Repeated environmental change mitigates inter-individual inequal food gain in a group foraging experiment of crow

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Abstract

Animal group foraging produces unequal distributions of food gains among participants because of individual differences, such as dominance rank. However, external environmental factors, such as fluctuation of food spatial distribution over time, may mitigate the impact of social features on food acquisition. Earlier experimental studies focused on a group's internal environment or were conducted in stable and unchanging environments. Here, we investigated how environmental fluctuations affect food acquisition at group and individual levels in captive large-billed crows (*Corvus macrorhynchos*) by changing the relationship between feeding sites and food quantity. We found that foraging efficiency and food distribution equality initially declined after environmental changes, gradually increased, and improved with repeated long-term environmental fluctuations. The influence of sex was found, while that of dominance rank was not. The present results provide the first experimental evidence to suggests that environmental fluctuations mitigate inequal food gain among individuals in group foraging.

Keywords: dominance rank, environmental fluctuation, group foraging, inequality, large-billed crows

1. Introduction

Inequality is a defining feature of animal society, including human society [1–3]. Animal groupings benefit individuals by efficiently finding potential predators [4,5] and food sources [6]. However, the cost of competition for scarce resources, such as habitat, mating opportunities, and food resources, comes with the grouping of individuals. This leads to unequal resource acquisition among group members because of different social attributes and phenotypes, such as kinship, age, sex, and dominance [7].

In group foraging animals, unequal food acquisition occurs among individuals because group members can compete for resources due to the uncertainty and finiteness of food distribution in space and time [8,9]. Dominance, which is thought to be based on an individual's resource-holding potential (RHP), is a significant factor contributing to inter-individual inequity in food acquisition [10,11]. Individual variations in RHP determine the relative priority of access to resources such as food, leading to the formation of dyadic dominant or subordinate relationships and dominance rankings within a group.

Both theoretical and empirical studies have explored individual variations in food gains related to dominance. Theoretical studies that used the game theory approach have proposed a stable strategy in group foraging in which subordinates act as "producers" to explore and find food, whereas dominants take the "scroungers" role to exploit the food produced by subordinates [12,13]. Several empirical studies have supported this theoretical suggestion. A field experiment on group-foraging capuchin monkeys (*Cebus apella*) found that subordinates took on a "producer" role in discovering and consuming new foods. However, their advantage in using the resource is only transitory because dominants monopolize the food once they arrive at the location by following the subordinates. Varying dominance-based tactics result in varying food gains; dominants gain more food than subordinates [14]. Similar dominance-associated differences in food gain have been found in group-foraging birds such as geese (*Branta leucopsis* [15]) and corvids (ravens, *Corvus corax* [16]; northwestern crows, *Corvus caurinus* [17]; Mexican jays, *Aphelocoma ultramarina* [18]).

Individual differences in food acquisition have been linked to both intrinsic factors such as dominance and extrinsic environmental factors such as the spatial distribution of food [19]. A previous study that used a foraging experiment on Ruddy turnstones (*Arenaria interpres*) found that dominants interfered with subordinates and gained more food when food was concentrated in one location. In other settings, however, the amount of food obtained did not differ between dominants and subordinates, as the same amount of food in the clumped treatment was disseminated throughout the experimental room [20].

The availability of food resources in the natural environment can vary in many ways, such as seasonal changes in foraging patches and different types of accessible food [21,22]. Even without such factors, repeated foraging at the same site reduces food availability, forcing foragers to relocate to another site that may offer food. Food at a previous foraging site may recover or increase because of the absence of consumption pressure when foragers visit other areas. Consequently, foragers must constantly determine whether to stay at their current location or go to other locations throughout their daily lives [23]. In group foraging, such staying-or-leaving decisions cannot be made only by individual foragers because inter-individual competition for the use of food-abundant locations arises and forces subordinates to leave other food-uncertain locations [13,14,16].

Unequal food gain among individuals associated with dominance has been suggested based on group-foraging experiments in stable and constant environments, such as food locations and amounts, over time. However, it is unclear whether uneven food gain among individuals in group foraging is facilitated, weakened, or maintained in a fluctuating environment of spatial distribution of food resources over time.

Crows and ravens are suitable for investigating this issue because they are known to forage in groups [24]. They also use producer or scrounger tactics while foraging depending on the dominant position, which results in unequal food acquisition among individuals [16,17,25]. Large-billed crows (*Corvus macrorhynchos*), the subjects of this study, form linear dominance hierarchies in captive groups [26, 27], where males are dominant over females.

At the group level, we measured the number of individuals successfully foraging and the time it took to search for and consume food to assess group foraging efficiency in a repeatedly changing environment. In addition, we used the Gini coefficient to assess the inequality in food distribution within the group. The group's foraging efficiency was expected to decline temporarily after changes in the location and amount because many individuals in the group would stay and use the previously learned food-rich location, taking time to find a new food-rich location. Furthermore, we conducted an individual-level analysis to determine whether social characteristics, specifically dominance rank and sex, influenced the amount of food obtained during environmental changes. As previously reported [14,20], dominant individuals may monopolize food in stable situations; however, immediately following an environmental change, subordinate individuals, known as explorers, may discover and consume food before others. Additionally, sex may alter food preferences and the use of social information [6, 28]. Such variations may potentially influence food acquisition in the present group-foraging experiment.

Our experiments show that inequalities in food acquisition within a group with a stable linear dominance hierarchy can be reduced in the face of repeated environmental changes. These results highlight the necessity of considering external environmental influences, as well as internal group factors such as dominance rank, when studying foraging in social animals.

2. Results

In this experiment, we placed feeding boxes containing different amounts of food ("RICH," "MID," "ZERO"; Figure 1) at three different positions ("A," "B," "C") within the outdoor aviary. The relationship between each feeding box and the amount of food it contained was changed for each block (one block consisted of 10 sessions). We recorded the behaviors listed in Table 1 and calculated four behavioral indices based on these records (Table 2).

(a) Group level

We used generalized linear models (GLMs) to examine the effects of environmental changes on group foraging. Furthermore, we performed two lines of model analysis on each response variable at distinct timescales: short- and long-term effects. The short-term scale analysis focused on the immediate effects of environmental change on each foraging index between sessions. The long-term scale analysis explored the cumulative effects of repeated environmental changes on each foraging index between blocks.

(i) Short-term effects

A GLM for the number of successful foragers (the number of crows that obtained at least one food item; Table 2) found that the null model was the best, showing that environmental change had no short-term effect on the number of successful foragers ($AIC_{best(null)}$ = 265.905, $AIC_{session\ model}$ = 266.995; Table 3 and Figure 2a). The best model for foraging duration (the time taken to consume all the food; Table 2) by GLM analysis yielded the significance of the post-session compared to the pre-session with a positive coefficient, indicating that foraging duration increased immediately after the environmental change ($AIC_{best(session)}$ = 451.164, AIC_{null} = 478.993; Table 3 and Figure 2b). The best model in terms of exploration duration (the time taken to explore for food around the feed boxes; Table 2) produced a negative

coefficient for the post-session compared with the pre-session, indicating a decrease in exploration duration immediately after the environmental change ($AIC_{best(session)}$ = 634.046, AIC_{null} = 661.451; Table 3 and Figure 2c). For the Gini coefficients (a measure of inequality ranging from 0 to 1, with values closer to 1 indicating greater inequality; Table 2), the best model showed a significant effect of the post-session compared with the pre-session with a positive coefficient, indicating an increase in the Gini coefficient immediately following the environmental change ($AIC_{best(session)}$ = -117.266, AIC_{null} = -97.262; Table 3 and Figure 2d). This implies that environmental change immediately results in a skewed food distribution among individuals.

(ii) Long-term effects

A GLM analysis of the number of successful foragers over time yielded the best model, which included session and *block* variables ($AIC_{best\ model}$ =865.462; AIC_{null} = 873.937). The best model showed no significant differences during the *session.* However, a significant difference was noted in the *block* with a positive coefficient (Table 4 and Figure 3a), implying that the number of successful foragers increased across the blocks. For foraging time, the best model selected using the GLM analysis showed significant effects of *session* and *block* with negative coefficients ($AIC_{best\ model}$ = 1474.716, AIC_{null} = 1548.145; Table 4 and Figures 3b and c). This finding implies that the foraging time decreased across sessions and blocks.

The GLM analysis revealed a significant positive correlation between the exploration duration and session × block, but there were no significant effects for either session or block ($AIC_{best\ model}$ = 2220.574, AIC_{null} = 2265.159; Table 4 and Figure 3d). This finding shows that exploring duration increased throughout sessions within blocks, and the effects increased as the blocks progressed. The GLM analysis for the Gini coefficient presented the best model, with a significant negative correlation with the interaction *session × block* but no significant correlation with *session* or *block* (AIC_{best} = -450.861, AIC_{null} = -386.852; Table 4 and Figure

3e). This result suggests that the Gini coefficient declined throughout the sessions, and the effects increased as the blocks progressed, implying that repeated environmental changes reduced skewed food gains among individuals.

(b) Individual level

A GLM analysis to examine the influence of dominance rank or sex on food gain produced the best model that included a significant negative correlation with *block* × *sex* but no significant correlation with either *sex* or *block* (AIC_{best} = 7549.073, AIC_{null} = 7560.038; Table 5, 6 and Figure 4). Stratified GLMs applied separately on male and female datasets produced the best model for males ($AIC_{best(block)}$ = 3712.150, AIC_{null} = 3712.712), and females ($AIC_{best(block)}$ = 3787.882, AIC_{null} = 3789.328; Table S1), both of which included blocks but showed no significant correlations. These findings indicate that the number of food items decreased in males but increased in females, with females gaining more food than males in later blocks.

3. Discussion

In this study, we examined how an experimentally fluctuating environment, specifically repeated changes in the relationship between food quantity and location, affected group and individual foraging performance in a captive group of large-billed crows.

We used two indices of foraging efficiency at the group level: foraging duration, which is the time taken to gather all the food, and exploration duration, which is the time from the first staying boxes to the last opening cups. Foraging duration increased briefly immediately following environmental changes but decreased as the sessions progressed. Furthermore, a long-term decline was seen. Exploration duration increased with each session, followed by fluctuations in all blocks. This result suggests that following the environmental changes, the subjects gradually began to postpone opening the cups with the ZERO condition. In addition, the exploration duration in the sessions after the changes (first and second sessions)

183 decreased with the block, implying that the time needed to learn a new association between
184 box locations and food quantities after the changes decreased with repeated changes.
185 Overall, foraging efficiency declined following environmental changes. However, as the
186 changes were repeated, individuals became more efficient at learning new associations
187 between location and food quantity with each change, resulting in a long-term increase in
188 foraging efficiency.

189 Changes in the Gini coefficient showed that inequality in food acquisition increased briefly
190 immediately after environmental changes. This implies that participants that could access
191 the newly abundant feeding boxes immediately after the changes could temporarily acquire
192 more food. However, given the number of successful foragers did not alter significantly
193 before and after the changes, extreme monopolization is unlikely to have occurred. At the
194 individual level, no previously assumed effect of social dominance on food acquisition was
195 found. Notably, often subordinate females increased their food intake in subsequent blocks.
196 As environmental changes repeat, subordinate individuals gain access to food, hence
197 lowering food inequality. This decrease in inequality could be attributed not only to the
198 subjects' adaptation to the repeated experiments, but also to the gradual development of
199 individual foraging strategies, which leads to increased foraging efficiency and role
200 differentiation [13,29]. These findings highlight the importance of factoring in external
201 environmental variations in experimental designs, which have been largely disregarded in
202 previous studies, and provide valuable insights for future group-foraging experiments.

203 We experimentally manipulated the external environment of the foraging group;
204 nonetheless, the group members remained unchanged. Previous studies on zebra finches
205 (*Taeniopygia guttata*) involved dividing stable groups and repeatedly introducing short-term
206 disruption events by reuniting them [30]. This experimental manipulation resulted in
207 recurrent short-term changes in the internal environment of the group, as well as a long-
208 term decline in foraging efficiency. These experiments contrast with those of our study, in

which repeated short-term changes in the external environment were observed. In our study, the group members stayed constant and stable, which may have aided them in using consistent social information from others. Individuals in a group have varying foraging habits [29, 31, 32]. Those unable to adapt to environmental changes on their own may rely on information from others, individuals who can adapt quickly, allowing group foraging efficiency to be maintained. Thus, our results highlight the need to establish a stable society even at the expense of inequality in ever-changing environments.

The spatial distribution and feasibility of monopolizing resources are significant factors [20, 33]. The food quantity and feeding boxes used in this study may make defense or monopolization difficult or cost ineffective. With 16 food items available to 10 individuals, the expected food acquisition per individual was less than 2 items. All foods were typically acquired within approximately 10 s in the subsequent trials. Furthermore, the feeding site could accommodate a maximum of five to six individuals at a time. In such situations, attempts to scrounge by chasing away other individuals may result in the loss of food to others. Therefore, the role of dominance rank as a determinant of food acquisition may be limited in specific situations. For example, in wild vulturine guinea fowl *(Acryllium vulturinum*), dominant individuals exclude subordinate individuals from feeding patches through agonistic interactions. However, displaced subordinates lead the group's departure from those patches, thus pulling dominant individuals to follow and abandon the feeding patch. [34]. In changing environments, cooperation with other individuals becomes critical, and dominant individuals may be unable to monopolize food because of the inherent social dynamics. Consequently, we should re-evaluate the role of dominance rank in food acquisition by considering the current status of resources in the environment, their changes, and the subsequent interactions within the group.

Individuals from social animal groups have a variety of characteristics [7]. In this study, sex

was selected as a biological and social characteristic influencing food acquisition. It has been proposed that females are more prone than males to use information from other individuals, which could be useful in a changing environment [6]. From the perspective of motivation for food, it has been observed that females have a stronger preference for palatable foods, and the use of cheese, which is highly preferred by the participants, may have influenced the results [28]. While this study focused on individual social characteristics, it would be useful to investigate social networks among individuals [19, 29]. Social networks are regarded as "relational wealth," a key factor influencing longevity and other aspects of animals, including humans [1,3,35].

Repeated short-term environmental changes caused a gradual decrease in the Gini coefficient. As frequent and intense climatic changes are likely to have prevented resource monopolization and promoted egalitarian societies in early human societies [2], short-term environmental changes may reduce inequality in social structures. The similarity between this and our results suggests that common mechanisms may underpin the formation of inequality across humans and other animal societies. Future research on group foraging should consider both internal and external social factors, as well as their interactions. This comprehensive approach may lead to a deeper understanding of the dynamics of social animal groupings.

In conclusion, we showed that repeated environmental changes can mitigate inequalities in resource acquisition within a group with a stable linear dominance hierarchy. Our findings suggest that group foraging research should consider the effects of external environmental factors and their fluctuations, as well as internal factors such as dominance rank. Researchers can better examine the effects of external environmental changes on group foraging dynamics by including and modifying them experimentally. In addition to field studies, future research using methodologies similar to this study could further investigate

259 the mechanisms that cause inequality in animal societies, including humans, and provide
260 deeper insights into the processes that lead to inequality within social groupings.
261

262 ## 4. Methods

263 ***(a) Animals***

264 We used 10 juvenile large-billed crows (five males and five females) aged 2 years, weighing
265 between 640 and 820 g. Sex was identified by analyzing DNA from blood samples. The birds
266 were captured as free-floater yearlings in the Yokohama and Kamagaya areas from October
267 to December 2022, with authorization from Japan's Ministry of the Environment (license no.
268 041454056). No individuals were paired during the experimental period. The captured birds
269 were group-housed in an outdoor aviary of 5 × 10 × 3 m. The aviary had sufficient wooden
270 perches for all the birds to perch at the same time, and tubs of water were supplied for
271 drinking and bathing. Slight food deprivation, specifically no food 1 h before the start of daily
272 sessions, was used to encourage the crows to forage in the experimental setting. Except for
273 deprivation and during experimental trials, food (dried dog food, eggs, and vitamin and
274 mineral supplements) was always available in each compartment. All experimental protocols
275 and housing conditions followed the Japanese National Regulations for Animal Welfare and
276 were authorized by the Animal Care and Use Committee of the Keio University (No. A2022-
277 348).
278

279 ***(b) Dominance rank assessment***

280 *(i) Observations of agonistic interactions*

281 Before starting the group foraging experiment, the dominance ranks of individuals in the
282 group were established using social interaction data collected through daily observations
283 from April to June 2023. Daily observations based on video recording were performed using
284 two omnidirectional video cameras (PIXPRO sp360 4 K; Eastman Kodak Co., Rochester, NY,

USA), which were placed at the center of the aviary ceiling to capture the entire space, including perches and floors, and to allow us to collect all social interactions. Video recordings were conducted for 30 min, twice a day, from 8:00-9:00 and 14:00-15:00. A researcher (M. T.) used the behavior coding software BORIS version 7 [36] to code agonistic interactions offline from video-recorded data. The dominance rank was determined using a total of 8.5 h of video data. We defined an agonistic interaction as a submission display (submissive begging) in which the recipient avoids or retreats from the antagonist's aggressive behavior. Aggressive behaviors include pecking, kicking, and displacement techniques, while submissive behaviors include avoiding and retreating [26, 27]. In each agonistic interaction, the bird that demonstrated submission, avoidance, or retreat was deemed the loser, whereas the other bird was the winner. We noted the winners and losers, as well as the identities of the combatants.

(ii) Determination of the dominant rank of the group.

Following confirmation of the linearity of the dominance hierarchy [37], the I & SI approach [38] was used to identify the dominance rankings of individuals in the experimental group. In each dyad, the individual winning ≥ 66% of their agonistic interactions was treated as dominant, whereas the other was considered the subordinate. In dyads with just four or three agonistic interactions in daily observation data, the individual who won ≥ 75% or 100% of the interactions was considered dominant. For dyads that did not match the winning (losing) rate criteria, we considered the birds' relationship to be tied with no dominance. If two or fewer agonistic interactions were seen in a dyad, the relationship between the two birds was deemed unknown.

A dominance relationship matrix was generated by allocating 1 and 0 to the dominant and subordinate individuals in a dyad, respectively, and 0.5 to two individuals with a tied relationship. We quantified the linearity of the dominance hierarchy using h', an index of rank linearity [37]. The chi-square test was used to determine the statistical significance of

linearity at a 1% level. Following confirmation of linearity, the dominance ranks of individuals were computed using the I & SI procedures [38]. A total of 458 agonistic interactions were recorded, with all 45 dyads showing unambiguous dominance patterns. We found significant linearity in dominance ranks across the 10 individuals ($h' = 0.95$, $\chi^2 = 61.26$, $df = 81$, $p < 0.01$). Using the I & SI method, we determined the ranks of 10 birds with only one inconsistency between the 4th- and 7th-ranked males, whose dominance relationship was reversed concerning their ranks (the 7th-ranked male was dominant over the 4th-ranked male).

(c) Experimental procedure

(i) Feeder box and experimental design

To examine the effect of fluctuated environments, specifically repeated changes of the spatial food distribution~~,~~ on foraging performance, we conducted a group foraging experiment in which the relationship between food amounts (none, middle, and rich) and locations was changed regularly over three months from October to December 2023. The experiment took place in one half of a home aviary, which was separated by a mesh door (5 × 5 × 3 m; Figures 1a and b).

Artificial foraging patches were created using three identical plastic feeder boxes in the shape of a regular octagonal prism (side length, 16.6 cm; height, 10.0 cm) mounted on an octagonal plate (side length, 24.9 cm). At the top of each box, 16 holes (4.5 cm in diameter) were placed at 6-cm intervals to accommodate a plastic food cup. At the start of the trial, the top of each cup was covered with opaque aluminum foil to prevent the crows from seeing the interior which contained either a piece of cheese (0.3 g) or nothing (empty), depending on the box condition. The subject crows had to break the foil with their beaks to obtain food.

Each experimental trial included three feeder boxes placed 2.5 m apart on the floor of the aviary (box locations A, B, and C in Figure 1a). The boxes at these locations were identical in shape and color, but the amount of food contained in the cups (the different conditions) varied, such as “RICH,” where 12 out of 16 cups contained food (Figure 1c), “MID,” where four out of the 16 cups contained food, and “ZERO,” where no cup contained food. In the RICH and MID conditions, the cups containing food in each box were arranged in a pseudo-random manner between trials.

The experiment included 240 trials divided into six blocks of 10 sessions (One session consisted of four trials). We implemented two sessions (2 × 4 trials each day) from 9:00−12:30 and 13:30–16:30 and the intervals between successive daily two sessions were ranged from 0 to 3 days. The relationship between food condition and box locations rotated clockwise over the blocks (Figure 1d). Crows in each block had 10 sessions (5 days × 8 trials) under stable conditions for five days. However, after the end of each block, the food conditions were changed for the first trial of the next session without any signals. Each trial began when the researcher (Y. N.) removed the covers from the three feeder boxes, allowing the crows to forage, and exited the experimental room. The trial was terminated 3 min after it began when the researcher removed the boxes. The inter-trial interval was approximately 20 min.

(ii) Coded behavior during the experiment

The behavior of the crows during the trials was video-recorded using an omnidirectional camera (SP360-4K, Kodak) on the ceiling of the aviary and three video cameras (HD CX535, Sony, New York, NY, USA) placed outside the aviary (Figure 1b). The coded behaviors were "*staying on a box*", "*opening a cup*" and "*gaining a food*" (Table 1). “Opening a cup" was coded up to a maximum of 48 times per trial (three boxes × 16 cups). Crows that investigated an already-opened cup were not considered. "Gaining a food" was recorded up to 16 times (RICH: 12 cups, MID: 4 cups). We recorded the individual identity and timing of

these actions. The time resolution for behavioral coding was approximately 0.3 s based on the video frame. The software BORIS v. 7 [36] was used for behavior coding.

(d) Analysis

Based on the observed behaviors, we derived indices of group foraging for each trial, such as "*number of successful foragers,*" "*foraging duration,*" and "*exploring duration,*" to evaluate foraging efficiency at the group level (Table 2). The "number of successful foragers" was defined as the number of crows that obtained at least one food item (one piece of cheese) in a trial. "Foraging duration" was defined as the time between the first “opening a box” and the final (16th) event of “gaining a food," regardless of box condition or individual. "Exploring duration" was defined as the time between the first “staying on a box” event and the 48th "opening a cup." In circumstances where not all 48 cups were opened for 3 min, we calculated the time from the initial “staying a box” event to the last "opening a cup" event. In addition, we estimated the Gini coefficient to evaluate the degree of inequality in food gain distribution among individuals. The Gini coefficient was determined using a Lorenz curve [39] derived from the cumulative ratio of participants to food gains, which ranged from 0 (not skewed) to 1 (highly skewed). We calculated and adjusted the Gini coefficient to account for the small sample size using the "ineq" R package [40]. Out of 240 trials, 18 were excluded from the analysis: one due to video recording issues, one where not all the food was consumed, and 16 from the seventh to tenth sessions of the sixth block due to individual withdrawal.

(i) Group-level analysis

We performed GLMs independently on group foraging indices as response variables, namely the number of successful foragers (with Poisson error distribution and log link function), foraging duration, exploration duration (with Gamma error distribution and log link function), and Gini coefficient (with Gaussian error distribution and identity link function).

The short-term scale analysis examined the immediate effects of environmental change on each foraging index between sessions; thus, GLMs included a session component as a fixed effect. For this short-term analysis, we divided the sessions into three types: "*pre-change session,*" which included the 10th (final) sessions of blocks as the data just before the environmental change; "*post-change sessio*n," which included the first sessions of blocks as the data just after the environmental change; "*post-change + 1 session,*" which included the second sessions of blocks as the data following the post-change session. The long-term scale analysis, on the contrary, investigated the cumulative effects of repeated environmental changes on each foraging index between blocks; therefore, GLMs included a block factor as a fixed effect.

(ii) Individual-level analysis

The effects of environmental changes and individual social characteristics, such as dominance rank and sex, on foraging performance were examined. We used GLMs, with the number of food gains per individual as the response variable, session number, block number, dominance rank, sex, and their secondary interactions as independent variables with negative binomial error distribution and log link function. To address multicollinearity, rank and sex were not included in the same model. Instead, in the individual-level model selection, the best model was chosen from those that included either rank or sex.

All these model analyses were conducted using the statistical software R v. 4.3.2 [42]. Before constructing the models, we checked for overdispersion of the response variable using the "performance" package [43]. We used Akaike's Information Criterion (AIC), based on smaller is better, to select the best model. Model selection was performed using the "MuMIn "package [44] and probabilities and confidence intervals were estimated using the "ggeffect" program [45] with a significance level of 0.05.

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Data availability

The data generated and analyzed during this study are available from https://doi.org/10.6084/m9.figshare.27124326.v2 .

Example videos of behavioral experiments are also available from https://doi.org/10.6084/m9.figshare.27124350.v1 (pre-session), https://doi.org/10.6084/m9.figshare.27124344.v2 (post-session), https://doi.org/10.6084/m9.figshare.27124356.v1 (post + 1 - session).

Code availability

The R script with all the code used during this study is available in https://github.com/2ki2ki/crow_RepEnvChange/tree/main .

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Author contributions (mandatory)

Y.N.: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

M.T.: Validation, Formal analysis, Investigation, Data curation.

E-I.I.: Writing – review & editing, Resources, Validation, Supervision, Project administration, Methodology, Investigation, Data curation, Funding acquisition, Conceptualization.

Competing interests (mandatory)

We declare we have no competing interests.

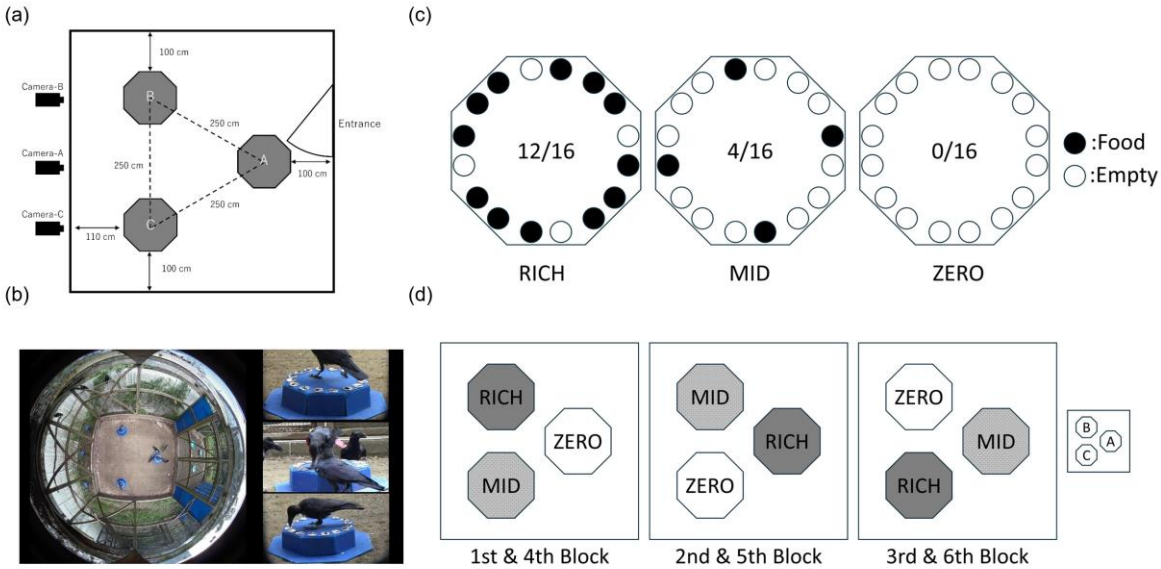

Figure 1. Experimental settings. (a) Feeding boxes (A, B, C) were place at three locations on the floor of the aviary. (b) Bird behaviors video recorded from above with a spherical camera and from the sides with three handy cams outside the aviary. (c) The number of cups containing food varied depending on the box condition: 12 cups in RICH, four cups in MID, and 0 cups in ZERO. The positions of food-containing cups in each box were pseudo-randomly varied between trials. (d) Box conditions at the three locations were maintained within blocks and moved to the next location with a clockwise direction between the blocks.

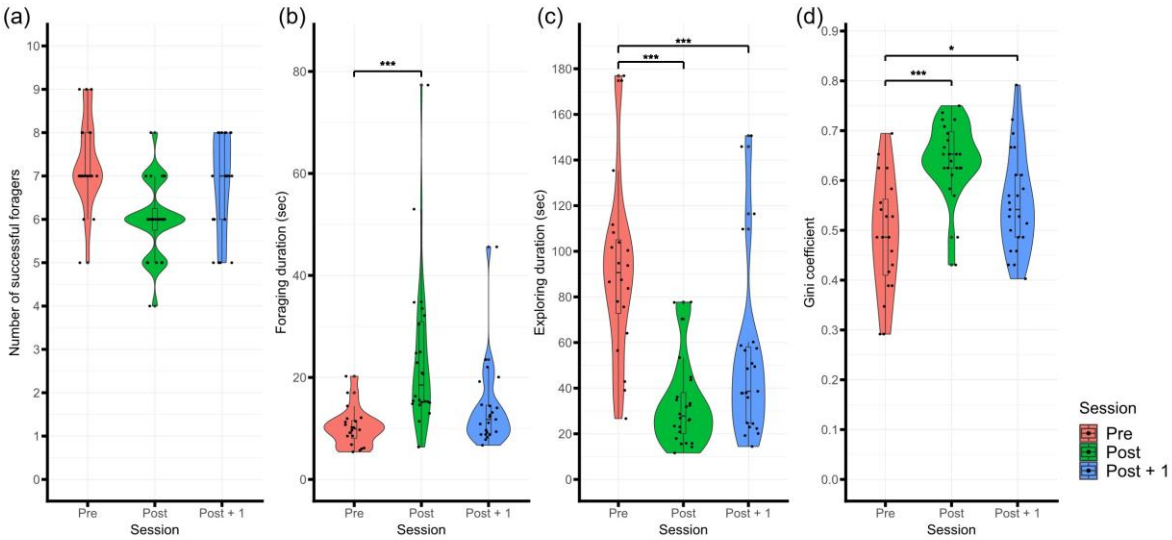

Figure 2. Short-term changes after environmental fluctuations. (**a**) No short-term effect was observed in the number of successful foragers. (b) The time required to consume all foods at each trial increased. (c) The time to open cups, including the ZERO condition box (without food), increased. (d) The inequality of food distribution increased. Pre: the 10th session of each block (immediately before fluctuations). Post: first session of each block (just after changes). Post + 1: second session of each block. Plots show the data at each trial. Asterisks indicate significant differences (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).

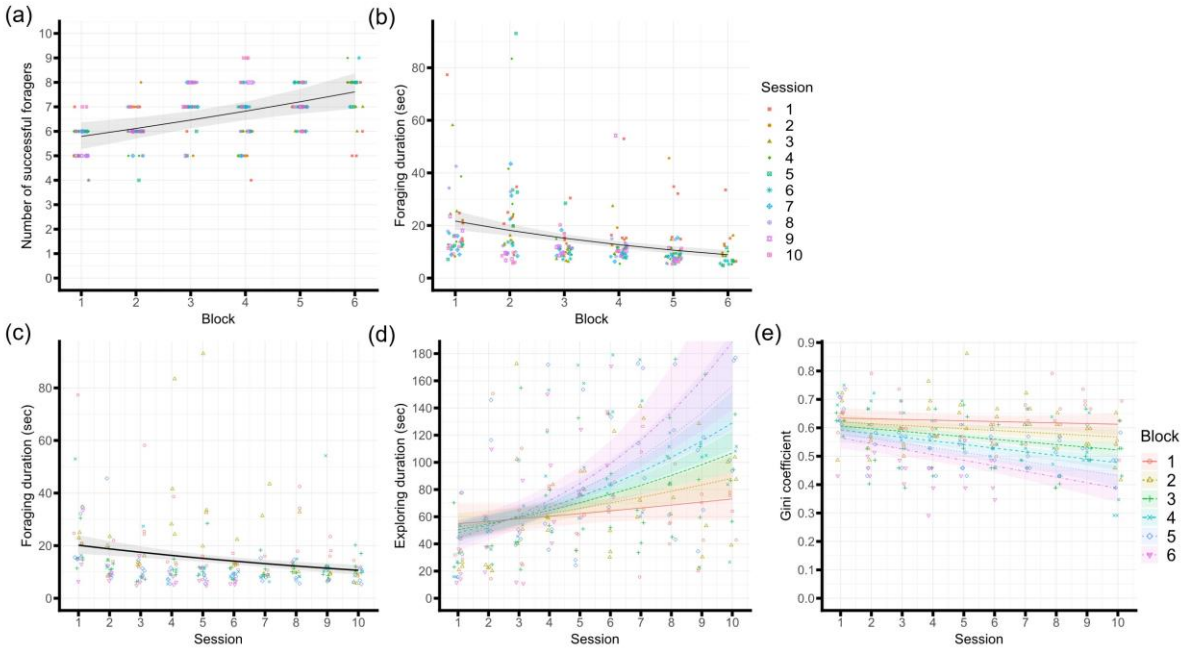

Figure 3. Long-term changes after environmental fluctuations. (a) As the blocks progressed, so did the number of successful foragers, with more individuals acquiring at least one food at each attempt. (b) The duration of foraging was reduced as the experiment advanced. (c) The time to consume all foods at each trial decreased as the sessions progressed. (d) The time to open cups increased as the session progressed. This effect became more marked with the passage of blocks. (e) The reduction of inequity in food distribution with session advancement became more pronounced as the blocks progressed. Plots show the data at each trial with colors indicating (a)(b) sessions, (c)(d)(e) blocks. The regression lines show the predicted value of the best model. The shaded areas around the lines indicate a 95% confidence interval.

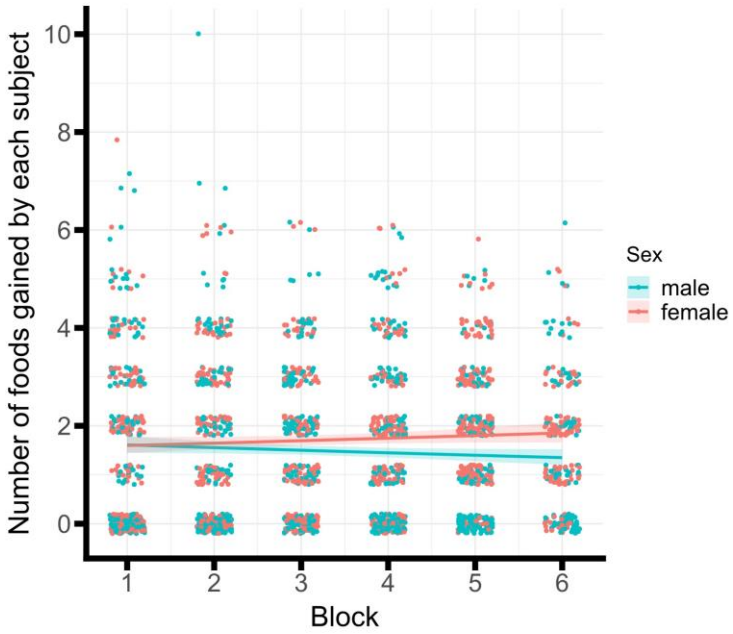

Figure 4. Effects of subjects' sex on the number of food items acquired by each subject. As the blocks progressed, the amount of food consumed by females surpassed that of males. The jitter plots show the data of each subject by trial. Regression lines show the predicted values of the best model. Shaded areas around the lines indicate a 95% confidence interval.

Table 1. Coded behaviors

Behavior	Definition
Staying on a box	Touching a feeder box including the bottom plastic board by any part of a bird's body (i.e., bill or foot).
Opening a cup	Breaking a lid of a cup by pecking.
Gaining a food	Picking up a food from the cup contained food.

Table 2. Indices of group foraging

Index	Definition
Number of successful foragers	The number of individuals that gained one or more food(s) in a trial.
Foraging duration	The duration from the first “opening a box” to the last "gaining a food" event in a trial. The individuals involved in the events were not considered.
Exploring duration	The duration from the onset of the first "staying on a box" event to the last "opening a cup" in a trial. The individuals and food gain involved in the events were not considered.
Gini coefficient	A measure of inequality in food-gain distribution, calculated from the Lorenz curve [39] obtained from the cumulative ratio of the number of subjects and food gains. This index ranged between 0 and 1.

Table 3. Outputs of the best model from a GLMs in short-term effect analysis

Index	Variables	Estimate	S.E.	Test Statistic	*p*
Number of successful foragers					
	Intercept	**1.898**	**0.047**	***z* = 40.125**	**< .001**
Foraging duration					
	Intercept	**2.328**	**0.124**	***t* = 18.819**	**< .001**
	Session				
	Post	**0.855**	**0.167**	***t* = 5.103**	**< .001**
	Post + 1	0.314	0.169	*t* = 1.854	0.068
Exploring duration					
	Intercept	**4.523**	**0.133**	***t* = 34.004**	**< .001**
	Session				
	Post	**-1.014**	**0.180**	***t* = -5.629**	**< .001**
	Post + 1	**-0.535**	**0.182**	***t* = -2.940**	**0.005**
Gini coefficient					
	Intercept	**0.490**	**0.022**	***t* = 22.555**	**< .001**
	Session				
	Post	**0.153**	**0.029**	***t* = 5.207**	**< .001**
	Post + 1	**0.066**	**0.030**	***t* = 2.237**	**0.029**

The "Session" term compared the sessions just before the environmental change ("Post" session: the 10th sessions of blocks) with the session after the changes (Post: the 1st sessions of blocks) and the session after that (Post + 1: the 2nd sessions of blocks). The number of successful foragers was analyzed using Poisson error distribution and log link function. Foraging duration and exploration duration were analyzed using Gamma error distribution and log link function. Gini coefficient was analyzed Gaussian error distribution and identity link function. Bold indicates statistically significant results.

Table 4. Outputs of the best model from a GLMs in long-term effect analysis

Index	Variables	Estimate	S.E.	Test Statistic	*p*
Number of successful foragers					
	Intercept	**1.632**	**0.085**	***z* = 19.304**	**< .001**
	Session	0.014	0.009	*z* = 1.502	0.133
	Block	**0.055**	**0.016**	***z* = 3.370**	**< .001**
Foraging duration					
	Intercept	**3.610**	**0.148**	***t* = 24.433**	**< .001**
	Session	**-0.071**	**0.029**	***t* = -4.244**	**< .001**
	Block	**-0.178**	**0.029**	***t* = -6.110**	**< .001**
Exploring duration					
	Intercept	**4.041**	**0.180**	***t* = 22.481**	**< .001**
	Session	0.006	0.030	*t* = 0.206	0.837
	Block	-0.068	0.047	*t* = -1.452	0.148
	Session × Block	**0.026**	**0.008**	***t* = 3.087**	**0.002**
Gini coefficient					
	Intercept	**0.647**	**0.028**	***t* = 22.839**	**< .001**
	Session	0.001	0.005	*t* = 0.223	0.824
	Block	-0.010	0.007	*t* = -1.401	0.163
	Session × Block	**-0.003**	**0.001**	***t* = -2.635**	**0.009**

The number of successful foragers was analyzed using Poisson error distribution and log link function. Foraging duration and exploration duration were analyzed using Gamma error distribution and log link function. Gini coefficient was analyzed Gaussian error distribution and identity link function. Bold indicates statistically significant results.

Table 5. Result of model selection in individual level

Model	Model Formula	AIC	ΔAIC	df
Best Model of Sex Model	**Intercept + Block + Sex + Block×Sex**	**7549.073**	**-**	**5**
Full Model of Sex Model	Intercept+ Block + Session + Sex + Block×Session + Block×Sex + Session×Sex + Block×Session×Sex	7554.709	5.636	9
Best Model of Rank Model (Null Model)	Intercept	7560.038	10.965	2
Full Model of Rank Model	Intercept+ Block + Session + Rank+ Block×Session + Block×Rank+ Session×Rank+ Block×Session×Rank	7571.504	22.431	9

Each model was analyzed using negative binomial error distribution and log link function. Bold indicates the best model of individual level models.

Table 6. Outputs of the best model from a GLM testing the effect of the sex on food gain

Variables	Estimate	S. E.	*z*	*p*
Intercept	**0.439**	**0.069**	**6.395**	**< .001**
Block	0.030	0.018	1.624	0.104
Sex	0.072	0.098	0.738	0.461
Block × Sex	**-0.065**	**0.027**	**-2.447**	**0.014**

Presence model was analyzed using negative binomial error distribution and log link function. Female was set at 0 for the sex variable. Bold indicates statistically significant results.