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Master's thesis in MSc in Biology

Supervisor: Jonathan Wright

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Abstract

The maintenance of behavioural variation among individuals in the same population, exposed to the same selection pressures, remains puzzling to evolutionary biologists because they should have evolved the same optimal (plastic) phenotypes. However, an individual's internal state, social environment, and resulting feedback mechanisms might provide an explanation. During social interactions, individuals may plastically adjust their behaviour in response to phenotypes expressed by social partners (social responsiveness) and/or elicit behavioural adjustments in their social partners (social impact). Such effects of social environment on behaviour remain poorly understood, particularly at an individual level. Therefore, I have studied these traits and how they are related to the internal state of individuals. This was approached through the framework of evolutionary game theory and the producer-scrounger game. To obtain behavioural data, we conducted repeated behavioural assays with groups of three House sparrows (*Passer domesticus*) and calculated best linear unbiased predictors using mean measures to estimate levels of responsiveness and impact in scrounging behaviour. I then calculated the effects basal metabolic rate (BMR), body mass and sex had on these social traits. The results indicated the presence of consistent, individual differences in social foraging behaviour, responsiveness and impact in this population. There was also support for a sex-dependent effect of both BMR and body mass on proportion of scrounging versus producing, as well as of an interaction between BMR and body mass on this tactic choice and social responsiveness. Importantly, it appears that we were not able to cleanly detect producer-scrounger dynamics in our assays, likely due to disturbance effects, and the biological implications of this are therefore not completely clear. Nonetheless, these state variables explained a significant amount of the variation in social behaviour and social plasticity and, as such, these findings contribute to the growing body of knowledge concerning the mechanisms underlying interindividual differences in behaviour and plasticity.

Sammendrag

Hvordan variasjon i adferd blant individer som er del av samme populasjon or er utsatt for de samme seleksjonstrykkene blir vedlikeholdt, er ennå uvisst blant evolusjonsbiologer, siden de forventes å ha utviklet de samme optimale (plastiske) fenotypene. Forklaringen på dette kan ligge i individers indre tilstand, sosiale miljø, og ‘feedback’-mekanismene mellom dem.

Under sosiale interaksjoner kan individer plastisk endre adferd i respons til fenotyper uttrykt av deres sosiale partnere (‘sosial responsivitet’) og/eller fremkalle adferdsendringer hos deres sosiale partnere (‘sosial påvirkningskraft’). Vi har fortsatt dårlig forståelse for slike effekter av sosialt miljø – særlig på individnivå. Jeg har derfor valgt å forske på disse trekkene og hvordan de henger sammen med individers indre tilstand. Dette ble tilnærmet ved hjelp av evolusjonær spillteori or ‘producer-scrounger-spillet’. Adferdsdata ble samlet inn ved å gjennomføre gjentatte eksperimentelle adferds-forsøk på grupper av tre gråspurver (*Passer domesticus*), for så å kalkulere ‘best unbiased linear predictors’ ved bruk av gjennomsnittsverdier for å estimere nivåer av responsivitet og påvirkningskraft i scrounger-adferd. Jeg kalkulerte så effektene av basal metabolsk rate (BMR) og kroppsmasse på disse sosiale adferdene. Resultatene indikerte tilstedeværelsen av konsekvente, individuelle forskjeller i sosial matsankingsadferd (‘foraging behaviour’), responsivitet og påvirkningskraft i denne populasjonen. Det så også ut til å være en kjønnsavhengig effekt av både BMR og kroppsmasse på proporsjonen av scrounger-adferd kontra producer-adferd, samt av en interaksjonseffekt mellom BMR og kroppsmasse på dette taktikkvalget og på sosial responsivitet. Det må nevnes at det kan virke som om vi ikke klarte å tydelig oppdage ‘producer-scrounger-dynamikk’ i forsøkene våre, antakelig grunnet ‘forstyrrelseseffekter’, og de biologiske implikasjonene av dette er derfor uklare. Likevel er det tydelig at disse ‘tilstandsvariablene’ kunne forklare en signifikant del av variasjonen vi observerte i sosial adferd og sosial plastisitet, og det er tydelig at våre funn har bidratt til bedre forståelse av de underliggende mekanismene som former individuelle forskjeller i adferd og plastisitet.

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Introduction

Personality is a concept traditionally applied exclusively to humans; however similar patterns of individual behavioural variation have also been frequently observed in species of non-human animals. ‘Animal personality’ can be defined as consistent individual differences in behaviour across contexts and over time, and ‘behavioural syndromes’ as covariation in such behavioural traits across individuals, and an increasing amount of research is focusing on these topics (Davies et al., 2012; Dingemanse et al., 2010; Dingemanse & Wright, 2020; Réale et al., 2007, 2010a; Sih et al., 2004). How such consistent individual variation might be maintained remains something of an evolutionary puzzle, as individuals from the same population, affected by the same selection pressures, are expected to have developed the same optimal levels of plastic and context-dependent behaviours. Many studies, however, found individual behaviour to be highly consistent over time with each individual only displaying a minority of the possible behavioural trait values available in the population (Bergmüller & Taborsky, 2010; Dingemanse et al., 2010). That is not to say that animal personality is non-plastic. Individual consistency in mean levels of a behaviour has been shown to exist alongside plasticity, and even levels of plasticity can be individually repeatable (Dingemanse et al., 2010). An example of this is seen in a study of aggressive behaviour in mice, where individuals that displayed overall higher levels of aggression were less likely to adjust their aggression in response to conspecifics, while overall less aggressive individuals would more readily adjust their behaviour (Natarajan et al., 2009). In relation to this, we can see how in a social environment an individual’s social behaviour might have fitness consequences not only for the focal individual, but also for its conspecifics (Maynard Smith, 1980; Maynard Smith & Price, 1973). Social evolution and its direct and indirect fitness consequences have historically been considered from a game theoretical perspective (see below) but is now increasingly being studied using tools from quantitative genetics as well (Araya-Ajoy et al., 2020). These methods allow us to study aspects of animal personality in social traits, because up until recently, most personality assays have had to be done in individual isolation in a non-social context to be sure of only including variation attributable to the individual itself.

The evolutionary potential of continuously varying phenotypic traits can be practically studied using a quantitative genetics approach. In this approach, the heritable phenotypic variation controlled by a multitude of genes is normally viewed in isolation from environmental effects, which are assumed to be unrelated to heritability (McGlothlin et al., 2010). When studying social behaviours using this approach, however, the assumption that the environment does not contribute to the heritable variation is no longer valid. In social traits, indirect genetic effects (IGEs, focal phenotypes resulting from genes expressed in social partners) operate in addition to direct genetic effects (DGEs, focal phenotypes resulting from the expression of the focal individual's genes), and they also carry an aspect of heritability (Dingemanse & Araya-Ajoy, 2015). A quantitative genetics approach that takes IGEs into account is therefore needed to get a comprehensive overview of the repeatability, heritability and evolution of social traits (Dingemanse & Araya-Ajoy, 2015; Wolf, 2003). Furthermore, IGE's have often been studied on a population scale, however when considering individuals, they not only respond to, but also affect their social environment (de Groot et al., 2023). There are therefore two apparent relationships that are interesting to assess in relation to IGEs – the degree to which a focal individual adjusts its phenotype to phenotypes expressed in social partners ('social responsiveness'), and the magnitude with which a focal individual elicits certain phenotypes in its social partners ('social impact') – see Araya-Ajoy et al. 2020). This is, for example, seen in interactions between parents and offspring in a variety of taxa, where the parents adjust their level of provisioning to the intensity of begging by their offspring, and the offspring increase or decrease their begging behaviour according to the effect on their hunger levels. That is, the parents display social responsiveness when providing more food to the offspring that beg more, and the offspring display social impact when their intensity of begging causes their parents to feed them more (Smiseth et al., 2008).

The traditional way of approaching the study of social evolution has been through the framework of evolutionary game theory (Davies et al., 2012; Maynard Smith, 1980; Maynard Smith & Price, 1973). In this approach, behavioural phenotypes are treated as possible tactics in an evolutionary game, with each tactic involving different pay-offs depending on the tactic adopted by other players. To justify this simplification, several assumptions are made, such as that phenotypes are perfectly heritable and that natural selection has always had time to operate until an equilibrium is reached. At this equilibrium, the population should have reached an optimal 'solution', in which no individual can do better by adopting a different strategy. Such a strategy is called an evolutionary stable strategy (ESS), and it can either

consist of a single tactic (a ‘pure’ ESS), multiple fixed tactics (a ‘mixed’ ESS), or multiple flexible tactics that individuals can readily switch between (a ‘mixed conditional’ ESS), with the ESS being maintained at a certain frequency between tactics in the population (Davies et al., 2012; Maynard Smith, 1986; Maynard Smith & Price, 1973). An example of the latter is seen in male natterjack toads (*Epidalea calamita*; Arak, 1988), where there are two prevalent mating tactics – calling to attract and mate with females or being a silent ‘satellite’ and trying to mate with the females that are attracted by calling males before they reach them.

Individuals have been found to choose which tactic to play by assessing their own attractiveness through comparing their call volume to that of neighbouring males. If a neighbouring male’s call is twice as loud, the focal individual will adopt the satellite tactic. This game theoretical perspective can be applied when studying actual populations of animals, with mathematical models providing qualitative predictions regarding the outcomes of such negative frequency-dependent natural selection to produce a stable variety of social behaviours (Davies et al., 2012; Maynard Smith, 1986).

The game theoretical model that will be the focus of this study is the ‘producer-scrounger’ game (Barnard & Sibly, 1981). In nature, resources often vary in availability and distribution, and so animals are expected to adopt foraging behaviours to try and maximize their fitness given a particular resource distribution. This model separates between two mutually exclusive foraging tactics: ‘producing’ in which individuals independently search for food patches, and ‘scrounging’ in which individuals join conspecifics that have already found food. Since both tactics cannot be played at the same time, individuals do not contribute to the collective foraging efforts of the group while scrounging. This causes the pay-offs of each tactic to be negatively correlated with the frequency of scroungers in the population (Figure 1.1), and we further see that both tactics do relatively better when rare – i.e. when the proportion of scroungers is high, producers do better than scroungers, while when the proportion is low, scroungers do better than producers (Giraldeau & Beauchamp, 1999). Scroungers do better when rare because there are more producers available to scrounge from and fewer scroungers to compete with, while producers do better when rare because they arrive at the food source first and thereby receive a larger share (‘producer bonus’ or ‘finder’s share’; Giraldeau & Beauchamp, 1999; Giraldeau & Caraco, 2000). Notably, if all individuals used only the producer strategy, the average absolute pay-off of the population would be even higher, however as the scrounging tactic does relatively well when rare, the ‘tragedy of the commons’ makes this all-producer scenario an unrealistic ESS. Hence, the mixed conditional

ESS is here predicted at the relative frequency of the two tactics where both provide the same fitness pay-offs, with individuals readily switching between the two and thereby keeping the population at the ESS (Figure 1; Katsnelson et al., 2008; Vickery et al., 1991). However, recent models suggest that individuals may also vary in their degree of plasticity, and that as long as enough individuals are conditionally switching tactics, even pure producer or scrounger tactics might be able coexist in the same population (Dubois et al., 2010; Katsnelson et al., 2011).

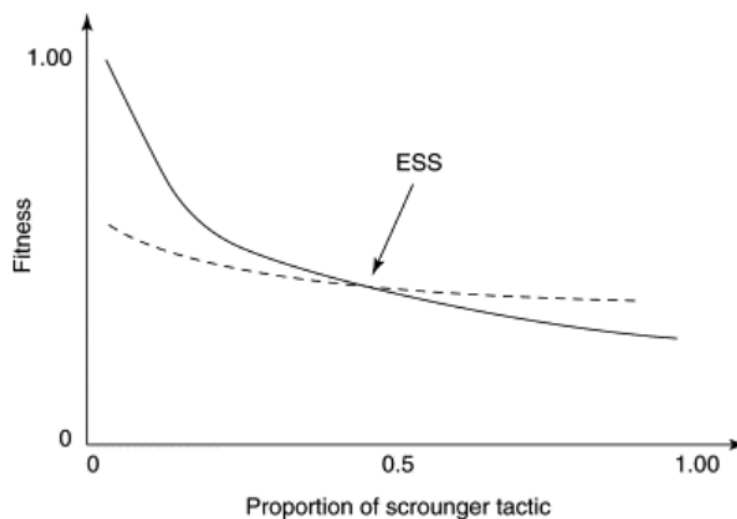


Figure 1.1: An example of the pay-offs of producer (broken line) and scrounger (solid line) strategies. The payoffs of both strategies decrease as the proportion of individuals employing the scrounger strategy increases. The scrounger strategy does relatively better when the proportion of scrounging individuals is low, while the producer strategy does relatively better when the proportion of scroungers is high. The equilibrium point at which these functions cross is the ESS, in which both strategies do equally well. Adapted from *Giraldeau & Beauchamp (1999)*.

Various mechanisms have been found to influence the conditional choice of producer versus scrounger tactics, mostly in experimental studies using house sparrows (*Passer domesticus*). One such mechanism is individual differences in state, and more specifically energetic state (Barta & Giraldeau, 2000; Lendvai et al., 2004). As the energy reserves of an individual decrease and immediate rewards increase in value (e.g. early in the morning), it should be gradually more inclined to employ the tactic that yields least variation in the food reward per energy spent – the most ‘risk-averse’ tactic (Barta & Giraldeau, 2000). In the producer-scrounger game, the scrounger tactic best fits this description, as it on average provides more consistent rewards than the producer tactic, where individual food searching efforts are not always successful, resulting in variable pay offs for invested energy (Lendvai et al., 2004).

Such an effect of energy reserves in turn suggests that differences in metabolism might also be a potential driver of personality; particularly for behaviours with strong consequences for energy turnover (acquisition or expenditure, e.g., foraging), as suggested by Mathot et al. (2019). A higher metabolic rate (MR) is generally associated with higher energetic costs, but there are two competing models predicting its relationship with energy reserves – the ‘performance model’ (also termed the ‘acquisition model’; Figure 1.2A) and the ‘allocation model’ (Figure 1.2B; Careau et al., 2008). The performance model suggests that individuals with higher MR also have larger internal organs, making them physiologically superior with regards to acquiring resources and sustaining energy-demanding behaviours (Daan et al., 1990). In their meta-analysis considering a wide range of taxa, Mathot et al. (2019) suggested that this model is most common, given the positive relationship between basal metabolic rate (BMR) and behaviours with significance for energy throughput in many of the reviewed studies. Conversely, the allocation model suggests that a higher MR does not entail higher energy availability, meaning individuals with a higher MR must allocate proportionately more energy to metabolism, resulting in relatively higher energetic costs. So, whether there is a positive or negative relationship between energy-demanding personality traits (e.g. activity) and MR depends on which of these proposed relationships is applicable. In Careau et al. (2008), the relationship considered involves resting metabolic rate (RMR) and activity. This thesis will instead consider basal metabolic rate (BMR), and while these are two different measures (BMR is measured at complete rest with very restricted conditions, while RMR is measured less strictly and may for example include light activity), their difference with regards to these models is sufficiently small that the same relationships can be predicted. Relating this directly to social foraging and the producer-scrounger game, there is evidence to suggest a relationship between BMR and tactic choice, such that individuals with higher BMR will more readily display scrounging behaviour when energy requirements are increased and/or food availability is decreased (Mathot et al., 2009). This might suggest that the allocation model (Figure 1.2B) is more likely, as individuals with higher BMR preferred the generally less active scrounger tactic, however it must once again be stated clearly that consensus is lacking with regards to the direction of this link, and the underlying mechanisms are not well understood.

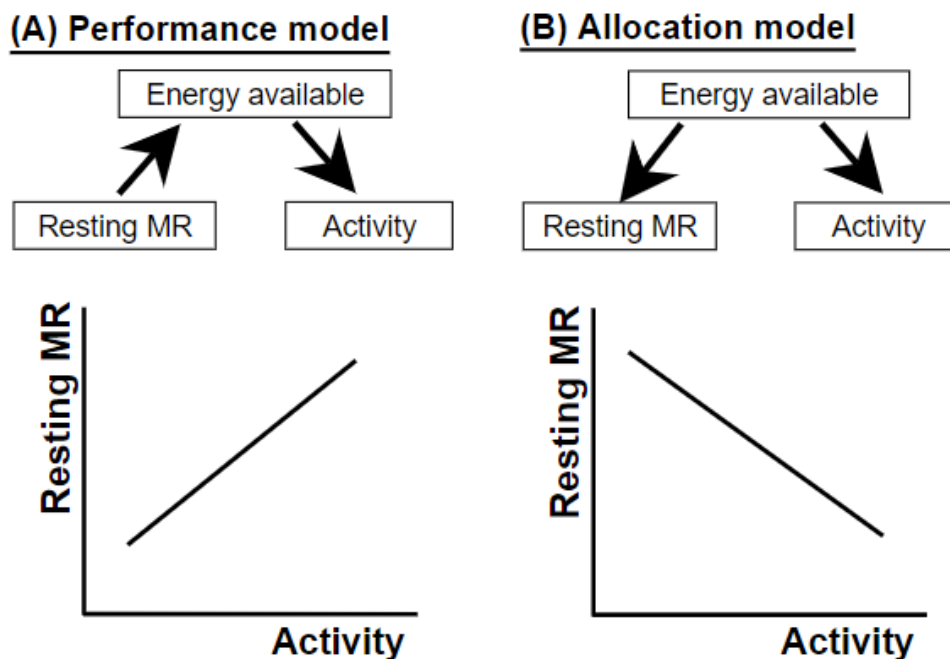


Figure 1.2: The two theories regarding the relationship between (resting) metabolic rate (MR), energy reserves, and activity. **(A)** the performance model predicts a positive relationship between MR and activity, while **(B)** the allocation model predicts a negative relationship. Adapted from *Careau et al. (2008)*.

Related to these ideas is the concept of a pace-of-life syndrome (PoLS). This concept builds upon the fast-slow inter-specific life-history continuum (which in turn builds upon the concept of *r*- and *K*-selection by MacArthur & Wilson (1967), which considers life-history traits observed to covary in most species in relation to the trade-offs between current and future reproduction, such as reproductive rate, clutch size, and age and size at maturation (Bielby et al., 2007; Gaillard et al., 1989). The PoLS-framework expands upon this by also considering physiological/morphological traits, such as BMR, hormone levels, and body size, as well as behavioural traits, such as boldness, aggressiveness, and activity (Hennemann III, 1983; Jones et al., 2008; Réale et al., 2010b; Wright et al., 2019). The concept of animal personality is relevant in relation to this, as a clear link between behavioural personality and physiological and life-history traits has been uncovered, both within populations and between populations and species (Réale et al., 2010b). Within the PoLS-framework, a fast-living individual might be expected to (among other things) display higher levels of aggressiveness, activity, exploration, boldness, and testosterone, as well as having a higher MR and be more dominant and less social than their slow-living counterparts, who exist on the opposite end of the continuum (Réale et al., 2010b). Frequent findings of correlations between these traits in the literature provide mixed support for this. For instance, BMR was found to have a positive

(in house sparrows; Buchanan et al., 2001), negative (in white-crowned sparrows (*Zonotrichia leucophrys*); Wikelski et al., 1999) and no (in house sparrows; Buttemer et al., 2008) relationship with testosterone levels. Testosterone has, in turn, repeatedly been found to be positively correlated with aggression, as demonstrated in multiple bird species by Soma (2006), from which we may infer a relationship between BMR and aggression. Aggression has further been found to be correlated with competitive ability and dominance (Liker & Barta, 2002; Riters et al., 2004), all of which are related to boldness (Dingemanse et al., 2007; Sih et al., 2004). If we again consider individual differences in IGEs, we may hypothesize that fast-living individuals could therefore also be less responsive and more impactful, as their dominant and competitive nature might make them more difficult for opponents to displace and more efficient at displacing opponents, lessening the adaptive value of being more plastic (Coppens et al., 2010; Damsgård et al., 2019).

In nature, scarcity of resources is not a rare occurrence, resulting in frequent observations of producer-scrounger dynamics in a variety of taxa (Ranta et al., 1996), and other factors than the aforementioned have been proposed as explanations for individual tactic choice. In addition to genetics, both the abiotic, developmental, and social environment of an individual could have an impact on this choice. This is, for example, seen in relation to predation risk, as scrounging can be conducted simultaneously with anti-predator vigilance (Ranta et al., 1996), and to group size, because it affects the number of producers available to scrounge from (Vickery et al., 1991). The patchiness of resources, through its influence on the profitability of producing via searching effort, has also been proposed as a key factor (Katsnelson et al., 2008). This may again connect with energetics through the different pay-offs for different types (e.g. sizes) of individuals under different levels of energy availability in the environment. Furthermore, as touched upon above, dominance is another factor that has been found to influence producer-scrounger strategy choice. Liker & Barta (2002) found that individuals in a population of house sparrows were generally flexible in their choice of tactic, and that there was a positive relationship between dominance rank and frequency of scrounging. When exposing individuals to energetic stress, Lendvai et al. (2006) found a similar relationship, with more dominant individuals increasing their propensity to scrounge considerably more than their less dominant conspecifics, suggesting a significant association between dominance and energetics, possibly also extending to metabolism. The relationship between strategy choice and dominance has also been investigated in relation to genetic relatedness. Tóth et al. (2009) found that individuals adjust their level of scrounging (and

aggressiveness) when foraging with more closely related conspecifics. Dominant males would less frequently use aggressive joining (scrounging) when foraging with relatives, and females were more readily allowed to use non-aggressive joining (scrounging), indicating that sex (and its dominance and size associations) has a significant effect as well, alongside relatedness. A final factor that has been demonstrated to impact foraging strategy is learning, both in fledglings and adults. Katsnelson et al. (2011) found that positive reinforcement from a learning task increased the propensity to produce in fledglings, and Belmaker et al. (2012) found that adult individuals are similarly able to adjust their producer-scrounger strategy in response to previous learnt experiences.

Through the framework of evolutionary game theory and the producer-scrounger game, we have the potential to gain greater insight into the complex topics of animal personality and social behaviour, and the mechanisms that drive individual choice of tactics. Previous master's projects have investigated these issues further, by trying to investigate the mechanisms underlying social plasticity, for which there is currently little evidence. Pettersen (2017) found evidence for repeatable individual differences in producer-scrounger behaviour, but not for repeatable social environment effects. Mohammad (2018) found evidence suggesting repeatable individual differences in both foraging behaviour and plasticity, as well as a varying effect of identity on scrounging behaviour in conspecifics. In this study, we aim to further these efforts by investigating social responsiveness and social impact using a different and more direct approach (see Methods section; de Groot et al., 2023). We also attempt to more thoroughly explain the underlying mechanisms shaping how individuals respond to and impact their social environment, and I here test for effects of BMR, body mass, and sex specifically. Expanding upon this knowledge will not only improve the quality of the design of future studies, as we learn about effects of differences in behavioural profile and stress tolerance, but also teach us about the adaptability of species in the face of changes to the environment. A better understanding of the relationship between these traits further enables us to make inferences about how selection operates and thereby to predict patterns of evolutionary trajectory.

Study objectives

The overarching aim of this study was to establish whether individuals are repeatable in their average level of producing versus scrounging, their social responsiveness and their social impact, and to quantify the covariances between these traits. Furthermore, I tested for covariances between these traits and physiological and morphological traits. The following hypotheses were addressed:

Hypothesis 1: Because the pay-offs of producing versus scrounging should be affected by individual body mass and BMR, individuals should show consistent variation in their propensity to produce versus scrounge.

Prediction 1.1: Individuals will display consistent differences in their propensity to produce versus scrounge.

Prediction 1.2: Larger (male) individuals with higher BMR will have a higher propensity to scrounge than smaller (female) individuals with lower BMR.

Hypothesis 2: Because the cost/benefit trade-offs of switching tactics should be affected by an individual's size and BMR, individuals should show consistent differences in their level of social responsiveness.

Prediction 2.1: Individuals will display consistent differences in their level of social responsiveness.

Prediction 2.2: Larger (male) individuals with higher BMR will display lower levels of social responsiveness than smaller (female) individuals with lower BMR.

Hypothesis 3: Because the cost/benefit trade-off of employing a strategy will depend on who in the population is playing what tactic, and competitive ability should be affected by size and BMR, individuals should show consistent differences in their level of social impact.

Prediction 3.1: Individuals will display consistent differences in their level of social impact.

Prediction 3.2: Larger (male) individuals with higher BMR will display higher levels of social impact than smaller (female) individuals with lower BMR.

Methods

Study species and location

This study was conducted on a wild population of house sparrows (*Passer domesticus*). The house sparrow is a small, passerine bird that is highly gregarious. It is well adapted to human habitats, mainly due to its flexibility in behaviour and its opportunistic and generalist nature, which has led to its distribution extending across most of the world (Anderson, 2006; Hanson et al., 2020). The combination of group living, behavioural flexibility and habituation to humans renders the house sparrow an appropriate model organism for a broad range of studies within the field of behavioural ecology, and it has previously been used as such in studies of social foraging and producer-scrounger interactions (Barnard & Sibly, 1981; Katsnelson et al., 2008; Lendvai et al., 2006; Tóth et al., 2009). The population used for this study was located on and around the island of Lauvøya in Åfjord municipality on the coast of Trøndelag. It is part of the larger study system established by the Centre for Biodiversity Dynamics (CBD) at NTNU for their long-running house sparrow project, which has been used to produce various ecological, genotypic, and phenotypic data for nearly 30 years (Holand et al., 2011; Jensen et al., 2007, 2013; Niskanen et al., 2020; Ringsby et al., 2006). The population at Lauvøya was established in 2012 for a study on the genetic basis of basal metabolic rate (BMR). The original population was translocated and replaced with a population consisting of 70 individuals with high BMR (from Leka) and 70 individuals with low BMR (from Vega), at an approximately equal sex ratio – see Nafstad et al. (2023). During the winter of 2022, when the data for this thesis was collected, the population was estimated to consist of approximately 180 individuals, residing in or around five local dairy farms.

Experimental set-up

Using mist nets, we were able to capture 168 individuals (approximately 93% of the population) between January and March 2022, which were divided into experimental groups of six individuals. The experimental groups were formed based on time and area of capture, as well as sex (groups ideally had an equal sex ratio with three males and three females), in order to ensure high likelihood of individuals being from the same wild social groups and familiar with each other. Upon capture, a variety of data was collected for each individual,

including age, body mass, wing length, tarsus length, beak length, beak colour (in males), and the size and category of mask and badge (also in males), as well as a blood sample (25µl) for DNA and hematocrit measurements. All individuals were also marked with a unique ring combination, plus a PIT-tag (passive integrated responder) on one of the colour-rings to be used together with RFID (radio frequency identification) antennae for behavioural tracking (see below).

The birds were then taken to a sealed central barn on Lauvøya, where they were kept in aviaries with a temperature of 10-12°C and *ad libitum* access to food (seed mix and bread) and water. All aviaries were customized to be similar with regards to factors such as lighting (artificial lights were turned on at 07:00 and off at 21:00) and environmental enrichment, the latter of which was provided in the form of perches (branches) and nest boxes for resting and sleeping. A total of eight aviaries were built: one was used to keep the birds prior to metabolic rate measurements, four (one of which was a spare aviary) were dedicated to habituation to the new environment and the feeders (see below), one aviary area was used for testing (experimental room), one was used for catching the birds when they were to be moved, and one was dedicated to keeping the birds after the assays before they were released.

To conduct the experimental trials, we used three ‘checkerboard’ feeders, which were rectangular 1 x 1.2 meter feeder plates with 6 x 6 evenly spaced wells, surrounded by a steel wire cage. The cages had a hatch in the front that could be opened to access the feeder, as well as three holes on the left side, from which the sparrows were released/caught before/after each trial using small, wooden nestboxes (Figure 2.1). To encourage the sparrows to search for food (produce), some of the wells contained no food and were filled completely with sand (22 wells), while the remaining wells contained both food (12 g of millet divided between these wells and covered by thin layers of sand) and sand (14 wells). The baited and un-baited wells were distributed in one of 12 different patterns, chosen randomly by roll of dice. Tarps were set up between each of the three feeders to allow three trials to be conducted simultaneously with minimal disturbance from other feeders. Every trial was recorded using two cameras per feeder (GoPro[®] Hero 8) – one mounted at the top of the cage, filming directly from above, and one mounted next to the left wall filming at approximately a 45-degree angle (Figure 2.1). Around each well were RFID antennae that are able to detect the PIT-tags, allowing us to track which individuals were present at what well at what time, as well as how long they stayed there (Figure 2.2).



Figure 2.1: Experimental set-up with 'checkerboard' feeders. The feeder plates are 1x1.2 meters, with 36 evenly spaced wells.



Figure 2.2: The RFID-antennae that are connected to each well. All antennae are compatible with the PIT-tags attached to the leg rings of all individuals.

Experimental protocol

For each group, we spent one day on catching, one night (the night of the day of capture) on metabolic rate measurements, two days on habituation to the feeders, and two days on behavioural assays (see below). The birds were then held in the release aviary (no birds were in captivity longer than two weeks) to ensure good condition before release at the site of capture. When the metabolic rate measurements were completed, the birds were fitted with “backpacks” (0.3-0.4g, Figure 2.3) with one of six different QR-patterns (for identification

during video analysis and potential integration with video tracking software; Alarcón-Nieto et al., 2018). Within the habituation aviaries, we placed dummy feeders resembling the experimental feeders and filled some wells completely with sand, and some with food (seed mix) and sand. During the day on the first day of habituation, the food was left visible, while when refilling during the evening of the first and second day, the food was concealed by a thin layer of sand. On the evening before the first day of trials, the birds were weighed (with a Pesola spring balance to the nearest 0.1 g) and placed in the experimental feeders with *ad libitum* access to food (40 g millet seeds provided in the same manner as in the trials). When we conducted trials on two groups simultaneously (most days), half of one group was kept overnight in a tarp-covered dummy feeder that was also located in the experimental room.



Figure 2.3: One of the QR- 'backpacks' that was worn by the sparrows during triadic assays.

Social foraging behaviour was quantified by testing all individuals in each group against each other in triadic assays - i.e. assays were conducted using all 20 possible combinations of three individuals in each group of six (conducted in a stratified random order), meaning every individual was assayed ten times. Furthermore, to get more datapoints and better assess the repeatability of the behavioural estimates, all assays were conducted twice (one for each day of testing), meaning there were 40 assays per group (20 per individual). A total of 40 minutes were spent per trial, with 15 minutes dedicated to the actual assays and 25 minutes dedicated to cleaning the cages, replacing the wells, rearranging the birds for the next trial, and allowing the birds to rest. We were able to test two groups in a day by running 14 cycles of parallel trials (Table 2.1). After the last trial on the second day, each individual was weighed again, allowing comparison with previous measurements to estimate the effect of captivity and assays on mass.

Table 2.1: Example of a schedule for testing two groups (represented by the two colours) of six individuals (represented by the different letters, A-F and G-L) simultaneously. Developed by Corné de Groot and Rori Wijnhorst.

	Feeder 1	Feeder 2	Feeder 3	Resting
08:20	GHI	ACF	JKL	BDE
09:00	BCD	HJL	AEF	GIK
09:40	HIJ	GKL	BDE	ACF
10:20	DEF	ABC	GIK	HJL
11:00	ACD	GHJ	IKL	BEF
11:40	GJL	ABD	CEF	HIK
12:20	HIL	BEF	GJK	ACD
13:00	CDE	HIK	ABF	GJL
13:40	HJK	GIL	CDF	ABE
14:20	BCE	ADF	IJL	GHK
15:00	ABE	GIJ	HKL	CDF
15:40	GHK	ADE	BCF	IJL
16:20	IJK	BDF	GHF	ACE
17:00		ACE		

Video analysis

Using the RFID-system, we were able to infer a variety of behavioural data based upon individual positions and how they relate to the positions of their opponents (and other criteria, such as the duration of visits and whether the well was baited). However, in order to visually confirm the accuracy of this data, as well as collect additional data (e.g. aggressiveness and amount of feeding), we also analysed the video recordings. There were a total of 1140 videos, from which we selected a subset of 114 videos for analysis, divided by 6 observers (i.e., 18-19 videos per person). The videos distributed to each observer were chosen in a stratified random order based on group and day, accounting for the time of year and time of day the trials were recorded.

To perform the analyses, we used the event logging software BORIS (Behavioural Observation Research Interactive Software; Friard & Gamba, 2016), for which we created an ethogram containing all the behaviours we are interested in and what characterises them (Table 2.2). Each behaviour was assigned a keyboard shortcut. Feeding events were divided into searching and joining (here used interchangeably with producing and scrounging) because they more accurately described the observed behaviours. Behavioural events were either characterised as state events, which are mutually exclusive behavioural states (e.g. an

individual cannot be searching and joining simultaneously) that have a starting point and an ending point (a duration); or as point events, which are behaviours that are only recorded for one exact point in time and can occur at the same time as a state event (e.g. an individual can be searching and feeding simultaneously). Before each trial, a PIT-tag was tapped near a well in order to be able to synchronise the videos, as well as make sure the RFID system was running when the birds were released. This point was marked by pressing “testtag”. The start of the 15-minute section that was scored was marked by pressing “release” when the first individual was released. Each video was analysed three times, each with a different focal individual in focus (distinguished by their unique QR-backpacks). Whenever the focal landed on the board, “board” was pressed, which was a state event that lasted until the focal left the board. This event is an exception from other state events, in that it is active at the same time as other state events (i.e. it is a prerequisite for individuals to be on the board for them to search/join). Searching was scored by pressing “search” whenever the focal was arrived at an unoccupied well and lowered its beak into the sand (only the first time per arrival). The event was stopped by pressing “search” again when the focal left the well or had not put its head down within the last 5 seconds. If there were clear visual cues for seeds in the well, the behaviour would be initiated and stopped by pressing “secondary search”. Joining was scored by pressing “Join” whenever the focal sampled/tried to sample from a well (or within 2 cm of it) that another individual was already sampling from. Upon pressing join, the mediator (the individual that the focal approached) and the outcome of the event were recorded. The potential outcomes were as follows: focal leaves within 5 seconds, resident leaves within 5 seconds, both leave within 5 seconds, both stay for more than 5 seconds, and latent join. Latent join was scored when the resident had left the well no more than 3 seconds before the focal arrived. The event was stopped by pressing “join” again under the same criteria as with search/secondary search. “Revisit” was pressed when the focal either left a well (or did not put its head down for more than 5 seconds) and returned to the same well within 10 seconds without sampling from another well. The event was stopped by pressing “revisit” again under the same criteria as search/join/secondary search. Whenever the focal could be seen eating a seed (both from a well and from the board) or was clearly sieving through sand at a baited well and then stopped, “feed” was pressed. “Attack” was pressed when the focal launched a short peck or an attack that was not directly reciprocated. When the attack was directly reciprocated and ended in a fight, “aggression” was pressed. Upon pressing “aggression”, the mediator, the outcome of the event (focal leaves, resident leaves, both leave, both stay) and the duration of the event (all 0.5 second intervals between 0 and 5 seconds, with the final

interval including all values above 5 seconds) were recorded. The sparrows would sometimes show a display or flap of their wings, which was scored by pressing “display”.

Table 2.2: An ethogram containing all of the behavioural events that were scored during the video analyses of the behavioural assays, including their type and description.

Event	Type	Description
Testtag	Point	The moment the test tag is tapped on the feeder.
Release	Point	The moment the first bird is released, which indicates the start time of the 15-minute trial.
Board	State	Standing on the board.
Search	State	Sieving through sand/beak is visibly in the well.
Secondary search	State	Same criteria as search, but the well has clear visual cues for seeds.
Join	State	Joining a well or feeding from seeds around a well (<2cm) that another individual is sampling from. Includes attempts at joining. Also includes the mediator (recipient) and outcome (whether one individual leaves, both either leave or stay, or it is a latent join) of the behaviour. Score as latent join when resident left shortly (no longer than 3 seconds) before focal arrived.
Revisit	State	Leaving the well and returning to the same well within 10 seconds (without visiting another well) or stopping feeding for longer than 5 seconds, but staying at well. Includes which behaviour was resumed (Search/Join/Secondary search).
Feed	Point	Consuming one seed either from board or a well.
Attack	Point	Short peck or attack launched and not directly reciprocated.
Aggression	Point	Fighting/directly reciprocated attack initiated by the focal individual. Includes the mediator (recipient), outcome (whether one individual leaves, or both either leave or stay), and duration (any 0.5 second interval between 0 and 5 seconds, or longer than 5 seconds) of the behaviour.
Display	Point	Wing display or flapping. Count each display or flap.
Stop event	Point	Stops state events (excluding board).

In order to ensure within- and between-observer repeatability in the video analyses, reliability tests were run on a subset of nine video clips (three of each of 1, 3, and 5 minutes long) that were analysed by all observers prior to starting the actual analysis. The clips were analysed in a different random order for each observer, and all clips were analysed a total of three times, each repeat on a different day. The repeatability was deemed satisfactory if it exceeded 0.8 - 0.9. Some of the behaviours did not achieve this value during the first round of reliability

tests, so the ethogram was improved to account for this, and another round of tests was conducted. This time, only the 3-minute videos were analysed (still for three repeats), and the results showed a satisfactory repeatability for all behaviours.

Basal metabolic rate

Data on basal metabolic rate (BMR) were collected for 12 hours during the night of the day of capture (for 127 of the individuals, four of which were measured twice), starting at 19:00. Using an open flow system, metabolic rate was measured as oxygen consumption rates (VO_2), which was calculated according to Withers (2001), applying a respiratory quotient of 0.71. BMR was represented as the lowest 10-minute running average VO_2 with an associated standard error of less than 1. At this same point, the mass of each individual was estimated based on the assumption of linear weight loss between 19:00 and 07:00. For more detail, see Rønning et al. (2016). These data were collected by PhD candidate Ådne Messel Nafstad.

Statistical analyses

All statistical analyses were performed using the statistical programming language R (R Core Team, 2022).

Before performing analyses using the RFID-data, we needed to confirm whether the behaviours inferred by individual and opponent positions usefully represented the actual behaviour or not. To achieve this, Pearson correlation analyses were conducted between the RFID-data and the more accurate subset of video analysis data, revealing a correlation of 0.65 for scrounging and 0.48 for producing. The slightly low correlation for producing notably increased when only including producing events on baited wells (to 0.66). However, in order to also capture the non-successful foraging efforts, all producing events (on both baited and non-baited wells) were included when using producing for the statistical models.

The sample size for the behavioural data was 167 individuals, but only the 127 individuals that also had their BMR measured in 2022 were included in this thesis. The total number of observations available for analysis was 2437 across 955 trials.

Four mixed-effect models were created to test the hypotheses ('lmer' or 'glmer' function from the lme4 package in R; Bates et al., (2015), with either proportion scrounging, mean total scrounging, social responsiveness or social impact as the response variables. Proportion scrounging was calculated as the total number of scrounging events divided by the total number of scrounging events plus total number of producing events per individual per trial (i.e. up to 20 values per individual). Since this variable is a proportion, and so a generalised linear mixed-effect model with binomial distribution was used. Mean total scrounging was calculated as the mean number of scrounging events per individual per trial day (i.e. a total of two values per individual). To account for the non-normal distribution of this variable, it was log-transformed, which improved the normality of the distribution. Both social responsiveness and social impact were estimated using the best linear unbiased predictors (BLUPs) for each individual. These BLUPS were derived from a linear mixed-effect model with focal scrounging in each trial as the response variable and average opponent scrounging (the mean of the two opponents) in each trial as a fixed effect. The random effects included were a random intercept for focal identity with a random slope for average opponent scrounging, and a random intercept for opponent identity for each opponent. All variables were mean centered so that each random intercept represented the average scrounging behaviour of that variable when the others were at their mean. The coefficients of each random effect could then be extracted to obtain measures of responsiveness and impact. Responsiveness was represented by the coefficients of the random slope, predicting a slope of how much the scrounging behaviour of the focal was changed from its mean in response to a one standard deviation increase in opponent scrounging behaviour. Impact could then be estimated by extracting the coefficients of each opponent's random intercept, representing how much the focal scrounging deviated from its mean at the opponent's average scrounging level. Thus, impact could be measured from the perspective of the opponent as how much focal scrounging on average deviated from its mean in response to that opponent. To obtain these values for each trial day, this procedure was carried out on sub-sets of the data for each trial day. These methods and the code for conducting them were provided by PhD candidates Rori Wijnhorst and Corné de Groot.

To address the predictions of consistent individual differences in behaviour, responsiveness, and impact, repeatability estimates were calculated between trial days in separate models for all four response variables. The tests were conducted using the 'rpt'-function from the rptR package (Stoffel et al., 2017), based on generalised linear mixed models (gaussian

distribution) with trial day as a fixed effect and individual identity as a random effect. We also ran the tests without including trial day in order to assess how much day effects impact our estimates. These tests were also conducted for the BMR estimates with multiples years of data, but with year as a fixed effect instead of trial day.

For all four main models, the same set of fixed and random effects were included. Individual identity and group identity were included as random effects to estimate how much of the variance was explained by natural fluctuations in the individual and social group alone. The fixed effects included were BMR, body mass (the measurements taken on the evening prior to the first trial), sex, and trial day, as well as all two-way interactions between them. Both BMR and body mass were mean centered in order for them to be on a more similar scale to the response variables. Although not inherently part of the research question, trial day and its interactions were included because it was thought to be a potential source of variation not explained by the other effects, which was confirmed by the output and better model fit (for all models AIC decreased by > 2 ; Forstmeier & Schielzeth, 2011). In the model with proportion scrounging as the response variable, there were two significant interactions with sex. To further investigate the nature of these interactions, two additional models using sub-sets of only males or females were analysed (see Appendix A).

To assess the potential issue of multicollinearity as a result of high covariance between predictors, a Pearson correlation analysis was conducted between all predictor variables prior to creating the models (see Appendix B, Table B1).

Additional analyses were conducted to gain insight into what mass actually tells us about these individuals and how it changes with time in captivity. Mass measurements were taken at four different points in time during this experiment: at capture, at BMR, on the evening prior to the first trial, and on the evening after the second trial. From these measurements, estimates of mass change between each of them, as well as overall mass change, were created. To get a more complete picture of how these covary between each other, as well as with other variables, Pearson correlations were conducted between all mass measurements, all mass change measurements, BMR, tarsus length, wing length, and David scores (see Table B1). Tarsus length and wing length were included to see how mass correlates to other measures of body size and how this might relate to adaptive mass change. David scores are estimates of individual dominance rank, and the data for this variable was provided by

Zeiner-Henriksen, (2023), who calculated these scores for these same individuals. To test for differences in these mass and mass-change estimates between sexes, two sample t-tests were conducted. Finally, four additional mixed-effect models were created, which were identical to the main models except that the mass change between capture and the BMR measurements were used as a fixed effect instead of body mass (see Tables B2 and B3).

Results

Hypothesis 1 – Proportion scrounging and mean total scrounging

Individuals were significantly consistently different in their average behaviour between the two trial days, and the repeatability of scrounging (without any fixed effects in the model except trial day) was quite high at 0.700 (0.666 without trial day in the model) for proportion scrounging and 0.705 (0.649 without trial day in the model) for mean total scrounging. This indicates the presence of consistent, individual differences in scrounging behaviour.

Table 3.1 shows the output from two models, one with proportion scrounging and one with mean total scrounging as the response variable, testing for effects of all two-way interactions between the fixed effects of BMR, body mass, sex and trial day.

Random effects

In the model with proportion scrounging as the response variable, individual identity accounted for 0.084 of the variation, indicating the presence of some variation between individuals (Table 3.1). Group ID accounted for 0.000 of the variation, indicating little to no variation between groups. Compared to true individual repeatabilities (above), these results indicate that most of the variation attributable to individual variation can be explained by variation in just a few fixed effects reflecting certain individual phenotypic attributes (Table 3.1). In the model with mean total scrounging as the response variable, individual identity accounted for 0.096 and group ID accounted for 0.107 of the variation, indicating the presence of some variation between individuals and between groups (Table 3.1). The results also indicate that 0.098 of the variation is residual and neither explained by random effects, nor fixed effects, but contains measurement error, within individual variation and other unexplained variation.

Table 3.1: Model output of two mixed-effect models: one with proportion scrounging (left) and one with mean total scrounging (right) as response variables. For the fixed effects, estimates (log-odds for proportion scrounging), standard errors and p-values are presented. For the random effects, variances explained and standard deviations are presented. The effect sizes of the mean total scrounging estimates are presented as deviations from 1, with values higher than 1 representing positive effects and values lower than 1 representing negative effects.

Fixed effects	Proportion scrounging	Mean total scrounging
Intercept	-1.735 ± 0.134 (p < 0.001)	8.822 ± 1.091 (p < 0.001)
BMR	0.033 ± 0.006 (p < 0.001)	0.999 ± 1.004 (p = 0.780)
Body Mass	-0.264 ± 0.071 (p < 0.001)	0.976 ± 1.037 (p = 0.500)
Sex	-0.281 ± 0.197 (p = 0.153)	0.904 ± 1.091 (p = 0.240)
Trial day	-0.162 ± 0.179 (p = 0.368)	0.780 ± 1.061 (p < 0.001)
BMR × Body Mass	-0.005 ± 0.003 (p = 0.083)	1.002 ± 1.002 (p = 0.270)
BMR × Sex	-0.070 ± 0.011 (p < 0.001)	0.999 ± 1.006 (p = 0.920)
Body Mass × Sex	0.346 ± 0.092 (p < 0.001)	1.036 ± 1.053 (p = 0.490)
BMR × Trial Day	-0.009 ± 0.008 (p = 0.268)	0.996 ± 1.003 (p = 0.130)
Body Mass × Trial Day	-0.065 ± 0.082 (p = 0.426)	1.005 ± 1.028 (p = 0.870)
Sex × Trial Day	0.092 ± 0.264 (p = 0.727)	1.089 ± 1.088 (p = 0.320)
Random effects		
Focal ID	0.084 (SD = 0.289)	0.096 (SD = 0.309)
Group ID	0.000 (SD = 0.000)	0.107 (SD = 0.327)
Residual	–	0.098 (SD = 0.313)

Fixed effects

The model with proportion scrounging as the response variable revealed a highly significant negative interaction between BMR and sex. With increasing BMR, the odds of scrounging decreased significantly for males and increased significantly for females (Table 3.1, Figure 3.1a, Appendix A). There was a highly significant positive effect of BMR as a main effect, suggesting an overall trend of individuals with higher BMR to prefer scrounging, and that the positive effect for females is stronger than the negative effect for males (Table 3.1).

Furthermore, there was a highly significant positive interaction between body mass and sex. With increasing body mass, the odds of scrounging decreased significantly for females and increased non-significantly for males (Table 3.1, Figure 3.1b, Appendix A). There was a highly significant negative effect of body mass as a main effect, suggesting an overall trend of larger individuals having lower odds of scrounging, and that the negative effect for females is stronger than the positive effect for males (Table 3.1). The interaction between BMR and body mass had a weakly significant negative effect, suggesting that with increasing BMR the odds of scrounging are lower for larger individuals compared to smaller (Table 3.1). No significant effects were found for the interactions with trial day, nor for the main effects of trial day and sex.

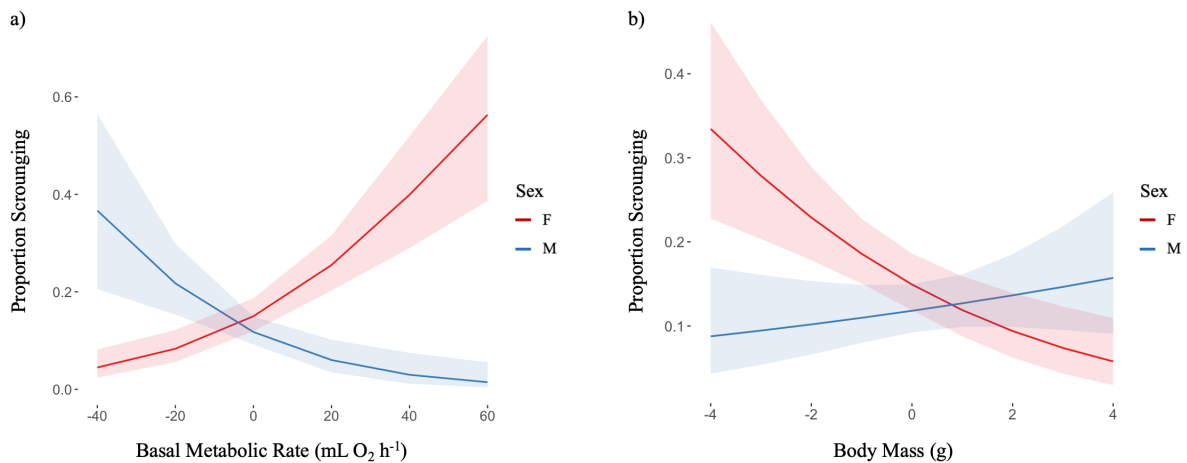


Figure 3.1: The estimated effect of a) mean centered BMR and sex, and b) mean centered body mass and sex, on proportion scrounging, with confidence intervals as shaded areas. The red line represents the effects for females (F), and the blue line represents the effects for males (M).

The model with mean total scrounging as the response variable revealed a highly significant negative effect of trial day as a main effect, suggesting an overall trend of individuals scrounging less on the second day (Table 3.1). No other significant effects were found.

Hypothesis 2 – Responsiveness

Table 3.2 shows the output from a model with social responsiveness as the response variable, testing for effects of all two-way interactions between BMR, body mass, sex and trial day. Responsiveness was measured as a slope value, and all values were unexpectedly positive, meaning that while a positive effect size here corresponds to a steeper slope and more responsiveness, a negative effect size indicates a shallower, but still positive slope and less responsiveness. Individuals were significantly different in their level of social responsiveness, and repeatability was estimated at 0.529 (0.396 without trial day in the model), which is sufficiently high to suggest the presence of consistent individual differences.

Table 3.2: Model output of a mixed-effect model with social responsiveness as the response variable. For the fixed effects, estimates, standard errors, and p-values are presented. For the random effects, variances explained and standard deviations are presented.

Fixed effects	Estimate	Standard Error	P-value
Intercept	0.575	0.0248	< 0.001
BMR	0.001	0.001	0.438
Body Mass	-2×10^{-4}	0.015	0.987
Sex	-0.040	0.035	0.257
Trial day	-0.127	0.024	< 0.001
BMR × Body Mass	0.002	0.001	0.024
BMR × Sex	-0.002	0.002	0.411
Body Mass × Sex	0.007	0.021	0.743
BMR × Trial Day	-0.001	0.001	0.345
Body Mass × Trial Day	-0.002	0.011	0.826
Sex × Trial Day	0.030	0.034	0.374
Random effects	Variance	Standard deviation	-
Focal ID	0.017	0.132	-
Group ID	0.000	0.000	-
Residual	0.016	0.125	-

Random effects

The results of the model indicate that individual identity accounted for 0.017 of the variation in social responsiveness, again indicating the presence of a small amount of variation between individuals once the fixed effects here were included in the model (Table 3.2). Group ID accounted for 0.000 of the variation, indicating little to no variation between groups (Table 3.2). The results also indicate that 0.016 of the residual variation is explained by neither the random effects, nor the fixed effects (Table 3.2). Overall, most of the variation is suggested to be explained by the fixed effects.

Fixed effects

It should be noted here that all the values for the slope (responsiveness) were unexpectedly positive (they range from 0-1.25), indicating that most individuals scrounged more in response to their opponents rather than less (as predicted by producer-scrounger scenarios). The model revealed a significant positive interaction between BMR and body mass, showing that with increasing BMR, larger individuals had a higher degree of social responsiveness whilst smaller individuals had a lower degree of responsiveness (Table 3.2, Figure 3.2). Furthermore, a highly significant effect of trial day was also revealed, indicating an overall trend of individuals being less responsive on the second trial day (Table 3.2). No other significant effects were revealed.

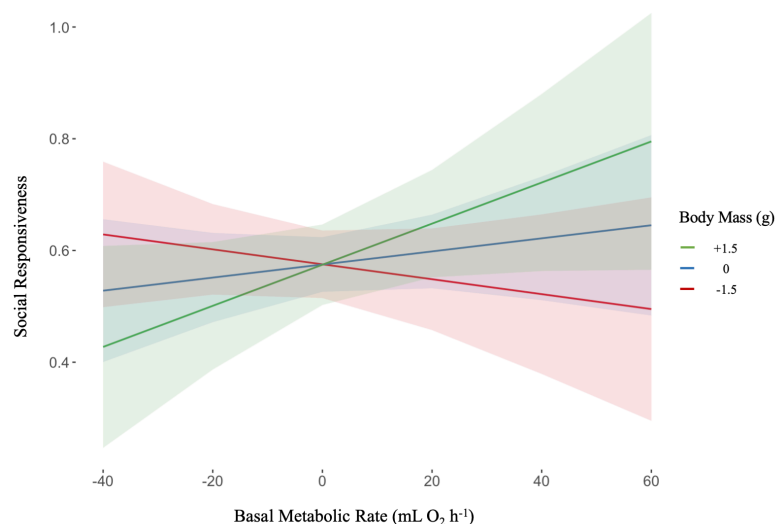


Figure 3.2: The estimated effect of mean centered BMR and mean centered body mass on social responsiveness. Three levels of body mass are represented by a red (smallest), blue (intermediate), and green (largest) line, displaying the effect of BMR for each of these body masses, with confidence intervals as shaded areas.

Hypothesis 3 – Impact

Table 3.3 shows the output from a model with social impact as the response variable, testing for effects of all two-way interactions between BMR, body mass, sex, and trial day.

Individuals were significantly different in their level of social impact, and the repeatability was estimated at 0.257 (0.000 without trial day as a fixed effect in the model), suggesting the presence of consistent, individual differences in impact.

Table 3.3: Model output of a mixed-effect model with social impact as the response variable. For the fixed effects, estimates, standard errors, and p-values are presented. For the random effects, variances explained and standard deviations are presented.

Fixed effects	Estimate	Standard Error	P-value
Intercept	0.494	0.072	< 0.001
BMR	0.005	0.004	0.180
Body Mass	-0.040	0.042	0.340
Sex	0.004	0.101	0.97
Trial day	-1.231	0.085	< 0.001
BMR × Body Mass	0.000	0.002	0.820
BMR × Sex	0.001	0.006	0.920
Body Mass × Sex	0.040	0.054	0.470
BMR × Trial Day	-0.007	0.004	0.110
Body Mass × Trial Day	0.029	0.040	0.470
Sex × Trial Day	-0.053	0.122	0.660
Random effects	Variance	Standard deviation	-
Focal ID	0.074	0.272	-
Group ID	0.001	0.034	-
Residual	0.200	0.447	-

Random effects

The results of the model indicate that individual identity accounted for 0.074 of the variation in social impact, indicating the presence of much less variation between individuals once these fixed effects were included (Table 3.3). Group ID accounted for 0.001 of the variation, indicating little variation between groups (Table 3.3). The results also indicate that 0.2 of the variation is explained by neither the random effects, nor the fixed effects, which is substantially more than in the other models (Tables 3.1, 3.2 and 3.3).

Fixed effects

The model revealed no significant effects of any of the interactions on social impact. There was a highly significant negative effect of trial day, indicating an overall trend of individuals having lower levels of impact on the second day of testing. None of the other main effects were significant (Table 3.3).

Repeatability of BMR measure

The between-year repeatability of the BMR measurements was relatively high at $R = 0.491$ (0.481 without year as a fixed effect), indicating that it is a somewhat consistent phenotype in this population.

Discussion

The aim of this study was to establish whether individuals in a population of house sparrows display repeatable differences in their average producer-scrounger behaviour, social responsiveness, and social impact (de Groot et al., 2023), and to investigate how this behavioural variation relates to their social environment. Moreover, as these traits are predicted to be affected by individual state, I tested for covariances with the state variables body size (body mass), basal metabolic rate (BMR), and sex. Specifically, I predicted that being larger and male, and having a higher BMR, would have a positive effect on scrounging levels (both mean total and proportion), a negative effect on levels of social responsiveness, and a positive effect on levels of social impact.

I found that individuals were indeed repeatable in both their producer-scrounger behaviour, social responsiveness, and social impact, supporting the prediction of consistent, inter-individual differences in foraging behaviour that are affected by the immediate social environment. BMR had a positive effect on scrounging behaviour only in females, while it had a negative effect in males. Body mass did not have a positive effect on scrounging behaviour (although there was a non-significant positive trend in males), and it had a negative effect in females. Both effects were stronger in females, leading to an overall trend of individuals with higher BMR having a higher propensity to scrounge and larger individuals having a lower propensity to scrounge. This was further indicated by a less steep positive effect of BMR with increasing body mass. The effect of BMR on social responsiveness was dependent on body mass, with larger individuals being more responsive with higher BMR and less responsive with lower BMR, and the opposite for smaller individuals.

Disturbance effects of lack of habituation

An unexpected finding from the statistical model explaining variation in social responsiveness, that should be kept in mind when interpreting these results, was that all behavioural shifts in response to opponent scrounging were positive. Producer-scrounger game theory predicts a negative frequency dependence between tactics (Barnard & Sibly, 1981; Davies et al., 2012), meaning that an increase in opponent scrounging should cause a decrease in focal scrounging, and so the observed positive social responsiveness in

scrounging behaviour might be more in line with a different type of dynamic. Furthermore, individuals were found to scrounge less and be less responsive and impactful on the second trial day. An explanation for all of this might be that the birds were not yet sufficiently habituated on the first trial day, causing them to be more careful and employ more anti-predator behaviours. A common anti-predator strategy in social species is to forage more closely together (Aplin et al., 2014; Carbone et al., 2003; Carere et al., 2009; Wilson et al., 1993), which is likely to increase the occurrence of foraging activity registered as ‘scrounging’. Although scrounging can also be conducted simultaneously with anti-predator vigilance, which should make it the preferable tactic in an environment with higher perceived predation risk (Ranta et al., 1996). Furthermore, in their dynamic state-dependent model, Rands et al. (2003) found that when foraging together in small groups, individuals would become highly synchronized in their foraging, and that this created a ‘leader-follower’ dynamic, where one individual is the ‘pace-maker’ (the ‘leader’, typically the one with lower energy reserves), who initiates the foraging, and the other uses that as a cue to join in. This dynamic provides a possible explanation for our finding of responsive shifts towards more scrounging as well, as foraging closer together should lead to more scrounging, independently of opponent tactic choice. The lower amount of scrounging, social responsiveness, and social impact on the second day further supports this explanation, since individuals would have had more time to habituate and thereby be more comfortable with foraging independently (i.e. ‘producing’), in turn resulting in fewer social interactions and perhaps more producer-scrounger-like dynamics on the second day. Therefore, these findings do not necessarily exclude the possibility that some form of the expected individual differences in behaviour, responsiveness and impact are present in our experiment. They might still be expressed in more of a ‘leader-follower’ dynamic, with responses to things such as opponent spacing and independent foraging or aggression/dominance, rather than just opponent scrounging.

Another factor that might support the presence of this suggested lack of habituation, is individual rate of mass change (gain or loss). Since both starvation risk and predation risk are affected by individual body mass, and the trade-off between foraging and vigilance/resting is affected by foraging predictability and perceived predation risk, the optimal body mass should be dependent on level of habituation, likely causing individuals to adapt their body mass thereafter (Bednekoff & Houston, 1994; Witter et al., 1995). To investigate these effects, I created four mixed-effect models similar to the main models, but with the mass

change during the first day of captivity as a fixed effect in place of body mass (see Methods; Appendix B, Tables B2 and B3). The output of these models provided little further insight. Still, the observed changes in body mass over time in captivity revealed a pattern within the population of an initial decrease, followed by an increase and then a decrease again in body mass (Figure B1). From an adaptive mass change perspective, this could be interpreted as the birds first decreasing their mass when provided with ad lib access to clearly visible food within a sheltered, (relatively) warm location (i.e. the foraging predictability was higher and the environment perhaps more familiar). Then, when moved to the more novel environment of the habituation aviaries to train with the feeder boards, their perceived uncertainty in foraging and safety increased, resulting in an increase in body mass as an insurance measure. The final decrease in body mass would then have occurred as a result of the birds becoming habituated to the experimental set-up as the trials progressed. Hence, when viewed in this context, these results support the proposition of an effect of lack of habituation being present during this experiment.

Modelling drawbacks

Before further discussing the findings of the statistical models, there are some issues that should be highlighted. The two response variables that were used to measure scrounging behaviour, proportion scrounging and mean total scrounging, provided quite different model outputs, with most effects of the model with mean total scrounging being very small and mostly non-significant, as compared to the model with proportion scrounging, where the effects were generally larger, and some were statistically significant. This makes sense, because these variables contain biologically different information. Since mean total scrounging does not consider producing events in addition to scrounging events (like proportion scrounging does), it does not necessarily serve as a good indicator of tactic-choice. That is, a high value of this variable does not equate to a preference for the scrounging-tactic, as it might just be an indication of more foraging in general (and similarly, a low value might just infer overall low levels of foraging, rather than a preference for producing). So instead, it serves as a measure of how often individuals foraged closely together and at the same well as others.

Furthermore, while proportion scrounging contains data for each individual for each trial, mean total scrounging uses the mean of all trials per individual per trial day, meaning that

some behavioural information in the form of within-individual variation is lost. This further means that the measure is more affected by outliers, whether they are biologically the case or not, and that the reported effects might be less biologically meaningful, as we are likely underestimating the amount of variance. This same issue applies to the measures of social responsiveness and social impact, which are also created based on mean values. Moreover, when using these measures in our models, we are relying on secondary statistics derived from primary statistical estimates (means), which adds additional layers of uncertainty to the analysis and makes the results less reliable and meaningful (Houslay & Wilson, 2017). The plan was initially to perform more sophisticated analyses accounting for within-individual variation in the responsiveness and impact measures, however this simplified method was applied due to time constraints. Likely due to having used only these summary measures that excluded much of the within-individual variation in the data, the effects of individual identity and group identity were very small for all models. The small effects of group identity on responsiveness and impact also make sense because they are estimated based on opponent scrounging, meaning they should capture a lot of the social environment effects. In combination with the small residual variance for all models (notably, it was quite a lot larger for the impact model, with 0.2), this suggests that most of the variation was explained by the fixed effects. Interestingly, the model with proportion scrounging, which does not use summary statistics, had similarly small random effects and residual variance, providing a more convincing argument for the variation being explained mostly by the fixed effects.

In addition, these mean values between trial days were also used in the repeatability calculations, which might have contributed to the values for proportion scrounging (0.700) and mean total scrounging (0.705) being relatively high compared with estimates found in other studies of social and non-social behaviours (Bell et al., 2009). For responsiveness and impact, the repeatability estimates were somewhat lower (0.529 for responsiveness and 0.257 for impact), but they are still large enough to suggest the presence of consistent individual differences for these variables as well. It should be noted, however, that when removing trial day as a fixed effect in the repeatability model for impact, the estimate was reduced to 0.000. This might suggest that including trial day as a fixed effect helped reveal individual consistencies that were obscured by differences between days, which is consistent with the effects found in the main model, where almost all values except for trial day were indistinguishable from zero.

Hypotheses

I will now move on to discussing the biological implications of the fixed effects in each of the models. When interpreting these results, it is important to keep in mind that there is still uncertainty regarding the relationship between metabolic rate and behaviour, and an argument can be made for both the ‘allocation’ and ‘performance’ model in relation to these findings (see Introduction; Careau et al., 2008). In addition, as previously discussed, it appears that this experiment might not have been able to cleanly create producer-scrounger dynamics, but rather that other behavioural drivers, such as leader-follower dynamics and disturbance effects of insufficient habituation in general, are at play. From this, four different scenarios can be imagined with regards to what explains the observed behaviours: (i) producer-scrounger dynamics and the allocation model; (ii) producer-scrounger dynamics and the performance model; (iii) leader-follower/disturbance effects and the allocation model; and (iv) leader-follower/disturbance effects and the performance model. Therefore, instead of discussing my results in order of my hypotheses, for clarity I will discuss them in relation to each of these four scenarios. It should be noted that the experiment was not designed to test for other dynamics than producer-scrounger, nor specifically to test for effects of BMR, and this might affect the meaningfulness of any interpretations of the statistical findings here.

Producer-scrounger dynamics and the allocation model

If we first view the results from the perspective of producer-scrounger dynamics and the allocation model, we might initially predict that larger and male individuals with higher BMR should express higher levels of scrounging (both proportion and mean total), lower levels of social responsiveness, and higher levels of social impact. In the producer-scrounger game, the scrounging tactic has been found to provide more consistent food rewards per energy spent (Barta & Giraldeau, 2000; Lendvai et al., 2004), and since larger individuals are expected to have greater competitive ability and be more dominant (Funghi et al., 2015), scrounging should be more readily available to them. This advantage of having a more independent choice of tactic further suggests that they less frequently must pay the costs of plasticity, perhaps resulting in lower levels of responsiveness and higher levels of impact. Having a higher metabolic rate (MR) entails higher energetic costs, and the allocation model suggests that individuals with higher MR have similar energy availability to those with lower MR (Careau et al., 2008). This means they have to allocate a proportionately larger amount of resources to maintaining these higher costs, in turn leaving less energy available for energy

demanding behaviours. Individuals with higher BMR might therefore be expected to have a stronger preference for the more consistent and risk-averse scrounging tactic, since they are more likely to be in a worse energetic state (be 'hungrier') and want to forage as efficiently as possible. A study by (Lendvai et al., 2004) found that house sparrows with artificially lowered energy reserves increased their use of scrounging. However, this effect was only documented very early in the morning (the first feed of the day), as predicted by the state dependent model by (Barta & Giraldeau, 2000), which suggests no further effects of hunger (energetic state) on tactic choice for most of the day, and even a preference for producing later in the foraging period. Furthermore, while scrounging is less variable in rewards compared to producing, that does not mean it is always less energetically expensive. If there are too few producers available to scrounge from (which might easily occur in this experiment with small groups of three individuals), the scrounging tactic will not be efficient, and so the hungry individuals might need to produce instead. This may be especially true when considering the potential costs of scrounging, both with regards to aggressive encounters and missed foraging opportunities while waiting for producers to succeed.

The results of this experiment provide only limited support for the predictions in this scenario. No effects were found for the model with mean total scrounging, suggesting that none of our fixed effects could sufficiently explain the variation in individual levels of scrounging. The weakly significant interaction between BMR and body mass on proportion scrounging revealed that individuals with higher BMR did indeed display a preference for scrounging, however this preference was weaker with increasing body mass, which is not what we would expect. Furthermore, there seem to be quite pronounced differences between sexes, with opposite effects of both BMR and body mass in males and females. The predicted positive effect of BMR was found in females, but not in males, and the positive effect of body mass was (non-significantly) found in males, but not in females. I included this non-significant effect because this same trend was found to be significant by Zeiner-Henriksen (2023) when analysing other aspects of this same data set but using a larger sample size regarding dominance instead of BMR.

One explanation for these sex differences might be that mass is a better indicator of competitive ability and dominance in males, while in females, the energetic aspect of body mass better predicts behaviour (i.e. their larger energetic reserves allowed them to forage independently without paying the potential costs of scrounging). So, mass might have

different implications for males and females. Males might also be larger in general, meaning the competitive aspect of size is more pronounced for them. However, my analysis revealed no sex differences ($p > 0.1$) in any of the body mass measures, apart from a small difference in the measure from the evening before the first trial (females = 29.71, males = 30.41, $p = 0.02$; Figure B1). Another explanation for these sex differences might be that females gain a disproportionate benefit from scrounging from kin. Tóth et al. (2009) found an effect of genetic relatedness on individual levels of scrounging that was dependent on both dominance and sex in house sparrows. When foraging with relatives, females would more frequently be allowed to use non-aggressive joining, and males and dominants would less frequently use aggressive and non-aggressive joining. So, while both males and females with higher BMR might prefer scrounging because of their higher energetic demands, females would more readily be able to, due to this sex-specific kin selection. Since our groups were constructed to hopefully mirror natural social groups, and our populations have displayed high levels of inbreeding (Jensen et al., 2007; Niskanen et al., 2020), it is reasonable to assume that such effects of relatedness might apply here (which will be testable when the genetic pedigree for this population is updated). Finally, the prediction of larger individuals with higher BMR having lower social responsiveness received inconclusive evidence from the model, as larger individuals were only less responsive with lower BMR, and *vice versa*.

Producer-scrounger dynamics and the performance model

If we now view the results from the perspective of producer-scrounger dynamics and the performance model, we might instead predict that individuals with higher BMR will display a lower proportion of scrounging, be more responsive, and less impactful. The performance model suggests that individuals with higher MR also have greater energy availability, due to enhanced physiological capacities and higher energy turnover resulting from larger internal organs (Careau et al., 2008; Daan et al., 1990). This means that the relative costs of having a high MR are not higher, and so these individuals can allocate more resources to energy demanding behaviours. Individuals with higher BMR might therefore display a preference for foraging behaviours that are more active and that carry higher costs and higher rewards. In the producer-scrounger game, this is most consistent with the producing tactic, since it generally requires higher levels of activity, provides higher rewards (the finder's share), and higher costs (variable rewards for the invested energy). However, as previously mentioned, the costs and benefits of both tactics can vary substantially. Since the scrounging tactic often

involves the displacement of opponents, affecting their tactic choice, individuals that display a higher propensity to scrounging should generally be more impactful and less responsive. Conversely, individuals that are more inclined to produce (the ones with higher BMR in this scenario), might then be less impactful and more responsive. Since such a preference for scrounging might be related to competitive superiority and dominance, the individuals that are more likely to produce might also tend to be smaller.

The results again provide only limited support for the predictions of this scenario as well. A lower proportion of scrounging by smaller individuals with higher BMR was only found in males, while the opposite was found in females. This opposite effect was also found in the weakly significant interaction between BMR and body mass, with smaller individuals with higher BMR displaying a higher proportion of scrounging. Interestingly, for both BMR and body mass, the effect was substantially stronger in females, perhaps indicating that this interaction effect (between BMR and body mass) is more representative of females than the population as a whole. The prediction concerning higher levels of responsiveness in individuals with higher BMR was only supported for larger individuals, which does not make complete sense with regards to our expectations of mass having a negative effect on responsiveness, regardless of other variables. This might suggest that body mass on its own is not a clear indicator of dominance in this population after all, which is supported by the very low correlations between all body mass measures and dominance ($r < 0.063$, see Table B1), as well as the differences observed between the sexes, despite small to non-existent differences in average body mass. Moreover, Araya-Ajoy et al. (2019) found that body mass was essentially equivalent to body size in this population, which is supported by the correlations between body mass and tarsus- and wing length in our experiment ($r < 0.415$ and $r < 0.246$ respectively, Table B1) being similar to those between (latent) body size and the same measures in their study. However, body mass also entails variation due to fat stores, and these individuals displayed considerable variation in body mass (Figure B1, Table B1), perhaps resulting from either adaptation to winter conditions (Brodin, 2007; Lima, 1986) or as artefacts of habituation levels (see above). If this means that body mass was not as representative of body size as thought, and body was a better indicator of dominance (e.g., through its correlation with bib size; Liker & Barta, 2001; Møller, 1987; Solberg & Ringsby, 2010), this may provide further clarification for the very low correlations between body mass and dominance.

Leader-follower dynamics/disturbance effects and the allocation model

As mentioned above, our results indicate that there might have been a disturbance effect from lack of habituation at play, where individuals forage more closely together on the first trial day as an anti-predator strategy. In this situation, everyone might prefer to stay vigilant, but some individuals must eventually be the first to turn to foraging away from the other two, resulting in a leader-follower relationship. Which individuals become the 'leaders' might be controlled by several factors, perhaps most likely energetic state (Rands et al., 2003) and/or boldness (Kurvers et al., 2010). In their model, Rands et al. (2003) suggested that the leaders should be the individuals with lower energy reserves, as the relative costs of not foraging are higher for them, and so they have greater incentive for taking larger risks to find more food. If viewed from the perspective of the allocation model, we might therefore expect that the leaders, who should have lower levels of both total and proportion scrounging, should be smaller individuals with higher BMR, due to lower fat reserves and higher energetic demands. Moreover, as it is in the nature of a leader-follower relationship that the leaders generate a behavioural response in the followers, these individuals should also have higher levels of social impact and lower levels of social responsiveness.

Once again, the results provide only incomplete support for these predictions. Smaller individuals with higher BMR displayed the predicted lower proportion of scrounging only in males, while in females and the interaction between BMR and body mass, the opposite relationship was found. The aforementioned potential effects of sex-specific kin selection as an explanation for the observed sex differences (above) might also make sense in a leader-follower setting. In their model, Koykka & Wild (2015) explored the leader-follower polymorphism in relation to dispersal behaviour in homogenous populations and found that it can be sufficiently promoted and maintained by kin selection alone, independently of individual state. This might suggest that the higher levels of joining (follower) behaviour in smaller females with higher BMR (i.e. in poorer energetic state, and likely less competitive) is the result of larger males more readily initiating leader behaviour and allowing related females to forage close to them. Furthermore, differences in reproductive strategy between the sexes might also explain the observed sex differences. Females may prioritize energy conservation in preparation for the upcoming breeding season, making them more inclined to display more reactive traits, such as shyness, neophobia and decreased superficial exploration. In their study on a naturally foraging flock of great tits (*Parus major*), Aplin et

al. (2014) found that more reactive individuals were more attracted to conspecifics (i.e. displayed more follower-like behaviour). This might apply to house sparrows where less competitive, smaller females may gain a disproportionate benefit from scrounging from kin (Tóth et al., 2009). As for the social responsiveness predictions, the interaction effect between BMR and body mass provides convincing support that smaller individuals with higher BMR are less responsive, and thus perhaps the leaders.

Leader-follower dynamics/disturbance effects and the performance model

For the final scenario, viewing this leader-follower dynamic from the perspective of the performance model, it is less clear exactly what effects we might expect. If we once again assume that the leaders have lower energy reserves, we may here expect them to be the smaller individuals with lower BMR, since a higher BMR is associated with greater energy availability (Careau et al., 2008). However, this greater energy availability is the result of a higher energy turnover and an ability to sustain more active and independent foraging, and so the energetic demands of these individuals should still be relatively higher (i.e. they might still generally have greater incentive to initiate foraging). We might therefore also expect the same relationship as with the allocation model here, with high BMR individuals being the leaders (displaying lower levels of mean total and proportion scrounging). Moreover, another mechanism that may determine which individuals become leaders is boldness, as shown in barnacle geese (*Branta leucopsis*) by Kurvers et al. (2010), and we might expect individuals with higher BMR to be bolder, due to their preference for more active and perhaps more explorative foraging (under the assumptions of the performance model). Such a behavioural syndrome between boldness and activity and superficial exploration has been found in a variety of taxa, for instance in great tits (Sih et al., 2004). Further support for the relationship between BMR and boldness can also be inferred from their correlation with dominance, aggression, and testosterone levels. Boldness has been found to be positively correlated with dominance and aggression, among others in a study on three-spined sticklebacks (Dingemanse et al., 2007), as well as various studies reviewed by Sih et al. (2004). Aggression, and its dominance implications (Liker & Barta, 2002; Riters et al., 2004), has in turn been found to be positively correlated with testosterone in a variety of bird species (Soma, 2006), which was further found to be positively correlated with BMR in a population of house sparrows (Buchanan et al., 2001; although studies on white-crowned sparrows and house sparrows have found opposing results; Buttemer et al., 2008; Wikelski et al., 1999).

Hence, leaders might tend to have higher BMR through its associations with boldness. This line of arguments is more convincing if viewed as part of a pace-of-life-syndrome, where fast-living individuals are expected to be, among other things, bolder, more aggressive, more dominant, less sociable, and have higher BMR (Réale et al., 2010b). In relation to this, we might also argue that the leaders should have higher body mass, since larger individuals are expected to be more dominant and aggressive (Funghi et al., 2015). The findings of Zeiner-Henriksen (2023) that heavier and more dominant individuals were less responsive and more impactful provides some support for this. However as mentioned above, there appears to be very little correlation between dominance and body mass in this population (Table B1).

When addressing the results in relation to this scenario, we see that it is not entirely clear what we would predict. If we first address the earliest prediction of smaller individuals with lower BMR being the leaders (lower proportion and mean total scrounging), this was supported with regards to body mass for males and BMR for females in the proportion scrounging model. The interaction effect between BMR and mass also provides an indication of smaller individuals having lower propensity to scrounge, however lower body mass had the opposite effect. Lower levels of social responsiveness for individuals with lower BMR was only supported for larger individuals and vice versa, again not clearly supporting these predictions. The alternative prediction that larger individuals with higher BMR are the leaders was supported for males with regards to BMR and for females with regards to body mass in the proportion scrounging model. The interaction effect between BMR and body mass indicates that larger individuals with higher BMR did indeed display a lower proportion of social responsiveness, supporting this prediction. The predicted lower levels of responsiveness for larger individuals with higher BMR received unclear support here as well, as they were only found for larger individuals with lower BMR and *vice versa*.

Concluding remarks on alternative scenarios

Therefore, overall, it appears that there is a lack of firm evidence for any single one of these scenarios, indicating that the discovered effects might either be better explained by some other dynamic that is not considered in this discussion, and/or that additional information is needed to clarify what the results imply. Nevertheless, from what has been discussed, I find the leader-follower dynamic with disturbance effects scenarios to be more convincing, especially when factoring in their much better correspondence with the trial day and positive

responsive shift results. So, what appears to be the most prominent social foraging dynamic is one where individuals become gradually more habituated over time, which creates a leader-follower relationship as some individuals turn to foraging ('producing') away from the group. That being said, this does not exclude the possibility that we have observed producer-scrounger dynamics here as well, as individuals may have been displaying such dynamics to an increasing extent as they became more habituated over time. Which relationship of BMR (allocation model or performance model) seems more likely within the leader-follower dynamic is not entirely clear, as the effects we might expect to see for each of them are not necessarily mutually exclusive. Additional data on body mass and BMR are therefore needed to be able to separate these and better understand what is going on. We might, for example, gain more detailed insight into mass change, vigilance and boldness during trials by looking at the amount of time individuals spent on the feeder board (rather than on the perch) and how much foraging they conducted per unit time on the board (as opposed to per trial). This is data that was collected during the experiment, but not used for this study. Further support for the proposed disturbance effects might also be uncovered by looking at data on the orientation of individuals while on the board, as we might expect less habituated individuals to stay closer to conspecifics and be more vigilant, and that they face away from their conspecifics when close together (but turning more towards each other as interindividual distance increases, as shown in starlings (*Sturnus vulgaris*) by Fernández-Juricic 2004). We might also test whether individuals were in fact grouping closer together by looking at data on the distance between individuals.

Methodological issues and future directions

This experiment and its findings carry certain limitations that should be considered when offering any interpretation of the statistical results. To begin with, it should be restated that the measures of mean total joining, social responsiveness, and social impact are all created using mean values. When using these variables in statistical models, we are essentially performing statistics on statistics, which entails several issues, such as loss of potentially interesting within-individual variation. Future studies should therefore attempt more sophisticated modelling approaches that can avoid such issues.

Perhaps the most prominent issue encountered in this experiment was that we were unable to cleanly create the producer-scrounger dynamics we were aiming for in sparrow social foraging, especially on the first trial day (above). A likely explanation for this is lack of sufficient habituation, causing a disturbance effect where individuals adapt their behaviour to a higher perceived predation risk. Future studies might therefore benefit from increasing the duration of the habituation period. Several studies have done this previously, such as (Lendvai et al., 2004, 2006), which habituated their sparrows for a minimum of one week. It should be noted, however, that due to the large amount of data required for quantifying behaviour with this approach, time constraints would in this case create a trade-off between duration of habituation and quality of behavioural estimates, as we would need to use a smaller sample size. There is also a consideration to make in relation to keeping the birds in captivity for too long, both regarding confounding effects and ethical considerations. Additionally, our sample size might already be somewhat smaller than what is ideal. A paper by Martin et al. (2011) on power analysis suggested that in order to detect significant variation in plasticity, a rule-of-thumb is to have sample sizes larger than 200 individuals. This would not be possible for with this setup, as the population in Åfjord only consisted of approximately 180 individuals at the time, and time constraints would further restrict including more individuals. However, that estimate addresses plasticity in general, while in this experiment, we specifically investigated reversible plasticity, which requires many fewer individuals to achieve sufficient power, provided there are enough repeated measures per individual (Hertel et al., 2020). Since a large number of measures were collected per individual, and the experiment was planned to be carried out across two years of data collection, this aspect of the experimental design likely does not need improving.

As discussed previously, the issue of individuals only showing positive values for responsiveness in opponent joining might not entirely exclude the possibility of social responsiveness in accordance with producer-scrounger game theory in this experiment. Future studies could benefit from looking into this data with other proxies for responsiveness, such as opponent searching, aggression, or dominance. Another factor likely to cause deviations from the expected behaviours, is that the groups used in the assays were artificially small. Triadic assays are generally not likely to represent natural groups, and this might contribute to altering individuals' behaviour from what it would be in the wild – especially when considering the proposed lack of habituation, since smaller groups provide less security. Otherwise, it should be noted that the RFID-data to some extent is confounded and

therefore not entirely accurate at inferring behaviour. It is, for example, not possible to completely separate producing from activity, superficial exploration, and habituation. Hence, future studies should emphasise calibrating the RFID data as well as possible, and perhaps create a more comprehensive data set for the video analyses by analysing more trials (although it should be noted that video analyses inherently carry certain data quality limitations as well).

Additional issues that should be emphasized here relate to BMR and how it is measured. First, while BMR and body mass did not have a very high correlation in this study ($r = 0.269$ for the measure used in the models, and $r < 0.371$ when considering all mass measures), they are generally thought to be closely correlated (Daan et al., 1990), and so looking at measures of relative BMR (e.g. mass-independent or mass-specific BMR) may help better separate these effects and provide more biologically accurate results. Furthermore, many species are known to significantly change their body mass over time, both between seasons and also within a single day (in kestrels (*Falco tinnunculus*) and blackbirds (*Turdus merula*); Dijkstra et al., 1988; Macleod et al., 2005), and the same has been shown with regards to BMR directly (in multiple species of waders; Kvist & Lindström, 2001). Therefore, it can be difficult to gain repeatable measures of BMR, and the estimates might generally become less reliable over longer time intervals. Stress from captivity can also be thought to influence individual BMR, meaning that despite being measured within the thermoneutral zone at rest, the birds might not be displaying their ‘true’ BMR. The between-year repeatability was here relatively high ($R = 0.491$) and consistent with similar findings in the literature (in multiple bird species; Nespolo & Franco, 2007; Versteegh et al., 2008), which might suggest that this is less of an issue than what was perhaps expected. To verify whether such variation in BMR across a smaller timeframe occurred, it might be interesting to take two BMR measurements for each individual during the experiment and see whether that repeatability differs significantly within and between years (this was done for only four individuals in this experiment).

Otherwise, it might also be helpful to look at MR outside the thermoneutral zone (for example at the natural ambient seasonal temperature), as it might be expected to more accurately represent MR in the wild, thus providing more direct ecological relevance. However, this would make it more difficult to remove potential behavioural influences affecting metabolism, which is problematic with regards to confounding, as we are testing its

effects on behaviour (Careau et al., 2008; Mathot & Dingemans, 2015). This issue is not solved for BMR either, as individual differences in BMR might be indirectly affected by behavioural differences, despite (and even somewhat because of) the strict conditions of the measurement (Speakman et al., 2004). One of these conditions is namely that individuals are in a post-absorptive state, and the time it takes to reach that state can vary. Individuals with higher levels of foraging might, for instance, need more time to reach this state, while other individuals might reach it more quickly and start metabolising energy stores earlier. This effect of foraging behaviour would perhaps be even more pronounced when considering the potential stress of being in captivity. RMR relaxes this assumption and might in that sense be a better alternative (Speakman et al., 2004). Furthermore, when using BMR as the only energetic measure to explain individual differences in foraging behaviour, we are essentially assuming that it serves as a good indicator of energy availability. This approach is likely not optimal, as it ignores the other contributing factors to the total energy expenditure of an individual (e.g. daily energy expenditure, DEE; Speakman, 1997). Instead, these two variables (BMR and DEE) should be considered together, since their relationship can work in several different ways (as seen with the performance model versus allocation model; Careau et al., 2008), and both are needed to determine which relationship is present (Mathot & Dingemans, 2015). It is, for example, not possible to exclude the allocation model based solely on a lack of decrease in the measured behaviour with increasing BMR, as individuals might have lowered their levels of other energy demanding traits to accommodate the observed levels of said behaviour. This would only be apparent if viewed in relation to total energy expenditure because the performance model would not predict such a clear trade-off. Therefore, the best approach for understanding how energetic constraints shape behaviour appears to be to use estimates of the slope values (with confidence intervals; Nakagawa & Cuthill, 2007) for the relationship between MR and DEE (Careau & Garland, 2012; Mathot & Dingemans, 2015).

Other interesting variables to look into for further research include data on genetic relatedness, as well as investigating social networks (Tóth et al., 2014; Wasserman & Faust, 1994). We assume that individuals caught at a similar place and time are part of the same social groups and that they have a high probability of being related. If given more time for the molecular analyses to be completed, we could have had actual data on this to provide empirical data on kin selection as part of the observed social dynamics. To better investigate the presence and effects of social networks, the experiment could be conducted using larger

groups, ideally natural ones. This might be achieved by placing experimental feeders with antennae in the environments where the populations naturally reside.

Finally, this thesis is part of a larger project conducted over several years (2 years of data collection), and the main aim of this project is not to test for effects of BMR. So, it is reasonable that some of the results of this thesis are not as clear as they might have been with a different experimental design. Furthermore, using an additional year of data from the same experimental setup and population might in itself allow for clearer and more reliable interpretations.

Conclusion

In conclusion, our findings indicate the presence of consistent individual differences in social foraging behaviour, social responsiveness and social impact (albeit less consistent for impact). This adds to the growing body of research investigating indirect genetic effects on behaviour at an individual level (Brichette et al., 2001; Santostefano et al., 2017; Wilson et al., 2009). The estimates of responsiveness and impact were statistically less sophisticated than initially planned, and we ended up using an approach in which within-individual variation in these traits was not included in the models and secondary statistical analyses were performed on primary statistical estimates. However, the results here can still be considered to have biological relevance, just with less information regarding the certainty around the effect size estimates. Furthermore, it seems that we were not able to cleanly detect any producer-scrounger dynamics in these data, as shown by a positive responsive shift in scrounging behaviour in response to opponent scrounging. This was accompanied by a decrease in the amount of scrounging, responsiveness and impact on the second day of testing. This suggests that the dominant social foraging dynamic reflected disturbance and gradual habituation over time, with individuals initially grouping together and being more alert, before some individuals eventually turned to producing away from the others, resulting in the emergence of more of a leader-follower dynamic. Then, as the birds became more habituated over time, they may have gradually turned to more producer-scrounger-like behaviour. This shift in habituation levels was therefore problematic for any hypothesis testing and data interpretation, and in the end it was not clear what theoretical frameworks best suit the findings here regarding the effects of BMR, body size (body mass) and sex on social foraging behaviour and plasticity. It is, however, evident that these variables are able to

explain a significant amount of variation in these traits (social behaviour and social plasticity), so future studies can benefit from applying a more tailored approach to clarify these effects, both with regards to study design and the sophistication of the statistical analysis.

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Appendix A – Verification of interaction effect in mixed-effect model

Table A1 shows the output of two mixed-effect models designed to test the validity of the sex-interactions found in the model with proportion scrounging as the response variable (See Results section, Table 3.1). This was achieved by running the same model on two subset data sets where data for either only males or only females are included.

Table A1: Model output of mixed-effect model with proportion scrounging as the response variable. The model was run on two subset data sets, one with only male individuals (left) and one with only female individuals (right). For the fixed effects, estimates (presented as log-odds), standard errors, and p-values are presented. For the random effects, variances explained and standard deviations are presented.

Fixed effects	Male	Female
Intercept	-2.082 ± 0.155 (p < 0.001)	-1.785 ± 0.141 (p < 0.001)
BMR	-0.049 ± 0.015 (p = 0.001)	0.036 ± 0.007 (p < 0.001)
Body Mass	0.152 ± 0.099 (p = 0.126)	-0.309 ± 0.080 (p < 0.001)
Trial day	0.062 ± 0.199 (p = 0.755)	-0.076 ± 0.187 (p = 0.683)
BMR × Body Mass	-0.007 ± 0.006 (p = 0.207)	-0.005 ± 0.004 (p = 0.216)
BMR × Trial Day	0.014 ± 0.019 (p = 0.462)	-0.014 ± 0.009 (p = 0.107)
Body Mass × Trial Day	-0.214 ± 0.125 (p = 0.088)	0.029 ± 0.110 (p = 0.793)
Random effects		
Focal ID	0.087 (SD = 0.294)	0.075 (SD = 0.274)
Group ID	0 (SD = 0)	0 (SD = 0)

Appendix B – Additional analyses exploring effects of mass change

Table B1 shows the output of a correlation analysis between 12 different variables, exploring potential indications of adaptive mass change and how it relates to other traits.

Table B1: Pearson correlations between the following measurements and estimates: BMR, body mass at capture (M1), body mass at BMR (M2), body mass evening before the first trial (M3), body mass evening after the last trial (M4), mass change between M1 and M2 (MC1), mass change between M2 and M3 (MC2), mass change between M3 and M4 (MC3), mass change between M1 and M4 (MC Total), mean tarsus length, mean wing length, and David score (an estimate of dominance rank; DS).

	BMR	M1	M2	M3	M4	MC1	MC2	MC3	MC Total	Tarsus	Wing	DS
BMR	-											
M1	0.218	-										
M2	0.371	0.662	-									
M3	0.269	0.590	0.823	-								
M4	0.199	0.520	0.756	0.735	-							
MC1	0.093	-0.639	0.154	0.067	0.091	-						
MC2	-0.161	-0.186	-0.392	0.200	-0.114	-0.157	-					
MC3	-0.089	-0.002	0.041	-0.214	0.505	0.046	-0.418	-				
MC Total	-0.059	-0.627	-0.040	0.020	0.339	0.786	0.101	0.463	-			
Tarsus	0.107	0.272	0.415	0.410	0.365	0.061	-0.064	0.007	0.026	-		
Wing	-0.043	0.131	0.132	0.246	0.147	-0.040	0.177	-0.097	-0.013	0.207	-	
DS	-0.122	0.012	-0.064	-0.048	0.012	-0.081	0.035	0.076	-0.003	0.028	0.017	-

Figure B1 illustrates the change in individual body mass across four body mass measurements, displaying how it progresses with time in captivity. It separates the sexes and illustrates a lack of any pronounced sex differences.

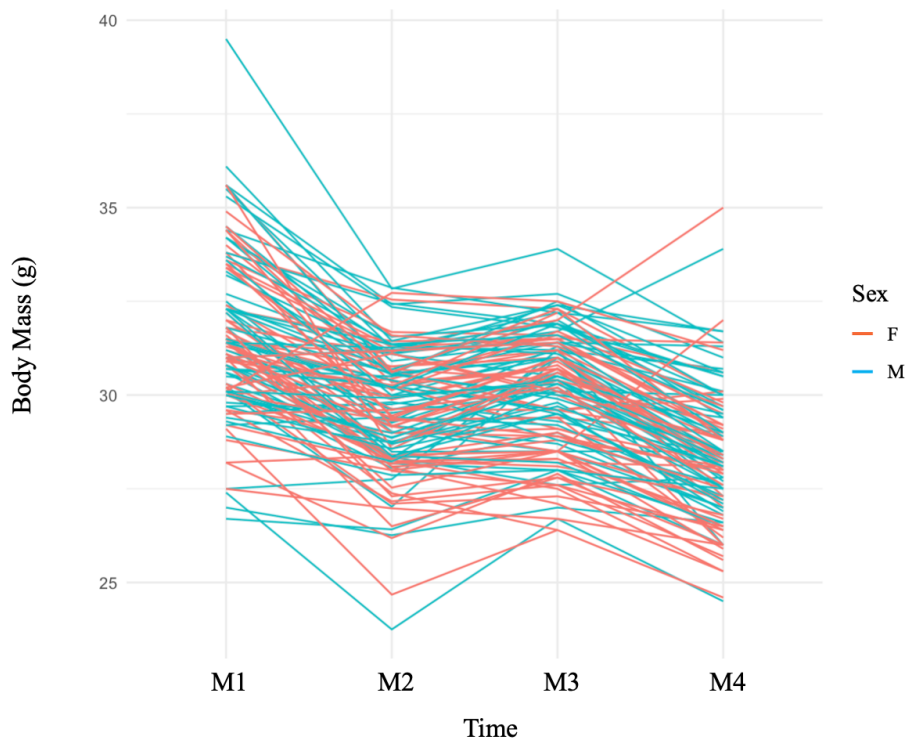


Figure B1: Individual changes in body mass over time in captivity, separated by sex. Illustrated as changes across four different measurements of body mass made in chronological order: body mass at capture (M1), body mass at BMR (M2), body mass evening before the first trial (M3), and body mass evening after the last trial (M4). The red lines represent females (F) and the turquoise line represents males (M).

The following two tables show the outputs of four mixed-effect models with proportion scrounging (Table B2), mean total scrounging (Table B2), social responsiveness (Table B3), and social impact (Table B3) as the response variables. They are identical to the models from the main analyses (Tables 3.1, 3.2, and 3.3), except that the body mass variable was replaced with the mass change estimate between the body masses measured at capture and at BMR.

Table B2: Model output of two mixed-effect models: one with proportion scrounging (left) and one with mean total scrounging (right) as response variables. For the fixed effects, estimates (log-odds for proportion scrounging), standard errors and p-values are presented. For the random effects, variances explained and standard deviations are presented. The effect sizes of the mean total scrounging estimates are presented as deviations from 1, with values higher than 1 representing positive effects and values lower than 1 representing negative effects.

Fixed effects	Proportion scrounging	Mean total scrounging
Intercept	-1.801 ± 0.195 (p < 0.001)	9.092 ± 1.130 (p < 0.001)
BMR	0.033 ± 0.008 (p < 0.001)	1.003 ± 1.005 (p = 0.581)
Mass Change	-0.091 ± 0.066 (p = 0.166)	1.010 ± 1.038 (p = 0.791)
Sex	-0.510 ± 0.268 (p = 0.057)	0.908 ± 1.142 (p = 0.467)
Trial day	-0.021 ± 0.232 (p = 0.929)	0.741 ± 1.085 (p < 0.001)
BMR × Mass Change	0.000 ± 0.002 (p = 0.717)	1.001 ± 1.001 (p = 0.094)
BMR × Sex	-0.064 ± 0.011 (p < 0.001)	1.001 ± 1.006 (p = 0.838)
Mass Change × Sex	-0.047 ± 0.087 (p = 0.592)	1.001 ± 1.050 (p = 0.999)
BMR × Trial Day	-0.011 ± 0.008 (p = 0.141)	0.996 ± 1.003 (p = 0.139)
Mass Change × Trial Day	0.050 ± 0.073 (p = 0.501)	0.974 ± 1.026 (p = 0.317)
Sex × Trial Day	-0.085 ± 0.256 (p = 0.740)	1.091 ± 1.088 (p = 0.300)
Random effects		
Focal ID	0.096 (SD = 0.309)	0.098 (SD = 0.313)
Group ID	0.000 (SD = 0.000)	0.112 (SD = 0.334)
Residual	–	0.099 (SD = 0.314)

Table B3: Model output of two mixed-effect models: one with social responsiveness (left) and one with social impact (right) as response variables. For the fixed effects, estimates, standard errors, and p-values are presented. For the random effects, variances explained and standard deviations are presented. It should be noted that the model with social responsiveness as the response variable failed to converge, making interpretations less meaningful.

Fixed effects	Responsiveness	Impact
Intercept	0.624 ± 0.038 (p < 0.001)	0.421 ± 0.108 (p < 0.001)
BMR	0.001 ± 0.002 (p = 0.472)	0.005 ± 0.005 (p = 0.282)
Mass Change	0.020 ± 0.014 (p = 0.150)	-0.035 ± 0.037 (p = 0.357)
Sex	-0.052 ± 0.052 (p = 0.318)	0.184 ± 0.140 (p = 0.191)
Trial day	-0.163 ± 0.032 (p < 0.001)	-1.278 ± 0.115 (p < 0.001)
BMR × Mass Change	0.000 ± 0.001 (p = 0.214)	0.000 ± 0.002 (p = 0.931)
BMR × Sex	0.000 ± 0.002 (p = 0.937)	0.001 ± 0.006 (p = 0.894)
Mass Change × Sex	-0.007 ± 0.019 (p = 0.733)	0.092 ± 0.049 (p = 0.063)
BMR × Trial Day	-0.001 ± 0.001 (p = 0.378)	-0.006 ± 0.004 (p = 0.123)
Mass Change × Trial Day	-0.019 ± 0.010 (p = 0.064)	-0.017 ± 0.037 (p = 0.653)
Sex × Trial Day	0.029 ± 0.033 (p = 0.375)	-0.027 ± 0.120 (p = 0.823)
Random effects		
Focal ID	0.018 (SD = 0.135)	0.071 (SD = 0.266)
Group ID	0.000 (SD = 0.000)	0.002 (SD = 0.047)
Residual	0.015 (SD = 0.123)	0.198 (SD = 0.445)



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