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4 Within-flock Diffusion of Foraging Skills in the Large-billed Crow

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I. Introduction

Learning the skill of foraging from other conspecifics is a crucial cognitive ability of group-foraging animals to reduce the risk and cost associated with the novel resources (Giraldeau & Caraco, 2000; Laland, 2004). Given the possible asymmetry in resource competition power between individuals, past theoretical studies predicted the evolution of complex foraging strategy such as scrounger and producer tactics particularly in opportunistic generalists (Laland 2004). Although numerous studies in the past revealed that social relationships between individuals had effects on the asymmetrical diffusion of foraging skills in social animals, most studies focused on affiliative relationships such as kin (Whiten et al., 1999; de Waal, 2001; Whiten et al., 2007; van de Waal et al., 2010; Hunt & Gray, 2003; Holzhaider et al., 2010). However, little is known about the effect of competitive relationships such as dominance (Izawa & Watanabe, 2011).

In this study, we examined (1) whether or not large-billed crows were able to learn the techniques through the observation of flock members and (2) the effect of dominance relationships between demonstrator and observer as well as that of sex on inter-individual diffusion of foraging skills. To examine these issues, we conducted the observational learning paradigm with a two-action method in a semi-natural group-foraging situation.

II. Materials and Methods

1. Subjects and housing

Eighteen wild-caught subadults of large-billed crows (9 females and 9 males) were served as subjects. Out of them, eight (4 males and 4 females) and ten (5 males and 5 females) were separately flock-housed in two outdoor aviaries ($5 \times 10 \times 3$ m^3). Each of the home aviaries consisted of two same-size compartments (Fig. 1a). The daily diet and water were freely available in the aviaries. No crows were pair-bonded during the experiment.

2. Apparatus

2.1. Test box

Two wooden boxes (yellow and white) of similar size were used (Fig. 2). Each box could be opened by using two different techniques to obtain the food rewards (small pieces of meat) hidden inside. The yellow box was a cube ($15 \times 15 \times 10$ cm^3) covered by a lid at the front end of which a 10-cm gray bar was fixed as a lever for manipulation (Fig. 2a). The yellow box could be opened by following two techniques: One involved the technique of vertical manipulation such as pulling or pushing action onto the lever to move it upward (Fig. 2b). Alternative technique was horizontal manipulation such as pulling or pushing action onto the lever to slide outward (Fig. 2c). In a pilot experiment, crows showed a clear disposition to use the horizontal technique (90.1% of 61 trials with 4 crows). Thus, vertical technique was used for demonstration in the yellow-box sessions in order to dissociate observation effects from the intrinsic disposition.

The white box was a cylinder (15 cm in diameter × 10 cm high) covered by a double-layered lid, each layer of which had an opening angle of 130º (Fig. 2d). A 10-cm gray bar fixed to the centre of the upper lid functioned as a lever to manipulate the lid. In the initial state, the lid was mounted on the white box with the two openings opposite one another (i.e., 180º apart) and the food reward was placed just below the opening of the lower lid. Food rewards could be obtained by vertical manipulation of the lever, such as pulling it upwards, which resulted in removal of the entire lid (Fig. 2e). Horizontal manipulation of the lever, such as pushing, caused the upper lid to turn clockwise or counterclockwise independently of the lower lid (Fig. 2f). Food rewards could be also obtained by turning the lever clockwise or counterclockwise to match the positions of the openings on the upper and lower lids. In a pilot experiment, we found no disposition of opening technique for the white box (53.0% of 66 trials with 4 crows).

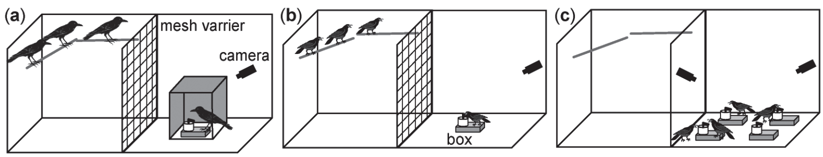

Figure 1. Schematic drawings of the experimental setup: (a) demonstrator training session, (b) observation session, and (c) test session.

For action data (on left half), the number in the bracket indicates the total number of birds that successfully opened the box by using the same technique as demonstrated. For technique data (on right half), the number in the bracket in each cell indicates the total number of birds that opened the box by either technique. Asterisks on the left denote the significant difference at the level of $p<0.01$. ns indicates no significance by two-tailed binomial tests. *NA* means that statistical test was not applicable.

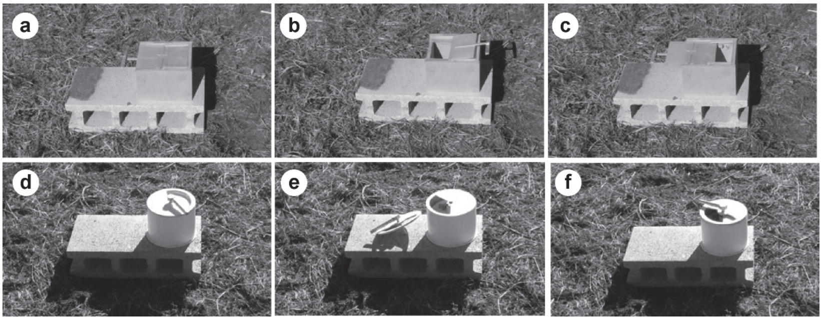

Figure 2. Two test boxes and the opening states. Both boxes could be opened using two different techniques involving either horizontal or vertical movements of the lid. (a) The initial state of yellow box. (b) An opened state by the vertical movement such as pulling / pushing up the lid. (c) Alternative opened state by the horizotal movement such as pulling / pushing outward the lid. (d) The initial state of white box. (e) An opened state by the vertical movement such as pulling / pushing up the lid. (f) Alternative opened state by the horizontal movement such as rotating clockwise / anticlockwise the lid.

2.2. Procedure

Assignment of demonstrator and observer roles

Dominance ranks of crows in each flock were determined based on the daily observation data of social interactions during September – November 2010. Win / loss outcomes in agonistic interactions were analyzed to determine the rank among flock members.

Each flock underwent two independent experiments which differed in demonstrator's dominance, box, and technique. In the Dom-demonstrator experiment, the most dominant male was served as demonstrator, while the most subordinate male as demonstrator in the Sub-demonstrator experiment. Note, however, that the demonstrators were participated in as observers in the alternative condition (i.e., the most subordinate and dominant participated as observers in the Dom- and Sub-demonstrator experiments, respectively). The other 14 crows were served as observers in the both experiments.

For flock 1, we used the most dominant as demonstrator to open the yellow box by the vertical-manipulation technique (pull / push up) in Dom experiment, while the most subordinate to open the white box by the horizontal-manipulation technique (turn clockwise / counterclockwise). The opposite scenario was given to flock 2; namely, the subordinate demonstrated to open the yellow box by the vertical manipulation (pull / push up), while the dominant demonstrated to open the white box by the horizontal manipulation (pull / push up).

Demonstrator training

Each demonstrator was trained to open the box by using specific one of the two techniques in the training compartment which was not seen from the other members in the opposite compartment during the training (Fig. 1a). To encourage the demonstrator to learn one technique, alternative lid movement was blocked by sticky tape inside the box. The learning criterion was successful opening the box within 10 min in the consecutive 8 trials in one daily session. All the demonstrators reached the criterion within 4–11 sessions.

Demonstration and test sessions

Observers were given 3 observation sessions and subsequent 20 test sessions under flock situation.

In each observation session, observers in the observation compartment were given the opportunities to observe 5 trials of successful open of a box which was presented at the centre of the demonstration compartment (Fig. 1b). Each demonstration trial was terminated when the demonstrator opened the box and ate a food reward. During the demonstration session, a mesh barrier was inserted between the compartments so that observers were allowed not to directly access the box but to see the demonstrator's behaviour.

Each test session consisted of one demonstration trial and a subsequent 20-min test period with a 10-min interval inbetween. During the 10-min interval, the experimenter removed the mesh barrier and set four boxes in the demonstration compartment for testing (Fig. 1c). Each test session was terminated when 20 min passed after the box presentation or when all the four boxes were opened within 20 min. Note that the demonstrator was also remained in the aviary during the test period and, thus, all of the flock members, including demonstrator and observers, were given the same opportunities to access the box. Behaviour of crows during the test period was video-recorded for offline analysis.

Behavioural coding

To assess the presence of emulation, we determined whether the box-opening technique of the observer in the first successful attempt matched or not to that of the demonstrator. Techniques used by each observer in each session were defined by the final opened states of the box (Fig. 2).

To examine the possibility of imitation, we investigated whether or not the observer's action in the first successful box-open matched the demonstrated actions. Actions shown by each observer were determined according to a frame-by-frame analysis of the video-recorded data. Specifically, we coded the six types of actions: 'pulling up' or 'pushing up' the lever by the bill, 'turning clockwise' or 'turning counterclockwise' the lever with the bill and 'pulling to slide outward' or 'pushing to slide outward' the lever with the bill.

III. Results

1. Dominance relationship

Strict linear dominance relationships were found among birds of both flocks (flock 1, $h' = 0.69$, $\chi^2 = 36.5$, $df = 21$, $p = 0.04$; flock 2 ($h' = 0.99$, $\chi^2 = 59.67$, $df = 20$, $p = 0.01$). In both flocks, males were dominant over females.

2. Emulation

As for the first box-open, the observers showed the technique same as demonstrated in the yellow-box experiment but did not in the white-box experiment. Table 1 shows the number of observers who used the demonstrated techniques for their first box-opening. The number of observers using the same techniques as demonstrated was significantly high for the yellow box ($p = 0.008$, two-tailed binomial test corrected by the expected probability of 0.1 for the technique of ‘lift’) but not for white box (*ns*, two-tailed binomial test). In addition, the number of observers using the same techniques as demonstrated was significantly high in the subordinate-demonstrator condition ($p = 0.008$) but not in the dominant-demonstrator condition. These results suggest that crows are able to emulate the demonstrated technique and that crows are more likely to use the emulation when demonstrators are subordinate.

3. Imitation

The actions of the observers using the same techniques as demonstrated did not match the demonstrators’ actions. The results are summarized in table 1. Although statistical test was not applicable due to the small number in each

Table 1. The numbers of observers showing the same actions (left) and technique (right) as demonstrated in the first successful box-opening.

	# of matched action			# of matched technique		
	white	yellow	total	white	yellow	total
Dom	0(1)	1 (1)	^{NA}1 (2)	1(4)	1 (3)	^{ns}2 (7)
Sub	0(3)	3 (4)	^{ns}3 (7)	3(6)	4 (6)	*7 (12)
total	^{NA}0(4)	^{NA}4 (5)	4 (9)	^{ns}4(10)	*5 (9)	9 (19)

cell, there was no clear evidence that the observers showed the same actions as demonstrated. These results, thus, do not support the imitation of crows in their first box-open attempts.

4. Effects of demonstrator's dominance on emulation across test sessions

The observers used the same technique as demonstrated more often when the demonstrator was subordinate than dominant through the 20 test sessions. Figure 3 shows the probability of the observers' use of the same techniques as demonstrated across the 20 test sessions. Although the trial-and-error learning could not be discarded for the analysis of population data based on the repeated test sessions, the significant bias toward the demonstrated techniques across the 20 test sessions were found in the individuals showing the same techniques as demonstrated in the first box-open. To examine the effect of demonstrator's dominance on the use of observers' techniques, GLMM analysis with logit-link function and Poisson error distribution was performed for the observer's technique (same = 1, different = 0) as the dependent variable and the demonstrator's-dominance (dominant = 0, subordinate = 1) and box-type (white = 1, yellow = 0) as fixed factors with considering individuals as a random effect. The best-fitted model re-

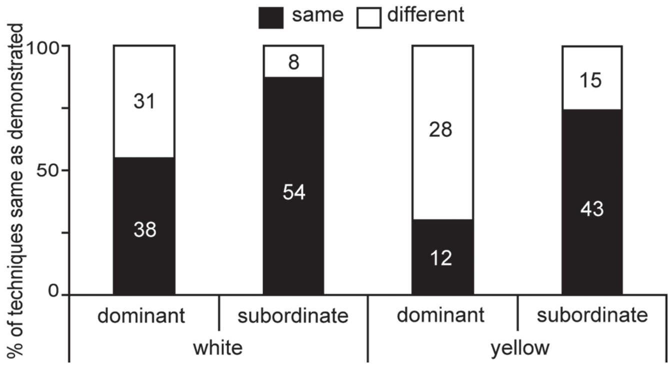

Figure 3. Probability of the observers' use of the techniques same as demonstrated through the 20 test sessions. In the Sub-demonstrator experiment, the observers showed the techniques same as demonstrated with higher probability than in the Dom-demonstrator experiment. The number in each graph exhibits the total number of successful box-open by the all observers through the 20 test sessions. See text for the statistical details.

vealed the significant main effects of dominance factor ($p < .001$, $z = 3.24$, 1.75 ± 0.54, $\beta \pm$ S.E.) and box factor ($p < .005$, $z = 2.66$, 1.48 ± 0.56), indicating the higher probability of using the demonstrated technique in the Sub-demonstrator condition. These results suggest that crows learned the foraging skills more preferably from subordinates than from dominant flock members.

IV. Discussion

The present results revealed the ability of the wild-caught large-billed crow to emulate the foraging techniques used by group members. Our study also showed that the information diffusion occurred preferably from subordinates to dominants but less for the reverse.

According to the results of the involvement of emulation in the first attempt and across 20 sessions, foraging skill diffused from subordinate to dominants but not from dominants to subordinates. Two possibilities could account for the asymmetrical social diffusion. One possibility is the poor ability of subordinate crows to emulate in comparison to that of dominants. However, the behavioural data in this study can discard this possibility. Although data was not shown here, moderately subordinate individuals successfully emulated the demonstrated skills from the most subordinate demonstrator. Further more, one subordinate male exhibited emulation even from the dominant demonstrator. These facts indicate that subordinate individuals have the capacity of observation learning of the demonstrated techniques. This eliminates the possibility of the poor social-learning ability of subordinates.

Another possibility is that dominant demonstrator inhibited the access of subordinates to the box even though the subordinates observationally learn the skills. This possibility is plausible because the boxes were often occupied by the dominant demonstrator even in the test sessions. These facts suggest the most dominant male could have an inhibitory effect on the other subordinate group members. Therefore, it is likely that asymmetry of inter-individual diffusion could be caused by the inhibitory effect of the dominant to limit the opportunity to show the socially-learned techniques by the subordinate individuals. Within-flock diffusion at the individual level is necessary to analyses in the next study.

References

de Waal, F. B. M. (2001) *The Ape and the Sushi Master: Cultural Reflections of a Primatologist*. New York, NY: Basic Boocks.

Giraldeau, L-A., and Caraco, T. (2000) *Social Foraging Theory*. Princeton, NJ: Princeton University Press.

Holzhaider, J. C., Hunt, G. R., and Gray, R.D. (2010) Social learning in New Caledonian crows. Learning & Behavior, 38, 206–219.

Hunt, G. R., and Gray, R. D. (2003) Diversification and cumulative evolution in tool manufacture by New Caledonian crows. Proceedings of the Royal Society B, 270, 867–874.

Izawa, E-I., and Watanabe, S. (2011) Observational learning in the large-billed crow (*Corvu macrorhynchos*): effect of demonstrator-observer dominance relationship. Interaction Studies, 12, 281–303.

Laland, K. L. (2004) Social learning strategies. Larning & Behavior, 32, 4–14.

van de Waal, E., Renevey, N., Favre, C. M., and Bshary, R. (2010). Selective attention to philopatric models causes directed social learning in wild vervet monkeys. Proceedings of the Royal Society B, 277, 2105–2111.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G.., Wrangham, R. W., and Boesch, C. (1999) Cultures in chimpanzees. Nature, 399, 682–685.

Whiten, A., Spiteri, A., Horner, V., Bonnie, K. E., Lambeth, S. P., Schapiro, S. J., and de Waal, F. B. M. (2007) Transmission of multiple traditions within and between chimpanzee groups. Current Biology, 19, 1038–1043.