# Social plasticity across contexts in bobwhite quail

***Running title**: Social plasticity in bobwhite quail*

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## Abstract

An animal's social network centrality has been linked to social benefits. However, the inverse effect of providing benefits to conspecifics on one's centrality has received less attention. We investigated effects of foraging success, and accompanying food access provided to others, on an individual's relationships in multiple social contexts using three captive groups of bobwhite quail (*Colinus virginianus*). The experiment used a novel automated feeder and included Phase 1 where the feeder was programmed to release food for any bird, Phase 2 where only one bird (producer) was able to release food from the feeder, and Phase 3 where all birds had access again. Individual RFID detection data recorded by the feeder were used to build networks reflecting interactions in which one bird followed another to the feeder. Temporal permutations of interactions showed the producer was followed significantly more in Phase 2 compared to Phase 1, but following interactions largely decreased after the producer lost its special access to the feeder in Phase 3. Our results suggest quail can display adaptive social plasticity, are sensitive to short-term changes in the benefits provided by others and may adjust their interactions in multiple social contexts in response to changes in a foraging context.

Keywords: adaptive social plasticity, social behavior, social networks, RFID, *Colinus virginianus*

## Introduction

Social animals can receive benefits from their social relationships, but there are also costs to being social. For example, well-connected individuals in a social group may be more likely to receive information from group members (Aplin et al. 2012; Claidière et al. 2013; Kulahci et al. 2016; Jones et al. 2017; Schakner et al. 2017), but they are also more likely to be infected than more peripheral individuals (Godfrey et al. 2009; Duboscq et al. 2016; Briard and Ezenwa 2021; Xu et al. 2022). Because social relationships and social network structure are both dynamic and can shift over time, these costs and benefits of associating with particular individuals can also change over time. In particular, social network positions can change due to feedback mechanisms where individual social decisions can change the presence and strength of connections within the network (Hobson and DeDeo 2015; Hobson et al. 2019; Kulahci and Quinn 2019; Cantor et al. 2021). These feedbacks between individual decisions and social structure can result in individuals gaining benefits from their social connectedness but can also affect sociality in the opposite direction. For example, if an individual increases the benefits it provides to others in the group, those group members may then change how they interact with that valuable individual.

Recent work has shown that a variety of animals adjust their decisions to interact with group members based on the benefits those group members provide, or their social value. A useful term for this process is adaptive social plasticity (see Kings et al. 2023). Evidence for social plasticity has been found in several species. For example, in vervets (*Chlorocebus aethiops*), where females  that solved a foraging puzzle, which directly benefited their group members through providing scrounging opportunities, received increased grooming in return (Fruteau et al. 2009). Similarly, lemurs (*Lemur catta*) have been found to increase their affiliative interactions toward individuals that have successfully solved a novel foraging task (presumably to gain opportunities to socially learn the skill; Kulahci et al. 2018). Firth et al. (2016) and Heinen et al. (2022) found that songbirds tended to learn the locations of food patches from individuals with whom they had greater foraging success following a manipulation of their food access, which suggests that these foraging partners were seen as more reliable sources of information. Jackdaws (*Corvus monedula*) similarly associated more with individuals who facilitated their access to food (Kings et al. 2023). Finally, bumblebees (*Bombus terrestris*) learned to associate conspecific appearances with food rewards, staying closer to demonstrators who had the same color marks as models that were previously associated with a reward (Romero-González et al. 2020).

Although there is increasing interest in the propensity for animals to exhibit adaptive social plasticity in response to changes in the social value of their group members, there is room for a greater understanding of how widespread adaptive social plasticity is among animals. Additionally, we have a limited understanding of if animals other than primates adjust their interactions in non-foraging social contexts. Previous studies on wild birds for instance have shown changes in interactions at feeders in response to foraging manipulations but have not been able to determine whether these translate into changes in interactions away from feeders (but see Firth and Sheldon 2015). Investigating changes in both foraging and non-foraging interactions would help provide insight into what birds understand about their group members and how broad the effects of changing foraging success may be on their social structure.

We investigated adaptive social plasticity in captive groups of Northern bobwhite quail (*Colinus virginianus*). Members of this taxonomic order (Galliformes) can have relatively complex social structures despite being relatively small-brained birds. For example, Vulturine guineafowl show evidence of living in multilevel societies; (Papageorgiou et al. 2019). Domestic chickens are well-known for forming dominance hierarchies (Gottier 1968; Chase 1982; Chase et al. 2022) and junglefowl form hierarchies and show evidence of mate choice (Collias and Collias 1996; Roth et al. 2021). Previous work has also shown that Japanese quail (*Coturnix japonica*) can socially learn foraging preferences from conspecific demonstrators (Boogert et al. 2013). Bobwhite quail are seasonally social and form mixed-sex social groups in during the nonbreeding season (Yoho and Dimmick 1972; Williams et al. 2003). These social groups are characterized by high fission-fusion dynamics (Yoho and Dimmick 1972; Williams et al. 2003), which would likely require them to be able to form new relationships or adjust their relationships, potentially based on the value provided by their group members. Experimental evidence has suggested that these birds show evidence for individual recognition of calls, where female quail appeared to be able to recognize the call of their mated male (Stokes 1967), so members of this species likely have the capacity for the individual recognition required for adjusting interactions toward specific group members. Finally, bobwhite quail are relatively small birds, making them a tractable option to study in captivity, where their access to food and familiarity with others can be more easily controlled.

To test whether bobwhite quail exhibited adaptive social plasticity, we used a selective feeder to control birds' access to food and measured how changing access to the food altered social interactions in two contexts: at the food site and away from the food. We conducted a three-phase experiment. In Phase 1, all birds could activate the feeder for themselves. In Phase 2, we artificially increased the foraging success of one focal individual (hereafter called the producer) relative to its group members, making it a valuable social partner. We did this by giving the producer the sole ability to activate the feeder while other group members could only gain food by scrounging from the producer. Lastly, in Phase 3, we eliminated the producer's valuable ability by setting the feeder so that every group member could once again activate the feeder for themselves.

We investigated three main questions in this study. First, to understand whether quail exhibited adaptive social plasticity, we asked whether quail adjusted their foraging interactions toward a focal individual (producer) in response to its increased value in Phase 2. If quail were able to exhibit adaptive social plasticity in a foraging context, we predicted that the number of times the producer was followed to the feeder would increase in Phase 2 compared to Phase 1. Second, to understand how quail responded to a decrease in the producer's value, we asked whether changes in foraging interactions from Phase 1 to Phase 2 persisted when the producer no longer had a foraging advantage in Phase 3. If the temporary change in the producer's foraging success in Phase 2 was enough to cause lasting changes in its incoming foraging interactions, we predicted the number of times it was followed to the feeder would remain high in Phase 3. However, if birds were able to recognize the loss of the producer's foraging success in Phase 3, the number of follows directed toward it could decrease back to levels seen in Phase 1. Lastly, we asked whether quail adjusted their affiliative or aggressive interactions in response to changes in the producer's value across phases of the experiment. If birds understood the role of the producer in providing them access to food in Phase 2, we predicted that they would increase their affiliative interactions and decrease their aggressive interactions with that bird compared to Phase 1. Changes in these non-foraging interactions in response to changes in the producer's foraging success would suggest that the foraging success of group members is an important piece of information for quail when making social decisions.

## **Methods**

### ***Study system***

Northern bobwhite quail were housed and studied in an indoor facility at the University of Cincinnati, Cincinnati, Ohio, USA. Quail were obtained from a commercial hatchery and raised in the lab. Prior to the experiment, most birds were housed in small groups (2-3 birds) in single-sex or mixed-sex groups; three birds were housed individually due to aggression. Birds in different cages were in auditory contact, but did not have visual contact. To encourage the birds to exhibit their natural social behavior the room was on an automated 8:16 hour light:dark cycle during the experimental period to mimic the natural day length the birds would experience in the Ohio winter, when members of this species live in social groups.

We tested three groups in this experiment, each comprised of six birds from separate housing cages. The birds used in the current study were used in a previous study in our research group and therefore had previous experience with one another. As group composition was not changed between experiments, birds within each test group were equally familiar with each other, although they had been separated for 16 to 17 months since the previous experiment.

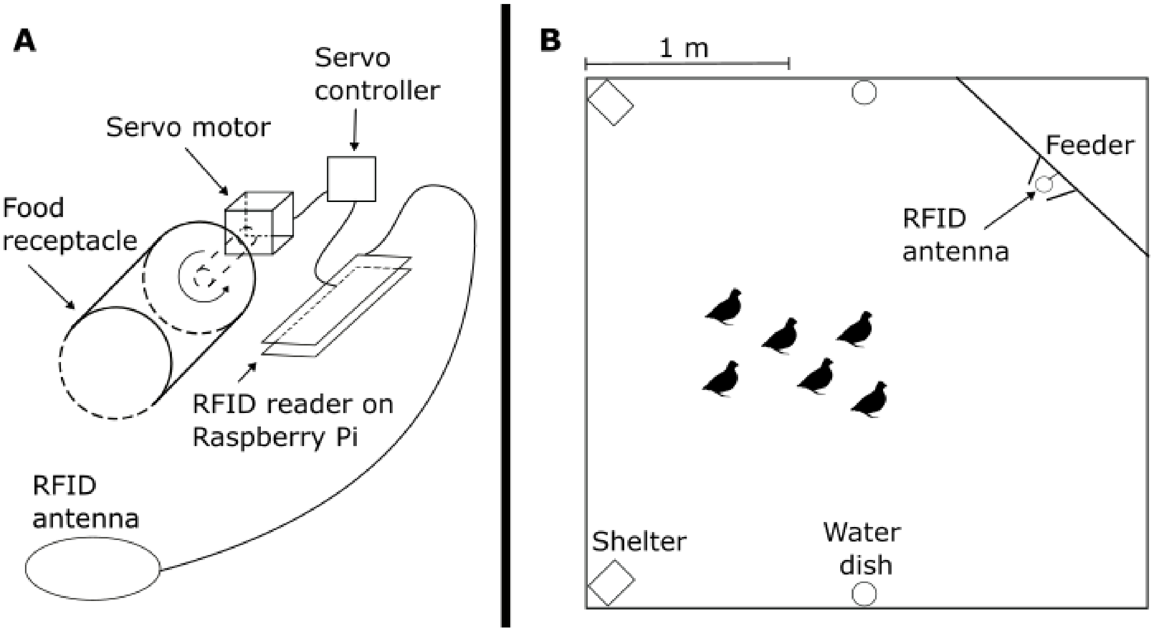

Figure 1. Diagrams showing the components of our feeder (A) and the layout of the flight pen (B). (A) We built a custom RFID-enabled feeder to control food access in the experiment. When a bird's PIT tag was detected at the antenna, the Raspberry Pi recorded the identification number with a timestamp. If appropriate, a signal would also be sent to the servo controller which caused the motor to rotate the food receptacle to drop food in front of the feeder. (B) Top-down schematic of the indoor flight pen in which experimental trials were conducted, showing the location of the feeder. The quail silhouette was made by Edwin Price and obtained from phylopic.org (https://creativecommons.org/licenses/by/4.0/).

### *Automated feeder*

We built a custom feeder (Fig. 1A) for our experiment, based in part on the feeder designed by Youngblood (2019). We equipped the feeder with a radio-frequency identification (RFID) reader and antenna (CognIoT, UK), and a Raspberry Pi computer (Raspberry Pi Zero W) to control the birds' access to food throughout the experiment. This feeder detected passive integrated transponder (PIT) tags at a resolution of one-second and automatically recorded the PIT tag identification numbers with a time stamp. The feeder was programmed to release food upon detection of any group member or only one specified group member depending on the phase of the experiment (see details below). To release food, the Raspberry Pi sent a signal to a servo controller (Pololu, USA) to activate a servo motor (SunFounder, China) which turned the food receptacle (taken from a Noodoky fish feeder), dropping some food into a dish in front of the feeder. Once food was released, the feeder could not be activated for the next five minutes, but feeder visits continued to be recorded during this time. In addition to feeder visits, the feeder also recorded the timing and identity associated with each feeder activation.

We used millet seeds in our feeder as they were a main ingredient of a seed mix provided to the birds as one of their regular forms of enrichment and was often consumed first during these presentations (SP personal observation). In addition to being a familiar food item, we found the seed mix to be preferred by the birds in a food preference test (see Supplemental Material 1). Finally, the round shape of millet compared to the other ingredients of the seed mix facilitated a more consistent food output and helped prevent blockages in the feeder mechanism.

Enough food was dropped into a receptacle at each activation of the feeder for one to three individuals to feed. When testing the amount of food released by the feeder over 50 activations, we found it released an average of 0.28 ± 0.18 SD grams of food per activation. The automated feeder was the only source of food for the birds during experimental trials.

***Experimental protocol***

Experimental trials were conducted in a 2.75 by 2.60 m indoor flight pen (Fig. 1B). We tested three experimental groups of six adult quail each (four males and two females) from September 2023 through December 2023. The experiment consisted of four phases, each five days in length: (0) training, (1) pre-manipulation, (2) experimental manipulation of foraging success, and (3) post-manipulation.

To initiate each experimental group, we caught and tagged the birds three days prior to beginning the training phase. This timing allowed the birds to acclimate to the tags and backpacks prior to the start of the experiment. Each bird was fitted with a passive integrated transponder (PIT) tag (dimensions: 0.6 by 2.6 cm; weight: 2.5 grams) with a unique identification number that we attached to each bird's left leg with zip ties. We also tagged each bird with a plastic "backpack" with one of six unique colors (white, blue, green, red, black, or yellow) to facilitate visual identification of individuals. Backpacks were rectangular cutouts of lightweight plastic (6 by 12.5 cm) with colored tape, secured to birds using elastic under the wings. Backpack attachments weighed roughly 3.45 grams (<2% of a bird's weight) and did not impede the regular movements of the birds. Similar backpack attachment styles have been used in previous studies of bird behavior (Alarcón-Nieto et al. 2018; Williamson and Witt 2021; Van Putten et al. 2025). We randomly assigned backpack colors to birds in each group. Each bird was weighed and then transferred to an individual cage in the flight pen room.

Once in these individual cages, birds within an experimental group had auditory, but no visual contact with each other. During a group's experimental period, birds were held in these individual cages outside of trials with ad libitum access to food (game bird feed) and nutrient-supplemented water, but no extra enrichment.

Every day’s trial was preceded by a 40 ± 10 minute food deprivation period to ensure birds were motivated to feed during the trial, by removing the food dish from each bird’s housing cage in the morning. To begin a daily trial, the experimenter turned off the lights in the room and transferred each bird from its individual cage to the flight pen. Birds were transferred in a random order each day. Once all six birds had been transferred, the start of a trial was marked by turning the lights in the room back on. Trials ran for a total of six hours and were video recorded top-down using one main and one backup camera (GoPro Hero 8 Black). To end each day’s trial, the experimenter ended the video recording and transferred each bird back to its individual cage where they had ad libitum access to food and water in the afternoon and overnight.

During trials, when birds were in the flight pen, the only source of food was the feeder. We conducted this trial in three phases, with an additional training phase at the start.

In Phase 0, we trained the birds to associate the feeder with food. During this 5-day training phase, a pile of millet seeds was available at the feeder throughout each day’s trial. To keep the pile of food stocked during each trial, the feeder was kept active such that it released some food when any bird was detected. The purpose of the training phase was to acclimate the birds to the flight pen, the appearance of the feeder, and the sound made by the motor upon feeder activation.

During Phase 1, all birds were able to activate the feeder when their PIT tag was within the reading distance of the RFID antenna (at a maximum of every five minutes). Thus, none of the birds were given a foraging advantage. After Phase 1, we explored the RFID detection data to choose a focal individual (producer) who would be the only individual able to activate the feeder in the next phase of the experiment. To be chosen as the producer, a bird had to meet three criteria. First, it had to have visited the feeder consistently during Phase 1 (Supplemental Fig. S2). Second, it had to be poorly connected in the Phase 1 joining network (see data collection information below; Supplemental Fig. S3). Third, it had to be a male because there could be confounding factors influencing interactions toward females.

In Phase 2, we set the feeder to release food only when the producer was detected. This allowed us to manipulate the producer's foraging success, resulting in an increase in its foraging success relative to its group members. Our goal was to determine if this increased foraging success increased the value of the producer within the group because its actions directly benefitted group members via its feeder activations.

In Phase 3, the feeder was re-set so that it released food to any detected individual and any group member could once again activate the feeder themselves.

### ***Data collection and analysis***

#### *Testing for social plasticity in foraging interactions*

RFID data were used to estimate the number of unique feeder visits made by group members and to infer "following" and "joining" relationships between birds occurring at the feeder based on how close in time two birds were detected. We defined a unique feeder visit from RFID data as a detection of an individual that was different than the previously detected individual, or that occurred after a 10 second or greater period of no detections. To infer following and joining relationships, we first identified potential leaders as birds with a feeder detection that occurred more than 10 seconds after the previous detection of any individual. Following was based on the timing of the potential leader's first reading at the feeder: the second individual was considered to have followed the potential leader if it was detected within 10 seconds of the potential leader's first detection (i.e., within 10 seconds of the potential leader's arrival at the feeder). Joining was based on the timing of the potential leader's most recent reading a second individual was considered to have joined the potential leader if it was detected within 10 seconds of the potential leader's most recent detection. Instances of following and joining were used to create separate social networks for each experimental phase resulting in three following networks and three joining networks per group. We calculated the in-strength of each bird in each network, representing how often it was followed or joined at the feeder by its group members. We focused our analyses on the following networks as following more accurately represents possible scrounging attempts by birds immediately after another group member's feeder visit.

To determine if the in-strength of the producer in the following network changed across experimental phases, we created permutation-based reference models (Hobson et al. 2021). For each directed dyad that had records of following interactions during the three experimental phases, we randomized the phase in which each following interaction occurred. Thus, we kept the identities of interacting dyads and their total number of following interactions stable, while randomizing the timing of interactions to isolate the effect of our manipulation. We rebuilt following networks from each permuted dataset and recalculated each individual's change in in-strength between phases to obtain reference distributions of difference values that could be expected if following interactions had no relationship to experimental phase. The producer's difference in in-strength was considered to be significantly different than the reference distribution for the equivalent of a two-tailed test if the observed value was more extreme than 97.5% or more of reference values. If the quail responded to our manipulation, we expected to see the producer's strength to have increased more than expected by our reference model from Phase 1 to Phase 2 (the proportion of reference values exceeding the observed would be <0.025). If the birds persisted in following the producer even when it was no longer the only one able to activate the feeder, we predicted that the producer's in-strength would remain high in Phase 3 and the change in the producer's in-strength from Phase 2 to Phase 3 would fall within the reference distribution (the proportion of reference values more extreme than the observed would be >0.025).

To test whether an individual's in-strength in the following network could have been explained by local enhancement (birds being attracted to the feeder by the sight of a feeding bird or by the sound of the motor) we ran mixed effects models and compared their fits to the data using the Akaike Information Criterion (AIC). We settled on a linear mixed model with the square-root transformed in-strength in daily following networks as the response variable. We set frequency of feeder activations per day, group identity, and the two-way interaction between them as fixed effects, and individual identity as a random effect. A nearly 1:1 relationship between an individual's in-strength and the number of times it activated the feeder would suggest that birds may have run to the feeder to scrounge whenever the feeder was activated. Alternatively, little to no relationship between the number of follows a bird received and the number of times it activated the feeder would suggest the actions of birds were driven by something other than local enhancement. We analyzed data from Phase 1 alone as the behavior of birds was not yet influenced by our experimental manipulation of feeder access.

### *Testing for social plasticity in affiliative and aggressive interactions*

To assess how changes to a producer's value in a group altered more general social interaction patterns, we investigated temporal patterns of affiliative and aggressive social interactions that could occur anywhere in the flight pen. To score social interactions, one experimenter (SP) and a group of four assistants conducted all-occurrence behavioral sampling from video recordings of trials using BORIS (Friard and Gamba 2016). We scored the first quarter and last quarter of each day's video (the first and last 1.5 hours). We recorded the affiliative and aggressive interactions listed in Table 1. Since our affiliation behavior, allopreening, was not an instantaneous behavior we counted the number of one-minute intervals in which dyads were observed allopreening and used this for analyses moving forward. We tested for inter-observer reliability for counts of affiliative and aggressive behaviors during a training phase, and observers only progressed to video scoring experimental data if inter-observer reliability was high. We found high inter-observer reliability for counts of both affiliative and aggressive behaviors (all weighted Cohen's Kappa > 0.92). During video scoring, we also recorded feeder visits to check that the RFID data were representative of the number of times birds actually visited the feeder by testing for a correlation between the number of unique detections recorded by the feeder and the number of feeder visits scored from the video during the same time period. We found a high correlation between the number of unique detections recorded by the feeder and the number of feeder visits recorded by human observers (Pearson's r = 0.914).

From social interactions scored in the videos, we created directed affiliation and aggression networks for each phase of the experiment resulting in three networks representing allopreening interactions and three aggression networks per group. We used permutation-based reference models to assess whether the producer experienced changes in its incoming affiliative and aggressive interactions between experimental phases. For each permutation, we took the total number of interactions recorded for directed dyads in each social context and randomly reassigned interactions to each phase of the experiment. As our cameras failed to record a full trial in Phase 1 for test Group 3, we chose to calculate rates of interactions per day. The metric we compared between the observed data and permuted datasets was the difference in the rate of interactions received by an individual between each experimental phase. An individual's observed difference in rate of interactions between phases was significantly different than the reference distribution for the equivalent of a two-tailed test if the observed value was more extreme than 97.5% or more of reference values. If birds saw the producer as a valuable social partner due to our manipulation, we predicted that they would direct more affiliation towards the producer causing the producer's rate of incoming affiliative interactions to significantly increase from Phase 1 to Phase 2 (the proportion of reference values exceeding the observed would be <0.025). We also predicted that birds would decrease their aggression towards the producer, leading to a significant decrease in the producer's incoming aggressive interactions from Phase 1 to Phase 2 (the proportion of reference values below the observed would be <0.025). If changes in the perceived social value of the producer were long lasting, we predicted that both the increase in affiliation and decrease in aggression would persist into Phase 3 and we would find no significant changes in producer's rate of incoming affiliative and aggressive interactions from Phase 2 to Phase 3.

To help explain some observed patterns in aggressive relationships, we calculated each group member's dominance rank in each phase of the experiment. We used the SpringRank algorithm developed by De Bacco et al. (De Bacco et al. 2018) to calculate each individual's continuous power and ordinal rank within the dominance hierarchy of the group. In the SpringRank algorithm, a network is imagined to be a set of nodes physically connected by directed springs and positions of nodes (SpringRank values) are calculated such that the total energy in the system is minimized (De Bacco et al. 2018). For networks of aggression, social support, faculty hiring, and basketball tournaments, SpringRank performed as well or better than other popular ranking methods (De Bacco et al. 2018).

**Table 1.** Behaviors recorded from video observations

| **Social Type** | **Behavior** | **Definition** |
|---|---|---|
| Affiliation | Allopreen | Gently preening head or neck feathers, esp. around eyes, of another bird. |
| Aggression | Wing raising | While directly facing another bird, from a horizontal position, wings raised and rotated with upper surface facing forward, primaries extended, and back end of the body raised. Individual may take a few steps toward the rival |

| | | |
|---|---|---|
| Aggression | Chase | Running after an escaping bird with body low and head held forward |
| Aggression | Displace | Lunge or charge toward rival with body held low, mouth of actor is often open. Actor may or may not make contact with the receiver. Receiver may be stationary or walking when the action begins and will usually move away from the actor. |
| Aggression | Jab | Peck, or quick series of pecks to the head of a rival, rival may attempt to duck or dodge to avoid jabs |
| Aggression | Feather pull | Grabbing and pulling the feathers of another bird, especially feathers of the head or nape |
| Feeder interaction | Feeder visit | Bird standing on or passing over feeder antenna |
| Feeder interaction | Feed | Bird eating from feeder |
| Feeder interaction | Co-feed | Two or more birds eating simultaneously at the feeder |

## **Results**

Across all three test groups, the birds were detected at the feeder a total of 14537 unique times and the feeder was activated a total of 2399 times. The feeder recorded a total of 2412 joins, and 829 follows. Observers recorded birds allopreening in a total of 3967 one-minute intervals and recorded 3021 aggressive interactions. Summaries broken down by group are shown in Table 2.

**Table 2.** Summary of overall feeder activity and quail interactions during the experiment. The count of affiliative behaviors represents the number of one-minute intervals that birds were recorded allopreening. The count of aggressive behaviors only includes interactions for which observers concluded there was a clear winner and loser.

| Group | Unique detections | Feeder activations | Joins | Follows | Affiliations | Aggressions |
|---|---|---|---|---|---|---|
| 1 | 4711 | 800 | 727 | 283 | 1158 | 797 |
| 2 | 5252 | 796 | 916 | 259 | 1472 | 968 |
| 3 | 4574 | 803 | 769 | 287 | 1337 | 1256 |

### *Did quail exhibit social plasticity in the foraging context?*

In all three test groups, our manipulation of the value of the producer resulted in a change in how other birds followed it. In all three social groups, the producer was followed most often out of all group members in Phase 2 (Fig. 2). The producer in each group received significantly more follows to the feeder in Phase 2 compared to Phase 1 (Fig. 3, $p = 0$).

Although there was a statistically significant positive relationship between a bird's in-strength in the following network and the number of times it activated the feeder each day in Phase 1 ($\beta = 0.0967$ , SE = 0.0208, $p < 0.001$ ; see full model results in Supplemental Table S1), it did not approach a 1:1 relationship in any of the three test groups (Fig. 4).

When we examined longer-term changes after the value of the producer was removed in Phase 3, we found that the number of times the producer was followed in Phase 3 decreased from the number of times it was followed in Phase 2 in all three groups, but not all of these decreases were significantly different from expectations. In two of our three groups (Groups 1 and 2), the number of follows received by the producer decreased significantly from Phase 2 to Phase 3 (Fig. 3, $p < 0.001$). However, the number of follows received by the producer in Group 3, while lower, did not significantly decrease between Phases 2 and 3 (Fig. 3, $p = 0.1424$).

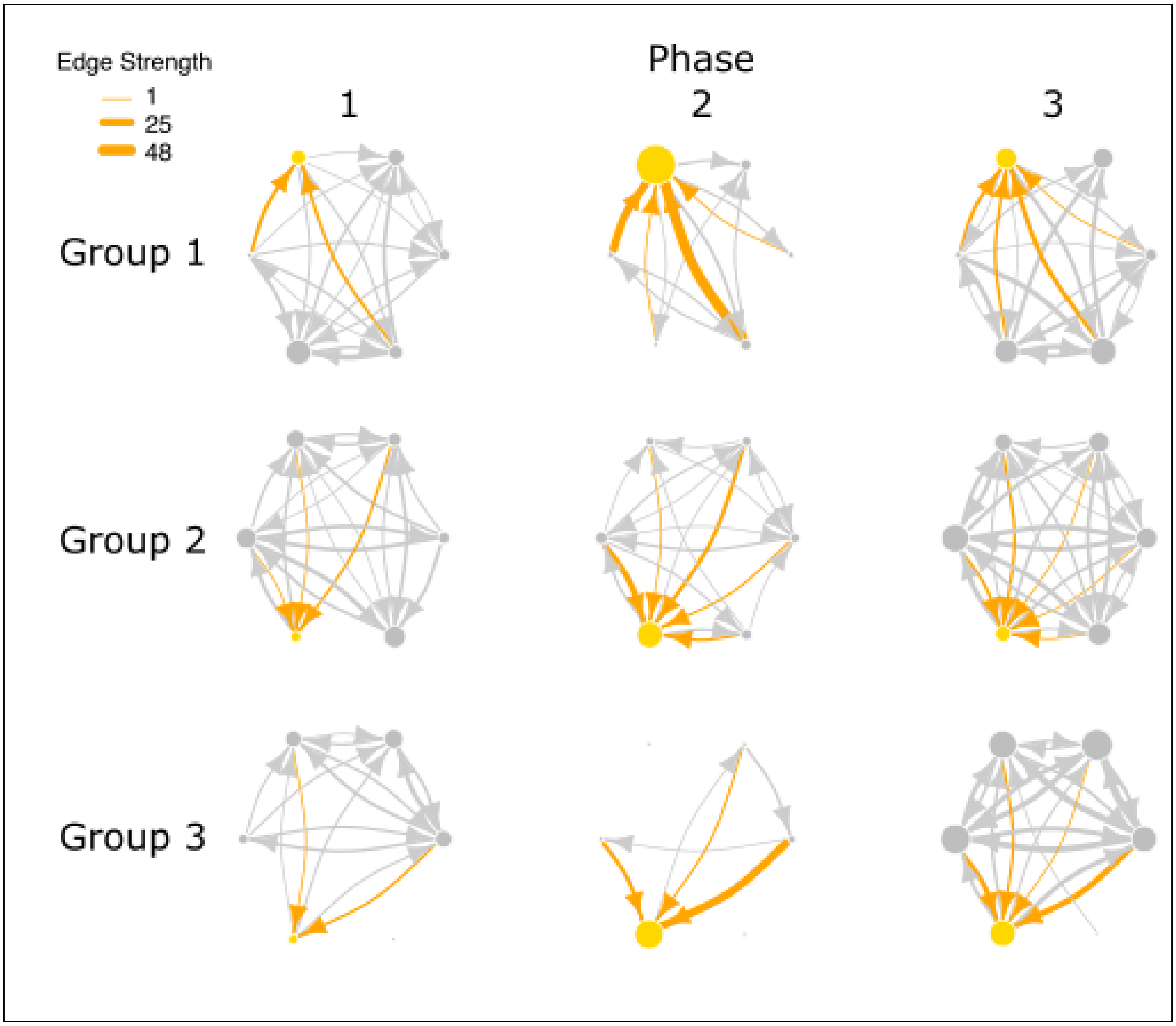

Figure 2. Following networks per phase for each test group across each experimental phase. The six birds are shown as nodes (circles) and are connected by an arrow if one bird followed another (arrow pointing at bird that was followed); the thickness of these lines shows the number of times following occurred. The producer is highlighted as the yellow node and its incoming following interactions are shown as orange edges.

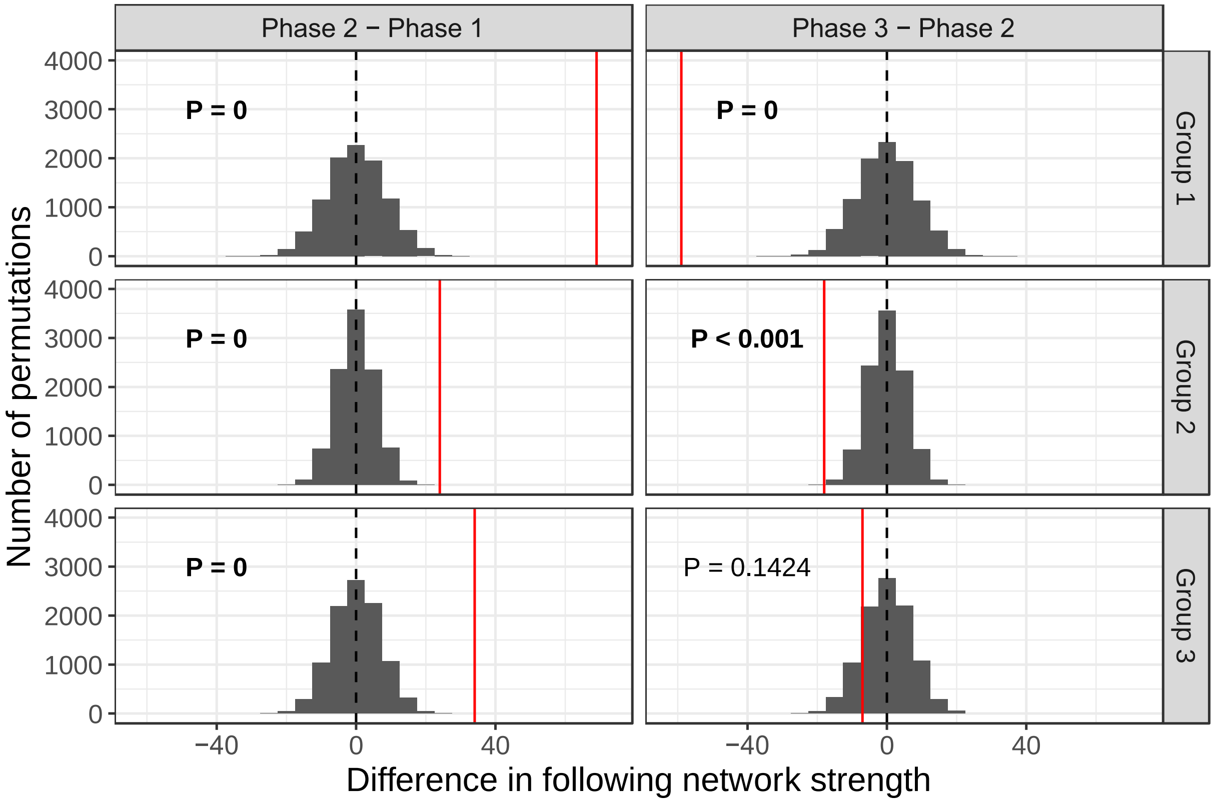

Figure 3. Producer's observed difference in following network strength between phases (red vertical line) relative to the expected distributions of differences calculated from the reference model which randomized the phase in which each following interaction occurred. The dashed vertical line indicates no change in strength between the two phases being compared. P values for significant differences with a two-tailed test are shown in bold text; all three groups followed the producer significantly more in Phase 2 compared to Phase 1 while two of the three groups followed the producer significantly less in Phase 3 compared to Phase 2.

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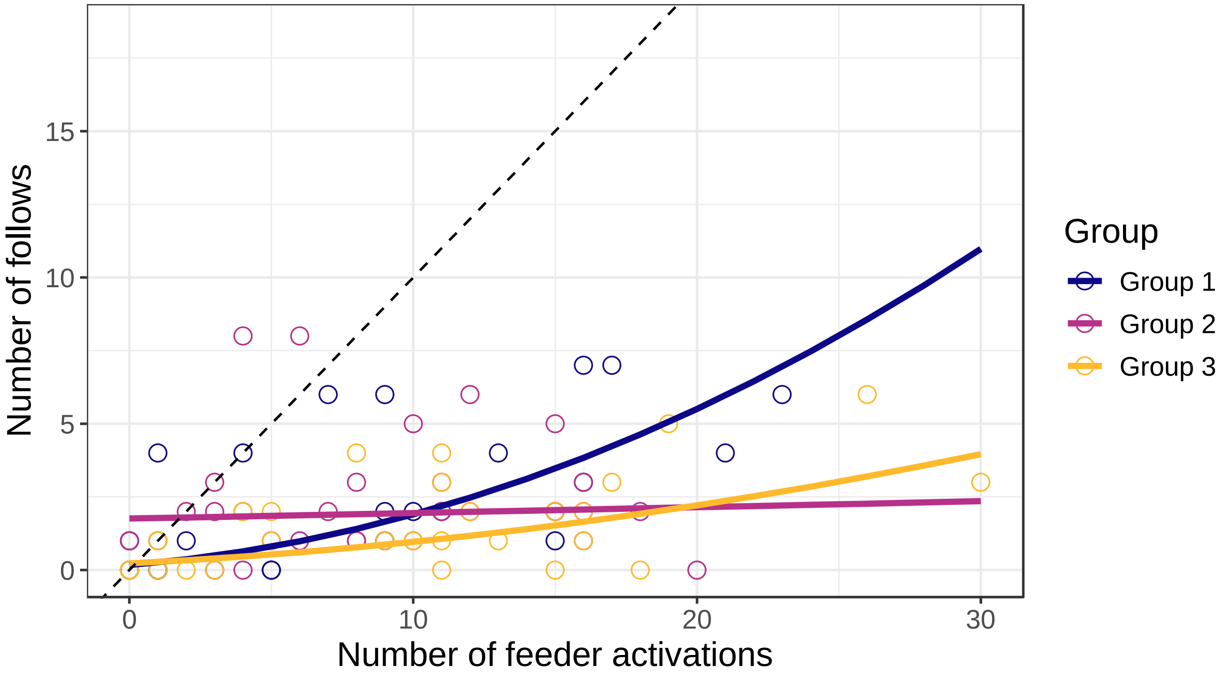

Figure 4. Relationship between each bird's strength in the following network and the number of times it activated the feeder each day in Phase 1. The slopes and 95% confidence bands indicate the estimated relationship based on a linear mixed model. The dashed line indicates a hypothetical 1:1 relationship.

### *Did quail exhibit social plasticity in the non-foraging context?*

Observers recorded affiliative and aggressive behaviors for 44 trials and a total of 132 video hours, translating to approximately 341 hours of video scoring time completed by observers.

Changes in affiliation were similar across all three groups. Contrary to our prediction, the producer in each group received allopreening from its group members at a lower rate in Phase 2 compared to Phase 1. This decrease was significantly different from random expectation for Groups 1 and 2 ($p < 0.025$) but not Group 3 ($p = 0.1674$). The producer received allopreening at a higher rate in Phase 3 compared to Phase 2 in all three groups, but this increase was only significantly higher than expectations in Group 3 ($p = 0$, Fig. 5).

Changes in aggression were more variable across the three groups, where Groups 2 and 3 exhibited similar patterns and Group 1 differed in aggression patterns. We had predicted that as the value of the producer increased in Phase 2, that it would receive less aggression from group members in Phase 2 compared to Phase 1. We saw this pattern in Groups 2 and 3, where the producer experienced a lower rate of incoming aggression in Phase 2 compared to Phase 1, but this was a significant change in Group 2 only (Group 2 $p = 0$; Group 3 $p = 0.0541$, see Fig. 6). In Group 1, there was no significant change in aggression received by the producer in Phase 2 (two-tailed test, $p > 0.025$), but the producer received no aggression from others in Phase 1 and very few aggressive interactions in Phase 2 so estimating random expectations for this individual was difficult.

Once the value of the producer was removed, aggression towards the producer increased slightly in Groups 2 and 3 in Phase 3 compared to Phase 2, but this change in aggression was not significantly higher than random expectations. The producer in Group 1 again received very few aggressive interactions in Phase 3. The pattern we see in Group 1 may be due to rank effects. The Group 1 producer was the most dominant group member, whereas the producers in Groups 2 and 3 were ranked second or third in their hierarchies (as determined by each individual's dominance power scores per phase via SpringRank; Supplemental Fig. S4).

We investigated two possible post-hoc explanations for the trends evident in the rates of affiliation and aggression received by the producer across phases. First, the producers' experience could simply have been a reflection of group-level patterns. For example, the producers could have experienced a decrease in affiliation and aggression in Phase 2 of the experiment because the group as a whole became less affiliative and aggressive. Second, the producers' decrease in rate of incoming affiliative and aggressive interactions could have reflected them spending more time at the feeder and away from others during Phase 2.

We found no evidence that the variability in producer strength in affiliation and aggression networks over time was associated with group level patterns for these behaviors. There was no significant correlation between the producer's affiliation network strength and the median affiliation strength of non-producers (Pearson's r = 0.047, n = 44, p = 0.761; Supplemental Fig. S5). Similarly, there was no significant correlation between the producer's aggression network strength and the median aggression strength of non-producers (Pearson's r = 0.195, n = 44, p = 0.206; Supplemental Fig. S6). These results suggest that the group level patterns of affiliation and aggression were not driving changes in producer strength.

We also found no strong evidence that patterns of affiliation and aggression directed towards the producer could be explained as a byproduct of the producer spending more time at the feeder and away from others in Phase 2. To investigate whether the producers' patterns were associated with the time they spent at the feeder, we pooled the data across groups and checked for a correlation between the producers' daily strength in the affiliation and aggression networks and their number of unique detections at the feeder per day. A negative correlation would suggest that the time that producers spent at the feeder could have detracted from the opportunities to receive affiliative and aggressive interactions from group members, whereas no correlation would suggest the time spent at the feeder did not influence its incoming interactions. We found no significant correlation between producer strength in their affiliation networks and their number of unique detections at the feeder (Spearman's r = -0.109, n = 44, p = 0.479; Supplemental Fig. S7). There was a weak negative correlation between the producers' strengths in their aggression networks and their number of unique feeder detections (Spearman's r = -0.299, n = 44, p = 0.048; Supplemental Fig. S8).

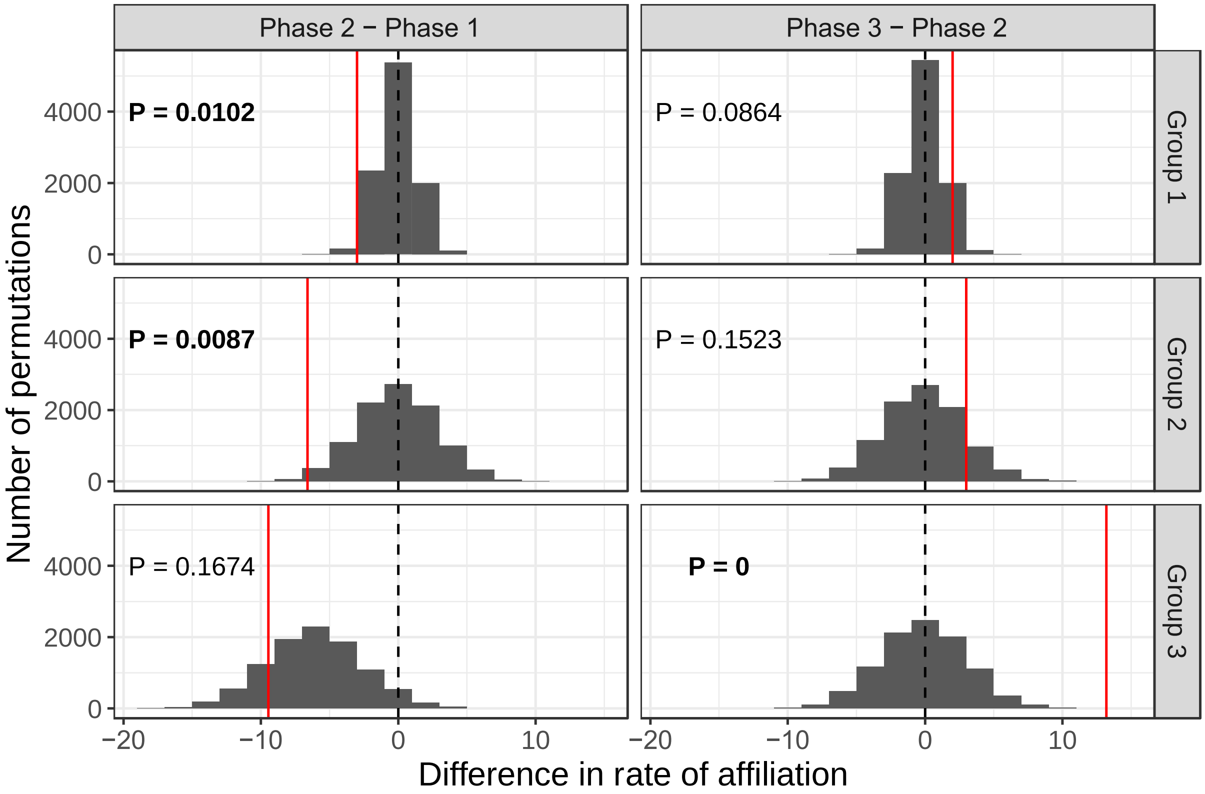

Figure 5. Producer's observed difference in rate of incoming affiliation between phases (red vertical line) relative to the distributions of differences calculated from the reference model. The dashed vertical line indicates no change in rate between the two phases being compared. P values for significant differences with a two-tailed test (p<0.025) are shown in bold text.

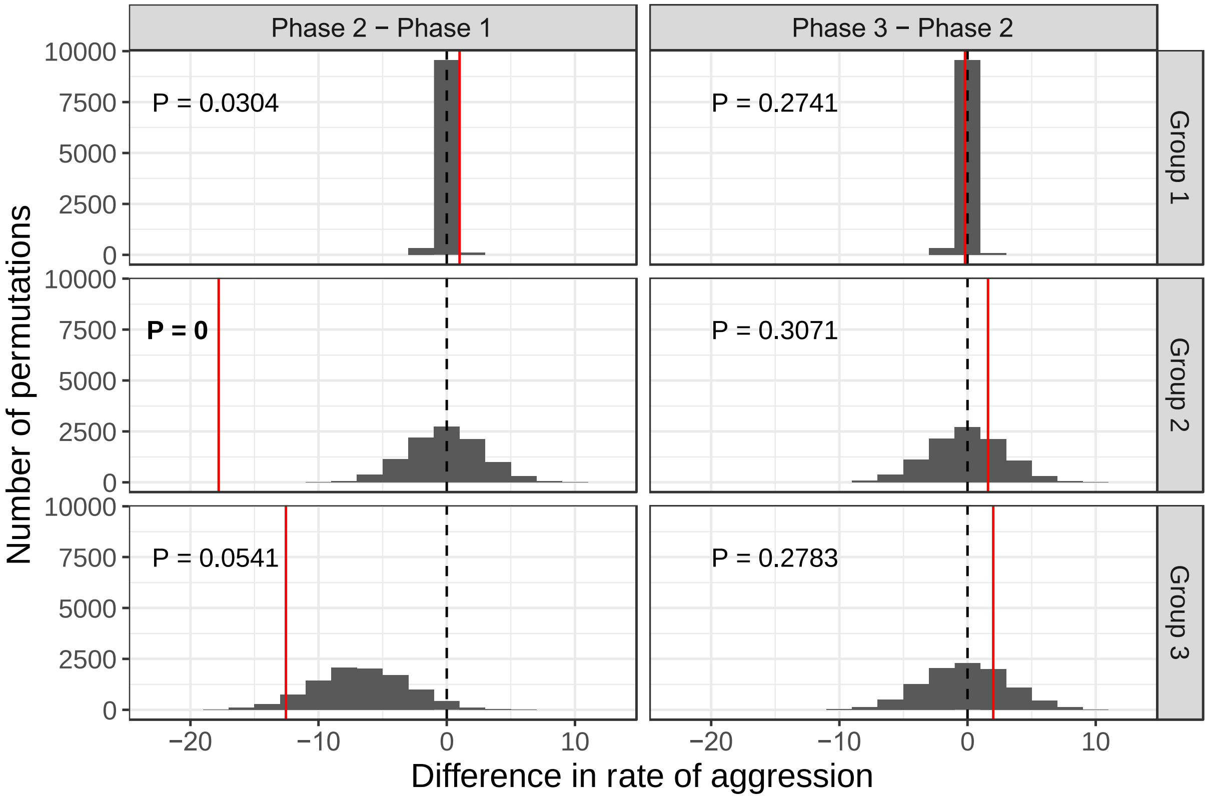

Figure 6. Producer's observed difference in rate of incoming aggression between phases (red vertical line) relative to the distributions of differences calculated from the reference model. The dashed vertical line indicates no change in rate between the two phases being compared. P values for significant differences with a two-tailed test (p<0.025) are shown in bold text.

## Discussion

Studies of animal social structure have shown that social connectedness comes with costs and benefits. However, social structure is dynamic and recent work has investigated how individual social decisions can influence social connectedness. Some animals have been shown to adjust their social relationships based on the value provided by their group members (e.g., Kulahci et al. 2018; Kings et al. 2023), but how widespread this phenomenon is across species and social contexts is an open question. We conducted a foraging experiment with captive quail to understand whether they showed evidence for adaptive social plasticity across social contexts. We asked whether individuals adjusted their interactions in response to an increase in a group member's social value and whether these responses persisted after the unique value of the group member was removed. We tested for changes in both a foraging context and a more general non-foraging context. Overall, we found the quail adjusted their foraging interactions following our experimental manipulation, but the persistence of this response varied across test groups. Away from the food, responses to changes in the value of one group member were more variable across groups.

### *Social plasticity in foraging interactions*

We first asked whether quail changed the number of times they followed the producer to the feeder during our experimental manipulation. We found that the producers' strength in the following networks increased in Phase 2 compared to Phase 1 in all three test groups. This result matched what we predicted if quail were capable of adaptive social plasticity and provides evidence for social plasticity in quail within this foraging context.

We found little evidence to suggest that this result could be solely attributed to foragers just being attracted by the sight of a group member feeding (local enhancement) or being attracted to the sound of the feeder being activated. We found a weak relationship between in-strength and number of feeder activations. A 1:1 relationship would have suggested that birds approached the feeder every time it was activated, with no regard for which bird activated it. Our results show that the birds' decisions to follow others to the feeder were not exclusively driven by local enhancement or attraction to the sound of the feeder.

Our results align with evidence for shifts in foraging patterns in other species of birds. For example, after foraging manipulations in which experimenters controlled which individuals could feed together, songbirds were found to favor socially learning the locations of new food patches from individuals with whom they had been matched in the experimental manipulation (Firth et al. 2016; Heinen et al. 2022). In another study, jackdaws learned to associate more at feeders with individuals who could facilitate feeder access (Kings et al. 2023). In all these experiments, birds responded to experimental manipulations by increasing their foraging interactions with individuals they associated with access to food. Our work adds the Northern bobwhite to the list of bird species that are able to exhibit adaptive social plasticity in a foraging context.

### *Persistence of initial plastic social responses*

Our second question was whether the temporary change in the producer's foraging success was enough to lead to persistent changes in following interactions. The number of following interactions directed toward the producer decreased from Phase 2 to Phase 3 in all test groups, but to varying degrees. This decrease was statistically significant in two out of the three groups. This result suggests our foraging manipulation was not enough to lead to persistent changes in foraging interactions perhaps because birds were able to recognize that the producer no longer had a foraging advantage in Phase 3. These results also support adaptive social plasticity, as the birds did not keep following the producer once the producer was not the only one who could open the feeder.

Our results show that the quail were sensitive to short-term changes in their social environment. Similar results for sensitivity to changes in the social environment have been found in other species. For example, a study in great tits (*Parus major*) in which experimenters successfully manipulated the foraging networks of birds by controlling which individuals could access the same feeders, found that these experimentally-induced social connections eroded after the period of experimental manipulation (Firth and Sheldon 2015). This was despite their manipulation period lasting much longer (90 days) than in our experiment (5 days). A similar study found that post-testing foraging networks of mountain chickadees (*Poecile gambeli*) did not show assortment by experimentally-induced connections (Heinen et al. 2022). In contrast, some studies in primates have found persistent changes in social interactions after experimental manipulations of social value. Stammbach (1988) found that increased proximity and grooming toward food providers persisted even after the foraging task was removed, suggesting monkeys treated food providers differently because they associated them with getting food rewards. Similarly, Kulahci et al. (2018) found lemurs directed more approach and grooming behaviors toward individuals able to solve a foraging task after the experiment compared to before foraging tasks were introduced. These differences in adaptability in response to changes in social circumstances may reflect differences in cognitive abilities across taxa.

### *Social plasticity in non-foraging interactions*

Our third question asked whether quail showed changes in rates of non-foraging interactions directed toward the producer across phases. Here, our goal was to investigate the influence that changes in an individual's social value in a foraging context may have on its broader social relationships. Increases in affiliation or decreases in aggression received by the producer, would suggest that quail associated the producer with access to food (i.e., seeing it as a valuable social partner) and chose to adjust their interactions with it accordingly. However, if they did not change their non-foraging interactions, that could be because their foraging interactions do not influence interaction decisions in other social contexts.

We found qualitatively similar patterns of change in the rates of affiliation directed toward the producer in each group, with the rate decreasing from Phase 1 to Phase 2 and increasing from Phase 2 to Phase 3. The rate significantly decreased from Phase 1 to Phase 2 and did not change from Phase 2 to Phase 3 in two of the three test groups. In the third group, the only statistically significant change in rate of affiliation was an increase from Phase 2 to Phase 3. Our results oppose our prediction for how affiliation toward the producer would change in response to our manipulation as well as findings of increased grooming directed toward valuable partners in primates (Stammbach 1988; Fruteau et al. 2009; Kulahci et al. 2018; Blersch et al. 2024).

In the context of aggression, we found qualitatively similar patterns of change in rates of aggression directed toward the producer in two of the three test groups, with the rate decreasing from Phase 1 to Phase 2 and increasing slightly from Phase 2 to Phase 3. These patterns match our prediction that aggression would decrease toward an individual whose social value was artificially increased. In the remaining test group, the rate of aggression slightly increased from zero interactions per day in Phase 1 to one in Phase 2 and 0.8 in Phase 3. All of the aggressive interactions recorded in Phases 2 and 3 came from a single individual. When calculating the dominance ranks of birds, we found that the producer in this group was the highest ranked while those in the other two groups were second or third in their hierarchy. This relationship between dominance rank and changes to a producer's incoming aggressive interactions further highlights the complex interplay between social position and social dynamics. Firth et al. (2015) and Kings et al. (2023) have previously shown that birds adjust their foraging interactions with others while keeping their long-term relationships intact, suggesting that long-term relationships act as a constraint on adaptive social plasticity. Our findings in the context of aggression suggest pre-existing dominance relationships are another factor that may constrain adaptive social plasticity in some study systems.

We explored two possible explanations for changes in non-foraging interactions with the producer. First, they could have reflected overall levels of affiliation or aggression in each group. However, we ruled out this possibility as changes in the number of affiliative and aggressive behaviors received by the producer did not correlate with the median strength of non-producers in the affiliation or aggression networks, respectively. A second possibility was that the producer experienced a lower rate of affiliative and aggressive interactions in Phase 2 because it was spending more time at the feeder, leaving less time for it to engage in social interactions in non-foraging contexts. Here too we argue this was not the case as we found little to no correlation between the number of non-foraging interactions received by the producer and the number of unique times it was detected at the feeder. Additionally, producers did not consistently have higher numbers of detections and lower incoming affiliative or aggressive interactions in Phase 2 compared to Phase 1.

Overall, our findings suggest foraging success may be an important piece of information for quail when making social decisions in multiple contexts. Other species have similarly been shown to adjust their interactions across contexts. Firth and Sheldon (2015) found co-occurrences recorded between prospecting birds at nest boxes matched experimentally-induced relationships at selective feeders. Multiple studies on primates show increased affiliative interactions towards food providers as group members associate them with a food reward (Stammbach 1988; Blersch et al. 2024), use grooming as a commodity to repay the provider for the benefits it provided (Fruteau et al. 2009) or perhaps approach them to increase opportunities for socially learning new foraging skills (Kulahci et al. 2018). It remains unclear why quail in our test groups tended to decrease the rate at which they affiliated with the producer in their group from Phase 1 to Phase 2. Finally, there have been few studies looking at the effects of changes in the foraging context on interactions in the context of aggression. In line with the decreases in rates of aggression we saw in Phase 2 in two of our three test groups, Stammbach (1988) found monkeys learned to refrain from displacing or chasing food providers during trials as they recognized they could benefit from their foraging actions. In contrast, Blersch et al. (2024) found that the provider in their experiment received more aggression from dominant group members perhaps as a result of competition or as a way to reinforce the existing hierarchy in the face of a perceived threat. More work is needed to understand what the quail understood about the producer in their group that led them to decrease the rates of both affiliative and aggressive interactions directed toward it.

### *Factors underlying adaptive social plasticity*

Adaptive social plasticity is likely driven by the underlying attention, learning, and memory capacities of animals. Individuals must be able to perceive the behavior of their group members, learn that their social value has changed, and remember this information long enough to act on it. Empirical studies like this one can help us infer what animals are paying attention to and learning about each other but cannot get at the underlying cognition directly. One way to test how cognitive factors might interact to affect social patterns is through simulations and modeling approaches. For example, we built an agent-based model resembling the three-phase structure of our experiment to investigate how cognitive factors influence emergent social relationships (Prasher & Hobson in review). Our model showed that strong tendencies to attend to the foraging activity of others and follow them based on this information led to the strongest responses to a change in one individual's relative foraging success. However, combinations of cognitive parameters reflecting a more flexible response to changes in group member foraging success were associated with the greatest benefits for non-producers. Simulations may prove useful in inspiring future experiments to dig deeper into the cognition driving adaptive social plasticity. More broadly, combining experimental and modeling approaches is likely to be a powerful technique to refine our understanding of complex social and cognitive interactions in animals.

### *Conclusions*

Our study demonstrates that quail can adjust their foraging interactions in response to short-term changes in a group member's social value. Additionally, plastic social responses can occur across social contexts, but pre-existing dominance relationships may influence the extent that responses can take place in an agonistic context. Future studies should aim to monitor interactions in multiple social contexts to understand the full extent of social dynamics that may be driven by adaptive social plasticity and the breadth of impacts an experimental manipulation may have. Modeling social scenarios in which individuals have varying levels of underlying cognitive skills could help gain insight into the minimum level of cognition required for adaptive social plasticity. Such work combined with empirical studies is essential to understanding the conditions leading to adaptive social plasticity.

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## Ethical Statement

All procedures were approved by the University of Cincinnati Institutional Animal Care and Use Committee protocols 21-02-23-01 and 24-04-16-01.

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## Supplemental Material 1

A food preference test was conducted to determine the most preferred food items of quail. The experimenter simultaneously presented individual birds with four dishes of food in their home cage, with each containing a unique food type. The four food types tested were an adult bird game feed, a chick bird game feed, a seed mix (containing majority millet seed with smaller amounts of niger seed, sunflower kernels, and canary seed), and sunflower seeds. Four dishes were fixed to a flat plastic surface to facilitate presenting the foods to the birds simultaneously. To begin a trial the experimenter filled each dish with a different food type (the same amount of food by weight was used in each dish), placed the dishes in the focal individual's home cage, removed the regular food dish from the cage, and started a timer. Each trial lasted 10 minutes, during which the experimenter observed the focal bird and recorded the number of pecks made to each food dish. At the end of the trial, the experimenter removed the introduced food dishes and returned the original food dish to the cage. Visibility between cages was blocked during trials to prevent the influence of one bird's preferences on the neighboring bird's food choices. A total of 31 birds and 23 of these pecked at least one food type.

We found that birds tended to direct the most pecks toward the seed mix.

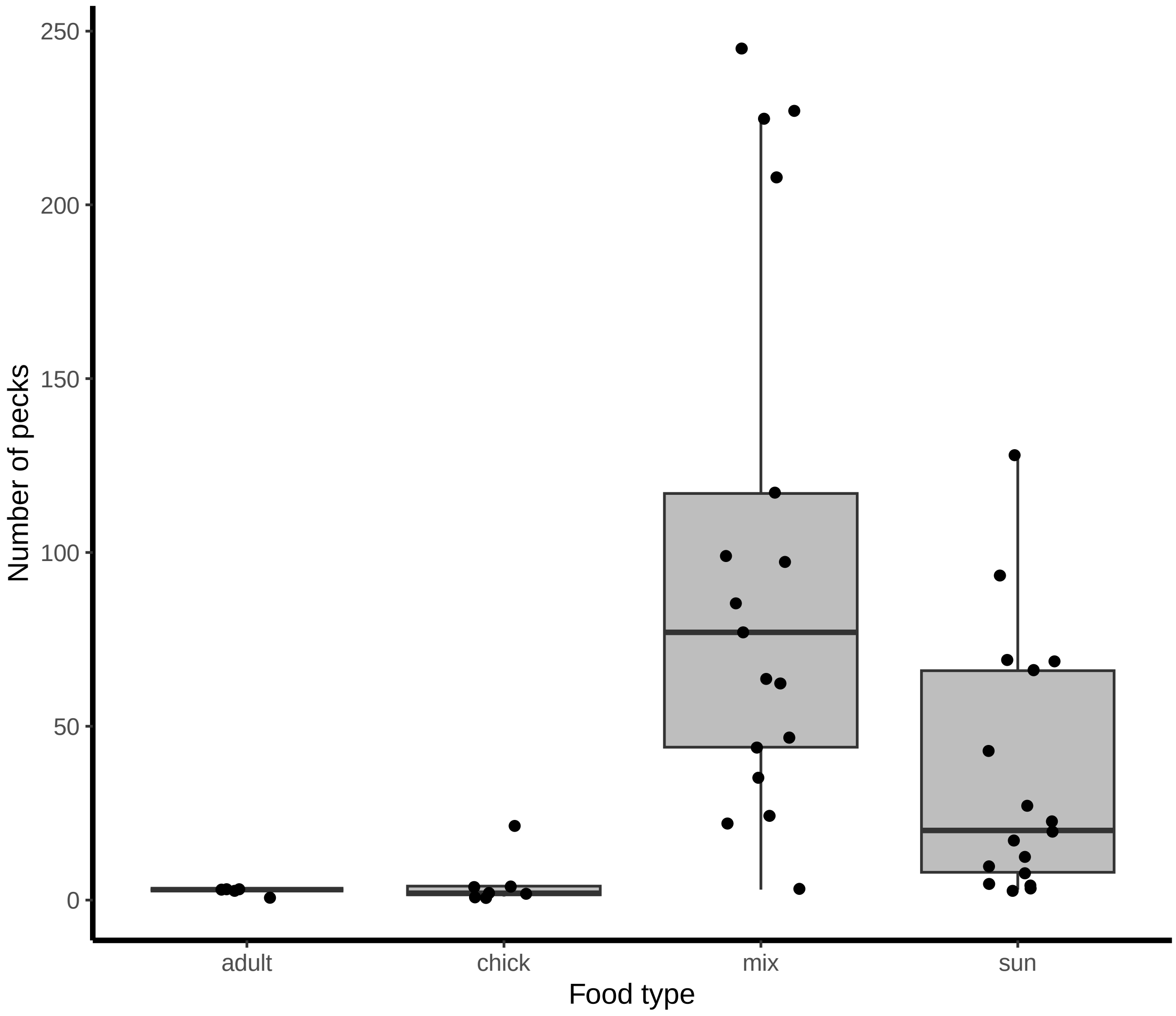

Figure S1. Number of pecks directed to each of four food types during food preference trials (adult = adult game bird feed; chick = chick game bird feed; mix = seed mix containing millet, niger seed, sunflower kernels, and canary seed; sun = sunflower seeds).

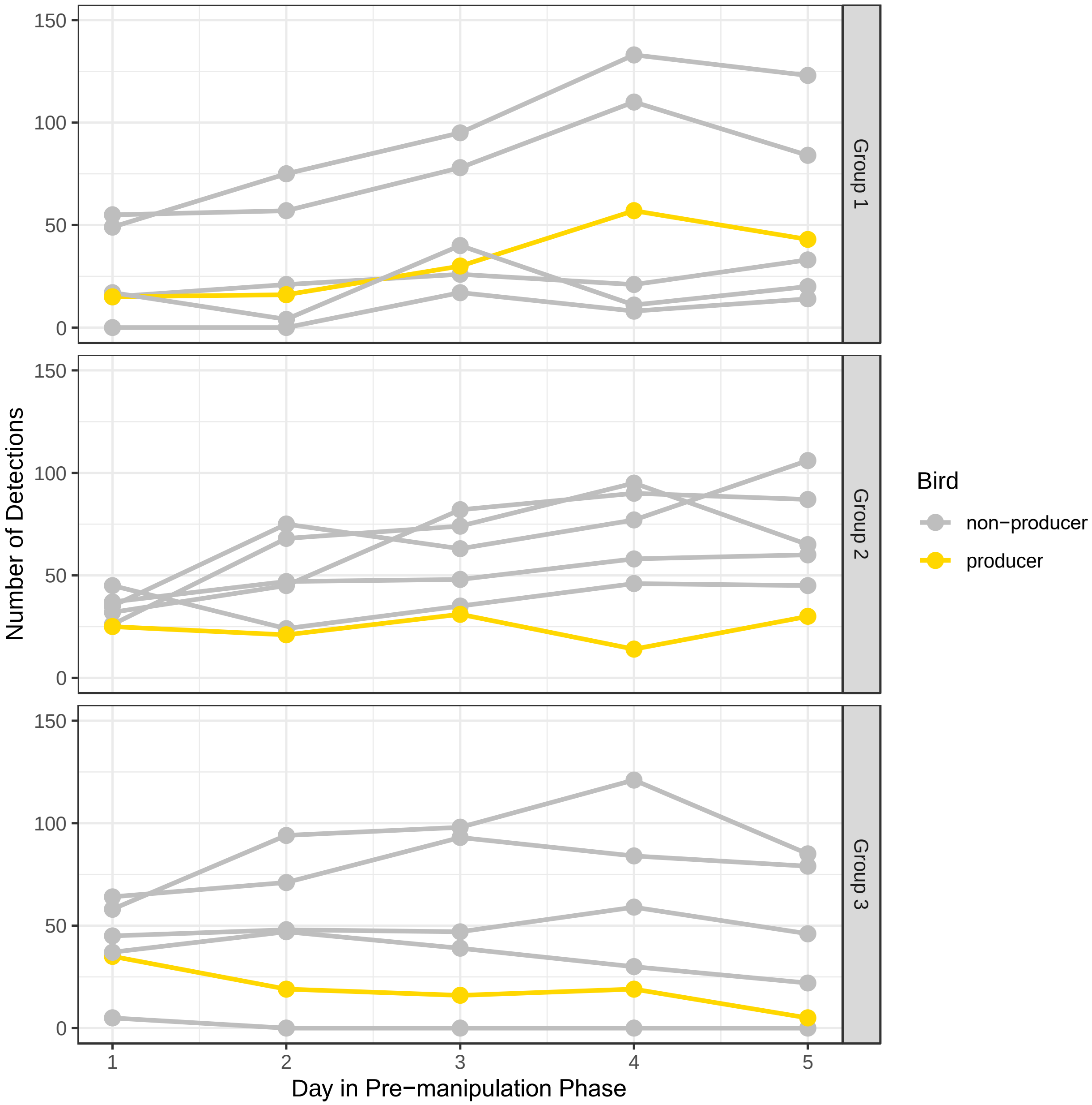

Figure S2. The number of feeder detections per bird in Phase 1 of the experiment. Birds that were chosen as the producer in each group are highlighted as the yellow line.

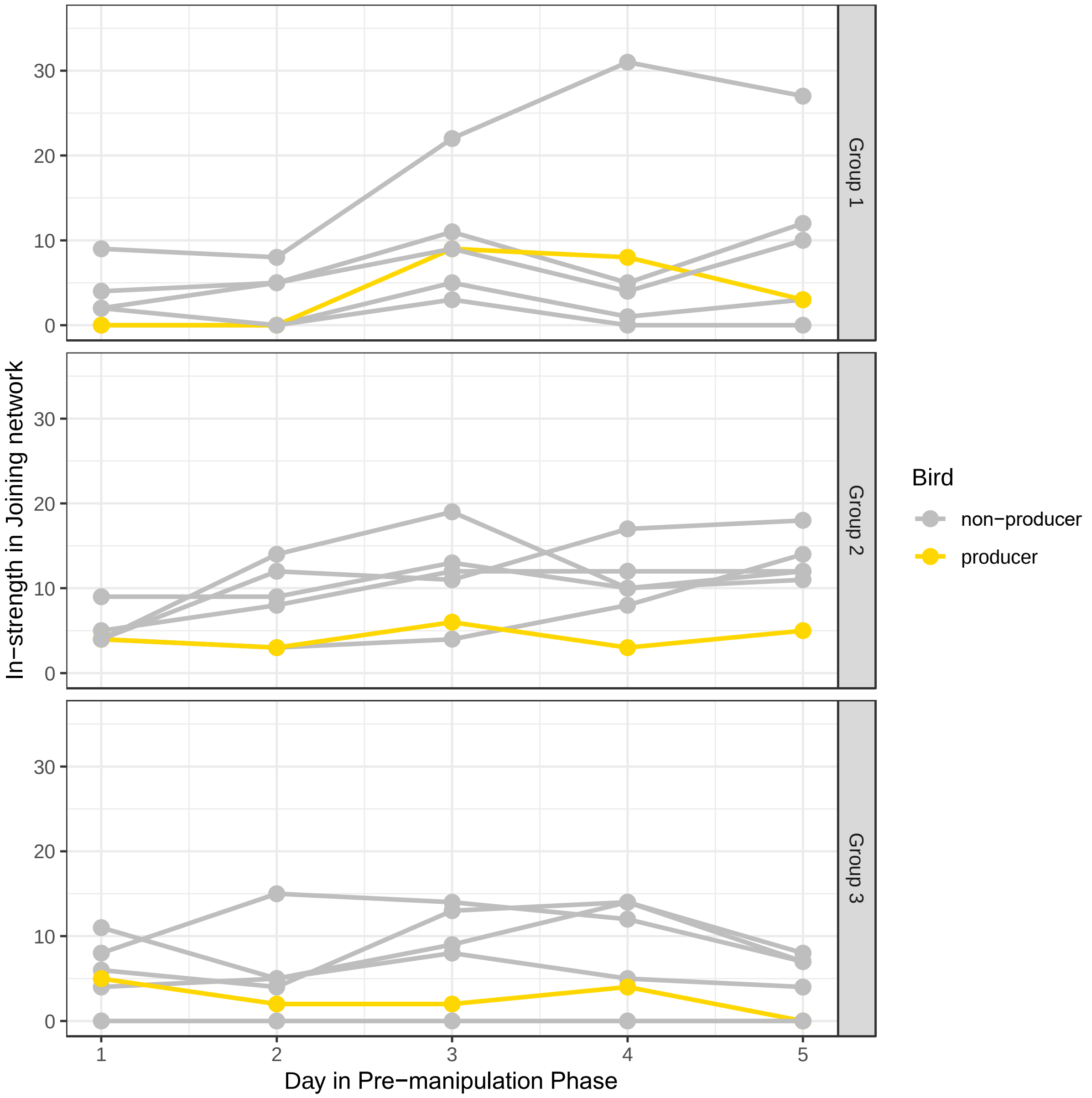

Figure S3. The in-strength of each bird in the joining network in Phase 1 of the experiment. Birds that were chosen as the producer in each group are highlighted as the yellow line.

Table S1. Model estimates assessing the influence of predictors on the square-root of the number of follows received by birds on each day of Phase 1 (n = 90). Statistically significant effects are highlighted in bold text.

| Predictor | Estimate | Standard Error | P-value |
|---|---|---|---|
| Number of activations | 0.09668 | 0.02083 | **0.000149** |
| Group 2 | 0.91483 | 0.33415 | **0.012124** |
| Group 3 | 0.06525 | 0.31387 | 0.837917 |
| Activations:Group 2 | -0.08977 | 0.03147 | **0.007445** |
| Activations:Group 3 | -0.04626 | 0.02753 | 0.107329 |

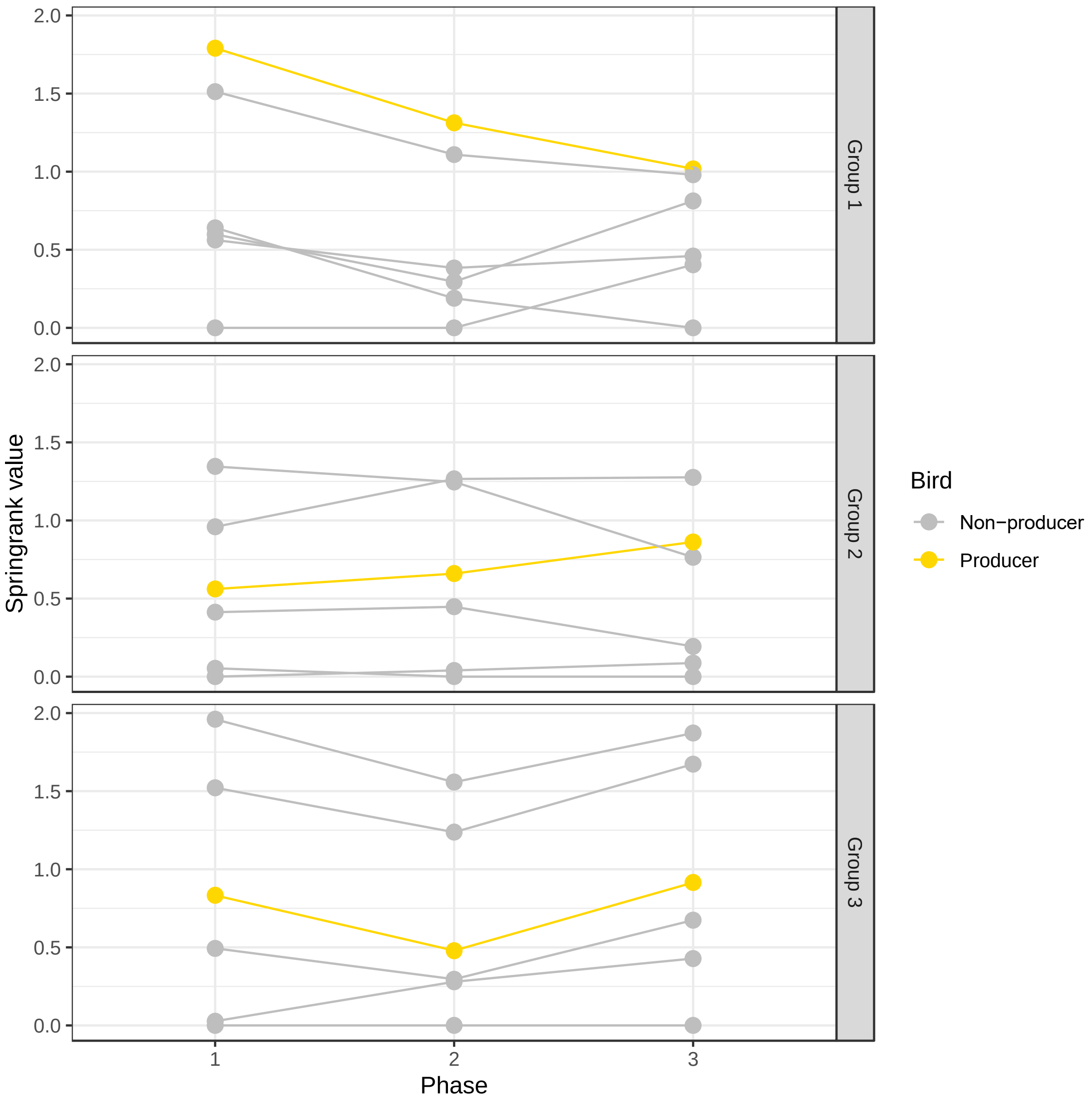

Figure S4. SpringRank values per bird in each test group over time. The producer in group 1 remained top-ranked throughout the experiment, while the producers in groups 2 and 3 remained in the middle of their hierarchies.

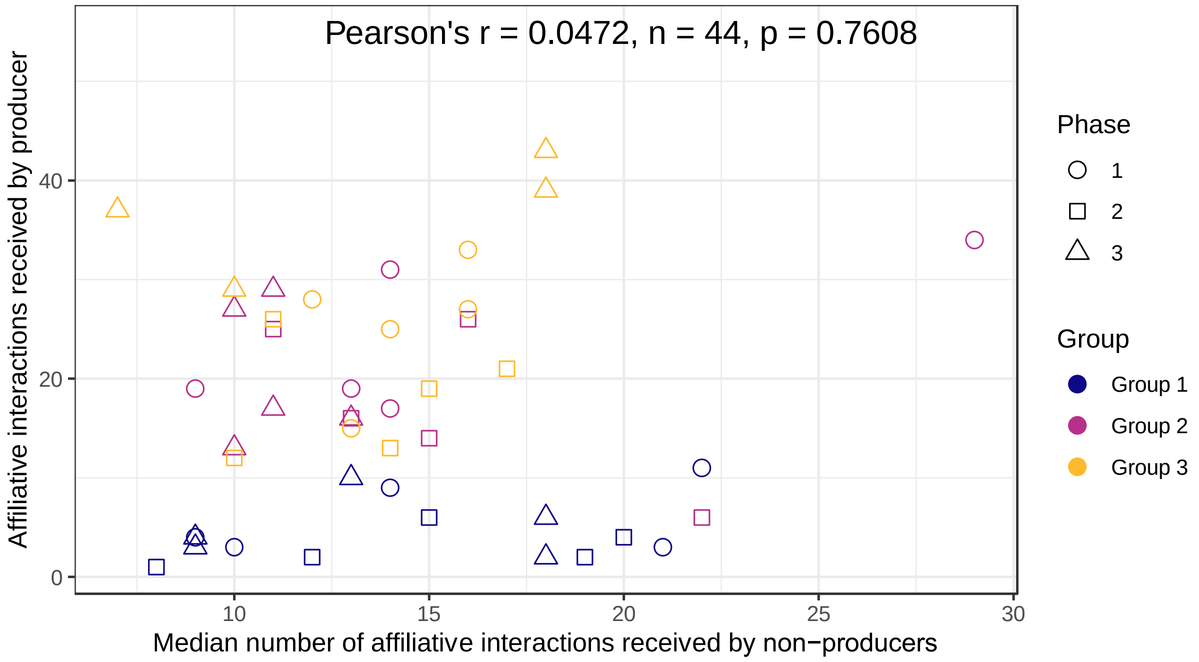

Figure S5 Correlation between the producer's strength in the affiliation network and the median affiliation strength of non-producers each day.

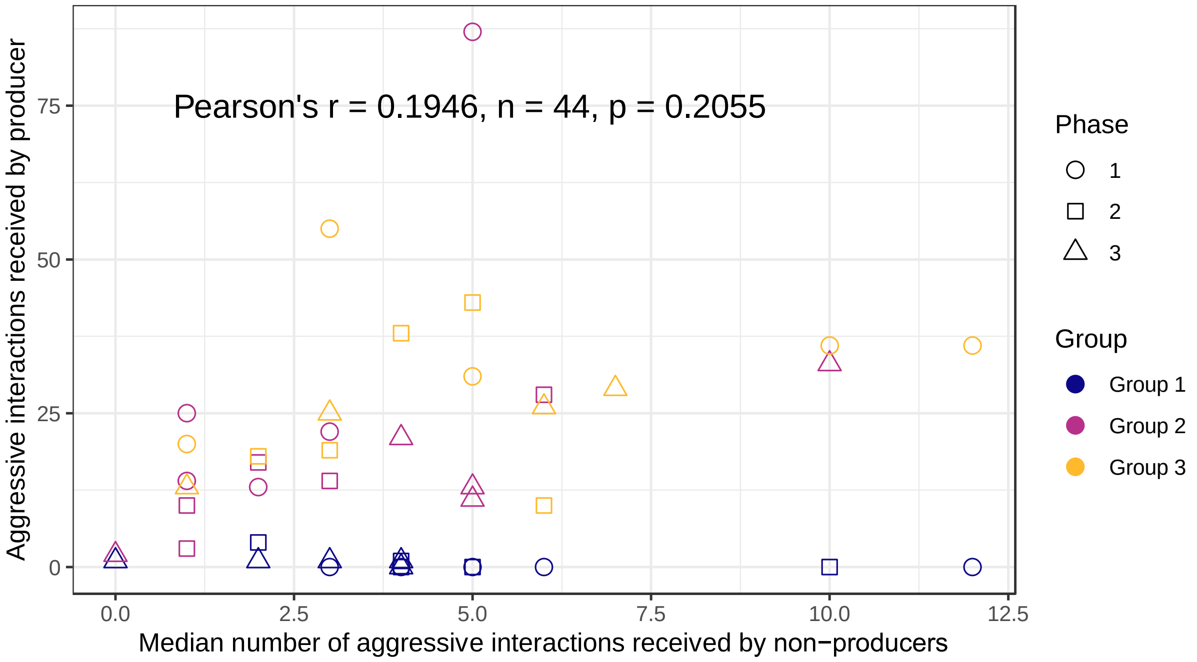

Figure S6. Correlation between the producer’s strength in the aggression network and the median aggression strength of non-producers each day.

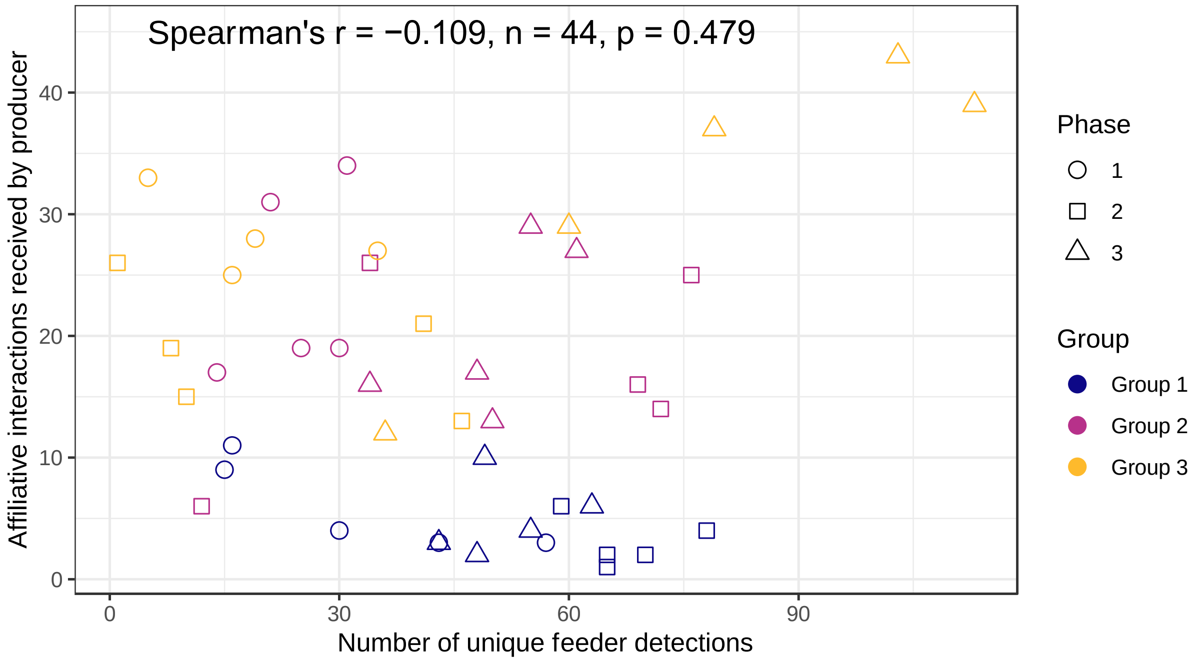

Figure S7. Correlation between producers’ affiliation strength and number of unique detections at the feeder per day

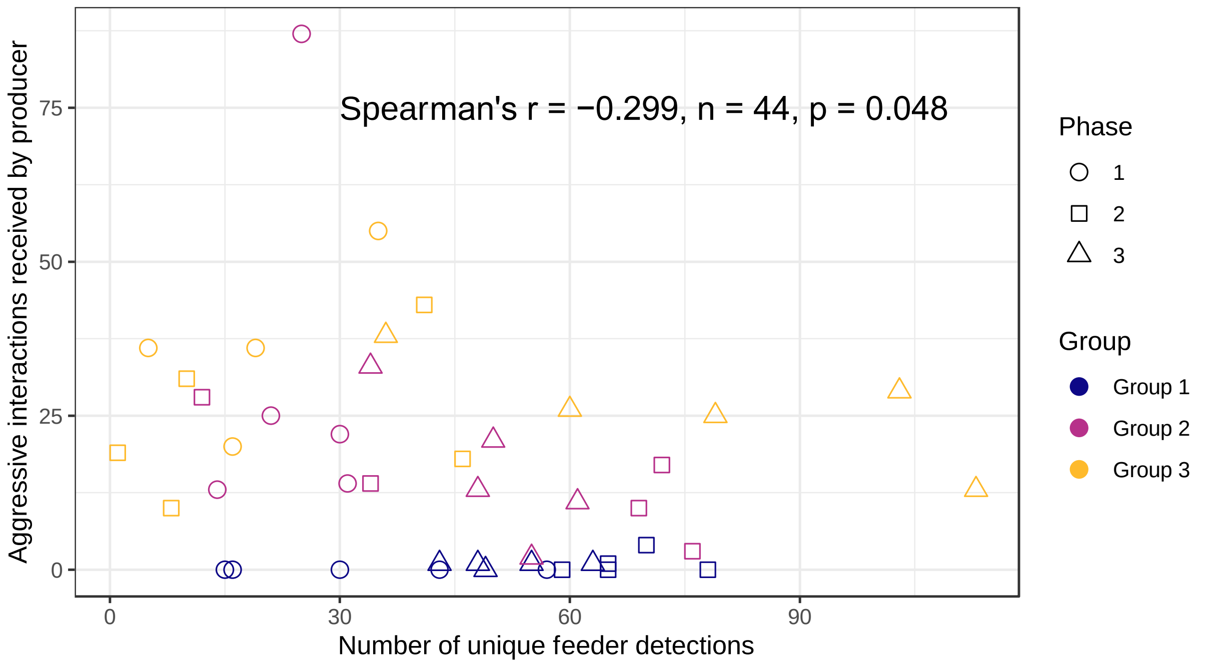

Figure S8. Correlation between producers' aggression strength and number of unique detections at the feeder per day