Master's thesis

NTNU
Norwegian University of Science and Technology
Faculty of Information Technology and Electrical Engineering
Department of Biology

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Individual variation and indirect social effects in producer-scrounger behavior in groups of house sparrows, *Passer domesticus*

Master's thesis in Lektorutdanning i realfag (MLREAL)
Supervisor: Jonathan Wright
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Abstract

Social foraging involves intraspecific competition over limited food availability that over time has shaped the evolution of social foraging strategies. Individuals are part of a dynamic social environment that often requires individuals to use mixed strategies where they switch between tactics to varying degrees, such as between ‘producing’ or searching for food versus ‘scrounging’ from the food discoveries of others. To test whether individual identities influence tactic of use, individual variation in producer-scrounger behavior were measured in several groups of house sparrows (*Passer domesticus*). Following a unique approach of two previous studies, this study was able to show individual differences in producing versus scrounging, and indirect social effects in the response to others – individuals scrounged more when there was more producing in the group. However, the majority of the results here were statistically non-significant due to the small number of social groups tested. Future work increasing the number of groups and trials should allow all of the planned comparisons using this effective experimental approach to exploring individual variation in producing-scrounging behavior.

Sammendrag

Sosial foringsatferd involverer intraspesifikk konkurranse over begrenset mattilgjengelighet som over tid har formet evolusjonen av sosiale forings strategier. Individer er del av et dynamisk sosialt miljø som ofte avhenger av at individer bruker blandingsstrategier der de bytter mellom taktikker i varierende grad, sånn som mellom 'producing' eller å lete etter mat versus å 'scrounge' fra andre sine matfunn. For å teste om individers identitet påvirker bruk av strategier, så ble individuell variasjon i producer-scrounger atferd målt i flere grupper av gråspurv (*Passer domesticus*). Ved å følge den unike fremgangsmåten til to tidligere studier, så kan dette studiet vise individuelle forskjeller i producing versus scrounging, og indirekte sosiale effekter i respons til andre – individer scrounget mer når det var mer producing i gruppen. Likevel, så var størsteparten av resultatene statistisk ikke-signifikante på grunn av få antall sosiale grupper som ble testet. Fremtidig arbeid som øker antallet grupper og forsøksrunder burde kunne gjennomføre alle de planlagte sammenligningene ved å bruke denne effektive fremgangsmåten til å utforske individuelle variasjoner i producer-scrounger atferd.

Acknowledgements

I would like to thank my supervisor Jonathan Wright for his guidance and for supporting me throughout this process. I would also like to thank my co-supervisors, Yimen Araya-Ajoy for providing expertise in the statistical work, and Bernt Rønning and Henrik Jensen for valuable input on the completion of my thesis. Lastly, I would like to give out a special thanks to Talal Mohammad, who voluntarily has spent much of his time explaining the methods and aiding in the statistical modeling of the dataset.

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1 Introduction

The individual fitness consequences of group living and the evolutionarily stable outcomes of social interactions have been extensively explored in theory. The ever-expanding theoretical framework that evolutionary social behavior research relies upon is heavily influenced by the mathematical modelling of evolutionary game theory. The players compete for a limited resource whilst deploying a strategy over repeated encounters, and the effectiveness of the chosen strategy depends on the strategy deployed by the opponent (see Davies *et al.*, 2012). Smith & Price (1973) first suggested that when strategies are frequency-dependent, the fittest strategy is an evolutionarily stable strategy (ESS), meaning that it can't be replaced by an alternative strategy once it has invaded the population. Barnard & Sibly (1981) incorporated this idea into their producer-scrounger model of social foraging animals. In this model, individuals can either search for unexploited resources as a 'producer' or use public information to pilfer resources discovered by a producer as a 'scrounger', or flexibly switch between both strategies (see Katsnelson *et al.*, 2011). The model assumes that scroungers will increase their foraging rate while avoiding the investment of producing and thus have a higher fitness than producers, but only as long as scroungers are sufficiently uncommon. This negative frequency dependence results in a mixed ESS; the ratio of scroungers to producers in the population that gives equal payoffs to both strategies (see Vickery *et al.*, 1991). That is, the population is predicted to be in an evolutionarily stable equilibrium when all individuals obtain equal net gain in their foraging effort (see Ranta *et al.*, 1996). Individuals that switch between producing and scrounging (i.e. a conditional ESS) will consequently achieve the maximum consistent fitness rewards if they match the same proportions of producing and scrounger as the ESS proportions at the population level (Vickery *et al.*, 1991).

Many empirical studies have investigated the effects of various factors on producer-scrounger frequencies, suggesting that the equilibrium ratio is altered with the adjusted values of their respective payoffs (e.g. Katsnelson *et al.*, 2008). A higher frequency of scroungers is expected with an increase in group size and thus more producers to exploit, and if there is a reduction in the producers' proportion of food due to their initially exclusive access to a patch, i.e. the 'finder's share' (Vickery *et al.*, 1991). In accordance with optimal foraging theory, this assumes that the foraging strategy that maximize the net intake-rate is favored by selection. However, state-dependent models of producing and scrounging (Barta & Giraldeau, 2000) suggest greater risk-averse scrounging when an individual is risking starvation, as it provides a less variable source of energy. Lendvai *et al.* (2005) tested this prediction by artificially reducing the energy-reserves of house sparrows (*Passer domesticus*) during the night, promoting a higher frequency of scrounging at dawn. Also, the optimal risk-sensitive foraging strategy is not necessarily the best option, but rather the strategy that minimizes the total risk of mortality (McNamara & Houston, 1990). Thus, the presence of scroungers and their attentive manner can provide additional anti-predatory benefits and tilt the equilibrium towards scroungers, provided it outweighs the energetic costs imposed on the producers (Ranta *et al.*, 1996).

With competition for limited resources, it is expected that the identities and the characteristics of the interacting individuals will impact the structure of the population as well. Individual asymmetries in competitive abilities were facilitated in an empirical study, again on house sparrows, with results suggesting that the tendency of dominants to scrounge successfully led to an increase the frequency of scroungers in the population as a whole (Liker & Barta, 2002). The effect of dominance rank and kinship should interact depending on an individual's physical condition or access to resources, due to discrimination in favor of relatives, as predicted by kin selection theory (Hamilton, 1964). Tóth *et al.* (2009) found that individual house sparrows adjusted the frequency and aggressiveness of scrounging behavior according to the relatedness of conspecifics, with the more dominant males being more likely to scrounge off non-relatives and the more subordinate females being allowed to scrounge off relatives.

Despite the extensive theoretical and empirical literature regarding factors affecting producer-scrounger dynamics, there is a scarcity of studies on the actual underlying mechanics. The unresolved problem relates to the extent to which an individual's behavioral decisions to produce or scrounge are determined by genetics or the early-life or on-going social environment (Belmaker *et al.*, 2012; Katsnelson *et al.*, 2008). There is evidence of a heritable component of traits relating to social foraging (Drent *et al.*, 2003; van Oers *et al.*, 2004) and that producer-scrounger tendencies due to learnt early-life predispositions may be further enhanced by learnt experiences as adults (Belmaker *et al.*, 2012; Katsnelson *et al.*, 2008, 2011).

The flexible adjustment of producer-scrounger strategies in response to different environmental and physiological states may therefore be further affected by internal or external cues relating to hunger, predation risk or public information (Belmaker *et al.*, 2012). Accordingly, plasticity in social foraging behavior may be a reaction to the social context and individual experience. Consistent individual variation in behavior, i.e. animal personality, is thus expected to influence and to be influenced by the phenotypes of the other individuals in a population (see Hamilton & Ligocki, 2012). Specifically, a phenotype can be directly affected by the individual's own genes, and/or indirectly affected by the genes expressed in the phenotype of the social partner – indirect genetic effects (IGEs). Consequently, individuals can be phenotypically plastic in response to the phenotypes expressed by their conspecifics, i.e., social responsiveness (Dingemanse & Araya-Ajoy, 2015). Applied to individual scrounging-producing behavior, further investigations are needed to assess the extent to which animal personalities is independent of the social context or socially responsive to certain individuals. Along with Mohammad (2018) and Pettersen (2017), these are the only studies that have attempted to asses consistent individual differences and social responsiveness in producer-scrounger behavior.

1.1 Purpose and Predictions

This study addresses the shortage of empirical studies on individual variation and social effects in producer-scrounger behavior (Grainger *et al.*, 2014; Hamilton & Ligocki, 2012; Kilgour & Brigham, 2013; Mohammad, 2018; Pettersen, 2017), further strengthening the scientific framework regarding the evolution of social behavior. The purpose here is to quantify repeatable individual levels of producing versus scrounging, plasticity and social responsiveness within social flocks of house sparrows (*Passer domesticus*), to determine the impact of both direct and indirect social effects in determining a producer-scrounger ESS.

Pettersen (2017) previously published a master of science (Msc) thesis concerning an experiment on house sparrows, where individual levels of producing and scrounging were quantified. Trials were repeatedly conducted on small mixed-sex flocks of six birds, and in uniquely paired combinations of two individuals, videotaped while foraging on chequerboards with wells mixed with sand and seeds. By comparing the results from the individuals in pair-wise assays, each individual's influence and social responsiveness was mapped and compared with the results seen in the group-wise assays. Some improvements were suggested for future studies, most obviously that greater rates of scrounging should be encouraged so as to make the experiment more realistic. The seed in the wells of the chequerboard was too easily accessible, reflected in the excessively high levels of producing (Pettersen, 2017). In response, Mohammad (2018) carried out an identical experiment but attempted to improve the experimental design by adding sand to all wells, including the wells with seeds plus a layer of just sand on the top of any seeds, thus adding a cost of searching for the seeds to the producing strategy. However, due to time-constraints, only the results from the pair-wise trials (see Methods for details) were published in Mohammad's (2018) MSc thesis, and the videos of the groups-trials remained unused.

This thesis therefore continues the work of Mohammad (2018), with the intent of comparing his results from the pair-wise trials with the group-wise trials analyzed by me. Consequently, Mohammad (2018) has been involved in this process in guiding me through the video-analysis and how to implement the data in the statistical models. Hence, the structuring of the sections and the presentations of the results in this thesis purposely corresponds to that seen in Mohammad's (2018) thesis. The following predictions were initially adapted from Pettersen's (2017) thesis, with grounds in empirical evidence from the aforementioned studies.

1) The average behavior (levels of producing vs. scrounging) of each individual will differ from the other individuals in the group. Sex and energy state are expected to have an impact, with males and hungry individuals displaying a heightened proportion of scrounging. The individual differences will be consistent and repeatable (figure 1.1) (Mohammad, 2018; Pettersen, 2017).

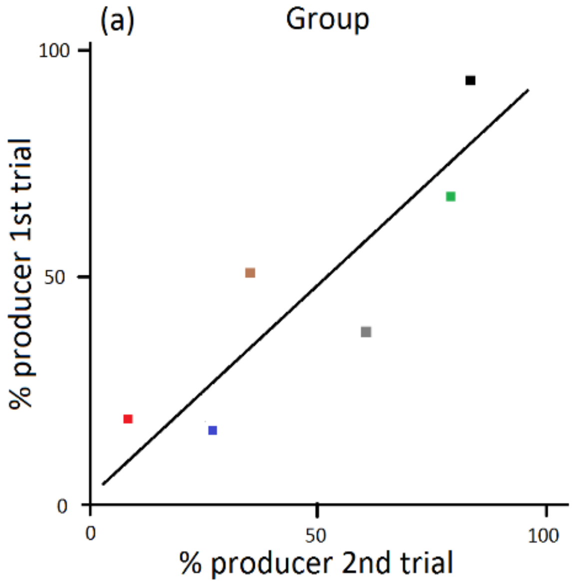

Figure 1.1: Each individual's (colored dots) expected repeatability in average producing (proportion producing of the total behavior) in the two group-trials. *

2) Each individual's extent of flexible use of the two strategies (behavioral plasticity) will differ from the other individuals in the group. The plasticity of an individual will consistently and repeatably depend on the strategies employed by individuals in its vicinity (figure 1.2) (Mohammad, 2018; Pettersen, 2017).

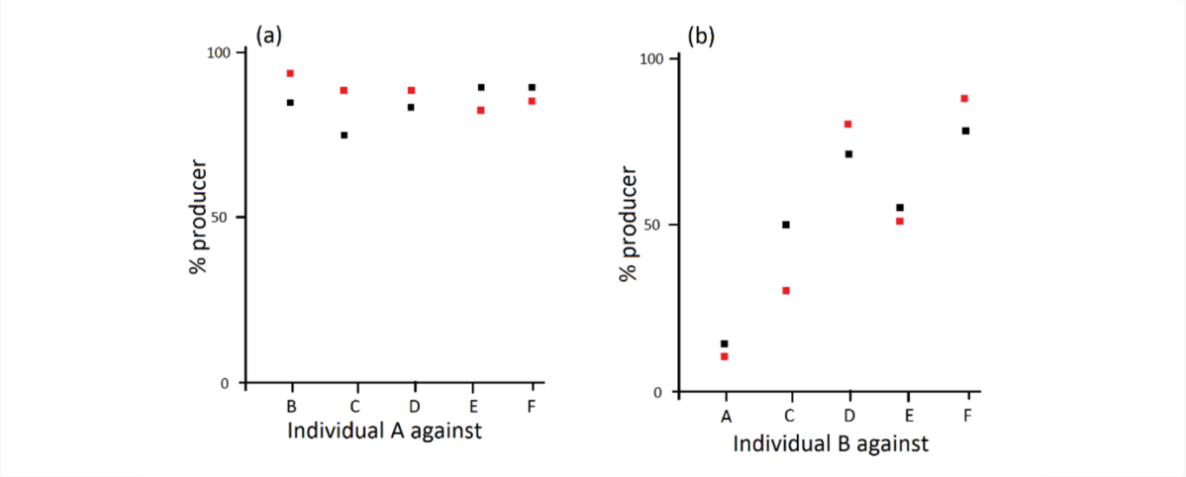

Figure 1.2: Comparison of the expected plasticity of two individuals A (left) and B (right). Individual A shows low variance in its level of producing in response to the varying behaviors of the other individuals (little plasticity), while individual B shows high variance (much plasticity). Red dot is group-trial 1 and black dot is trial 2. *

3) The behavior of an individual will affect the behavior of the individuals in its vicinity. The magnitude of influence each individual exerts will vary between them. Individuals consistently exerting pure/fixed strategies (little plasticity) is expected to have the largest impact on the behavior of more plastic individuals (figure 1.3) (Mohammad, 2018; Pettersen, 2017).

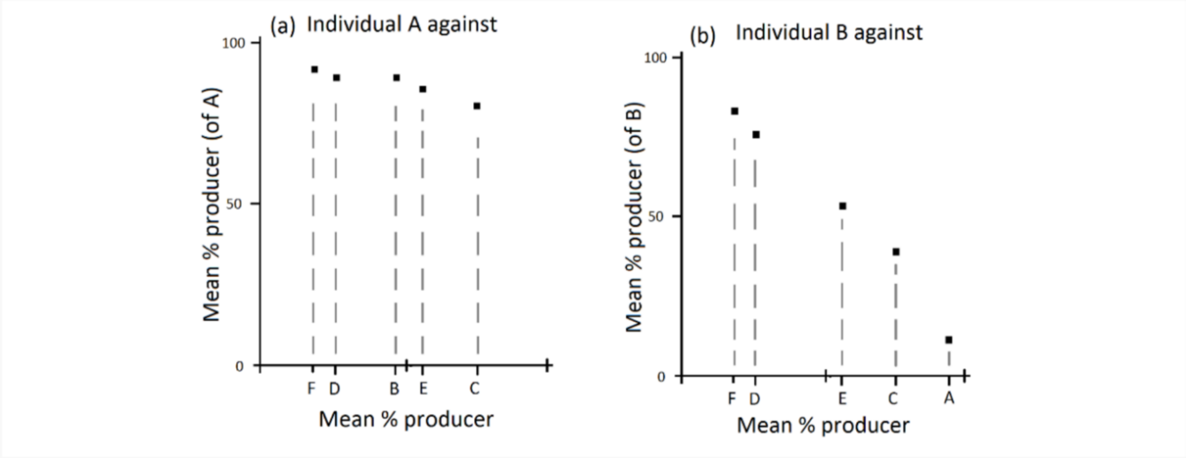

Figure 1.3: How the levels of mean producing of individual A (left) and individual B (right) is impacted by the levels of mean producing of other individuals in their vicinity. The little plasticity of individuals such as A shown in the left graph is predicted to have the largest effect on plastic individuals such as B, shown by the great decrease in mean level of producing of individual B in the right graph. *

*Adapted with permission from Pettersen (2017). Copyright 2017 by NTNU.

These hypotheses were confirmed in Mohammad’s (2018) results of the pair-wise trials. The results showed 1) consistent and repeatable individual differences in producing and scrounging, 2) repeatable plasticity of producing and scrounging that varied from each individual, and 3) opponent identification significantly affected the scrounging on all other individuals with varying magnitude, but had no effect on producing. The question now is whether these results were reflected in Mohammad’s (2018) group-wise trials, as expected from the preliminary results of Pettersen (2017).

2 Methods

This section is largely taken from the methods section in Mohammad's (2018) thesis, as I was never involved in the design or execution of the experimental work. This experiment is also part of a larger house sparrow project by NTNU's Centre for Biodiversity Dynamics (CBD). Over the last 25 years they have gathered a comprehensive data set on genetics, pedigrees, morphology, fitness and dispersal of all the inhabitant house sparrows on 17 islands on Helgeland coast in Norway. In 2012, many individuals were translocated to the population of the island of Lauvøya where this study was conducted. In addition to the detailed mapping of the study subjects and their relations, the house sparrow is widely known as a social species that exhibit producer-scrounger behavior (see Introduction), making it an ideal choice as this project's study species.

2.1 Study Location and Set-up

The experiment on Lauvøya involved 19 of the island's 20 resident sparrows plus 17 subjects from the mainland Åfjord. The 36 individuals; 21 adult males and 15 adult females were captured in late winter/early spring 2017 and placed into 6 groups of 6 individuals each. As much as possible, each group contained 3 males and 3 females that had been captured at the same place and time to maintain their presumed familiar social groups. The individuals were captured with mist nets and moved to a sealed barn that the experiment was conducted in. Here they resided for 14 days, from 1st to 14th of March 2017, and with temperatures of approximately 7 to 13 °C. Each individual was marked with a unique combination of a numbered metal-ring and three colored plastic rings. During this time, data on the individuals were also collected for CBD's wider project, including weight, tarsus length, wing length, beak length and depth, breathing irregularities (indicating the presence of lung parasites), sex, age, and a 25µL blood sample for genetic analysis. The six individuals in each group had two feathers of tails colored with acrylic paint to be distinguishable from each other in the video analysis; orange, blue, green, white, yellow and pink.

The training and experiment rooms were each equipped with a communal checkerboard feeder; a panel (1,2m x 1,2m) with 144 sand-filled wells / 50mL tubes. 60 of these wells were added browntop millet seeds. The bottom of the wells were filled with 45mL clay so that the sparrows could always reach the bottom of the sand or sand and seeds. The clay was topped by either 5mL sand or a priorly-made mixture of 5mL sand and ca. 30 seeds, and then topped with a thin layer of sand. The feeder was designed this way so that food had to physically be discovered. Figure 2.1 shows the barn and one of the rooms with a large feeder, whereas figure 2.2 shows the general organization of the sealable rooms in the barn. The training rooms and group room each contained a large checkerboard (144 wells), and the pair-wise room contained three small checkerboards (49 wells) that were 34% the size of the greater variant.

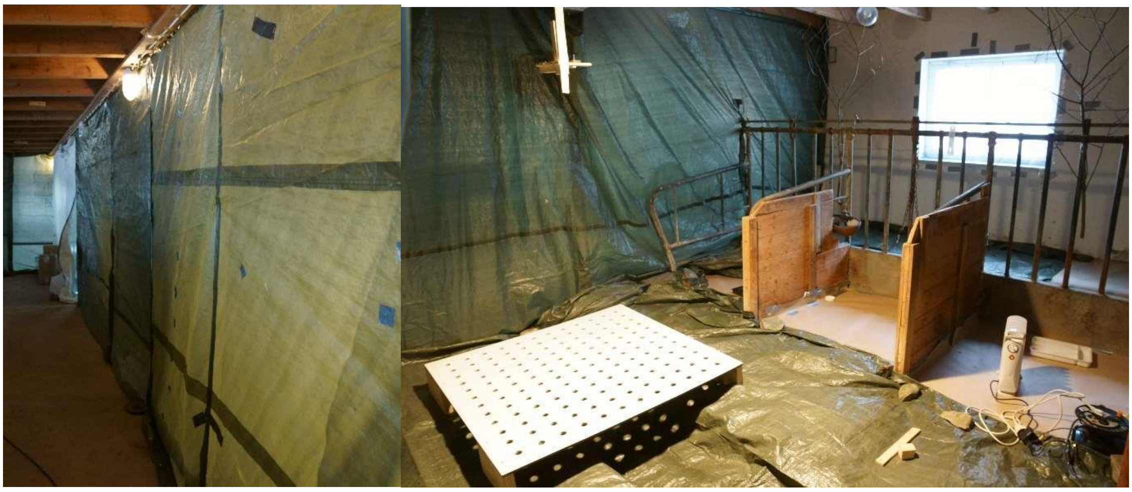

Figure 2.1: The inside of the barn (left photo) and one of the experiment rooms with its feeder (right photo). *

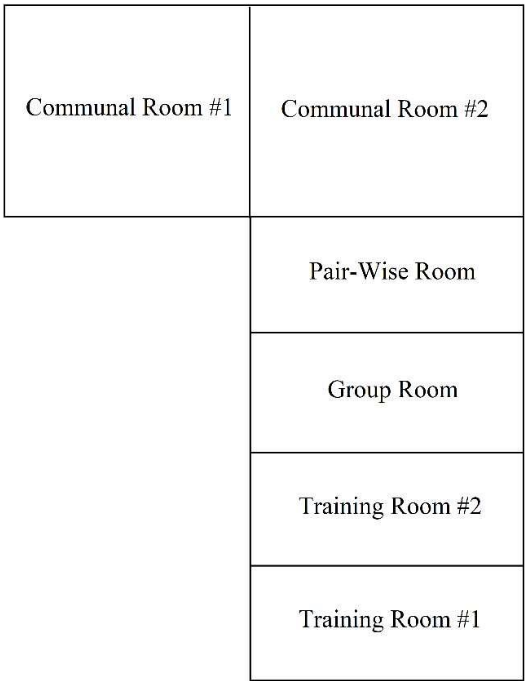

Figure 2.2: The general room-organization in the barn. The videos were recorded in the "Group Room". *

*Adapted with permission from Mohammad (2018). Copyright 2018 by NTNU.

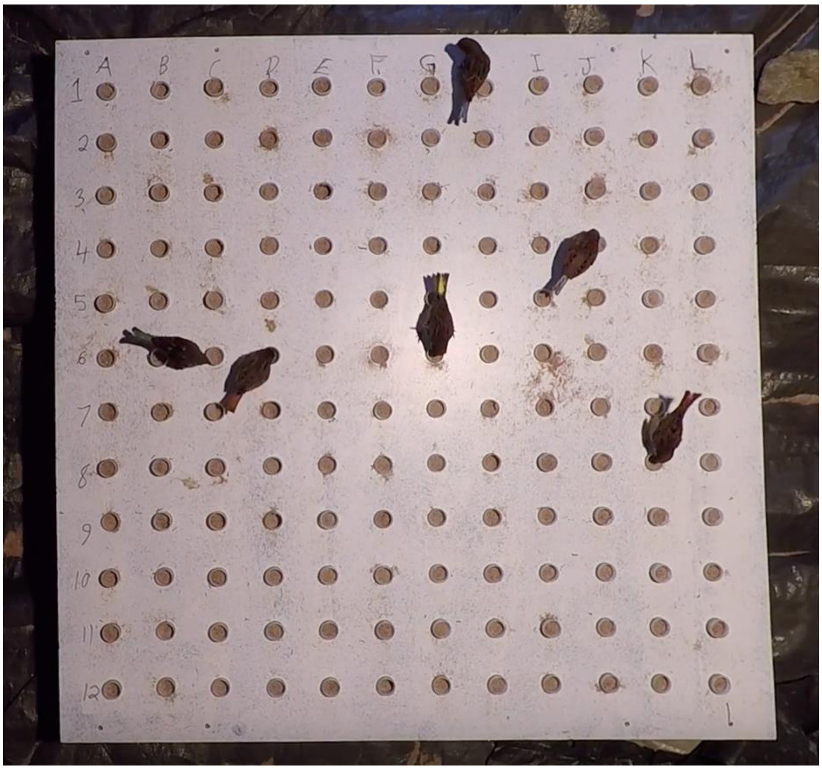

Figure 2.3: Video screenshot showing one group during a trial of the experiment. The communal checkerboard feeder contains 144 wells that were labeled to keep track of the individuals' visits. The individuals are identified by the color painted on their tail.

The pair-wise trials lasted around 15 minutes, whereas the group-trials lasted around 90 minutes. See Mohammad (2018) for more information about the pair-wise trials. In sequence, each group spent four consecutive days in the training and experimental rooms. For one group, day 1 was spent in training room #1 and day 2 in training room #2. On day 3, the group participated in its two first trials; the whole group together in the group room in the morning, and one vs. one individual in the pair-wise room in the afternoon. Day 4 entailed the same experiments in the same rooms, but in opposite order; pair-wise in the morning and group-wise in the afternoon. The next group in line used training room #1 the day after it was occupied by the previous group, then training room #2 and so on. When not participating in any trials, the rest of the birds resided in one of the communal rooms divided into the island and mainland populations. Training room #1 provided unlimited access to sunflower, oat and millet seeds mixed in the sand and on top of all the wells to get the birds used to the feeders as sources of food. Likewise for training room #2, but with the exception that all the wells were altered in the afternoon to not have any seeds on top, and some wells to not include any seeds at all. The purpose was to gradually acclimate the individuals to the real experiment. The food was removed at 21:00 every night in all these rooms, but the feeders in rooms with residing groups that had an experiment the next morning were also covered at 21:15. Whenever an individual was caught and moved from one room to another, it was weighted, but also re-painted if the tail-color was diminishing. Individuals that had completed the trials on day 4 recouped in the communal room, and when all individuals were finished with the experiment, they were released at the location they were caught.

2.2 Video Analysis

The video footage involved a total of 35 individuals; 6 individuals in group 1 to 5, and 5 individuals in group 6. Each group participated in 2 trials (1 trial is approximately 1 hour and 30 minutes of video). However, because 3 individuals of group 5 barely had any paint left on their tails, they were too difficult to differentiate from each other while watching the videos and the group had to be excluded. The video analysis and the consequent results of this study are therefore based on 29 individuals in 5 groups.

The videos were recorded with a Wi-Fi-enabled GoPro-camera connected to an external power supply to prevent power-failure during the trials. The camera was attached to a mount approximately 1 meter from the ceiling above the communal feeder. The recordings were monitored live via the GoPro app to ensure proper execution of the trial, that the camera was recording, and that no individual seemed too stressed to participate. At the end of the same day a trial was conducted, the video footage was secured from the camera's microSD-card to an external hard-drive. The recording commenced before the birds was let in and out of the room, whereas the actual start- and end-times of the trials were noted when the first individual landed on the feeder and the last individual departed. The time shown in the videos were accordingly adjusted for the actual start-time when analyzing the material.

The experiment therefore consists of 10 trials; 1 morning-trial and 1 afternoon-trial for each of the 5 groups. When analyzing a group, its members behavior was analyzed individually and in sequence. The observer noted the arrival and exit time and duration of a well visit if the individual foraged for more than 2 seconds, and the observation was recorded as producing if that well contained seeds. The observer noted the time the focal individual interacted or was interacted with, as well as the duration of any aggression occurring at that well. Additionally, the time when an individual flew away or landed at the feeder was recorded, as a measure for the time it was absent from the feeder. In any of these scenarios, the present number of other individuals on the feeder and neighbors to that well were noted. Table 1 shows the parameters and table 2 the social interactions more in detail.

Observation Name	**Parameters**
Trial Start	The time when the first individual lands on the board and the trial begins.
Trial End	The time when the last individual leaves the board and the trial ends.
Square	The designation of a well on the feeder. Each well has a combination of a letter and a number: A to L for the columns and 1 to 12 for the rows.
Well Order	The order of the well the focal individual currently visits. A well-visit only counts if the focal individual forage for more than 2 seconds, if it interacts with another individual, or if it leaves or lands at the feeder.
Square Arrival Time	The time the focal individual arrives at a well.
Square Exit Time	The time the focal individual leaves a well.
Well Duration	The duration the focal individual resides at a well.

Board Number	Number of other individuals present on the feeder at the time the focal individual visits a well.
Neighbor Number	Number of other individuals currently residing in the wells next to the well at the time the focal individual visits it.
Excluded	A well-visit where the focal individual feeds for more than 2 seconds, interacts with another individual, or leaves or lands on the feeder. It is recorded as a number from 0-3: 0 = Feeds 1 = Interacts 3 = Leaves the feeder (recorded as duration absent from the feeder until it lands again) 2 = Lands on the feeder (Brief landings lasting less than 4 seconds before leaving again are not recorded)
Flying	The focal individual feeds for more than 2 seconds (excluded = 0) before it flies away or after it lands on the feeder. It is recorded as a number from 1-2: 1: Lands and feeds 2: Feeds and leaves
Seed Present	If there are seeds present or absent in a well. Seeds needs to be present for feeding (excluded = 0) to be considered successful producing by the individual. It is recorded as either 0 or 1: 0: Seeds absent 1: Seeds present
Join Act	When the focal individual interacts with another individual residing at a well. The type of interaction is recorded as a number from 1-15 (see table 2).
Intruder Act	When another individual interacts with the focal individual residing at a well. The type of interaction is recorded as a number from 1-15 (see table 2).
Intruder Time	The time the intruder act occurs.
Fight Duration	The duration of a fight occurring at a well. Fight duration is recorded when both individuals give continuous aggression of more than 1 second, or repeatedly within a timeframe of less than 10 seconds.

Table 2.1: The parameters used in 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 2.2: The types of interactions used in the video analysis.*

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2.3 Data and Statistical Analysis

The data from each video file was coded and entered in the data base. The data were then checked for any obvious typos or missing inputs. The data was manipulated and analyzed using the statistical software R (2019), in the same manner as for the pair-wise trials (Mohammad, 2018). Each individual was given a unique identifier from 1 to 29, the various producing or scrounging observations were turned into binaries, and statistical parameters such as means, min/max, and frequency of observations were estimated.

Variation around the intercept of the response variable caused by random and fixed predictor variables was modelled using linear and generalized mixed-effect models in the lme4-package (2019) in R. It is then possible to distinguish between the effects of the random variables, namely the total effect of all opponents in a group (Group ID), and the focal ID (Dingemanse & Araya-Ajoy, 2015). The following response variables were used: (a) Producing Count, (b) Scrounging Count, (c) Producing Duration, (d) Scrounging Duration Ratio (Scrounging Duration divided by the total duration of producing plus scrounging as a measure for potential scrounging-opportunities), and (e) Scrounging Count Ratio (Scrounging Count divided by the total counts of producing plus scrounging).

Variation in the phenotype of the focal individuals was analyzed in mixed-effects models using the so-called variance partitioning (VPA) and hybrid approaches (HA). In VPA, Focal and opponent ID acts as the random intercepts, so that variance relating to the focal individual and opponent is estimated. HA involves a fixed covariate of a specific trait (i.e. opponent levels of behavior) that helps reveal the effect of the opponent’s behavior on the focal individual’s response variable. If the trait value proves to explain nearly or all the variance seen in the ID effect, then the random ID effect is almost all accounted for by that trait. The summed producing by all other members in a group was estimated to generate this covariate of ‘opponent total producing’. Comparing these two models thus quantifies the magnitude of opponents’ behavioral trait-effect on the response behavior of the focal individual (Dingemanse & Araya-Ajoy, 2015). Both models included sex and day as fixed effects along with their interaction in order to highlight any differences in response behavior between the sexes or due to different (i.e. first versus second) days of the experiment.

All the models were run in R. The significance of the random effects in the models was assessed using P-values from likelihood ratio tests. Likelihood-ratio tests were used to compare each model against its null model to determine the increase of fit when including the random effect of focus. The statistical significance was measured as the P-values of the loglikelihood ratio tests with 0.5 degrees of freedom. The focal individual’s consistencies in behavior and plasticity with regard to level of behavior of an opponent were measured as repeatabilities. Repeatability values were measured as the proportion of variance attributed to random effects of the total variance not associated with any fixed effects (Han *et al.*, 2016). Repeatability was measured this way as a mean to distinguish between the proportion of total variance belonging to the focal individual and that of an opponent. The repeatability measures taken from the binomial models were calculated using a method described by Nakagawa & Schielzeth (2010). Finally, the ANOVA summaries from all the models were put into tables, and figures of interest were made with the ggplot2-package (2019) in R.

Unfortunately, the sample sizes did not allow some of the models to converge and the following measures are therefore not included in table 3.1: Scrounging count ratio (e), repeatability for scrounging count (b), residuals for scrounging count (b) and scrounging duration ratio (d). The values for focal ID slopes of all the response variables (a-e) in response to opponent total producing are also left out because of runoff overparameterization. Additionally, the results in table 3.1 need to be interpreted with care as the convergence was poor.

3 Results

There was a large variation between individuals in total counts and duration of producing and scrounging, ranging from 13 individuals that did not scrounge once to 1 individual that scrounged 22 times, and 5 to 270 producing counts (see appendix).

The majority of the results regarding focal ID and group ID variance have statistically non-significant effects, apart from the group ID results concerning producing count and duration. Thus, confident claims cannot be made regarding the apparent patterns described in section 3.1 and 3.2. However, the proportion of the variance explained by these random effects is considerable in all models, suggesting that they explain important aspects of these social behaviors.

Fixed Effects	**(a) Producing Count [Normal]**		**(b) Scrounging Count [Poisson]**	
	VPA	**HA**	**VPA**	**HA**
Intercept ± SE	**-0.219 ± 0.492**	**0.212 ± 0.484**	**1.587 ± 0.002 (p < 0.001**	**2.637 ± 0.002 (p < 0.001)**
Sex ± SE	-1.069 ± 0.627 (p = 0.008)	-1.032 ± 0.582 (p = 0.076)	-1.637 ± 0.002 (p < 0.001)	-1.342 ± 0.002 (p < 0.001)
Day ± SE	-0.036 ± 0.288 (p = 0.001)	-0.322 ± 0.282 (p = 0.119)	-0.129 ± 0.002 (p < 0.001)	-0.887 ± 0.002 (p < 0.001)
Day x Sex Interaction ± SE	1.024 ± 0.368 (p = 0.007)	0.993 ± 0.336 (p = 1.000)	0.654 ± 0.002 (p = p < 0.001)	0.472 ± 0.002 (p < 0.001)
Opponent Total Producing ± SE		0.334 ± 0.122 (p = 0.006)		0.677 ± 0.002 (p < 0.001)
Random Effects				
Focal ID	0.012 (p = 1.000)	0.380 (p = 1.000)	0.200 (p = 0.975)	0.443 (p = 1.000)
Group ID	0.381 (p = 1.000)	0.024 (p < 0.001)	0.746 (p = 0.975)	0.215 (p = 1.000)
Residual	0.455	0.379		
Repeatability				
R among	0.014	0.486		
R opponents (group)	0.500	0.031		

Fixed Effects	**(c) Producing Duration [Normal]**		**(d) Scrounging Duration Ratio [Binomial]**	
	VPA	**HA**	**VPA**	**HA**
Intercept ± SE	-0.399± 0.505	-0.111 ± 0.508	-2.037 ± 0.338 (p < 0.001)	-1.671 ± 0.329 (p < 0.001)
Sex ± SE	-0.577 ± 0.643 (p = 0.032)	-0.534 ± 0.620 (p = 0.097)	-1.753 ± 0.436 (p < 0.001)	-1.759 ± 0.416 (p < 0.001)
Day ± SE	0.052 ± 0.296 (p = 0.006)	-0.132 ± 0.297 (p = 0.184)	-0.463 ± 0.057 (p < 0.001)	-0.719 ± 0.076 (p < 0.001)
Day x Sex Interaction ± SE	0.742 ± 0.379 (p = 0.050)	0.700 ± 0.361 (p < 0.001)	0.343 ± 0.079 (p < 0.001)	0.342 ± 0.081 (p < 0.001)
Opponent Total Producing ± SE		0.251 ± 0.129 (p = 0.047)		0.253 ± 0.047 (p < 0.001)
Random Effects				
Focal ID	0.008 (p = 1.000)	0.0368 (p = 1.000)	0.524 (p = 0.998)	0.380 (p = 0.999)
Group ID	0.392 (p = 1.000)	0.386 (p < 0.001)	0.643 (p = 0.998)	0.666 (p = 0.999)
Residual	0.482	0.436		
Repeatability				
R among	0.009	0.043	0.118	0.088
R opponents (group)	0.445	0.449	0.144	0.154

Table 3.1: The number of events of producing (a) and scrounging (b), and the duration (sec) of producing (c) and scrounging ratio (d), using variance-partitioning approach (VPA) and hybrid approach (HA) models (see Methods for details). Focal individual sex and the day, and their interaction are included as fixed effects, and 'Opponent Total Producing' in the group as a whole is added to the HA models as a covariate. The parameter estimates ± standard errors and p-values are given, along with the random effects variances explained and p-values. Only the producing models (a) include repeatability and residuals, because the other models had poor convergence.

3.1 Focal ID

Figures 3.1, 3.2, 3.3 and 3.4 illustrate the means and ranges of producing and scrounging for individuals both within and among groups, showing apparent differences between individuals and suggesting that there are animal personalities even if the random effect of Focal ID in table 3.1 was not always significant. The following paragraphs compare the VPA and HA models in table 3.1 to assess the responses to the producing of others versus variability of the measured phenotypes due to individual and group differences.

The variation in individual producing frequency (table 3.1 (a) and figure 3.1) was not at all explained by focal ID in the VPA model. However, the focal ID variance increased to a substantial value (0.380) in the HA model when the opponent total producing covariate was added as a fixed effect. This increase in variance was probably explained by the characteristics of some individuals (e.g. shyness or friendships) causing them to produce in response to the level of producing in the group, also reflected in the noticeable reduction of random within individual variation (residuals) from 0.455 to 0.379. Furthermore, the covariate considerably increased the non-existent repeatability (R among = 0.014) to a fair amount (0.486), possibly because levels of producing provided stability in the environment.

The producing duration variation (table 3.1 (c) and figure 3.2) was not explained by focal ID in neither of the models, no matter the incremental increase in variance and repeatability in the HA model. This implies that the total time the focal individuals spent producing did not vary according to repeatable individual differences. However, the decrease in residual variance suggests that some of the within individual variance was absorbed by the opponent producing covariate. Yet, it was a bit surprising that focal ID was markedly responsible for the number of well-visits, but not at all for the total duration of the producing events.

The variance explained by the Focal ID for the scrounging count (table 3.1 (b) and figure 3.3) nearly doubled (0.200 VPA vs. 0.443 HA), suggesting that the covariate further revealed any individual differences that affected the propensity to scrounge. This effect is believed to be caused by individual characteristics that encourage individuals to scrounge in regard to the increase in scrounging opportunities that producing provides. However, the two models were not able to provide residuals and repeatability estimates due to low sample sizes.

For the scrounging duration ratio (table 3.1 (d) and figure 3.4) the covariate tended to show the opposite pattern (0.524 VPA vs. 0.380 HA), so that individual differences were less important in explaining the proportional scrounging duration when controlling for the producing duration of others. Furthermore, the scrounging count is too low in both models to show consistency in this behavior in both trials. Additionally, the amount of residual variation and the information that this provides was also unavailable. The lack of information makes this effect unclear, but the scrounging ratio was in fact intended to measure the actual use of scrounging opportunities that was argued for in the paragraph above.

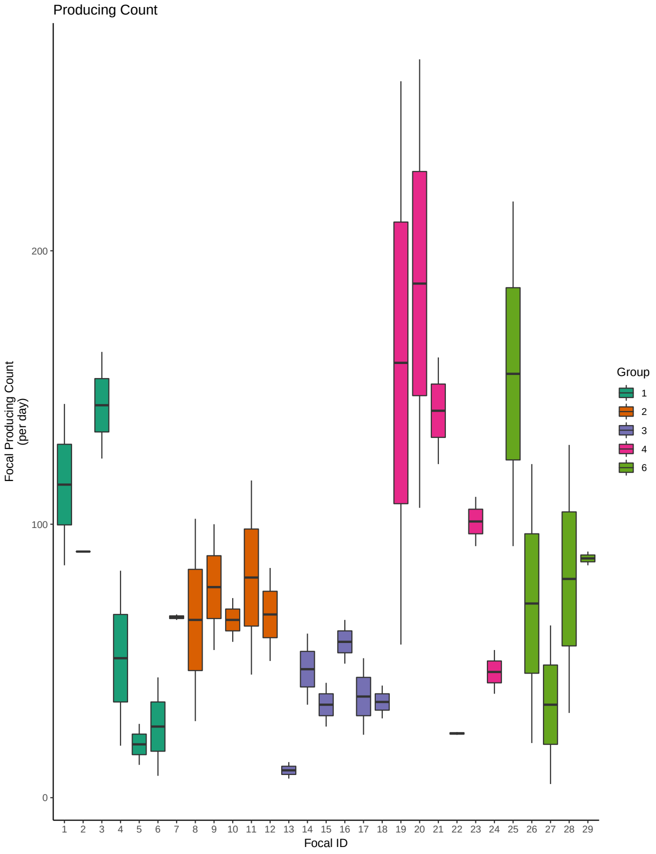

Figure 3.1: Individual frequency of producing per day. The 29 individuals are colored by their associated groups.

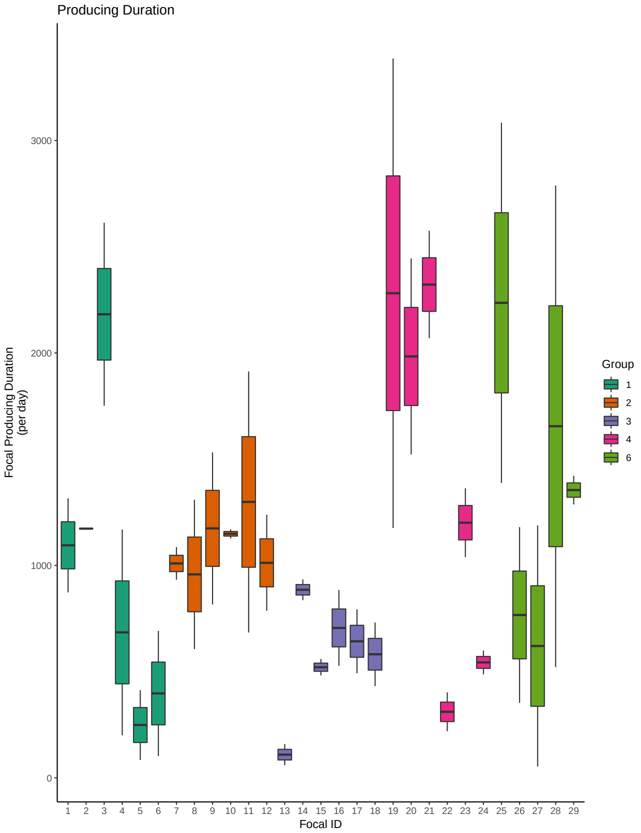

Figure 3.2: Individual duration of producing per day. The 29 individuals are colored by their associated groups.

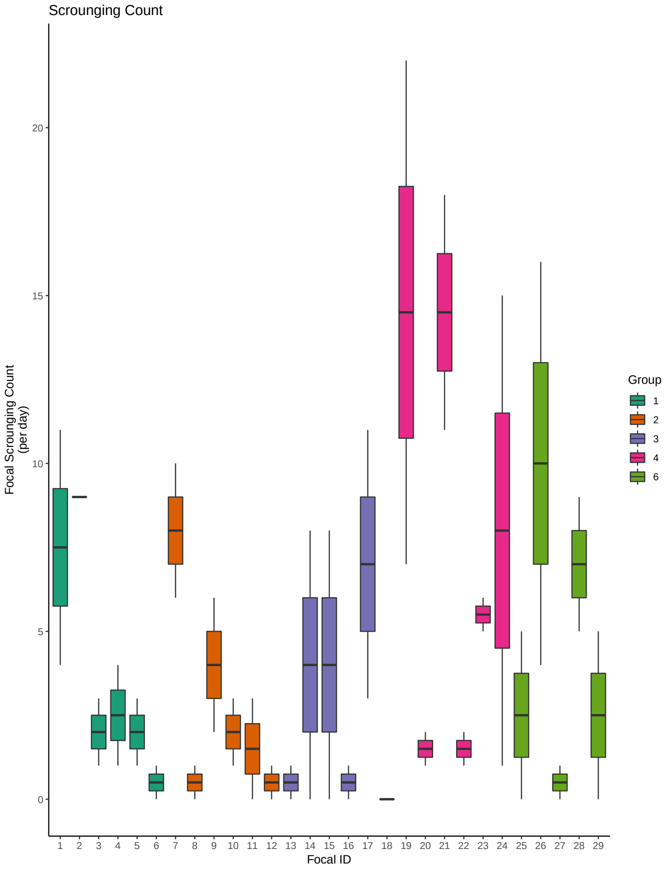

Figure 3.3: Individual frequency of scrounging per day. The 29 individuals are colored by their associated groups.

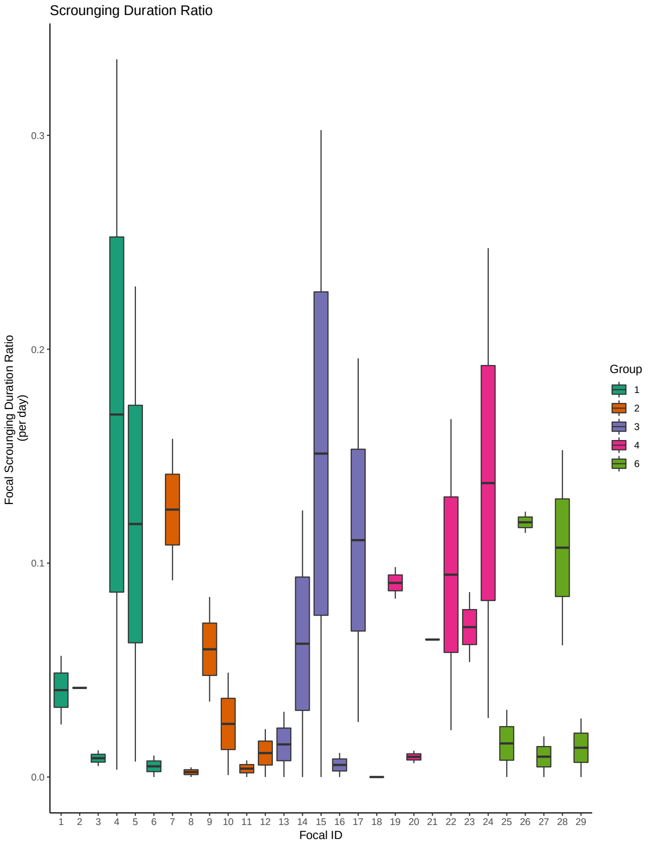

Figure 3.4: Individual scrounging duration ratio per day. The 29 individuals are colored by their associated groups.

3.2 Group ID

Figures 3.5, 3.6, 3.7 and 3.8 illustrate different means and ranges of the collective behavior in the groups when separately influenced by specific opponents. This provides information of the extent of influence each group members had on each other. Note that these figures don't show the individual contributions to the group ID effect. However, the combined producing frequency and duration (figure 3.5 and 3.6) shows similar means and ranges in group 2, implicating that the group ID effect is less important, and that the opposite is true for group 4 and 6 that shows large contrasts within. It thus follows that all the groups have important group ID effects for scrounging duration ratio (figure 3.4). The importance of the group ID effects on individual scrounging and producing is reflected in table 3.1:

Individual responses seemed to depend a lot on the group ID in their frequency of producing (table 3.1 (a) and figure 3.5) when considering only the VPA model (var = 0.381). Moreover, the variance essentially dropped to zero (0.024) in the HA model with inclusion of the covariate total producing effort in the group. This suggests that all of the variation in individual producing frequency previously explained by the group ID can be explained by the measured levels of producing by the group in the covariate rather than any other effect of the group itself (e.g. levels of disturbance, aggression or anti-predator behaviors). The group effect was statistically significant ($p < 0.001$), but not consistently repeatable across trials (R opponents = 0.031).

For the producing duration (table 3.1 (c) and figure 3.6), the addition of the covariate did not change much of the Group ID variance (0.392 VPA vs. 0.386 HA), but the considerable random group ID effect was statistically significant ($p < 0.001$) and fairly repeatable (R opponents = 0.449). These results suggest that the opponents had a consistent and repeatable effect on the producing duration of focal individuals.

The variance for the scrounging count (table 3.1 (b)) was the highest measured value (0.746 VPA) regarding all the response variables, presumedly because of the distinctiveness of group 4 (figure 3.7). This means that a large proportion of the phenotypic variability was probably due to the random group ID effect. The covariate was able to explain a large amount of this variance, suggesting that the producing of the other group members provides an explanation for most, but not all of this effect. The remaining variance (HA = 0.215) is possibly due to characteristics of the group, such as patterns of dominance or relatedness. However, no repeatability estimates are available.

For the scrounging duration ratio (table 3.1 (d)) both models explain similar variance (0.643 vs. 0.666), and these high values build support for the strong group ID effects within all of the groups (figure 3.8). This suggests that the characteristic of the group had a considerable effect on the individuals, and that the producing with the consequent scrounging opportunities was not influenced by the group ID effect. Yet, the repeatability estimates are not able to show consistent and repeatable opponent effects.

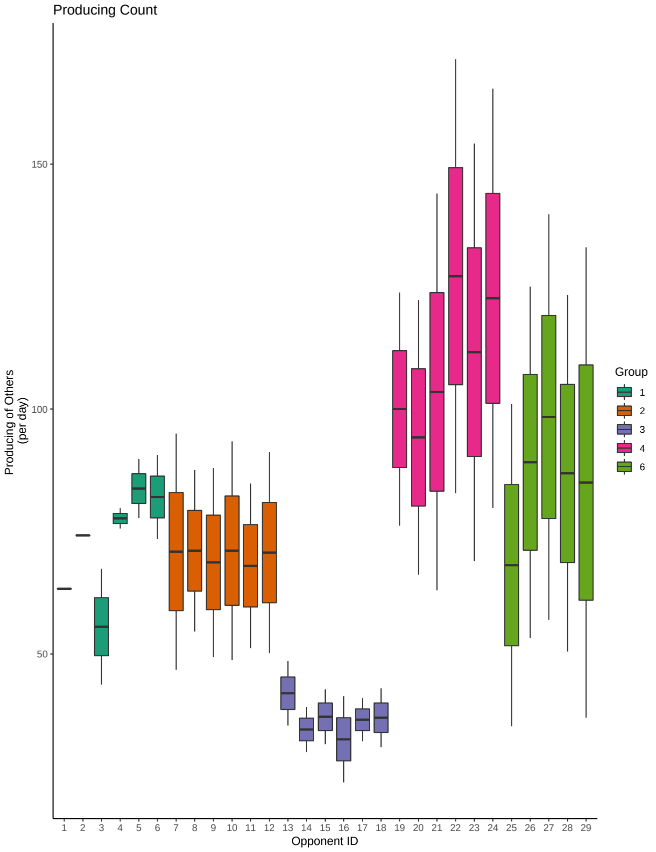

Figure 3.5: The producing frequency of the other individuals (colored by group) when faced against a specific opponent (ID 1-29), per day.

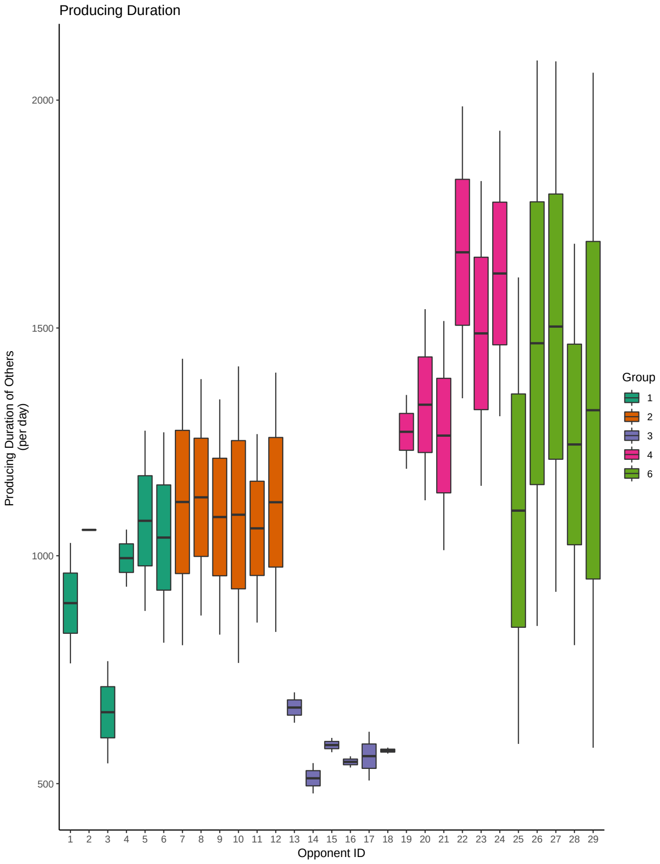

Figure 3.6: The producing duration of the other individuals (colored by group) when faced against a specific opponent (ID 1-29), per day.

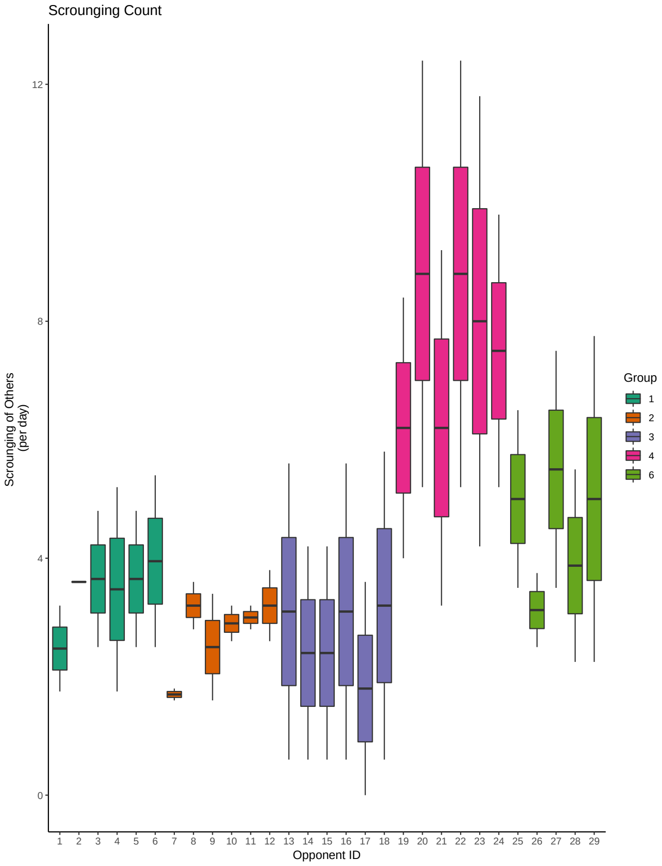

Figure 3.7: The scrounging frequency of the other individuals (colored by group) when faced against a specific opponent (ID 1-29), per day.

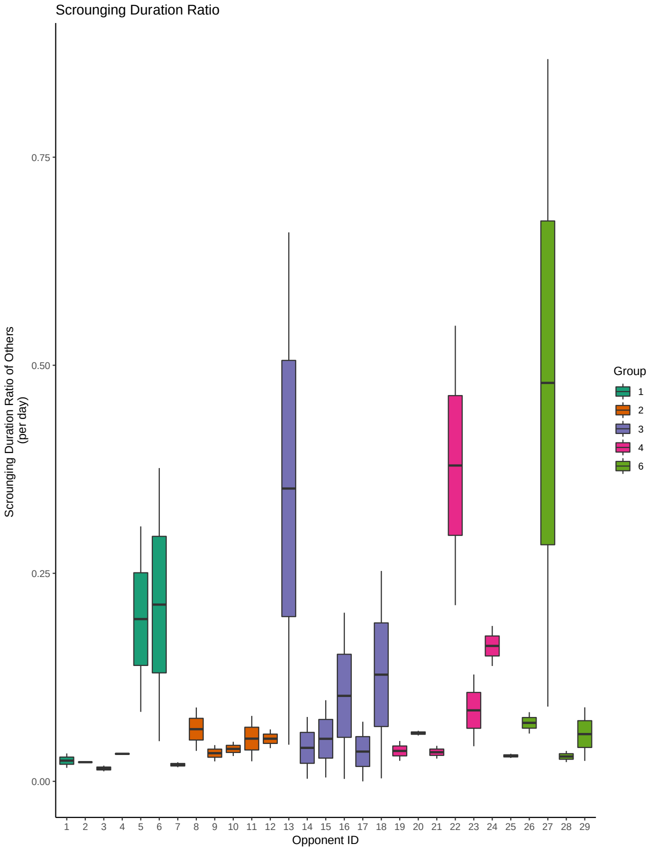

Figure 3.8: The scrounging duration ratio of the other individuals (colored by group) when faced against a certain opponent (ID 1-29), per day.

3.3 Sex and Day

Sex and day relate to factors that caused females to act or be treated different than males or factors that had changed the second day. The combined effect of the sex and day interaction was very statistically significant in all the models apart from the HA model of producing count (table 3.1 (a)), ensuring that the separate sex and day effects were entangled and thus problematic to interpret on their own. As such, there is evidence of specific combinations of these two variables having effects on individual rates of producing and scrounging.

The slopes representing the sex x day predictor variables (table 3.1) are positive for the producing count (a) and duration (c), meaning that sex and day effects is responsible for the pattern seen, that males produced considerably more than females on the second day (figure 3.9 and 3.10).

For the scrounging count (table 3.1 (b)), the positive slope decreased substantially (0.654 VPA vs. 0.472 HA), because the opponent total producing covariate made the sex and day interaction effect on scrounging behavior less important. This covariate has possibly absorbed some of this variation to explain sex effects or day effects within or among individuals in their frequency of scrounging. Figure 3.11 and 3.12 reflects the value and decrease of the slope, that females on average scrounged more than males on both days, but less the second day for example due to disturbances. Furthermore, it becomes apparent that many of the individuals that scrounged negligible or not at all (appendix) were males (figure 3.13 and 3.14).

The slopes are equal for the two models of scrounging duration ratio (table 3.1 (d)), so the opponent total producing is not able to explain the differential ratios relating to sex and day. However, figure 3.13 and 3.14 provide some insight into sex and day differences in individual plasticity regarding scrounging opportunities, whereas the females seem to display most plasticity, especially for scrounging duration ratio. The specific extent of this plasticity is not known due to the missing slope values, because of the unsuccessful implementation due to insufficient sample size to detect these differences.

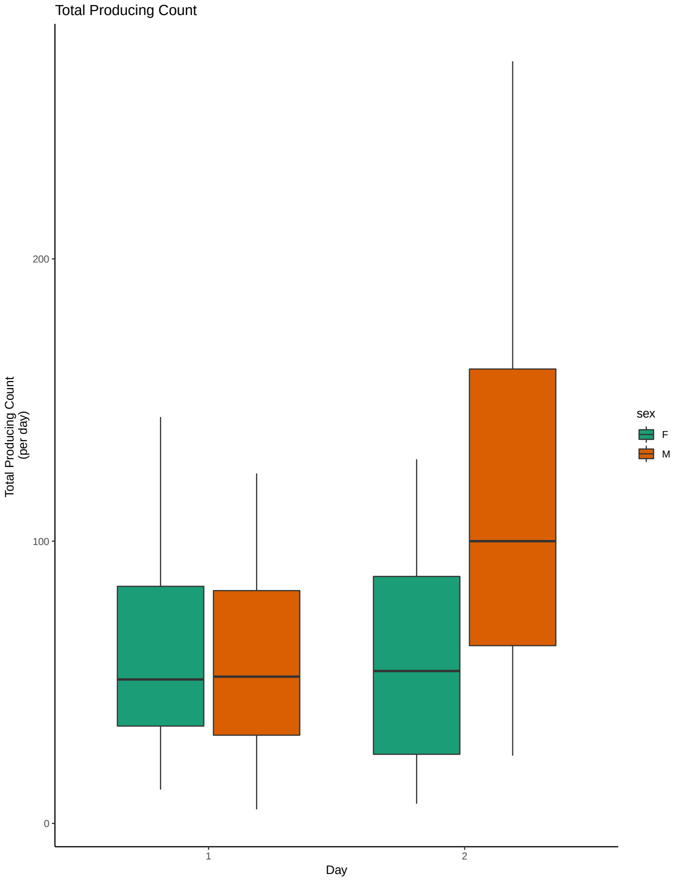

Figure 3.9: The total frequency of producing across all groups per day, colored by sex.

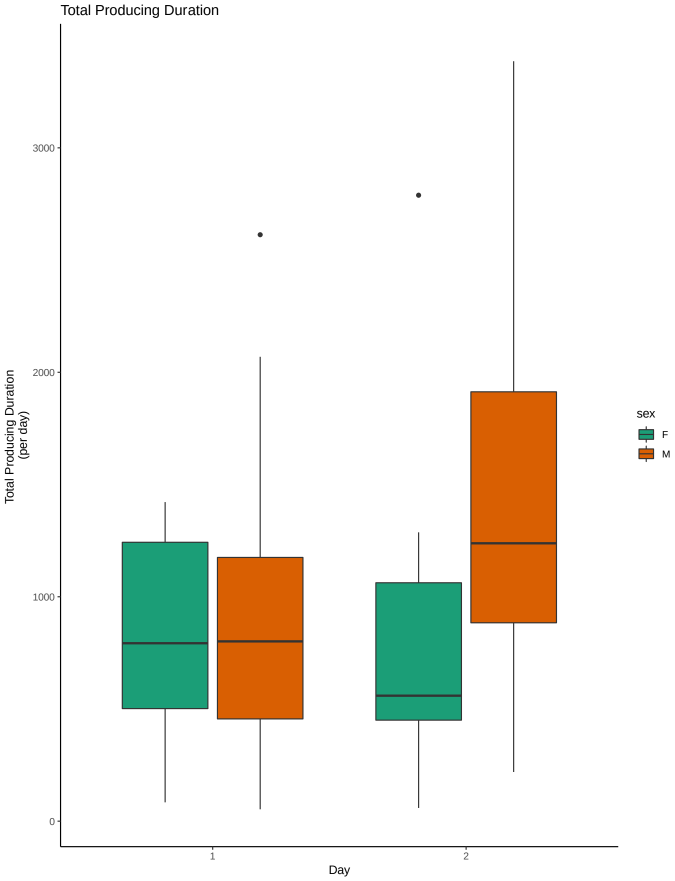

Figure 3.10: The total duration of producing across all groups per day, colored by sex.

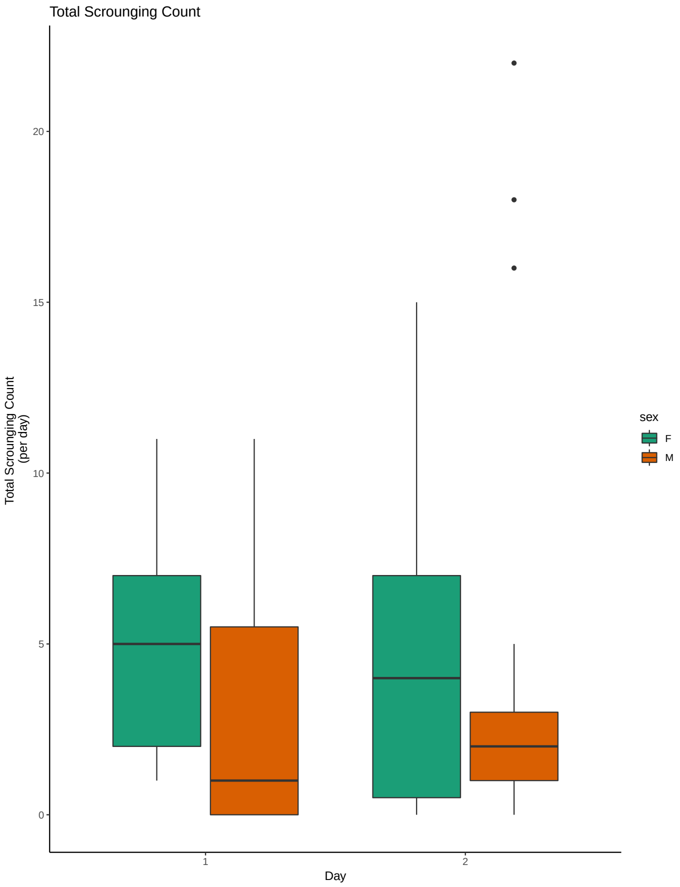

Figure 3.11: The total frequency of scrounging across all groups per day, colored by sex.

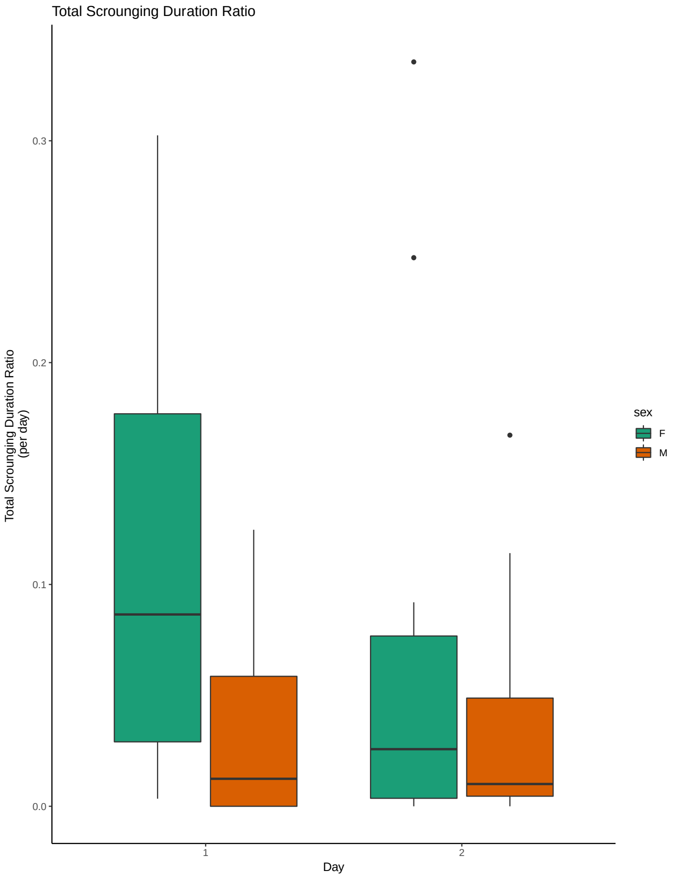

Figure 3.12: The total scrounging duration ratio across all groups per day, colored by sex.

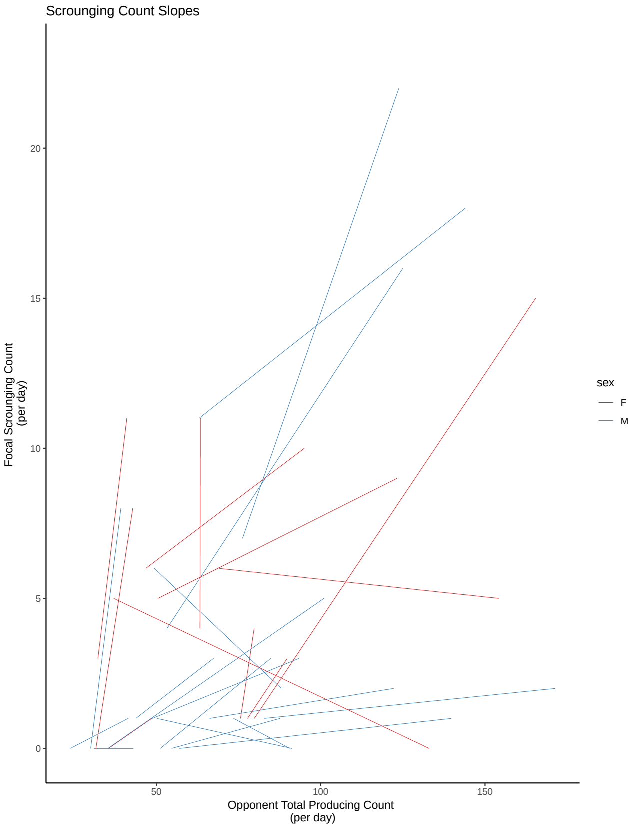

Figure 3.13: The change in individual scrounging frequency as the total producing of the group changes. The start-point and end-point of the slope corresponds to day 1 and 2. The individuals are colored according to sex.

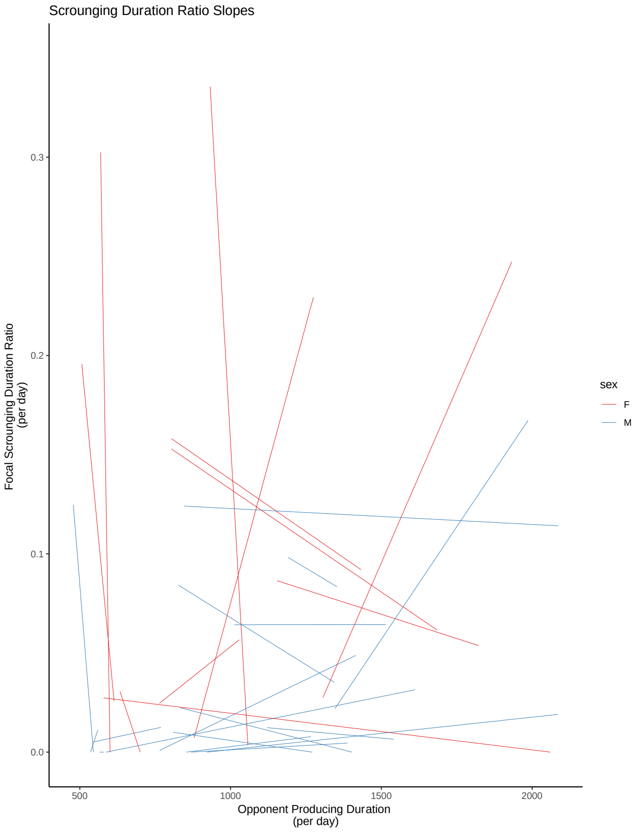

Figure 3.14: The change in individual scrounging duration ratio as the total producing of the group changes. The start-point and end-point of the slope corresponds to day 1 and day 2. The individuals are colored according to sex.

4 Discussion

The objective of this study was to investigate consistently repeatable foraging behavior within flocks of house sparrows (*Passer domesticus*). Specifically, to what extent did individual differences and indirect social effects explain individual rates of producing and scrounging in an ESS context Mohammad (2018) measured the indirect social effects of specific opponents, whereas this study aimed to assess the collective effect of all the identities of the same individuals (Group ID).

The results of this study revealed individual differences, reflected in the focal ID random variance that was able to explain much of the phenotypic variation within the groups. However, despite the relatively high producing count repeatability (0.486), the individual repeatability of the various behaviors was generally low (< 0.118). Moreover, there was not enough statistical power to claim that the measured variance in these two trials were due to actual individual differences. These uncertain results cannot provide firm evidence of the first hypothesis (figure 1.1); that average levels of producing and scrounging differ consistently and repeatably within a group. However, a claim as such would be rather uncontroversial, and this study clearly explained enough individual variance to be meaningful in a study with more groups.

This study also aimed to assess individual differences in phenotypic plasticity, but the small sample size prevented the rendering of the random-slope models. Martin *et al.* (2011) suggests a sample size of N > 200 to be able to detect significant variation in plasticity, which is considerably more than the 72 individuals of the 130 Lauvøya residents used in the study of Pettersen (2017). Pettersen (2017) ran into the same problem due to low levels of scrounging that probably created a social environmental range too small to detect individual differences. However, Pettersen (2017) believed that the high number of repeated measurements (628 pair-wise and 115 group-wise assays) would suffice had the study design stimulated enough scrounging and thus introduced sufficient variation into the data set. The year this experiment was conducted only 36 individuals of the population were still alive, yet 278 pair-wise trials proved enough to provide evidence of individual differences in plasticity, presumedly because of the improved rates of scrounging (Mohammad, 2018). The 57 (6 individuals * 5 groups * 2 days (1 individual attended only 1 day)) group-wise assays of this study did not suffice. The scrounging pattern was very similar to the pair-wise assays (compare appendixes of both studies), so it is probable that there were too few group-wide assays for a such small sample size. The complications this had for the study was that the second prediction (figure 1.2) could not be tested.

The results regarding the last hypothesis (figure 1.3) is what we were truly interested in, and the interpretations proved a bit more nuanced. Firstly, it was predicted that the behavior of certain individuals would differentially affect the behavior of opposing individuals, and that this would happen in a consistent and repeatable manner. Secondly, it was predicted that individuals deploying fixed strategies, i.e. displaying low plasticity, would exert the greatest influence on the behavior of more plastic individuals. Because in this case all the opponent IDs was summed to create the group ID, the individual proportion of the collective effect a group exerted on a focal individual was not always clear, if only due to the small number of groups and limited measures per group (i.e. only one per trial for all individuals in the group). This is different from models of pair-wise trials where the individuals were pitted one versus one in all combinations to see the individual effects clearly (Mohammad, 2018; Pettersen, 2017). Thus, this study lacks the sensitivity to provide evidence of particular individuals affecting more plastic individuals to a larger extent. However, it was evident in many of the random effects of group that different combinations of individuals affected the mean and range of behaviors within the groups to a varying degree, reflecting contrasting importance of the group phenotype on its members. Regarding the actual results, the individual frequency of producing was not affected by the group ID, but was significantly affected by the collective amount of producing in the group. This might reflect what was previously pointed out by Pettersen (2017), that producing is not necessarily a social behavior, and that food abundance and lack of group ID effect could have led to a more stable environment with consequent increase in repeatability (0.486) of the feeding behavior. A simpler explanation relates to the fact that house sparrows prefer to forage in flocks, so that group producing promotes individual producing. However, the most interesting results was probably the extensive effect the collective producing had on focal scrounging frequency. Large amounts of producing – and thus more scrounging opportunities, were expectedly followed by increased rates of scrounging. However, the remaining random group ID effect could also tell us that there was something else about the social structure that influenced individuals propensity to scrounge of their conspecifics. Willingness of individuals to scrounge depending on the IDs of the opponents and at given level of producing can provide such an answer, for example due to social bonds, dominance ranks (Liker & Barta, 2002) or relatedness (Tóth *et al.*, 2009). Characteristics such as these could also possibly explain the large increase in focal ID variance regarding the first prediction, simply because some individuals scrounge more given the opportunities.

The only consistently solid statistical results in this study were the fixed effects of sex and day. The significant interactions here mean that the separate variance estimates for sex and day are hard to interpret. Nevertheless, the combined effect of these two factors highly suggests that sex and day had a particularly positive influence on male rates of producing the second day, but also on the relatively higher female rates of scrounging that was reduced the second day. It is likely that these effects were due to persistent differences between males and females, e.g. higher metabolic rate in females (Mathot *et al.*, 2009), and small or large dissimilarities within the location over the time-span of the study, such as sources of disturbance. It was attempted to keep the physical environment stable, but some possibly unrelated differences were revealed in the videos. Examples are that one individual did not attend a whole trial of 90 minutes, and periodically long stretches passed without the presence of individuals on the feeder. On other occasions the individuals simultaneously scattered, whereas one event was surprisingly caused by a rock hitting the floor (camera did not see why). Furthermore, birds sometimes displayed puffed feathers, indicating e.g. stress, illness, cold – not excessive in extent or duration, but seemingly at random. Other day and sex variations could be related to internal energetic state, and so the ample supply of food and water was to ensure the well-being of the study subjects, but also served to equalize the effect of hunger (Mohammad, 2018).

It follows that weight is closely related to internal state and metabolic rate, thus conditionally prompting individuals to scrounge (Barta & Giraldeau, 2000; Lendvai *et al.*, 2005). Yet, that was not controlled for due to time constraints, but is something that should be included in future studies. That said, the individuals were weighted at capture and before the trials (Mohammad, 2018), so the relative change in weight could possibly have been used to this purpose. Sex and day interactions possibly makes the focal and group ID effects even harder to interpret, as it suggests complex and unclear differences in the day to day behavior between the individuals. Part of the unknown variance currently partitioned to the different predictor variables may possibly instead relate to dominance ranks and relatedness. These two factors could possibly have acted on their own or intertwined, or even entangled with sex (Liker & Barta, 2002; Tóth *et al.*, 2009) and/or day to day variabilities such as energetic state (Mathot *et al.*, 2009). Considering that the females scrounged more than males in this study, investigations on relatedness and dominance could prove useful in explaining the underlying causes. The timing and location the individuals were captured at were supposed to serve as an indicator of their endemic social groups (Mohammad, 2018), and are likely to hold higher relatedness than the average population. Genetics and pedigrees on all the inhabitant house sparrows on the Helgeland coast in Norway are available, so future studies should take use of that information.

The overall results in this study were not at all what was hoped for, but the low p-values do not necessarily contradict the results from the previous studies (Mohammad, 2018; Pettersen, 2017), however they also mean that we are not able to confirm them. It is obvious that too few trials were conducted on too few groups, and that such a small sample size might generate random trends in the data rather than true effects. Hence, there is a very low probability that the measured individual differences reflect the actual individual differences. The small sample size was also likely what caused problems when trying to fit the data into the models (see methods section), effectively ensuring that crucial information was missing in order to answer the predictions. The aim of this study was also to compare the pair-wise and group-wise results, but as Mohammad (2018) had to exclude group 6 due to excessive signs of stress, and that group 5 had to be excluded in this project (see methods), only data from group 1, 2, 3 and 4 from both projects were available for direct comparison. In itself, that says something about the importance of overestimating the number of study subjects in case of unfortunate events that disqualify experimenting on certain individuals. Combined with the fact that much information in the models was missing and the somehow unreliable results in this study, a decision was made not to delve into the details for comparison.

However, this study did provide a few good p-values and repeatability estimates, and the random effects generally explained large proportions of variance. Pettersen (2017) was not able to provide sufficient repeatability estimates and scrounging rates, presumably because of low levels of scrounging in that study (see purpose and predictions), but he still got overall positive results in pair-wise and group-wise assays. Mohammad (2018) attempted to improve the design, and the results from this study were also in line with the predictions for the most part, albeit also showing somehow low repeatability estimates, some high p-values, but also fully non-significant effects such as opponent ID on individual producing. Fewer individuals (30 vs. 29) and trials (5 vs. 2) were conducted for the group-trials in this study compared to the pair-wise trials (Mohammad, 2018), and 1 of the 29 individuals only attended one trial. Considering that the group-assays in the study of (Pettersen, 2017) conducted 2 trials for each of the 12 groups with 70 individuals, it could maybe have been foreseen that the sample-size and/or number of trials was insufficient before enduring the video analyses. However, these decisions were based on the already small population on Lauvøya and with considerations of the time available during one season. An alternative would be to spend two seasons, but that would cause problems with between-year effects to some extent. Pettersen (2017) proved that it’s possible to fit a much larger experiment with more individuals and trials in one season, so that should be encouraged for future studies.

Furthermore, this study lacked some sensitivity in detecting small changes in behavior that could possibly reveal biological significant effects. Lack of such was wholly explained by the limited time that was available for the extremely time-intensive video analysis. Parameters such as preening, pacing, sleeping, stress and observing should have been implemented as suggested by Mohammad (2018), as it is likely to have influenced behaviors to some extent. Firstly, it would allow for a much more precise estimate of actual foraging time. Observing for example, as it can't be combined with simultaneous producing, would downgrade the producing duration estimates at each well, consequently improving the estimates of each individual. Admittedly, one of the pitfalls relates to one of my own adjustments of the video analysis operation that differ from the original instructions (Mohammad, 2018). The well-visits of 2 seconds and less were not recorded, with the attempt to lessen the overwhelming work-load. It remains unknown how this trade-off is reflected in the results. Perhaps the consequences were minuscule, but it is likely that some individuals were more prevalent in producing within the timeframe that was cut off, falsely incurring narrower ranges and higher mean estimates. Thus, the slightly different methodology may have additionally reduced the sensitivity in detecting the effects in question, followed by the problems with the dataset. For a 30-credit master student, it is thus worth questioning if attempting to investigate producing duration was time better spent than simply recording all of the producing counts. That said, I strongly encourage future studies that have more time or human resources available to include important aspects such as these in the video analysis. On that note, I resolutely support Mohammad (2018) in suggesting that the basic procedure of quantifying producer-scrounger behavior is automated. PIT radio frequency identification devices can track ID and wells with accurate measurements of counts and duration. It has the potential to spare the experimenter for hundreds of hours of video analysis that could be better spent elsewhere and ensure that the measurements are completely accurate. By increasing the sample size and trials, more videos could be analyzed with the sole intent of recording other important aspects that might improve the estimates and the usefulness of the results. Examples could be stress, observing, sleeping, preening, time away from the feeder, unforeseen events, the details of the scrounging (aggression, who initiates etc.). The remaining time can be used investigating effects of sex, energetic state, dominance and relatedness and implementing all that's possible in the models.

This study was set out to reveal consistent and repeatable individual differences and social responsiveness in producer-scrounger behavior, but the biological significance largely remains unanswered. Instead, this study might stand as an example of the sample size being too small and the number of trials insufficient. However, the main problem was the quantity and not necessarily the quality of the data, so the study was not completely uninformative. Because of this, I strongly advocate future studies on the implications of the social environment on producer-scrounger ESS and the evolution of social foraging behavior.

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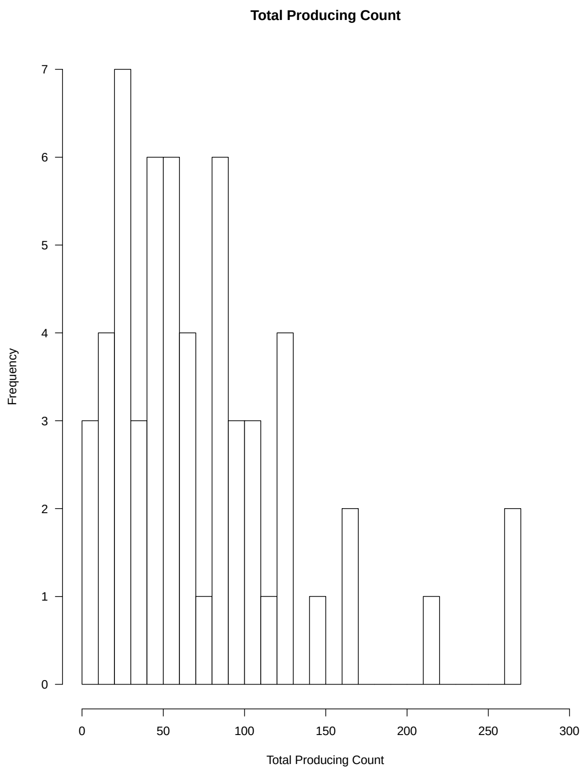
Appendix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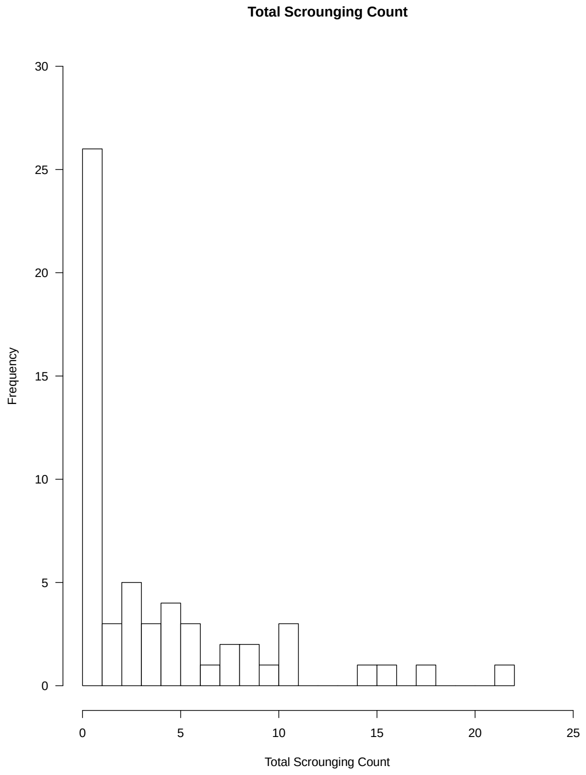
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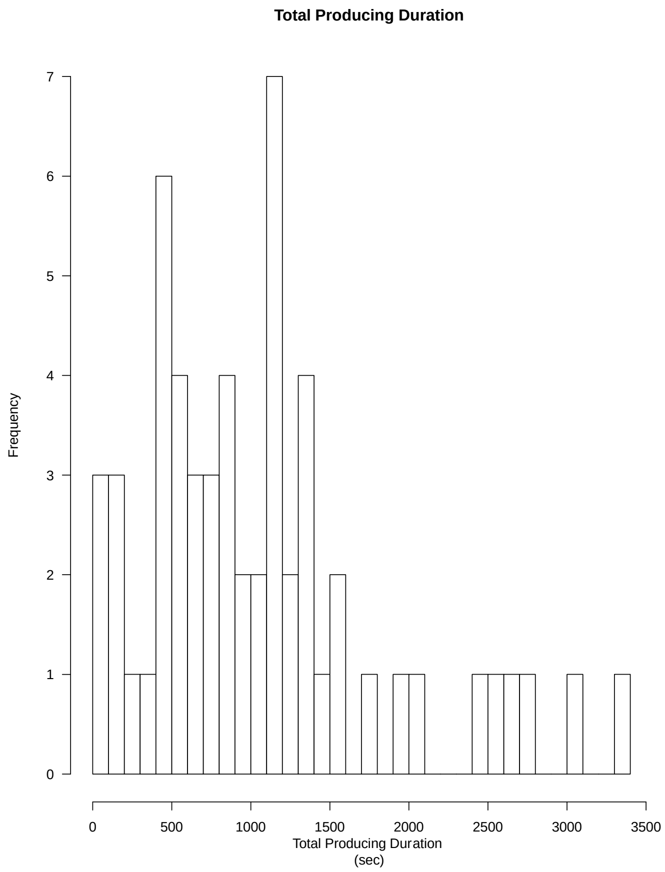
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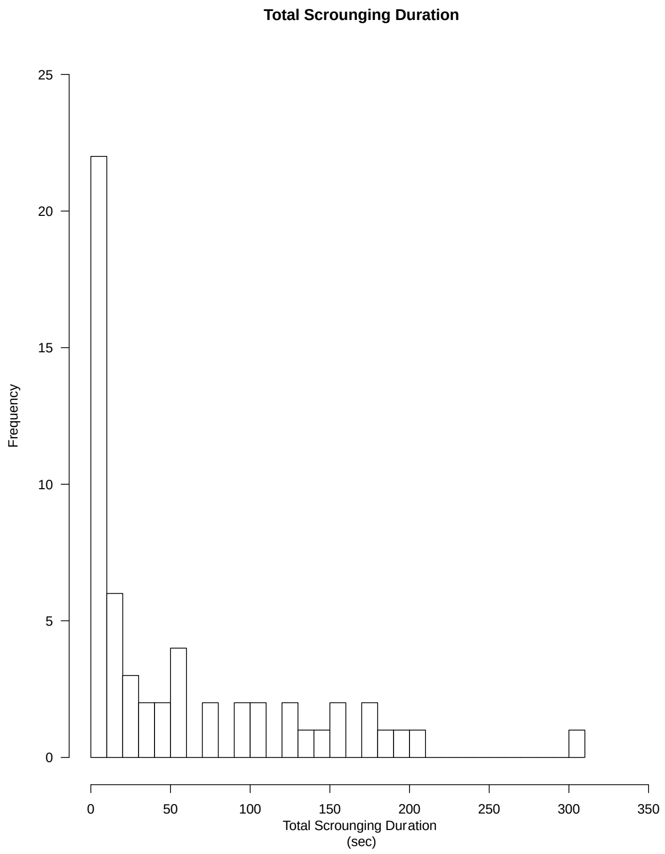
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