To preen or not to preen: aggressive and association networks predict allopreening interactions in wild parrots

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To preen or not to preen: social predictors of allopreening in a wild parrot

Abstract

Allogrooming is fundamental to social relationships in many mammals. In primates, allogrooming has been the subject of decades of research, and has been shown to play an essential role in maintaining social affiliations, and often exchanged for social tolerance and support. Yet, while the equivalent behaviour of allopreening occurs in many avian species, most description has been limited to its role in pair formation and maintenance, with little known about non-breeding contexts. Here we investigated the decision-making associated with allopreening in wild sulphur-crested cockatoos, conducting detailed observations of 182 allopreening events between 126 individuals while concurrently recording rank, aggressive interactions, and social networks. We found no influence of sex, as predicted if allopreening was primarily about pair bonding, but instead a positive correlation between allopreening and aggression (given and received). Within interactions, individuals were influenced by social bond strength and rank, with individuals preening for longer and with more turn-taking when interacting with stronger social associates, and individuals investing more in interactions initiated by higher-ranked individuals. Our results are highly suggestive that allopreening may serve a convergent function in wild parrots to primates, both in maintaining social bonds and in negotiating social tolerance.

KEYWORDS: allopreening and allogrooming, *Cacatua galerita*, parrots, social cognition, social network analysis

Introduction

Allogrooming is considered a fundamental component of sociality in many mammals, including in primates, social mongoose, bats, and social rodents (Rowell, 1974; Kutsukake & Clutton-Brock, 2006; G. Carter & Leffer, 2015), where individuals can spend up to one-fifth of their time combing through the fur of group members (Dunbar, 1991). Allogrooming is assumed to have significant hygienic benefits, such as the removal of ectoparasites that one can't remove oneself (Stopka & Graciasova, 2001; Zamma, 2002; Mooring et al., 2004). Yet, in social primates, the total amount of time spent grooming is often better predicted by group, rather than body size (a proxy for parasite load), suggesting that allogrooming provides benefits beyond the removal of parasites (Dunbar, 1991). For example, research on primates and other mammals has suggested that grooming interactions reduce stress levels (Boccia et al., 1989: Feh & de Mazieres, 1993; Gust et al., 1993: Wittig et al., 2008), play an important role in creating and strengthening social bonds (Mitani, 2009; G. G. Carter et al., 2020), and may increase fitness (Silk et al., 2003; Cameron et al., 2009; Silk et al., 2009).

Time budgets are limited, and the time individuals engage in social interactions must be traded off against other activities such as foraging or resting (Dunbar, 1992; Dunbar et al., 2009). Therefore, individuals should be selective regarding whom to groom. In Seyfarth's (1977) classic model of primate grooming, he proposed that individuals should groom up the hierarchy and those close in rank, in exchange for agnostic support or tolerance (Schino, 2001; Tiddi et al., 2012; Wubs et al., 2018). Further studies extended this model with biological market theory (BMT) to argue that grooming is a commodity to be traded for a range of benefits (Noe & Hammerstein, 1994, 1995). For example, grooming can be exchanged for tolerance (Carne et al., 2011; Borgeaud & Bshary, 2015; Garcia, Lemieux, et al., 2021), but also grooming (leading to reciprocal interactions Carne et al., 2011; Tiddi et al., 2011; Schino and Alessandrini, 2018), infant-handling (Gumert, 2007; Fruteau et al., 2011; Yu et al., 2013), mating opportunities (Norscia et al., 2009; Yu et al., 2013) or food-sharing (G. G. Carter & Wilkinson, 2013; Jaeggi et al., 2013). Evidence for both Seyfarth's model and BMT remains mixed, but has been reported from primates (Tiddi et al., 2012), bats (Carter & Wilkinson, 2013), and meerkats (Kutsukake & Clutton-Brock, 2006)

In birds, allopreening (the equivalent of allogrooming) has been observed in over 400 species (Kenny et al., 2017), yet in contrast to mammals, allopreening has almost exclusively been described in the context of breeding. Allopreening is commonly performed from parent to dependent offspring. Between adults, allopreening plays an important role in courtship, in strengthening bonds between mated pairs (Kushlan, 2011), in promoting cooperation for offspring feeding (Kenny et al., 2017) or the re-establishment of familiarity in mates after periods of separation (Erickson, 1973; Kushlan, 2011). Previous research has therefore highlighted that allopreening is more likely to occur in co-operatively or colonial breeding species, or in socially monogamous species with stable mate-bonds (Lewis et al., 2007; Gill, 2012; Kenny et al., 2017).

Studies have suggested a wider, multifunctional social role for allopreening in birds, similar to that observed in social mammals. For example, at the group-level, allopreening may function to reduce aggression between neighbouring pairs in the colonially breeding common guillemot (*Uria aalga),* (Lewis et al., 2007), with reduced aggression in turn increasing breeding success. And at the individual level, dominant birds in groups of cooperatively breeding woodhoopoe *(Phoeniculus purpureus)* are more likely to receive preenings than subordinates (Radford & Du Plessis, 2006), and barn owl *(Tyto alba)* nestlings preen siblings in exchange for food (Roulin et al., 2016). Yet, by far most evidence for a multi-faceted role of allopreening in birds has come from corvids. For example, in common ravens (*Corvus corax),* allopreening events predict agonistic support (Fraser & Bugnyar, 2012), and in common ravens and carrion crows (*Corvus corone),* preening serves as reconciliation after aggressions with valuable interaction partners (Fraser & Bugnyar, 2011; Ikkatai et al., 2016; Sima et al., 2016; Sima et al., 2018). Yet, these studies predominantly focused on mixed-sex dyads, thus not fully removing potential effects of breeding context on preening.

There are multiple similarities between the social systems of many corvids and parrot species, and between these groups and primates (Fraser & Bugnyar, 2010). For example, all groups have been shown to form differentiated social bonds that are stable over time (corvids: reviewed by (Boucherie et al., 2019), parrots: (Aplin et al., 2021; Penndorf et al., 2023)). Yet, perhaps surprisingly, allopreening in parrots has almost exclusively been described as between potential mates or with dependent offspring (Brockway, 1964; Garnetzke-Stollmann & Franck, 1991: Hobson et al., 2014) and studied for its role in pair formation (Rogers & McCulloch, 1981; Garnetzke-Stollmann & Franck, 1991). This view has been recently challenged in a comparative study in captive parrots and corvids showing that: (i) preening rates were similar to those measured in chimpanzees, (ii) preening interactions occurred outside the pair, and (iii) preening interactions were predicted by physical proximity and reduced aggression (Morales Picard et al., 2020). Yet, these results may need to be interpreted with caution, as data were collected in captivity, and artificial provisioning is highly likely to change the rate and the pattern of affiliative interactions (Garcia, Farine, et al., 2021).

In a previous study, we observed social allopreening in wild groups of sulphur-crested (SC-) cockatoos (*Cacatua galerita),* whereby individuals preferentially preened kin while also preening other unrelated individuals outside of the pair (Penndorf et al., 2023). SC-cockatoos are a large parrot, commonly observed across northern and eastern Australia that forms large stable roosting communities, with a minority of adults breeding in tree hollows near the main roost site, and roosting groups foraging in fission-fusion flocks in a shared home range (Penndorf et al., 2023). In this species, individuals form stable monogamous pair bonds *(personal observation),* but will also hold long-term, differentiated, social bonds outside the pair with both kin and unrelated individuals (Aplin et al., 2021). Individuals also exhibit evidence of social cognition in aggressive interactions, forming dominance hierarchies and strategically aggressing those below them in the dominance hierarchy (Penndorf et al., 2025). In this study we identify social predictors of preening interactions and test the assumptions of Seyfarth's model (Seyfarth, 1977). We assessed whether-and if so, how-rank difference

within a dyad contributes to the relative contribution (number of events within a sequence, and duration) of allopreening interaction by each individual involved.

Methods

Study population

Our study population comprised birds at four neighbouring roosting communities in northern Sydney, during winter in 2018 (one roost: BG), 2019 (three roosts: BA, CG & NB) and 2022 (two roosts: CG & BG-Figure la). Under each roost, individuals were attracted to the ground using small amounts of sunflower seeds. Once individuals were habituated, i.e. could be lightly touched on their back without inciting an adverse response, they were individually marked using non-toxic fabric dye (MARABU Fashion dye); (Penndorf et al., 2023) that lasted for three to four months. In addition, 144 birds were ringed and wing-tagged with plastic cattle ear-tags as part of the ongoing Citizen Science project *Big City Birds* (Davis et al., 2017; Aplin et al., 2021), and some were present in the study population, as individuals regularly engage in localised between-movements (Aplin et al., 2021; Fehlmann et al., 2024).

Overall, 713 uniquely recognizable birds were observed in the study (2018: 136 paint-marked, 14 wing-tagged, 2 individually recognizable; 2019: 536 paint-marked, 17 wing-tagged, 8 individually recognizable; 2022: 233 paint-marked, 24 wing-tagged, 0 recognizable). Birds were aged by eye colour as juvenile (<7 years) or adult (>7 years), and amongst adults as male or female. In 2019 and 2022, feather samples were non-invasively collected, allowing verification of morphological sexing, and molecular sexing of juveniles. This also allowed identification of individuals between these two study periods.

Figure 1: Allopreening in sulphur-crested cockatoos. (a) Location of the roosting communities in Sydney included in this study. These include: Royal Botanic Garden (BG—2018, 2022), Balmoral Beach (BA—2019), Clifton Gardens (CG—2019, 2022) and Northbridge (NB—2019). In addition, social associations were recorded at Spit Road, where individuals of all three northern roosts associated while being fed by a local residents. The map was constructed in QGIS (QGIS Development Team, 2009), using OpenStreetMap (OpenStreetMap contributors, 2017). (b) An example observation of two individuals allopreening.

Social data collection

Social associations and interaction data were recorded in late winter, over 14 days in 2018 for a total of 42 hours in BG, over two 10 days periods for a total of 165 hours in 2019 (55 hours at BA, CG and NB respectively) and 14 days for a total of 84 hours in 2022 (42 hours at BG & CG respectively; Figure 1 a). Birds were attracted to begin ground foraging in parks close to the roost using small amounts of sunflower seeds scattered over a 300-680m area (see Penndorf et al., 2023). Foraging flocks were then observed for 2.5 to 3 hours per day. During this time, *group scans* (Altmann, 1974) were conducted every ten minutes to record the identities of all birds present. Between scans, *all occurrence sampling* (Altmann, 1974) was used to record aggressive interactions and allopreening interactions. In all possible cases, the full sequence was recorded, including the initiator (hereafter *individual* 1), receiver (hereafter *individual* 2), and subsequent reciprocity (allopreening) or escalation (aggression). Additionally in 2022, a second observer (LF) filmed all preening interactions while other social interactions were recorded by JP.

To make association networks, we constructed a *group-by-individual* matrix, where individuals were assigned to the same group if observed in the same presence scan. We then used the *simple ratio index* (SRI, R-package *asnipe*, Farine, 2013) to create an undirected association network for each year of the study. Edges between individuals were scaled from 0 (never associated) to 1 (always associated).

Aggressive interactions

Overall, we recorded 9.908 aggressive interactions (BA_{2019}=1.737, CG_{2019}=2.735, CG_{2022}=1.935, NB_{2019}=l.005, BG_{2018}=686, BG_{2022}=l,810). These interactions were converted into a directed aggressive network for each year separately by the following formula:

$$F_{\text{aggressions 1->2}} = \frac{N(ind1 \rightarrow ind2)}{N(ind1)+N(ind2)}$$

where $F_{aggressions\ 1->2}$ is the frequency of aggression between individual 1 and individual 2, $N_{ind1->Ind2}$ the number of aggressions from individual 1 towards individual 2, N_{ind1} the total number of aggressions initiated by individual 1, and N_{ind2} the total number of aggressions initiated by individual 2. This result in a directed network, in which $F_{aggression}$ from 0 (individual 1 never aggressed individual 2) to 1.

In order to calculate a dominance hierarchy for each roosting community, we subset this data to include only individuals with more than ten aggressive interactions recorded at a given location (Sanchez-T6jar et al., 2018), and included all types of aggressive interactions in the analysis as simple *'wins'* and *'losses'*. Dominance ranks were calculated using randomized Elo-ratings package *aniDom* version 0.1.5, (Farine & Sanchez-Tojar, 2021). Hierarchies were both linear and relatively stable over at least 3 years, with males tending to be dominant over females, and adults over juveniles, but with no other clear predictors of rank (Penndorf et al., 2024).

Allopreening interactions

Altogether, we collated two types of allopreening data: (i) allopreening bouts including the initiator, receiver, and how often roles were exchanged, (ii) full durations of bouts and of episodes within bouts. Initiators were considered to be the individual first presenting to or preening the other individual (receiver).

Analysis of social correlates of allopreening

To test initiation of preening interactions are correlated with social associations and/or aggressive interactions, we ran a Bayesian multi-membership model for proportions (zero-inflated beta binomial family, R-package *brms* Bürkner, 2017a, 2017b, 2018, 4 chains, 2,000 iterations). We used the number of preenings within the dyad as response variable, modulated by the number of *trials—i.e.* the total number of preenings initiated by individual 1 (including preenings with third parties). The predictors were the social association index (SRI) and the proportion of aggressive interactions from individual 1 towards individual 2 (hereafter referred to as *aggression given)* and the proportion of aggressive interactions directed from individual 2 towards individual 1 (hereafter referred to as *aggression received)* during the entire study period.

Analysis of investment in preening interactions

To investigate the investment of both individuals in an allopreening interaction, we considered: (i) the number of behavioural components (preenings) contributed by each individual to the interaction, (ii) the duration each individual preened the other during the interaction.

First, for each individual we quantified the number of behavioural components contributed to the allopreening interaction. For example, if individual 1 preened individual 2, then individual 2 preened individual **1** before retreating, each individual would be considered having contributed one behavioural component to the interaction. To test whether the number of behavioural components contributed by each individual within the interaction was influenced by characteristics of the dyad, we then fitted multivariate Bayesian model (number of elements contributed by individual 1: Poisson family, number of elements contributed by individual 2: hurdle-Poisson family, R-package *brms*, Bürkner, 2017a, 2017b, 2018, 4 chains, 4,000 iterations). Response variables were the number of behavioural components each individual contributed to a given interaction, with the initiator considered as individual 1 and the initial receiver involved in the preening was considered as individual 2. One of the predictors was the rank difference defined as the rank of the receiver minus the rank of the initiator, divided by the total number of individuals in the hierarchy. As previous work on parrots suggested that allopreening is more frequent between pairs (Brockway, 1964; Trillmich, 1976; Garnetzke-Stollmann & Franck, 1991; Hobson et al., 2014) and close-associates (Morales Picard et al., 2020), we additionally added the dyad was mixed or single sex (binary, TRUE/FALSE), and dyadic association strength (SRI). For the number of behaviours contributed by individual 1, we added an additional binary predictor of whether or not the receiver preened in return. The same predictor variables were used to predict the likelihood of individual 2 not reciprocating the allopreening.

Second, to test whether the investment of each individual-measured in time spend preening during the interaction-was influenced by characteristics of the dyad, we fitted a multivariate Bayesian model (shifted-normal family for $preen_{ID1}$, and hurdle gamma family for $preen_{ID2}$, R-package *brms*, Bürkner, 2017a, 2017b, 2018, 4 chains, 2,000 iterations). The response variables was the preening duration given by the individual in seconds. Similar to the analysis for the investment in terms of behavioural components, the predictors were the rank difference, sex (mixed/same) and dyadic association strength (SRI). The same predictors were used in hurdle part of the model, to predict the likelihood of non-reciprocation of the preening. For the duration individual 1 spent preening, we added an additional binary predictor, whether or not the receiver preened in return.

Results

We recorded 182 allopreenings between 126 individuals, of which 21% occurred in same-sex dyads, 34% in between-sex dyads, and 45% in dyads where the sex of at least one individual was unknown

(Figure 2a). For 167 of 182 interactions where the full allopreening sequence was observed, initiation involved an active allopreening of the receiver, rather than a presentation.

Perhaps counter-intuitively, individuals that exchanged more aggression were more likely to be observed allopreening. The initiation of allopreening was positively predicted by both aggressions directed towards (es=13.51, se=5.16, 95% CI: [5.05, 25.16] —Figure Sla), and received by (es= 24.47, se=8.56, 95% CI: [10.20, 43.77] —Figure Slb), the receiver of the allopreening. Association strength, however, was not correlated with the initiation of allopreening (es=0.09, se=0.34, 95% CI: [-0.57, 0.77]).

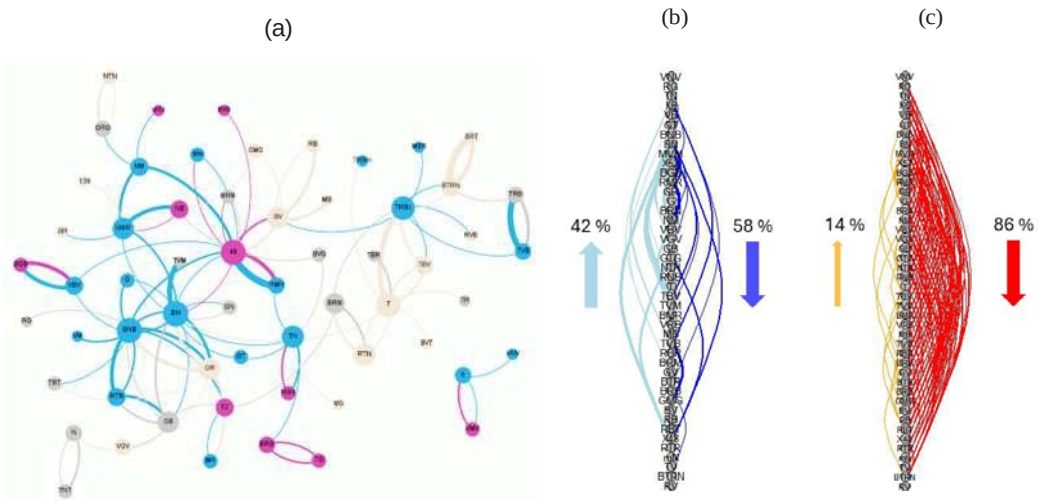

Figure 2: Interaction patterns in BG group (2018). (a) Directed allopreening network (n=85). Females are represented in pink, males in blue, juveniles in beige, and individuals of unknown age and sex in grey. Edges are coloured according to direction of the preening. (b) Aggressive interactions, and (c) preening interactions. Individuals are ordered according to dominance rank, from highest ranking (top) to lowest ranking (bottom). For each graph, darker edges on the right represent interactions directed down the hierarchy, while lighter edges on left are those directed up the hierarchy. Arrows surmise the relative proportion of interactions in each direction.

Social factors influencing the numbers of behavioural elements within a sequence

Number of elements contributed by the initiator

Within a single interaction, the length of the sequence was influenced by the association strength and the rank difference of the dyad, with initiators directing more behavioural elements towards strong associates ($preen_{ID1}$: es= 0.49, se=0.20, 95% CI: [0.17, 0.95]—Figures 3a & S3a), increasing their preening effort if the higher ranking individual was the first to preen, and with larger rank difference between the individuals ($preen_{ID1}$: es= 0.39, se=0.13, 95% CI: [0.12, 0.65]—Figures 3a & S4a). Additionally, the number of behavioural elements contributed by the first individual was higher if it

received preening(s) in return (*preen*$_{ID1}$: es= 0.35, se=0.13 95% Cl: [0.10, 0.61]—Figure 3a). The sex of the dyad (same or mixed sex), however, did not influence the number of behavioural components contributed by the initiator (*preen*$_{ID1}$: es= 0.02, se=0.14, 95% CI: [-0.25, 0.28]—Figure 3a).

Number of elements contributed by the receiver

Whether or not the receiver reciprocated the preening was best predicted by association strength and the sex of the dyad (same or mixed). Receivers were less likely to reciprocate preening(s) of close associates (*preen*$_{ID2}$: es= 2.34, se=0.82, 95% Cl: [0.93, 4.10]—Figure 3c), and more likely to reciprocate interactions when in a mixed sex dyad (*preen*$_{ID2}$: es= -0.70, se=0.35, 95% Cl: [-1.39, -0.04] —Figure 3c). The rank difference between the two individuals, however, did not predict the likelihood of reciprocation (*preen*$_{ID2}$: es= -0.09, se=0.26, 95% CI: [-0.59, 0.41] —Figure 3c).

If the receiver reciprocated the interaction, the number of preenings was positively correlated with the association strength (*preen*$_{ID2}$: es= 0.86, se=0.35, 95% CI: [0.30, 1.66]-Figure 3e). Individuals tended to also increase their preening effort if the first individual to preen was higher ranked, and with larger rank differences between individuals (*preen*$_{ID2}$: es= 0.36, se=0.21, 95% Cl: [-0.06, 0.77] —Figure 3e).

Social factors influencing the duration of preening interactions

Focusing on the subset of preenings for which video recordings were available (N= 34), we found that the duration given by each individual was highly correlated with the number of elements each individual contributed to the sequence (initiator: Spearman correlation, rho=0.53, p<0.001, Figure S2a; receiver: Spearman correlation, rho=0.72, p<0.001-Figure S2b).

Duration of preening given by the initiator

Similarly to the analysis on behavioural components, the duration of preening given by the initiator was predicted by association strength (preen$_{ID1}$: es= 0.98, se=0.44, 95% Cl: [0.32, 2.01]—Figures 3b & S3c) and rank difference, with the duration of preening given by individual 1 tending to increase with increasing rank difference(preen$_{ID1}$: es= 0.41, se=0.24, 95% CI: [-0.07, 0.86]—Figures 3e & S4b). The sex of the dyad (mixed/same) did not influence the relative time investment of individual 1 (preen$_{ID1}$: es= -0.19, se=0.30, 95% Cl: [-0.84, 0.37]—Figure 3b). Whether an interaction was reciprocated or not did not affect the duration given by the initiator (*preen*$_{ID1}$: es=0.13, se=0.30, 95% Cl: [-0.46, 0.73]—Figure 3b).

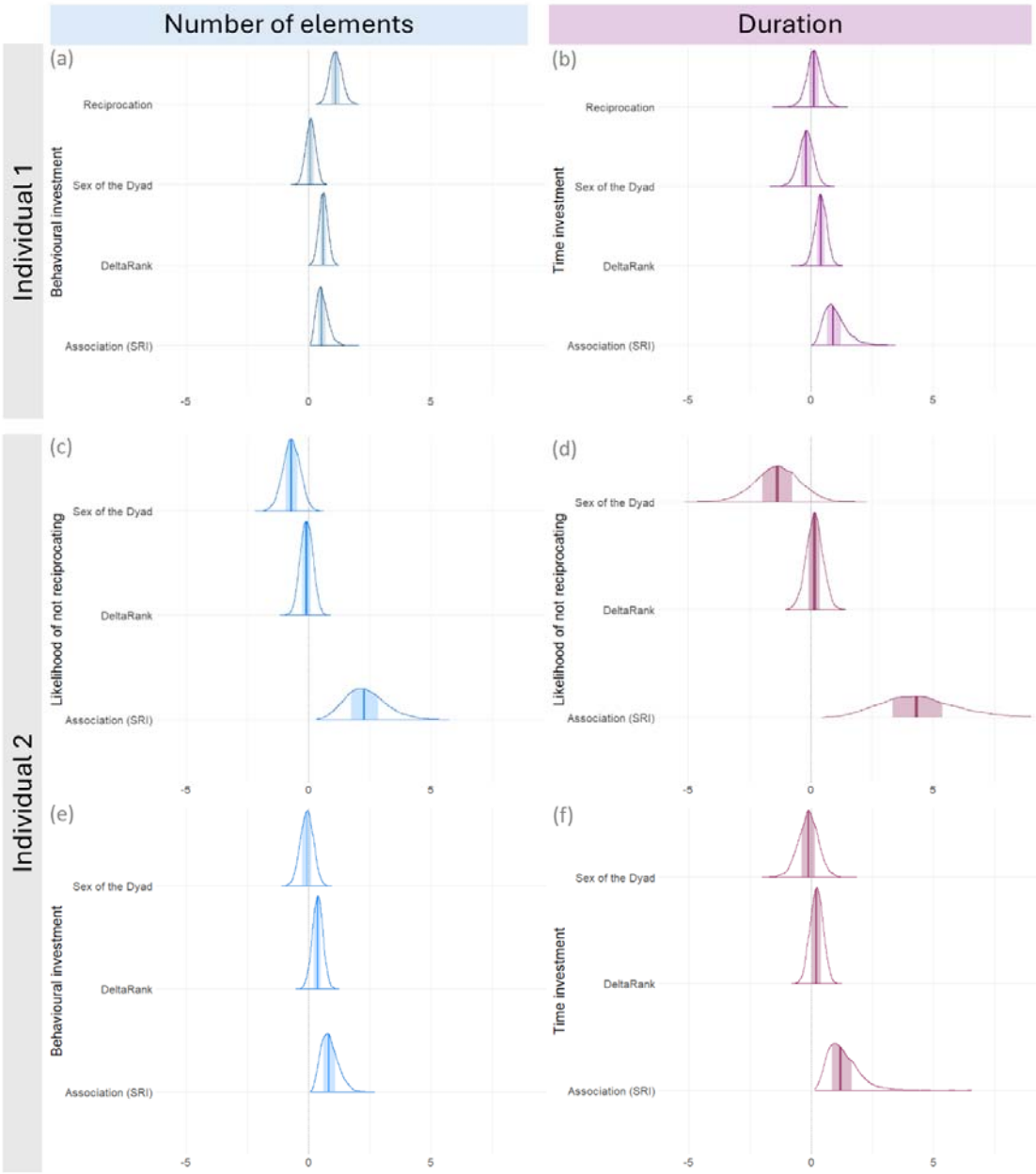

Figure 3: Posterior distributions with medians and 80% intervals. The left column (panels (a), (c) and (e)) correspond the posterior distributions for analysis of the behavioural investments, measured as number of elements each individual contributed to the preening sequence. The right column (panels (a), (c), (d) and (f)) represent the posterior distributions for the analysis of time investment, measured as duration each individual preened (in seconds). The first row (panels (a) and (b)) corresponds to the contributions of individual 1 (initiator). The second and third row (panels (c), (d), (e) and (f)) correspond corresponds to the contributions of individual 1 (receiver). For each posterior distribution, the shaded area represents the 80% intervals, and the coloured line corresponds to the median.

Duration of preening given by the receiver

The reciprocation of a preening event was again best predicted by association strength, with the likelihood of individual 2 not reciprocating the preening (hu) increasing with increasing association strength ($preen_{D2}$: es=4.49, se=1.57, 95% CI: [1.84, 7.97]—Figure 3d). Additionally, the likelihood of

individual 2 not reciprocating tended to be lower mixed sex dyads (*preen*$_{ID2}$: es=-1.39, se=0.96, 95% CI: [-3.29, 0.48]—Figure 3d). The rank difference between of the dyad did, however, not affect the likelihood of individual 2 not reciprocating (*preen*$_{1D2}$: es=0.15, se=0.96, 95% CI: [-0.52, 0.80] — Figure 3d).

If individual 2 reciprocated the preening, the duration of the preening given by individual 2 was best predicted by the association strength of the dyad, with the duration of the preening increasing with increasing association strength (*preen*$_{ID2}$: es=l.29, se=0.62, 95% CI: [0.39, 2.77]—Figure 3f). Neither the sex of the dyad (same or mixed-preen$_{ID2}$: es=-0.14, se=0.42, 95% CI: [-1.01, 0.67]—Figure 3f), nor the rank difference (*preen*$_{ID2}$: es=0.21, se=0.26, 95% CI: [-0.31, 0.72]—Figure 3f), influenced the duration of the preening given by the receiver.

Discussion

In previous work, we found that wild SC-cockatoos engaged in allopreening with multiple partners, with allopreening more likely to be observed between related individuals and individuals belonging to different roosts (Penndorf et al., 2023). Here we extend these results by using intensive observations over three years to examine the potential social functions of allopreening. We confirm our previous results, and additionally find that: (i) birds with strong social associations exchanged longer preenings with more elements; (ii) individuals that share more aggression also share more allopreening, and (iii) while preening roles are frequently exchanged within one interaction, the investment of each individual—both in terms of number of elements contributed and overall duration—is dependent on their relative rank, and whether the higher ranking individual was the first to preen. Altogether, our results provide, to our knowledge, the first wild confirmation of a multi-faceted social function for allopreening interactions in parrots.

As allopreening has been suggested to play an important role in maintaining social bonds (Spencer et al., 2005; Spoon et al., 2006; Kenny et al., 2017), individuals should invest more into preening close associates to strengthen or maintain existing social bonds. This can for example result in longer allopreening sequences. Perhaps counter-intuitively, we found the opposite, with the length of preening sequences decreasing with increasing association strength. This suggest that frequent associates exchange longer sequences, and overall have a higher frequency of preening interactions, thus aligning with previous suggestions in other parrot species (Morales Picard et al., 2020). Support for this hypothesis also comes from a previous study on SC-cockatoos, suggesting that allopreening interactions at population level were predicted by the association network (Penndorf et al., 2023).

The higher investment, both in terms of number of behavioural elements and duration, combined with our previous finding in this species showing a high degree of preening between individuals of different roosts when assembling at foraging sites (Penndorf et al., 2023), suggests that individuals may invest into maintaining rare relationships such as with kin or dispersed former close-associates.

Alternatively, when preening infrequent associates, individuals could adopt a tit for tat strategy. In this context, offering short preening bouts can serve as a way of testing whether this relationship is worth investing time into, i.e. whether the other individual will reciprocate. Some support for this hypothesis comes from our findings (i) that preenings given by the initiator where longer-both in terms of number of individuals and duration-if the receiver reciprocated, and (ii) that individual 2 was more likely to reciprocate preenings of rare associates.

Intriguingly, we did not find any evidence that preening sequences are longer between males and females, as opposed to same-sex dyads. This could be an artefact of the protocol, as we recorded social interactions within a feeding context. Allopreening between pairs are frequent at their nest-hollow *(personal observation)*, and social interactions are limited by feeding constraints (Garcia, Lemieux, et al., 2021). Therefore, within feeding associations, individuals may instead preferentially direct preening towards important social partners outside of the pair. Some evidence comes from a previous study on SC-cockatoos, suggesting that allopreening is maintained with kin even after dispersal (Penndorf et al., 2023).

Alternatively, individuals can favour allopreening with high-ranking individuals, as the latter may provide support or increase tolerance (Koyama et al., 2006; Carne et al., 2011; Tiddi et al., 2011; Borgeaud & Bshary, 2015; Garcia, Lemieux, et al., 2021). Our results support this hypothesis in two ways. First, the investment of higher ranked individual was decreased with increasing rank difference. Second, the investment into the preening interaction increased if the interaction was initiated by the higher-ranking individual. One explanation comes from power differentials between preening partners. A number of studies described rank bias within allopreening (allogrooming) interactions, with preening bouts being disproportionately directed towards the higher-ranking individual (Barrett et al., 2002; Schino et al., 2003; Kutsukake & Clutton-Brock, 2006; Radford & Du Plessis, 2006; Ventura et al., 2006; Miyazawa et al., 2020). Our study did not focus on the asymmetry of preening interactions, yet we provide intriguing insight on how rank differences influence affiliative interactions.

When considering the wider pattern of preening interactions, we found a positive correlation between preening and aggression. While perhaps initially surprising, this result is similar to that described in several primate species (Barrett et al., 2002; Schino et al., 2003; Port et al., 2009) and meerkats (Kutsukake & Clutton-Brock, 2006). One potential explanation proposed for the positive correlation between preening and aggression has been the need for reconciliation with valuable interaction partners. Reconciliation after aggressive interaction has been shown to occur in corvids (Fraser & Bugnyar, 2011; Sima et al., 2018), and has been suggested to occur in captive budgerigars *Melopsittacus undulatus* and monk parakeets *Myiopsitta monachus* (Morrison, 2009; Ikkatai et al., 2016). However, we did not observe any obvious close temporal correlation between aggressive and affiliative interactions in SC-cockatoos, making this explanation seem unlikely. A more directed study testing temporal correlation between aggressive and affiliative interactions could perhaps better

reveal any less obvious patterns of reconciliation.

Alternatively, a different, but non-exclusive, explanation is that such patterns may emerge when subordinates invest in preening (grooming) to appease potential aggressors (Schino et al., 2003), therefore exchanging preening (grooming) for future tolerance. Such an explanation would fit with both our findings, of unbalanced reciprocity in preening, and of a correlation between preening and aggression networks. Such a correlation has been suggested to exist only within dyads close-by in rank (Roubova et al., 2015). In this case, our limited sample size restricted a detailed analysis of this question. However, our recent work has identified that SC-cockatoos use strategic heuristics when choosing where to direct their aggressions (Penndorf et al., 2025). So, it seems reasonable that allopreening may also be used to consolidate or improve rank, or in exchange for tolerance, in addition to its affiliative role strengthening bonds within mates and close kin (Penndorf et al., 2023).

If preening is exchanged for tolerance, this might further suggest the intriguing possibility of the presence of a biological market in SC-cockatoos. This, to our knowledge, would be the first such description in a wild parrot. Yet, preening being directed up the hierarchy is, by itself, not support for a biological market. Further evidence is needed that commodities are exchanged, and that the outcome of the exchange is affected by the availability of traders on the marked (Port et al., 2009). While currently lacking in this case, support for the biological market theory could be provided by identifying (i) if, and which, commodities are exchanged, and (ii) whether the exchange is affected by the availability of providers or commodities. For example, tolerance may serve as commodity in Vervet monkeys: dominant increase their tolerance (measured as in the distance at which individuals foraged on artificially provided food), after being groomed by subordinates (Borgeaud & Bshary, 2015; Garcia, Lemieux, et al., 2021). This thus provides an exciting avenue for future research in wild birds.

Conclusion

Our previous study on SC-cockatoos found that aggressive interactions are influenced by relative rank within the dyad, suggesting that knowledge about their place in the local hierarchy informs social decision within this species (Penndorf et al., 2025). We also previously found evidence that SC-cockatoos preferentially preen kin, as well as preening associates from other roosting groups when encountering each other in intermediate locations, suggesting that allopreening plays an important in maintaining bonds in this fission-fusion society (Penndorf et al., 2023). Here, we build on these findings with a final scale analysis that uncovers additional social predictors of preening patterns in wild SC-cockatoos. Our findings therefore add to the evidence for differentiated social relationships within SC-cockatoos, with individual exhibiting a multi-faceted affiliative and aggressive response to other individuals that depends on roost membership, social network ties, rank and kinship. Our work also suggests intriguing directions for future work in this species that could add further valuable

comparisons to primates and corvids.

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