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Different patterns of allopreening in the same-sex and opposite-sex interactions of juvenile large-billed crows (*Corvus macrorhynchos*)

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Abstract

Allogrooming, where an individual grooms another, has been extensively studied in various social animals to understand its role in the evolution of cooperation/prosociality. In existing studies in mammals, allogrooming has been suggested to exhibit not only a hygiene but also a social function. Allopreening, a topic of increasing interest in mammals but recently also in birds, has been studied mostly with mature animals. However, in some species immature individuals also show allopreening and its function remains poorly understood. Crows, *Corvus spp.*, are an ideal model to study this phenomenon, because juveniles form year-round aggregates during their long juvenile stage (e.g., throughout 3–4 years). Here, we investigated the function of allopreening in juvenile groups of wild-caught large-billed crows (*C. macrorhynchos*). Allopreening frequency and duration for three groups of wild-caught juveniles were analysed to determine whether there was a symmetrical (i.e., reciprocal) or asymmetrical allopreening pattern, and if sex composition of the dyad and/or relative dominance of donor and recipient had an effect. We found that both the frequency and duration of male allopreening correlated with frequency of aggression. Allopreening between both males and females occurred unidirectionally from dominants to subordinates but not in the opposite direction. On the contrary, allopreening between a male and a female was found to be reciprocated, though the absolute frequency and duration were both greater in males than in females. These results suggest that the social function of allopreening in juvenile crows differs depending on the sex composition of the dyad, functioning as a dominance signal for same-sex dyads, and serving a social bonding function for opposite-sex dyads. These findings may reflect the potentially crucial roles of allopreening in within-sex competition and opposite-sex attraction during the 3 year-long juvenile stage affecting future mate choice in lifelong monogamy.

KEYWORDS
altruism, corvids, dominance, grooming, preening, reciprocity

1 | INTRODUCTION

Allogrooming, where an individual grooms another, has been extensively studied in different social animals to understand the adaptive function of allopreening as a costly, seemingly altruistic behaviour and its role in the evolution of cooperation/prosociality (Hamilton, 1964; Trivers, 1971). Two hypothetical functions, not mutually exclusive, of allogrooming have been suggested: a hygiene function and a social function. From the hygiene function perspective, allogrooming is an anti-parasite behaviour wherein donors benefit recipients by removing ectoparasites from body parts that cannot be accessed by autogrooming (Barton, 1985; Bush & Clayton, 2018; Clayton, 1991; Radford & Plessis, 2006). The social function hypothesis postulates that allogrooming is an affiliative behaviour serving to form and maintain affiliative relationships within the group and to avoid and resolve social conflicts within the group. The social function hypothesis predicts that allogrooming will occur in specific patterns that relate to differences in social factors among group members. Indeed, it has been reported that allogrooming between individuals can occur in symmetric or asymmetric patterns depending on their respective social class and/or relationship in various taxa. Reciprocity is a symmetrical pattern of allogrooming, where two individuals exchange groomer and groomee roles in iterated interactions (Trivers, 1971), and has been observed in several species (e.g., chimpanzees, *Pan troglodytes*, Hemelrijk & Ek, 1991; Watts, 2002; chacma baboons, *Papio ursinus*, Barrett, Henzi, Weingrill, Lycett, & Hill, 1999). Similarly, allogrooming has been observed in reciprocal exchange of other commodities such as conflict aid (e.g., long-tailed macaques, *Macaca fascicularis*, Hemelrijk, 1994; ravens, *C. corax*, Fraser & Bugnyar, 2012), food sharing (e.g., chimpanzees, de Waal, 1997; Norway rats, *Rattus norvegicus*, Schweinfurth & Taborsky, 2018) and infant handling (e.g., Henzi & Barrett, 2002). These findings regarding reciprocal exchange of affiliative behaviour are theorised as "biological market" to describe their role in the formation and maintenance of affiliative relationships in group-living animals (Noë & Hammerstein, 1995; Seyfarth, 1977).

Asymmetrical patterns of allogrooming have been documented in various social animals, largely in cooperative breeding mammals. In meerkats (*Suricata suricatta*), for example, it was found that allogrooming occurred more from subordinate females to dominant females than the reverse. Such a unidirectional pattern of allogrooming from subordinates to dominants supports the hypothesis that allogrooming serves to reduce the aggressive tension of dominant recipients and reduce the likelihood that subordinates will be attacked or harassed by dominants (i.e., tension reduction or harassment avoidance hypotheses; Kutsukake & Clutton-Brock, 2006; Terry, 1970). On the contrary, allogrooming has been also observed from dominants to subordinates in the dwarf mongoose (*Helogale parvula*; Rosa, 1987). In this species, dominant females allogroom subordinate females more than vice versa. Their asymmetric allogrooming has been interpreted as a dominance signal discouraging subordinates from challenging the dominants, and/or

encouraging them to stay within the cooperative breeding group (i.e., handicap signal, Zahavi, 1975; costly signal, Grafen, 1990). A similar allogrooming pattern was reported in the cooperative breeding common marmoset (Callithrix jacchus, Lazaro-Perea, Fátima, & Snowdon, 2004).

Although avian allopreening (equivalent to mammalian allogrooming) has been little investigated compared to mammals, it has been suggested to play a social function in forming and maintaining the affiliative relationships between individuals, as a basis for cooperation in their social lives (Harrison, 1965; Radford & Plessis, 2006; Lewis, Roberts, Harris, Prigmore, & Wanless, 2007; see also Picard et al.,. in this issue). Like in mammals, both symmetric and asymmetric patterns have been reported in avian allopreening. Reciprocal pattern of allopreening has been found in pair-bonded males and females (cockatiels, *Nymphicus hollandicus*, Spoon, Millam, & Owings, 2006; wrens, *Cantorchilus leucotis*, Gill, 2012), conforming to the social bonding hypothesis. From an evolutional perspective, this hypothesis was further supported by a phylogenetic analysis of 50 avian species which suggests an association between the presence of symmetrical allopreening and stable pair-bonds or parental cooperation (Kenny, Birkhead, & Green, 2017). Yet, asymmetrical patterns of allopreening have also been reported in birds, namely in cooperative breeding green woodhoopoes (*Phoeniculus purpureus*). In this species, subordinate non-breeding helpers allopreen dominant breeding pairs more often and for longer than the other way around, conforming to the tension reduction and harassment avoidance hypothesis (Radford & Plessis, 2006). Further, an allopreening pattern from dominants to subordinates, serving a signal function, was pointed out in an earlier review by Harrison (1965). This extensive review described instances of allopreening from dominants to subordinates in a variety of avian species and proposed that allopreening serves an aggressive signal. Surprisingly, however, no empirical study has ever been reported to support the dominance signal hypothesis. Many of these previous studies on avian allopreening investigated its social function in matured adult individuals such as in pair-bonded partners. To understand social function of allopreening from the perspective of evolution of cooperation and prosociality, it is necessary to expand our study scope of allopreening to include a broader range of social contexts, not only in matured adults, but also in unmatured juveniles.

Crows and related species (i.e., *Corvus* spp) are an ideal model to investigate social functions of allopreening in juveniles as a basis for affiliative relationships and cooperation. This group of birds show lifelong monogamy, alloparental care (Coombs, 1978; Kuroda, 1990) or cooperative breeding systems (Baglione, Marcos, & Canestrari, 2002; Bresgunova, 2016). In addition, pair-bonded individuals remain together year-round (Braun & Bugnyar, 2012; Kuroda, 1990). Young birds (unpaired adults as well), after being independent of parental care, form fission–fusion aggregations with both males and females and freely float in a wide range of areas for their long juvenile period, for example, 3–4 years in ravens (*C. corax*), carrion crows (*C. corone*) and large-billed crows

(*C. macrorhynchos*; Boucherie, Loretto, Massen, & Bugnyar, 2019; Coombs, 1978; Izawa, 2011; Loretto et al., 2017; Uhl et al., 2019). In both captive and wild populations, it has been reported that affiliative relationships are formed between unpaired adults and unmatured juveniles by exchanging affiliative behaviour such as allopreening, active food giving and conflict aiding (rooks, *C. frugilegus*, de Kort, Emery, & Clayton, 2006; Emery, Seed, Bayern, & Clayton, 2007; Scheid, Schmid, & Nöe, 2008; jackdaws, *C. monedula*, von Bayern, Kort, Clayton, & Emery, 2007; ravens, Braun & Bugnyar, 2012; Fraser & Bugnyar, 2012). Formation of affiliative relationship between individuals was found to increase the dominance rank and the likelihood of success for competing foods in a captive group of rooks (Emery et al., 2007) and in the wild ravens (Braun & Bugnyar, 2012) as well. These findings suggest an advantage of the affiliative relationship in group lives. In recent experimental studies, the affiliative relationship between individuals was found to affect the task performance requiring cooperation, suggesting that affiliative relationship could endow the cooperative or prosocial behaviour in birds (Jelbert, Singh, Gray, & Taylor, 2015; Massen, Ritter, & Bugnyar, 2015; Seed, Clayton, & Emery, 2008). Despite these findings to suggest the crucial role of affiliative behaviour at the proximate and ultimate levels for prosociality and cooperation, social functions of allopreening in corvids, but also in birds in general, have been poorly understood (von Bayern et al., 2007; Emery et al., 2007; Frasers & Bugnyar, 2012).

In this study, we examined social functions of allopreening in captive groups of wild-caught juvenile large-bill crows (*C. macrorhynchos*). Large-billed crows, similarly to other corvids, form lifelong pair-bonds and breed siblings by biparental care in their territory during the late spring to summer (April–August; Kuroda, 1990). Juveniles, leaving the parents' territory at a few months after hatching, aggregate as free floaters for 3 years or more until the formation of pair-bonds after having reached maturity at the end of the third years (Islam, Zhu, Aoyama, & Sugita, 2010; Izawa, 2011; Kuroda, 1990). Pair-bonded adults also join this non-breeder aggregation outside the breeding season. It has been found that in captivity, males form and maintain stable dyadic dominance relationships and, in a group setting, a strict and stable linear hierarchy, where males are dominant over females (Izawa & Watanabe, 2008; Kitagawa, 1980; Nishizawa, Izawa, & Watanabe, 2011; Ode et al., 2015).

The present study aimed at determining social functions of allopreening based on three hypotheses introduced above, each of which is characterised by a specific pattern of allopreening between individuals. If indeed allopreening serves a social bonding function as hypothesised for juvenile large-billed crows, their allopreening should be reciprocated by allopreening or other behavioural commodities such as conflict aid. On the other hand, if tension reduction is involved, it is predicted that allopreening should occur asymmetrically from subordinates to dominants. Finally, if the social (i.e., dominance) signal function is at work, allopreening should be expected to occur asymmetrically from dominants to subordinates.

2 | METHODS

2.1 | Animals and housing

This study utilised 32 juvenile large-billed crows that composed three groups (groups A, B and C). All of the birds were caught as free-floater yearlings in various cities of Japan (i.e., Tokyo, Mizuho, Kamagaya, Tsukuba, Moka, Toyohashi, Iida, etc.) during November 2014 for group A, January 2016 for group B and March 2017 for group C, with authorisation from the Japanese Ministry of the Environment (permission numbers 2025575, 27924005, 29030001). The birds captured in each year were housed in group of mixed sex in outdoor aviaries (180 m^2 × 3 m high): thus, each group consisted of 5–6 males and females with matched age (see Table S1 for the group composition). Age of the first yearling was determined by black/pink pigmentation of tongue and oral cavity (Kitagawa, 1980), and sex was determined by blood DNA analysis (Fridolfsson & Ellegren, 1999). Kinship among the group members was unknown as the birds were not caught from the nest. Food (i.e., dog food, boiled eggs, raw meat and cheese) and water were freely available, and a sufficient number of tree branches for perching were placed in the aviary. Experimental protocols and housing conditions adhered to the Japanese regulations for animal welfare and were approved by the Animal Care and Use Committee of Keio University (No. 08005, 15092, 16059).
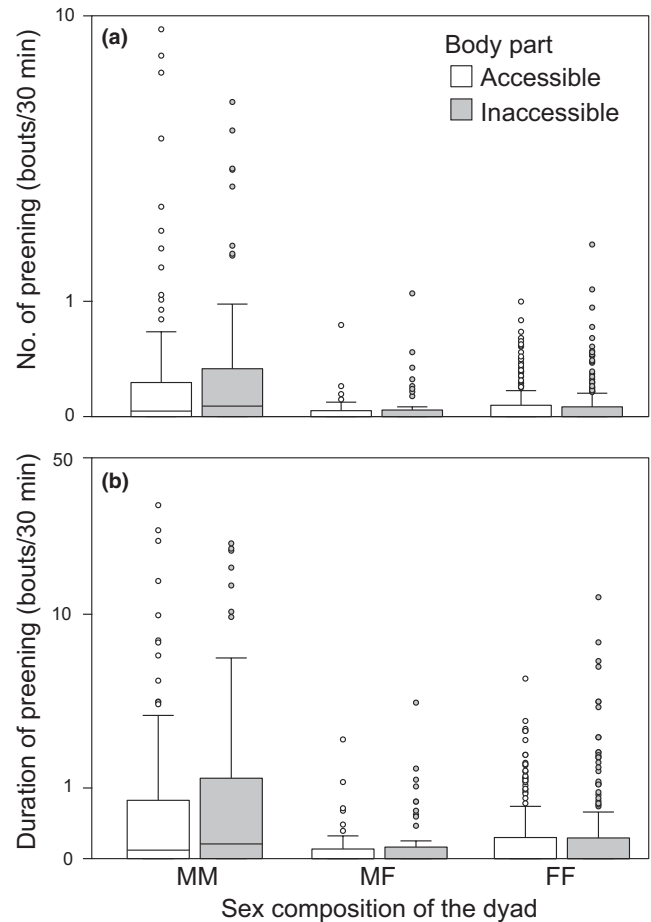
2.2 | Observations

Observation of social interactions was conducted through March 2015–February 2017 for group A, July 2016–February 2018 for group B and April 2017–February 2018 for group C. These study periods correspond to the immature juvenile stage for birds of all groups, namely the second and/or third years after hatching. Mean observation time was 63.4 hr across the three groups (69.7 hr for group A, 78.9 hr for group B and 41.6 hr for group C). A single observation session was 15 min, including one of five experimenters (E. M., A. S., N. T., A. M. and E.-I. I), conducted either by direct or indirect video-recording observation. For direct observation, one experimenter directly observed the social interactions and their participants' identities randomly in a focal group (random sampling method; Altman, 1974). For indirect video-recording observation, one experimenter placed 2–4 video cameras outside a focal group aviary to video record the social interactions on all the perches in the aviary. During video-recording session, the experimenter hid (in a hut) out of crows' sight. These two methods were not performed simultaneously in the same session. Proportions of direct and indirect observations were comparable among the three groups (direct and indirect: 70.1% and 29.9% for group A, 68.3% and 31.7% for group B and 75.4% and 24.6% for group C). Each video-recorded data was scored offline by the experimenter who video-recorded the session. Eight sessions (i.e., 2 hr) were performed at a maximum per day between 900 and 1,500. The

five experimenters took part randomly in observation sessions of both groups throughout the study period. Inter-observer agreement between the five observers was calculated using a randomly chosen 10.5 hr of video data. Mean kappa was 0.802 with 0.78–0.82 of the 95% confidence interval, indicating relatively high inter-observer reliability of behavioural coding.

2.3 | Analysis

Instances of allopreening, agonistic interactions and conflict aid were collected from the observation data for analysis. Allopreening was defined as one bird passing its bill through the feathers of another bird. For each instance, we scored identities of the preening donor and the recipient as well as the body part being preened. We scored in terms of number of bouts (i.e., frequency) and duration (i.e., seconds). Two sequential allopreenings of the same donor and recipient occurring within 2 s were considered the same bout, and those separated by more than 2 s were considered separate bouts. We measured the duration of each bout. It is notable that allopreening in some corvids has been reported to be initiated by bowing behaviour of the recipient as an invitation signal to the donor's allopreening (e.g., jackdaws; Harrison, 1965; Katzir, 1983). However, allopreening initiated by bowing behaviour of the recipient was observed in very few instances of allopreening in our study populations (<0.6%). The allopreening initiated by the receiver was very rare even if they had a different function than allopreening initiated by the donor and were therefore excluded from the analysis. We scored immediately reciprocated allopreening within a dyad as separate bouts, although such immediately reciprocated allopreening was seldom observed in our study (2%). An instance of agonistic interaction was defined as (a) a submissive display of the victim to the aggressive behaviour of an aggressor or (b) by a displacement where an individual retreated from an approach of another individual. Aggressive behaviour includes peck, jab, kick and chase, and submissive behaviour consisted of fuzzy head, submissive begging vocalisation, and escaping (see details; Izawa & Watanabe, 2008; Ode et al., 2015). We also scored instances of conflict aid where a bystander showed aggression to one of the combatants during or within 10 s after an agonistic conflict. Specifically, the identities of the donor of the conflict aid and the recipient were scored in each instance. All of these behavioural variables were scored separately between the second and third years of age because in some dyads of groups A and B the dominance relationship changed. For this calculation, the data were separately pooled from spring to the next winter for each year, in particular: group A, March 2015–February 2016 and March 2016–February 2017 for the second and third years of age, respectively; group B, July 2016–February 2017 and March 2017–February 2018 for the second and third years of age, respectively; group C, April 2017–February 2018 only for the second year of age. It is also noted that allofeeding and other affiliative behaviour, which could be reciprocated for allopreening, did not occur in our study population, so we used only conflict aid for the analysis below.

FIGURE 1 Allopreening occurred with different frequency (a) and duration (b) among the sex compositions of the dyad

To test the hygienic and social function hypotheses, we performed generalised mixed models (GLMM) to examine the effects of dominance relationships, sex and body part on allopreening of dyads. GLMMs were run separately for the number of allopreening bouts and the duration of allopreening as dependent variables. For both GLMMs, "dominance," "number/duration of allopreening bout received," "number of aggression initiated," "number of aggression received," "sex composition," "body part," "age" and "conflict aid" were included as independent variables, and the donor's identity and the group were treated as random factors. Gamma error distribution with log link function was applied to the GLMMs. The "dominance" factor was the dominance of the preening donor to the recipient in each dyad, and fell into three categories: dominant, subordinate or tied (no dominance). Dominant was defined as an individual winning ≥70% of the total number of agonistic interactions in each year, and the other one was defined as subordinate. Individuals in a dyad with <70% win/loss asymmetry were defined as tied. This dominance category was applied only to those dyads that showed four or more agonistic conflicts in a year. We excluded dyads exhibiting fewer than three conflicts from the analysis. The "sex composition" factor consisted of three categories: male–male (MM), male–female (MF) and female–female (FF). The "body part" factor denotes the part of the body where the donor preened the recipient and was categorised

into two categories: accessible (trunk, back and wing) and inaccessible (head, neck and bill) by autopreening. "Age" factor considered the age of the birds, thus falling into two categories: the second or third year. Behavioural variables, such as allopreening and aggression initiated/received, were calculated as mean frequencies (as well as duration for allopreening) per 30 min for each dyad in each year of age. The best-fit model was selected by stepwise reduction, starting from the full model including all possible interactions, to attain the smallest AIC (Akaike's information criterion). In this analysis, we predicted that if allopreening had a social function, dominance and/or sex would exert an effect on allopreening. If allopreening had a hygienic function, more preening of inaccessible body parts would be expected. All of these analyses were performed using R 3.4.4 software with the "lme4" package for mixed models.

3 | RESULTS

A total of 5,277 allopreening bouts, 5,790 agonistic interactions and 43 instances of conflict aid were recorded through the entire observation period of the three groups added together. Both the number of bouts and duration of allopreening were clearly different across the sex composition categories (no. of bouts: $F_{2, 168.9}$ = 6.68, p < .002, Figure 1a; duration: $F_{2, 193.1}$ = 9.50, p < .001, GLM after log-transformation, Figure 1b). Thus, analyses were conducted separately for the different sex-combination categories.

Note that in all the analysis separately for each sex composition below, the body part and the age factors were dropped from the initial runs of GLMMs. Thus, in the following GLMM analysis, we did not describe the age factor and used the pooled data of allopreening of different body parts.

3.1 | Between males

All of the 50 male–male dyads exhibited dominance relationships but none had tied or unknown relationships. The GLMM analysis selected the full model as the best, which included the significant effects of dominance, the number of aggressions initiated, and that of aggression received, and also the significant interaction between dominance and the number of aggressions received (Table 1). These results indicate that in terms of frequency, allopreening was not reciprocated by either allopreening or conflict aid, but occurred almost unidirectionally from dominant to subordinate males (Figure 2a,b).

To further examine the mixed effect of dominance and the number of aggressions initiated, stratified GLMMs consisting only of the number of aggressions initiated as an independent variable were performed separately for allopreening from dominant males and allopreening from subordinate males. For allopreening from dominant males, a GLMM analysis selected the best model that included the number of aggressions initiated with its significant effect and a positive coefficient (Table 2). Another GLMM for allopreening from subordinates selected the best model that included the number of

TABLE 1 Output of the best model from a GLMM for the number of allopreening bouts between males

AIC$_{best}$ = −271.6 (AIC$_{full}$ = −258.8, AIC$_{null}$ = −227.6)				
Variables	**Estimate**	**SE**	**t value**	**p**
Intercept	**−1.511**	**0.534**	**−2.830**	**.005**
Dominance[a]	**−1.829**	**0.673**	**−2.716**	**.007**
No. of allopreening bouts received	2.981	1.819	1.639	.101
No. of aggressions initiated	**1.498**	**0.445**	**3.366**	**<.001**
No. of aggression received	**−6.530**	**3.155**	**−2.069**	**.038**
No. of being aided	8.453	5.502	1.536	.124
Dominance[a] × No. of allopreening bouts received	−2.499	1.832	−1.364	.172
Dominance[a] × No. of aggressions initiated	**5.899**	**3.006**	**1.963**	**.049**
Dominance[a] × No. of aggressions initiated	5.670	3.185	1.780	.075

Note: Bold indicates statistically significant results.
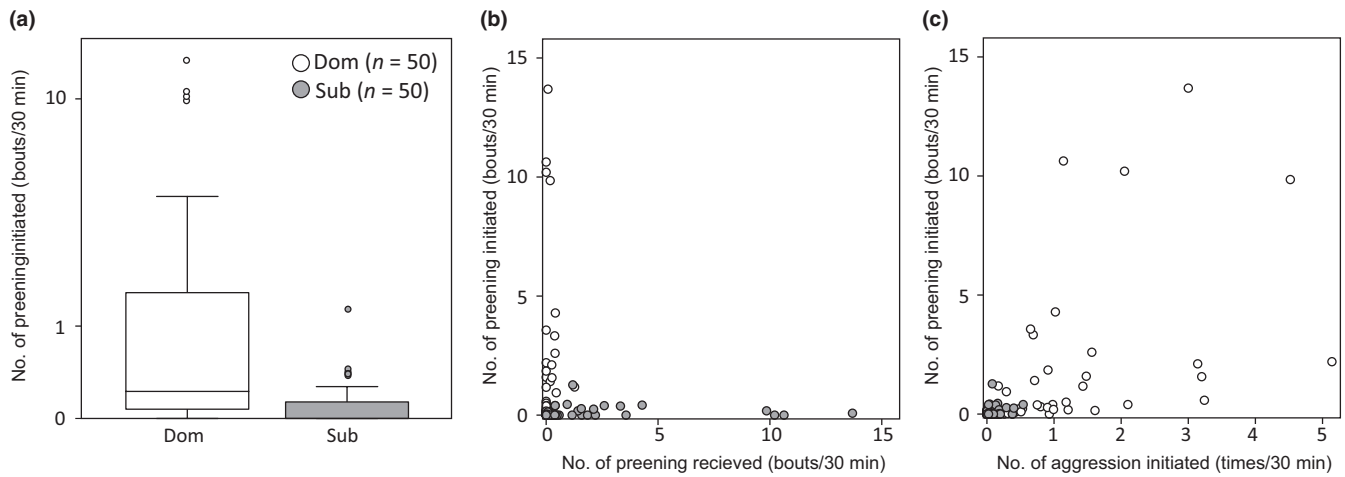[a]Dominant was set at 0.

aggressions initiated without its significance (Table 2). These results indicate that dominant males who allopreened subordinate males more often also showed more aggressions to those subordinate males.

Consistent results were obtained for the duration of allopreening. A GLMM analysis selected the best model that contained dominance and the number of aggressions initiated both with significant effects (Table 3). A negative coefficient of the dominance variable (when the "dominant" category was set at 0) indicates that the duration of allopreening was longer from dominant to subordinate males than the reverse. A positive coefficient of the number of aggressions initiated denotes that dominants who showed more aggression to subordinates allopreened the subordinates for longer durations.

The results indicate that both in terms of allopreening frequency (number of bouts) and duration, allopreening occurs unidirectionally from the dominant to the subordinate male rather than occurring reciprocally. Also, the more aggressive dominant males allopreen the subordinate males more frequently and for longer durations.

3.2 | Between males and females

Out of 129 dyads, 103 showed males dominant over females, six exhibited females dominant over males, five dyads displayed a tied relationship and 15 were unknown. Only three of the 15 unknown dyads showed allopreening (with a few agonistic interactions), and the other 12 exhibited no allopreening or agonistic interactions at all. According to our criterion, these 15 unknown dyads were not used for

FIGURE 2 Unidirectional allopreening from dominants to subordinates between males. (a) Dominant males provided allopreening more often than did the subordinate males. (b) Dominant males provided allopreening to, but received very little allopreening from, subordinate males (open circles). On the contrary, subordinate males rarely provided allopreening to, but received allopreening from, the dominant males (shaded circles). (c) Dominant males, that showed more aggression, more allopreened more the subordinate males, but the subordinate males did not. Note that the vertical axis in (a) is displayed as log scale

TABLE 2 Output of the best model from a GLMM for the number of allopreening bouts between males

Variables	Estimate	SE	t value	p
From dominants				
AIC = 34.6 (AIC$_{null}$ = 47.2)				
Intercept	**−1.150**	**0.438**	**−2.622**	**.009**
No. of aggressions initiated	**1.081**	**0.355**	**3.043**	**.002**
From subordinates				
AIC$_{best}$ = −301.2 (AIC$_{null}$ = −301.1)				
Intercept	**−2.713**	**0.410**	**−6.615**	**<.001**
No. of aggressions initiated	3.787	3.238	1.169	.242

Note: Bold indicates statistically significant results.

TABLE 3 Output of the best model from a GLMM for the duration of allopreening between males

AIC$_{best}$ = −83.0 (AIC$_{full}$ = −81.8, AIC$_{null}$ = −41.3)				
Variables	Estimate	SE	t value	p
Intercept	0.1798	0.536	0.335	.737
Dominance[a]	**−1.461**	**0.572**	**−2.554**	**.011**
No. of aggressions initiated	**1.181**	**0.454**	**2.602**	**.009**

Note: Bold indicates statistically significant results.
[a]Dominant was set at 0.

the analyses. For male–female allopreening, analyses were conducted separately from male to female and female to male allopreening.

A GLMM analysis of the number of allopreening bouts from males to females produced the best model that included the following variables: number of allopreening bouts received, number of aggressions
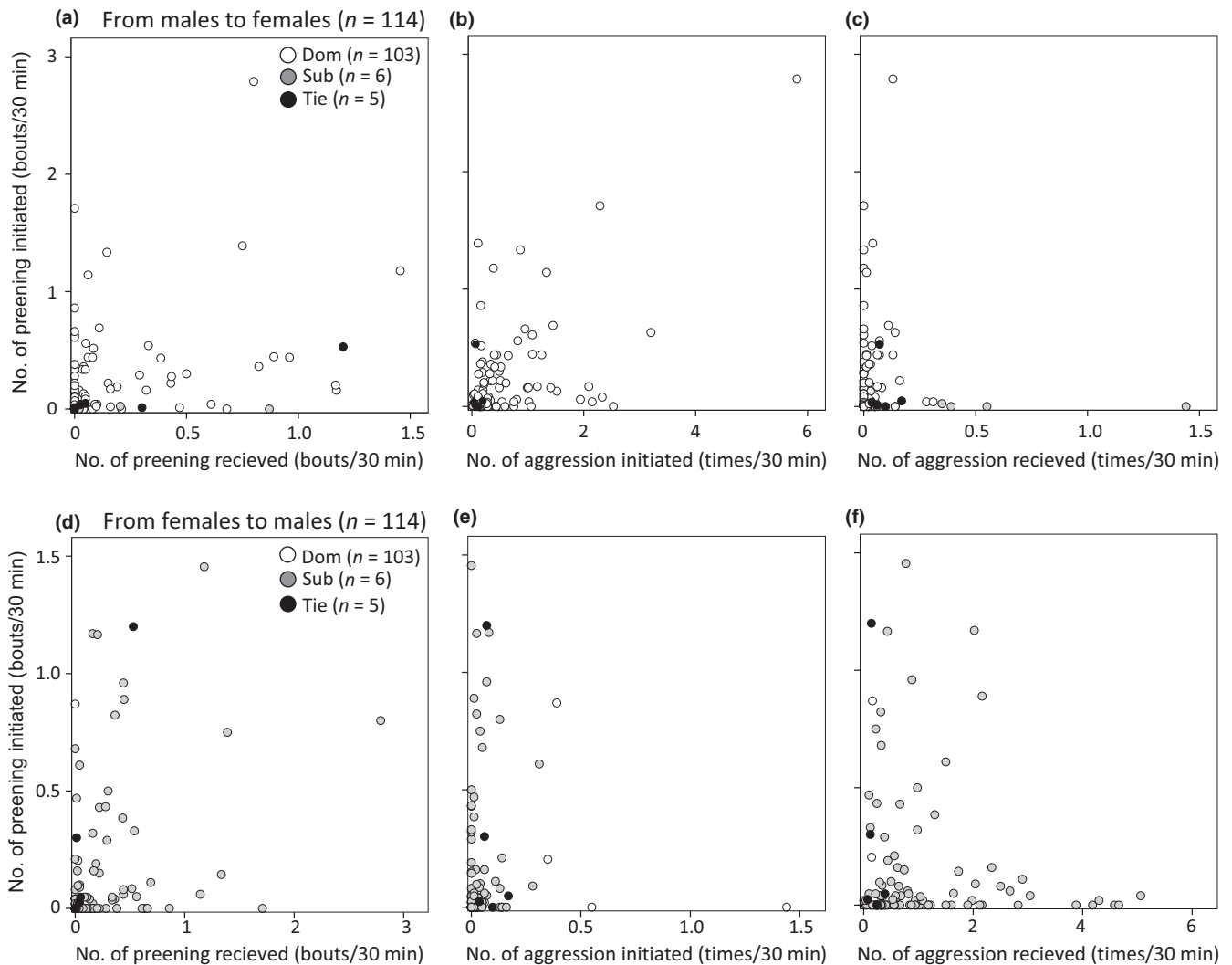
TABLE 4 Output of the best model from a GLMM for the number of allopreening bouts between males and females

Variables	Estimate	SE	t value	p
From males to females				
AIC$_{best}$ = −359.5 (AIC$_{full}$ = −348.9, AIC$_{null}$ = −342.9)				
Intercept	**−2.455**	**0.265**	**−9.276**	**<.001**
No. of allopreening bouts received	**1.672**	**0.611**	**2.738**	**.006**
No. of aggressions initiated	**0.908**	**0.292**	**3.105**	**.002**
No. of aggressions received	**−5.100**	**0.926**	**−5.510**	**<.001**
From females to males				
AIC$_{best}$ = −600.7 (AIC$_{full}$ = −598.9, AIC$_{null}$ = −592.5)				
Intercept	**−2.492**	**0.320**	**−7.784**	**<.001**
No. of allopreening bouts received	**2.461**	**0.811**	**3.034**	**.002**
No. of aggressions initiated	3.792	2.4260	1.563	.118
No. of aggressions received	**−0.721**	**0.344**	**−2.094**	**.036**

Note: Bold indicates statistically significant results.

initiated and number of aggressions received with significant effects (Table 4). In the final model, coefficients of both the number of allopreening received and of aggressions initiated were positive, whereas the coefficient for the number of aggressions received was negative. These results indicate that those males that allopreened more females showed more aggression to the females but received more allopreening and less aggression from the females (Figure 3a–c).

Similar results were obtained from the analysis of the duration of allopreening from males to females. A GLMM selected the best model

FIGURE 3 (a, d) Allopreening occurred reciprocally between males and females irrespective of dominance relationships. (b) Males that allopreened more females showed more aggression to the females but (c) received less aggression from the females. (e) Female allopreening of males had no correlation with aggression to the males. (f) Females that allopreened more males received less aggression from the males

that consisted of the variables of duration of allopreening received, the number of aggressions initiated and the number of aggressions received with significant effects (Table 5). Coefficients of both the duration of allopreening received and the number of aggressions initiated were positive, whereas that of the number of aggressions received was negative. These results reflect that those males that allopreened females for longer durations showed more aggression to those females but vice versa received more allopreening and less aggression from them.

The same trend was found in the allopreening from females to males. A GLMM analysis of the number of allopreening bouts produced the best model that included the variables of the number of allopreening bouts received, aggressions initiated and aggressions received (Table 4). Significant effects were found for the variables of allopreening bouts received (with a positive coefficient) and of aggressions received (with a negative coefficient), but no significance was found for the number of aggressions initiated. These results reflect that those females that allopreened more males received more allopreening but less aggression from the males (Figure 3d–f).

A GLMM performed on the duration of allopreening from females to males selected the best model that contained the duration of allopreening received, the number of aggressions initiated and the number of aggressions received (Table 5). Significance was found only for the duration of allopreening received, with a positive coefficient. These results indicate that those females that allopreened males for a longer time received allopreening from the males for a longer time.

In summary, these results of allopreening between males and females indicate that in terms of both frequency and duration, allopreening was reciprocated within male–female dyads.

3.3 | Between females

Out of 48 female–female dyads, 34 showed a dominance relationship, two dyads displayed a tied relationship, and 12 were unknown. Only one of the 12 unknown dyads exhibited allopreening (with a few agonistic interactions), and the remaining 11 dyads did

TABLE 5 Output of the best model from a GLMM for the duration of allopreening between males and females

Variables	Estimate	SE	t value	p
From males to females				
$AIC_{best} = -121.7$ ($AIC_{full} = -111.1$, $AIC_{null} = -108.5$)				
Intercept	**−0.927**	**0.296**	**−3.132**	**.002**
Duration of allopreening received	**0.408**	**0.178**	**2.295**	**.022**
No. of aggressions initiated	**0.896**	**0.317**	**2.830**	**.005**
No. of aggressions received	**−6.118**	**1.055**	**−5.800**	**<.001**
From males to females				
$AIC_{best} = -400.8$ ($AIC_{full} = -398.2$, $AIC_{null} = -396.9$)				
Intercept	**−0.811**	**0.338**	**−2.401**	**.016**
Duration of allopreening received	**0.385**	**0.162**	**2.376**	**.017**
No. of aggressions initiated	3.214	2.495	1.288	.198
No. of aggressions received	−0.735	0.408	−1.802	.071

Note: Bold indicates statistically significant results.

TABLE 6 Output of the best model from a GLMM for the number of allopreening bouts between females

$AIC_{best} = -362.0$ ($AIC_{full} = -354.7$, $AIC_{null} = -359.6$)

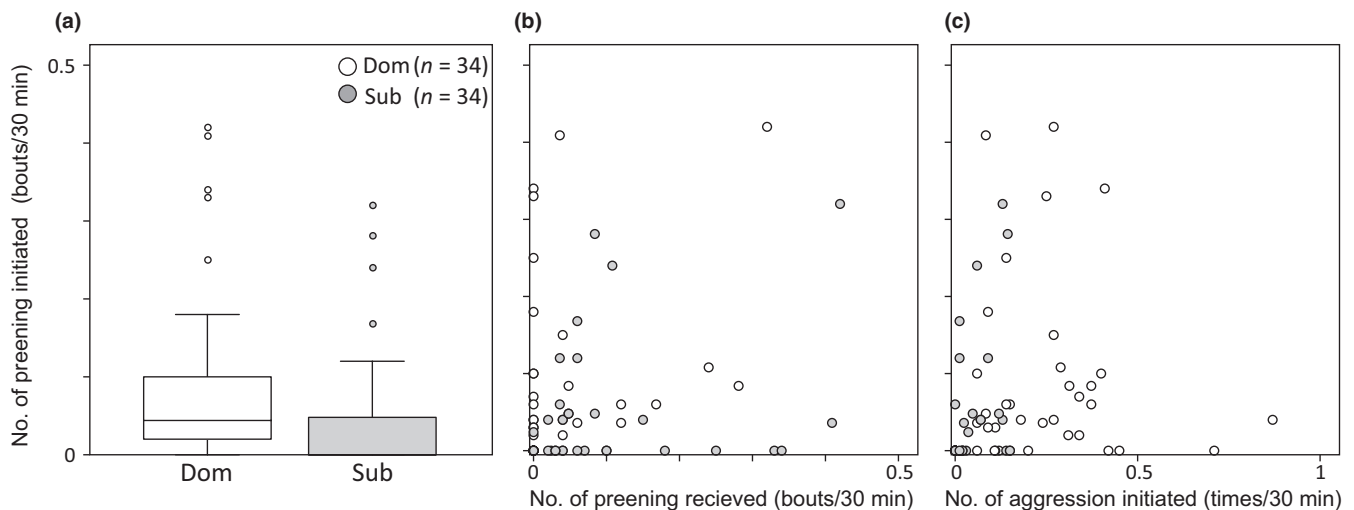| Variables	Estimate	SE	t value	p
Intercept	**−2.156**	**0.623**	**−3.460**	**<.001**
Dominance[a]	**−1.903**	**0.763**	**−2.496**	**.012**
Dominance × No. of aggressions initiated	16.896	7.403	1.782	.076

Note: Bold indicates statistically significant results.
[a]Dominant was set at 0.

to subordinate females than the other way around (Figure 4a), but that this did not relate to the degree of aggression initiated (Figure 4b,c).

Similarly, a GLMM performed on the duration of allopreening between females yielded the best model that contained the dominance variable with a significant effect and an interaction between the number of aggressions initiated and the dominance variable without significance (Table 7). The coefficient of the dominance variable was negative, indicating that allopreening between females occurred longer from dominant to subordinate females than the other way around.

These results suggest that allopreening in female–female dyads

FIGURE 4 (a) Allopreening between females occurred more from dominant to subordinate individuals than the reverse. (b) Allopreening was not reciprocated within female–female dyads. (c) There was no clear correlation between the number of allopreening bouts and that of aggressions initiated in females

not show both allopreening and agonistic interactions at all. Based on our criteria, the 12 dyads were excluded from the analysis. Owing to the small number of dyads with a tied relationship, we excluded them from the following GLMM analysis. A GLMM analysis for the number of allopreening bouts selected the best model that included the dominance variable with a significant effect and an interaction between the number of aggressions initiated and the dominance variable without significance (Table 6). The coefficient of the dominance variable was negative, which indicates that allopreening between females occurred more from dominant

occurred, similar to that in male–male dyads, unidirectionally from dominant females to subordinate females, but with lower frequencies relative to male–male dyads and male–female dyads.

4 | DISCUSSION

The present study revealed different patterns of allopreening between dyads of different sex composition in wild-caught juvenile

TABLE 7 Outputs of the best model from a GLMM for the duration of allopreening between females

AIC$_{best}$ = −243.0 (AIC$_{full}$ = −235.6, AIC$_{null}$ = −239.3)				
Variables	Estimate	SE	t value	p
Intercept	−0.518	0.699	−30.741	.459
Dominance[a]	**−2.441**	**0.849**	**−2.876**	**.004**
Dominance[a] × No. of aggressions initiated	18.926	8.108	0.204	.840

Note: Bold indicates statistically significant results.
[a]Dominant was set at 0.

large-billed crows. Allopreening in dyads of same-sex individuals occurred unidirectionally from dominants to subordinates, and not in the opposite direction. In contrast, allopreening in opposite-sex dyads was exchanged reciprocally, although in terms of absolute number and duration, males allopreened females more often and for longer durations than females allopreened males within the dyad. It was also turned out that allopreening occurred evenly between accessible and inaccessible body parts. These results suggest that allopreening in juvenile large-billed crows has a crucial social function rather than a hygienic function and that the social function differs according to whether the interacting individuals are of the same or of different sex. Specifically, it serves a dominance signal function in male–male and female–female interactions, while serving a social bonding function in male–female interactions.

The reciprocal pattern of allopreening observed in male–female interactions supports the social bonding hypothesis. Given that reciprocal allopreening has been found between pair-bonded males and females in various avian species (e.g. cockatiels, Spoon et al., 2006; wrens, Gill, 2012), the present results may indicate that male–female allopreening contributes to pair bond formation. We could not directly examine the possibility that male and female juvenile crows directly used allopreening to evaluate its donor as a potential partner for lifelong pair bond in this study because pair-bonds were not formed during the study period. However, in our preliminary observations after the study period, three pair-bonds were formed and allopreening was clearly reciprocated between the partners of pair-bonds (Takahashi & Izawa, unpublished). These preliminary data suggest that establishing reciprocal allopreening in male–female dyads in the juvenile group might lead to pair bond formation after sexual maturation. However, longitudinal observation of male–female allopreening is necessary to investigate how male–female allopreening rates during the juvenile stage relate to their future pair-bonding. More detailed studies in the future may elucidate if and what behavioural and/or morphological characteristics play a crucial role in lifelong partner choice during the juvenile stage in crows and related species (i.e., corvids).

The present results of unidirectional allopreening from dominants to subordinates was robust between males but less obvious between females in terms of number and duration though statistical significance emerged in both sex combinations. Such active allopreening between males could reflect that the dominance signal function of allopreening was more prominent for male–male dyads than for female–female dyads. In large-billed crows, we previously found that males form and maintain stable dyadic dominance relationships and, in a group setting, a strict linear hierarchy, whereas those of females are less robust (Izawa & Watanabe, 2008; Nishizawa et al., 2011; Ode et al., 2015). Such stable formation of dyadic dominance relationships and hierarchical group structure indicate that juvenile males must actively affirm dominance status among the members in the aggregation. Under such socio-ecological conditions, reaffirming the dominance by using affiliative allopreening, but not aggressive behaviour, could be beneficial to reduce the cost associated with agonistic conflicts.

Our finding of unidirectional allopreening from dominants to subordinates is, to our knowledge, the first empirical evidence to support the dominance signal hypothesis in the context of allopreening in birds. Surprisingly, no empirical study has ever reported evidence for this hypothesis since Harrison proposed this possibility in his extensive review of allopreening in various avian species (Harrison, 1965). In mammals, allogrooming from dominants to subordinates has been observed, but can have several social functions, such as playing a role in promoting group cohesion, and does not just serve as a dominance signal. Common marmosets, which possess a matrilineal cooperative breeding system, were found to show unidirectionally allogrooming from dominant to subordinate females and did not have a correlation between allopreening and aggression such as that found in our study (Lazaro-Perea et al., 2004). In light of this, it was claimed that allogrooming might serve not to reaffirm dominance but rather to enhance the incentive of subordinates to stay within the group and not disperse. This staying incentive hypothesis, however, cannot be applied to male–male allopreening because our study populations were non-breeding juvenile groups. Therefore, our finding of allopreening from dominant to subordinate males still supports the dominance signal hypothesis rather than the staying incentive hypothesis.

The dominance signal hypothesis for juvenile male large-billed crows still requires further investigation to elucidate the relationship between allopreening and aggression. For instance, if allopreening indeed plays a prominent role as a dominance signal to avoid conflict in male–male interactions, it is expected that aggressive interactions between males would be replaced in the course of the formation and maintenance of stable dyadic dominance relationships and a stable dominance hierarchy within each group. Some previous studies on corvids conducted longitudinal analyses to examine changes in social behaviours over time within the experimental group (von Bayern et al., 2007; Emery et al., 2007; de Kort et al., 2006; Scheid et al., 2008). However, our present study could not conduct a similar longitudinal analysis because observations began at a different point in time after the experimental group was formed and it was difficult to assess changes in allopreening and aggression in the three study groups across the time after group formation. Future longitudinal studies should be conducted to examine if the replacement of aggression occurs

among males outside of the breeding season as stable dominance relationships form.

Similar unidirectional patterns of allopreening from dominants to subordinates in other altruistic/prosocial behaviours have been confirmed in other avian species, such as allofeeding. Scheid et al. (2008) showed that allofeeding in captive male rooks occurred more from dominants to subordinates than the reverse. Wild Arabian babblers (*Turdoides sqamiceps*), cooperative breeders, were also found to allofeed from dominants to subordinates but not in the opposite direction or reciprocally (Carlisle & Zahavi, 1986). These previous findings and the present study suggest that not only allopreening, but also allofeeding, and even altruistic/prosocial behaviour in the broader context, might function as a dominance (or costly) signal to avoid conflict in some avian species. Yet, evidence for the dominance signalling hypothesis, as we report in juvenile large-billed crows, is rare even generally in non-human animals. Only one experimental study on long-tailed macaques by using a cooperation task found out that dominants, not subordinates, obtained food not only for themselves but also for others, potentially suggesting a dominance signal (Massen, Berg, Spruijt, & Sterck, 2010).

The dominance or costly signal hypothesis should be tested for the effect not only on the direct receivers but also on bystanders that observe third-party interactions as this hypothesis predicts signal propagation of donor's altruistic/prosocial quality to the direct receivers, as well as third-party bystanders, such as same-sex rivals and/or potential future mates (Grafen, 1990; Zahavi, 1975; see also Roberts, 1998). If allopreening in juvenile large-billed crows indeed serves as dominance or costly signal, it is expected that bystander males and females would show a preference to observe allopreening of dominant males and that the dominant males would facilitate allopreening in the presence of audience males and females. Although no study has yet tested, these possibilities might be likely, given the cognitive capacity of corvids to use the information of third-party's behaviour via observation (Izawa & Watanabe, 2011; Massen, Szipl, Spreafico, & Bugnyar, 2014; Müller, Massen, Bugnyar, & Osvath, 2017) and to adjust behaviour in the presence of bystanders (Szipl, Ringler, & Bugnyar, 2018).

These future research directions should be conducted by considering the effect of kinship. Although kinship was unknown and, thus, untested in our present study, effects of kinship on affiliative behaviour between group members have been reported in previous studies on corvids (von Bayern et al., 2007; Emery et al., 2007; Fraser & Bugnyar, 2012). Thus, future studies on allopreening to test dominance or costly signal hypothesis, together with kin effects during the developmental stage in corvids, will shed light on the social roles of allopreening of juveniles in immediate benefits for their group lives and also in the long-term payoff for future mating and breeding success based on lifelong cooperation.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.