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Individual variation and indirect social effects in Producer-Scrounger behavior in the House Sparrow, *Passer domesticus*

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MSc in Biology

Submission date: June 2018

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Acknowledgements:

First and foremost, I would like to thank Jonathan Wright for his supervising, guidance, and insights into behavioral ecology. I would also like to thank my co-supervisors, Henrik Jensen, Thor Harald Ringsby, and Bernt Rønning. Nils Håkon Pettersen proved to be an invaluable resource with his help, experience, and knowledge from previous years of working on behavioral experiments with sparrows. I would also like to thank Yimen Araya-Ajoy for helping guide me with the statistical analysis. Bernt Rønning provided invaluable field expertise, and had a large role in helping organize the field work and the site for setting up the experiment. I would also like to thank Léo Lusardi, Jeffrey Kohld, and Dilan Saatoglu for their assistance in setting up and running the experiment. Finally, I would like to thank my family and friends for their support throughout this process.

Abstract:

Game theory is a scenario where, at its simplest, two alternative tactics may yield different costs and benefits. Many organisms are tied to a dynamic environment where the actions, social behaviors, or even presence of each organism may affect one another – such as with the producing and scrounging model. Producing involves searching for unexploited resources, and scrounging involves competing for already discovered resources. The unique approach of this study is its ability to measure individual variation in a game theory context for producing and scrounging behavior. *Passer domesticus* was chosen as the model species to test the following predictions on producing/scrounging: 1) Individuals differ consistently in their average behavior across the pair-wise trials, 2) Individuals have different propensities in switching between producer/scrounger strategies (plasticity), and 3) A particular opponent will influence the behavior of all the other individuals in that group (indirect social effect), to varying degrees. The following was demonstrated with 30 individuals (21 male, 15 female) over 278 trials: 1) Individual, repeatable variation in an individual's producing and scrounging, 2) Individuals exhibited repeatable plasticity that varied from one another for producing and scrounging, and 3) A opponent's identity significantly affected all other individuals scrounging, and to varying degrees, but had no effect on others' producing. Therefore, this study provides evidence for significant opponent effects and indirect effects, as well as the presence of repeatable strategies, variation, and plasticity for individuals.

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Introduction:

Individuals and conspecifics present in a space constitute a social environment which evolves alongside the individual social phenotype (Maynard Smith, 1982). A social behavior is one in which has fitness costs/benefits both for the individual propagating the behavior and the individual(s) receiving said behavior (Giraldeau, 2000). Social behavior and its evolution is challenging to understand and decompose due to its reciprocal nature on the fitness of the several individuals that could be involved. Insight into the evolutionary equilibriums of alternative strategies for groups or populations was provided by the advent of Game Theory. Game Theory provides methods to model the evolutionarily stable strategy (ESS) (Maynard Smith, 1982; Davies *et al.*, 2012). A strong assumption of perfect heritability of phenotypes is made due to the lack of understanding of the genetic determinants of behavior, which is true in many instances, and all of which is subject to natural selection (i.e. the phenotypic gambit, Grafen, 1984). The varying behaviors of individuals can be seen as different tactics or strategies in a game theory context, where each behavior or combination of behaviors yields certain costs and benefits and affects all the other individuals present in the social environment. These models, known as evolutionary game theory models, are essential tools for exploring the dynamics involved in the natural selection of the various social behaviors in species (Davies *et al.*, 2012).

An example of an evolutionary game theory model is with producing and scrounging, which was based upon the social foraging of house sparrows, *Passer domesticus* (Barnard & Sibly, 1981). Due to the patchiness of resources, and its variation over time, individuals often employ the tactics of either 'producing' (searching for unexploited resources; i.e. pure producing) or 'scrounging' (competing for already discovered resources; i.e. pure scrounging), or a combination of the both at varying degrees (i.e. mixed strategies). The producer-scrounger game was defined by Barnard and Sibly (1981) when attempting to

describe the occurrence of exploitative behavior, or stealing, during the feeding observations of house sparrows. Sometimes individuals behave as ‘producers’ and look for food patches on their own, and at other times they may be ‘scroungers’ where they join patches being exploited by producers. Producing has its advantages – when a patch is discovered, the producing has initial access to the resource called the ‘producer’s bonus’ (Caraco & Giraldeau, 1991). The utilization of public information allows for the possibility of scroungers to take a larger proportion food in comparison to the energy and effort used to find the food (Ranta *et al.*, 1996). Although, the potential costs for the scrounger can be high as they can receive aggression from producers during scrounging. The producer/scrounger model is negative frequency dependent, where scroungers do not do well when there are many scroungers proportionally present (in this case, the scroungers do worse than producers) but are able to gain larger benefits when scroungers present are proportionately rare (in this case, scroungers perform more well than producers) (Vickery *et al.*, 1991). A population can contain pure producing/scrounging tactics (only one or the other) and/or mixed (generalist) tactics (Vickery *et al.*, 1991; Belmaker *et al.*, 2012). If either pure or mix, or even both, an ESS is expected to occur (Vickery *et al.*, 1991; Katsnelson *et al.*, 2008; Tóth *et al.*, 2009). Due to the producer’s bonus mentioned before, the benefits of producing are always greater than zero in an ESS frequency models, whereas a population of pure scroungers are able to have a benefit of zero (especially since there are no individuals to scrounge from).

Individuals within various species have been shown to use the producing and scrounging strategies flexibly, by employing mixed strategies of both behaviors (e.g. Lendvai *et al.*, 2004). It is plausible that there are both genetic and social/environmental factors involved where evolution has led individuals to use public information, and possible experience, in making the decision to produce and/or scrounge (Belmaker *et al.*, 2012). More experiments

and investigations are necessary to understand the genetic basis underlying the predispositions of producing and/or scrounging (Katsnelson *et al.*, 2008). Levels of producing and scrounging may be affected by group size (more individuals and producers allows for more scrounging opportunities) (Vickery *et al.*, 1991), whether predators are present (vigilance may take effect, and the public information taken could be used towards scrounging) (Ranta *et al.*, 1996), and by the distribution of resources (which may affect the cost/benefits of staying at a well or searching) (Katsnelson *et al.*, 2008). Studies concerning house sparrows have shown scrounging to be affected by dominance, where it increases with higher dominance (Liker & Barta, 2002). Lower energy levels were also shown to increase scrounging (Lendvai *et al.*, 2004). Furthermore, individuals were less likely to utilize aggressive joining and took less food when scrounging on more related individuals than with less related/unrelated individuals. This effect was observed to be sex dependent as the degree of kin exploitation differed between males and females (Tóth *et al.*, 2009). In addition, learning was shown to affect strategies within the producing/scrounging model (Belmaker *et al.* 2012; Katsnelson *et al.* 2008). Learning is presumed to have evolved in this context to provide advantages within the dynamics of producing/scrounging (Katsnelson *et al.*, 2012).

The next step to understand the evolution of producer/scrounger behaviors is to measure individual variation and plasticity, which in this context is the change in producing and scrounging rates in response to certain social environments. This would allow statistics on quantitative genetics to be carried out in regards to producing and scrounging behaviors, would open avenues for the assessment of genetic versus social environment influences, and allow the assessment of the fitness consequences of different behavioral strategies in real populations. Notably, the research mentioned before involved large flocks, which does not allow for the ability to assess the effect of an individual on its social environment nor does it allow us to differentiate how individuals react to and cause changes in the social environment

based on their identity. In order to separate an individual's plasticity within said individual's behavior and to measure the impact they have on other individuals' behavior, all individuals need to be matched in pair-wise combinations and tested with one against the other in all the possible combinations of pairs within the group (Dingemanse & Araya-Ajoy 2015).

Furthermore, the social (both direct and indirect) and environment effects could theoretically be filtered to explore the genetics and influence of certain (or many) genes on social behavior. Direct genetic effects are those in which an individual's genes effect its own phenotype/behavior, whereas indirect genetic effects are those where an individual's phenotype is influenced by the expression of genes/behavior in a conspecific (Dingemanse & Araya-Ajoy 2015). Not many studies have been designed to allow for the quantification of the impact of the individual on other's behavior and the reactivity of the individual to others' behaviors (but see Hamilton & Ligoeki, 2012; Pettersen, 2017)).

Purpose and Predictions:

The aim of this project was to quantify producing and scrounging in the house sparrow at the individual level, as well as to measure individual level plasticity and social responsiveness.

This was done by testing individuals in a series of pair-wise assays consisting of all the possible combinations of individuals within the group using captured social groups of house sparrows from wild populations in mid Norway.

The following predictions were formed from previous empirical evidence and from hypothesizing the effect of individual (and genetic) differences on social behavior:

1. Individuals will differ consistently in their average behavior across the pair-wise trials. Some individuals will tend to produce more often and others will tend to scrounge more often than the population/group averages. Sex, energy levels, and health may affect the levels of producing and scrounging, such as individuals with low energy levels producing more.

Ultimately, we predict that these individual differences in behavior will be consistent and repeatable (Figure 1).

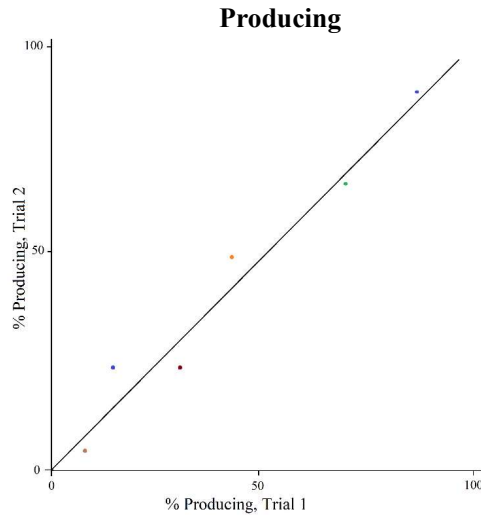


Figure 1. Describes the expected repeatabilities of an individual's percent producing versus scrounging in their first and second trials in the pair-wise assay. Each dot, color represents a different individual within a group of six individuals. *

*Adapted from "Indirect social effects of the individual strategy in producer-scrounger foraging interactions," by N. H. Pettersen, 2017, *Master Thesis*, p. 4. Copyright 2017 by NTNU. Adapted with permission.

2. Individuals have different propensities in switching between producer/scrounger strategies (plasticity). This plasticity depends on the behaviors of an individual's conspecifics/opponents (such as their rates of producing and/or scrounging). Individual repeatability in plasticity should result in some individuals being consistently more plastic than others across different sets of pair-wise assays. Plasticity may then also differ consistently due to sex or state, but even when controlling for these it is predicted that repeatable individual differences in plasticity will still emerge (Figure 2).

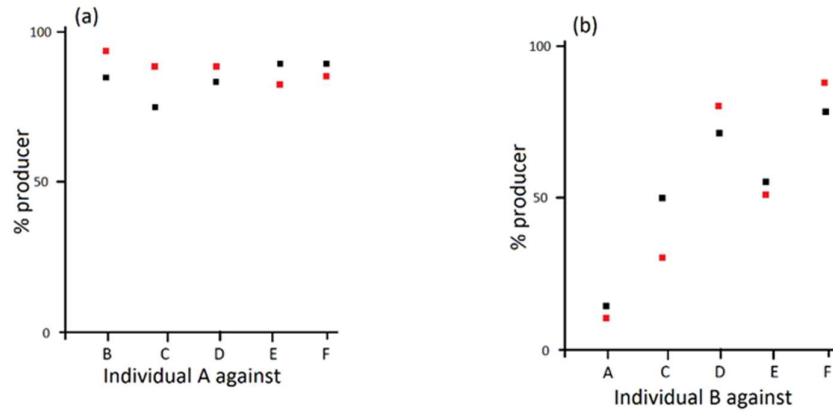


Figure 2: Examples of two different types of behavioral variation for two individuals showing the percent producing versus scrounging for individual A (a) and individual B (b) against all the other opponents. Individual A shows a consistently fixed, non-plastic response in its level of producing regardless of the identity of its opponents, and individual B shows a consistently more plastic, sensitive response towards its various opponents. The colored points represent trial one (black) and trial two (red). In this case, repeatabilities may vary depending on the opponent, such as individual B against individual E compared to B against individual C.*

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3. An individual’s behavior will influence the behavior of all the other individuals in that group.

The degree of this influence will differ repeatedly between individuals over the trials. Certain individuals are predicted to have larger effects on an opponent’s levels of behavior than other individuals. Individuals with more fixed strategies, such as nearly-pure producing or scrounging, may have the largest effect on the behavior of more plastic individuals (Figure 3).

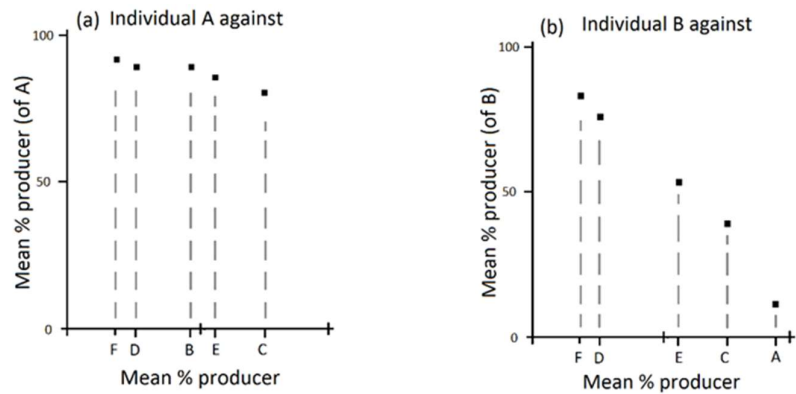


Figure 3: Predicted impacts of different mean percent producing versus scrounging of opponents on the mean percent behavior of individual A (a) and individual B (b). The fixed, non-plastic behavior of individual A is predicted to have the largest impact on the changes in behavior of others, as seen by the decrease in plasticity of individual B when against A.*

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Methods:

The house sparrow was selected as the study species due to its fit as a model social species which displays producer/scrounger behavior. The experiment here is connected to a larger, extensive study on house sparrows by the Centre for Biodiversity Dynamics (CBD) and the Norwegian University of Science and Technology (NTNU). It has been ongoing for over 20 years, and includes extensive genetic, dispersal, morphometric data, and a large genetic pedigree.

Study Location and Set-up

The experiment was conducted on the island Lauvøya, located in the municipality of Åfjord on the coast of mid-Norway. The island contained approximately 20 birds, which were all, more or less, part of one flock. Before catching the birds, we built the experimental rooms within a sealed, heated barn (Figure 4). Power, heating, lighting, and natural materials such as branches were placed in each room. Checkerboard feeders, which were made beforehand were placed in the training and experiment rooms (Figure 5).

We were able to catch almost, if not all, the house sparrows on the island which totaled to 19 individuals. In addition, 17 birds were caught nearby from mainland Åfjord. This allowed us to reach our total goal of 36 birds, which consisted of with 21 adult males and 15 adult females.

The birds were placed in groups of 6 individuals, preferably 3 males and 3 females, and grouped as much as possible according to capture site/timing to match the presumed familiar social groups in the wild. All individuals were captured using mist nets, and then held in the sealed central barn (with *ad lib* food, where the temperature approximately ranged from 7-13°C), for a period of 14 days, from the 1st to 14th March, 2017. The birds were marked with an individual, unique ring combination (consisting of one numbered metal ring and three colored plastic rings), and then measured and analyzed as part of CBD's long-term study. The measurements included: weight, tarsus length, wing length, beak length and depth, and any difficulties in breathing (i.e. presence of lung parasites). Furthermore, each individual's sex and age was recorded, as well as a small blood sample (ca. 25µL) in order to obtain DNA for genetic analysis.

The large feeders, which were placed in the training and group rooms, were 1.2m x 1.2m panels with 144 small sand-filled, recessed wells in each feeder. The wells were equally distanced from each other. The aim was for only some of the wells to contain seeds in order to create a clumped resource that could be discovered by producers and then also exploited by the scroungers that joined them. The wells themselves were made by filling 50mL tubes up to the 45mL mark with clay in order to create sturdy, nearly filled wells that the birds could reach the bottom of. For a well that would contain seed, ~30 seeds and 5mL sand were mixed and then added to that well in order to provide the birds with a substrate to search through for the seeds and slow down consumption (i.e. by the producer before being joined by any scrounger) once they were discovered. The seed used in the experimental trials was brown millet. The 'Group' experiment boards contained 13.04 ± 0.8 grams seed while the 'Pair' boards contained 4.34 ± 0.5 grams seed per trial. If the well did not contain seed, then it was filled with 5mL sand. All the wells were then covered with a thin layer of sand in order to conceal any seeds laying on the top, preventing possible visual cues as to which wells contained seed – i.e. producers had

to physically search for wells containing seeds by disturbing the sand surface. By filling only 60 of the 144 wells with sand-seed mix for the ‘Group’ boards and covering all wells with sand during the experimental trials, it was presumably more difficult to be a producer since searching would be required. Group trials lasted around 90 minutes with each 6 bird flock/group although group trial data is not included in the results or analysis here (due to time constraints).

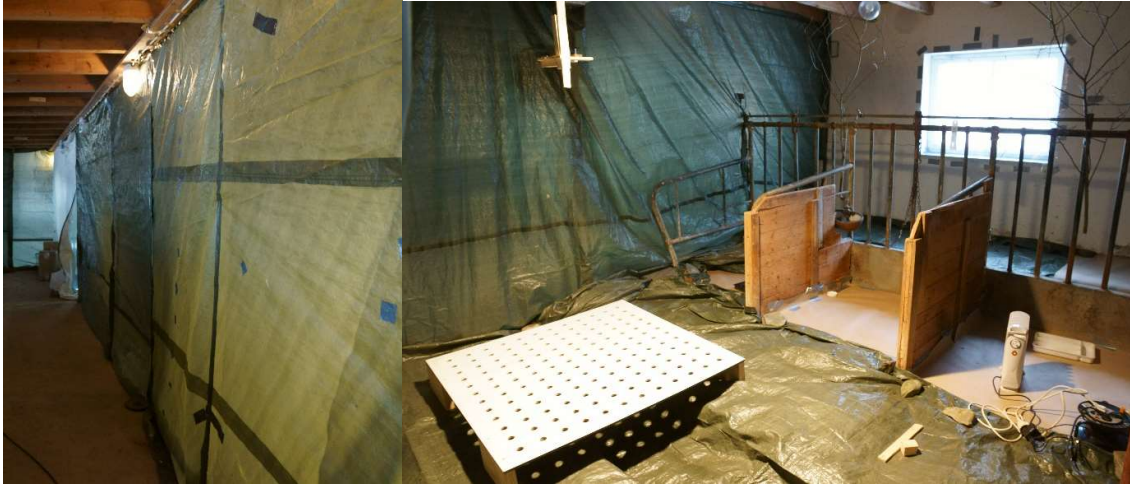


Figure 4. Photos of the inside of the barn and the setup of one of the rooms, which contains a group feeder with its 144 wells.

Communal Room #1	Communal Room #2
	Pair-Wise Room
	Group Room
	Training Room #2
	Training Room #1

Figure 5. The layout of the rooms is presented in this diagram. Each room had a sealable entrance, and the two communal rooms served to separate the island and mainland populations after the groups finished their time in the experiment



Figure 6. A frame from one of the videos showing a pair of individuals feeding during a pair-wise trial. The pair-wise checkerboard feeder contains 49 wells that were labeled to identify both the board and the wells visited by an individual.

During the individual sparrows' stay in the central barn, we conducted both group-feeder trials per flock and pair-wise trials for all combinations of individuals within those flocks. Water was continuously provided in all the rooms and between the trials. The birds of a single group of 6 spent their first day training on a communal checkerboard feeder in training room #1 (see Figure 5) with *ad lib* access to food (a variety of seed both such as sunflower, oat, and millet on top of and in the wells), before their food was taken away for the night. Then, the second day involved training on a communal checkerboard feeder in training room #2, with *ad lib* access to millet and having the food taken away for the night at 21:00. Feeders were covered at 21:15 every night in groups that were given *ad lib* access to food and which were going to be in an experimental trial the next day. The difference in training room #2 from training room #1 was that in the morning the birds in training room #2 were presented with a sand and seed

mixture in the wells of the feeder with seeds on top of the sand and a sand/seed mixture in only some of the wells during the afternoon with no seed on top of the wells. Some wells were filled with the sand/seed mixture, but the birds couldn't know until they searched through the sand. This was done to acclimate the birds to the sand and the presence of seeds within some of the wells. The trial days began on days 3 and 4 for each group. Each bird was marked on their tail with a different colored acrylic paint, which allowed them to be readily distinguished on video by the overhead GoPro® cameras in both the group and pair-wise trials. On the third day, the birds were presented with the communal (large checkerboard) group feeder assay in the morning with sand covered wells (with a hidden seed/sand mix under the sand of some of the wells), and a pair-wise (small checkerboard) feeder trials in the afternoon (with a hidden seed/sand mix under the sand of some of the wells). After the afternoon trials, they were given *ad lib* food access that was taken away for the night at 21:00. On the fourth day in captivity they experienced a repeat of the pair-wise assays in the morning (but in a different pairing order), and a repeat of the group feeder assay in the afternoon. At the end of the fourth day, each experimental flock was placed in the main barn holding area with *ad lib* food before being released back within close proximity to their capture location. Therefore, the experiment order in day 3 and 4 was group, then pair-wise, then group, then pair-wise trials. From Group 3 onwards, the order was changed and only one group was tested at a time in the experimental rooms instead of two (one in group-wise and one in pairwise). These groups had the group trial in the morning of day 3, pair-wise trial in the afternoon of day three, and then returned to the group room for *ad lib* food which was removed at 21:00. For day 4, the group would undergo the group trial in the morning and the pair-wise trial in the afternoon, and then released in the communal room. Any time the birds were caught, such as to move them from the group trial room to the pair-wise trial room, they were weighed and their tails were repainted with the same colors if they showed signs of fading.

In the pair-wise assays, we tested every combination of two individuals within the same group, chosen in a stratified, random order each time. Since each group contained 6 individuals, this resulted in 15 unique pair-wise combinations and allowed to check for opponent (partner of the focal individual in a pair-wise trial) and order effect. Three pair-wise combinations were tested simultaneously at a time thus constituting a trial, and this was done 5 times in order to get all 15 unique combinations during the pair-wise assay. There was a 20-minute pause between each pair-wise trial. During the 20-minute pause, the birds were placed back in their cages, the remaining seed was collected from each pairwise board, the boards were cleaned, and then the wells were refilled in their specific pre-determined random orders. Each trial started approximately 30 seconds after the experimenters left the room and when the birds began to settle down. The pair-wise trials lasted for 15 minutes, where at the end the birds were placed back in their cages and the feeders reset. The pair-wise feeders were 34% of the size of the group feeders (i.e. $7 \times 7 = 49$ wells with only 20 containing seeds). The data recorded included the well identity visited and any social interaction at the well and thus amount of producing and scrounging, and additional variables concerning the social interaction, etc., as described in Table 1.

The birds from Groups 1 and 2 were kept and assayed at the same time, and they were staggered by one day from each other so that only one group of was doing the pair-wise assay at any one time. The staggering was increased by one day and only one group was assayed at a time from Group 3 onwards. This allowed the whole experiment to be completed in 14 days, in addition to a few days at the start to set-up and catch the birds and at the end to dismantle and return the birds to their capture sites.

Video Analysis

The pair-wise feeders were equipped with GoPro[®] cameras to the top of the cages covering the feeders, and the room containing the communal feeder for the group assay was fitted with a GoPro about 1 meter from the ceiling on a mount. All the GoPro's[®] were connected to an external power supply in order to allow for continuous recording. Recording began before the start of a trial and ended at the end of each trial. The GoPro[®] app was used in tandem with wifi-enabled GoPro[®] cameras in order to observe a live-feed of the ongoing trials. This was a safety measure to ensure every trial was running properly, the cameras were recording, and to stop the trial if the birds appeared too stressed to continue for that trial or round (note, round here specifies the first and second trial days as round 1 and round 2, respectively). At the end of each day, the videos stored on each GoPro[®] camera's microSD cards were transferred to an external hard drive. Only the pair-wise videos were analyzed for the results due to time limitations, but the group trial videos are available for further analyses in the future. The pair-wise videos were analyzed by one individual and under specific guidelines. The observer kept track of the identity of the pair in the trial, the trial start time, trial end time, the wells visits and n^{th} well visited, if producing or scrounging occurred, the rank of any interaction, the start and end time of a well visit, the duration of a well visit, if a well visit was excluded, the duration of any fight, the observable stress level of the focal bird, if the bird showed significant levels of observing/monitoring, if the individual paced, flew, preened, and/or slept at any point. Table 1 details all the observations and their parameters. Table 2 details the social interactions and their parameters. Producing was recorded when an individual occupied a well with food, and scrounging was recorded when an individual joined/interacted at the well in which the other individual was producing from. Observations were measured in minutes and seconds and were then converted to seconds.

Observation Name	Parameters
Pre-Pair Round Weight	The weight of an individual before the start of the pairwise trials, and it is measured in grams to the nearest tenth of a gram.
Well Order	The n^{th} well visited for the focal individual. It counts only when the individual stays 1 second or longer at the well or if the individual interacts with the well such as searching through sand or scrounging from another individual producing at a well.
Square	Each of the 49 wells is designated a label with, and the wells are labeled in a grid format with the columns as a letter from A to G and the rows from 1 to 7 (for ex. A1, A2,...,G7).
Neighbor	An opponent is recorded as a neighbor if they are within a one well distance from the focal individual when a new well visit occurs for the focal individual. It is only recording if a neighbor was present during the beginning of the visit to the well.
Square Arrival Time; Square Exit Time; Well Duration	These measures are for the time when the focal individual has arrived at a well, the time it has left a well, and the duration of the stay at the well. It is measured to the nearest second.
Join Act	When an individual joins another individual at a well, it is given a rank for the type of interaction that occurs. See Table 2 for the various interactions measures.
Intruder Time; Intruder Act	When an individual is at a well, intruder time is the time when an intruder joins the focal individual. The intruder act is the interaction which occurs. It is measured to the nearest second. See Table 2 for the various interactions measured.
Fight Duration	This is the duration of interactions (in seconds, to the nearest second) where aggression is given by both individuals. Fight times only greater than or equal to one second are recorded. An act can be considered a fight if it includes repeated attacks and defending. It does not have to be a continuous fight, but it should occur repeatedly in a short period of time (less than 10 seconds) to count.
Trial Start; Trial End	The time a trial begins after all the experimenters have left the area and when the trial ends (approximately after 15 minutes). The time is measured in minutes and seconds, to the nearest second.
Sleeping	It is recorded (to the nearest second) when an individual sleeps at any point during a well visit or in close proximity to a well
Pacing	Pacing is recorded (to the nearest second, as a behavior which consists of rapid movement along the edges of the feeder. No feeding is involved during pacing, and it is not recorded as pacing if it occurs between flights of the focal individual which are less than 30 seconds apart.

Flying	Anytime the focal individual leaves the board, that is considered flying. When the individual returns to the board, that is one flight. The time which the first flight occurred and the last flight are recorded for the duration (to the nearest second) and number of flights. The flight duration end at the last flight before a well visit. Flights occurring after 30 seconds between each other are recorded as different flying events. Pacing often occurs between flights, but it is not included in the pacing measurement unless consecutive flights are greater than 30 seconds apart.
Preening	Preening is recorded as occurring anytime an individual preens and cleans its feathers.
Observation	<p>Observation is recorded as a factor from 0-5 to approximate the degree an individual is observing (the rest of the feeder or another individual) and not feeding during a well visit.</p> <p>0 = little to no observation (0-10%)</p> <p>1 = some observation (11-30%)</p> <p>2 = nearly half observation (31-50%)</p> <p>3 = half observation (51-70%)</p> <p>4 = mostly observation (71-90%)</p> <p>5 = only observation (91-100%)</p>
Stress	<p>Stress is recorded as a factor from 0-5 to describe the observable stress level of the bird, especially how puffed the feathers are.</p> <p>0 = appears normal (mobile, quick)</p> <p>1 = Active, but slightly fluffed (slightly slower, still mobile)</p> <p>2 = Active, very fluffed (wings visibly droopy, slow, less mobile)</p> <p>3 = Inactive, fluffed (almost no mobility, lethargic, slow head movements, no eating, little to no interaction with the well)</p> <p>4 = Inactive, very fluffed (almost no mobility, lethargic, slow head movements, no eating, wings outstretched and very droopy, little to no interaction with the well)</p>
Excluded	Recorded if the focal individual has no interaction with the well the it is residing at, and must be more than a one second break from foraging (for example: resting at well, sleeping at well, preening at well, only observing at a well with no feeding). Note, this serves to measure wells with (long) periods of inaction.

Table 1. Shows the different parameters used for the video analysis

Type of interaction		Intruder Aggression	Resident Aggression
0	No interaction	None	None
1	Nothing happens	None	None
2	Resident moves to make place, but stays at the well	None	None
3	Displacement, the resident moves to another well	Giving	Receiving
4	Resident pecks but both stays	Receiving	Giving
5	Intruder pecks but both stays	Giving	Receiving
6	Both pecks and both stays	Both	Both
7	Resident pecks and leaves	Receiving	Giving
8	Intruder pecks and leaves	Giving	Receiving
9	Resident pecks and intruder leaves	Receiving	Giving
10	Intruder pecks and resident leaves	Giving	Receiving
11	Both pecks and intruder leaves	Both	Both
12	Both pecks and resident leaves	Both	Both
13	Both pecks and both leaves	Both	Both
14	Resident pecks and both leaves	Receiving	Giving
15	Intruder pecks and both leaves	Giving	Receiving

Table 2. Shows the classification of interactions used for the video analysis.*

*Adapted from “Indirect social effects of the individual strategy in producer-scrounger foraging interactions,” by N. H. Pettersen, 2017, *Master Thesis*, p. 10. Copyright 2017 by NTNU. Adapted with permission.

Data and Statistical Analysis

The total number of pair-wise trials that could be used was reduced from 360 (6 individuals * 6 groups * 5 trials per day * 2 days) to 278. This was due to several factors: Group 6 had to be removed completely because of signs of high stress and non-participation (leaving there to be n = 30 individuals), some pair-wise trials had to be cut short or individuals removed because of high stress and non-participation, and due to some human/technical errors. The human/technical errors involved videos which did not record the entire trial, battery failures, or issues of the videos saving properly to the memory cards. Note that due to this, there are several pairs that do not meet twice and, thus, do not have repeated measurement for the pairs. This is accounted for, as are several other factors, with the use of mixed effect models. First, all the pair-wise data taken from the video analysis were extracted and combined into a single .csv file. This file was then checked in MSEXcel for any missing data or mistakes due

to human error. Each individual was given a unique identifier from 1 to 30, observations such as producing and scrounging were turned into binaries (1 when it occurred, 0 when it did not) in order to allow for simpler statistical analyses. The statistical software R (R Core Team, 2018) was used to extract general statistical parameters from the data set, such as the means, min/max, and frequency of observations and variables. Plots were created using these results within R for visualization. The distribution of the data was visualized in various plots to help determine the method and models to utilize.

Linear mixed effect models and generalized mixed effect models were employed using the lme4 (Bates *et al.*, 2014) package within R. These models allow for the assessment of variance by utilizing different random and fixed effects, including the effects of the individual and its opponent in the pair-wise trials. The fixed effects are the predictor variables, and the random effects account for the variance within the model. There are random effects with random slopes and intercepts, such as focal ID and opponent ID with the opponent's behavior as the slope (i.e. level of producing or producing versus scrounging). This allows for closer analysis of the effect of the opponent on an individual via its ID or its level of behavior. The following focal response variables were used: (a) Producing count (the amount of producing per trial), (b) Producing Duration (the time spent producing per trial), (c) Scrounging Count (the amount of scrounging per trial), (d) Scrounging Count Ratio (total scrounging divided by the total of producing and scrounging; this gives a proportion representing the total opportunities to scrounge) (e) Scrounging Duration (the time spent scrounging per trial, given in a ratio similar to (d) but with durations instead). In addition to the normal mixed modeling, response variables (c), (d), and (e) were modeled with the opponent total producing in the slopes of the 'Focal ID' random effect (Table 5).

Variance partitioning (VPA) and hybrid approaches (HA) mixed-effect models were utilized. These statistical methods allow for analysis of the variation in the phenotype of the focal

individual, which can possibly be due to among-opponent effects and variation in phenotypes. The VPA models have the focal ID and opponent ID as the random effects and intercepts. The random factor of 'trial' was added as well in order to account for any trial-specific effects such as order. With the VPA used in this manner, it allows for the decomposition of the variance into two target areas: the focal individual and the opponent. HA uses the same method, but adds the opponent behavior of interest in the fixed effects. This opponent behavior is added a covariate and it helps account for the potential effect of the opponent behavior(s) on the focal's response variable. When this covariate was added the effect of the opponent behavior on the focal individual is entirely accounted for, and the random effect of opponent ID can potentially drop to zero since it no longer accounts for any of the variance in the model, unlike in the VPA model with no covariate added. The comparison of these two methods of approach (VPA versus HA) allows for the quantification of the magnitude of effect of behavioral traits of the opponent individuals on the response behavior of the focal individual that is of concern (Dingemanse & Araya-Ajoy, 2015). Both the VPA and HA models contained the fixed effects of day, such as 1 or 2 of the experiment, and of sex. An interaction of these two fixed factors was also included in the models, and this allowed for the assessment of the significance of any potential differences of the sex's response behavior in relation to the day of the experiment.

The 'Producing Count' and 'Producing Duration Count' assumed a Gaussian error distribution of residuals for its models, the 'Scrounging Count' assumed a Poisson distribution, and the 'Scrounging Count Ratio' and 'Scrounging Duration Count Ratio' assumed a binomial distribution since their response variables were incorporated as a binomial trait that represented the proportion of scrounging to the total producing and scrounging. All the models were tested in R, and the values were extracted from ANOVA

summaries and transferred to the summary tables in Tables 3, 4, and 5. A correlation matrix was also produced in R to check for any confounding factors.

In Tables 3, 4, and 5, the significance of the random effects was measured and represented by their probability values (p-values). Likelihood ratio tests are χ^2 distributed tests that test a model of concern against a null version of that model, and they were measured as two times the difference in log-likelihood between models in which the random effect of concern was present to those in which they were not present, essentially forming the null models (Shaw 1991). These tests reveal the likelihood of the effect to be in one model over the other, which are revealed as a p-value in the ANOVA summaries comparing the two models (the model and its null) in R. These likelihood ratio tests when applied to the variance can have their p-value calculated with the degrees of freedom (df) equal to 0.5. This is due to variances always being positive and with the assumption of equal combinations of p with df=1 and df=0 (Self & Liang 1987; Visscher 2006).

Repeatability values were measured in order to test whether individuals were consistent in their behavior and respond plastically to repeatable measures and differences of the opponent's behavior/trait. This repeatability value is measured as the proportion of variance explained by the random effects to the total variance which is not explained by or attributable to the fixed effects (Santostefano *et al.*, 2016). This allows for the separation between the focal individual and opponents' proportion in the total variance observed. The binomial models' repeatabilities were calculated using the method described by Nakagawa and Schielzeth (2010). Once the analysis was complete, the residuals and effects were once again visualized with ggplot2 (Wickham, 2009) and served as aids to understand trends signified by the models of interest. Nearly all the averages reported in the statistics include their standard error (SE).

Results:

General Statistics

In the pair-wise trials, the mean total producing count for all individuals was 33.23 ± 1.17 times, with the range being from 0-113 times. The mean total scrounging count was 2.06 ± 0.24 , with the range being from 0-36 times. Total producing duration had a mean of 335.19 ± 12.10 seconds, with the range being from 0-731 seconds. The total scrounging duration had a mean of 13.90 ± 1.75 seconds, with the range being from 0-256 seconds.

The proportion of scrounging to producing was slightly less in the duration measurements than in the counts. There was an instance of one individual who produced 0 times and for 0 seconds, which was a female from Group 3. In addition, all the individuals, except for one, had at least one instance in which they did not scrounge at all during a trial. The mean number of instances in which an individual scrounged 0 times during an entire trial was 3.8 ± 2.5 times out of 5 times 2 trials per individual (i.e. around 40% of trials).

(See Appendix for distributions of producing and scrounging)

The mean capture weight of all the individuals involved in the analysis (Groups 1-5; 30 individuals) was 30.18 ± 0.10 grams. The mean pre-pair round weight was 28.52 ± 0.10 grams. The mean total trial time was 893.88 ± 2.35 seconds and the mean number of well visits per trial was 61.31 ± 1.91 visits. In addition, a neighbor was present on average 11.52 ± 0.58 times per trial. On average, the amount of seed remaining after a trial was 3.39 ± 0.03 grams.

Count Data

Fixed Effects	(a) Producing Count [Normal]		(b) Scrounging Count Ratio [Binomial]		(c) Scrounging Count [Poisson]	
	VPA	HA	VPA	HA	VPA	HA
Intercept ± SE	-0.301 ± 0.280	-0.161 ± 0.255	-2.584 ± 0.294 (p < 2e-16)	-2.492 ± 0.294 (p < 2e-16)	0.370 ± 0.282 (p = 0.189416)	0.674 ± 0.273 (p = 0.01361)
Sex ± SE	0.015 ± 0.374 (p = 0.984)	-0.075 ± 0.336 (p = 1.000)	-1.879 ± 0.447 (p = 2.66e-05)	-1.995 ± 0.450 (p = 9.19e-06)	-1.518 ± 0.417 (p = 2.74e-04)	-1.801 ± 0.405 (p = 8.74e-06)
Day ± SE	0.194 ± 0.139 (p = 0.098)	0.108 ± 0.133 (p = 1.000)	-0.080 ± 0.117 (p = 0.493)	-0.170 ± 0.123 (p = 0.168)	0.261 ± 0.100 (p = 0.009)	0.014 ± 0.108 (p = 0.89569)
Day x Sex Interaction ± SE	0.016 ± 0.189 (p = 0.934)	0.061 ± 0.179 (p = 1.000)	0.536 ± 0.208 (p = 0.010)	0.619 ± 0.215 (p = 0.004)	0.311 ± 0.183 (p = 0.090)	0.516 ± 0.193 (p = 0.00752)
Opponent Total Producing ± SE	X	0.304 ± 0.056 (p = 1.15e-06)	X	0.212 ± 0.055 (p = 1.22e-04)	X	0.480 ± 0.053 (p < 2e-16)
Random Effects						
Focal ID	78.870 (p = 1.14e-09)	0.264 (p = 3.57e-10)	0.608 (p < 2.2e-16)	0.577 (p < 2.2e-16)	0.566 (p < 2.2e-16)	0.443 (p < 2.2e-16)
Opponent ID	2.90e-12 (p = 1.000)	0.055 (p = 1.000)	0.119 (p = 9.89e-08)	0.115 (p = 1.22e-06)	0.197 (p < 2.2e-16)	0.215 (p < 2.2e-16)
Trial Number	31.270 (p = 1.000)	0.000 (p = 1.000)	1.03e-08 (p = 1.000)	0.001 (p = 0.848)	0.002 (p = 0.7671)	0.014 (p = 0.114)
Residual	0.604	0.538	X	X	X	X
Repeatability						
R among	0.400	0.308	0.151	0.145	0.140	0.112
R opponent	0.000	0.064	0.030	0.029	0.049	0.054

Table 3. Results from mixed effect models for the following ‘count’ (frequency) response variables: (a) producing, (b) scrounging ratio, and (c) scrounging. The response variables each have models using the variance-partitioning approach (VPA) and the hybrid approach (HA). The hybrid approach includes a fixed covariate predictor variable of the total level of producing per trial for the opponent (Opponent Total Producing). The estimates, standard errors and p-values are provided for the fixed effects, and the variance and p-values are provided for the random effects. Repeatability measurements are provided for each model as well. Residuals are only provided for the linear mixed effect model (a)

Time Data

Fixed Effects	(a) Producing Duration [Normal]		(b) Scrounging Duration Ratio [Binomial]	
	VPA	HA	VPA	HA
Intercept ± SE	-0.051 ± 0.284	-0.018 ± 0.262	-3.206 ± 0.390 (p < 2e-16)	-3.291 ± 0.400 (p < 2e-16)
Sex ± SE	0.404 ± 0.372 (p = 0.504)	0.266 ± 0.349 (p = 1.000)	-1.956 ± 0.471 (p = 3.31e-05)	-2.193 ± 0.472 (p = 3.32e-06)
Day ± SE	-0.045 ± 0.137 (p = 0.488)	-0.053 ± 0.136 (p = 1.000)	-0.003 ± 0.048 (p = 0.947)	0.021 ± 0.050 (p = 0.675)
Day x Sex Interaction ± SE	-0.099 ± 0.186 (p = 0.5917)	-0.037 ± 0.184 (p = 1.000)	0.291 ± 0.078 (p = 1.87e-04)	0.372 ± 0.080 (3.17e-06)
Opponent Total Producing ± SE	X	0.230 ± 0.055 (p = 5.45e-05)	X	0.488 ± 0.029 (p < 2e-16)
Random Effects				
Focal ID	0.41497 (p = 1.89e-09)	0.298 (p = 1.71e-08)	1.442 (p < 2.2e-16)	1.430 (p < 2.2e-16)
Opponent ID	0.00000 (p = 1.000)	1.16e-16 (p = 1.000)	0.666 (p < 2.2e-16)	0.775 (p < 2.2e-16)
Trial Number	0.015 (p = 0.159)	4.93e-03 (p = 1.000)	0.054 (p < 2.2e-16)	0.076 (p < 2.2e-16)
Residual	0.581	0.571	X	X
Repeatability				
R among	0.410	0.294	0.264	0.257
R opponent	0.000	1.32e-16	0.122	0.139

Table 4. Results from mixed effect models for the following ‘duration’ (seconds) response variables: (a) producing, (b) scrounging ratio. The response variables each have models using the variance-partitioning approach (VPA) and the hybrid approach (HA). The hybrid approach includes a fixed covariate predictor variable of the total level of producing per trial for the opponent (Opponent Total Producing). The estimates, standard errors and p-values are provided for the fixed effects, and the variance and p-values are provided for the random effects. Repeatability measurements are provided for each model as well. Residuals are only provided for the linear mixed effect model (a)

Non-Random Slopes Data

Fixed Effects	(a) Scrounging Count [Poisson]	(b) Scrounging Count Ratio [Binomial]	(c) Scrounging Duration Ratio [Binomial]
	HA	HA	HA
Intercept ± SE	0.875 ± 0.301 (p = 0.004)	-2.329 ± 0.321 (p = 3.82e-13)	-3.183 ± 0.428 (p = 1.11e-13)
Sex ± SE	-1.944 ± 0.438 (p = 8.85e-06)	-2.116 ± 0.472 (p = 7.27e-06)	-2.934 ± 0.471 (p = 4.76e-10)
Day ± SE	-0.074 ± 0.124 (p = 0.551)	-0.275 ± 0.136 (p = 0.043)	-0.168 ± 0.056 (p = 0.003)
Day x Sex Interaction ± SE	0.540 ± 0.208 (p = 0.009)	0.662 ± 0.224 (p = 0.003)	0.872 ± 0.094 (p < 2e-16)
Opponent Total Producing* ± SE	0.443 ± 0.113 (p = 8.22e-05)	0.213 ± 0.101 (p = 0.035)	0.627 ± 0.189 (p = 8.85e-04)
Random Effects			
Focal ID	0.504 (p < 2.2e-16)	0.680 (p < 2.2e-16)	1.980 (p < 2.2e-16)
Focal ID Slope [Opponent Total Producing*]	0.171 (p = 0.006)	0.106 (p < 2.2e-16)	0.951 (p < 2.2e-16)
Correlation of Intercept-Slope	0.09	-0.35	-0.59
Opponent ID	0.203 (p = 4.28e-14)	0.123 (p = 1.15e-06)	0.814 (p < 2.2e-16)
Trial Number	0.012 (p = 0.167)	0.002 (p = 0.772)	0.096 (p < 2.2e-16)

Table 5. Results from mixed effect models for the following response variables: (a) scrounging count (frequency), (b) scrounging count ratio, and (c) scrounging duration ratio. The response variables each have models using the hybrid approach (HA) which includes a fixed covariate predictor variable of the total level of producing per trial for the opponent (Opponent Total Producing). Opponent Total Producing is included as an effect in the slopes of Focal ID, and a correlation of Opponent Total Producing to Focal ID slope is given. The estimates, standard errors and p-values are provided for the fixed effects, and the variance and p-values are provided for the random effects.

*Opponent total producing is count for the count models and duration for the duration models

Focal ID

Focal ID as a fixed effect was significant in all the models and, in each case, explained the highest proportion of variation of the intercepts in the models (Tables 3-5). The VPA model had an among individual (R among) repeatability of 0.400 (Table 3 (a)). This suggests that there was consistent, and repeatable, levels of producing among individuals. In Table 3 (b) and Table 4 (b), the among individual repeatabilities were 0.151 and 0.145 and 0.264 and 0.257, in that order. This suggests that the Total Scrounging Duration models in Table 4 (b) have a higher level of ability to detect among individual repeatabilities (~1.75x) than in the Total Scrounging Count models in Table 3 (b). In terms of repeatabilities, these results are still not too high.

In regard to prediction 1, the results suggest that there were individual differences in producing that are repeatable, but less so for scrounging count and scrounging duration. Both producing and scrounging, in all the models, showed levels of variation for the individual (Figures 7 and 8).

Opponent Effect

The opponent can have varying magnitudes of effect on all the other individuals in regards to producing and scrounging, and their respective plasticities (Figures 11 and 12; see plasticity below). The effect of an opponent on the other individuals is key to answering predictions 2 and 3.

The opponent ID has no significant effect on the total producing (Table 3 (a), Table 4(a)) but it has a very significant effect on total scrounging. Tables 3 (a) and 4 (a) show p-values = 1.00 for the opponent ID in all the models, including both the VPA and HA models. The

non-significance of the effect can also be seen in Figure 11 below, where the means of total producing of others against a focal ID are nearly the same. The opposite is the case for scrounging, where scrounging has a very significant effect in all the models in Tables 3-5. The opponent ID is also significant in Table 5, where the opponent total producing count/duration has a significant effect in the slope of the focal individual's scrounging (see 'Plasticity' below).

Regarding prediction 3, the opponent has no significant effect on a focal individual's total producing (Figure 11), but the opponent does have a significant effect on the focal individual's scrounging (Figure 12). Sex plays a role in the opponent's effect on a focal individual's rate of scrounging, and the fixed effect of sex was significant in all the models. For the repeatable effect of the opponent's measured response onto the focal individual's response, the repeatability of the opponent was negligible or very small for producing (Table 3 (a) and Table 4 (a)). The scrounging opponent repeatabilities were very small in Table 3. On the contrary, the opponent repeatability was higher, such as $R_{\text{opponent}} = 0.139$, in the Scrounging Duration models in Table 4 (b). This suggests that there is some repeatability in the opponent's phenotype in how it affects the focal individual's scrounging (Figure 12).

Prediction 2, concerning the effect of the opponent's total producing on the slope of the focal ID is answered below in 'Plasticity' and can be seen in Figures 9 and 10.

Plasticity

The plasticity of an individual in its ability to adjust its rates of producing and/or scrounging are key to answering prediction 2. Table 5 provides scrounging models that address the prediction and Figures 9 and 10 provide the slopes from the pair-wise data. Producing is not

included since it was seen earlier that the opponent does not have a significant, observable effect on the levels of producing of others (including the focal).

Table 5 (c) shows a clear correlation of -0.59 in the focal slope in response to opponent total producing duration, and all the fixed and random effects, including the slope and opponent, are significant. The scrounging duration ratio model (Table 5 (c)) shows the most significant effects and pronounced correlations that the scrounging count and count ratio models (Table 5 (a) and (b)). This suggests that scrounging duration ratio provides necessary, important information in producing-scrounging models that should not be overlooked. In Table 5 (c), the fixed effect of sex was significant; there appears to be a difference between the slopes of males and females (Figures 9 and 10), which is supported by the differences in rates of scrounging between males and females where females scrounge more than males (Figure 15).

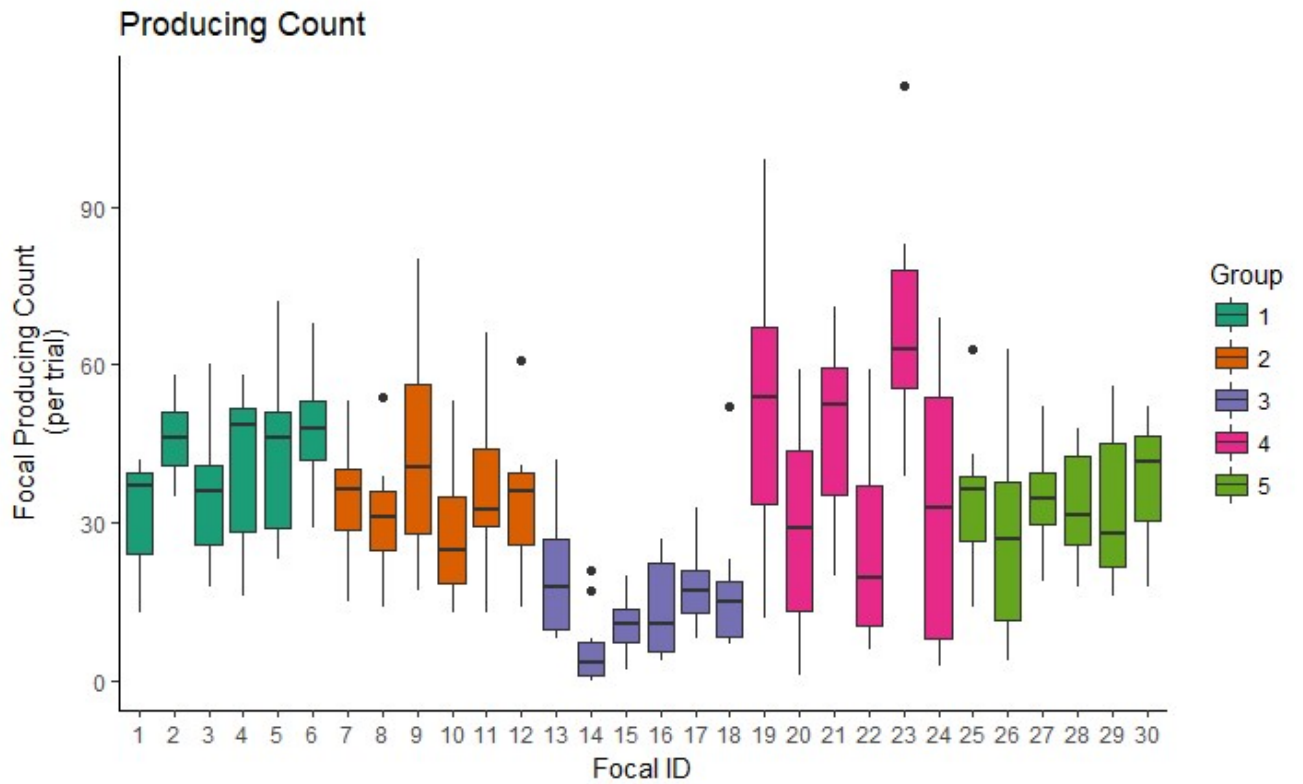


Figure 7. The focal individual's producing count (per trial), colored by group

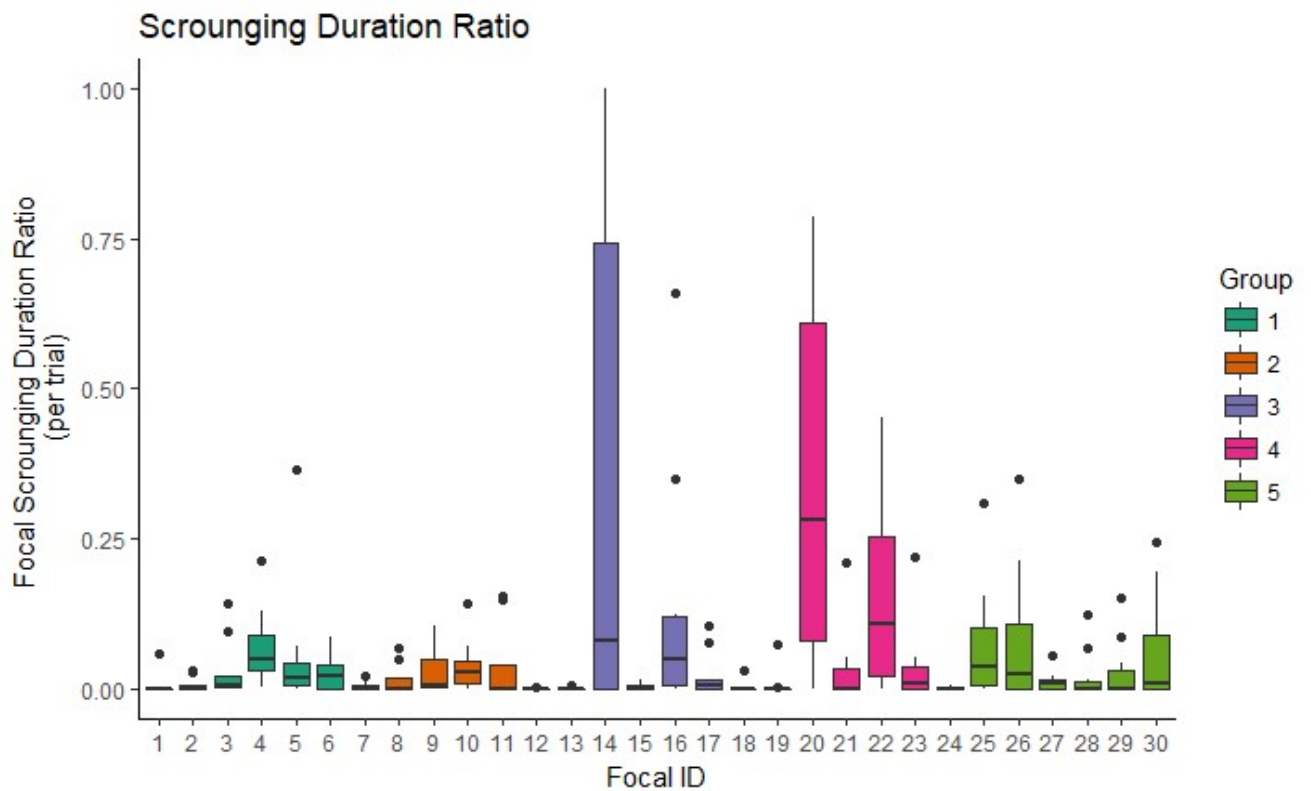


Figure 8. The focal individual's scrounging duration ratio (per trial), colored by group

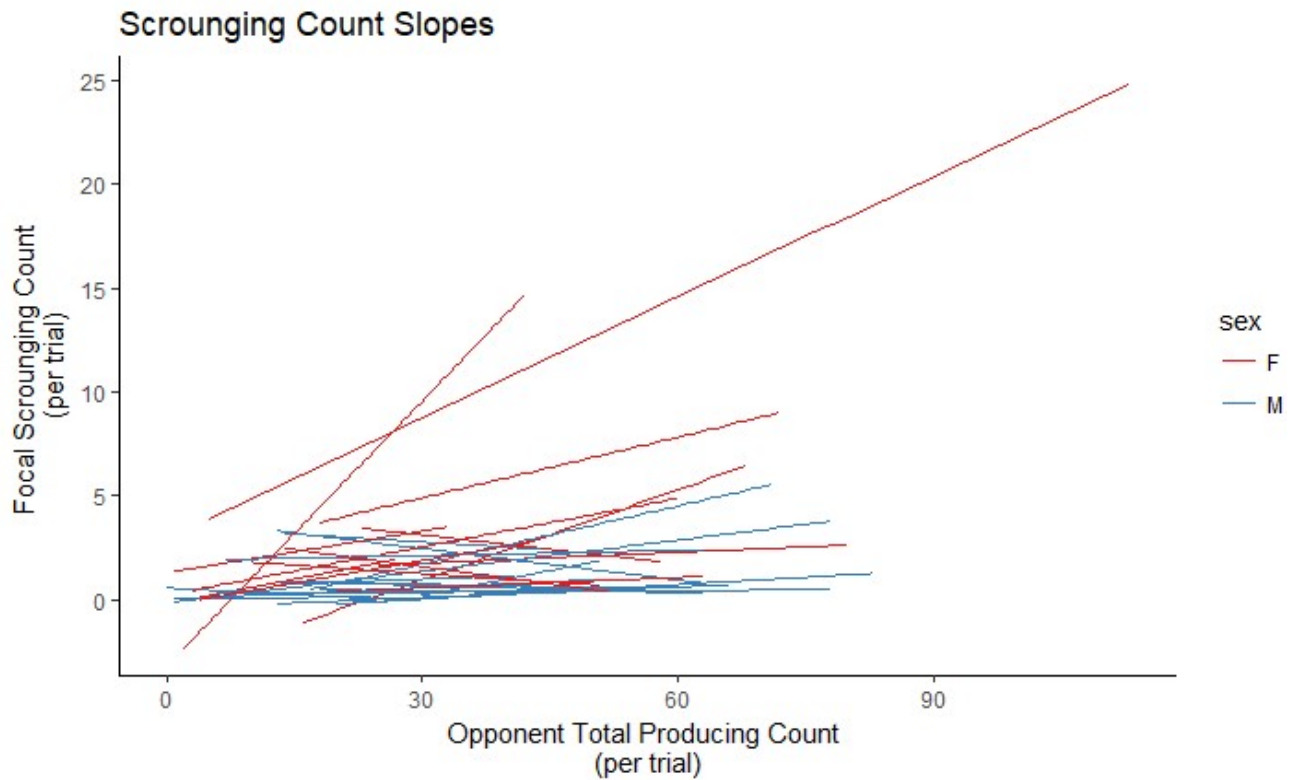


Figure 9. The change in focal scrounging count (per trial) slopes as the opponent total producing changes, colored by sex.

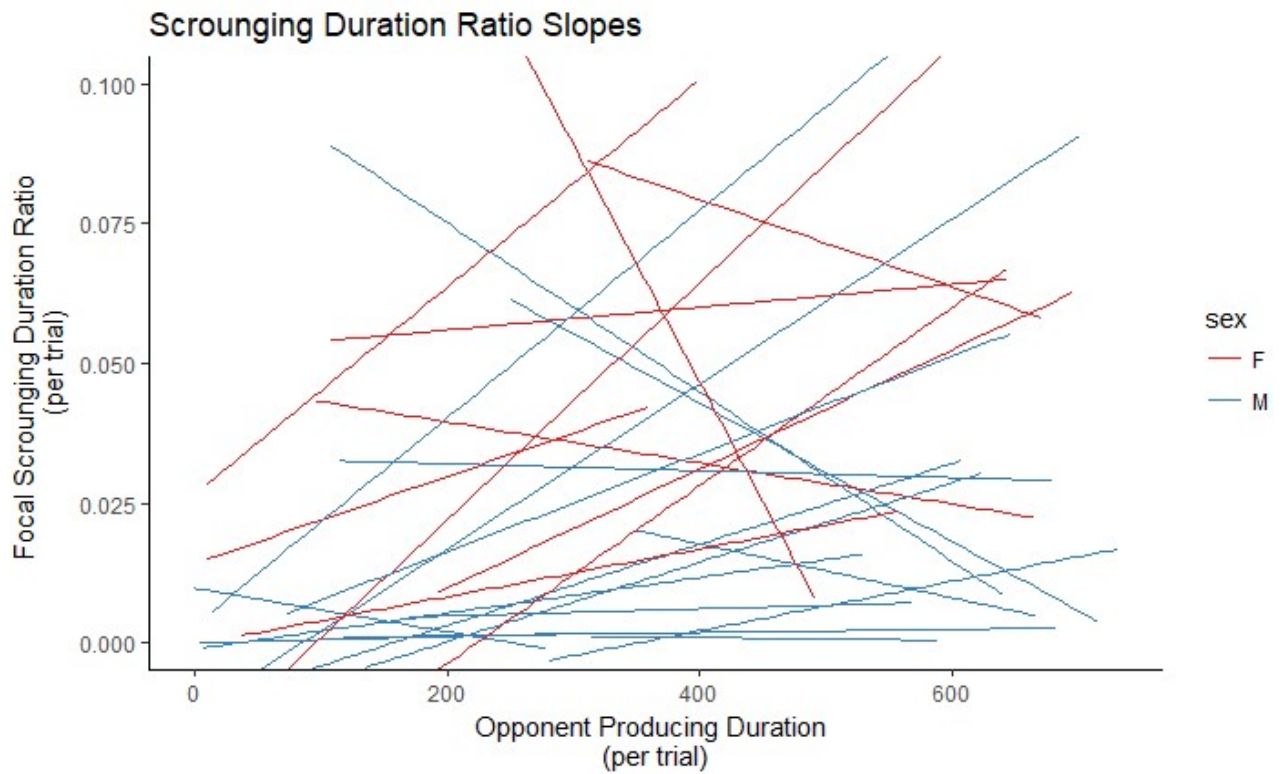


Figure 10. The change in focal scrounging duration ratio (per trial) slopes as the opponent total producing changes, colored by sex.

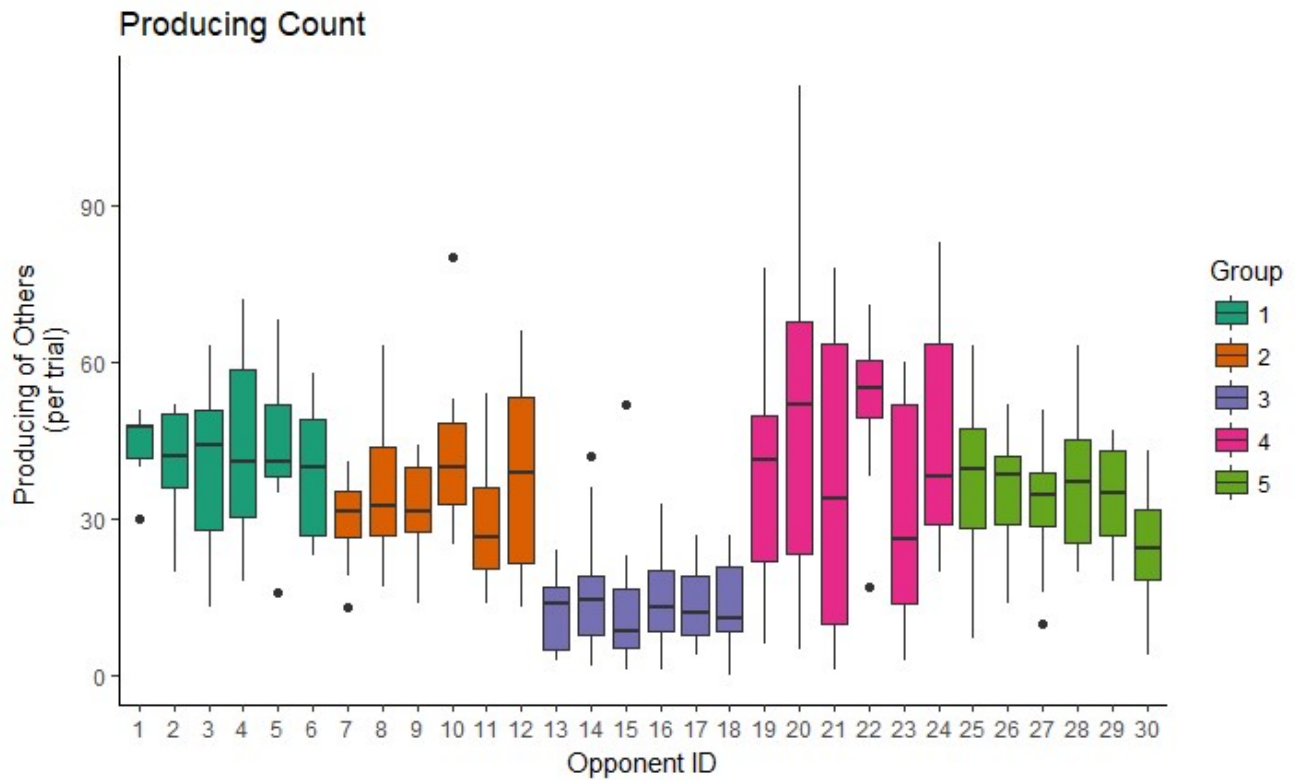


Figure 11. The producing count of other individuals (per trial) when faced against a particular opponent (opponent ID), colored by group

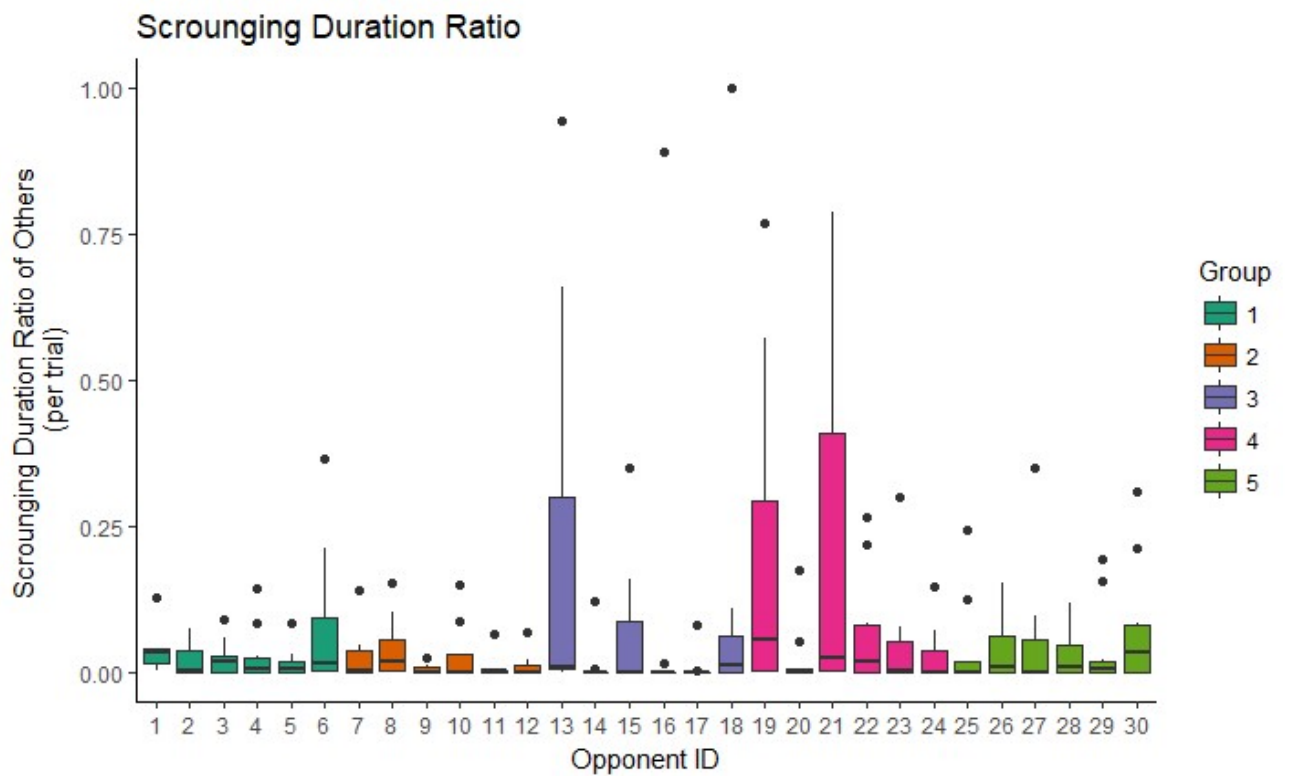


Figure 12. The scrounging duration ratio of other individuals (per trial) when faced against a particular opponent (opponent ID), colored by group

Sex and Day

There were no significant differences between sexes in any of the producing models. On the contrary, sex was very significant for all the scrounging models in Tables 3-5. These models support the observations seen from Figure 15.

Any significance of day implies possible order effects and acclimation to the pair-wise feeders. The fixed effect of day was significant only in the VPA model for scrounging count (Table 3 (c)). Once opponent effect was added in the HA models, the p-value was no longer significant. In all the other models in Table 3 and 4, day was not significant. Day was also significant in Table 5 (b) and (c), where the non-random slope effect of opponent total producing was added to the scrounging ratio binomial models. This suggests that day is significant when all the effects of the opponent phenotype are accounted for, and that an order effect of day is present.

The day*sex interaction as a fixed effect was not significant for any of the producing models but was very significant for all the scrounging models, apart from the VPA scrounging count model in Table 3 (c) where it was nearly significant. In all the cases where the interaction is significant, the separate effects of day and sex are no longer interpretable due to the nature of interactions.

There was variation in the levels of producing and scrounging both among genders and between genders. For males, the mean total producing was 33.45 ± 1.51 times and the mean total scrounging was 1.12 ± 0.15 times. The mean for the total producing duration was 355.16 ± 17.17 seconds and the mean total scrounging duration was 9.15 ± 1.67 seconds. For females, the mean total producing was 32.97 ± 1.83 times and the mean total scrounging was

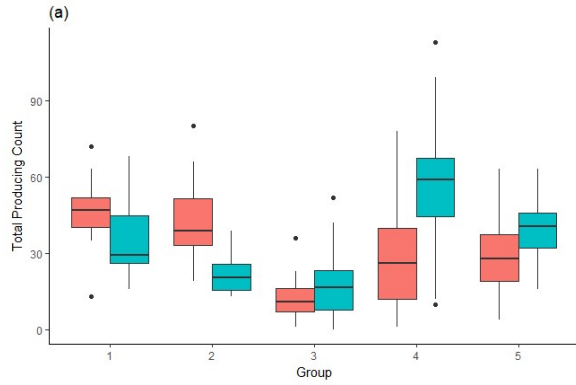
3.22 ± 0.49 times. The mean for the total producing duration was 310.75 ± 16.61 seconds and the mean total scrounging duration was 19.72 ± 3.25 seconds.

Males produced more than females on average, which can be seen in the total producing count and especially in the total producing duration. Also, males had higher means of well visits, neighbors present, and slightly higher pre-pair round weights than females. As can be seen, females scrounged nearly 2-3x more than males (Figure 15), and females were scrounged on less by their opponents than their male counterparts were. When it comes to aggression, females were more than 2x more likely to give aggression and were less likely to receive aggression than males.

As seen in Figures 13 and 14 the mean producing varied day to day from both within and among groups. The difference in mean producing from day 1 to day 2 also varied between groups. There was also variation in total levels of scrounging between the days and groups, which is especially visible in Figure 13 (d).

The total producing count and well visits increased from day 1 to day 2, but, despite these increases, the total producing duration decreased. The total scrounging count and duration, as well as the instances of aggression and neighbors present, increased from day 1 to day 2. There was also a slight increase in the pre-pair round weight and almost no change in the seed remaining after trials.

Producing



Scrounging

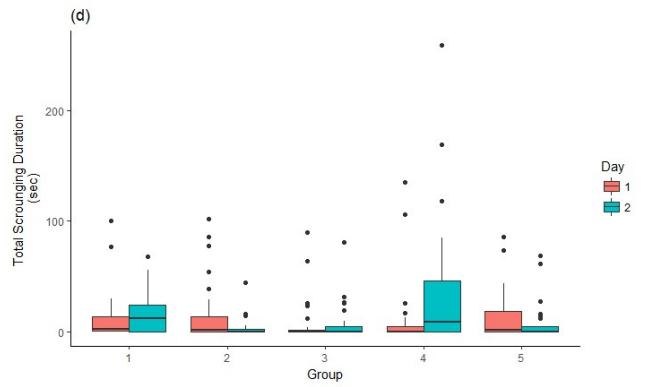
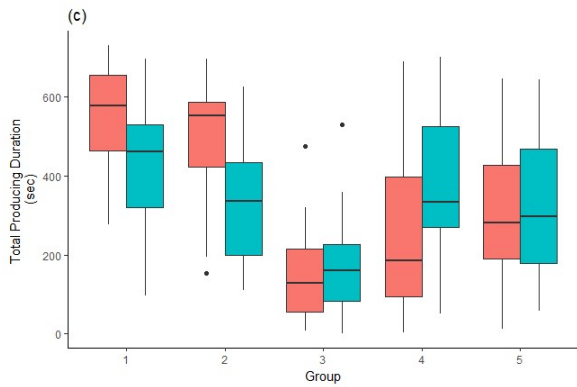
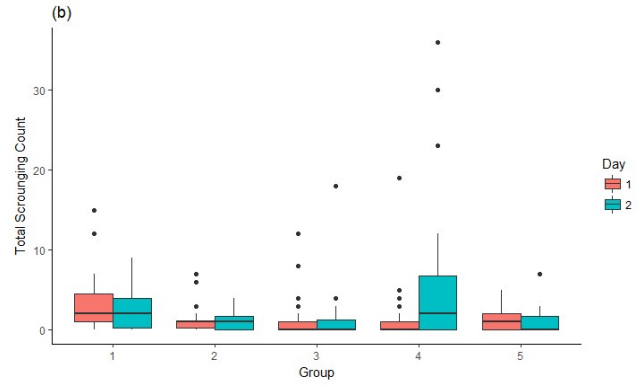


Figure 13. Boxplots showing median and interquartile values $\pm 95\%$ CIs and outliers for (a) Total Producing Count, (b) Total Scrounging Count, (c) Total Producing Duration, and (d) Total Scrounging Duration. The data is separated by Group on the x-axis and is colored by day. Each data point represents the total from a trial, with $n = 278$ trials (involving 21 males and 15 females).

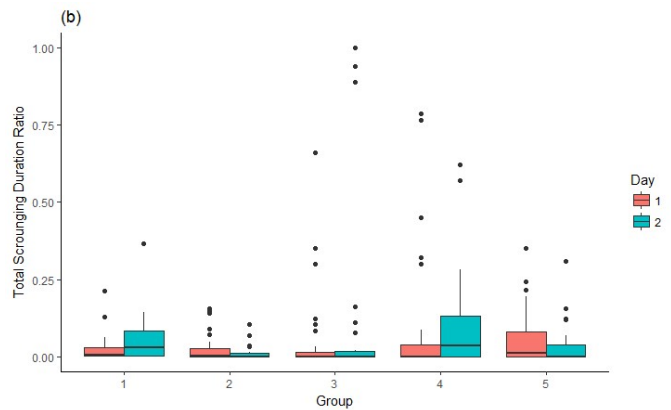
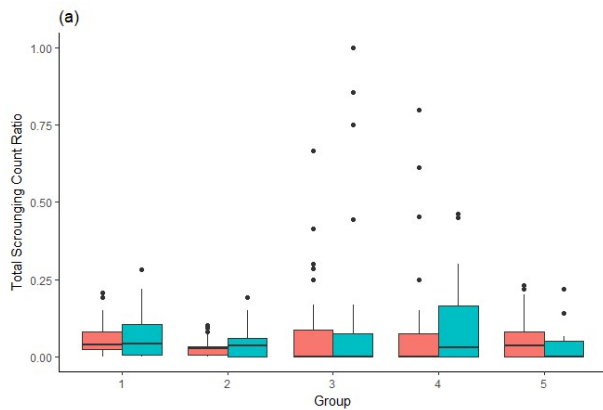


Figure 14. Boxplots showing median and interquartile values $\pm 95\%$ CIs and outliers for (a) Total Scrounging Count Ratio, (b) Total Scrounging Duration Ratio. The data is separated

by Group on the x-axis and is colored by day. Each data point represents the total from a trial, with $n = 278$ trials (involving 21 males and 15 females).

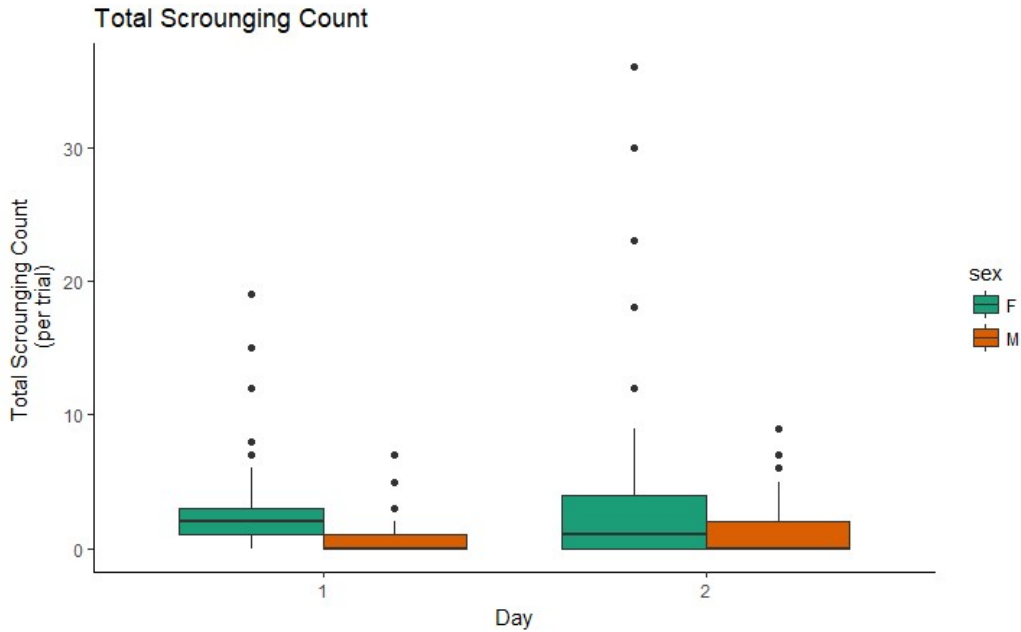


Figure 15. A box plot for Total Scrounging Count per trial which is separated by day and gender

Trial and Group

Trial was only significant in the models for scrounging duration ratio as the response variable (see Tables 4 and 5). In these cases, an order effect is present since the trial effect is significant (see Figure 16). This suggests that the scrounging duration ratio gives important insight into the effect of trial/order on the scrounging response which is missed when considering scrounging count models.

Group is not included in the models, but a possible trend is apparent. Figures 7, 8, 11, 12, and 16 show observable effects and differences amongst groups in their levels of producing and scrounging, thus suggesting that there may be possible biological group effects.

Although, the differences between groups are more likely explained by the disturbance/stress effects of different groups as they experienced different conditions while going through the trials. Due to this complexity, the effect of group was not incorporated so that simplified models could be maintained.

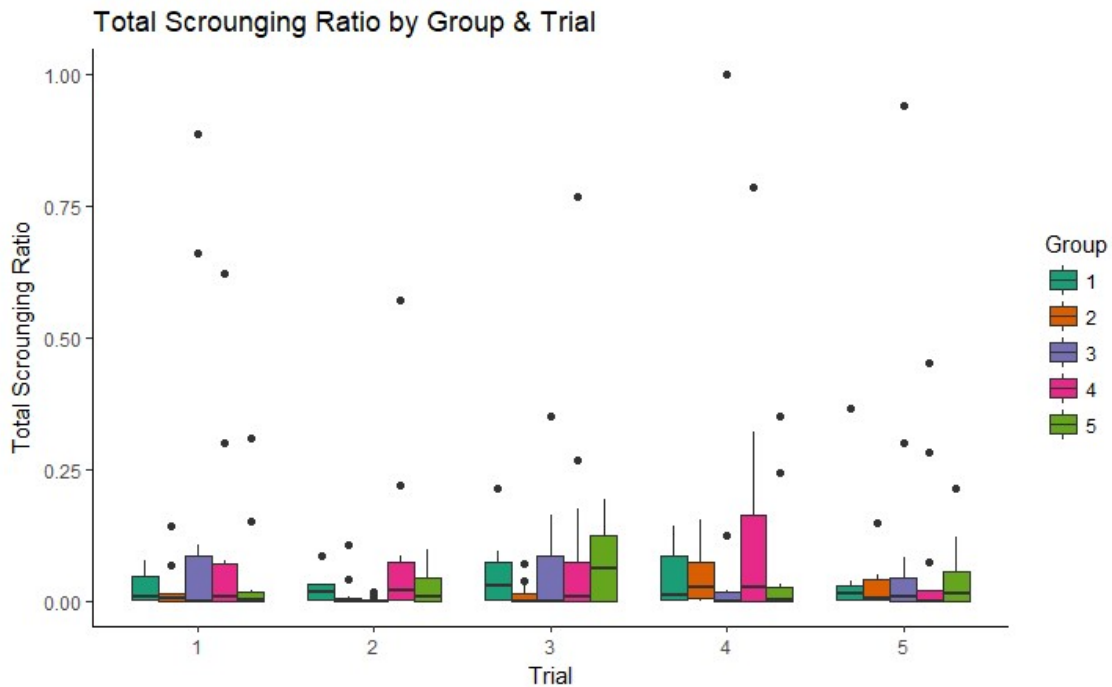


Figure 16. Shows the Total Scrounging Ratio from trial to trial and it is separated by group

Discussion:

The aim of the study was to identify the indirect social effects of the opponent, the degree of these effects, as well as to test if individuals varied independently of this in their own strategies, and if those strategies were repeatable among individuals and opponents. The house sparrow, *Passer domesticus*, was employed as the model species due to its social nature and use in previous empirical studies exploring the nature of producing/scrounging models. It was predicted that there would be individual variation and repeatability in strategy for producing and scrounging. This held to be true, according to our results, as there were significant effects of the focal individual's identity on its levels of producing and scrounging

as well their being repeatability and variation in its levels of producing and scrounging (the repeatability was smaller, less noticeable for scrounging). Albeit low in some cases, these repeatabilities were mostly in line with those from other various studies concerning a social behavior and its repeatability (Wilson *et al.*, 2013; Santostefano *et al.*, 2016; Pettersen, 2017). In addition, the focal identity accounted for the largest proportion of variation around all the models' intercepts.

The second prediction intended to test the responsiveness of focal individuals towards a continuous opponent phenotype, such as total producing of the opponent, and to observe how it may affect the focal' response variables of producing and scrounging. The results and models showed that for focal producing, the opponents' rates of producing (fixed effect of opponent total producing) seemed to have a significant effect on the amount of focal producing, but the opponent identity was not significant. In addition, the opponent repeatabilities were very low. A significant effect was not seen in opponent identity in this case due to the high rates and variation with the levels of producing both within and between individuals, or perhaps the opponent total producing wholly accounted for the variance of the opponent identity within the producing models. Both the opponent identity (random effect) and opponent total producing (fixed effect) were very significant in models for focal scrounging and there was observable opponent repeatability. As seen in Table 5 the opponent total producing in the slope of the focal ID random effect was very significant and had a -0.59 correlation on the slope of the focal individual's rate of scrounging. This effect was harder to show visually, perhaps due to the small sample size, but theoretically the model predicted that as the slopes fan in to the right with the slopes becoming shallower with the increased height of the intercepts. This means that the opponent's rate of producing did have an effect on a focal individuals' rate of scrounging, it's plasticity, and therefore it's propensity to switch between producing and scrounging. It also revealed that for scrounging

there were repeating, individual differences in the plasticity, similar to the Dingemans (2012) where stickleback exhibited differing individual plasticities.

The third prediction intended to test for the effects of a particular opponent on all the other individuals in their respective groups through the pair-wise trials, thus serving as an indirect social effect. For focal producing, these indirect social effects and the repeatability of the opponent were not significant. It was observed that the rates of producing were independent of the opponent's identity. It was predicted that particular opponents would have a weaker effect on some individuals and stronger effects on others. This was contradicted by the producing models and results, but seemed to be the case for when it came to scrounging. For scrounging, the opponent identity was significant in all cases with some opponents having stronger effects on individuals than others.

Scrounging itself can come with risks such as aggression, fighting, or injury, and house sparrows have previously been observed using aggression over food resources (Liker & Barta, 2002; Lendvai *et al.*, 2004). Compared to a study done previously by without sand (Pettersen, 2017), this study had far higher rates of scrounging. One of the aims was to build on this study by creating a sand-seed mix and more difficult searching structure. Other such studies which utilized a sand-seed mix in the wells saw higher rates of scrounging, so this only further supported the decision to incorporate it into the study (Liker & Barta, 2002; Belmaker *et al.*, 2012). Some studies had very large groups and no sand incorporated, but in these studies the presence of many individuals may have increased competition and scrounging (Lendvai *et al.*, 2004; Tóth *et al.*, 2009). The disadvantage of such studies is that they did not allow for a strong analysis of the individual and its role in the social environment, whereas this experiment allowed for the individual to be addressed at a higher degree.

Several studies of producing/scrounger with house sparrows, using captive flocks and feeders, had several weeks of acclimatizing the birds to feeders and their environments (Liker & Barta, 2002; Lendvai *et al.*, 2004; Belmaker *et al.*, 2012). This setup becomes more difficult for analysis in quantitative genetics which requires large sample sizes, and this study shows some of the advantages of having a shorter training period while still obtaining the desired producer/scrounger dynamics. Although, it is uncertain how the stress levels of individuals could have been affected if the training period were extended. Still, these experiments are conducted in non-natural environments and this is important when considering the biological significance of factors/conclusions and their translation to natural contexts.

Stress was a concern once the experiment was conducted and the videos were analyzed. This is because stress had the potential to disrupt trials and effect the stress levels of the paired individual experiencing a stressed opponent. It could have had the possibility to create a negative feedback loop of stress, where individuals feed less and less, scrounge less, and/or produce less due to the stress and stress interactions. If there were repeatable, consistent stress levels for certain individuals/pairs, then perhaps it was accounted for by focal identity as a random effect, or by adding the random effect of pair identity. There is still the possibility for it to be a non-repeatable effect if certain disturbances, noise during trials, or perhaps some other stressor created more stress in some trials than in others. If this is the case, then it would not be reflected in the pair identity as random effect. For possible future analysis, several stress variables and disturbances were recorded during the video analysis. These can help by accounting for variation within the models due to stress, such as flying or pacing, but at the effect of creating more complex models. One individual died after the experiment, some groups were stopped early, the order of pair-wise to group-wise was altered, and group 6 was taken out completely. These were all largely due to stress and non-

participation, so it is integral to minimize stress for future experiments. One way to do this is by removing the cages from the pair-wise feeders and to have an open space or stall when the pair in a pair trial can feed. Another method that could be used is to utilize radio-frequency identification (RFID) with a tag as a leg ring and each individual well on a checkerboard feeder as a reader. The advantage of this is that it would keep accurate measurements of time, location, identification, and duration at wells, thus significantly reducing the intensive human resources needed for the video analysis.

The group-trial videos were not analyzed due to time constraints. If they were analyzed, it would have been done as follows. We would have recorded social behaviors and foraging, as well as the presence of conspecifics on the feeder. The behaviors measured would include: (i) First individual to come to the feeder (boldness), (ii) An individual leaving the feeder when too many opponents/conspecifics present (shyness), (iii) aggressiveness, and (iv) producing, (v) scrounging, and many of the stress behaviors measured for the pair-wise trials in Table 1.

Little research in this area has explored the effect of the opponent phenotype and opponent identity on the focal individual and its response (Wilson *et al.*, 2013; Santostefano *et al.*, 2016; Pettersen, 2017). The studies managed to find some evidence supporting a repeatable effect of the other individuals present. These dynamics are important to consider when observing social organisms and interactions. Producing showed the highest repeatabilities with its among-individual repeatability. It is possible that this is a consequence of producing-biased feeding behavior if not enough difficulty is present in searching for food patches, although this is not believed to be the case in this experiment. It is possible that producing is a behavior that is not very socially influenced since opponent identity was not significant. If the behavior is not socially influenced, it could lead to more predictable, stable environments since social environments add a degree of variability from individual to individual. The

repeatabilities in producing were comparable to those of other studies which measured activity when individuals were isolated and had no feed present (Beauchamp, 2000; Dingemanse *et al.*, 2007; Santostefano *et al.*, 2016), in addition to other studies using populations of house sparrows from Norway (Finnøen, 2016; Pettersen, 2017).

The lower-than-expected repeatabilities of scrounging may be due to several factors. If the trial duration or sample size were too small, the measured scrounging could seem very biased. It may also have to do with how stressed the birds were within enclosures. An open enclosure could provide insight into how the producer/scrounger dynamics may change with less stress. The food available within each seed-filled well and during a trial could be reduced in order to increase competition, but it is suspected that this may not be much of an issue for this experiment since scrounging was observed. It is important to note that enough seed needed to be provided to maintain safe energy levels for the individuals, so this limits the difficulty possible for searching on the feeders. Further analysis with the group trials could provide many useful insights into the possible changes of producing/scrounging dynamics between the pair and group feeders.

This study revealed very significant effects of sex on scrounging behavior but not on producing behavior. Females had 2-3x the rate of scrounging than males, revealing a large difference in the rates. Previous studies have found these differences in scrounging behavior as well. It has been shown that females, which serve as the primary dispersers in these populations, tend to scrounge more from close kin than males (Tóth *et al.*, 2009). The pedigree and genetic data from the individuals in the experiment could be utilized to further explore the relationship of scrounging with sex and relatedness. This data could account for some of the differences between sexes.

An individual's state may also have played a role in the rates of producing and scrounging. A decrease of rates in producing was found for those in lower energy states (Lendvai *et al.*, 2004). The food availability may affect the producing/scrounging strategy employed (Mathot *et al.*, 2009). Differences in metabolic rates could be explored, although this was partially accounted for with the catch and pre-pair weight measurements recorded. For zebra finches, it was shown that individuals with higher basal metabolic rates scrounged more than those with lower ones (Mathot *et al.*, 2009).

Furthermore, the result from a sparrow and behavior study done by Hammerås (2016) support our observed results that some behaviors exhibit repeatabilities – in that specific case being number of well visits and well visit durations. Differences in the rates of feeding at a well while producing/scrounging may give more detailed insight into the predictor variables for producing and scrounging. This was accounted for during the video analysis as 'Observation Level' and served to give a relative rate of producing and scrounging for individuals. It may be of interest to continue the models and investigations with these relative values in order to explore the effects of relative feeding rates, metabolism, and state. It could also allow for the exploration of effects of the location of opponents and their behaviors within time and space, such as the duration they are neighboring a producer. The models support the inclusion of duration models and experimental designs, especially for scrounging, as they give the most information on the specific behaviors and may lead to more accurate models. Another advantage is that these models can be translated to other behaviors observed during the trials, using the same/similar methods of analysis for the producing and scrounging models.

For the experiment and its predictions, a large enough sample size is integral to detect certain observed effects. It is suggested to have at least $n > 200$ for experiments attempting to detect variation in plasticity (Martin *et al.*, 2011). Improvements in the experiment could be made to increase the effect size and to have more repeatable values for individuals and pairs.

Although the whole population at Lauvøya was captured, it was significantly reduced from ~130 individuals in the previous year due to predation (Pettersen, 2017). The consequence of utilizing a larger population is the time that is required to execute the experiment. Methods such as preparing the wells before entering the field and automating the feeders with RFID readers can allow for the analysis of larger populations.

On a concluding note, this study yielded many interesting results that can further future research and insight into social behaviors and dynamics within a complex environment. Individuals were shown to have repeatabilities, plasticity, and sensitivity towards different opponents for certain behaviors within their social environment. This experimental design can be expanded to other species as well, especially those which feed in groups.

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Appendix:

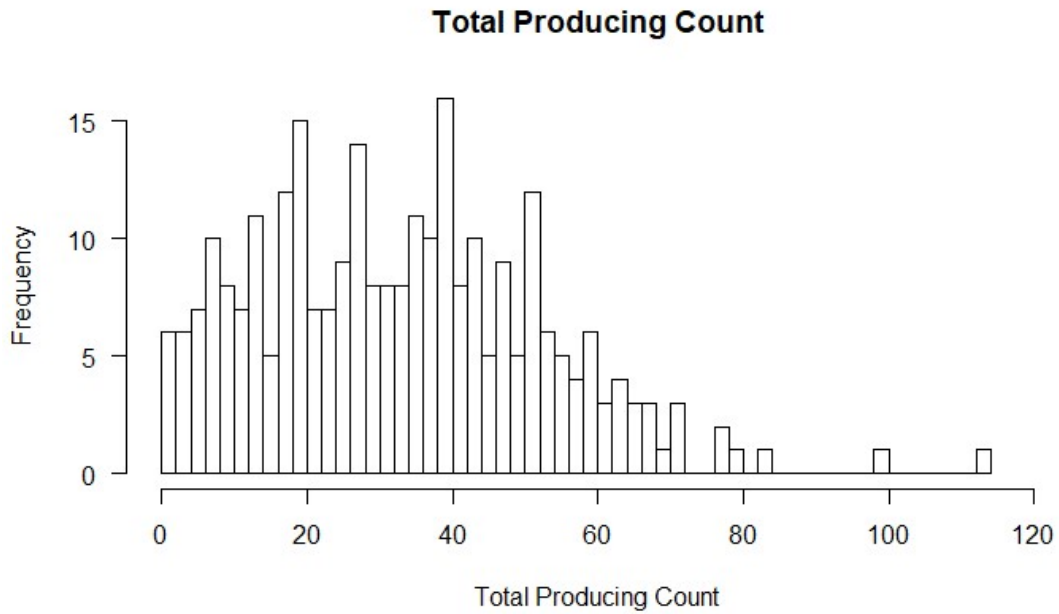


Figure A1. A histogram of the Total Producing Count per trial and the frequency of those total producing counts. ($n=30$ individuals)

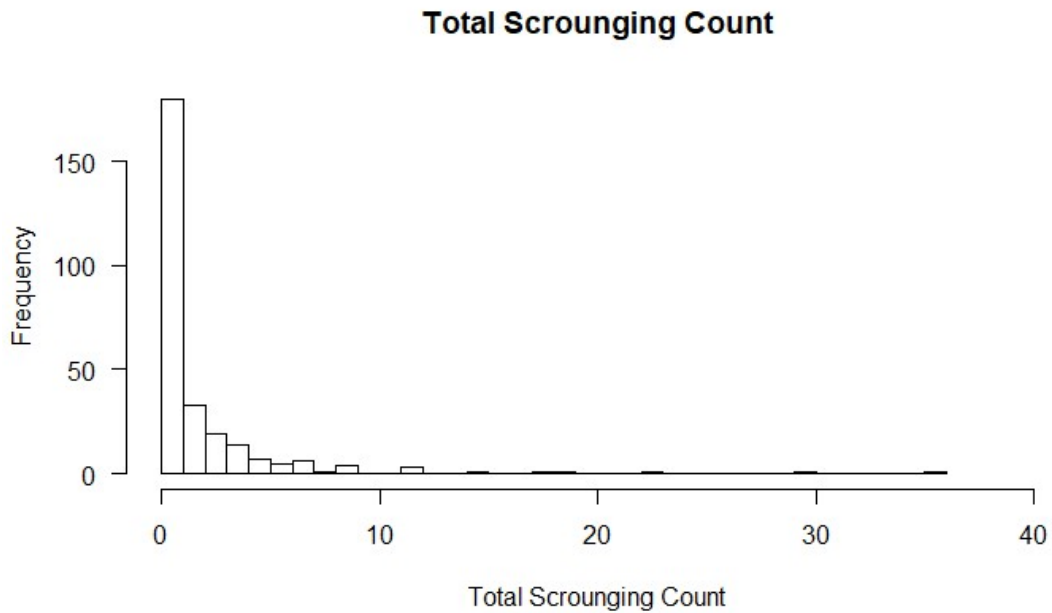


Figure A2. A histogram of the Total Scrounging Count per trial and the frequency of those total scrounging counts. ($n=30$ individuals)

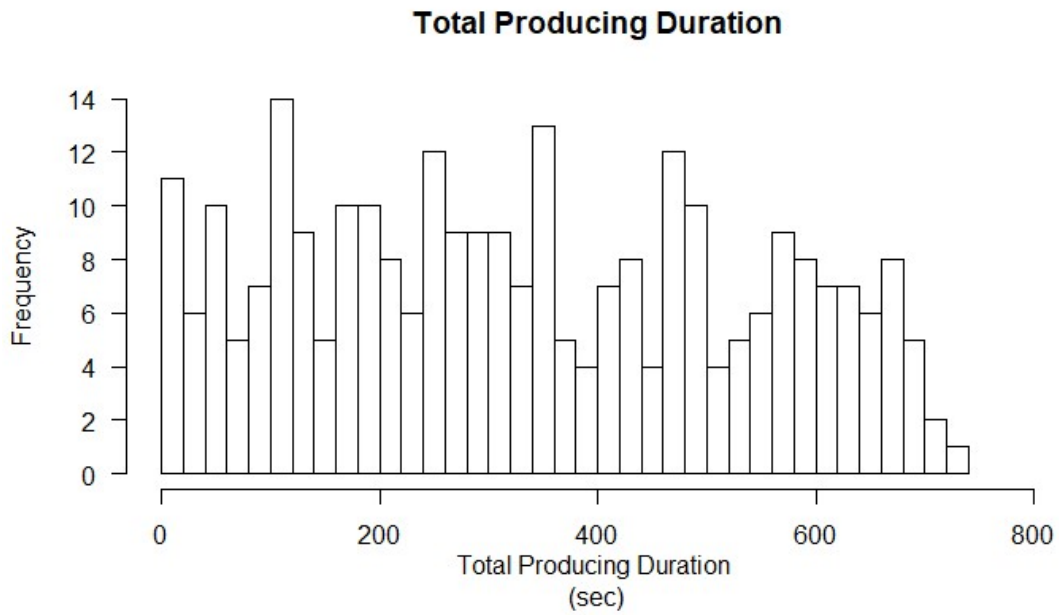


Figure A3. A histogram of the Total Producing Duration per trial and the frequency of those total producing durations. ($n=30$ individuals)

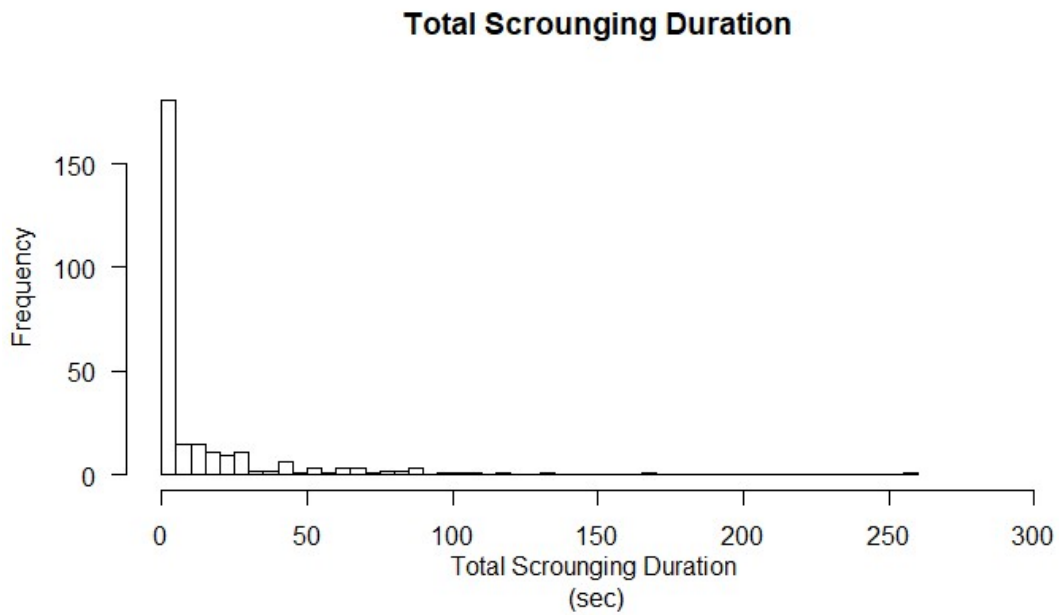


Figure A4. A histogram of the Total Scrounging Duration per trial and the frequency of those total scrounging durations. ($n=30$ individuals)