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Indirect social effects of the individual strategy in producer-scrounger foraging interactions

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Abstract

When animals interact socially they experience and react to phenotypes of their social partners. Such interactions can affect behaviours and fitness, and therefore opponent effects (i.e. indirect social effects) can maintain or prevent the existence of certain phenotypes in a population. In this study, I repeatedly assayed individual producer-scrounger behaviour in house sparrows (*Passer domesticus)* in both group- and pair-wise assays, to be able to assess indirect effects in whether different opponents affect the behaviour of focal individuals, and to what magnitude. I show repeatable individual differences in feeding behaviour, and that individuals behaved consistently across the group- and pair-wise contexts. However, I found no evidence for repeatable social environment effects, most likely due to high abundance and availability of food, causing scrounging rates to be low. This study therefore suggests that dividing naturally flock-feeding individuals into pairs is an effective way of assessing individual variation in social behavioural responses to individual partners, and the profitability of different foraging and social strategies.

Sammendrag

Når dyr interagerer sosialt, opplever de og reagerer på fenotypene til sine sosiale partnere. Slike interaksjoner kan påvirke atferd og fitness, og derfor kan motstanders effekter (dvs. indirekte sosiale effekter) opprettholde eller forhindre eksistensen av visse fenotyper i en populasjon. I denne studien analyserte jeg gjentatte ganger individuell ‘‘producer-scrounger’’-atferd hos gråspurv (*Passer domesticus*) i både gruppevise og parvise analyser for å kunne vurdere indirekte effekter i hvorvidt ulike motstandere påvirker gitte individers oppførsel og til hvilket omfang. Jeg viser repeterbare individuelle forskjeller i fôringsadferd, og at individer oppførte seg konsekvent over gruppevise og parvise kontekster. Imidlertid fant jeg ikke noe bevis for repeterbare sosiale miljøeffekter, mest sannsynlig på grunn av overflod og tilgjengelighet av mat, som antageligvis forårsaker scrounging-andelen til å være lav. Denne studien antyder derfor at det å dele naturlig flokkspisende individer inn i par er en effektiv måte å vurdere individuell variasjon i sosiale atferdsresponser til individuelle partnere, og lønnsomheten til ulike spisestrategier samt sosiale strategier.

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Introduction

When animals interact with each other, the social behaviour characteristic of each individual becomes a part of the social environment of all the other individuals in its social group. Therefore, the type of individual and its physical environment are not the only factors affecting the consequences of the individual's action (i.e. its fitness), because it also depends upon the behaviour of others (Maynard Smith, 1982). In essence, this is the definition of social behaviour: a behaviour that has fitness consequences for both the actor and the recipient (Hamilton, 1964). One problem in trying to understand the evolution of social behaviour is the complexity of such reciprocal effects on the fitness between different individuals. Game theory provides a solution by exploring the evolutionary stability of alternative social strategies within a population, in order to ascertain the evolutionarily stable strategy or ESS (Maynard Smith, 1982; Davies *et al.*, 2012). The genetic basis of behaviour tends to be poorly understood in most cases, and it is therefore easier to assume perfectly heritable phenotypes under simple natural selection (i.e. the phenotypic gambit, Grafen, 1984). Different phenotypes can thus be treated as different strategies in an evolutionary game, because each will lead to different rewards in terms of fitness when played against other individuals (or players). The mathematical modelling of such games, or evolutionary game theory, has become a widely used tool for explaining natural selection for a range of different social behaviours (Davies *et al.*, 2012). One such game theoretical model of animal social interactions is the producer-scrounger game (Barnard & Sibly, 1981). Since there is often an uneven distribution of resources, both in time and space, animals can use alternative behavioural tactics when searching versus competing for these resources. This is especially apparent in social foraging, where group members vary in their contribution to searching and the discovery of new sources of food. Barnard & Sibly (1981) presented the producer-scrounger game when trying to explain the frequency of exploitation behaviour where some individuals uses the resources found by other individuals. The tactic of the 'producer' is to search for food independently, while the 'scrounger' joins others who have already discovered food. The scroungers use public information and may take a disproportionately larger share of the food compared to their food-searching efforts (Ranta *et al.*, 1996). The producer-scrounger game involves negative frequency dependence, where scroungers do poorly when in the majority, but do better when rare (Vickery *et al.*, 1991). A population may consist of a mix of pure producers and pure scroungers, or it may include individuals playing

a mixed strategy of producer some of the time and scrounger the rest of the time (Vickery *et al.*, 1991; Belmaker *et al.*, 2012). Either way, the two strategies are expected to coexist in a stable equilibrium (i.e. the ESS), making it evolutionarily stable (Vickery *et al.*, 1991; Katsnelson *et al.*, 2008; Tóth *et al.*, 2009).

Studies have shown that individuals of numerous species use a mixed strategy, switching readily between producing and scrounging (e.g. Lendvai *et al.*, 2004). This indicates that the producer-scrounger game might involve a combination of genetic components and a process in which individuals have evolved to use environmental cues and/or personal experience to choose among strategies (Belmaker *et al.*, 2012). There is still some uncertainty whether the producer-scrounger game is under genetic control or not, due to the lack of direct investigations of the genetic basis of the producer-scrounger tendencies (Katsnelson *et al.*, 2008). However, levels of producing and scrounging are theoretically expected to differ according to group size (i.e. the potential number of producers to scrounge from) (Vickery *et al.*, 1991), predation risk (i.e. scrounging and anti-predator vigilance can be done together) (Ranta *et al.*, 1996), and the patchiness of resources (i.e. the profitability of searching) (Katsnelson *et al.*, 2008). Furthermore, in studies on house sparrows (*Passer domesticus*), the frequency of scrounging increased gradually with increasing dominance rank (Liker & Barta, 2002), and with lowered energy reserves during the first feed of the day (Lendvai *et al.*, 2004). Tóth *et al.* (2009) used kin selection theory to predict the frequency of scrounging from relatives, and found that house sparrows used aggressive joining less often and obtained less food by scrounging from their close kin than from unrelated flock mates, although this result was dependent of the sex of the individual concerned. In addition, Katsnelson *et al.* (2008) and Belmaker *et al.* (2012) published the first pieces of experimental evidence (again, in house sparrows) for an effect of learning in the context of the producer-scrounger game, with such a learning rule presumably evolving to some optimum under genetic control (Katsnelson *et al.*, 2011).

The producer-scrounger paradigm has revealed much about the evolution of a variety of very sophisticated social strategies, supported by the simultaneous development of game theoretical models and closely related empirical studies (mostly on house sparrows). It would seem that we are very close to being able to quantify the individual variation in such producer-scrounger behaviour, and more interestingly the individual plasticity (i.e. propensity to switch between producing and scrounging, depending upon the social conditions). Only in this way can we assess the fitness consequences of these different behavioural strategies in

real populations. However, nearly all of the research cited above has involved flocks of many individuals at a time, which necessarily conflates the contribution that each individual makes to the social environment and how each individual is differentially affected by such changes in their social environment. To be able to dis-entangle the plasticity that each individual shows in its own behaviour and the effect that it has on the behaviour of other individuals in the group, all the individuals must be tested in pairwise assays against each other. Interestingly, very few studies exist where each individual in a social group has been tested against all (or a sample) of the others, in pairwise behavioural assays, in order to quantify individual social effects and sensitivities (but see Hamilton & Ligocki, 2012; Kilgour & Brigham, 2013; Grainger *et al.*, 2014).

The aim of the present study was therefore to quantify individual levels of producing and scrounging in social groups of house sparrows held in captivity, and to test how these compare to the same measures collected in pairwise assays between all combinations of the same individuals.

Study objectives

Based on the theory and empirical knowledge from previous studies (see above), and the hypothesis of evolved producer-scrounger behaviour based on individual (i.e. genetic) differences, the following predictions were addressed;

1. We predict that there will be individual differences in behaviour, both in the group and pairwise experiments. More specifically it is expected that some individuals will behave more producer-like (i.e. searching more independently for food), and others more scrounger-like (i.e. joining occupied food patches). Some of this will be due to the sex and state (i.e. body condition) of the individual, with males and hungry individuals scrounging more on average, but we predict that these individual differences in behaviour will be repeatable over time and between the group versus pairwise contexts (Figure 1).

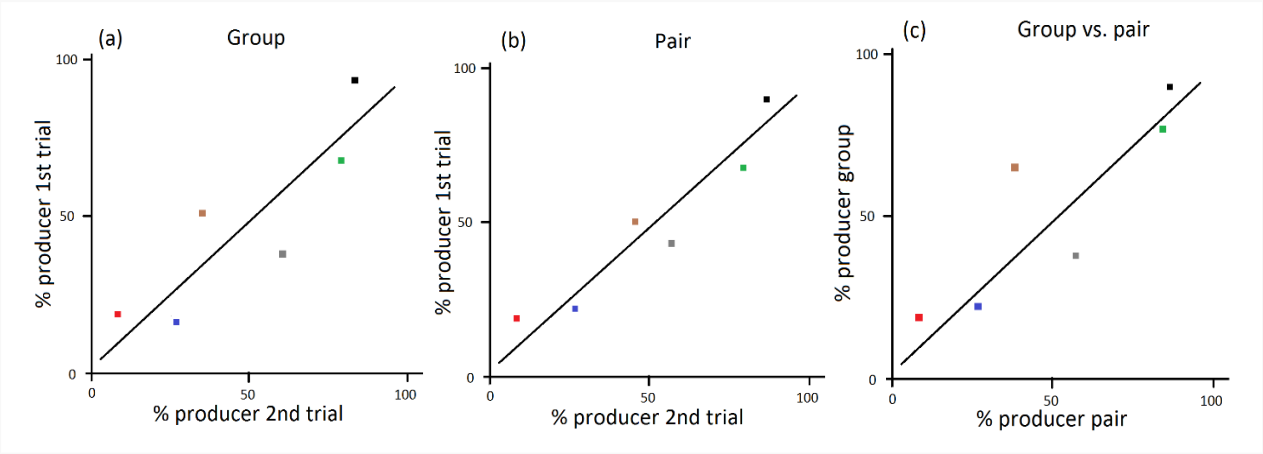

Figure 1. *Prediction-graphs describing the expected repeatabilities between individual levels of producing (i.e. versus scrounging – see text for details) in the first and second trials for both the (a) group- and (b) pair-wise assays, and also the repeatability predicted between the mean individual level of producing in the (c) pair-wise versus group assays. Each coloured dot represents a different individual within a single example group of six birds.*

2. We predict that individuals will differ in their propensity to switch between the different strategies producer and scrounger, depending upon the strategies employed by other individuals (i.e. whether they produce or scrounge). It is not clear whether such differences in behavioural plasticity will differ between the sexes, or simply follow changes in state (i.e. hunger), but we predict individual differences in plasticity that will be repeatable over time and between the group versus pairwise contexts (Figure 2).

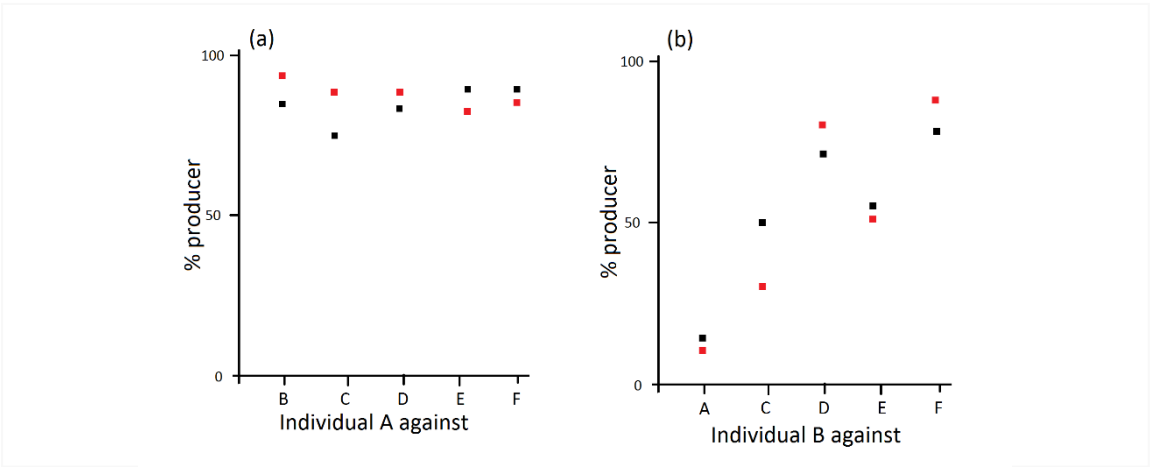

Figure 2. *Prediction-graphs describing two contrasting examples of the expected within-individual variation in levels of producing (i.e. versus scrounging – see text for details) in pair-wise assays against the five other individuals within a group of six. The graphs show (a) individual A that is non-plastic in response to the behaviour of other individuals, and (b) individual B that is more responsive and plastic in its producing behaviour than player A. Red and black dots represent individual levels of behaviour in the first and second trials, respectively. Note that producing is more repeatable against some opponents (e.g. individual E) than others (e.g. individual C).*

3. We predict that the behaviour of each individual will affect the behaviour of others, but that the magnitude of this interaction will vary consistently between individuals over time and between the group and pairwise contexts. Essentially, the behaviour of some individuals will have a greater impact on the plasticity of others. This individual effect may correspond to the differences seen in prediction 1. and 2. above, such that extreme individuals that mostly just produce or mostly just scrounge, and perhaps show the least plasticity in switching between the two, will have the greatest impact on the behaviour of less extreme and more plastic individuals (Figure 3).

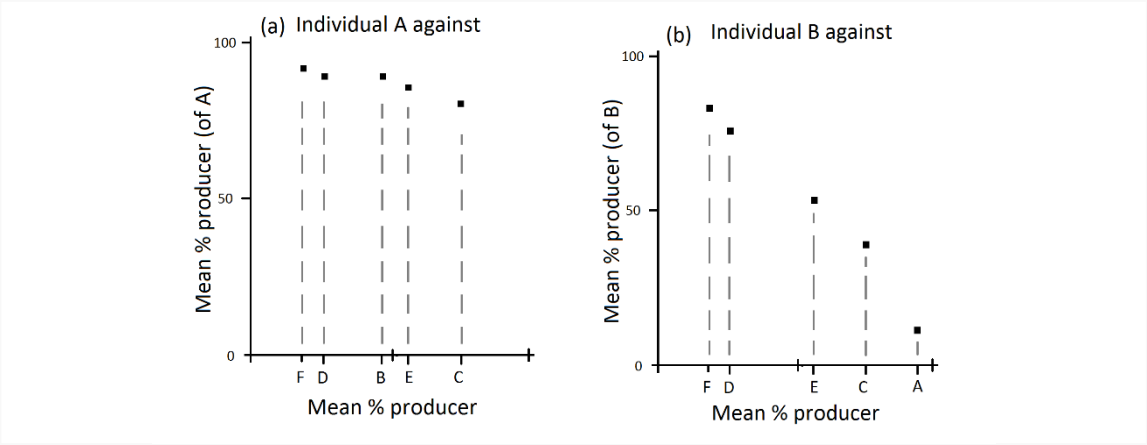

Figure 3. *Prediction-graphs describing two examples of the predicted impact of the mean level of producing of different individuals on the mean producer behaviour of two individuals (A and B) during the pair-wise assays within a group of six. The consistently high non-plastic levels of producing by A in the first graph (a) means that this individual A then has the largest effect on the plastic decreases in producing behaviour by individual B in the second graph (b).*

Methods

Study site

We studied a population of house sparrows on the island of Lauvøya, located in the municipality of Åfjord on the coast of Sør-Trøndelag, Norway. The house sparrow population on this island contains approximately 130 birds, all more or less part of one flock. This study population is part of a larger study system from the Centre for Biodiversity Dynamics (CBD) at the Norwegian University of Science and Technology (NTNU). In 2012, nearly all (97%)

of the 72 indigenous house sparrows on Lauvøya, and 83% of the 18 house sparrows on the mainland closest (<2.5 km) to Lauvøya were moved across mountains and fjords and released in a suitable habitat >80 km away, prior to translocation of individuals from Leka and Vega, two islands further north in Norway. From Leka, the 70 individuals with the highest levels of basal metabolic rate (BMR), which is the lowest level of metabolic output of an endothermic organism not using energy to regulate body temperature and represents an animal's maintenance cost (McNab, 2002), were translocated to Lauvøya. Similarly, from Vega the 70 individuals with the lowest BMR were translocated to Lauvøya. By introducing approximately twice as many individuals as the original population on Lauvøya, the aim was to compensate for the fact that many of the translocated birds would not establish and breed on the island (see Skjelseth *et al.*, 2007). The focus of this wider study was the genetic basis for BMR, as well as selection and evolution of this and other traits in common-garden population of house sparrows.

During February 2016, nearly all the birds in the population were caught with mist nets in or close to farm buildings around the island, and 72 individuals (12 groups * 6 individuals, i.e. more than 50% of the population) were used in the behavioural experiment. We managed to get an equal number of males and females (i.e. even sex-ratio) for most of the groups.

Experimental set-up

After capture, the sparrows caught on that day were divided into groups of six individuals according to place, time of capture, and sex ratio (three males and three females). We could then assume that all individuals were from the same natural social groups. After ringing with a unique combination of rings (i.e. one metal ring with a unique ID number plus 3 plastic colour rings for visual identification) and measuring (i.e. wing length, tarsus length, bill length and depth, plumage characters, body mass), all individuals in each group of six were also painted with a different colour of acrylic paint, chosen randomly, on the top of their head for video identification. Each flock was then placed in a room with a dummy feeder with *ad lib* food, both in the wells and on top of the feeder. The dummy feeder was designed as a 1.2m x 1.2m white panel with 144 small recessed wells equally distanced from each other, to hold some seeds and to create a spatially clumped resource (see Figure 4).

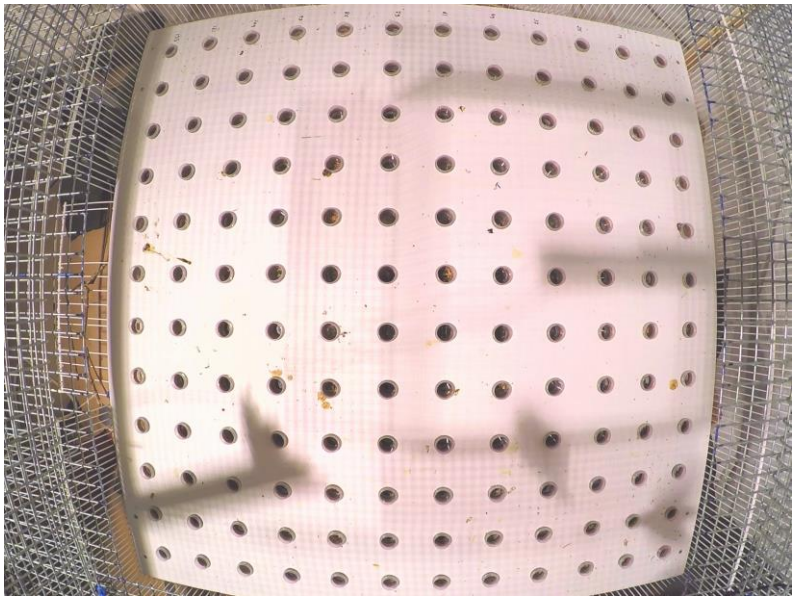

Figure 4*. Photo of the group-wise feeder. A 1.2m x 1.2m white panel with 144 small recessed wells equally distanced from each other, surrounded by walls, roof and an entrance. See text for more details on the dummy- and pair-wise feeders.*

This was done to familiarise the sparrows with the experimental artificial feeder. The food used in the dummy feeder was a mixture of different seeds (e.g. millet, sunflower, etc.) and bread. The food was then taken away at 22:00 hrs, so that the sparrows would be food deprived before the behavioural assays the following morning. Each group was tested in a group assay (see below) the first morning, and in pair-wise assays (see below) in the first afternoon, and then a second round of pair-wise assays on the second morning, and a second group assay on the second and final afternoon (Table 1).

Table 1*. Schedule of when each group was involved in the different parts of the experiment. * = dummy feeder (training period), G = group-wise assays, P = pair-wise assays, followed by group number (1-12) and the final numbers -1 and -2 for the first or second time, respectively.*

Day	Morning trials		Afternoon trials		
1					*1
2		G1-1		P1-1	*2
3	P1-2	G2-1	G1-2	P2-1	*3
4	P2-2	G3-1	G2-2	P3-1	*4
5	P3-2	G4-1	G3-2	P4-1	*5
6	P4-2	G5-1	G4-2	P5-1	*6
7	P5-2	G6-1	G5-2	P6-1	*7
8	P6-2	G7-1	G6-2	P7-1	*8
9	P7-2	G8-1	G7-2	P8-1	*9
10	P8-2	G9-1	G8-2	P9-1	*10
11	P9-2	G10-1	G9-2	P10-1	*11
12	P10-2	G11-1	G10-2	P11-1	*12
13	P11-2	G12-1	G11-2	P12-1	
14	P12-2		G12-2		

Before the first group assay, the birds were caught in the dummy feeder room using a mist net, and then individually weighed. After that, the birds were released into the group assay room, containing a feeder identical to the dummy feeder, but also with cage walls and roof (Figure 4). The walls and roof made it possible to connect the camera (see below) from above, but also to have just one large entrance and exit point to be able to capture the coloured leg rings on the entrance cameras. This was done for identifying which individuals entered and left the feeder during the trial, in case the paint on the heads was not enough. The feeder was filled with 12.7 to 13.9 g (mean = 13.61, SE = 0.06) of a mixture of millet and other small seeds (Versele Laga, Premium Prestige Budgie), divided evenly into 30 randomly chosen wells out of the 144 available. The assays started between 07:25 to 10:35 hrs and lasted from 2.0-3.5 hours, depending on when individuals were first seen using the feeder. After the trial ended, the birds were again caught and weighed, and then placed into cloth bags before being placed in individual cages and deprived of food from one to two hours prior to the pair-wise assays. The seeds not eaten in each group assay were then collected and weighed before preparing the feeder with new seeds for the next group.

Before the pair-wise assays, the birds were placed in six individual cages covered with cloth and given *ad lib* access to water. The individual cages made it possible to easily switch different individuals between the three pair-wise feeder set-ups for each successive trial, and the cloth helped to block vision out of the cage and reduce stress in between trials. The three pair-wise feeders were similar to the group feeder, but approximately one third of the size, and with 49 wells and also holes in the cage walls for the attachment of two removable cages. Each feeder was filled with 4.1 to 4.9 g (mean = 4.53, SE = 0.01) of seeds, divided evenly into 10 randomly chosen wells out of the 49 available. The first pair-wise assays started between 13:00 and 15:45 hrs. Each individual met all the other 5 individuals in their flock once with a randomly assigned order (i.e. 15 combinations, run as five times three pairs simultaneously). This resulted in five trials, lasting 17 to 24 minutes each, for each individual. At approximately 15 minutes into each pair-wise trial, all birds were disturbed by a loud clapping with the aim to simulate disturbance and to assess how long it took for each individual to resume feeding again. At the end of each trial, the individuals were moved without handling back into their individual cages, and the seeds left in the feeders were collected and weighed before cleaning and refilling the feeders with new seeds prior to the next set of pair-wise assays.

When the first set of 15 pair-wise assays was finished in the afternoon of the first day, all individuals were given *ad lib* food and water in their individual cages, and left undisturbed until the food was removed at 22:00 hrs. On the following morning, the same flock was given the second set of pair-wise assays, starting between 07:25 and 09:10. The procedure was the same as above, but a different random order of pairs was used, with the aim of providing assessments of repeatability for all the behavioural measures taken in these pair-wise assays. After the second set of pair-wise assays, all individuals were again weighed and left without food from one to two hours prior to the second group-wise assay.

The second group assay started between 12:05 and 15:25 hrs on the second day, and lasted 2.0-3.5 hours, with the same procedures as in the first group assay. After this second group assay was finished, all individuals were caught using a mist net, weighed for the last time and released into a big communal room containing all of the other birds with *ad lib* access to food and water.

Birds were kept for a further one to twelve days, depending on which group they were in (group 1 = 12 days, to group 12 = 1 day), before being released back to the place from which they were captured. Of the 72 individuals used in this experiment, two managed to escape during group-wise (both recaptured later, but not used further in the experiment), three were excluded during pair-wise and given *ad lib* food and water in a separate cage, because they showed no sign of feeding/activity and their feathers were fluffed. One of those individuals was later confirmed dead, while the other two recovered well. In addition, one individual was found dead under a big rock in the communal room, multiple days after being released into it, so the cause of death of this individual was probably not related to participating in the experiment. All in all, despite being caught, handled and disturbed as much as this experiment required, the majority of the house sparrows coped well with the experiment and appeared to return to life in the wild with no lasting detrimental effects.

Video analyses

Each feeder (except the dummy feeder) had a GoPro Hero4 camera connected above on the cage roof, capturing the whole floor of the feeder. In addition, the group-wise feeder had two Sony Action Cams connected on each side of the cage entrance, to be able to identify the birds entering and exiting the feeder. All cameras filmed in 1440p video resolution, with 60 frames per second. The behavioural data were collected manually by watching the videos of

the group and pair-wise assays in random order. After identifying the entrance and exit times and how many birds were present at the feeder for those times (for the group assays), and individual identities whilst foraging at the feeders, the number of producing events was recorded as an individual visiting an unoccupied well, defined as clearly moving its head into the well. If the individual visited the same well twice in a row, it was only counted as a new producing event if it had moved across the feeder for at least two wells distance in between those visits. Number of scrounging events was recorded as an individual moving to an already occupied well, or if that well had been occupied in the last 2 seconds. The identities of the scrounger and the individual that it scrounged from, as well as different types of social interaction and levels of aggression (see Table 2), were recorded per event. In addition, if an individual visited a well when an individual was feeding from one of the neighbouring wells, this was recorded as area copying. Also, the time from disturbance (i.e. clapping) until each individual resumed feeding again was recorded (only for the pair-wise assays).

***Table 2**. List of how 16 different social interactions (including direction of aggressive behaviour) was classified in the video analyses of both group- and pair-wise assays.*

	Description of interaction	**Aggression (By intruder)**	**Aggression (By resident)**
0	No interaction	No	No
1	Nothing happens	No	No
2	Resident moves to make place, but stays at the well	No	No
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

Statistical analyses

The number of pair-wise assays used in the analyses was reduced from 720 (6 individuals/group * 12 groups * 5 trials/day * 2 days) to 628, due to removal of individuals that did not eat at all, or due to memory card failing to save videos. This resulted in some individuals meeting just once (i.e. no repeated measurements), but this is not a problem due to

the use of mixed effect models. A combination of linear mixed effect and generalized mixed effect models were used to assess the amount of variance explained by individual and partner identity effects in the pair-wise assays for the three different response variables: (a) amount of producing (as a count per trial), (b) probability of scrounging (given the opportunity via the rate of producing by one's partner), and (c) the ratio of scrounging to producing (number of scrounging events versus the number of new wells visited). To be able to statistically estimate the probability of scrounging (b), the number of scrounging events per individual per pair-wise trial was transformed to a binary variable (# scrounging events<1 = 0, # scrounging events >0 = 1). All mixed effect models presented in this thesis were fitted using the package lme4 (Bates *et al.*, 2014) in the statistical programming language R (R Core Team, 2016).

For each response variable, both a variance partitioning approach (VPA) and a hybrid approach (HA) were used to estimate the variation in the focal individual's phenotype due to phenotypic among-opponent variation. VPA is characterised as a mixed-effect model with focal- and opponent ID as random intercepts. In this way, the total phenotypic variance is decomposed into variance created by focal ID and opponent ID. HA is similar to VPA, but in addition a specific quantified opponent trait is fitted as a fixed (covariate) effect to the model, to explain the potential opponent effect according to the opponent trait value. If the trait is completely responsible for this opponent effect, the variance explained by opponent ID in the VPA model will be reduced to zero in the HA model. Thus, by comparing these two models, it is possible to assess how a specific behaviour (producing) of the opponent affects the behavioural measures (a-c) of the focal individual (Dingemanse & Araya-Ajoy, 2015).

All models included the fixed effects day (1 vs. 2) and sex (male vs. female), as well as the interaction between them. The amount of producing was modelled assuming a Gaussian error distribution, the probability of scrounging as a binomial trait, and the scrounging ratio assuming a binomial distribution. Within individual variation in the scrounging ratio was modelled using an observation level random effect, which also accounted for overdispersion in the data.

The number of group-wise assays was reduced from 144 (6 individuals/group * 12 groups * 2 days) to 115, due to four groups not entering the feeder the first day, and also some excluded individuals (see above). The group-wise assays were assessed using the same type of models for the same response variables (a-c) as pair-wise, but with group instead of individual opponent as the second random effect alongside individual ID. The fixed covariate effect of

opponent levels of producing in these group-wise HA models also had to be calculated for the group as a whole minus the amount of producing by the focal individual. Also, note that the models for probability of scrounging (b) in the group-wise assays did not converge, probably due to very few individuals not scrounging at least once (i.e. too few zero levels of scrounging), and so the results of these models are not presented here.

To be able to compare variance components of variables on different scales (i.e. effect sizes of categorical vs. continuous variables), all fixed effects were mean centred in relation to the population mean and standardised by dividing by 2 * standard deviations (SD) before use in the different models (Araya-Ajoy *et al.*, 2015).

Likelihood ratio tests (LRT) were used to test statistical significance of the different random effects. This is a χ^2-distributed test, and is calculated as twice the difference in log-likelihood between a model where a target random effect was fitted versus not fitted (Shaw 1991). Since variances are always positive, the probability (p) of a LRT applied to a variance was calculated assuming an equal mixture of p (χ^2, df = 0) and p (χ^2, df = 1), that is, df = 0.5 (Self & Liang 1987; Pinheiro & Bates 2000; Visscher 2006).

Repeatability estimates were calculated as the proportion of each random effect's contribution of variance to the total phenotypic variance not attributable to fixed effects (Santostefano *et al.*, 2016). In this way, focal and opponent ID's contribution to the total phenotypic variance can be separated, and this makes it possible to evaluate the hypothesis that focal individuals respond (plastically) to repeatable individual differences in partner behaviours. For the models with binomial error distribution, the repeatability estimates were calculated following the paper of Nakagawa & Schielzeth (2010), accounting for logit link function.

Mixed effect models were used to analyse the correlations of the different behaviours (a-c) across contexts (Araya-Ajoy *et al.*, 2015). Amount of producing was transformed to producing per 10 minutes to account for the two contexts (i.e. group- and pair-wise assays) differing in length, while the probability of scrounging and scrounging ratios were calculated by summarising the values from the five pair-wise trials into one value per individual per day.

Validation of model assumptions was done by visually inspecting residual plots.

Results

Group-wise results

Results for two of the three focal response variables (a and c, see Methods) that were possible to analyse from the group-wise assays are shown in Table 3. These results mainly explain among individual repeatability in the group-wise trials and the total effect of all opponents in a group on a focal individual, and are therefore compared with the pair-wise results (see below) to assess the different predictions in this study.

Table 3. *Group-wise data summaries for selected mixed effect models for two different response variables: (a) producing and (c) scrounging ratio. Each response variable has one model from the variance partitioning approach (VPA) and one from the hybrid approach (HA), with the latter including the summed producing by all opponents in the group (Prod_opp). Estimates (log-odds for the binomial model), standard errors and p-values are given for the fixed effects, variance and p-values are given for the random effects, in addition to repeatability measurements for all the models.*

	Producing (normal)		**Scrounging ratio (binomial)**	
Fixed	**VPA**	**HA**	**VPA**	**HA**
Intercept ± SE	135.613 ± 11.146 (p = 0.000)	137.990 ± 6.292 (p = 0.000)	-3.335 ± 0.114 (p < 0.001)	-3.335 ± 0.114 (p < 0.001)
Sex ± SE	-25.706 ± 12.692 (p = 0.043)	-28.735 ± 12.639 (p = 0.023)	-0.476 ± 0.218 (p = 0.029)	-0.477 ± 0.219 (p = 0.030)
Day ± SE	114.475 ± 11.980 (p = 0.000)	49.256 ± 16.800 (p = 0.003)	-0.938 ± 0.169 (p < 0.001)	-0.954 ± 0.280 (p < 0.001)
Day * Sex interaction ± SE	-53.568 ± 23.038 (p = 0.020)	-40.974 ± 21.490 (p = 0.057)	-0.165 ± 0.333 (p = 0.620)	-0.163 ± 0.334 (p = 0.625)
Prod_opp ± SE		81.701 ± 17.264 (p < 0.001)		0.021 ± 0.291 (p = 0.941)
Random				
Focal ID	195.200 (p = 0.199)	854.100 (p = 0.072)	0.350 (p = 0.022)	0.351 (p = 0.022)
Group ID	1040.100 (p = 0.007)	0.000 (p = 0.500)	7.51e-10 (p = 0.500)	4.02e-10 (p = 0.500)
Residual	3610.900	3046.800	0.483	0.482
Repeatability				
R among	0.049	0.219	0.085	0.085
R within	0.758	0.781	0.915	0.915
R opponents (group)	0.193	0.000	1.82e-10	9.74e-11

Focal ID effects in group-wise assays

Focal ID explained a significant amount of variation around the intercept of the scrounging ratio models (Table 3). Although this was statistically significant, there was very low repeatability among individuals in scrounging ratio (Figure 5), which does not provide support for the hypothesis concerning repeatable individual differences in this behaviour in prediction 1 (Introduction, Figure 1).

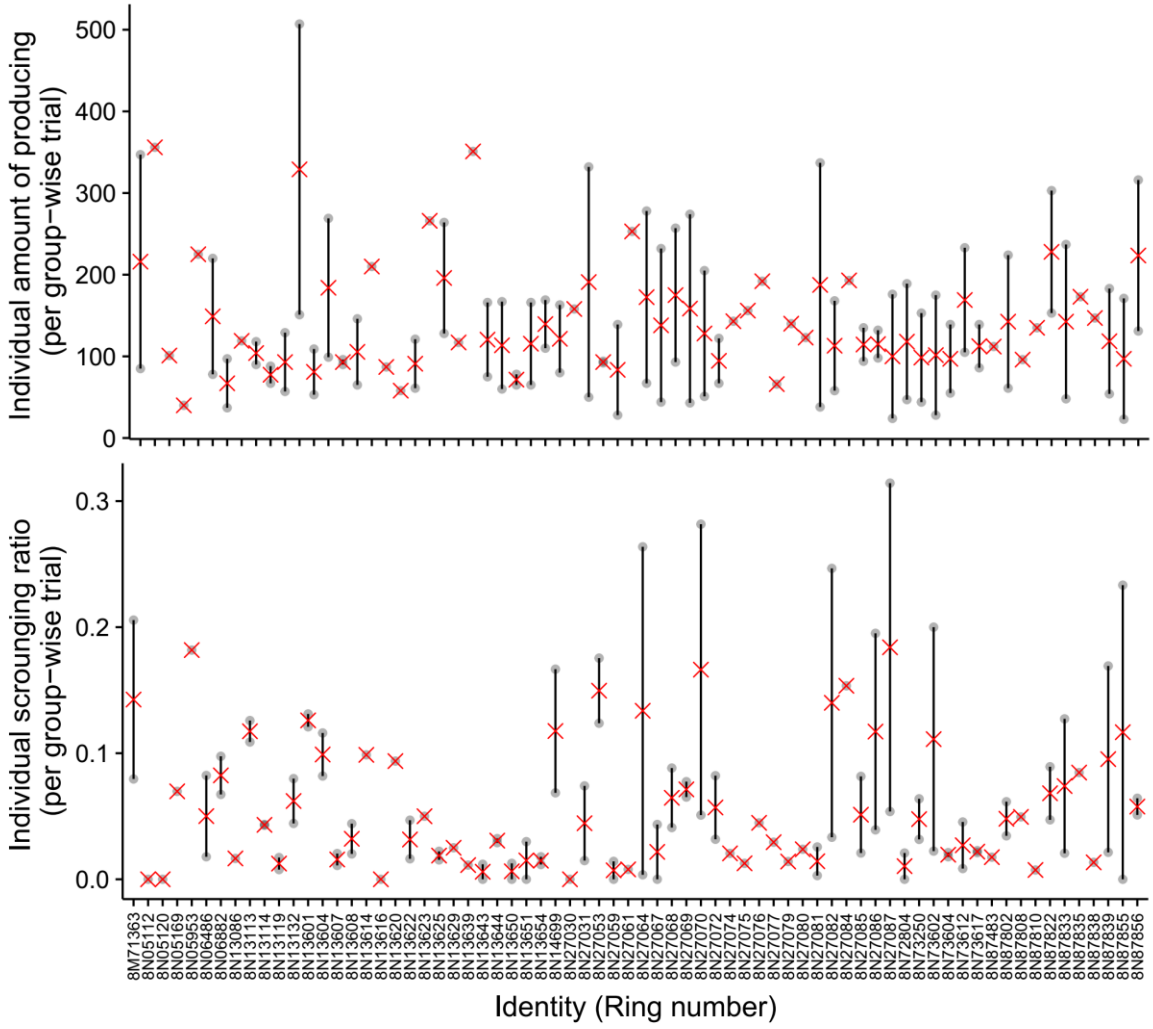

Figure 5*. Individual (n=70) amount of producing (top) and producing ratios (bottom). Each point is from a different group-wise trial (≤ 2 / individual), and the mean of all trials are represented by a red X.*

The amount of variation around the intercept explained by focal ID in the amount of producing was non-significant in the VPA model, but this increased and became marginally non-significant in the HA model when the covariate of producing by all opponents was added

as a fixed effect (HA, Table 3). This is probably the result of the significant effect of producing by all opponents reducing the within individual (i.e. residual) variation, and thus increasing the relative amount of among-individual variation. This is also reflected in the repeatability measures, since adding producing by all opponents caused the among-individual repeatability to increase from 0.049 to 0.219 (VPA vs. HA in Table 3, Figure 5).

Group ID effects in group-wise assays

Group ID explained a significant amount of variation around the intercept of the amount of producing (VPA, Table 3). This means that the focal individuals responded predictably and consistently to some aspect of the behaviour of all the individual phenotypes making up a group in the two group-wise trials. Once the producing by the opponents was added as a fixed effect to this model (HA, Table 3), it had a significantly positive effect on the focal individual's amount of producing, and additionally caused the group ID random variance to drop to 0. This means that all the variation previously explained by the group ID was caused by the amount of producing by the opponents, and that focal individuals responded by increasing their amount of producing when their social partners produced more. Interestingly, group ID did not explain any variation in scrounging ratio, and the amount of producing by the opponents did not affect this ratio either (Table 3). This lack of an effect was not as expected, since more producing by opponents should theoretically have provided focal individuals with more opportunity to scrounge (or at least more in proportion to the amount of producing).

Sex effects in group-wise assays

There was a significant effect of sex on the focal individual rate of producing and scrounging ratio (Table 3, Figure 6). Females had a higher average level of producing and a higher scrounging ratio than males in the group-wise assays. This means that females visited more wells than males, regardless of what strategy (i.e. producing or scrounging) they used, but also that females used proportionally more scrounging than males (see below).

Day effects in group-wise assays

There was significantly more producing and thus a lower scrounging ratio by both sexes during the second day of the experiment, compared to the first (Table 3, Figure 6). There was also a significant day-by-sex interaction in the VPA model of producing with the effect of day being stronger in females than males, but when adding producing by the group as a fixed effect in the HA model this effect was reduced and became marginally non-significant (i.e. p = 0.057). Even so, this leaves a high chance for type II-error, and is therefore treated as a significant effect. There was no significant day-by-sex interaction in any of the other models.

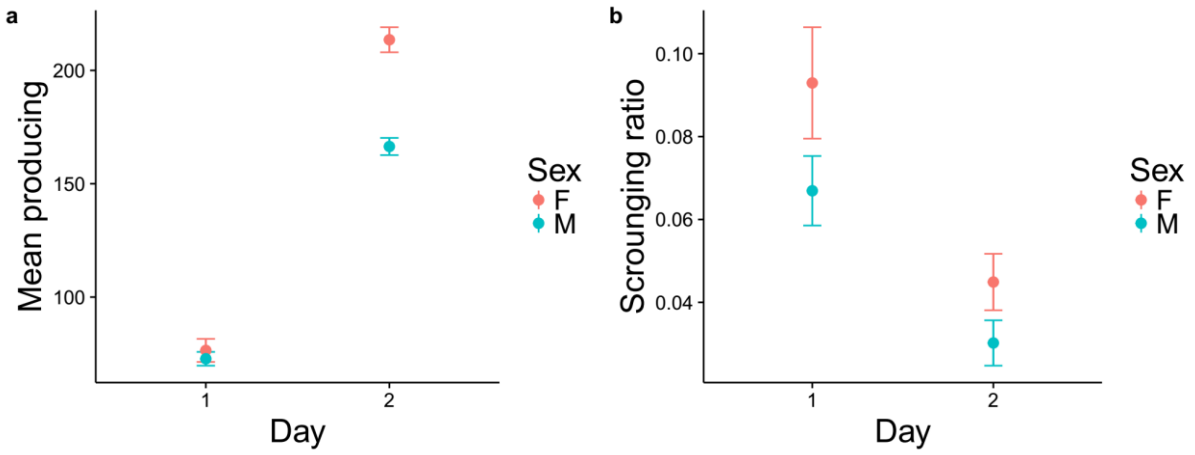

Figure 6*. Effect of day and sex in the group-wise assays on (a) mean amount of producing per trial and (b) the scrounging ratio (amount of individual scrounging to producing) of the focal individuals. Means (±SE) are shown grouped as females (F, red points) and males (M, blue points).*

Pair-wise results

Results for all three of the focal response variables (a-c, see methods) from the pair-wise assays are shown in Table 4. These results show the among individual repeatability in the pair-wise trials and individual opponent effects, which are used to assess prediction 1 and 3 (see Introduction; for prediction 2, see below), in addition to other sources of variation (e.g. sex and day).

Table 4. *Pair-wise data summaries for selected mixed effect models for three different response variables; (a) producing, (b) P(scrounging) and (c) scrounging ratio. Each response variable has one model from variance partitioning approach (VPA) and one from hybrid approach (HA), with the latter including the fixed covariate effect of level of producing by the opponent (Prod_opp). Estimates (log-odds for the binomial models), standard errors and p-values are given for the fixed effects, variance and p-values are given for the random effects, in addition to repeatability measurements for all the models.*

	Producing (normal)		**P(scrounging) (binomial)**		**Scrounging ratio (binomial)**	
	VPA	**HA**	**VPA**	**HA**	**VPA**	**HA**
Fixed						
Intercept ± SE	20.493 ± 1.238 (p < 0.001)	20.486 ± 1.193 (p < 0.001)	-0.969 ± 0.178 (p < 0.001)	-0.982 ± 0.001 (p < 0.001)	-4.029 ± 0.140 (p < 0.001)	-4.036 ± 0.141 (p < 0.001)
Sex ± SE	-5.072 ± 2.288 (p = 0.027)	-5.064 ± 2.269 (p = 0.026)	-0.179 ± 0.337 (p = 0.595)	-0.160 ± 0.001 (p < 0.001)	-0.036 ± 0.251 (p = 0.887)	-0.033 ± 0.253 (p = 0.896)
Day ± SE	-6.260 ± 1.270 (p < 0.001)	-5.413 ± 1.123 (p < 0.001)	-1.444 ± 0.220 (p < 0.001)	-1.335 ± 0.001 (p < 0.001)	-0.702 ± 0.129 (p < 0.001)	-0.690 ± 0.130 (p < 0.001)
Day * Sex interaction ± SE	1.444 ± 1.609 (p = 0.370)	1.761 ± 1.622 (p = 0.278)	0.324 ± 0.413 (p = 0.432)	0.325 ± 0.001 (p < 0.001)	0.247 ± 0.255 (p = 0.333)	0.250 ± 0.255 (p = 0.327)
Prod_opp ± SE		3.516 ± 0.901 (p < 0.001)		0.576 ± 0.001 (p < 0.001)		0.095 ± 0.136 (p = 0.487)
Random						
Focal ID	78.870 (p < 0.001)	77.930 (p < 0.001)	1.233 (p < 0.001)	1.331 (p < 0.001)	0.723 (p < 0.001)	0.736 (p < 0.001)
Opponent ID	2.90e-12 (p = 0.500)	0.000 (p = 1.000)	0.000 (p = 0.500)	0.000 (p = 0.485)	0.030 (p = 0.268)	0.032 (p = 0.256)
Trial ID	31.270 (p <0.001)	18.780 (p < 0.001)	0.036 (p = 0.412)	5.95e-07 (p = 0.486)	3.43e-09 (p = 0.500)	7.05e-10 (p = 0.500)
Residual	85.990	90.140	-	-	0.059	0.052
Repeatability						
R among	0.396	0.411	0.222	0.237	0.176	0.179
R within	0.445	0.490	0.772	0.763	0.816	0.813
R trial	0.159	0.099	0.007	1.06e-07	8.37e-10	1.72e-10
R opponent	0.000	0.000	0.000	0.000	0.007	0.008

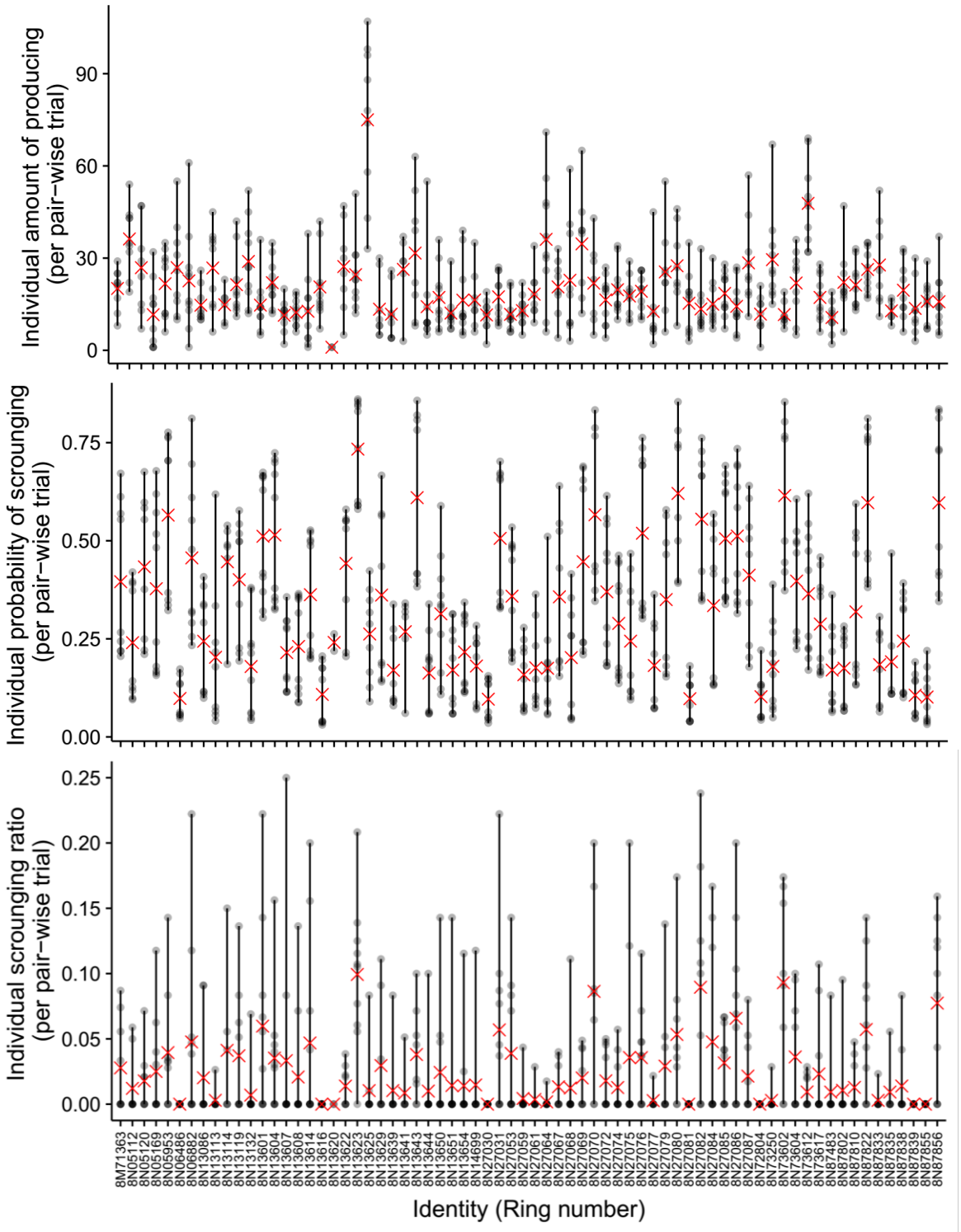

Figure 7*. Individual (n=70) amount of producing (top), probability of scrounging (middle) and scrounging ratios (bottom). Each point is from a different pair-wise trial (≤ 10 / individual), and the mean of all trials are represented by a red X.*

Focal ID effects in pair-wise assays

Focal ID explained a significant amount of variation around the intercept of all the models (Table 4, Figure 7). The among-individual repeatability for amount of producing was 0.411 (HA, Table 4), which means that individuals were fairly consistent in this behaviour. However, for the probability of scrounging and scrounging ratio, this repeatability was only 0.237 and 0.179, respectively (HA Table 4, Figure 7), which is not very high. These results therefore provide support for the hypothesis of repeatable individual differences in behaviour for amount of producing, but not so much for the probability of scrounging or scrounging ratio (prediction 1 in Introduction, Figure 1).

Plasticity in pair-wise assays

Prediction 2 (Introduction, Figure 2) could not be tested statistically, due to low power of the data needed to test the scrounging ratio model with random slopes (Table 4). However, Figure 8 shows that there was a tendency for individual differences in plasticity in producing ratio, but an overall positive effect of producing ratio by the partner, which is the opposite of what was expected.

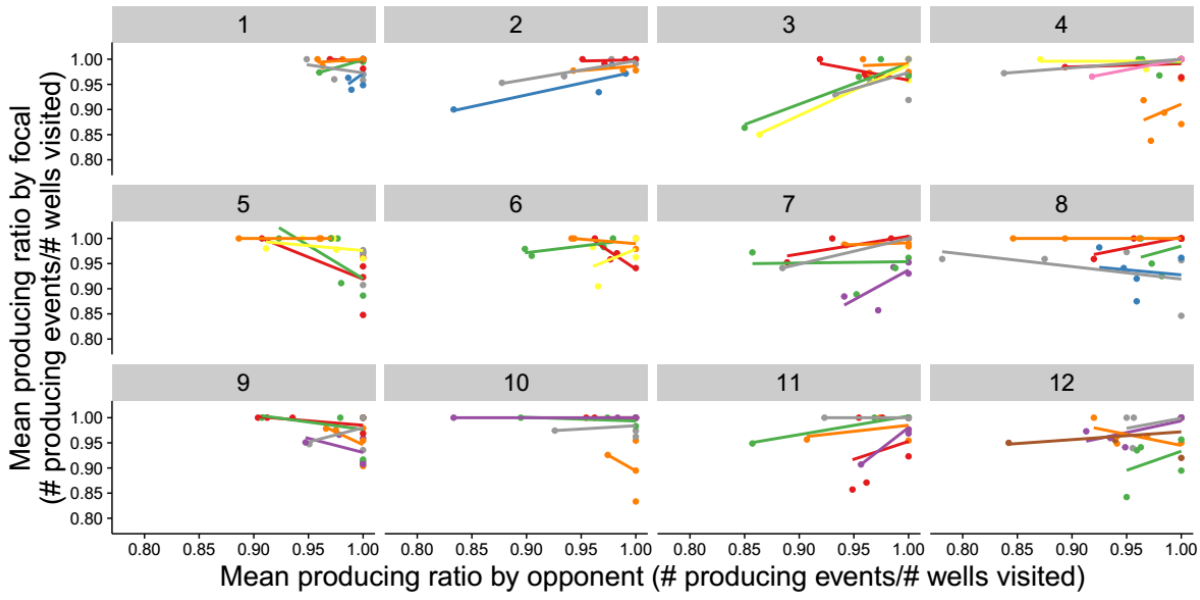

Figure 8. *Behavioural reaction norms of mean producing ratio by opponent against mean producing ratios by focal, for all groups (1-12) from the pair-wise assays. Different colours within each sub plot represents the different individuals within each group. From raw data.*

Partner effects in pair-wise assays

There was no apparent repeatable effect of the opponent's phenotype on any of the focal response variables, contrary to prediction 3 (Introduction, Figure 3). The amount of producing by the focal individual increased significantly with increased producing by the opponent, while this effect was non-significant for the scrounging ratio (Table 4, Figure 8).

This positive effect of producing behaviour by the opponent on focal producing implies that there was a social environment effect on the two behaviours of the focal. However, the opponent ID random effect did not explain significant amounts of the variation around the intercept in the variance partitioning models. This suggests that the positive effect of producing by the opponent (Table 4, Figure 8) was not because of effects of the particular social relationship with the opponent, as we might have expected from effects such as dominance or kinship. Instead, something else must have been making both birds produce (i.e. forage) more whilst in the same trial together in certain instances, such as similarities in state (hunger) or in social compatibility (e.g. lack of stress, disturbance and/or aggressive interference) to foraging socially.

We tested for a possible kin-effect, that could explain this. Since different pairs of birds reflected each other's behaviour (i.e. both individuals in a pair produce more/less at the same time), it could be that e.g. kinship was causing this effect. We therefore tested this by adding the pair combinations as a random factor to the HA model for amount of producing, to see if different combinations of birds had a repeatable effect on each other, but this did not explain any of the variation around the intercept of the model (see Table A1 in Appendix).

There was a clear positive effect of the rate of the opponent level of producing on the probability of scrounging, as predicted. Unfortunately, interpretation of this effect was complicated by the fact that the hybrid model in this case failed to converge. However, the estimates between VPA and HA model in this case are similar, and the effect size of opponent producing on rate of scrounging is fairly large and in the expected direction (from prediction 3), since more producing should lead to a higher scrounging probability. It therefore seems likely that the estimates are reliable, but that the SEs around them are not.

Sex effects in pair-wise assays

There was a moderately significant effect of sex on focal rate of producing, but not on the probability of scrounging or the scrounging ratio (Table 4). Males produced on average

21.9% less than females (Figure 9), when controlling for all other effects in the model. This means that even though males produced less than females, they did not tend to scrounge more, so the tendency to use the two different feeding strategies (i.e. the scrounging ratio) did not differ between the two sexes (see below).

Day effects in pair-wise assays

The average amount of producing, the probability of scrounging and the scrounging ratio decreased significantly from the first to second day of the pair-wise trials (Table 4, Figure 9). The decrease in both the probability to scrounge and scrounging ratio might reflect the decrease in producing between the first and second day, because producing and scrounging are linked by the fact that an individual cannot scrounge when there are no producers. So, when the amount of producing by an individual goes down, its partner has less scrounging opportunities. There were no significant day-by-sex interactions in any of the pair-wise models.

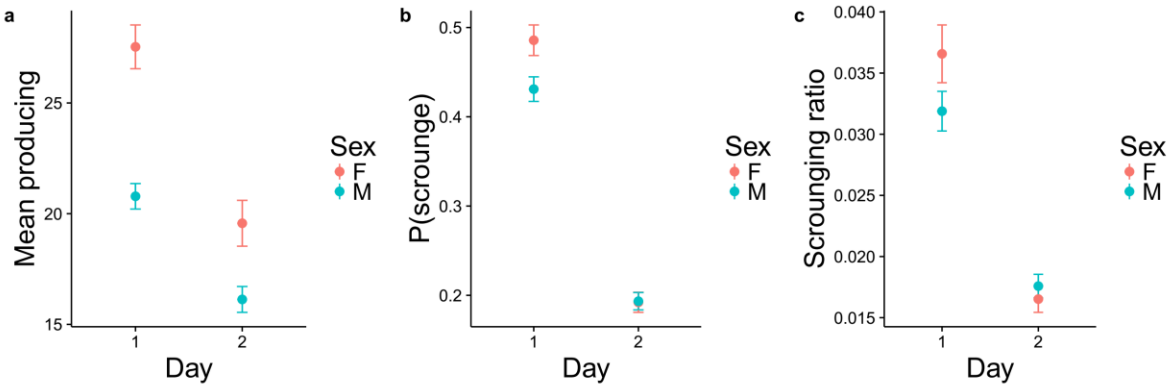

Figure 9. *Effect of day and sex in the pair-wise assays on (a) mean rate of producing per trial, (b) probability of scrounging (P(scrounge) - scrounges per opponent producing event), and (c) the scrounging ratio (amount if individual scrounging to producing) of the focal individual. Means (±SE) are shown grouped as females (F, red points) and males (M, blue points).*

Experimental trial and group identity effects in pair-wise assays

There was also a significant amount of variation around the intercept of producing explained by the random effect of the experimental trial identity, but not for the probability to scrounge or scrounging ratio (Table 4, Figure 10). This suggests that there was a repeatable order effect of the pair-wise trials per group, because something caused individuals to behave predictably to the particular sequence of experimental trials. Additionally, when adding producing by the

opponent as a fixed factor (HA, Table 4), this effect of trial identity was reduced by 38%. This suggests that the experimental trial order effect in the VPA models reflected some of the variation caused by producing behaviour by the opponent. However, the random effect of experimental trial identity remained significant in the HA models, mostly due to high levels of producing in the first trail in the sequence (Figure 10), perhaps due to hunger following food deprivation. The amount of producing dropped in trial 2, and then gradually increased during the rest of the trials (Figure 10), perhaps reflecting increasing familiarity with the pair-wise experimental set-up. It is therefore interesting to see that the decrease in producing between the first and second days (Figure 9) was the result of this effect of trial order being more exaggerated on day 2 as compared to day 2 (see Figure 10).

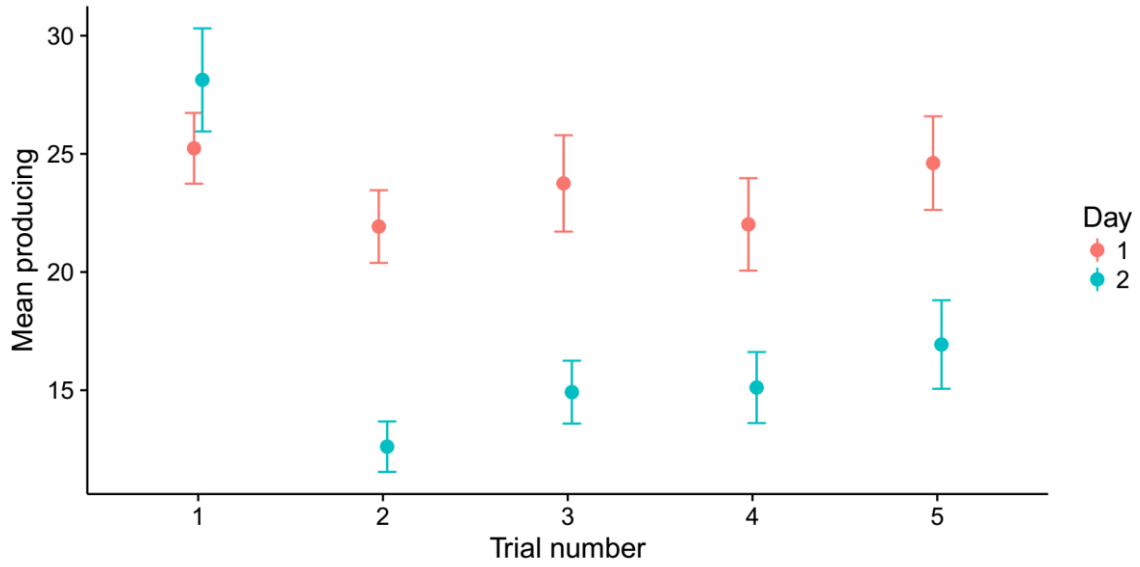

Figure 10. *Effect of trial number and day in the pair-wise assays on the mean amount of producing for all individuals. Means (±SE) are shown for each trial number in both day 1 (red points) and day 2 (blue points).*

To address this issue further, Figure 11 shows that the mean amount of seeds eaten largely reflects the mean amount of producing in the different trials and days. However, as the mean amount of producing gradually increases from trial 2 to 5 (Figure 10), the mean amount of seeds eaten gradually declines (Figure 11), causing more mismatch between the two measurements. This suggests that the birds increased their producing effort, while decreasing the food eaten from each well in the later trials.

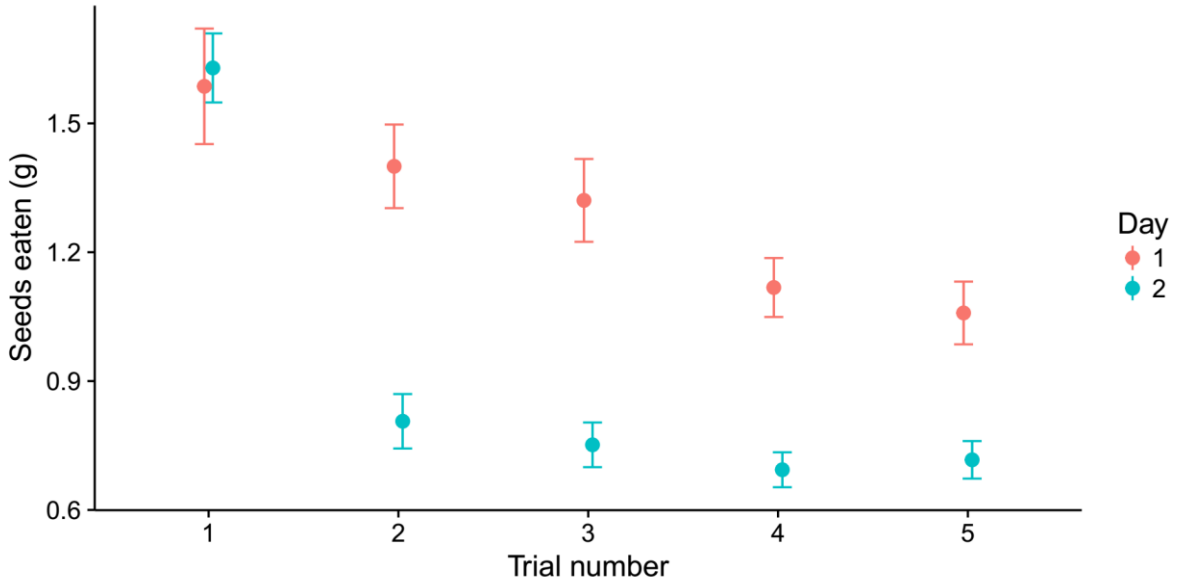

Figure 11. *Effect of trial number and day in the pair-wise assays on the mean amount of seeds eaten (in grams) for all pairs. Means (±SE) are shown for each trial number in both day 1 (red points) and day 2 (blue points).*

Cross-context analysis

Individuals behaved consistently in the amount of producing per unit time between the pair- and group-wise assays (corr = 0.39, p = 0.022; Figure 12), as well as in the scrounging ratio (corr = 0.50, p < 0.001; Figure 12), while probability of scrounging failed to converge due to very little variation in the pair-wise context. The two former results give support for prediction 1c (see Introduction). This means that dividing these house sparrows into pairs in the pair-wise assays did not cause the individuals to behave too differently compared to being tested in larger (i.e. more natural) groups.

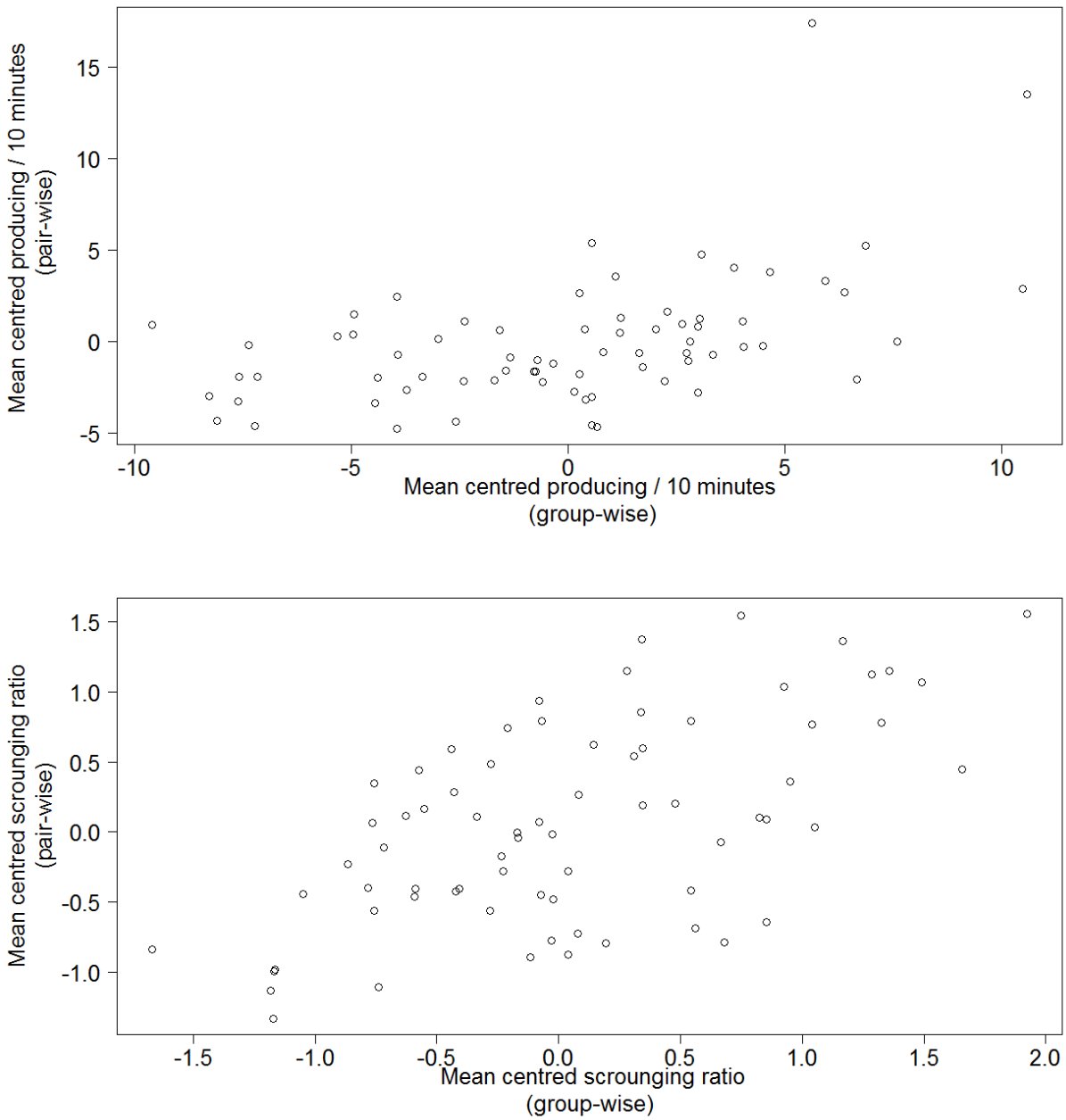

Figure 12*. Mean centred amount of producing (top) and scrounging ratio (bottom) by individuals across group- and pair-wise assays.*

Females produced more than males in both group- (Table 3; Figure 6) and pair-wise (Table 4; Figure 9) assays. In general, females also started each trial with a lower state (at a lower percent of their catch weight) than males (Figure 13), which could mean they tended to be more hungry and thus foraged (i.e. produced) at a greater rate.

The day effect on the amount of producing was positive in the group-wise (Table 3; Figure 6) and negative in the pair-wise assays (Table 4; Figure 9). Interestingly, these differences were

not reflected in the pre-assay state of the birds (Figure 13). There was not a large difference in the state before the group-wise assays in day 1 and 2, which might have explained the increase in amount of producing in the second day. In addition, the birds had a higher state before the pair-wise assay in day 1, compared to day 2, which might reflect time of day differences, but it is the opposite of that expected from the lower rate of producing in day 2 in the pair-wise assays, assuming amount of producing reflects amount of food eaten. However, if this was the case, then the amount of seeds eaten per producing event should have stayed relatively stable across assays. Figure 14 shows that the mean seed weight eaten per producing event for all individuals combined varied across assays, and there was fewer seeds eaten per producing event in the group-wise, compared to the pair-wise assays.

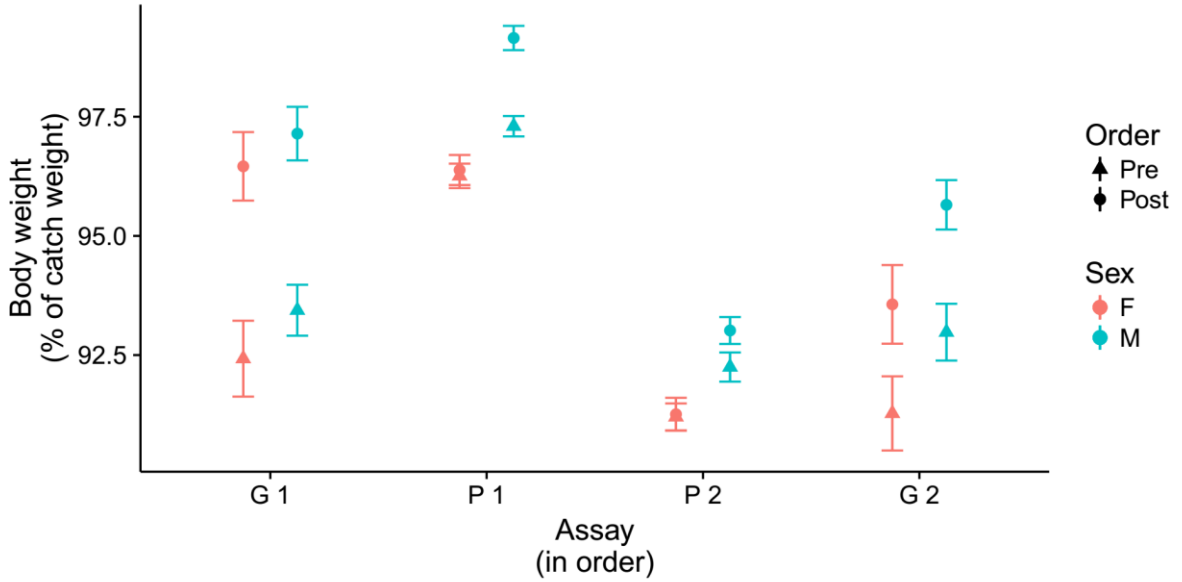

***Figure 13**. Body weight in percent of catch weight in both pre- (triangles) and post- (circles) assay. G = group-wise, P = pair-wise, and the following numbers means day (1 and 2). Means (±SE) for each assay are shown for both females (red) and males (blue).*

Interestingly, females produced more than males in general (Figure 15), but they did not increase their body weight from pre- to post pair-wise assays, while males always did (see Figure 13). This suggests that females experienced a higher number of "unsuccessful" producing events, where they ate fewer seeds during each producing event, or that they got less benefit from each seed eaten in the pair-wise assays, compared to males.

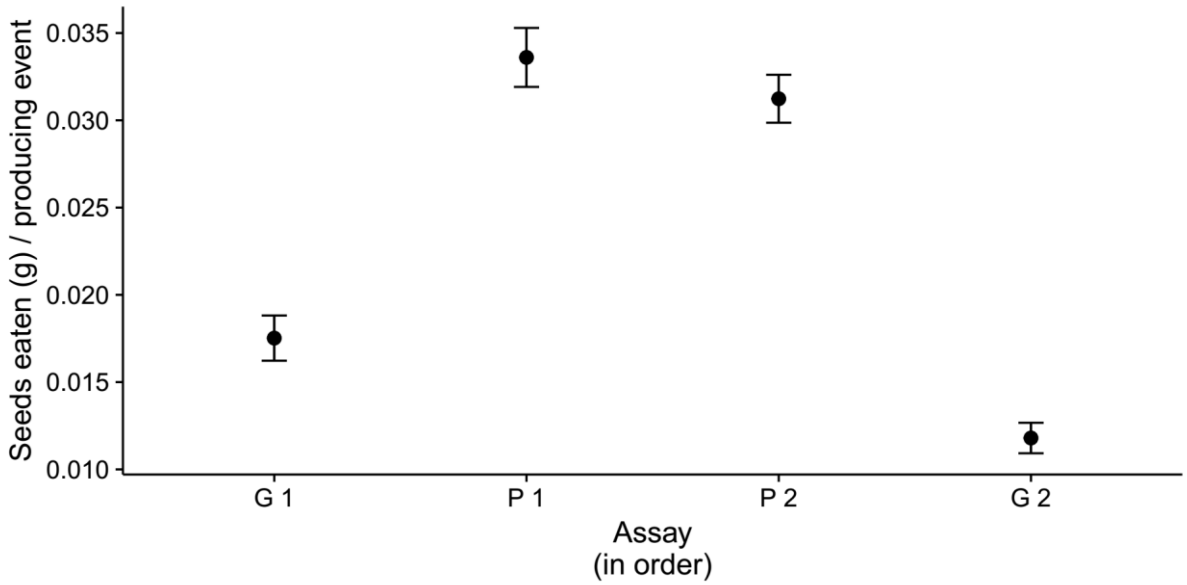

Figure 14. *Amount of seeds eaten per producing event in* each *assay. G = group-wise, P = pair-wise, and the following numbers means day (1 and 2). Means (±SE) for each assay are shown for all individuals combined.*

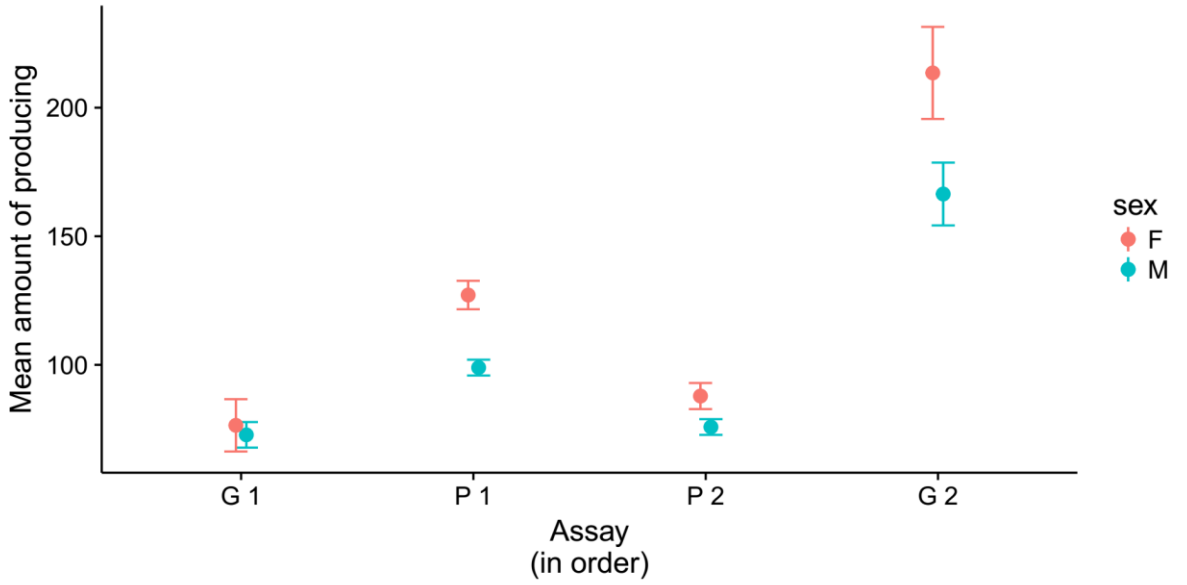

Figure 15*. Amount of producing in each assay. G = group-wise, P = pair-wise, and the following numbers means day (1 and 2). Means (±SE) for each assay are shown for both females (red) and males (blue).*

Discussion

The aim of this study was to investigate indirect social (partner) effects on individual producer-scrounger foraging strategy in house sparrows (*Passer domesticus*). First, we predicted repeatable individual differences in behaviours for the group-wise and pair-wise assays, in addition to correlations in individual behaviour between these two. Focal ID explained a significant amount of variation around the intercept of all models, except for the amount of producing from the group-wise assays. As expected, we found repeatable individual differences in the amount of producing in the pair-wise assays and individuals behaved consistently in the amount of producing and scrounging ratio relative to the mean between group and pair-wise assays. In addition, individuals were also moderately repeatable in the probability of scrounging and scrounging ratio from the pair-wise assays, and although somewhat low, these repeatabilities were mostly in the same range as reported in other studies on social behaviours (Wilson *et al.*, 2009, 2011, 2013; Han *et al.*, 2016; Santostefano *et al.*, 2016). In contrast, both the amount of producing and the scrounging ratio showed very low repeatabilities in the group-wise assays. So even though there was a statistically significant amount of variation explained by focal ID for the scrounging ratio models, the low repeatability scores indicate that the biological significance may be less meaningful (i.e. variance components can be statistically significant even though they contribute very little to the total amount of variation). There are two possible reasons for these results. First, individual levels of scrounging were very low over both the group assays and the pair-wise assays. This may very well be because the amount of food in each trial was too high, and/or too accessible, reducing the competition for food in addition to the theoretical "scrounger bonus". Some other producer-scrounger studies used a sand and seed mixture in the wells, and observed much higher levels of scrounging (Liker & Barta, 2002; Belmaker *et al.*, 2012), while other studies had larger groups (i.e. less food provided per individual), but without sand (Lendvai *et al.*, 2004; Tóth *et al.*, 2009). Scrounging also comes with a risk of injury, and house sparrows have been shown to use aggressive fighting over food patches (Liker & Barta, 2002; Lendvai *et al.*, 2004). This risk could easily be avoided by increasing the amount of producing because of the low competition for food patches in this study. Secondly, four of the twelve groups (i.e. 24 individuals) did not feed in the first of the two group-wise assays. This means the sample size for estimating the behavioural consistency in the group-wise trials were reduced by one third, although including individuals with only one measurement (as we

did) is expected to increase the power (Martin *et al.*, 2011). We also had a very short acclimatisation period of just one day, due to time and space limitations. Other producer-scrounger studies with a similar setup (i.e. in captivity with an artificial feeder) allowed several days to weeks for familiarising the birds with the feeders and each other (Liker & Barta, 2002; Lendvai *et al.*, 2004; Katsnelson *et al.*, 2008; Belmaker *et al.*, 2012). However, this would not be possible for the kinds of high throughput sample sizes intended for future quantitative genetic studies of these indirect social effects in the sparrows. So, one aim of the current study was to see if short acclimatisation was a viable option here.

The second prediction about repeatable differences in individual phenotypic plasticity could not be tested statistically, due to low power of the data needed for testing random slopes in a (generalized) linear mixed effect model. The main reason for this is probably due to the low levels of scrounging (i.e. the social environment range being too small for detecting responses by the focal individuals), compared to other studies (Liker & Barta, 2002; Lendvai *et al.*, 2004; Katsnelson *et al.*, 2008; Belmaker *et al.*, 2012). The power to detect significant variation in plasticity also depends on sample size, and a power analysis article from Martin *et al.* (2011) suggests data sets of $N > 200$ as a rule of thumb when it comes to detecting significant variation in plasticity. However, this also depends on the effect size and number of measurements per individual, and we think that the high number of repeated measurements per individual in this study would have been sufficient, if the scrounging levels had been higher. In addition, increasing the sample size to $N > 200$ would require the study to be done in a location where the population size is much larger than the population size at Lauvøya (approximately 130 individuals), where this study was conducted. It also would take over a month of fieldwork, if done with the same experimental setup, and consequently, that study would be out of range for a master thesis for one student.

The third prediction about indirect social effects had nearly no support in this study. There were no repeatable effects of partner phenotypes on focal individuals in any of the behaviours except for the combined phenotype of all opponents in a group on the amount of producing. Interestingly, the amount of producing by opponents explained all of this variation, and also had a significant effect in the pair-wise trials, but not on any of the other behaviours. This positive effect of producing by the opponent on producing by the focal was not as expected. This means that something caused both the focal and the opponent(s) to produce more/less in the same trials. A possible explanation could be that stress levels of an individual spills over on the social partner(s), creating inter-individual dependence for the level of stress. This could

possibly result in increased feeding when all individuals are relaxed, and if some birds become stressed, they may feed less and their social partners react by doing the same. If this was due to repeatable differences in stress among individuals (e.g. some individuals were consistently more stressed in the pair-wise trials), this should be reflected in the pair ID effect we tested for, but this did not explain any of the variation. However, it could still be that a non-repeatable factor caused some individuals to become more stressed in certain pair-wise trials (e.g. noises inside the barn), because this would not be reflected in the pair ID random effect. Unfortunately, we had no additional recording or measurement that allowed us to be able to test for such effects.

There are a few other studies that have investigated opponent identity effects on focal behaviours, but none of these have been done on social foraging behaviour or with house sparrows (Wilson *et al.*, 2009, 2011, 2013; Han *et al.*, 2016; Santostefano *et al.*, 2016). Still, all of these studies have found (at least some) evidence for a repeatable social partner effect. However, social feeding behaviour might be less repeatable. The most repeatable behaviour in this study was the amount of producing. This might just reflect activity in the feeder, due to the availability of the food, since it is not necessary a social behaviour. This may also be the reason for no opponent ID effect for this behaviour, because non-social behaviours are not necessarily affected by the social environment. This could therefore explain why this repeatability was the highest of all behaviours, because it would lead to a more stable environment, compared to a social environment that may vary substantially between trials. The repeatability for this behaviour was also similar to other studies measuring simple individual activity when alone in an empty cage without food (e.g. Beauchamp, 2000; Dingemanse *et al.*, 2007; Santostefano *et al.*, 2016), and in previous studies of this type on these Norwegian sparrow populations (Sommerli, 2015; Finnøen, 2016).

Differences between the sexes in producer-scrounger behaviour have been found previously in other studies. In the present study, females had a higher ratio of scrounging than males in the group-wise assays (but not in pair-wise). This could support results from Tóth *et al.* (2009), who used kin-selection theory to argue that females, who are the dispersing sex in house sparrows, have had lower selection pressure for kin recognition, and thus scrounge more from close kin. However, we used the assumption of catch time and place as an indicator of natural social groups, but we have not used (soon to be available) data on genetic

relatedness of the individuals in the different groups. It would be interesting to see if relatedness could explain some of this effect. Males also produced significantly less than females in both group- and pair-wise assays. This could be linked to females having a lower state compared to males before each assay, and therefore producing more. However, a previous study found a decrease in producing for individuals in a lower state (Lendvai *et al.*, 2004), although only at the first feed of the day, but this study had lower food abundance per individual compared to our study, which may (as stated above) influence the choice of tactics used (but see Mathot *et al.*, 2009). The reason why females seemed to have a lower state before each assay could be because they possibly have a higher metabolic rate, as shown in zebra finches, *Taeniopygia guttata*, (Rønning *et al.*, 2005). This could also explain why females maintained their weight during the pair-wise assays, while males gained weight, since individuals with high metabolic rate get less benefit from a given food item, compared to individuals with low metabolic rate. In a study on how basal metabolic rate (BMR) affects producer-scrounger strategy use in zebra finches (Mathot *et al.*, 2009), they found that high BMR individuals invested more in scrounging, compared to low BMR individuals, which could also be the reason why females had a higher scrounging ratio in the group-wise assays in our study.

The negative effect of the second day on scrounging ratio in both group- and pair-wise assays could possibly be related to the birds being familiarised with the experimental setup, and thus having a better expectation about the amount of food in the feeders, i.e. due to the short acclimatisation period prior to the first day trials (see above). This could also be the reason for the increased amount of producing in the second day in the group-wise assays. As mentioned in the methods, four of the groups did not enter the communal feeder at all the first day, and some other groups took a long time before they started feeding, and this problem disappeared totally in the second day. It therefore seems that this effect of day might have been reduced by allowing one more day of acclimation of the birds to the artificial feeders. There was also variation in producing rate within each pair-wise assay, with more producing and more seeds eaten in the first trial in both days. This is probably due to individuals being hungrier in the first trial, since they were food deprived overnight prior to this.

Differences in hunger level could also explain why females produced more than males in both the group- and pair-wise assays, since females in general started each trial with a lower state than males. However, amount of producing did not always reflect amount of seeds eaten, and there was also less seeds eaten per producing event in the group-wise, compared to pair-wise

assays. This could possibly be because the amount of food in the group-wise assays got depleted, while the feeders were refilled between each pair-wise trial. This could have caused the birds to get less food from each producing event as the feeder got depleted. Such effects could have been assessed more carefully if the number of seeds eaten per producing event had been recorded (e.g. as number of pecks in each well). We therefore recommend future studies to have some measure of food obtained per producing event for each individual.

In conclusion, this study revealed repeatable individual differences in feeding behaviour in both group- and pair-wise producer-scrounger assays on captive house sparrows. Even though some of these behaviours were not as repeatable as expected, we argue that the high abundance and/or availability of food at the feeder was responsible for this. This is probably also the reason for the overall low rates of scrounging, which could then explain the absence of repeatable social environment effects. It might be that the expected ESS is shifted towards less percentage of scrounging in the population when the competition for food is reduced – i.e. the producer bonus became excessively large. This therefore suggests that relative strategy use of producing and scrounging is affected by resource availability, but more empirical studies are needed on this, to investigate how strongly this affects the use of the different strategies. We therefore suggest that adding sand in the wells to increase the effort needed to obtain the food will therefore probably increase the scrounging rates (see Mohammad 2017). We also showed that individuals behaved consistently when tested in groups and pairs. This is a critical requirement when dividing a naturally flock-feeding organism in pairs to be able to assess focal behaviour response to individual partners. Still, we recommend future studies to include this comparison, particularly if done on different populations and/or species.

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Appendix

Table A1. *Pair-wise data summaries for selected mixed effect models of amount of producing, showing there was no variation explained by including pair ID in the HA model.*

	Producing (normal)		
	VPA	**HA**	**HA + Pair ID**
Fixed			
Intercept ± SE	20.493 ± 1.238	20.486 ± 1.193	20.486 ± 1.193
	(p < 0.001)	(p < 0.001)	(p < 0.001)
Sex ± SE	-5.072 ± 2.288	-5.064 ± 2.269	-5.064 ± 2.269
	(p = 0.027)	(p = 0.026)	(p = 0.026)
Day ± SE	-6.260 ± 1.270	-5.413 ± 1.123	-5.413 ± 1.123
	(p < 0.001)	(p < 0.001)	(p < 0.001)
Day * Sex interaction ± SE	1.444 ± 1.609	1.761 ± 1.622	1.761 ± 1.622
	(p = 0.370)	(p = 0.278)	(p = 0.278)
Prod_opp ± SE		3.516 ± 0.901	3.516 ± 0.901
		(p < 0.001)	(p < 0.001)
Random			
Pair ID			0.000
Focal ID			(p = 1.000)
	78.870	77.930	77.930
	(p < 0.001)	(p < 0.001)	(p < 0.001)
Opponent ID	2.90e-12	0.000	0.000
	(p = 0.500)	(p = 1.000)	(p = 1.000)
Trial ID	31.270	18.780	18.780
	(p <0.001)	(p < 0.001)	(p < 0.001)
Residual	85.990	90.140	90.140