	**7**
	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
	Jackdaw	**.00**	**.00**	**na**	**na**	**na**	**na**	**na**	**na**	**9**
	New Caledonian crow	**.07**	**.05**	**1.15**	**1.18**	**na**	**na**	**na**	**na**	**2**
	Rook	**.02**	**.03**			**na**	**na**			**10.23**
	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
Juvenile corvid groups	**Eurasian jay**	**.00**	**.00**	**na**	**na**	**na**	**na**	**na**	**na**	**13**
	Common raven	**.05**	**.04**	**1.01**	**.95**	**na**	**na**			**9**
	Jackdaw	**.03**	**.01**	**na**	**na**	**na**	**na**	**na**	**na**	**14**
	Rooks	**.06**	**.04**	**na**	**na**	**na**	**na**	**na**	**na**	**12**
Apes	**Bonobos**									
	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
	Chimpanzees									
	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

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

Table 7

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

Model	term	est.	OR	SE	lower Cl	upper Cl	χ^2	df	P	min	max
3a	Intercept	-4.966	0.007	0.539	-21.359	-4.435			(1)	-17.679	-4.484
3a	feeding(2)	-1.424	0.241	1.321	-14.368	1.295	1.397	1	0.237	-9.630	0.229
3a	agon(3)	-0.400	0.670	0.696	-6.751	0.625	0.384	1	0.535	-5.283	0.021
3a	proximity(4)	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(2)	0.598	1.818	1.457	-3.325	4.047	0.159	1	0.690	-1.074	1.031
3b	proximity(4)	4.000	54.624	0.781	2.629	7.831	13.801	1	0.000	3.024	4.774

(1) not shown because of having a very limited interpretation

(2) dummy coded with no feeding observed being the reference category

(3) dummy coded with no agonistic behaviors observed being the reference category

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

Table 8.

Percentage of preening behaviors subjects (N = 7 species) directed to partners that focused on preening the head/neck area) and anatomical preening mechanism (G = urypoigal gland, P = 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)†
Orange-winged amazon	76.14	P (Vincze et al., 2013)

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

Table 9.

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

Model	term	est.	SE	OR	lower Cl	upper Cl	χ^2	df	P	min	max
4a (H)	Intercept	-5.257	0.978	0.005	-35.132	-4.277			(1)	-24.260	-4.887
4a (H)	feeding(2)	5.443	1.622	231.176	2.947	45.825	14.769	1	<0.001	4.691	20.312
4a (H)	proximity(3)	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			(1)	-4.684	-3.959
4a (B)	feeding(2)	0.981	1.032	2.667	-4.376	16.724	0.836	1	0.361	-3.262	2.463
4a (B)	proximity(3)	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

(1) not shown because of having a very limited interpretation

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

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

[4] dummy coded with Blue and gold macaw being the reference category; the indicated test refers to the overall effect of species

Figure legends

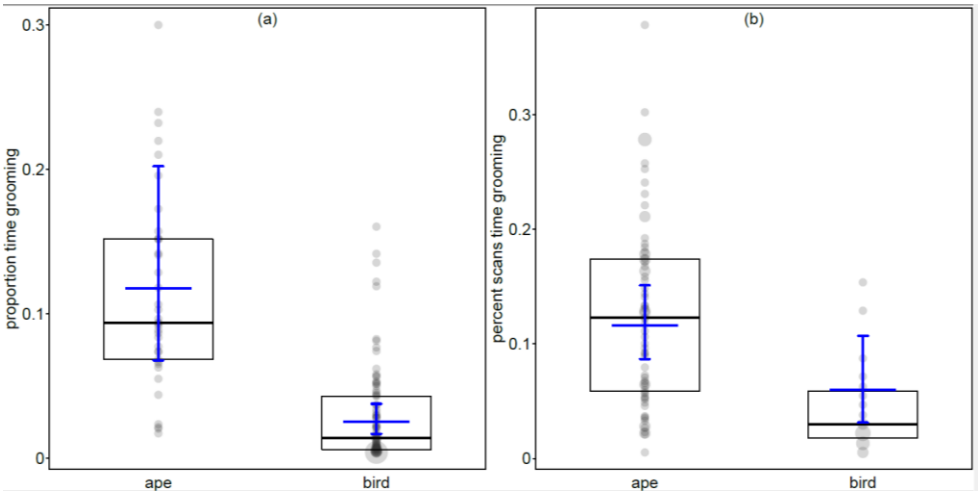


Figure 1. Proportion time (a) and percent scans (b) spent grooming, separately for apes (chimpanzees/bonobos) and birds (corvids/parrots). Depicted are the raw data (grey dots), whereby the area of the dots is proportionate to the number of observations per value of the response (N =1 to 9). Thick black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

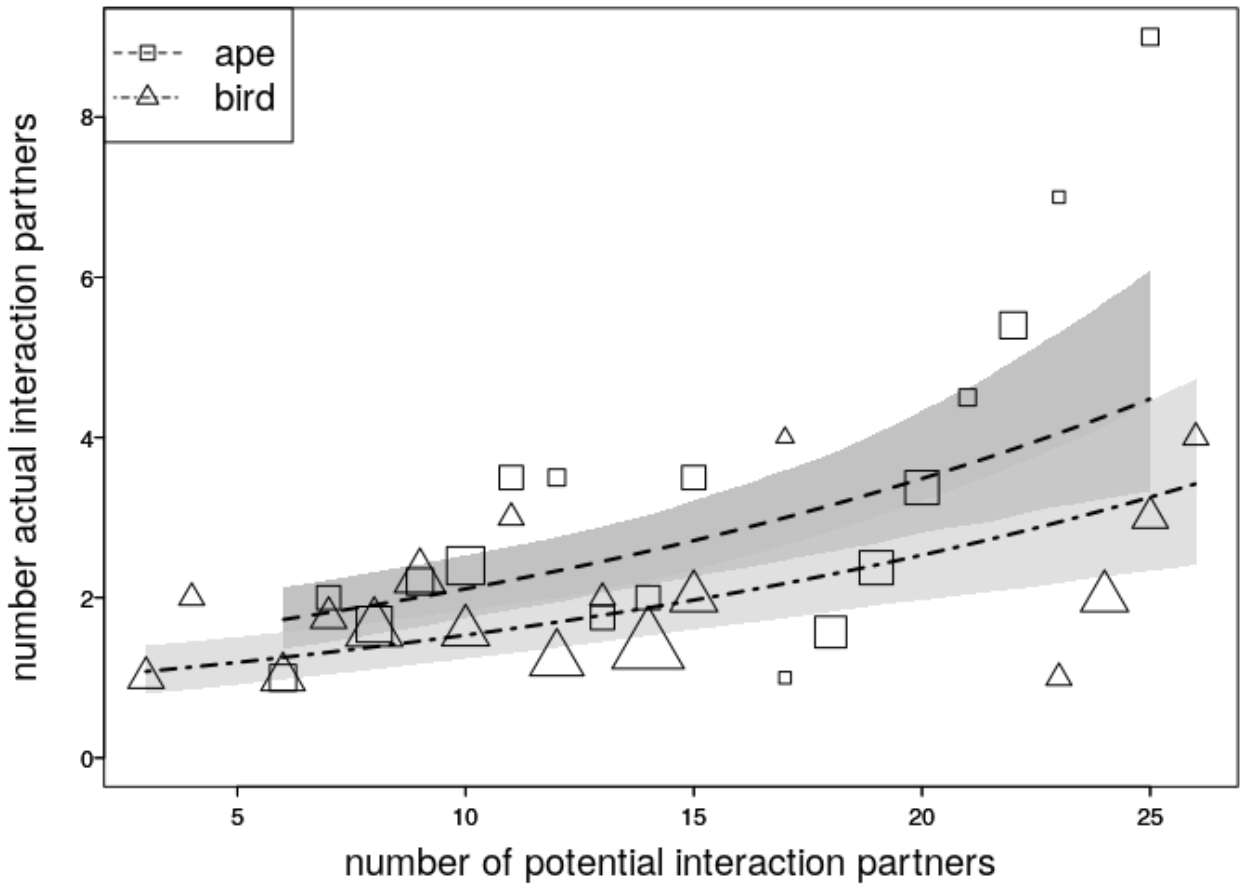


Figure 2. Number of grooming interaction partners as a function of the number of potential interaction partners, and separately for birds (corvids/parrots) and apes (chimpanzees/bonobos). Indicated are average numbers of interaction partners per number of potential interaction partners, whereby the area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

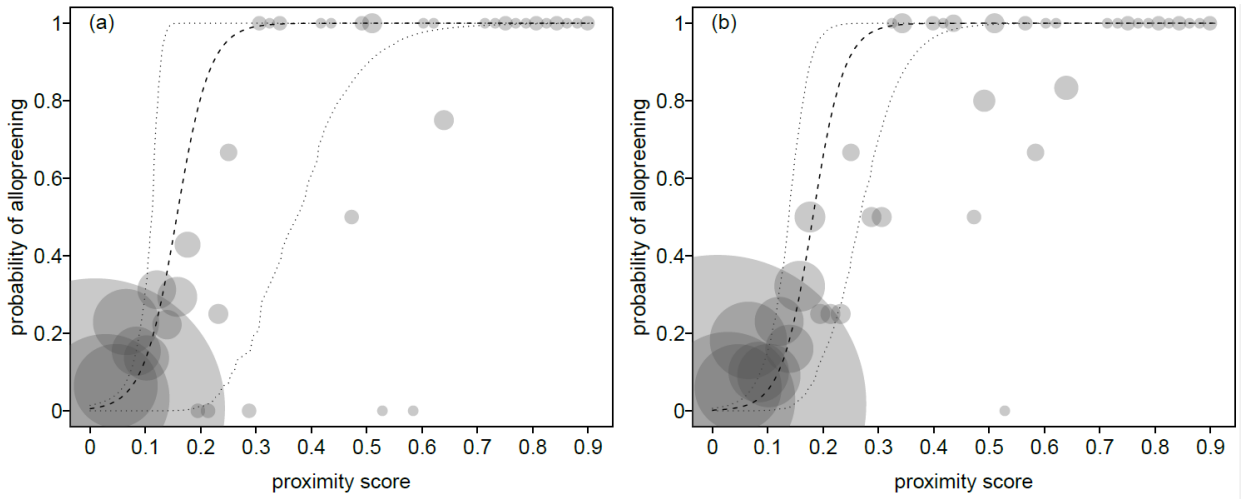


Figure 3. Probability of dyadic allopreening to be observed within a given dyad, as a function of their proximity score. (a) illustrates the relationship from Model 3a where proximity, active feeding and agonistic interactions were included as fixed factors (N = 77 individuals from six species) and (b)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

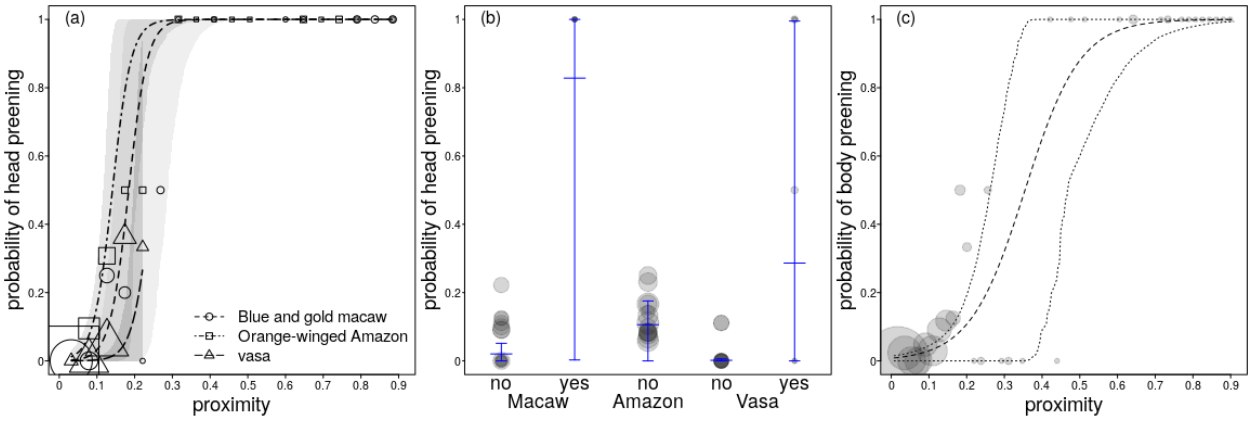


Figure 4. Probability of head preening (a, b) and body preening (c) as a function of dyadic proximity (a, c) or separately for three species and dyads that exhibited or did not exhibit active feeding (b). Dots in (a) and (c) show the average probability per bin of the dyadic proximity, and dots in (b)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

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