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6 Social Function of Allopreening to Maintain Dominance Hierarchy in Large-billed Crows (*Corvus macrorhynchos*)

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I. Introduction

Allogrooming, where an individual grooms another, has been extensively studied in a variety of social mammals with close inter-individual proximity, to understand its altruistic nature in relation to cooperative behaviour from an evolutionary framework (Hamilton, 1964; Trivers, 1971). Two functions of allogrooming have been proposed. The first is hygiene function. Allogrooming benefits groomees by removing ectoparasites from the body parts inaccessible by autogrooming (Clayton, 1991).

The second is social function. Allogrooming has been suggested to play a critical role to maintain social relationships between group members with symmetrical or asymmetrical patterns in relation to social systems. One of the most common mechanism is 'reciprocity.' Reciprocity is characterized as a symmetrical pattern of allogrooming between donor and recipient and, thus, is considered as a mechanism for social bonding and cooperation among non-kin individuals (Trivers, 1971). Reciprocity of allogrooming hypothesizes that allogrooming is reciprocated by grooming *per se* (Hemelrijk & Ek, 1991; Mitani et al., 2000; Kutsukake & Clutton-Brock, 2006) or even interchanged by other social commodities such as conflict aid (Barrett et al., 1999).

Allopreening, homologous to allogrooming of mammals, has been widely observed in birds (Harrison, 1965). However, less has been known whether allopreening are functionally similar to allogrooming or not, due to only a few studies on allopreening function. Green woodhoopoes (*Phoeniculus purpureus*), a species breeding cooperatively in group territory, have been found to use allopreening for both hygienic and social functions (Radford & Du Plessis, 2006). In respect to the social function, subordinate woodhoopoes donated allopreening dominant ones than the reverse, suggesting the role of allopreening in reduce the aggressive tension of dominants. Allopreening in colonial breeding guillmots (*Uria aalge*) was found from males to females within pairs, suggesting that allopreening could work as a signal for mate choice but also can be interpreted as social bonding function for cooperative breeding partnership (Lewis et al., 2007).

In this study, we examined the social function of allopreening in non-breeding flock of large-billed crow juveniles. Specifically, we tested four hypotheses: (1) social bonding, (2) dominance signal, (3) temper reduction, and (4) mate signal. If allopreening functions as social bonding, reciprocity (or interchange) should be observed between preeners and preenees. If allopreening play a role of dominance signal, allopreening is expected to occur asymmetrically from dominants to subordinates. If temper reduction works in allopreening interactions, subordinates should allopreen dominants more than the reverse. Finally, if allopreening operates as sexual signal, males are predicted to engage allopreening predominantly towards females but not males.

II. Materials and methods

1. Animals and housing conditions

Wild-caught eight large-billed crows (*Corvus macrorhynchos*; four males and four females) were used in this study. All the eight crows were caught during January – March 2008 and determined as yearlings based on their tongue pigmentation (Kitagawa, 1980). All birds were colour-bonded on their legs for individual identification and housed in an outdoor aviary (5 x 10 x 3H m^3) where dog food with dry fruits and meat as diet and water were freely available.

2. Observation

Observation was conducted by one of the experimenters (E-I. I.) during July 2008 – November 2010. Focal sampling (Altmann, 1974) was employed with a 10-min session for each bird during 900-1700. Focal observation on each bird was conducted only once a day. Random sampling with a 30-min session was also performed in addition to focal sampling. A total of 160-hours observation was conducted with the equal amount of focal observation time across the birds.

Observations were performed to analyze instances of allopreening, agonistic interaction, and conflict intervention. Allopreening was defined as one bird passing the bill through the feathers of another bird. Allopreening has been reported to follow an invitation display, such as bowing head, by the bird to be allopreened (e.g., Harrison, 1965; Katzir, 1983). However such invitation display was observed in a few instances of allopreening (< 0.6%) in the present study. Thus we discarded the instances of allopreening which was initiated by invitation bowing display.

Each instance of allopreening was scored with identities of preener and preenee and also with body parts being preened. For agonistic interactions, winner and loser were determined based on aggressive or submissive display of the contestants according to our previous study (Izawa & Watanabe, 2008). We also recorded instances of conflict intervention where a bystander individual showed aggression to one of two contestants during an agonistic interaction or within 10 sec after the conflict. Specifically, identities of the donor of the conflict intervention and the recipient were scored for each instance.

3. Data analysis

To test the hygienic and social function hypotheses at the dyad level, we performed a Generalized Linear Mixed Model (GLMM) to examine the effects of dominance relationships, sex, and body part on the instances of allopreening. GLMM with a Poisson error distribution and log link function was applied for ‘dominance of preener,’ ‘dyad type’ and ‘body part’ as categorical independent factors and the number of allopreening as an explanatory variable. Preener’s identity was considered as a random effect.

‘Dominance of preener’ was categorized as dominant, subordinate, and tie. These categories were determined according to the win / loss outcomes

in agonistic interactions based on the following criterion. Dominant was defined for an individual of a dyad that won ≥75% of interactions and, consequently, the opponent in the dyad was defined as subordinate. Individuals in a dyad resulting in < 75% win / loss asymmetry were defined as tie (i.e., no dominance). 'Dyad type' factor comprised three categories such as male-male (M-M), male-female (M-F), and female-female (F-F). 'Body part' factor fell into two categories such as trunk and wing regions, accessible by auto-preening, and head and neck regions, inaccessible by auto-preening.

The best-fit model was selected by stepwise reduction procedure, starting from the full model including all possible interactions to attain the smallest score of Akaike's Information Criterion (AIC). In this analysis, we could predict the effects of dominance and/or sex on allopreening if social function involved. If hygienic function was operated, the effect of body-part factor was expected and, namely, more preening of inaccessible body part (i.e., head) would be found.

To investigate reciprocity of allopreening and/or conflict intervention (i.e., interchange) at the population level, the data of allopreening, agonistic interaction, and conflict intervention were separately represented in matrix forms.

Reciprocity and interchange hypotheses were examined by a matrix correlation analysis with Mantel Z test with 10 000 permutations and Pearson *r* correlation (Hemelrijk, 1990a, b). To test reciprocity of allopreening, Mantel Z test was performed on preener-preenee matrix and its inverse preneepreener matrix. Interchange between allopreening and conflict aid examined by Matel Z test on preener-preenee matrix and the matrix of recipient-donor of conflict intervention. In addition, to assess the effect of dominance relationships on reciprocity and interchange, these analyses were separately performed for the dyads with dominance relationships and with no dominance (i.e., tie).

III. Results

We observed 1271 instances of agonistic interactions, 1861 instances of allopreening, and 10 instances of conflict intervention. Figures 1 show the summary of observed instances of agonistic interactions (fig. 1a) and allo-

(a)

Loser \ Winner	W	Or	RY	WW	s	rb	y	g	sum
W		209	91	137	28	164	53	50	732
Or	4		62	35	15	103	14	48	281
RY	8	4		10	3	16	6	18	65
WW	5	8	16		4	11	10	17	71
s	0	2	2	5		4	9	5	27
rb	2	2	1	1	6		33	11	56
y	6	4	3	0	2	3		6	24
g	0	2	1	1	5	4	2		15
sum	25	231	176	189	63	305	127	155	1271

(b)

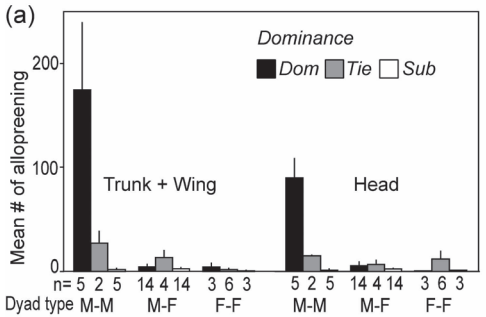
Preener \ Preenee	W	Or	RY	WW	s	rb	y	g	sum
W		305	119	519	0	68	15	6	1032
Or	0		220	159	0	6	0	29	414
RY	0	7		32	0	1	0	4	44
WW	1	10	53		5	10	1	9	89
s	0	2	2	51		0	1	19	75
rb	0	3	6	54	2		1	7	73
y	9	1	2	3	1	2		4	22
g	0	3	6	27	69	5	2		112
sum	10	331	408	845	77	92	20	78	1861

Figure 1. Outcomes of agonistic interactions (a) and allopreening (b) in a captive flock of juvenile large-billed crows. a. Winner / loser matrix. The value in a cell is the number of times the crow in that row (winner) won in an agonistic encounter against the crow in that column (loser). b. Preener / preenee matrix. The value in a cell is the number of times the crow in that row (preener or donor) allopreened an individual in that column (preenee or recipient). In both matrices, individuals are shown in dominant-to-subordinate order from top to bottom. Capital and small letters indicate males and females, respectively.

preening (fig. 1b). Out of 28 dyads in total, 22 and 6 dyads were found as dominance and tied relationships, respectively.

Mantel Z test revealed the significant correlation between preener-preenee and its inverse matrices for the 6 dyads with tie relationships (r = 0.46, p = 0.012) but not for the 22 dyads with dominance relationships (r = -0.08, p = 0.67, ns). No significant correlations were found between allopreening and conflict intervention matrices both for the dyads with dominance relationships (r = -0.09, p = 0.71, *ns*). Dyads with tie relationships exhibited no conflict intervention at all. These results suggest the reciprocity of allopreening between individuals with tie relationships.

The results from the analyses with GLMM are summarized in figure 2. Mean numbers of allopreening trunk / wing and head for each dyad type and dominance of preener were separately shown in figure 2a. The best-fitted model with GLMM analysis produced the significant interaction between dyad type and dominance of preener factors and the significant main effects of these two factors (fig. 2b). Summary of GLMM outputs in figure 2b showed that more allopreening were found in M-M dyads from dominant individuals to subordinate ones. These results indicate that allopreening was not reciprocated in dyads with dominance relationships but rather occurred unidirectionally from dominant to subordinate individuals.



(b)

GLMM (poisson, log link)

dom + **dyad** + body + **dom x dyad**

Factors	*b* ± *SE*	*Wald* X^2	*df*	*p*
Dyad type				
M-M	0	-	-	-
M-F	-3.62 ± 0.13	745.2	1	<0.001
F-F	-4.65 ± 0.49	107.5	1	<0.001
Dominance				
Dominant	0	-	-	-
Tie	-1.85 ± 0.14	176.5	1	<0.001
Subordinate	-4.37 ± 0.30	207.7	1	<0.001

Figure 2. Most instances of allopreening were found to occur asymmetrically from dominants to subordinates within males. a. Mean number (± s.e.m.) of allopreening of wing/trunk and head are represented for each dyad type and dominance. *n* indicates number of dyads. b. Summary of GLMM analysis. A formula above the table shows the final model. Factors in bold letters depict the significant effects.

IV. Discussion

The results in the present study suggest two social functions of allopreening in juvenile large-billed crows. First, reciprocity of alloreening in the dyads with tie relationships supports the social bond hypothesis. Second, the asymmetrical pattern of allopreening from dominants to subordinates supports the dominance signal hypothesis.

Social bond hypothesis was supported in the dyads with tie relationships. As far as we observed for approximate 3 years, however, we did not observe any explicit cooperation, such as alliance, in the dyads with tie relationships. These reciprocal allopreening might be examined with considering a possibility of post-conflict bystander affiliation. Post-conflict bystander affiliation is known as a behavioural solution for stress reduction in group living animals, typically in primates (de Waal & van Roosmalen, 1979). Post-conflict bystander affiliations were found in other corvids (Seed, Clayton, & Emery, 2007; Fraser & Bugnyar, 2010). In the further study, it is worth to examine the possibility that individuals with tie relationships might provide allopreening one another in separate occasion after either individual receives aggressive attacks from third-party opponents.

Dominance signal function of allopreening is necessary to be investi-

gated further because our study just provides the fact of within-male asymmetrical pattern but does not reveal its functional role in the flock. If within-male allopreening indeed functions as dominance signals to inhibit the challenges by subordinates, the most dominant male (individual W) should allopreen the second dominant male (Or). However, this was not the case. Allopreening of individual W directed not to individual Or but to the most subordinate male, WW. This fact does not support the dominance signal for suppressing subordinates' challenge. In the further study, we need to examine the benefits of this asymmetric allopreening pattern for both dominant preeners and subordinate preenees.

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