Hovedoppgave

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Fakultet for naturvitenskap
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Tuva Zeiner-Henriksen

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Hovedoppgave i Master of Science in Biology
Veileder: Jonathan Wright
Medveileder: Rori Wijnhorst, Corné de Groot, Ådne Messel Nafstad, Henrik Jensen
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Abstract

Animal personality is defined as consistent individual differences in average behaviour. In a social environment, such differences can be shaped by individual intrinsic attributes as well as indirect fitness effects through social interactions, and feedbacks between the two. In this study, using a producer-scrounger framework, I have assessed behavioural differences in foraging strategy, responsiveness and impact in the house sparrow (*Passer domesticus)* and their covariation with differences in dominance, body mass and sex by repeatedly observing birds in three-wise group assays. I found that birds repeatably differ in their propensity to scrounge and that an individual increase in scrounging was associated with sex-specific effects of body mass and dominance. Dominant females scrounged proportionately more, which was also true for dominant and heavy males, while heavy females scrounged less. Individuals also differed repeatably in how much they plastically adjusted their behaviour in response to differences in social contexts (social responsiveness), and heavier and more dominant males were less responsive, while females were generally more responsive than males. I also found that individuals differed in how much they impacted the behaviour of their opponents, and increased impact was associated with the same traits as reduced responsiveness. There was also substantial evidence for disturbance effects and a lack of habituation to the experimental set-up, which disrupted the expected producer-scrounger foraging dynamics. In conclusion, my results show that individual differences, responsiveness and impact in social foraging are consistent and repeatable, and associated with individual sex, dominance and body mass.

Sammendrag

Personlighet hos dyr blir definert som konsekvente individuelle forskjeller i gjennomsnittlig atferd. I et sosialt miljø kan slike forskjeller bli formet av individuelle iboende egenskaper, samt indirekte fitness-effekter som oppstår under sosiale interaksjoner og `feedback`- effekter mellom de to. Ved å gjentatte ganger observere individer i triadiske gruppe-analyser, har jeg i dette studiet undersøkt atferdsforskjeller i fôringsstrategi, responsivitet og påvirkningsevne i gråspurv (*Passer domesticus)* i en `producer-scrounger`-kontekst, og deres kovariasjon med individ-forskjeller i dominans, kroppsmasse og kjønn. Jeg fant at en individuell økning i `scrounging`-atferd var assosiert med kjønnsspesifikke effekter av kroppsmasse og dominans. Dominante hunner brukte `scrounging` proporsjonalt mer, noe som også var tilfelle for dominante og tunge hanner, mens tunge hunner brukte `scrounging` mindre. Individer varierte også repeterbart i hvor mye de justerte atferden sin plastisk i respons til ulike sosiale kontekster (sosial responsivitet), og hanner som var tyngre og mer dominante hadde lavere responsivitet, mens hunner generelt sett var mer responsive enn hanner. Jeg fant også at individer varierte i hvor mye de påvirket atferden til sine motstandere, og økt påvirkningsevne var assosiert med de samme egenskapene som redusert responsivitet. Det var også vesentlig bevis for forstyrrelseseffekter og en mangel på habituering til det eksperimentelle oppsettet, noe som forstyrret den forventede `producer-scrounger`-dynamikken. For å konkludere så viser disse resultatene at individuelle forskjeller, responsivitet og påvirkningsevne i sosial fôringsatferd er konsekvente og repeterbare, samt at de er assosiert med kjønn, dominans og kroppsmasse.

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Introduction

An increasing amount of research suggests that animals within the same population express consistent inter-individual variation in average behaviour, meaning that one individual does not express all available behavioural characters in the population ('animal personality': Dingemanse et al., 2010; Réale & Dingemanse, 2010). Additionally, such repeatable behavioural traits have been observed to covary across contexts, such as the positive correlation between exploratory behaviour and aggression ('behavioural syndromes': Sih et al., 2004; Verbeek et al., 1996). These individual differences are potentially perplexing from an adaptive perspective, where individuals within the same environment should have been subject to the same selection pressures, and are therefore expected have evolved to the same optimal and plastic levels of context-dependent behaviour (Réale & Dingemanse, 2010; Sih et al., 2004). A current consensus is lacking regarding the ultimate explanation behind these differences and how they can be selected for and be evolutionarily stable (Dall et al., 2012). However, feedback loops between factors of an individual's intrinsic and extrinsic environment and behaviours may shape adaptive individual variation (Luttbeg & Sih, 2010). Even though behaviour can be plastic, the cost-benefit trade-off of an individual's actions will be affected by variables such as condition and size, meaning that the same behaviour will likely yield different results for different individuals, and that optimal behaviour will differ inter-individually. The properties altering the cost-benefit trade-offs may refer to a number of factors, including fixed attributes (e.g. sex) or slow-changing state-variables (e.g. size, energetic state) of the individual, as well as social attributes (e.g. dominance) and properties of the social environment (e.g. traits of conspecifics). Thus, behavioural differences may arise as an adaptive outcome of consistent individual differences in any of these properties (Luttbeg & Sih, 2010; Sih et al., 2015; M. Wolf & Weissing, 2010).

When considering animals in a social environment, feedbacks may arise based on both individual properties, as well as properties of conspecifics in their social environment, as social animals will affect each other. Thus, feedback influences between interacting individuals may alter evolutionary dynamics and further contribute to the emergence of consistent individual differences (McGlothlin et al., 2010; Wolf, 2003). To date, the link between inter-individual differences in personality and social behaviour remains insufficiently explored, despite the prominence of sociality in nature (Székely et al., 2010; Webster & Ward, 2011). Assessments of animal personality have in the past been carried out in the absence of a social environment, comparing behaviour in social isolation versus in natural conditions (see Aplin et al., 2013). However, the selective environment underlying personality may be misinterpreted if the multivariate nature of focal and conspecific behavioural phenotypes and their interactions in social environments are ignored (Santostefano et al., 2016, 2017). For instance, when studying conspecific aggression in pair-wise interactions in wild-caught field crickets (*Gryllus campestris)*, Santostefano et al. (2016) found a positive correlation between the behavioural traits aggression, exploration and activity. Comparatively aggressive individuals also showed comparatively high degrees of exploration and activity in two different contexts. Furthermore, this trait correlation was linked with elicitation of aggressiveness in conspecifics, and it was also demonstrated that focal levels of aggression were plastically adjusted to inter-individual phenotypic differences in opponents. Such findings emphasize that among-individual differences in behaviour can constitute a significant effect on individual behaviour, and studies incorporating effects of interaction partners are therefore of importance.

Social interactions are abundant in nature and can be found in almost every species (Székely et al., 2010). In a social environment where individuals interact, a focal individual's fitness does not only depend upon its own phenotype in relation to the abiotic environment, but also on the phenotypes expressed in conspecifics in its social environment. In turn, the social environment is further affected by the focal individual and any change in its phenotype, meaning that if a heritable genetic basis exists for the affected traits, both the individual and the environment will be under selection with the ability to evolve (McGlothlin et al., 2010; Moore et al., 1997; Wolf, 2003). The effect that the social environment has on a focal's phenotype can be described as indirect genetic effects (IGEs) and thus differs from the more obvious direct genetic effects (DGEs) utilized in traditional evolutionary models, which describe how an individual is directly affected by its own genes. To understand the evolutionary potential of traits, a quantitative genetic approach is commonly utilized to differentiate the phenotypic variation of heritable origin, excluding nonheritable environmental variation that do not contribute to evolution. Consequently, this approach traditionally relies on the effect on trait evolution of DGEs alone. By including an additional source of phenotypic variation (i.e. in the social partner) that is in itself under selection, namely IGEs, the direction and rate of evolution on traits expressed in a social context can change (McGlothlin et al., 2010; Wolf, 2003). Thus, if positive or negative genetic correlations between DGEs and IGEs occur, the reciprocal effects arising from interactions have the potential to either accelerate or restrict evolution respectively (Bijma, 2010; McGlothlin et al., 2010). For example, Wilson et al. (2008) found that phenotypic expression of aggression in deer mice (*Peromyscus maniculatus*) depends on the genotype of the social partner and that DGEs on aggression in the focal individual positively covaried with IGEs on aggression in the opponent. This positive correlation is expected to accelerate evolution of aggression as a social trait (Moore et al., 1997; Wilson et al., 2008). Conversely, Brichette et al. (2001) found a negative covariance between DGEs and IGEs in mussel cultures (*Mytilus edulis*), where the most genetically competitive growers also inhibit growth in neighbouring conspecifics, limiting the social evolution of such competitive growth. Consequently, IGEs correlated with an individual's DGEs could alter the direction and rate of evolution on traits expressed in social behaviour, as well as non-social traits covarying with these. If the correlation is negative, IGEs could reduce the amount of available genetic variation for that respective trait that is unconstrained by additive genetic covariances, effectively halting directional selection by imposing evolutionary constraints in the sense that there is less variation for selection to act upon. This effect of IGEs on trait variance and evolutionary dynamics is potentially an important contribution to the existence and maintenance of inter-individual differences (Santostefano et al., 2017).

Since the first inclusion of game theory in evolutionary biology by Maynard Smith and Price (1973), this approach has been applied to study of adaptive social behaviours across the field of behavioural ecology (Davies et al., 2012; van den Berg & Weissing, 2015). In game theoretical models, each alternative perfectly heritable strategy is associated with different costs and benefits based on the strategies present in other members of the social group. If for example the majority of individuals in a social group choose a strategy where they never fight over resources and share ('dove'), the ones choosing a strategy where they do fight ('hawk') would have a higher payoff on average because they generally will gain the benefit of not sharing without suffer the cost of potential injury. Thus, the strategy that confers the greatest fitness will be positively or negatively frequency-dependent in the population. The model then proceeds to identify the evolutionarily stable strategy (ESS), meaning the optimal long-term strategy that can always invade against any other and such that when it is at fixation no other strategy can invade the population (Davies et al., 2012; Maynard Smith, 1986). Further, the ESS in a population can be either pure or mixed. In a pure ESS, all individuals will stick to the same fixed strategy, while in a mixed ESS individuals may deploy one of several phenotypically fixed strategies or change flexibly (i.e. conditionally) between the different strategies (Davies et al., 2012). For example, male ruffs (*Calidris pugnax*; a lekking bird) deploy one of three genetically determined mating strategies, either settling and defending territories (independents) or entering territories already settled and protected by other males (satellites) or female mimics (Lank et al., 1999). This dynamic constitutes a mixed ESS likely upheld by negative frequency-dependence (Widemo, 1998). However, such fixed mixed ESSs are rare in nature, because the short-term flexibility of phenotypic plasticity in conditional mixed ESSs means that they are more likely to maintain the population at the ESS where relative individual fitness is optimised.

A classic example of a conditional mixed ESS is the social foraging game of Producer-Scrounger, where individuals utilize one of two strategies to obtain unpredictably distributed food resources and receive pay-offs in terms of food items acquired: ‘scroungers’ join food patches already found by others, while ‘producers’ search for undiscovered food patches (Barnard & Sibly, 1981). Thus, the producers pay a cost of actively searching for food but can benefit from gaining first access to a resource (the ‘producer bonus’), while the scroungers avoid search cost by utilizing social information from successful producers. This dynamic yields negative frequency dependence, where the payoffs associated with each strategy decrease as the proportion of each strategy increases (Figure 1). Consequently, the expected ESS will be mixed and individuals should play one of the two strategies so that the average frequency of strategies in the population equals the ESS.

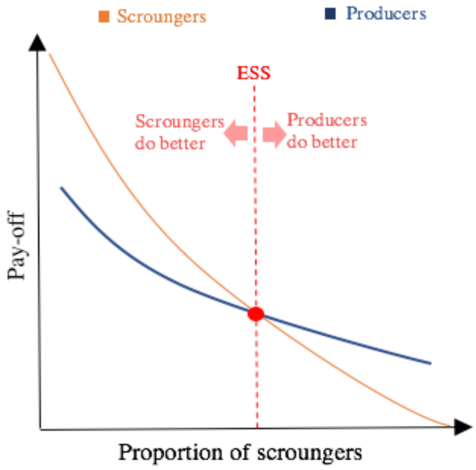


Figure 1: *Pay-off associated with producing and scrounging relative to proportion of scroungers in the population. Scroungers do better when there are proportionately more producers. Producers do better when there are proportionately more scroungers. At the ESS, each strategy has equal pay-offs and no one can do better by switching. (Figure adapted from Davies et al. (2012) and Barnard & Sibly (1981)).*

Figure 1 illustrates the classic model proposed as to how the producer-scrounger dynamic of two alternative foraging strategies can be stable and maintained in a population. In theory, individuals could either play fixed all-producer or all-scrounger strategies, or switch flexibly (i.e. conditionally) between the two, and the ESS for the population will be a certain frequency of mixed tactics (Giraldeau & Dubois, 2008). However, these models do not consider the complexity of how different types of individual should arrive at an optimal strategy, and the payoffs modelled do not depend on who is playing what strategy, for example male versus female or dominant versus subordinate (Aplin & Morand-Ferron, 2017; Giraldeau & Dubois, 2008). Thus, the pay-offs obtained by an individual may be dependent on their phenotype, meaning that strategy choice is not just determined by frequency (Giraldeau & Beauchamp, 1999). Due to inevitable inter-individual differences (e.g. genes, age, sex, energetic state), individuals may well differ consistently in what strategy they use based upon what will best maximize their fitness, which in turn will therefore be phenotype- and frequency-dependent (Giraldeau & Beauchamp, 1999; Gross, 1996) and the ESS may shift according to cost-benefit tradeoffs of the alternative strategies (Giraldeau & Dubois, 2008). Thus, if the tradeoff changes due to labile (e.g. body mass), fixed (e.g. sex) or social (e.g. dominance) individual attributes, these properties may change the ESS ratio. How the dynamics of strategies used in Producer-Scrounger games will be affected by individual difference in state, sex, dominance, etc., depend on the lability of the respective effects. More or less stable individual characteristics, such as sex and dominance rank, will impact behaviour and thus foraging strategy consistently across time and context, thus possessing the potential to induce consistent differences in behaviour and strategy. Conversely, labile characters, such as body mass and energetic state, can vary continuously, creating feedbacks between state and foraging behaviour. If these feedbacks are positive, state and behaviour may stabilize each other, further contributing to consistent individual differences (Luttbeg & Sig 2010; Wolf & Weissing, 2010).

In addition to consistent individual differences in mean levels of behaviour, individuals are expected to differ in their propensity to switch between strategies, playing more fixed or flexibly (Lendvai et al., 2006; Morand-Ferron et al., 2010), also based on individual cost/benefit-trade-offs such as differences in experience (Dubois et al., 2010). In a social environment, which is a prerequisite of the producer-scrounger dynamic, the cost versus benefit of a strategy like scrounging should also depend upon things like the dominance of any conspecifics, and thus not only the frequency at which they produce or scrounge. Hence, the cost of scrounging from an individual with low competitive ability may be lower compared to scrounging off a more superior competitor (e.g. a larger, more dominant individual). Individuals conditionally adjusting their strategy according to type of social partners may consequently do better than fixed individuals, but perhaps only if they are subordinate. However, switching conditionally upon the pay-offs is not always expected by all individuals in producer-scrounger contexts, even when the population is at the ESS. This is because more fixed strategies involving set levels of more or less producing versus scrounging, that do not pay the costs of plasticity, can invade whenever there are enough sufficiently flexible individuals adjusting to keep the social group or population at the ESS (Dubois et al. 2010; Katsnelson et al. 2011). This then creates another level of frequency-dependence, between the proportions of fixed versus conditional players. At the stable equilibrium, a variable number of players might therefore be fixed strategists maintained by the buffering frequency-dependent flexibility of the conditional players. In real producer-scrounger systems, we might therefore expect an ESS where the population involves a range of types in both their average levels of producing versus scrounging and in the flexibility or willingness to switch between producing and scrounging in response to social conditions (Afshar & Giraldeau, 2014), and such differences in strategy should correspond to individual competitive ability (i.e. dominance and perhaps energetic state as well as the opponent's competitive ability). More dominant individuals might be predicted to scrounge more, and to do so unconditionally from all other individuals. Whereas subordinates might produce more, on average, and be more responsive in switching to scrounging whenever it is likely to be more profitable (e.g. from other subordinates or kin). Dominants might therefore also have a larger 'impact' on others in terms of forcing most individuals to adjust their behaviour, but subordinates will have less 'impact' on the behaviour of the average group member.

Producing and scrounging strategies are found throughout nature in a range of behavioural contexts involving limited resources, for example in competitive foraging (e.g. Barnard & Sibly, 1981; Harten et al., 2018) and mating (e.g. Arak, 1988; Widemo, 1998) scenarios, suggesting that this is a common dynamic in wild populations. As discussed, individuals could in theory play all-producer, all-scrounger, or a mixed (conditional) strategy on average, depending upon both internal and external factors. The strategy played is expected to vary according to genetics (as assumed in ESS models), developmental environment (e.g. body size, dominance) and the current social environment (e.g. predation risk, group size, food availability and distribution, etc.: Giraldeau & Dubois, 2008; Ranta et al., 1996; Reader, 2015; Vickery et al., 1991). The source of inter-individual differences in strategic predispositions are likely a combination of genetic control and environmental assessment, based on the observation of flexible strategy use dependent on both reversible and irreversible individual and social attributes, both within and between species (Belmaker et al., 2012; Giraldeau & Dubois, 2008; Lendvai et al., 2004, 2006; Morand-Ferron et al., 2010). In the house sparrow (*Passer domesticus),* experimental evidence has shown that individuals differ both in their producer versus scrounger conditional strategy use, based on energetic state, dominance and sex (smaller females often being subordinate to larger males in winter flocks). For example, Liker and Barta (2002) found that scrounging frequencies increased with increasing dominance ranks and that most sparrows varied in what strategy they played, utilizing both foraging strategies. Similarly, Lendvai et al. (2006) found that individuals of different dominance rank reacted differently to cope with energetic stress, with dominants increasing their affinity for scrounging significantly compared to subordinates, while Lendvai et al. (2004) found strategic choice to depend on hunger level, where scrounging was used increasingly by birds with lower energy reserves at the start of the day. Additionally, Katsnelson et al. (2010) showed that foraging strategy relates to individual learning during early life, where the tendency to produce increased subsequent to positive reinforcement from a learning task in fledglings. Belmaker et al. (2012) also found a similar effect of learning in adult birds, and showed that individuals were able to learn from experience and accordingly apply the more successful strategy. Producer-Scrounger dynamics in the house sparrow may also be expected to depend on kinship, and Tóth et al. (2009) demonstrated experimentally a sex-specific inclination for males to scrounge less and be less aggressive during scrounging events from relatives, whereas females were allowed to scrounge more from relatives without the need for aggressive intrusions.

In this study, I will look at repeatable differences in individual behaviour (i.e. foraging strategy), social responsiveness (i.e. propensity to switch between foraging strategies) and social impact (i.e. effect of social partner's phenotype on the foraging strategy of others) in relation to dominance, body size and sex in semi-natural flocks of house sparrows. These variables are likely to be interdependent, and dominance is not an inherent property of the individual, but rather a social structure arising from sequential agonistic interactions between dyads (Strauss et al., 2022), and the outcome of these interactions is likely affected by phenotypic properties such as body size and sex (Bergeron et al., 2010; Chase & Seitz, 2011; Funghi et al., 2014; Lindström et al., 2005; McElligot et al., 2001). Frequently, dominance is defined by your ability to control access to resources which will be affected by your competitive ability, again affected by phenotypic traits (Bergeron et al., 2010; Chase & Seitz, 2011; Haley et al., 1994;). However, phenotypical attributes are likely not the sole contributors in dominance rank orders. Experience has been shown to play a part in the outcome of competitive interactions, and winner-loser effects may arise where experiencing a win or a loss will increase your chances of winning or losing in the future (Franz et al., 2015). In addition, social information likely plays a part in the establishment of hierarchies through eavesdropping and transitive inference: Individuals can observe others behaviour, as well as predict the likely outcome of a fight by inferring the relative strength of an individual based on their previous wins or losses, finding their place in the hierarchy while avoiding direct interaction (Grosenick et al., 2007; Olivera et al., 1998). Together, individual variation in competitive ability, winner-loser effects and social information can create hierarchies characterised by bigger or smaller asymmetries between group members (Strauss et al., 2022). These asymmetries refer to the steepness of a hierarchy, meaning how different the scores used to infer dominance are between individuals. If the hierarchy is steep and linear, contest outcomes are consistent, and the rank order is clear. In more shallow hierarchies, individuals likely have similar competitive ability and rank orders can be unclear, often resulting in a more circular hierarchy (de Vries et al., 2006). In turn, the linearity and steepness of the hierarchy can have behavioural consequences in a social context. For instance, high-cost aggression has been shown to be preferentially aimed at competitors close in rank in several species (Hobson et al., 2021) thus steeper hierarchies could result in less overall costly fights, and hierarchies could have evolved to mitigate long-term costly conflict that could be detrimental at an individual- and group level (Heitor et al., 2006; Richards, 1974).

The evolution of adaptive individual differences likely results from a multivariate selective landscape, including inter- and intra-individual state-behaviour feedbacks, social interactions and frequency-dependent selection (Sih et al., 2015; Wolf & Weissing, 2010), and these behavioural differences may be embodied in different foraging strategies and explored using the producer-scrounger game. Consequently, studying behaviour in producer-scrounger social foraging and separating individual effects may allow us to identify sources of individual variation due to the social environment, abiotic environment and genes, further enabling us to quantify individual variation and plasticity to explore its effect on fitness and thus evolution. A link between producer-scrounger strategy use and personality has previously been found in house sparrows in MSc theses by Pettersen (2017) and Mohammad (2018), where Pettersen demonstrated repeatable differences in individual strategy use and Mohammad demonstrated repeatable differences in both individual strategy use, plasticity and social impact. This study will build on this work with the aim of providing– clearer evidence for the role of inter-individual differences and sociality in evolution. This will be done in association with Prof. Niels Dingemanse and funding from the German Research Foundation (DfG) for PhD candidates Corné de Groot and Rori Wijnhorst, all from the Ludwig-Maximillian-Universität (LMU), München. This project is also part of the long-term sparrow project conducted by members of the Center of Biodiversity Dynamics (CBD) and its associates at the Norwegian University of Technology and Science.

Objectives

With the aim to contribute to the knowledge on indirect genetic effects and how sociality can shape and maintain individual differences, this study will address a number of hypotheses regarding consistency in personality, responsiveness and social impact:

Hypothesis 1: Producer-scrounging foraging strategies should be negatively frequency dependent, but the relative costs and benefits of these two social foraging tactics will vary between individuals based on sex, body size and social dominance.

Predictions:
1a) Sparrows will show repeatable individual differences in their average proportion of producing versus scrounging (Figure 2).
1b) Males and larger, more dominant individuals will show proportionately more scrounging on average relative to smaller, female and more subordinate individuals that should proportionately produce more.

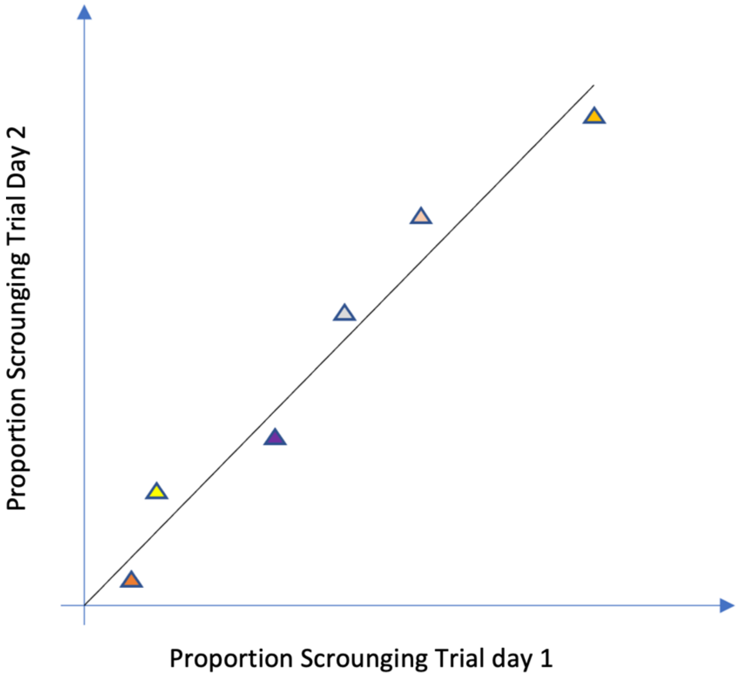


Figure 2: *Predicted repeatabilities for proportion scrounging per individual across the two trial days. Each datapoint and colour represents a different individual. (Figure adapted from Pettersen (2017)).*

Hypothesis 2: Conditional mixed producer-scrounger strategies require individual responsiveness to social cues (e.g. the proportion of producers versus scroungers, or the relative pay-offs from the two tactics), but the relative costs and benefits of switching between producing and scrounging will be based on sex, body size and dominance, resulting in different individuals showing more or less fixed versus conditional producing versus scrounging.

Predictions:
2a) Sparrows will show repeatable individual differences in their level of social responsiveness in switching between producing versus scrounging according to the social context (Figure 3).
2b) Males and larger and more dominant individuals will be more fixed and show less social responsiveness in switching between producing versus scrounging as compared to more socially responsive smaller, female and more subordinate individuals.

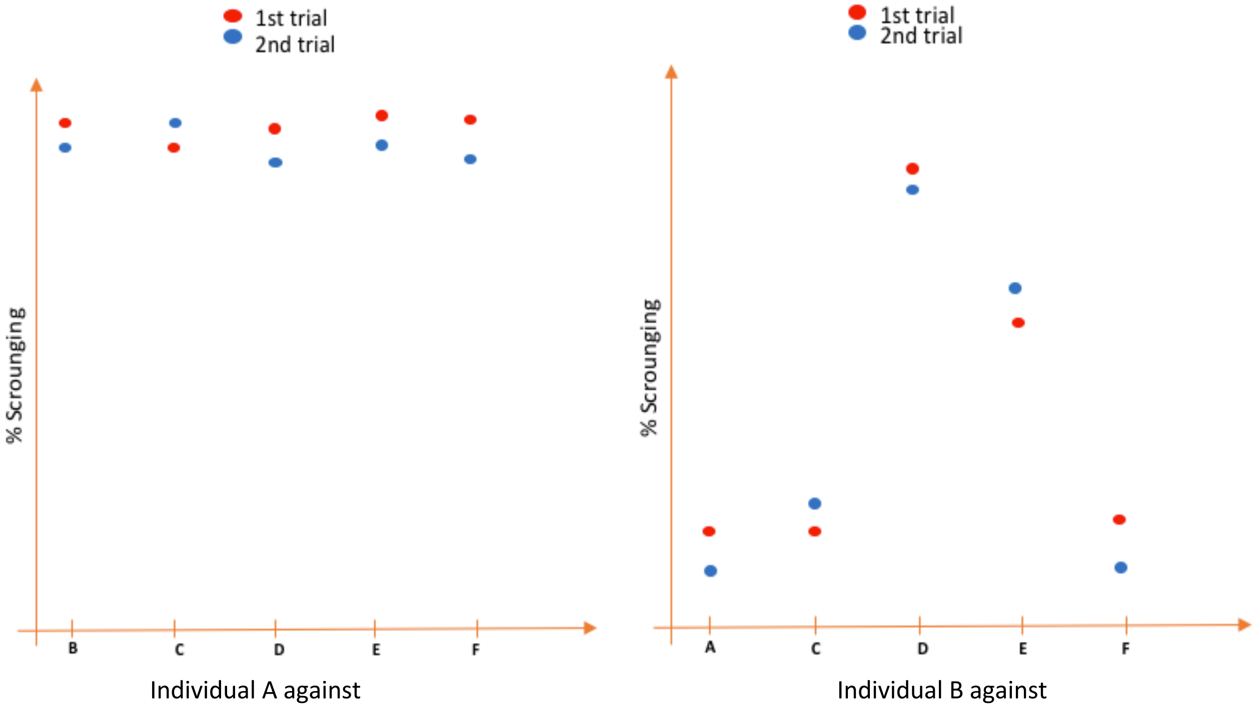


Figure 3: *Predicted patterns for individual differences in responsiveness. The X-axis represents the social environment with different individuals, while the Y-axis represents proportion scrounging by the focal individual in two different trials. Individual A has a consistently high level of scrounging, while individual B consistently adjusts its proportion of scrounging in different social environments, meaning that A is not responding to its social partners, while B is. (Figure adapted from Pettersen (2017)).*

Hypothesis 3: Individual responsiveness in mixed producer-scrounger strategies should be conditional on who in the foraging group is doing the producing versus scrounging, because the relative costs and benefits of these two tactics will depend upon the social partner's sex, body size and dominance, resulting in different individuals having more or less of an impact on the changes between producing versus scrounging by others in the flock (Figure 4).

Predictions:

3a) Sparrows will show repeatable individual differences in their social impact on the producing versus scrounging tactic choices of others.

3b) Males and larger and more dominant individuals will have a greater social impact on the producing versus scrounging tactic choice of others compared to smaller, female and more subordinate individuals

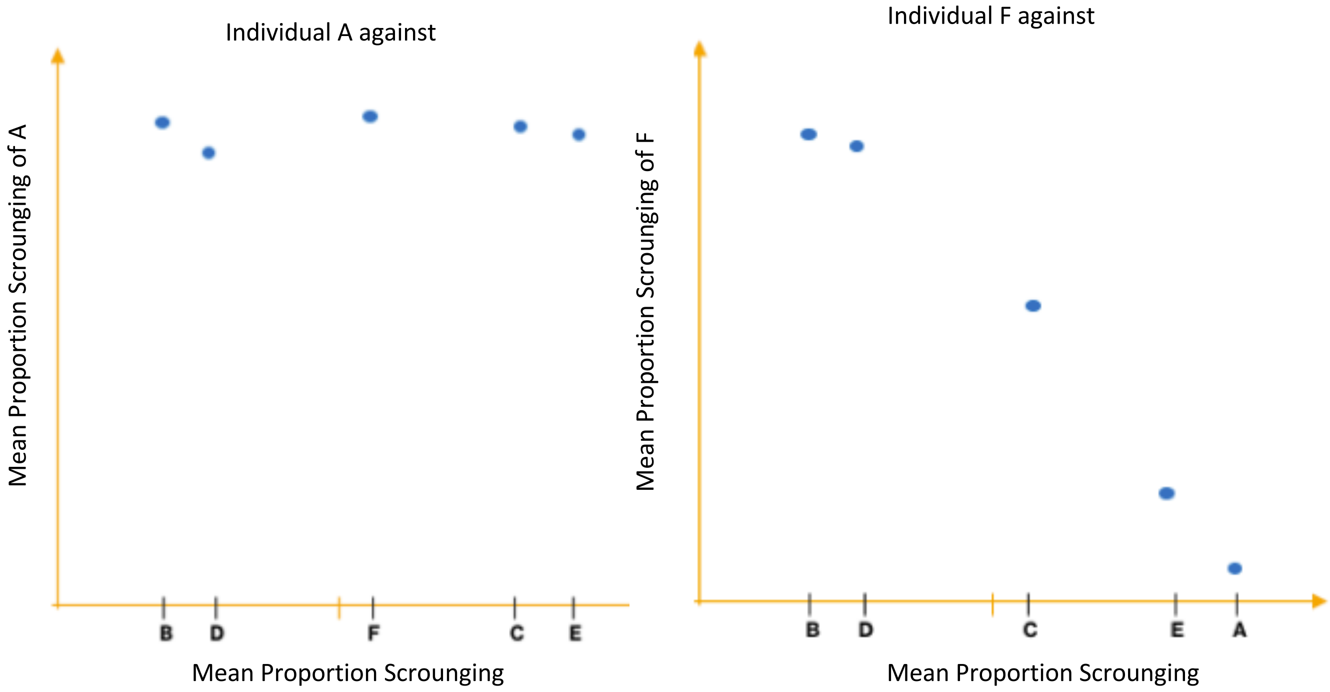


Figure 4: *Predicted responses of a focal individual to social partners with different social impact. The X-axis represents the social environment and the proportion scrounging of each social partner. The Y-axis represents mean proportion scrounging of the focal individual. Indivdiual A consistently has a high scrounging-proportion and is unresponsive. Further, the scrounging level of individual A has the larger impact on the scrouging behaviour of individual F, as seen from how F's scrounging proportion lowers in response to individual A. (Figure adapted from Pettersen (2017)).*

Methods

This study was conducted on natural flocks of the house sparrow (*Passer domesticus),* a small passerine bird. The house sparrow is behaviourally flexible and highly abundant, and its social nature and producer-scrounger foraging dynamics makes it a fitting model species for the research in question. The specific population of sparrows used in this study was established in 2012 but is also part of a large longitudinal project under the Centre of Biodiversity Dynamics (CBD), where various data have been gathered on genetics, physiology, morphology and demographics for almost 30 years (Jensen et al., 2004, 2007, 2013; Nossen et al., 2016; Ringsby et al., 2006; Rønning et al., 2016).

Study Location and Set-up

The experiment was conducted on Lauvøya with populations from the surrounding area, on the northwest coast of Trøndelag in central Norway (Figure 5) from January 22nd to March 9th 2022 to avoid the breeding season and allow for easier bird catching. The sparrow population in this area is largely associated with the local dairy farms and consists of approximately 170-200 individuals of which 168 were captured and used in the study. The study set-up was constructed inside an unused barn in which we put up experimental rooms with natural enrichment, perches and bird boxes. We constructed 4 habituation and training rooms with dummy checkerboard feeders, 1 catching aviary, 1 experimental room and 1 large release aviary (Figure 6).

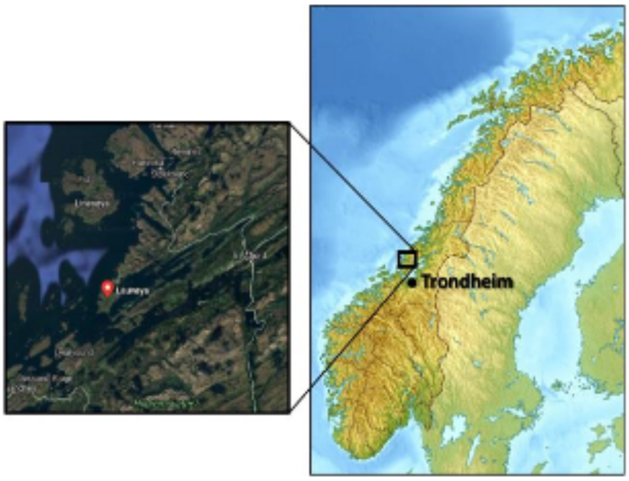


Figure 5: *Map of the study location, Lauvøya.*

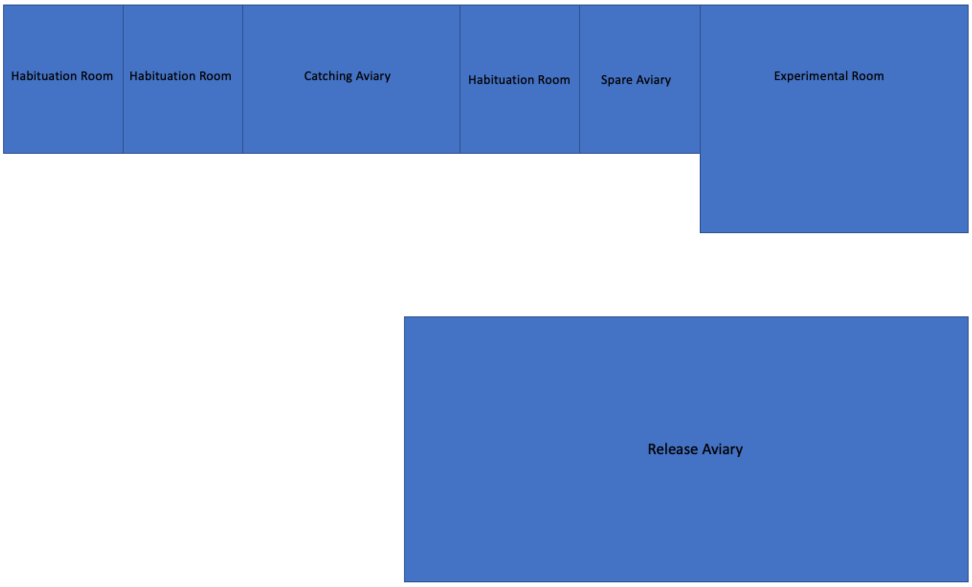


Figure 6: *Room setup and organisation.*

The birds were captured using mist nets at 5 different farms. At capture, before being used in any procedures, all birds were banded with an alphanumerical ring, fitted with a PIT-tag (passive integrated responder) on one tarsus, and sampled for blood (25 µL) by brachial venipuncture. Their resting metabolic rate (RMR) was measured using an open flow respiratory system (Rønning et al., 2016) as part of a project conducted by PhD candidate Ådne Messel Nafstad. Simultaneously with the blood sampling and ringing, characteristics such as sex, age, body mass, bib size (for males), beak depth and length, tarsus length (to the nearest 0.01 mm) and wing length (to the nearest mm) was measured as part of the longitudinal CBD house sparrow project. After capture the birds were divided into artificial groups of 6 based on adjacent capture times and more or less even sex ratios. They were then housed in the aviaries in the central barn (Figure 2) at 10-12 °C with *ad libitum* food and water access. All individuals stayed in their respective groups until the end of their trials and each group was kept in the barn for a period of minimum 5 and maximum 14 days. During this period they were exposed to RMR measurements (1 night), habituation (2 days) and testing (2 days). Lastly, they were put in a release aviary for some time to ensure good state before they were released at the site of capture.

Before starting the experiment, each bird was fitted with backpacks with visually distinguishable QR-codes (Figure 5) to aid tracking and identification during video analysis before they underwent a habituation and training period. On the first training day, a chequerboard feeder plate was placed with exposed food in wells, so that the birds would habituate to the wells and the feeder plate itself. In the afternoon of the first day, the food in the wells was covered with sand, so the birds would habituate to search the wells for food throughout the second training day. All rooms were swept and fitted with new food (*ad libitum* access to seed mix and bread) and water every night. The lights were turned off at 22:00 and turned on at 08:00 every day to keep a diurnal rhythm. On the night before the start of the trial, the birds were captured in the catching aviary using mist nets before they were weighed and then placed in the specifically designed trial feeders in the experimental room overnight (Figure 7). The trials would start the following morning at approximately 08:20 after encouraging the birds into nestboxes fitted on the feeders and preparing the feeders for trials.

The experiment was conducted on a chequerboard feeder plate consisting of 6 x 6 equally spaced wells on 1*1.2 m. feeder plates within wire cages (Figures 7 & 8). The wells were filled with either just sand (22 wells), or a mixture of sand and seeds (14 wells, 12 g. millet), so that the food was limited and randomly spatially distributed, to encourage the need for ‘producer’ searching. All the wells were filled with the same total volume and the wells containing seeds were topped off with sand so that they were indistinguishable from the other unfilled wells. Each well was fitted with four RFID (Radio Frequency Identification) antennae to automatically track and identify each bird by their PIT tag. In total, we used three of these feeders, visually separated, enabling three assays to be performed at a time (Table 2). Each feeder was equipped with two GoPro® Hero 8 cameras (linear view, 1080p, 24fps) at different angles; one at the top of the feeder and one on the left side.

Figure 7: *Chequerboard feeder plates used in the behavioural assays, with the small wooden nestboxes in the top left part of the cage, and perches and ad libitum water in the red pot on the right.*

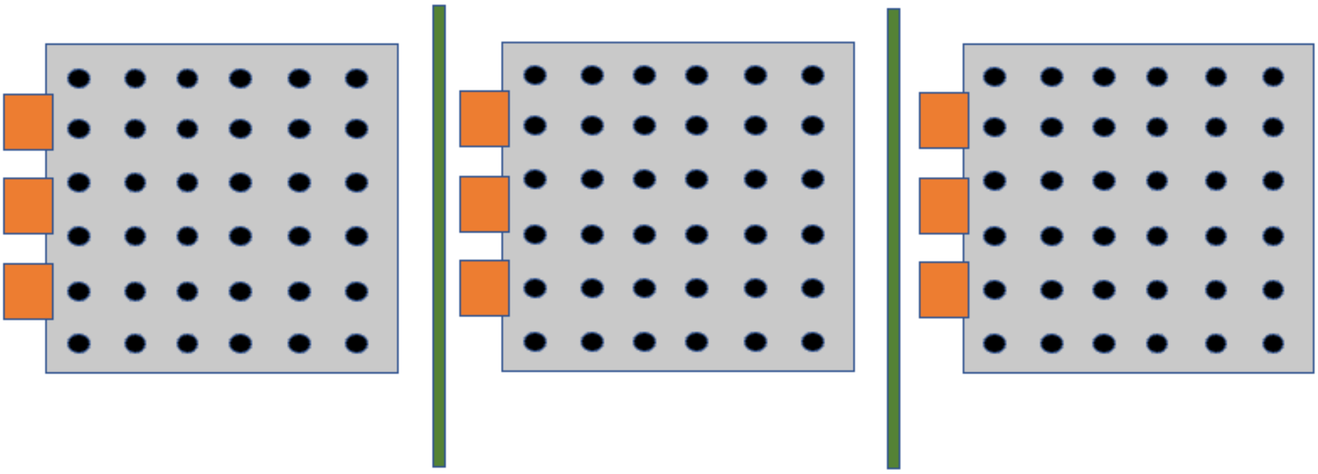
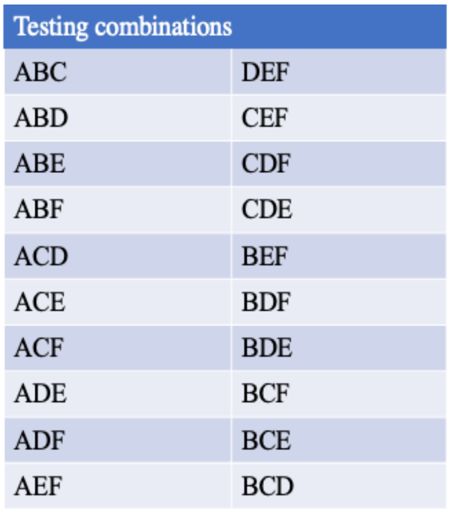


***Figure 8:** Organisation of the parallel feeders. Orange squares represent the fitted nestboxes.*

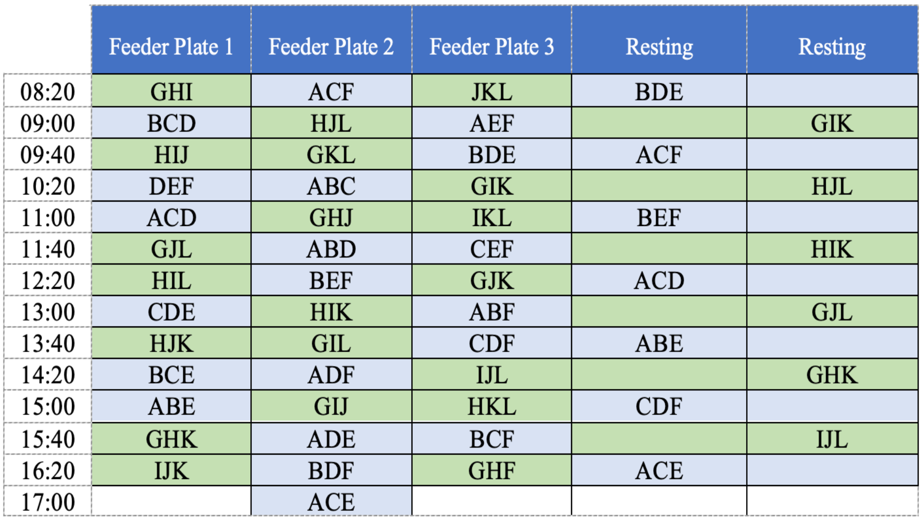
To quantify individual consistency, social responsiveness and impact in producer-scrounger behaviour (see Introduction), individuals were assayed with each other in the feeders (Figure 7) while being tracked and filmed. By manipulating who interacts with whom, the birds were exposed to different social environments and the effect of different triadic interactions could be measured. As portrayed in Tables 1 and 2, two groups of 6 were kept and tested in parallel on three feeders (Figure 8): Three individuals from the same group were tested at a time, and all possible combinations of individuals were assayed (20 combinations – Table 1), meaning that each bird was assayed 10 times per day. This was done for every group over two consecutive days, so that each group combination was assayed twice as a repeated measure. Each separate assay was conducted in 40-minute cycles, which included 15-minute trials and 25-minute rest (14 cycles per day). Between each trial, all feeders were cleaned and provided with newly filled wells according to different predetermined random patterns that were randomly chosen by rolling dice. The composition of birds in each feeder was changed according to an order randomly decided for both days. To start the trials, observers would enter the experimental room after the end of the resting period, start the cameras and then release the birds from the nestboxes before closing up the room and setting a 15-minute timer. At the end of each trial, observers would enter the experimental room after the 15-minute trial period, turn off the cameras and then encourage the birds into the nestboxes to start the 25-minute resting period. To account for differences in state (i.e. within-individual variation in body mass, as a proxy for fat reserves), all individuals were weighed before and after the trials (to the nearest 0.1 g) using a pesola balance.

Table 1: *All combinations of individuals assayed within groups (Group: ABCDEF).*



Testing combinations	
ABC	DEF
ABD	CEF
ABE	CDF
ABF	CDE
ACD	BEF
ACE	BDF
ACF	BDE
ADE	BCF
ADF	BCE
AEF	BCD

Table 2: Schedule and layout for the behavioural assays describing how the three feeders were used to test two groups in parallel. The two different colours portray two different groups (A-F and G-L; scheme developed by Corné de Groot and Rori Wijnhorst).

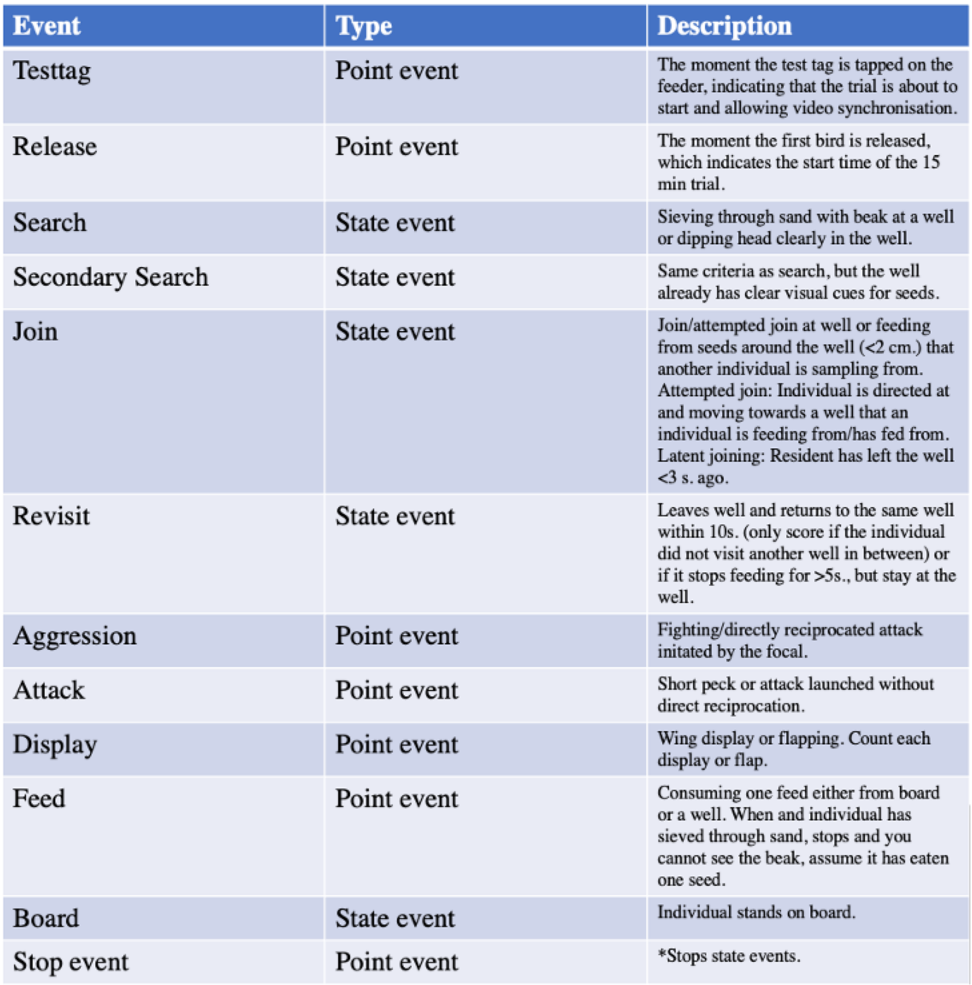


	Feeder Plate 1	Feeder Plate 2	Feeder Plate 3	Resting	Resting
08:20	GHI	ACF	JKL	BDE	
09:00	BCD	HJL	AEF		GIK
09:40	HIJ	GKL	BDE	ACF	
10:20	DEF	ABC	GIK		HJL
11:00	ACD	GHJ	IKL	BEF	
11:40	GJL	ABD	CEF		HIK
12:20	HIL	BEF	GJK	ACD	
13:00	CDE	HIK	ABF		GJL
13:40	HJK	GIL	CDF	ABE	
14:20	BCE	ADF	IJL		GHK
15:00	ABE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

Video analyses

During the experiment all trials were filmed using the aforementioned GoPro cameras. During trials, all the cameras were connected to power banks to avoid flat batteries, and the videos were imported to external hard disks every night, together with the bird position data obtained from the RFID trackers. To extract data from the videos, they were analysed manually by 6 observers according to a specialized ethogram (Table 3). Due to time constraints, not all of the videos were analysed, but a subset was randomly assigned to each observer. This subset was chosen according to a random stratified design: they were spaced out all through the total duration of the experiment so that every group of birds was repeatedly sampled on two consecutive days, 2 trials in day 1 and 2 trials in day 2. This way, we avoided confounding by season and time-of-day effects, and we get at least one repeated measure per individual and group. For this, an ethogram (Table 3) was specifically designed to extract the necessary variables. Subsequently, reliability tests and optimization of the ethogram were performed. Between- and within-observer reliability was determined based on all observers scoring the same set of 9 video clips until a repeatability of above 0.9 was reached.

Table 3: *Ethogram explaining all variables recorded during the video analyses.*



Event	Type	Description
Testtag	Point event	The moment the test tag is tapped on the feeder, indicating that the trial is about to start and allowing video synchronisation.
Release	Point event	The moment the first bird is released, which indicates the start time of the 15 min trial.
Search	State event	Sieving through sand with beak at a well or dipping head clearly in the well.
Secondary Search	State event	Same criteria as search, but the well already has clear visual cues for seeds.
Join	State event	Join/attempted join at well or feeding from seeds around the well (<2 cm.) that another individual is sampling from. Attempted join: Individual is directed at and moving towards a well that an individual is feeding from/has fed from. Latent joining: Resident has left the well <3 s. ago.
Revisit	State event	Leaves well and returns to the same well within 10s. (only score if the individual did not visit another well in between) or if it stops feeding for >5s., but stay at the well.
Aggression	Point event	Fighting/directly reciprocated attack initated by the focal.
Attack	Point event	Short peck or attack launched without direct reciprocation.
Display	Point event	Wing display or flapping. Count each display or flap.
Feed	Point event	Consuming one feed either from board or a well. When and individual has sieved through sand, stops and you cannot see the beak, assume it has eaten one seed.
Board	State event	Individual stands on board.
Stop event	Point event	*Stops state events.

Figure 9: *Fitted backpack with specific QR pattern.*

For video analysis, we used Behavioral Observation Research Interactive Software (BORIS) (Friard & Gamba, 2016). The main variables extracted from the videos were 'searching'(here used interchangeably with producing), 'joining' (here used interchangeably with scrounging) and 'aggressive' behaviour (Table 3). In addition, number of 'feeds' and presence duration on the feeder plate was recorded. The observers were able to keep track of the identity of the birds using the QR codes on their backs, which could be further confirmed by checking the RFID tracking data. The data was extracted as follows: all videos were analysed three times where a new focal individual, identified by its backpack QR pattern (Figure 9) was specified and followed for each round. The events recorded were either ‘state events’ or ‘point events’. State events were ongoing and had a duration, and they excluded all other state events. For example, ‘searching’ as a state event excluded ‘joining’ as a state event, since these cannot happen at the same time. Point events on the other hand happen at a single point in time and can happen on top of state events. For example, a ‘display’ (point event) can happen within a ‘join’ (state event). Before recording any other events, ‘board’ was pressed to record presence on the feeder and would be an ongoing, non-exclusive, state event for everything happening on the feeder. All other variables were recorded according to the descriptions in the ethogram (Table 3).

Recording of both ‘joining’, ‘aggression’ and ‘attack’ behaviours included several levels. For all of them, the mediator of the behaviour was specified, namely what individual the behaviour was aimed at (Figures 10, 12 & 13). For both ‘join’ and ‘aggression’, the outcome of the behaviour was also recorded (Figures 10 & 12), and for ‘aggression’ the duration was scored according to the closest 0.5 seconds (Figure 10). The ‘revisit’ behaviour was also scored with one additional level, namely what behaviour the focal individual had initially used to obtain the well it was revisiting (‘join’ or ‘search’, Figure 11).

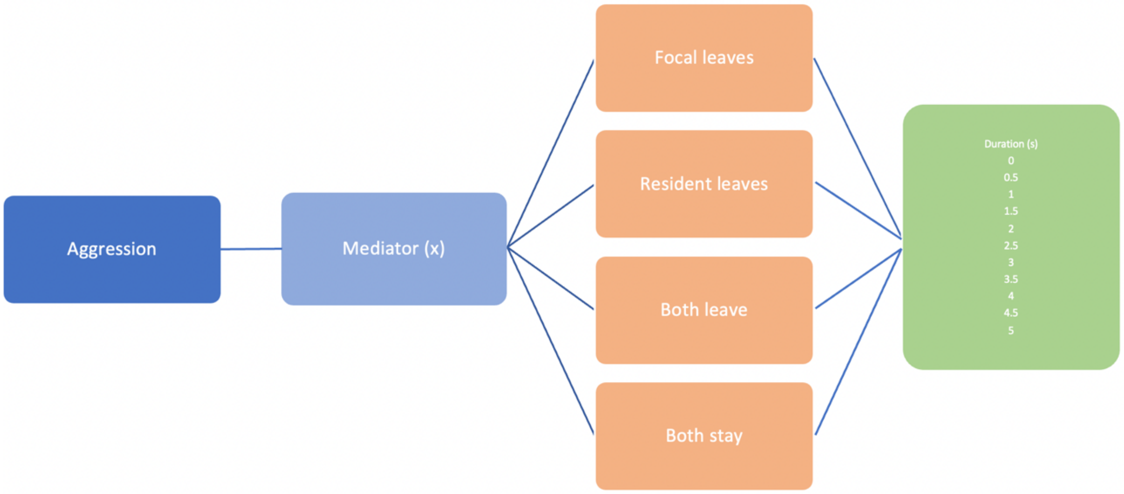


Figure 10: *Levels included in the “aggression” state event.*

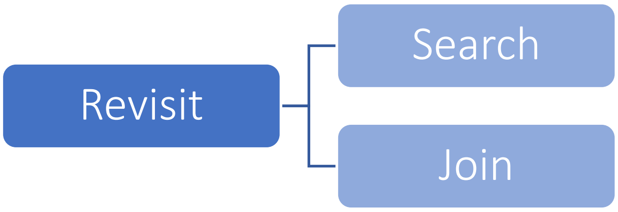


Figure 11: *Levels included in the “revisit” state event.*

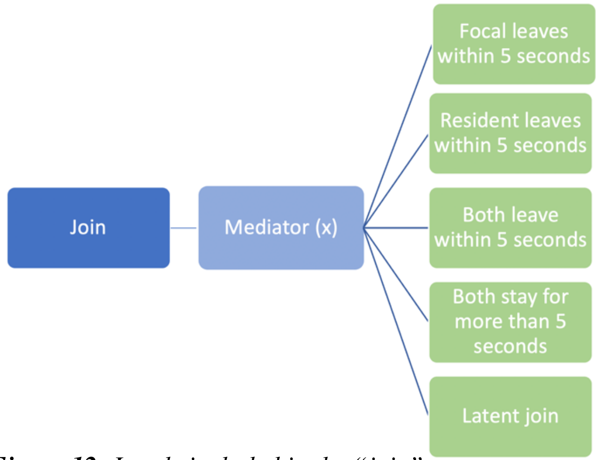


***Figure 12:** Levels included in the "join" state event.*

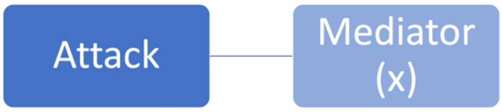


***Figure 13:** Levels included in the "attack" point event.*

RFID Data

In the subset of videos analysed by eye, all individuals were measured in two trials on different days, meaning one repeat per individual. In the data gathered from the RFID, all trials were used, meaning 10 repeats per day and 20 repeats in total per individual (note that if an individual did not land on the feeder plate for one or more trials, it has not been tracked, thus some individuals had slightly fewer repeats). For feeding behaviours, producing and scrounging measures could be obtained from the trackers by registering when one individual was recorded by a well followed by another bird recorded at that the same well. What individual was displaced in the joining interaction could be measured by the trackers by recording which individual was first registered at another well following the join.

Producing and scrounging measures were obtained from the RFID data and then optimised based upon the more precise measures obtained from the video analysis (sample sizes for each provided in Table 4). In the final data sets, scrounging in the RFID and video analysis data were correlated by a Pearson correlation of 0.65, while producing was correlated by a Pearson correlation of 0.48, mainly because measures of producing at unbaited wells (i.e. wells not containing food) contained a lot of noise (producing at baited wells alone had a Pearson correlation of 0.66). Even so, total producing efforts, including events at both baited and unbaited wells, were used as a proxy for producing in the further analysis to match the proxy for scrounging that includes both successful and unsuccessful events. For the other foraging behaviours, such as secondary searches, a reliable measure could not be obtained from the RFID trackers.

Table 4: *Sample size for individuals and trials, and occurrence of foraging events in the full RFID dataset versus the subset analysed by video. Pearson correlations between the two foraging measures in each dataset is provided.*

	RFID Data	**Video Subset**	**Correlation**
Individuals	168	158	-
Trials	1140	112	-
Producing	68856	2548	0.48
Scrounging	29067	1795	0.65

Measuring Dominance

Within groups, David Scores (DS) (Gammel et al., 2003) were calculated for each individual to infer dominance hierarchies. David Scores are calculated based on win matrices according to the formula:

$$DS = w + w_2 - l - l_2 \ ,$$

where w and w_2 are the wins and the weighted wins of the focal individual, while l and l_2 are the losses and the weighted losses of the focal individual (See Table 5 for calculation). By using this method, we can consider the weighted wins and losses of each individual, meaning that individuals get a higher score by displacing another individual that proportionately wins a lot than it does by displacing an individual that proportionately loses a lot. By considering weighted wins and losses, disproportionately lowering or increasing scores based on single wins or losses is avoided. For example, if relatively unsuccessful or successful individuals win or lose against relatively successful or unsuccessful individuals respectively, you avoid illogical hierarchies where the dominance relationships are confounded by single dyadic deviations from the main dominance direction (Gammel et al., 2003).

Table 5: Calculation of David Scores according to a 6*6 example matrix. Rows indicate wins and columns indicate losses. For each cell and each dyad, the integer numbers indicate number of wins while italics indicate proportion of wins. w equals the summed proportion of wins for the row individual (e.g. w for individual A = (0.00+0.75+0.50+0.00+0.20 = 1.45), while w_2 equals the sum of weighted proportion of wins (eg.: w_2 for individual A = (0.00*2.73)+(0.75*2.27)+(0.50*2.3)+(0.00*1.66)+(0.20*2.58) =3.37). l and l_2 are calculated in the same way, but horizontally for column individuals. Table adapted from Gammel et al. (2003).

	A	B	C	D	E	F	w	w_2	DS
A	–	**0**(*0.00*)	**3**(*0.75*)	**2**(*0.50*)	**0**(*0.00*)	**1**(*0.20*)	1.45	3.37	-3.16
B	**3**(*1.00*)	–	**2**(*0.40*)	**0** (*0.00*)	**1**(*0.33*)	**2**(*1.00*)	2.73	5,49	0.08
C	**1**(*0.25*)	**3**(*0.60*)	–	**1**(*0.20*)	**1**(*1.00*)	**2**(*0.22*)	2.27	4.69	-1.85
D	**2**(*0.50*)	**1**(*1.00*)	**4**(*0.80*)	–	**0**(*0.00*)	**0**(*0.00*)	2.3	5.27	-0.7
E	**0**(*0.00*)	**2**(*0.66*)	**0**(*0.00*)	**3**(*1.00*)	–	**0**(*0.00*)	1.66	4.10	-1.47
F	**4**(*0.80*)	**0**(*0.00*)	**7**(*0.78*)	**3**(*1.00*)	**2**(*1.00*)	–	2.58	6.89	4.68
l	2.55	2.26	2.73	2.7	2.33	1.42			
l_2	5.43	5.88	6.08	5.57	4.90	3.37			

Four different dominance hierarchies were calculated based on different displacement data: (a) aggressive interactions from the video analysis; (b) join interactions from the video analysis; (c) join interactions from a subset of the RFID data corresponding to the trials from the video analysis; and (d) join interactions from the RFID dataset containing all trials. In all of them, wins and losses were classified as obtaining or losing a resource respectively, which in this case would correspond to staying at or leaving a well. Lastly, the steepness of each hierarchy was examined, both within and between groups and between sexes. In steep hierarchies, each individual is further apart in terms of their dominance scores, meaning that there will be a greater distance from the most dominant to least dominant bird than in flat hierarchies. The steepness was measured by assigning a rank (1-6) to each individual within groups and then plotting their normalised DS against rank. The slope of this relationship is the steepness, and a steepness approaching 1 is steep and one approaching 0 is considered shallow (de Vries et al., 2006).

Statistical Analyses

Before hypotheses testing, correlation analyses were performed across all explanatory variables (Appendix 2: Table A8). Both within variable repeatability across individuals and between variable correlations were calculated using Pearson correlations or the rptR package in R (Stoffel et al., 2017). Correlations were performed on all key explanatory traits of interest in this thesis, namely sex, body mass, different dominance measures and different foraging behaviours, to determine any problematic levels of covariance. For foraging behaviours and dominance measures, individual repeatability estimates were calculated between trial days using generalised mixed models (rpt function from rptR library) (Nakagawa & Schielzeth, 2010). In all repeatability models, individual ID was included as a random effect to measure variation attributable to the individual. For the different dominance measures, a random intercept for Group ID was added as an additional random effect, as dominance does not make sense to measure without the context of a social environment but is relative to a focal’s conspecifics.

For all models used in the main analyses, the distributions of the response variables were assessed by eye and model assumptions were controlled using residual plots. The response variables used were: (a) total mean scrounging per individual across trial days; and (b) proportion scrounging per individual per trial, calculated as the number of scrounges per individual per trial divided by total feeding events (producing + scrounging) in that trial. Mean scrounging was log-transformed and modelled using a normal distribution, while a binomial distribution was used for proportion of scrounging. Furthermore, the consistency of individual differences in scrounging behaviour across the two trial days was estimated separately from the main models by calculating mean total scrounging and mean proportion scrounging per individual per day and modelling this in response to individual ID as a random effect in generalized mixed effect models, using the rpt function in the rptR package. The models were run both without any fixed effect and with only trial day as a fixed effect in order to derive adjusted repeatability. By including trial day, variation introduced by day effects rather than individual attributes is accounted for, isolating variation caused by individual trait differences (Nakagawa & Schielzeth, 2010).

The fixed effects used in the main models were individual body mass, obtained the night before the trial (mean centred to better fit the scale of the response variable), individual David Scores (either based on joins or aggressions), sex and trial day. The initial model was always based upon the variables and interactions predicted to have an effect from the different hypotheses, and thus included all of the fixed effects of the predictor variables of primary interest (mass, dominance and sex) and their two-way interactions in addition to trial day. As trial day had a highly significant effect, all two-way interactions between trial-day and the other primary predictor variables were included and the models assessed based on Akaike's Information Criteria (AIC). The final model, including all two-way interactions with trial-day, was selected as the AIC was lowered by >2 (Forstmeier & Schielzeth, 2011) and model fit was significantly improved. Furthermore, in order to evaluate interaction effects found to be significant in the main models, individual mixed models were run including datapoints for only males or females, only events on the first versus second trial day, or for only the more dominant or subordinate half of the population in the response variable, excluding the respective predictor from the model.

To assess the amount of additional variance explained by individual and group identity effects, mixed effect models included individual ID and group ID as random effects. A random slope for dominance was also included in the group ID to account for possible group-specific differences in the effects of social dominance.

For simplicity and due to time constraints with this thesis, the additional measures of ‘impact’ and ‘responsiveness’ were modelled and quantified per individual using best linear unbiased predictors (BLUPs, i.e. the coefficients of each random effect). The model and methods used for extracting the appropriate BLUPs were assembled by PhD candidates Rori Wijnhorst and Corné de Groot. An assumption of minimal within-individual error around the estimate of the coefficients had to be made here in order to justify using statistical predictions (BLUPs for responsiveness and impact) as the responses in further statistical testing. To obtain these measures, total scrounging for each individual in each trial was modelled as a response to opponent scrounging in a mixed effect model. Opponent scrounging was chosen as the predictor as we expect both within-individual and between-individual producing and scrounging to be negatively correlated: High amounts of opponent scrounging should equate to lower amounts of opponent producing and thus fewer scrounging opportunities for the focal. So, if this assumption is true, high opponent scrounging is expected to predict low focal scrounging and vice versa. Opponent scrounging was calculated as the mean scrounging of the focal individual’s opponents in each trial, and both the response and the predictor where mean centred so the intercepts would represent the mean level behaviour. Individual ID, with opponent scrounging as a random slope, and random intercepts for the individual ID’s of the two opponents in each trial were added as random effects, then the model was run and the coefficients of each random effect was extracted from the model. Thus, the coefficients of the random intercepts for individual ID and opponent IDs indicate the average level of scrounging of either variable when the other variables are at their mean level of scrounging. The coefficients of the random slope represent the effect of a one standard deviation increase in opponent scrounging behaviour on focal scrounging behaviour, creating a predicted slope for each focal individual’s response to opponent scrounging (i.e. its ‘responsiveness’). In turn, if things are viewed from the perspective of the opponent, how much the focal’s average joining deviates from the population mean is the opponent’s ‘impact’: The coefficients associated with each opponent ID’s random intercept represents the difference in scrounging behaviour between the opponent and the focal at the opponents average scrounging level, meaning how much the focal deviates from its average scrounging level in response to that opponent’s average scrounging.

In order to then model ‘responsiveness’ and ‘impact’ as a function of individual attributes, linear mixed models were run with either individual responsiveness or impact as the response variables. Dominance, body mass (mean centred), sex and trial day were included as fixed effects, with all their two-way interactions (see above for any additional model selection procedures on these initial models, and for visualisation and interpretation of certain interaction effects). Individual ID and groupID with a random slope for dominance were included as random effects. To be able to use individual ID meaningfully as a random effect, responsiveness and impact were calculated for each individual on each trial day, enabling the use of two responsiveness and impact values for each individual as a response in the model. Furthermore, a Pearson correlation was performed to assess the among-individual relationship between the two.

All analyses were conducted using the statistical programming language R (R Core Team, 2023), and all mixed models used were fitted with lme4 package (Bates et al., 2015).

Results

Assessing Dominance

Figure 14 shows frequency distributions of the data used to assess dominance in terms of the number of aggressive interactions compared to scrounging interactions from the video analysis, the RFID subset corresponding to the video analysis trials and the whole RFID dataset respectively. For the video analysis data (Figure 14a and b), there are zero-inflated Poisson distributions for both scrounging and aggressive interactions. In the RFID subset and RFID data, distributions have substantially less zeros, with the complete RFID dataset having very few. Table 6 describes the frequency of interactions per individual for the different dominance measures. The RFID data includes far more interactions, but might also be a less accurate measure, as aggressive and non-aggressive scrounging events could not be distinguished. Thus, aggressive scrounging events are likely captured within the RFID data as well.

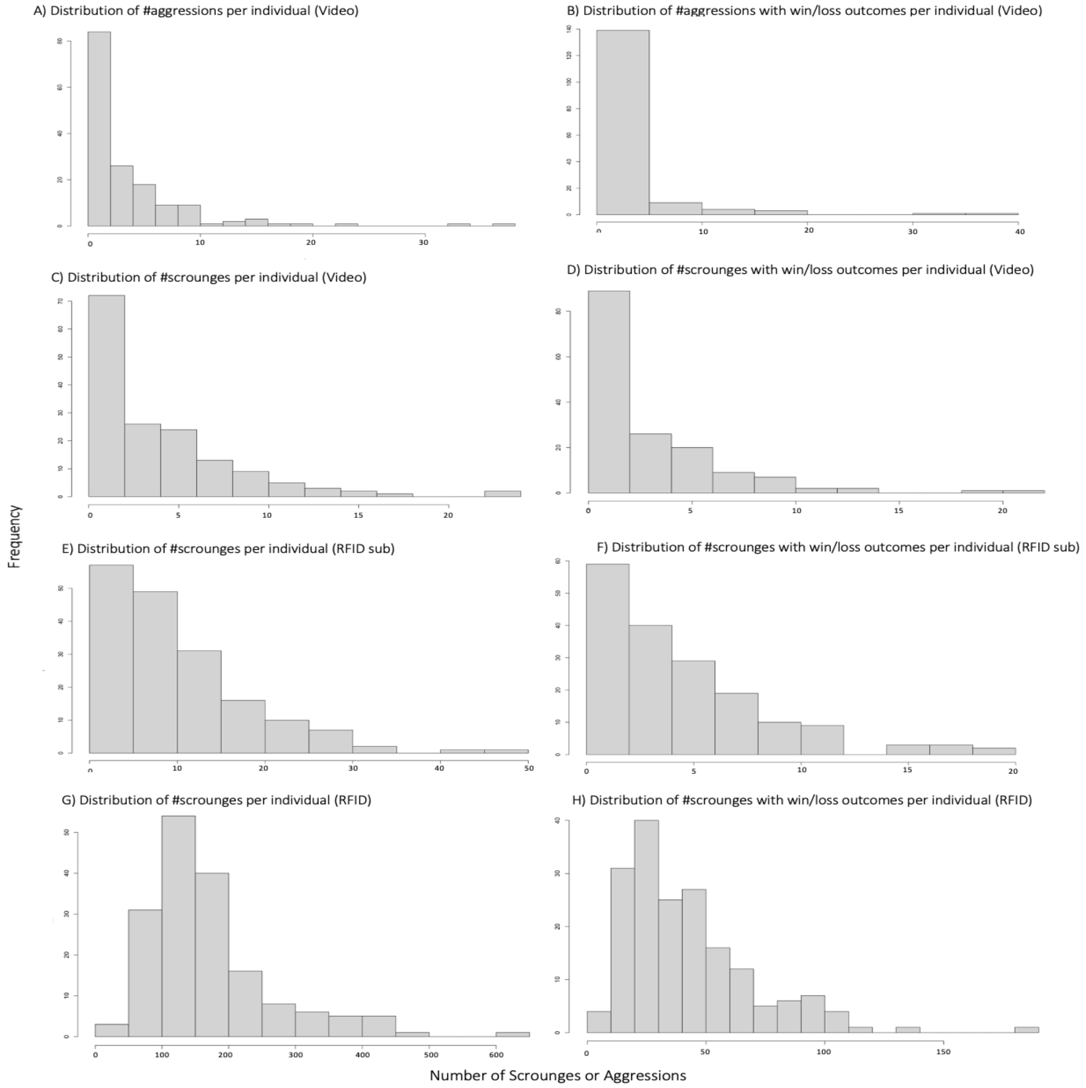


Figure 14: *Frequency distributions for variables used in assessing dominance. A) and B): Aggressive interactions from video analysis data. C) and D): Scrounging interactions from video analysis data. E) and F): Scrounging interactions from RFID subset. G) and H): Scrounging interactions from the complete RFID data. Left panels: all interactions included. Right panels: only win/loss interactions included.*

Table 6: *Mean number of interactions in scrounging and aggressions per individual for the different types of data (sub-set of videos analysed versus the full RFID data set), and the mean only when a clear winner and loser could be determined, plus the total number of interactions.*

	Mean	*Mean Win/Loss*	*Total*
Video (Aggression)	4.00	2.68	628
Video (Scrounging)	4.20	3.14	660
RFID Subset (Scrounging)	10.32	4.78	1795
RFID (Scrounging)	170.30	43.20	28951

The zero-inflated frequency distributions from the video analysis data (Figure 14) and the mean values in Table 6, show that aggressive interactions and even scrounging were relatively rare in most trials and a large portion of individuals had very few aggressive interactions. This is probably due to the inclusion of only two trials per individual in the video analysis, and thus a dominance hierarchy based on aggressions or even scrounging from these data might well be less reliable due to a lack of information. In contrast, the few zero values for scrounging in the RFID data mean that it could provide a more reliable hierarchy because there are more interactions to base the dominance calculations on (Gammel et al., 2003). The general trend observed while watching videos was that most trials did not contain many or any aggressions, and that most scrounges and displacements happened without any obvious physical conflict.

Correlations between different David Scores (DS) measures of dominance are shown in Table 7. The correlation between DS measured based on aggressions versus scrounges in the video data indicates similar but not identical aspects of dominance. Importantly, the correlation between DS based on scrounging from the video analysis and DS based scrounging from the sub-set of the RFID data indicates that the RFID data provides reliable information on scrounging interactions (Table 7). Still, the additional interactions per individual across more trials introduced in the full RFID dataset do reduce this correlation. This suggests a certain amount of non-repeatable scrounging behaviour by the same individuals across the different trials.

Table 7: *Pearson correlations for DS based on different interactions and data. "DSA" indicates DS based on aggressions, while "DSJ" indicates DS based on scrounging. "Video" indicates interactions from the video analysis data, while "RFID sub" indicates interactions from the RFID subset corresponding to the trials analysed by video and "RFID" indicates interactions based on the whole RFID dataset. Corresponding colours represent correlations between the same two measures. P-values are provided in parentheses. Standard deviation for each measurement is given in its corresponding white box.*

	DSA (Video)	**DSJ (Video)**	**DSJ (RFID sub.)**	**DSJ (RFID)**
DSA (Video)	*1.292*	0.53*(2.35e-16)*	0.20*(.011)*	0.31*(5.91e-9)*
DSJ (Video)	0.53*(2.35e-16)*	*1.648*	0.47*(3.21e-14)*	0.42*(2.23e-12)*
DSJ (RFID sub.)	0.20*(.011)*	0.47*(1.32e-14)*	*1.581*	0.39*(1.86e-10)*
DSJ (RFID)	0.31*(5.91e-9)*	0.42*(2.23e-12)*	0.39*(1.86e-10)*	*3.522*

Repeatability across trial days for different measures of DS are shown in Table 8. The most repeatable measure was DS based on scrounging in the video data. However, repeatability was generally low for all measures. This again suggests that individuals interacted somewhat differently with each other across the different trials. The addition of GroupID as a random effect in all rpt-models did not change the correlation coefficients, but in all instances lowered the P-values (reported in Table 8), which means that group explains a portion of variation in DS scores.

Table 8: *Repeatability across trial days for DS based on different interactions. "DSA" indicates DS based on aggressions, while "DSJ" indicates DS based on scrounging. "Video" indicates interactions from the video analysis data, while "RFID sub" indicates interactions from the RFID subset corresponding to the trials analysed by video and "RFID" indicates interactions based on the whole RFID dataset.*

DSA (Video)	0.21 *(.0055)*
DSJ (Video)	0.29 *(.00011)*
DSJ (RFID sub.)	0.21 *(.0042)*
DSJ (RFID)	0.12 *(.0064)*

As the DS based on scrounging in the complete RFID data captures the scrounging measured in the video analysis and in the RFID subset, we can conclude that there are in essence two different dominance measures we can use here: (i) DS based on aggression in the video analysis; and (ii) DS based on scrounging in the complete data.

Figure 15 shows the hierarchy steepness across groups, as well as the average steepness in the population, for both dominance measures. In both cases, the steepness varies, but most groups have relatively flat hierarchies. The average slope is substantially steeper for the hierarchies based on RFID scrounging events.

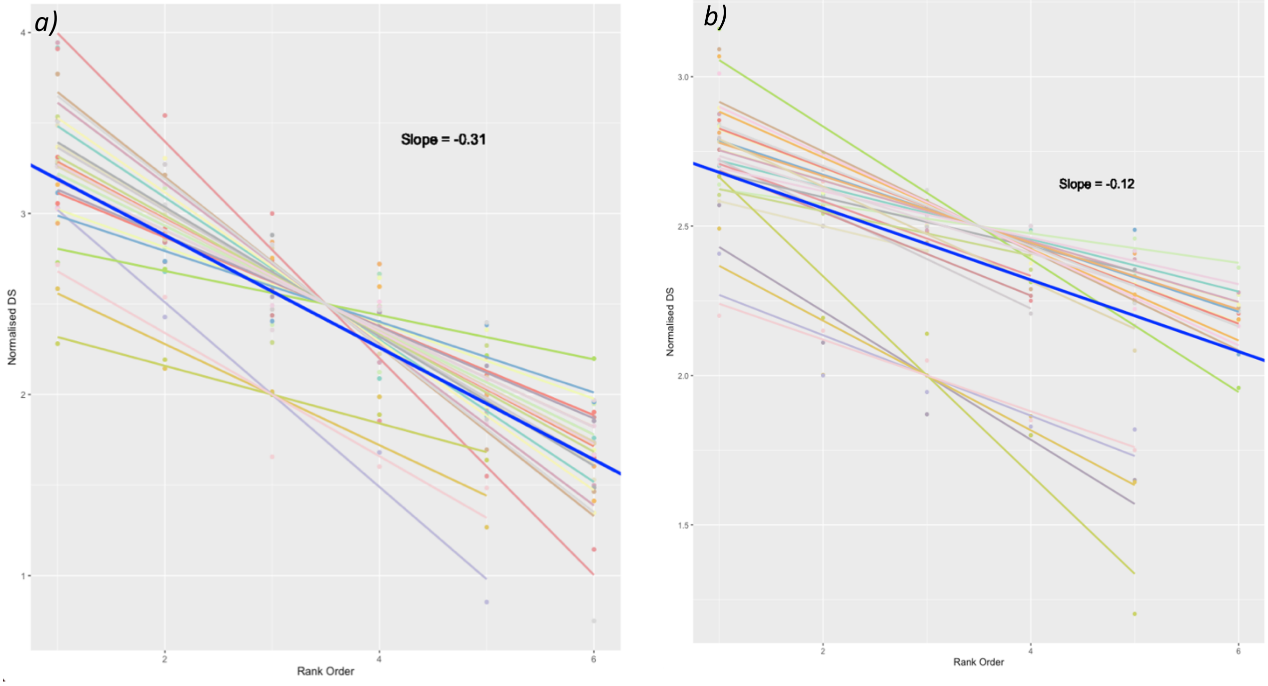


Figure 15: *Hierarchy steepness between groups for dominance based upon RFID scrounging data (a) and video aggression data (b). Different colours represent different groups, while the overall steepness is given by the contrasting blue line and described by the slope. For each group, the line extends across the ranks in that group. If dominance data is missing for any individuals, there will be fewer ranks and a shorter line. In groups with deviating elevations, the most dominant individual had a low David Score, but the highest relative to its group.*

Dominance measured based on RFID scrounging events includes more interactions per individual, which is indicative of more reliable hierarchies (Gammel et al., 2003), and there will be fewer missing pair-wise dominance relationships. This measure also portrays steeper hierarchies, and thus more likely captures meaningful differences due to dominance. It was also acceptably correlated with the dominance measures based on more accurate assessment of scrounging events in the video analysis (Table 7). Thus, dominance measured based on RFID scrounging events will be of main focus in the upcoming analyses.

Hypothesis 1 – Individual Levels of Scrounging

- Do dominant, larger and male individuals scrounge more?

Table 9 shows results for mean total scrounging (defined as mean total scrounging of all trials per trial day for each individual) and proportion scrounging (defined as total scrounging events per individual in each trial divided by total foraging events by that individual in the respective trial), in response to individual properties, including the two different measures of dominance. Dominance based upon scrounging in the RFID data seems to be the most appropriate measure here (see above), and so this will be used to determine the main effects. A separate model using dominance based upon video aggressions has been included to further assess how the results from the two measures compare.

Focal ID Effects

Focal ID accounted for 0.113 and 0.055 of the variation in mean total and proportion scrounging respectively (Table 9). The true individual repeatability, calculated based on mixed models only including focal ID as a random effect and only trial day as a fixed effect (see Statistical Analyses), was 0.710 (0.634 without trial day as a fixed effect in the model) for mean total scrounging behaviour, and 0.693 (0.638 without trial day) for individual mean proportion scrounging (Figure 16).

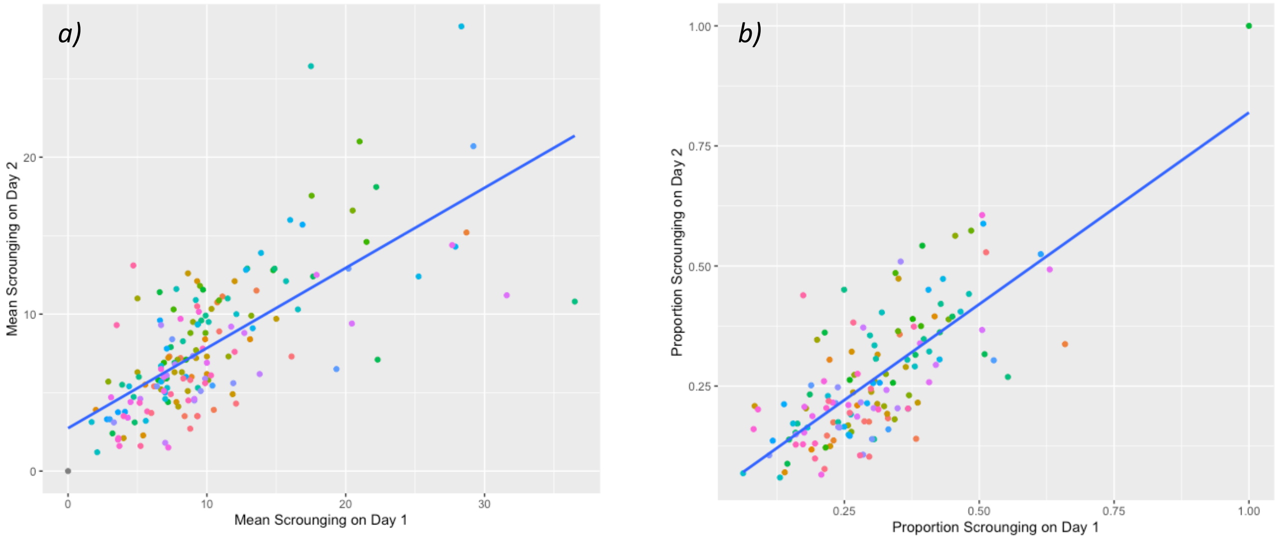


Figure 16: *Repeatabilities for mean total scrounging (a) and proportion scrounging (b) per individual shown as the relationships between values on trial day 1 and 2. Each point represents one individual and the different colours indicate the different social groups.*

Group ID Effects

Group ID explained only 0.099 and 0.000 of the variance around the intercept in mean total and proportion scrounging respectively (Table 9). The random slope for David Scores explained <0.001 of the variance in mean total scrounging and 0.025 of variance in proportion scrounging in the models based on RFID scrounging (Table 9). In the models based on video aggressions, the random slope for David Scores explained 0.002 of the variance in mean total scrounging and 0.321 of the variance in proportion scrounging (Table 9). This indicates that the effect of dominance on scrounging behaviour only differed to a meaningful extent between groups for video aggression dominance.

Table 9: *Mixed-effect model results explaining individual mean and proportion scrounging for each of the two different dominance measures (RFID scrounging or Video aggressions), with the fixed effects of sex, body mass, trial day (1 versus 2) and their two-way interactionsThe output for the fixed effects in mean scrounging is reported as the exponent of the original output, as the log of mean scrounging was used in the models. Values <1 equals negative effects, while values >1 equals positive effects. The output for the fixed effects in proportion scrounging is reported as log odds, as models were fitted with a binomial distribution. Positive or negative values are associated with higher or lower odds of the outcome respectively (e.g. an effect size of 0.5 equals a 50% increase in the odds of the outcome). All fixed effects are reported with standard errors and p-values, while all random effects are reported as proportion variance explained.*

Fixed Effects	a) **Mean Scrounging** *Joins RFID*	b) **Mean Scrounging** *Aggression Video*	c) **Prop. Scrounging** *Joins RFID*	d) **Prop. Scrounging** *Aggression Video*
Intercept	9.021 ±*1.084* *(p <0.001)*	9.027 ±*1.087* *(p <0.001)*	-1.693±*0.116* *(p <0.001)*	-1.674±*0.114* *(p <0.001)*
Dominance	0.950 ±*1.017* *(p=0.003)*	0.949 ±*1.042* *(p =0.206)*	-0.183±*0.046* *(p <0.001)*	-0.188±*0.13* *(p =0.175)*
Body Mass	0.940 ±*1.034* *(p=0.068)*	0.967 ±*1.034* *(p =0.323)*	-0.252±*0.067* *(p <0.001)*	-0.182±*0.062* *(p =0.003)*
Sex	0.885 ±*1.080* *(p=0.114)*	0.904 ± *1.081* *(p =0.199)*	-0.343±*0.169* *(p=0.042)*	-0.263±*0.166* *(p =0.114)*
Trial Day	0.754 ±*1.052* *(p<0.001)*	0.755 ±*1.053* *(p <0.001)*	-0.362±*0.158* *(p=0.022)*	-0.338±*0.161* *(p =0.035)*
Body Mass*Sex	1.059 ±*1.047* *(p=0.215)*	1.032 ±*1.047* *(p =0.493)*	0.434±*0.086* *(p<0.001)*	0.174±*0.078* *(p =0.026)*
Body Mass*Dominance	0.981 ±*1.007* *(p=0.012)*	1.016 ±*1.019* *(p =0.416)*	-0.059±*0.013* *(p<0.001)*	-0.024±*0.040* *(p =0.556)*
Sex*Dominance	1.046 ±*1.021* *(p=0.034)*	0.981 ±*1.057* *(p =0.724)*	0.230 ±*0.041* *(p<0.001)*	-0.110±*0.109* *(p =0.312)*
Dominance*Trial Day	1.026 ±*1.010* *(p=0.008)*	1.043 ±*1.027* *(p =0.132)*	0.060 ±*0.031* *(p=0.057)*	0.326±*0.086* *(p <0.001)*
Sex*Trial Day	1.082 ±*1.072* *(p=0.263)*	1.083 ±*1.075* *(p =0.270)*	0.145 ±*0.231* *(p=0.531)*	0.187±*0.227* *(p =0.411)*
Body Mass*Trial Day	0.998 ±*1.023* *(p=0.937)*	0.996 ±*1.023* *(p =0.854)*	-0.162±*0.073* *(p=0.026)*	-0.167±*0.071* *(p =0.019)*
Random Effects				
Focal ID	0.113 *(p<0.001)*	0.114 *(p<0.001)*	0.055 *(p=0.015)*	0.015 *(p<0.001)*
Group ID	0.099 *(p<0.001)*	0.108 *(p<0.001)*	0.000 *(p=NA)*	<0.001
Dominance|GroupID	<0.001 *(p=0.421)*	0.002 *(p=0.306)*	0.025 *(p<0.001)*	0.321 *(p<0.001)*
Residual	0.092	0.095	-	-

Fixed phenotypic effects: Models based on RFID dominance

- Mean total scrounging

For mean total scrounging there was a significantly positive interaction between sex and David Scores (i.e. relative dominance within each group of 6 birds) (Table 9a). Males had a very slightly positive, but non-significant relationship, while the relationship was significantly negative for females (Figure 17, Appendix 1: Table A1), and the main effect of David Scores on mean total scrounging was significantly negative (Table 9a). Higher David Scores indicate greater dominance, so in females, more dominant individuals scrounged less. There was also a significant negative interaction between body mass and dominance (Table 9a), with the amount of scrounging decreasing faster for heavier individuals if they were also more dominant (Figure 18). The effect of body mass was however found to be non-significant for both dominants and subordinates (Table A4). Overall, the main effect of body mass was negative and weakly significant (Table 9a). A significant positive interaction was found between trial day and dominance (Table 9a), showing that the negative relationship between dominance and scrounging was less pronounced on the second trial day compared to the first (Figure 19, Table A1). Trial day as a main effect also showed this significant negative effect (Table 9a).

No significant relationships were found for the main effect of sex, the interaction between body mass and sex, the interaction between body mass and trial day, or the interaction between sex and trial day (Table 9a). However, both sexes scrounged significantly less on the second trial day, and males scrounged significantly less than females on the first trial day (Table A1).

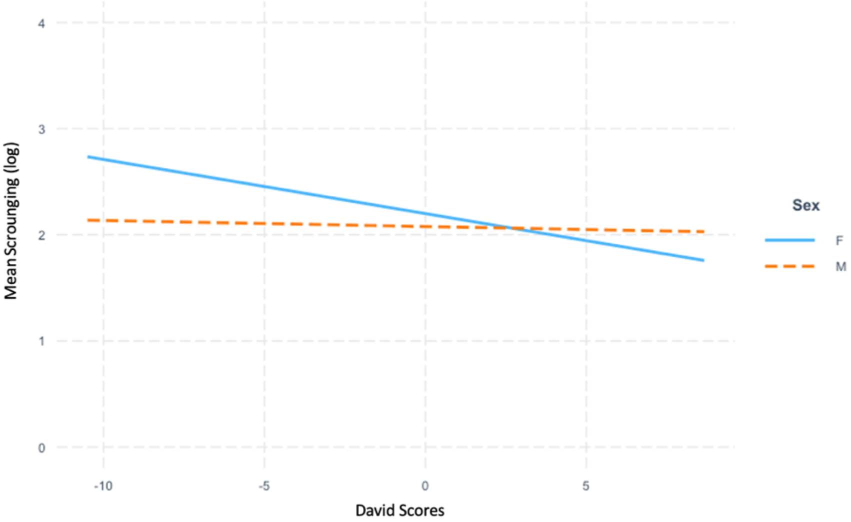


Figure 17: *Plot showing the interaction between David Scores (i.e. relative dominance within each group of 6 birds) and sex on mean total scrounging. Females are showing a negative relationship between mean total scrounging and dominance, while males showed no relationship.*

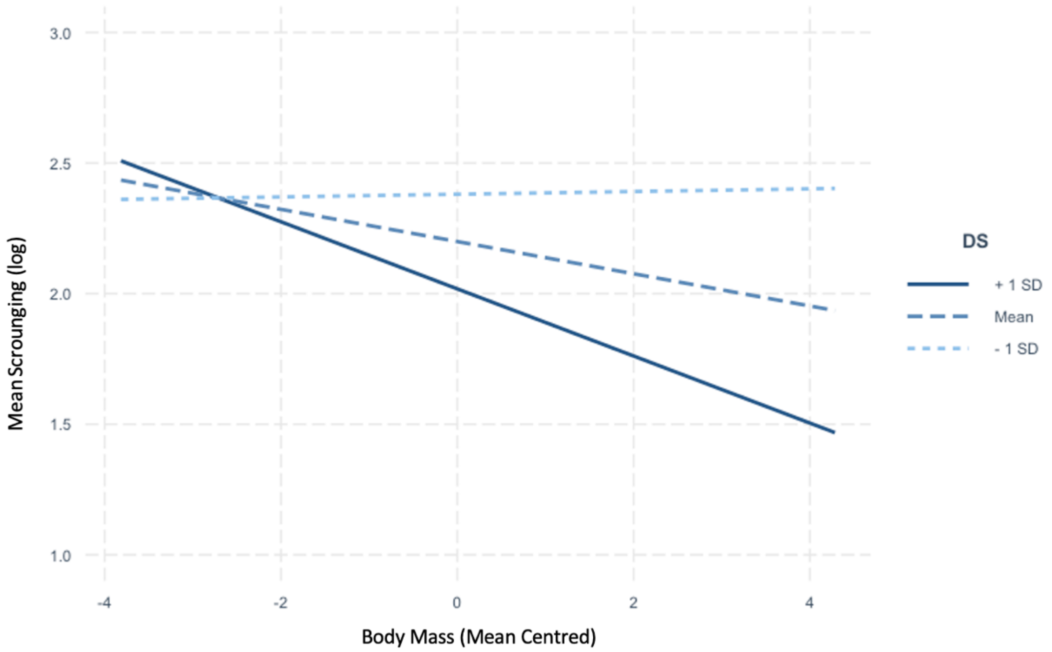


Figure 18: *Plot showing the interaction between body mass and David Scores (DS) (i.e. relative dominance within each group of 6 birds) on mean scrounging. The upper standard deviation of David Scores, meaning the more dominant part of the population, has a steeper negative relationship between scrounging behaviour and body mass.*

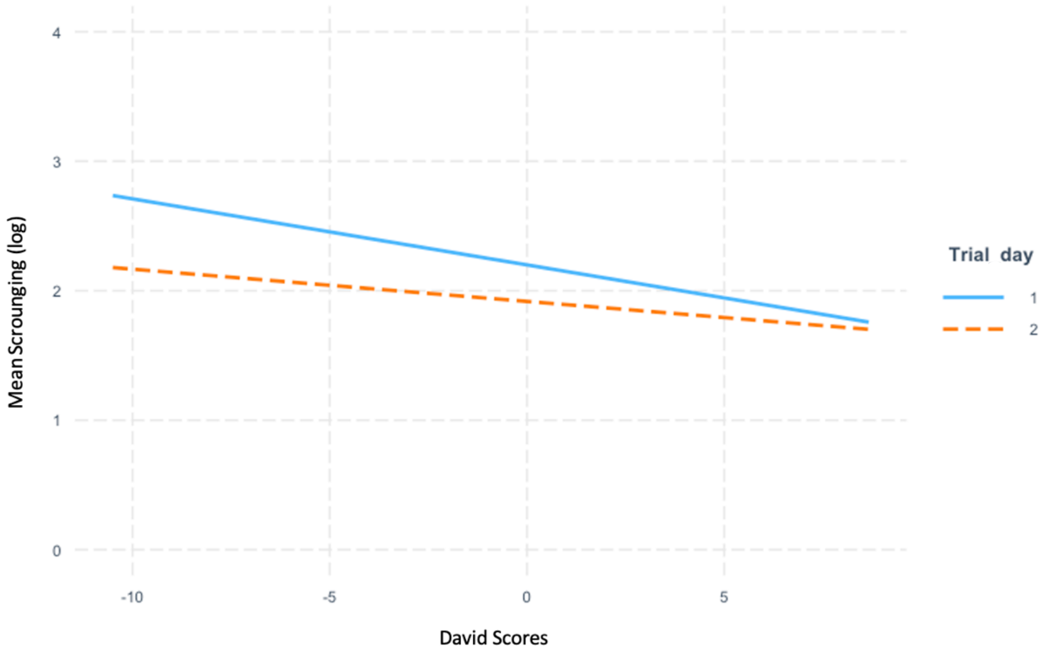


Figure 19: *Plot showing the interaction between David Scores (i.e. relative dominance within each group of 6 birds) and trial day on mean total scrounging. The relationship is more negative on the first day compared to the second day.*

- *Proportion scrounging*

For proportion scrounging, there was a significant positive interaction between sex and David Score (Table 9c). Males showed a positive non-significant relationship with dominance, while the relationship was significantly negative for females (Figure 20, Table A2), and the main effect of David Scores overall was significantly negative (Table 9c). Higher David Scores indicate greater dominance, so in females the odds of scrounging decreased for more dominant individuals. Furthermore, a significant positive interaction was found between body mass and sex (Table 9c), with mass having a significant positive effect on scrounging behaviour in males compared with a non-significant negative effect in females (Figure 21, Table A2). The main overall effect of sex was significantly negative, suggesting that males overall used scrounging less (Table 9c). There was also a significant negative interaction between body mass and dominance (Table 9c), with the odds of scrounging having a steeper decline for heavier individuals if they were also more dominant (Figure 22). The effect of body mass was, however, found to be non-significant for both dominants and subordinates (Table A4), but the main effect of body mass was significantly negative (Table 9c). Body mass also had a mildly significant negative interaction with trial day, with body mass having slightly more of a negative effect on the second day (Figure 23). A significant positive effect was found for the interaction between dominance and trial day, showing that the negative relationship between dominance and scrounging was less pronounced on the second trial day compared to the first (Figure 24, Table A2), and trial day as a main effect also showed a significant negative effect (Table 9c). The only clearly non-significant effect found was for the interaction between sex and trial day.

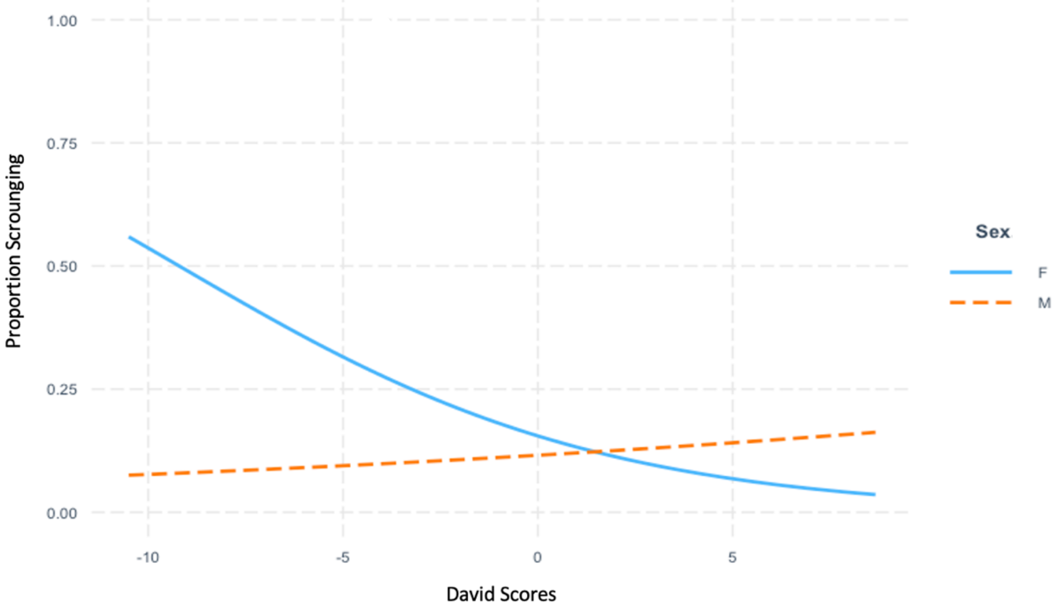


Figure 20: *Plot showing the interaction between David Scores (i.e. relative dominance within each group of 6 birds) and sex on proportion scrounging. Females are showing a negative relationship between proportion scrounging and dominance, while males showed a slightly positive relationship. The curvature in the plot is an artefact of the binomial distribution used in the model.*

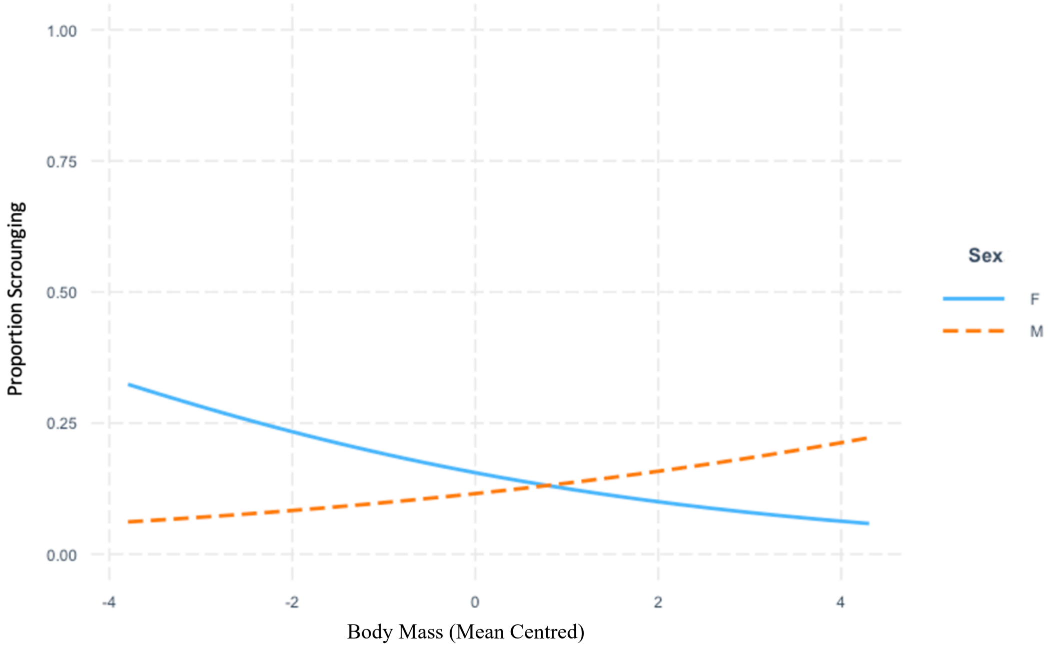


Figure 21: *Plot showing the interaction between body mass and sex on proportion scrounging. Females are showing a negative relationship between proportion scrounging and body mass, while for males the relationship is positive. The curvature in the plot is an artefact of the binomial distribution used in the model.*

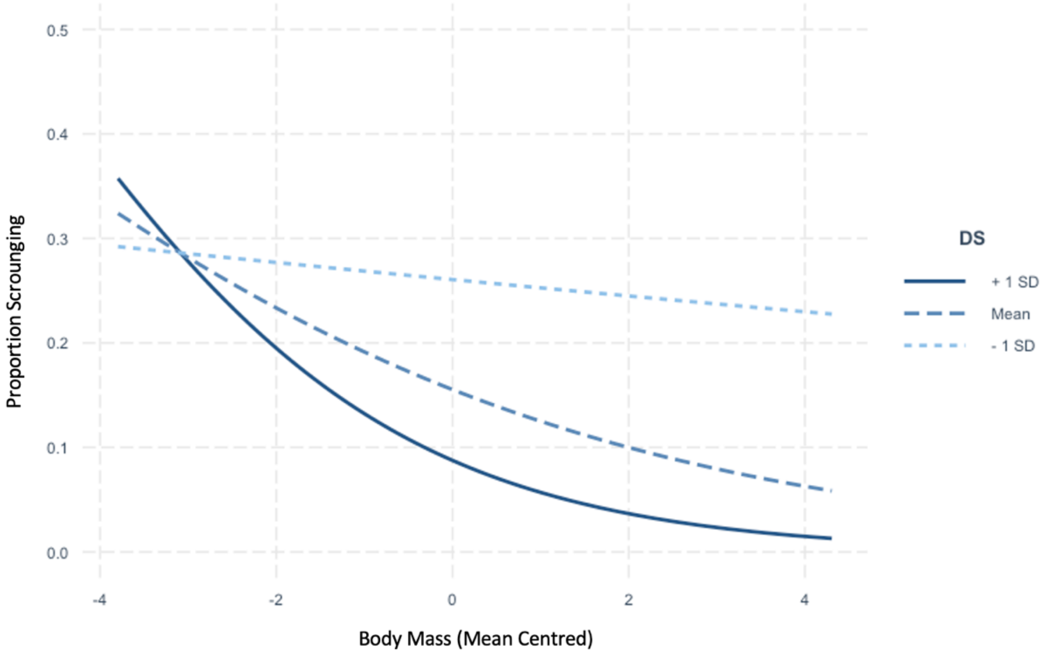


Figure 22: *Plot showing the interaction between body mass and David Scores (DS) (i.e. relative dominance within each group of 6 birds) on proportion scrounging. The upper standard deviation of David Scores, meaning the more dominant part of the population, has a steeper negative relationship between scrounging behaviour and body mass. The curvature in the plot is an artefact of the binomial distribution used in the model.*

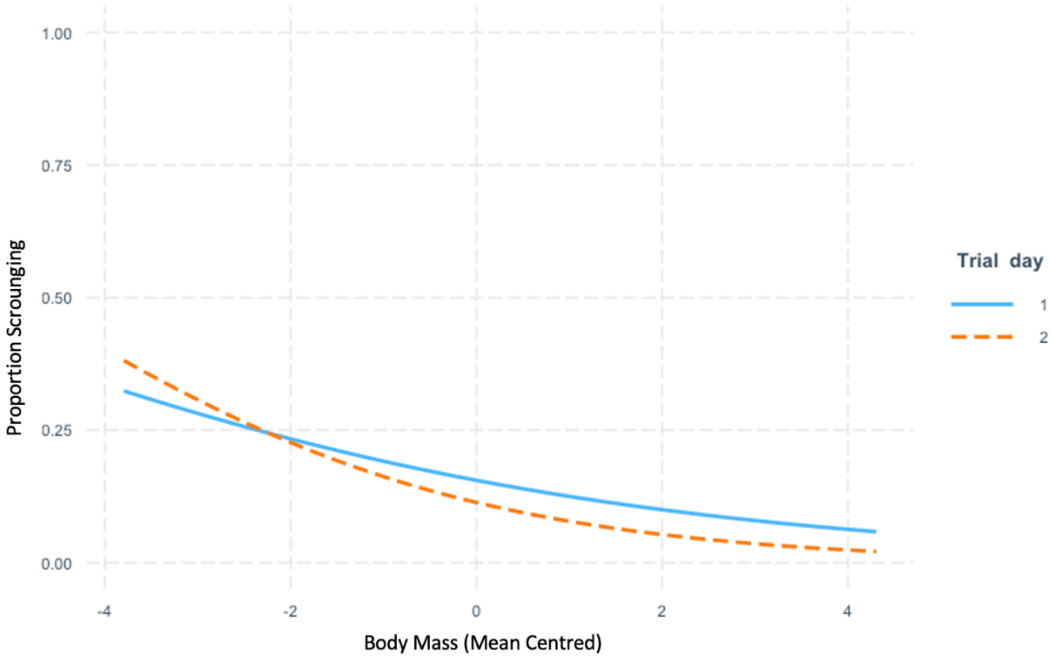


Figure 23: *Plot showing the interaction between body mass and trial day on proportion scrounging. The relationship between proportion scrounging and body mass is slightly more negative on the second trial day than on the first. The curvature in the plot is an artefact of the binomial distribution used in the model.*

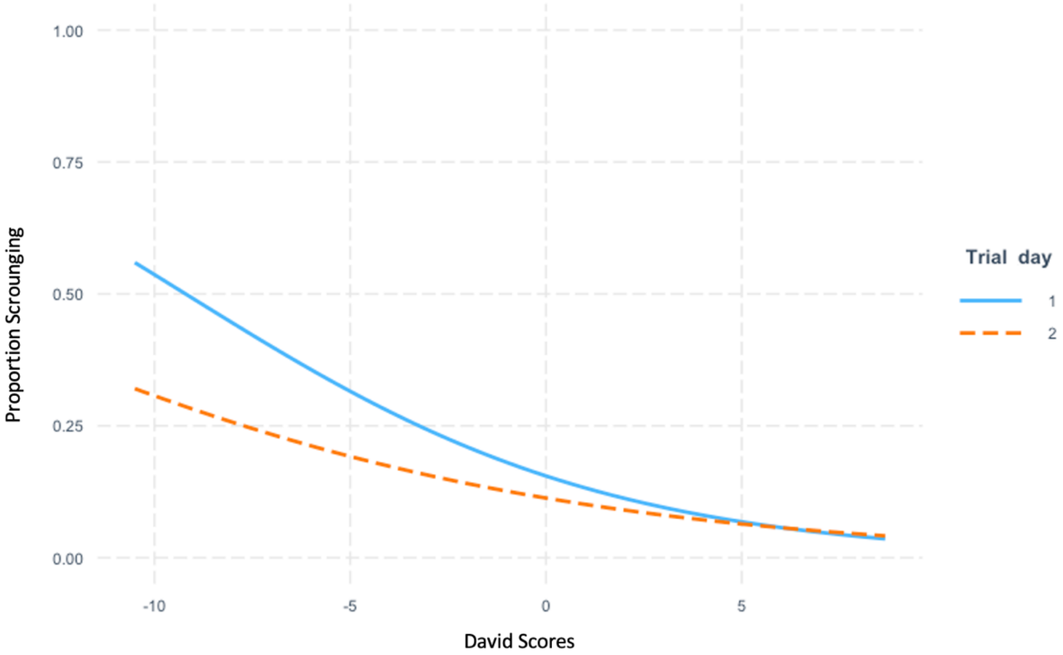


Figure 24: *Plot showing the interaction between David Scores (i.e. relative dominance within each group of 6 birds) and trial day on proportion scrounging. There was a negative relationship between David Scores and proportion scrounging on both days, but the relationship is steeper on the first day. The curvature in the plot is an artefact of the binomial distribution used in the model.*

Fixed Phenotype effects: Models based on aggression dominance

- Mean total scrounging

For mean total scrounging using David Scores based upon video aggression data, the only significant relationship found was a negative effect of trial day, suggesting that individuals scrounged less on the second trial day compared to the first (Table 9b). All other fixed effects were found to be non-significant, but all effect sizes, apart from the interaction between body mass and dominance and sex and dominance, had the same directional relationships as the models based on RFID scrounging data (Table 9b).

- Proportion scrounging

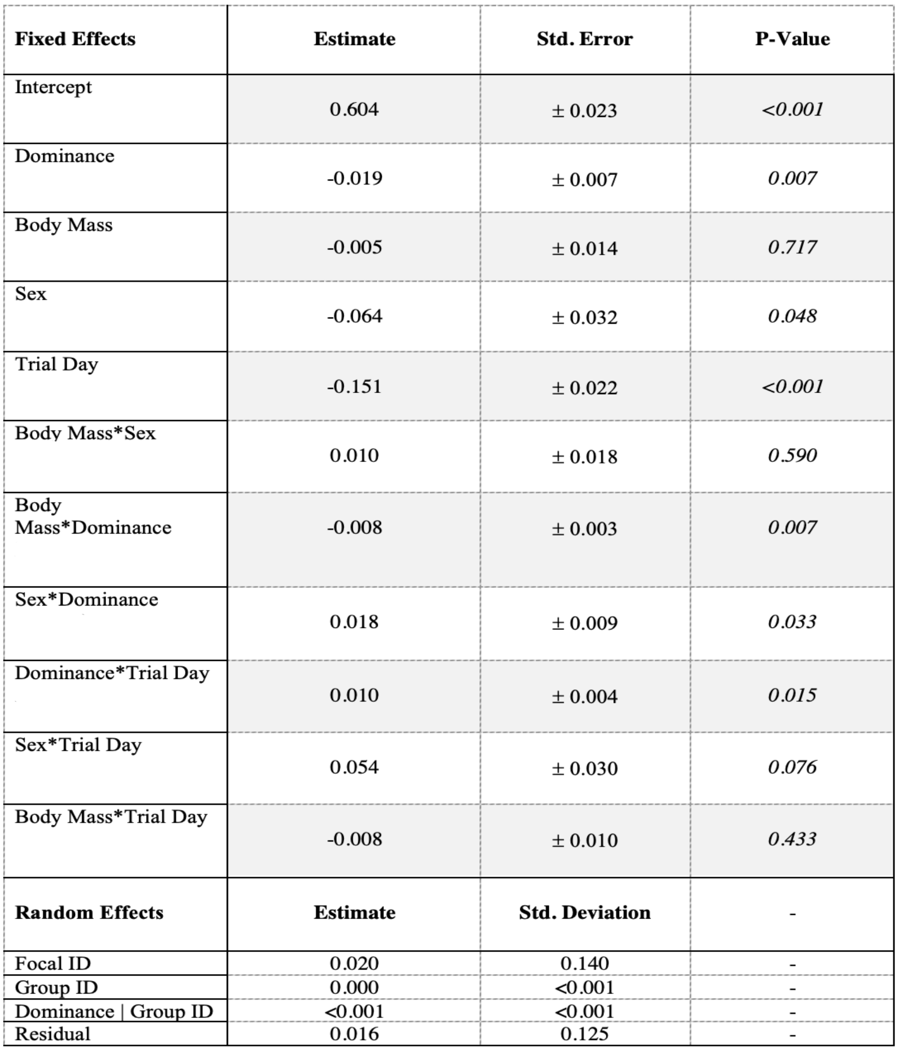
For proportion scrounging using David Scores based on video aggression data, there was a significant positive effect of the interaction between body mass and sex, displaying similar relationships as for the models based on the RFID scrounging data (Table 9d, Figure 22). There was also a significantly positive interaction between dominance and trial day (Table 9d). This means that the relationship between dominance and scrounging was more positive on the second trial day compared with the first. The relationship was negative on the first day, but, in contrast to the models based on RFID scrounging data, it was slightly positive on the second day. On both days, the effect was non-significant (Table A3). The interaction between body mass and trial day was significantly negative, showing a similar relationship as in the models based on the RFID scrounging data (Table 9d, Figure 23). This means that body mass had slightly more of a negative effect on the second trial day, but the negative effect was still significant on both days (Table A3). Overall, this resulted in a significant negative main effect of trial day (Table 9d). All other fixed effects were non-significant, but all effect sizes, apart from the interaction between dominance and sex, were of the same directional relationship as those in the model based on RFID scrounging data (Table 9d).

Hypothesis 2 – Individual Levels of Responsiveness

-Are dominant, larger and male individuals less responsive?

Table 10 shows results for individual levels of ‘responsiveness’, represented by individual BLUPs for changes in total scrounging (see Statistical Analyses), as a function of individual phenotypic properties. As responsiveness is a slope for each individual, a higher value for responsiveness equals a steeper slope, representing a bigger change in behaviour. For all fixed effects, the effect sizes appear very small, but they are operating on slope values ranging from ~ 0 to 1.25. This means that all slope values are positive, meaning that all individuals responded to opponent scrounging by increasing their own scrounging, which is the opposite of what is predicted by producer-scrounger dynamics.

Table 10: *Output from mixed- effect models explaining individual levels of ‘responsiveness’ in response to dominance (based on RFID scrounging), body mass, sex, trial day (1 versus 2) and all their two-way interactions. Fixed effects are reported with standard errors and p-values, random effects are reported as variance explained.*



Fixed Effects	**Estimate**	**Std. Error**	**P-Value**
Intercept	0.604	± 0.023	*<0.001*
Dominance	-0.019	± 0.007	*0.007*
Body Mass	-0.005	± 0.014	*0.717*
Sex	-0.064	± 0.032	*0.048*
Trial Day	-0.151	± 0.022	*<0.001*
Body Mass*Sex	0.010	± 0.018	*0.590*
Body Mass*Dominance	-0.008	± 0.003	*0.007*
Sex*Dominance	0.018	± 0.009	*0.033*
Dominance*Trial Day	0.010	± 0.004	*0.015*
Sex*Trial Day	0.054	± 0.030	*0.076*
Body Mass*Trial Day	-0.008	± 0.010	*0.433*
Random Effects	**Estimate**	**Std. Deviation**	-
Focal ID	0.020	0.140	-
Group ID	0.000	<0.001	-
Dominance | Group ID	<0.001	<0.001	-
Residual	0.016	0.125	-

Focal ID Effects

Focal ID accounted for 0.020 of the variance around the intercept for responsiveness (Table 10). The true repeatability for individual responsiveness, calculated based on a mixed model only including focal ID as a random effect and only trial day as a fixed effect (see Statistical Analyses), was 0.524 (0.380 without trial day as a fixed effect in the model). This means that individuals expressed individual differences in responsiveness (Figure 25), and that they are repeatable.

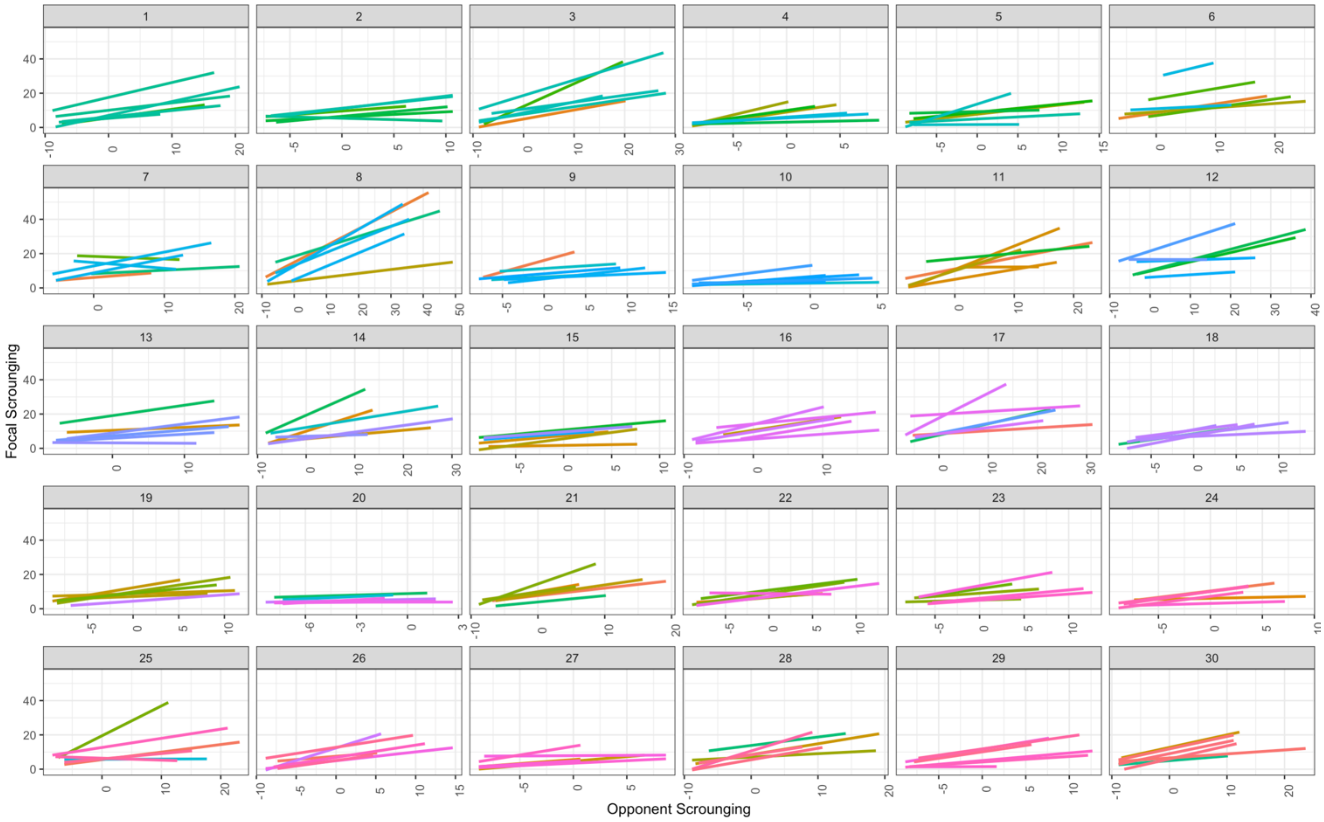


Figure 25: *Behavioural reaction norms for individual scrounging across trials against average opponent scrounging in each trial. Each plot represents a different group, while each line represents an individual within that group.*

Group ID Effects

Group ID explained 0.000 of the variance around the intercept in individual responsiveness (Table 10), suggesting that no remaining variation is attributable to differences between groups after the fixed effects are accounted for. Furthermore, the amount of variance explained by the random slope for David Scores (i.e. relative dominance within each group of 6 birds) was negligible, indicating that the effect of dominance on responsiveness did not differ meaningfully between groups.

Individual phenotypic effects

For responsiveness slope values, there was a weak positive interaction between David Scores (i.e. relative dominance within each group of 6 birds) and sex (Table 10). Higher David Scores indicate more dominance, meaning that the general trend was that individuals who were more responsive were less dominant. This effect was slightly stronger in females (Figure 26, Table A5), but the overall significant negative effect of sex indicated that females were slightly more responsive than males (Table 10). Furthermore, the interaction between trial day and David Scores was significantly positive (Table 10), but the relationship was negative on both days (Figure 27). Overall, the effect of trial day was significantly negative, but in reality, only significantly negative on the first day (Table 10 & Table A5). There was also a significant negative effect of the interaction between body mass and dominance (Table 10), suggesting that the effect of body mass depends on dominance. This means that heavier individuals that were also more dominant responded less to their opponent's behaviour, giving them lower slope values for responsiveness (Figure 28). However, the effect of body mass was non-significant for both dominants and subordinates (Table A7). No significant relationships were found for any of the fixed effects including trial day (Table 10).

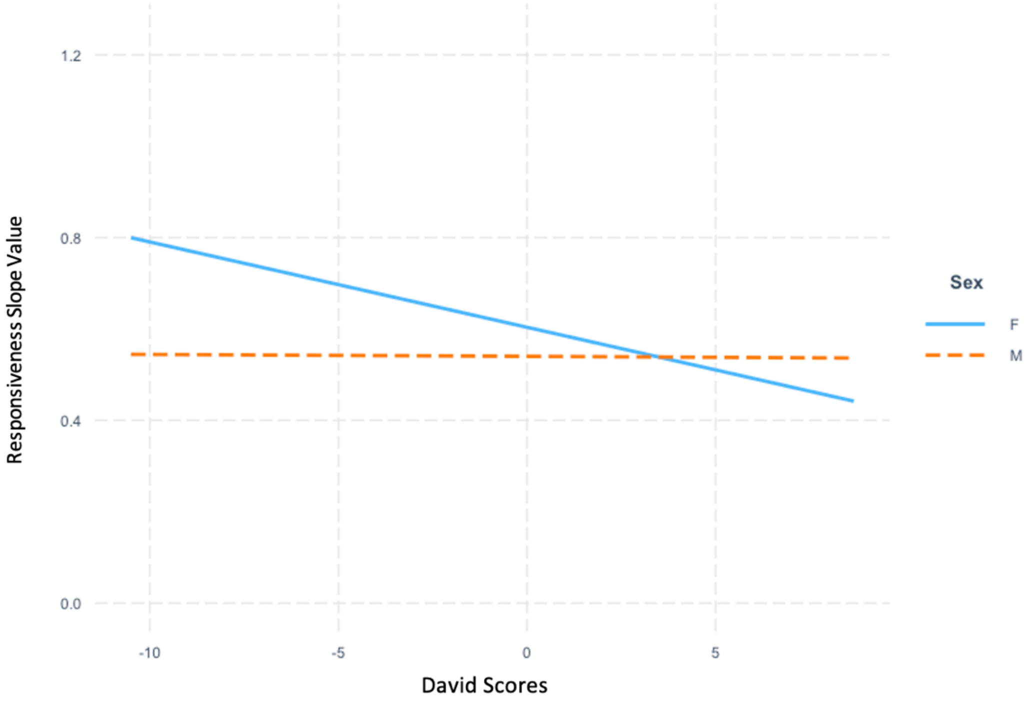


Figure 26: *Plot showing the interaction between David Scores (i.e. relative dominance within each group of 6 birds) and sex on responsiveness. Females are showing a negative relationship between responsiveness and dominance, while males are nearing a 0 relationship.*

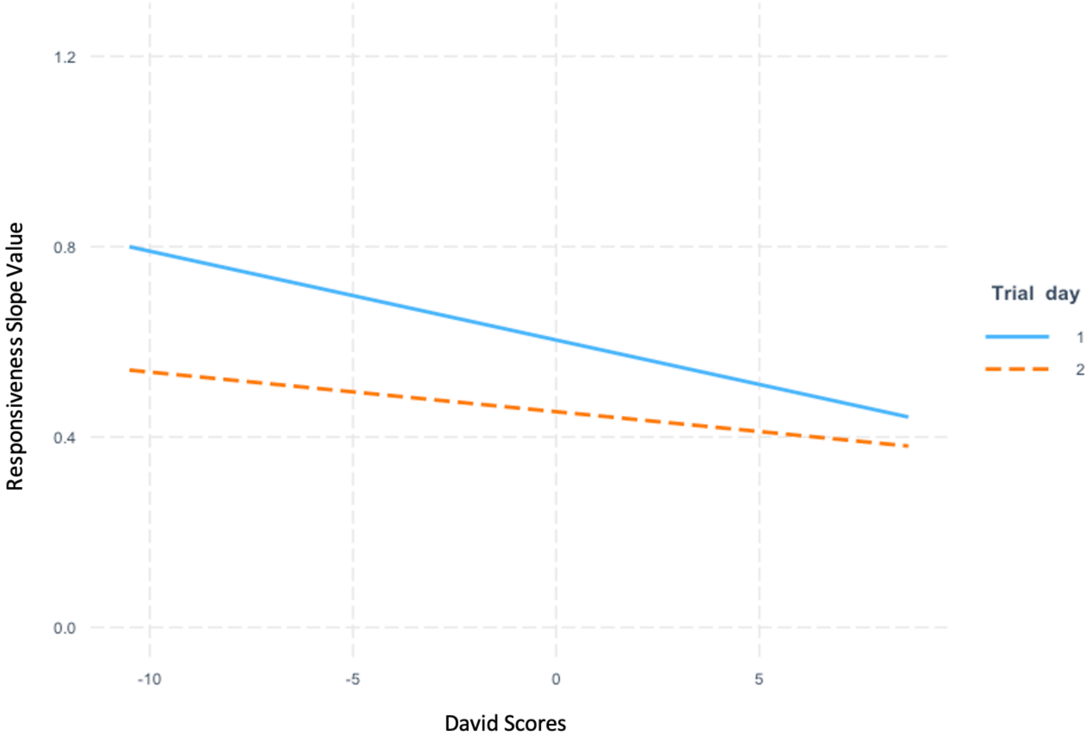


Figure 27: *Plot showing the interaction between David Scores (i.e. relative dominance within each group of 6 birds) and trial day on responsiveness. The relationship is more negative on trial day 1 compared to trial day 2.*

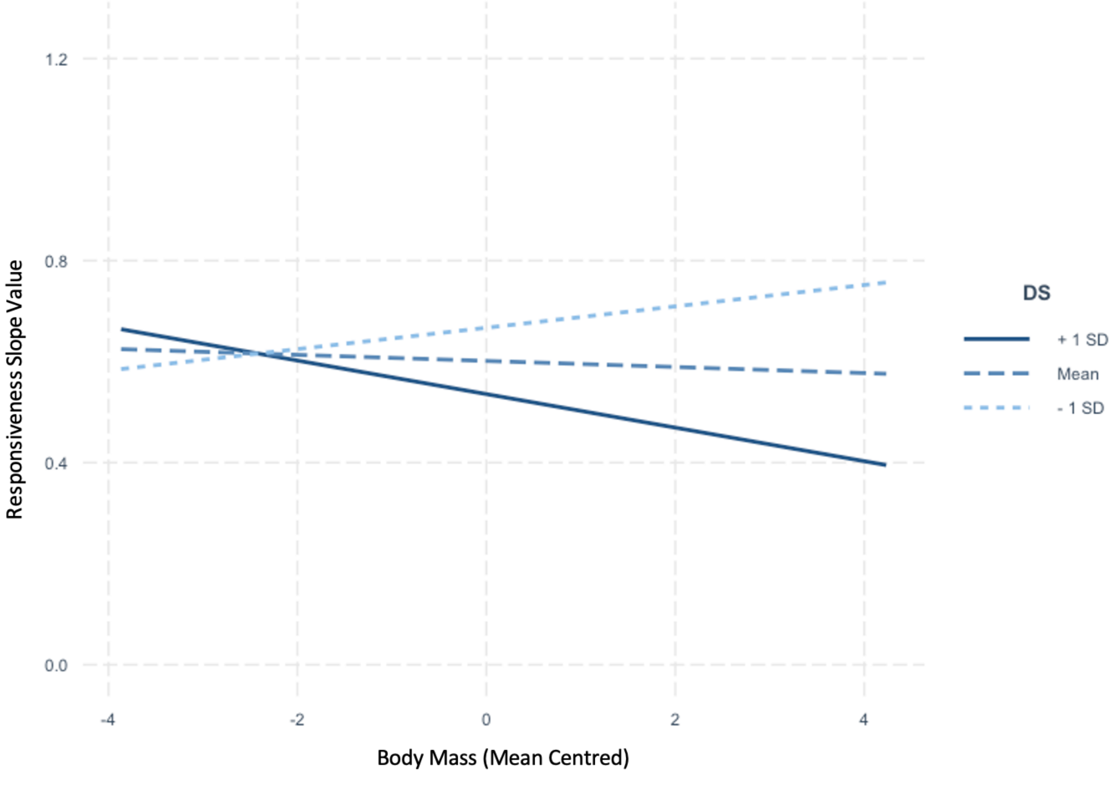


Figure 28: *Plot showing the interaction between David Scores (DS) (i.e. relative dominance within each group of 6 birds) and body mass on responsiveness. The upper standard deviation of the population has a more negative relationship between responsiveness and body mass, compared to the mean that has slightly negative slope and the lower standard deviation that has a positive slope.*

Hypothesis 3 – Individual Levels of Impact

-Do dominant, larger and male individuals have a bigger impact?

Table 11 shows results for individual levels of 'impact', represented by individual BLUPs for opponent's average deviation from mean scrounging levels (see Statistical Analyses), as a function of phenotypic properties and social environment. There are both positive and negative values for impact, indicating more or less scrounging than average for the impacted individual (i.e. a positive relationship means that individuals of a certain property makes their opponents scrounge more).

Table 11: *Output from mixed-effect models explaining individual levels of 'impact' in response to dominance (based on RFID* scrounging*), body mass, sex, trial day (1 versus 2) and all their two-way interactions. Fixed effects are reported with standard errors and p-values, random effects are reported as variance explained.*

Fixed Effects	**Estimate**	**Std. Error**	**P-Value**
Intercept	0.529	± 0.071	*<0.001*
Dominance	0.046	± 0.019	*0.019*
Body Mass	-0.006	± 0.040	*0.878*
Sex	-0.018	± 0.095	*0.848*
Trial Day	-1.263	± 0.086	*<0.001*
Body Mass*Sex	0.047	± 0.048	*0.334*
Body Mass*Dominance	0.013	± 0.008	*0.079*
Sex*Dominance	-0.042	± 0.023	*0.064*
Dominance*Trial Day	-0.019	± 0.017	*0.253*
Sex*Trial Day	-0.023	± 0.119	*0.848*
Body Mass*Trial Day	-0.001	± 0.038	*0.972*
Random Effects	**Estimate**	**Std. Deviation**	-
Focal ID	0.059	0.243	-
Group ID	0.009	0.094	-
Dominance | Group ID	<0.001	0.015	-
Residual	0.245	0.495	-

Focal ID Effects

Focal ID accounted for 0.059 of the variance around the intercept for individual impact (Table 11). The true individual repeatability for individual impact, calculated based on a mixed model only including focal ID as a random effect and only trial day as a fixed effect (see Statistical Analysis), was 0.206 (0.000 without trial day as a fixed effect in the model), suggesting that individuals were weakly repeatable in their impact across trial days.

Group ID Effects

Group ID explained 0.009 of the variance around the intercept for individual impact (Table 11), suggesting that very little remaining variation is attributable to differences between groups after the fixed effects are accounted for. The random slope for David Scores (i.e. relative dominance within each group of 6 birds) also explained a negligible amount of the variance, indicating that the effect of dominance on impact does not differ meaningfully between groups.

Individual phenotypic effects

For impact, there was a weakly significant negative interaction between sex and David Scores (i.e. relative dominance within each group of 6 birds), but the main effect of David Scores was significantly positive (Table 11). Higher David Scores indicate more dominance, suggesting that generally, opponents of individuals who were more dominant were impacted to scrounge more, and that this effect was stronger in females compared with males (Figure 29, Table A6). There was also a weakly significant positive interaction between body mass and dominance (Table 11), suggesting that heavier individuals that were also more dominant made their opponents scrounge more (Figure 30). However, the effect of body mass was non-significant for separate models for both dominants and subordinates (Table A7). Additionally, there was a significant negative effect of trial day (Table 11), indicating that overall opponent scrounging behaviour was less impacted on the second trial day compared to the first. All interactions including trial day were also found to be non-significant (Table 11).

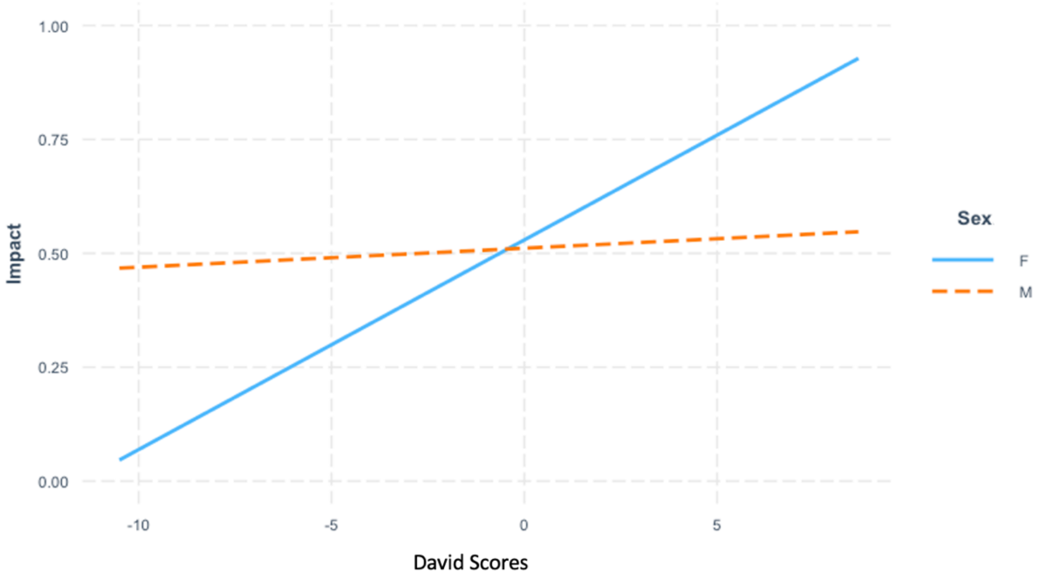


Figure 29: *Plot showing the interaction between David Scores and sex on impact. Females are showing a positive relationship between impact and dominance, while males have a slightly positive relationship.*

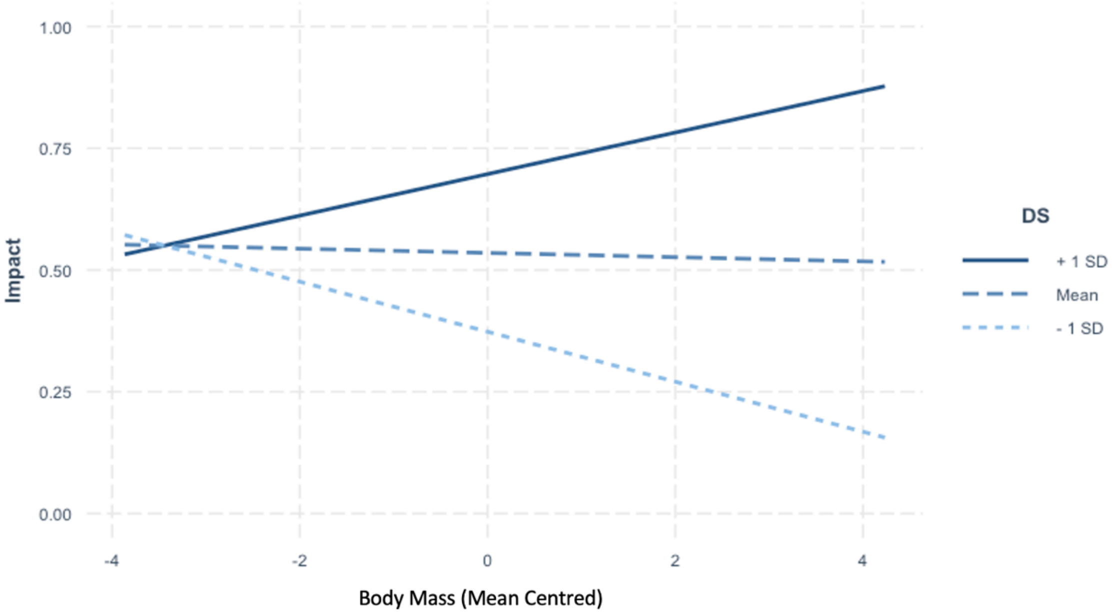


Figure 30: *Plot showing the interaction between David Scores (DS) and body mass on impact. The upper standard deviation of the population has a more positive relationship between impact and body mass, compared to the mean that has slightly negative slope and the lower standard deviation that has a negative slope.*

Discussion

In this thesis, the aim has been to explore mechanisms shaping consistent individual differences, social 'responsiveness' and social 'impact' (de Groot et al., 2023) in the context of producer-scrounger behaviour, and its integration with individual phenotypic attributes and social environment effects in the house sparrow (Barnard & Sibly, 1981; Giraldeau & Beauchamp, 1999; Giraldeau & Dubois, 2008). We hypothesised within- and among-individual variation in the costs and benefits of producing versus scrounging, and being more or less responsive, based upon phenotypic attributes of the individual and in relation to its social partners. This allowed predictions to be made that sparrows would repeatably differ in their amount of scrounging, their 'responsiveness' in switching between tactics and their social 'impact' on others. Specifically, because males and larger more dominant individuals are expected to have a higher competitive ability, and thus should not have to pay the cost of searching for food or being plastic, it was predicted that individuals with these properties should scrounge more, be more fixed in their strategy and less responsive, and have a larger impact on the producer-scrounger behaviour of its social partners.

Mean versus proportion scrounging

When assessing variation in strategy use, two main models were compared, concerning differences in mean total number of scrounging (joining) events and proportion scrounging (calculated as number of scrounges per individual in each trial divided by total number of producing and scrounging for that individual in the respective trial). The directional relationships for all effects were found to be the same between the model based on mean total scrounging and proportion scrounging, thus the main difference involved which of the effects were significant. More effects were found to be significant in the model for proportion scrounging, which is likely because this measure captures more biologically meaningful variance in terms of the behavioural strategy used by individuals. Mean total scrounging does not tell us how much an individual uses one strategy versus the other and can therefore be conflated by the effect of individuals simply foraging more (and more closely together), independent of foraging strategy. Thus, using proportion scrounging also makes it easier to compare individuals that might have differed in their overall foraging activity for reasons other than those related to strategy use. Likewise, the models using mean total scrounging could also be more heavily affected by outliers, even if these extreme values were real in biological terms. A few individuals were observed to use an excessive amount of scrounging compared to most, which was not a measurement error, but will still result in values far outside the general range in the population that could inflate the mean. This would increase the variability of the data, which could bias parameter estimates (Kwak & Kim, 2017). Conversely, proportion scrounging will be less sensitive to outliers, while also capturing the propensity of an individual to use one strategy versus the other, thereby accounting for individual variation in producing behaviour as well scrounging behaviour. Furthermore, using mean values as the response in a statistical model, as done with the mean total scrounging model, will mean that any within-individual variation is lost. Even though using mean scrounging value per day provides some variation for each individual, the complete range is missing, while this is not an issue for the model concerning proportion scrounging where proportion scrounging was calculated per individual in each trial, thereby capturing the complete range of within-individual variation. So, because the statistical model concerning mean total scrounging assumes the within-individual variation to be very small, the residual variance may be underestimated which can in turn lead to biased estimates of the other random and fixed effects, and thus less accurate model estimates.

Comparing dominance measures

When comparing the models including dominance measured based on joins versus aggression, all effects that were significant in both models had the same directional relationships, whether for mean total or proportion scrounging. This suggests that the two measures of dominance represented the same general biological or social processes, but perhaps to different degrees or for different socials contexts. The main difference was that for proportion scrounging the random slope for dominance based on aggression explained substantially more variation than in the other models, thus the effect of dominance differed to a meaningful extent between groups. However, this does not necessarily represent a biologically important effect. The aggression dominance was based on a relatively small subset of the data, and so in the randomly selected trials chosen for video analysis there could have been a comparably high ratio of aggressive interactions by chance for just some individual and just some groups and not others. As seen from the frequency distributions, most individuals were involved in few fights, and so this chance effect is plausible. To be able to avoid this issue in the future, it would be useful to obtain a measure of aggression that is based on a more comparable amount of data as the scrounging dominance. For example, a larger subset of videos could be analysed to be able to better compare the two measurements and minimise the likelihood that patterns are observed by chance. Furthermore, previous research on dominance effects in the house sparrow has used aggression as the proxy for dominance (Jawor, 2000; Lendvai et al., 2006; Liker & Barta, 2001, 2002). A possible reason why some of the findings in this study do not agree with these previous studies could therefore be due to us measuring a different type of dominance. Dominance can vary contextually (Hand, 1986; Kaufmann, 1983), and thus dominance measured in different social contexts could have different behavioural implications, and it is a plausible assumption that dominance measured based on joins could capture different variation than aggression dominance. While scrounging occurs during foraging and year-round, aggressive behaviour is more likely to fluctuate over time and contexts, and how aggressive individuals are during foraging could be related to other aspects such as mating competition. The sample size for scrounging events was also slightly bigger than for aggressions and events were more evenly distributed between individuals, also within the video subset (Table 6). Had dominance been measured at another point in time, aggressions could have been more prevalent among certain or all individuals, and one would expect for example increased intrasexual conflict which could manifest in different patterns when predicting foraging behaviour based on a dominance measure more related to a non-foraging context.

There is also a certain amount of circularity when predicting scrounging behaviour based upon dominance scores that were themselves determined from scrounging displacements. There is a possibility that we recorded more (and thus more accurate) dominance data for the individuals that were already inclined to scrounge more. Therefore, some biological patterns may have been hidden from these analyses, because of inaccurate hierarchies due to missing dominance data for some less represented individuals, but this issue is likely small when using the large RFID dataset. In the context of this study, and studies such as Lendvai et al. (2006), it was evident from the video analysis that aggressive behaviour was also mostly happening in the context of scrounging, so there is a possible issue of circularity here as well. However, in this case aggression and scrounging are distinctly different behaviours, which somewhat reduces this complication, and would argue for changing the main dominance measure to aggression dominance. So, in the future it would be useful to compare our results with ones using dominance based on aggressive interactions outside any foraging contexts. Within this dataset, however, one could somewhat reduce the confounding of dominance and scrounging by distinguishing between displacements during initiated scrounges and displacements during patch defence. It is likely that the defender of the patch has obtained it by producing, and so wins and losses calculated based on the defending of a patch can be used as a separate dominance measure that can be compared with dominance calculated on wins and losses from only initiated scrounges. Furthermore, to increase the number of interactions to base the dominance measurements, the dominance measures used in this thesis is based on wins and losses during both initiation and defence, which is likely to somewhat reduce the bias that is more dominance data for scrounging individuals.

Defining 'responsiveness' and 'impact'

When testing individual differences in responsiveness and impact in the context of scrounging behaviour, it is likely that measures chosen to quantify such traits could affect the patterns that will emerge. Different variables can reflect different aspects of the social dynamics, and just like dominance, they can be context dependent (Hand, 1986; Kaufmann, 1983). Therefore, this must be true of responsiveness and impact, as is somewhat indicated by how responsiveness and impact decreased on the second trial day. For example, while dominance was found to be negatively related to responsiveness, and to have an impact on scrounging behaviour (note that responsiveness and impact was considerably negatively correlated. Appendix 2: Table A9), dominants could be responsive in another context or other properties could evoke impact when using another behaviour, such as producing, as the proxy for impact. Importantly, in this study we found that focal scrounging behaviour was positively related to scrounging behaviour in social partners. In terms of the negative frequency dependence in the producer-scrounger game, where both strategies should do better when proportionately rare, this positive change in scrounging behaviour in response to opponent scrounging behaviour does not make sense. In theory, flexible individuals should produce more due to the increasing benefit of the finders advantage when the amount of scrounging increases. This indicates that the responsiveness we are seeing is not a result of frequency dependence in the producer-scrounger game, but possibly the result of social mechanisms promoting coordinated versus independent foraging, probably as a product of group 'anti-predator' cohesion in response to a lack habituation to a relatively novel social foraging environment.

Related to the explanation of responsiveness in terms of synchronised foraging as a result of foraging close together, in tree sparrows (*Passer montanus*), it was found that scrounging behaviour increased during high predation risk, and it was proposed that even subordinates that should normally produce could prefer scrounging in this scenario because the cost of scrounging would be relatively small compared to the cost of being preyed upon if they do not have the reserves to wait for safe foraging opportunities (Barta et al., 2004). This could contribute in explaining the coordinated scrounging response, but it still requires an underlying producer-scrounger dynamic that the present study lacks. Furthermore, the negative relationship between dominance and responsiveness was weaker on the second trial day. If the birds were more habituated to the experimental setup during the second day, the coordinated foraging effect might be expected to be smaller on this day because individuals felt safer and thus foraged more independently of each other. Likewise, if they felt less safe on the first day, this could motivate them to forage closer together for anti-predator reasons (Carere et al., 2009), which would incidentally lead to more scrounging in the form of joining or foraging more closely together. Overall, in light of the emergent patterns, there is a question if this study failed to produce producer-scrounger dynamics in the theoretical sense due to lack of individual habituation, and this must be considered as part of any further interpretation of these data.

Disturbance effects of lack of habituation

Trial day influenced the propensity to use scrounging behaviour, and both the effect of dominance and body mass differed between trial days, perhaps due to differences in habituation versus disturbance in these foraging groups. The relationship between scrounging and dominance was more negative on the first day, while the relationship between body mass and scrounging was more negative on the second day, and in general, scrounging behaviour was more pronounced on the first day. This relates back to the finding of more responsiveness on the first day, and more independent foraging on the second. If the birds were less habituated on the first day, causing more disturbance effects, less scrounging by dominants could be explained by dominants being more cautious and waiting for safe foraging opportunities because they have the reserves or priority of access to do so, and again, if the food abundance has not yet been properly assessed on the first day, the same effect would not exist in subordinates that do not have the reserves to wait for safe foraging opportunities, but should then choose scrounging for anti-predator reasons as the cost of scrounging would be relatively small compared to the cost of being preyed upon (Barta et al., 2004).

Furthermore, the disturbance (or lack of habituation) effect could have a negative effect on foraging overall, meaning a reduction in both producing and scrounging. This could have resulted in more of a producer-scrounger dynamic on the second day, while the observed scrounging patterns on the first day could be more related to (perceived) anti-predator effects or another mechanism promoting benefits of synchronised behaviour in more threatening environments. If so, individuals foraged more independently on the second day, and the stronger negative effect of body mass on scrounging behaviour could be a continued effect of heavier individuals having sufficient reserves not to scrounge. In a dynamic, state-dependent modelling approach, Rands et al. (2003) showed that sufficiently high benefits of foraging together, for example through lower predation risk, can promote synchronised behaviour and the emergence of leader versus follower roles. Additionally, Koykka & Wild (2015) determined in their model that kinship is sufficient to promote leader and follower roles even if there is no initial difference in condition. So, the patterns observed in this study could be a result of leader-follower dynamics based on both or either kinship and differences in state, rather than dynamics expected from producer-scrounger theory. Relating this back to the all positive scrounging adjustment in responsiveness, this is further supported by a study on great tits (*Parus major)* where reactive individuals were found to be more socially attracted to their conspecifics (Aplin et al., 2014). If this is true for the sparrows as well, this dynamic can explain why scrounging behaviour by dominants led subordinates to scrounge more, and differences in responsiveness and propensity to scrounge between days could follow different dynamics on the two days.

Furthermore, there might be spatial component to the observed dynamics. In sparrows, there is evidence that vigilance behaviour is affected by distance between flockmates (Elgar et al., 1984), indicating potential anti-predator benefits of foraging closer together. Boujja-Mijor et al. (2018) also found that house sparrow males with larger bibs (indicative of higher dominance) spent less time being vigilant, demonstrating inter-individual differences in perceived predation risk and also a lower need for social monitoring in dominants. This could further support the synchronised foraging response, where lower perceived chances of predation in dominants drives them to be the initiators of group foraging positions and flock movements. Supporting this, Kurvers et al. (2010) demonstrated a difference in independent decision making where bolder individuals had a greater influence on group decisions and Tóth et al. (2014) found that male house sparrows were more consistently followed than females. So, in light of greater disturbance effects and presumably higher perceived predation dangers on the first day, anti-predator group density effects and leader-follower dynamics could have played a large role in shaping what was recorded as 'producing' on the edges of the flock versus 'scrounging' nearer the middle of the flock. Meanwhile, on the second day when the birds are more habituated, the more traditional (and not mutually exclusive) producer-scrounger dynamics and independent foraging could have been more prominent within our data. If so, the more negative effect of body mass on scrounging behaviour found on the second trial day could be explained by them having sufficient reserves and thus being even less inclined to scrounge on this day because they have had more of chance to assess the food availability in the experimental setup and observed it to be abundant.

Hypothesis 1 – Differences in scrounging behaviour

For the hypothesis testing, which one should remember *a priori* related specifically to producer-scrounger rather than leader-follower dynamics, we first tested the individual consistency and differences in use of scrounging behaviour, in terms of mean total scrounging and proportion scrounging. Individuals were found to be repeatable in both mean total and proportion scrounging (0.71 and 0.693, respectively), supporting the suggestion that the observed differences in scrounging behaviour were biologically meaningful. This is further supported by the findings of similar repeatabilities in other social behaviours (Aplin & Morand-Ferron, 2017; David et al., 2011; Trnka et al., 2013) and slightly higher than those found in some non-social behaviours (Dingemanse et al., 2002; Hardman & Dalesman, 2018; Ligorio et al, 2020). As a social behaviour, scrounging (or joining or foraging close to others) is likely affected by both internal and external factors. So, the high repeatability found across days suggests that individuals either act consistently different in each distinct social environment on each day, or that they consistently express similar proportions across all social environments. Within the mixed-effect models, both FocalID and GroupID explained only small amounts of variation in both mean and proportion scrounging because most of the variation in scrounging behaviour was explained by the fixed effects (FocalID: 0.113 and 0.055, GroupID: 0.099 and 0.000, respectively).

As predicted, heavier males showed a higher proportion scrounging. This same relationship was negative in females, suggesting sex-specific differences in the conditional costs and benefits of scrounging. This could be explained body mass as a stronger predictor of competitive ability in males, making scrounging more beneficial. In pigeons (*Columba livia)*, artificial mass loading caused an increase in dominance hierarchy positions in males, but not in females (Portugal et al., 2020), also illustrating sex-specific effects of mass. The sparrows used in our trials were obtained from house sparrow populations where a certain level of inbreeding has previous been recorded (Jensen et al., 2007), so the limited rates of natal dispersal here mean that it is likely that a fair number of the groups tested contained related individuals, and so there could be kin-effects at play. So, if our birds were related, these findings also contrast with those of Tóth et al. (2009), demonstrating that males (that have the choice due to dominance) should scrounge less from kin, and (more subordinate) females should be allowed to scrounge more from kin. The genetic relatedness in these birds could be tested in the future, as blood to assess relatedness was collected on the birds used in this experiment, although the results of any molecular analyses were not available in time for use in this thesis.

A similar negative relationship was found for the effect of dominance in females on both mean total and proportion scrounging, while for males there was no significant relationship. Thus, there are several indicators of sex-specific effects on scrounging behaviour. In this population of house sparrows, males were found to be slightly more dominant than females on average (Table A8). If females were comparatively less dominant than males, dominant and heavier females could use their competitive advantage to produce with minimal disturbance while somewhat avoiding the costs of being scrounged upon, rather than engage in higher cost scrounging. Furthermore, Tóth et al. (2009) found in their study that females scrounge more from relatives, while this was not true for males, so if individuals are related, more subordinate females could scrounge from dominant males inclined to kin-helping, and they also found that dominants scrounge less from kin than subordinates. If then also taking into consideration the finding that reactive individuals have been found to be more socially attracted to their conspecifics (Aplin et al., 2014), and that females in this study were found to be somewhat more responsive than males, it is plausible that dominant males might allow these scrounging efforts because there are social bonds or kinship present and they are acting as leaders. This is then supported by the finding that leader-follower dynamics could occur due to kinship alone (Koykka & Wild, 2015), in addition to differences in individual energetic state.

There was also a significant negative interaction between dominance and body mass, which suggests that scrounging behaviour, in general, decreased with increasing body mass, but more so if individuals were dominant, even though a non-significant main effect of body mass for both dominants and subordinates suggests that this effect was in reality small. In great tits (*Parus major*) during group foraging in winter, dominant individuals have been found to have a generally lower body mass in predictable environments, as their primary access to resources means they do not have to pay the cost of maintaining a constantly high body mass (Krams et al., 2010). There was a very slight negative correlation between dominance and body mass, and in our experimental set-up, there was plenty of food and predictable food access, so the heavier dominants may have had access to sufficient reserves to not focus their efforts on scrounging. However, this dominance mass effect should be assessed with more careful considerations. The essentially *ad lib* food access in this experiment could suggest that this should be true for subordinates as well. However, dominants might still be defending resources for monopolization reasons, giving the subordinates lower food access, and thus we might predict greater mass loss by dominants whilst in captivity. Supporting this claim, Lendvai et al. (2006) found that more dominant individuals increased their scrounging in an energetically challenging situation. This matched Barta and Giraldeau's (2001) state-dependent model prediction that individuals with low reserves increased their scrounging (especially early in the day), which is in line with our finding that individuals with higher reserves that also have access to primary resources would scrounge less in a predictable, abundant environment. Still, our finding here of proportionately less scrounging by dominants is in contrast to other studies, and it as previously been found that scrounging frequency increases with dominance (Liker & Barta, 2002).

Hypothesis 2 – Differences in responsiveness

In the second *a priori* hypothesis, I tested the consistency and individual differences in 'responsiveness' in changing between producing versus scrounging behaviour. Firstly, consistent individual differences in responsiveness across trial days was predicted, and individuals were found to be moderately repeatably in their slope values (0.524 and 0.380

without trial day). This value is within the repeatability range found for responsiveness measures in other studies (Strickland et al., 2021), and thus there is support for responsiveness as a biologically meaningful property of the individual. However, in the mixed-effect models, FocalID explained only a very small amount of the variation in responsiveness (0.020), and GroupID explained none (0.000), and so it seems to be the phenotypic attributes that were captured by the fixed effects that explained most of the within- and among-individual variation in responsiveness. The steepness of each individual's responsiveness slope that is used as the response in this model was extracted based upon the focal individual's change in scrounging as a response to average opponent scrounging (see Statistical Analyses), and so the variation in the social environment across groups (i.e. the GroupID effect) was essentially captured by this response variable.

In females, the relationship between dominance and responsiveness was significantly negative, meaning that this study's prediction of more dominant individuals being less responsive was met in females. Similarly, heavier individuals were found to be less responsive if they were also more dominant, meaning that the prediction of larger individuals being less responsive was met for dominants. Natarajan et al. (2009) found that the ability to plastically adjust levels of aggressive behaviour in different social contexts was lower for very aggressive individuals, also demonstrating individual differences in social responsiveness. For subordinates, the relationship appeared to be opposite, and the interaction term involved a positive relationship where heavier individuals seemed to be scrounging more in response to the scrounging of others. These patterns should be interpreted in the context of what this responsiveness measure is, namely a change in scrounging behaviour. No individuals had negative responsiveness slopes, meaning that all individuals that responded to an increase in scrounging by their opponents did so by increasing their own scrounging. Then, looking back at the finding that dominant females scrounged less, the lack of responsiveness in scrounging behaviour in dominant females could result from the same proposed mechanism that makes them scrounge less in general, namely an affinity for producing with minimal disturbance. Alternatively, if the birds were genetically related, it could again be related to the findings of Tóth et al. (2009) that dominant individuals scrounge less from kin. Furthermore, dominant individuals that are also heavier should, according to our predictions, be less responsive because they do not need to pay the cost of social plasticity. It is, however, less obvious why heavier subordinates should be more responsive, but this could be related to predation trade-offs. If individuals felt unsafe, it would prompt them to forage closer together, and while lighter subordinates might not have the option to scrounge more, heavier subordinates do because of increased competitive ability, giving them an increased benefit of foraging closer together in addition to the lowered predation-risk. While the differing effect of mass between dominants and subordinates was significant and can somewhat be reasoned, it is necessary to remember that the effect of body mass alone on responsiveness was non-significant for both parts, and so the real-life expression of the discussed effect is likely small.

Hypothesis 3 – Differences in impact

The third *a priori* hypothesis tested the consistency and individual differences in social 'impact'. Given by the positive slopes for responsiveness, impact was not what we intended in light of producer-scrounger dynamics, but rather seemed to be a result of a leader-follower dynamic where individuals deemed impactful were indirectly impacting their conspecifics by acting as the leader in a coordinated feeding response and then the impact would in turn be the responsive individual's change in behaviour due to this synchronisation of foraging. Even so, the consistency in individual impact across trial days was predicted, and a repeatably value of 0.206 (0.000 without trial day, meaning that variance masking individual consistencies may have been accounted for by including day effects) was obtained. Thus, individual repeatability in impact was somewhat low to possibly non-existent, which might have been influenced by the fact that a large proportion of the impact estimates were approaching zero. Furthermore, it is difficult to determine what is expected in terms of consistency for individual impact, because for repeatability of social impact as a trait we lack the full data set needed here to properly assess its variation within and among individuals. FocalID and GroupID both explained only very small amounts of the variation in individual impact (0.059 and 0.009, respectively), with the residual variation being 0.245, meaning that there was a considerable amount of variation in social impact not captured by the effects included in the model. This could mean that there are other, more meaningful traits to explore as the predictor of social impact in this system. However, these results could also be an artefact of underfitting in the model. The assumption concerning a normal distribution of the residuals was perhaps not fulfilled here, and even though a normal distribution still provided the best model fit, residuals were not sufficiently normally distributed and could have biased any model estimates.

There was a significantly positive effect of dominance on impact, meaning that the prediction of dominants having more impact was met in the sense that dominant individuals made their opponents scrounge more. Again, this must be interpreted in the context of the solely positive responsiveness slopes and the scrounging behaviour on which the impact was estimated. In this case, ‘impact’ represents how much an individual’s scrounging behaviour made opponents scrounge more. So, scrounging behaviour by dominants made opponents on average scrounge more. If dominants are bolder, taking more risks and thus foraging more independently, this effect is supported by the finding that bold individuals often lead collective group decisions (Kurvers et al., 2010). Furthermore, Tóth et al. (2014) found that individuals that were more frequently followed were more often involved in aggressive interactions, which could relate being followed to dominance, as aggressiveness has been positively correlated with dominance rank in the house sparrow (Riters et al., 2004). These findings would then support the positive effect of more dominant individuals having more impact in terms of initiating collective foraging. Likewise, the finding by Aplin et al. (2014) that reactive individuals are more socially attracted to conspecifics would support that the response elicited is a synchronisation of scrounging behaviour as a result of foraging closer together. They also found that reactive individuals were drawn to central positions in the group, while pro-active individuals, who are generally also bolder and more aggressive, acted more in the peripheries, arguing that this difference can emerge from different trade-offs in risk. Further, if relatedness is high, dominants could be less responsive in their scrounging behaviour because they are less inclined to scrounge from relatives (Tóth et al., 2009), while they could also be more inclined to let kin scrounge from them due to higher reserves. Subsequently, dominants can monopolize a resource using scrounging and then help kin by letting them scrounge from this resource, essentially acting like leaders. Still, this does not tell us why specifically scrounging behaviour by dominants should make their opponents scrounge more, but one possibility is that dominants can monopolize a resource using scrounging and subsequently help kin by letting them scrounge from this resource, acting like leaders.

For impact, there was also a weakly significant interaction between dominance and body mass, as well as for dominance and sex. Firstly, in line with earlier predictions, heavier individuals that were also more dominant had a higher impact, while the interaction plot showed that this trend was negative for subordinates. This could be related back to the reasoning that scrounging by dominants made individuals scrounge more because heavier dominants could monopolize resources and then help kin or social partners at a low cost because of their even higher reserves. Additionally, female dominants were found in this study to use scrounging behaviour significantly less, but overall, females scrounged slightly more than males, and the positive interaction between dominance and mass on impact was strongest in males. This finding could be supported by the study by Tóth et al. (2014), demonstrating that male house sparrows were consistently followed more than females, and then the effect of mass could indicate even higher reserves and increased opportunity to allow scrounging.

In more of a leader-follower (edge versus centre flock) dynamic like the one described above, it is intuitive to think that leading individuals should be at the front edge of groups, and hence scrounging is likely to increase when individuals were foraging closer together. Producing should therefore intuitively occur more at group peripheries, making producers the instinctive group leaders. For the impact variable it was scrounging behaviour in the leading individuals that initiated a response in their conspecifics, so this indicates the leading individuals pursued producing individuals. Hirsch (2007) argue that it can be advantageous for dominant individuals in a producer-scrounger scenario to obtain front central positions, rather than a position at the very front, and this spatial pattern has been documented empirically (Robinson, 1981). So, while the aforementioned leader-follower dynamic could indicate that leading individuals should be at the group peripheries, Bode et al. (2012) predicted in their model that leading does not have to happen from frontal positions. So, this spatial pattern can explain why the leading individuals are scroungers. Again, while the difference in dominance is likely to represent a real effect, it is necessary to remember that the main effect of body mass was non-significant for both subordinates and dominants, so the effect of mass here likely represents only small real-life consequences. Furthermore, the kind of impact found in this study is not what was originally expected, as the prediction was that social partners of dominants should scrounge less due to the conditional cost of scrounging from traditionally high competitive individuals. Even so, dominant and heavier individuals were still impacting the behaviour of their social partners, but not in the way expected based on producer-scrounger dynamics, but rather by acting as leaders.

Conclusions and future directions

The accuracy of the findings discussed in this study might also be affected by the inaccuracy of the RFID dataset used. For instance, the RFID data cannot accurately distinguish between foraging events and events where individuals incidentally appear in the vicinity of a well. Thus, one should aim to improve the accuracy of the RFID estimates for example by analysing a larger video subset for optimisation. Additionally, there is the issue of performing statistics on statistical estimates here, especially when explaining variation in responsiveness and impact. To obtain the necessary measurements within the time limits of this thesis, we had to adopt this approach and thus make an assumption of limited within-individual variance in the data. This assumption is, however, not in line with the possible error in the RFID data, and even if this error was reduced, one should aim to use more appropriate full statistical modelling approaches to avoid this issue. We also suggest that responsiveness and impact should be measured based on other traits than opponent scrounging, such as opponent producing or dominance, to assess whether more typical patterns will be displayed.

Overall, this study has revealed consistent individual differences in both tactic use and responsiveness, as well as individual differences in impact, although the consistency in this latter trait was less clear. Differences in phenotypic traits consistently explained most of the variation in the main responses of interest, and there was evidence fort both dominance, body mass and sex effects, although not always in the expected direction. Further observed phenotypic variation could likely be explained by a mix of additional information on energy reserves, kin selection, inter-individual spacing in relation to predator avoidance whilst foraging, and data on leader-follower dynamics in the place of the expected effects of competitive ability and producer-scrounger negative frequency dependence. There was also evidence for plastic adjustment of behaviour in response to conspecifics, thus if the individual traits associated with differences in responsiveness and impact are rooted in genetic variation, this could indicate the presence of feedbacks between DGEs and IGEs in social interactions affecting evolution. Furthermore, the responsiveness and impact patterns observed were not in the direction expected, suggesting that the patterns could be better explained by a lack of habituation to the experimental set-up and thus disturbance effects promoted spatially tighter foraging groups and apparent leader-follower dynamics in who moved away from the others to ‘produce’. This dynamic could be better assessed in the context of larger social groups, because of greater flock cohesions and because the three-bird assays likely caused larger disturbance effects due to higher stress of foraging in smaller groups than normal. Any patterns the leader-follower and group spacing dynamics should also be easier to study in a larger group context, seeing as the central versus periphery positions is hard to distinguish between only three individuals. To conclude, this study has revealed that consistent individual differences are apparent in a population of house sparrows, that these differences are integrated with phenotypic attributes and that behaviour is affected by social environment. Still, across year comparisons and further empirical testing of proposed explanations should be performed to evaluate these results within the larger study here.

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Appendix 1 – *Mixed-Effect Models on Data Sub-Sets by Sex and Trial Day*

Output for further verification of interaction effects for Hypothesis 1 (Table A1, A2, A3 & A4), Hypothesis 2 (Table A5 & A7) and Hypothesis 3 (Table A6 & A7). For mean scrounging based upon RFID scrounging dominance, the data and models have been divided by sex and trial day (Table A1), and by dominance (Table A4). For proportion scrounging based on RFID scrounging dominance, the data has been filtered by sex and trial day (Table A2), and for dominance (Table A4). For proportion scrounging, the model based on aggression dominance has also been filtered by sex and trial day (Table A3). The models for responsiveness and impact have also been filtered by sex and trial day (Table A5 & A6), as well as for dominance (Table A7).

Table A1: *Output from mixed-effect models explaining individual total mean scrounging for males versus females and first versus second trial day. The data used in the model has been divided to include datapoints for only females or males, or only trial day 1 or 2. The fixed effects for the sex models include dominance (based on RFID scrounging), body mass, trial day and all their two-way interactions. The fixed effects for the trial day models include dominance (based on RFID scrounging), body mass, sex and all their two-way interactions. Fixed effects are reported with standard errors and p-values, and effect sizes have been exponentiated as the response variable was log transformed. Random effects are reported as variance explained.*

Fixed Effects	**Trial Day 1** *Mean Scrounging*	**Trial Day 2** *Mean Scrounging*	**Female** *Mean Scrounging*	**Male** *Mean Scrounging*
Intercept	8.890± *1.090* *(p <0.001)*	6.861± *1.078* *(p <0.001)*	9.015± *1.086* *(p <0.001)*	7.826± *1.079* *(p <0.001)*
Dominance	0.942± *1.016* *(p=0.008)*	0.996± *1.017* *(p =0.170)*	0.950± *1.019* *(p=0.008)*	1.004± *1.016* *(p =0.801)*
Body Mass	0.943± *1.032* *(p=0.078)*	0.977 ± *1.031* *(p =0.607)*	0.938± *1.037* *(p=0.078)*	1.007± *1.041* *(p =0.002)*
Body Mass * Dominance	0.980± *1.007* *(p=0.019)*	0.990 ± *1.008* *(p =0.006)*	0.993± *1.010* *(p=0.464)*	0.964± *1.012* *(p <0.001)*
Body Mass*Sex	1.035± *1.048* *(p=0.635)*	1.007± *1.048* *(p =0.705)*	-	-
Sex	0.893± *1.072* *(p=0.033)*	0.944 ± *1.087* *(p =0.493)*	-	-
Sex*Dominance	1.055± *1.020* *(p=0.052)*	1.001 ± *1.019* *(p =0.030)*	-	-
Trial Day	-	-	0.755± *1.052* *(p <0.001)*	0.820± *1.050* *(p <0.001)*
Dominance*Trial Day	-	-	1.045± *1.016* *(p=0.005)*	1.013± *1.013* *(p =0.315)*
Body Mass*Trial Day	-	-	1.001± *1.033* *(p=0.977)*	0.998± *1.033* *(p =0.942)*
Random Effects				
Focal ID	0.161	0.242	0.094	0.121
Group ID	0.136	0.059	0.111	0.078
Dominance|GroupID	<0.001	<0.001	<0.001	0.001
Residual	0.002	<0.001	0.092	0.093

Table A2: *Output from mixed-effect models explaining individual proportion scrounging for males versus females and first versus second trial day. The data used in the model has been divided to include datapoints for only females or males, or only trial day 1 or 2. The fixed effects for the sex models include dominance (based on RFID scrounging), body mass, trial day and all their two-way interactions. The fixed effects for the trial day models include dominance (based on RFID scrounging), body mass, sex and all their two-way interactions. Fixed effects are reported with standard errors and p-values, and on log odds scale as the model follows a binomial distribution. Random effects are reported as variance explained.*

Fixed Effects	**Trial Day 1** *Prop. Scrounging*	**Trial Day 2** *Prop. Scrounging*	**Female** *Prop. Scrounging*	**Male** *Prop. Scrounging*
Intercept	-1.732± *0.120* *(p <0.001)*	-2.003± *0.133* *(p <0.001)*	-1.362± *0.261* *(p <0.001)*	-1.790± *0.260* *(p <0.001)*
Dominance	-0.190± *0.049* *(p<0.001)*	-0.074± *0.053* *(p =0.158)*	-0.309± *0.109* *(p=0.004)*	0.031± *0.073* *(p =0.677)*
Body Mass	-0.293± *0.073* *(p<0.001)*	-0.345± *0.085* *(p <0.001)*	-0.345± *0.171* *(p=0.043)*	0.480± *0.170* *(p =0.005)*
Body Mass * Dominance	-0.068± *0.017* *(p<0.001)*	-0.049± *0.019* *(p =0.010)*	-0.015± *0.024* *(p=0.514)*	-0.096± *0.021* *(p <0.001)*
Body Mass*Sex	0.487± *0.112* *(p<0.001)*	0.269± *0.121* *(p =0.027)*	-	-
Sex	-0.282± *0.170* *(p=0.096)*	-0.218± *0.183* *(p =0.232)*	-	-
Sex*Dominance	0.278± *0.055* *(p<0.001)*	0.167± *0.057* *(p =0.003)*	-	-
Trial Day	-	-	-0.302± *0.165* *(p =0.068)*	-0.193± *0.164* *(p=0.240)*
Dominance*Trial Day	-	-	0.112± *0.056* *(p=0.044)*	0.029± *0.043* *(p =0.495)*
Body Mass*Trial Day	-	-	0.044± *0.109* *(p=0.686)*	-0.263± *0.106* *(p =0.013)*
Random Effects				
Focal ID	0.006	0.095	0.000	0.009
Group ID	0.001	<0.001	0.010	0.000
Dominance|GroupID	0.015	0.023	0.092	0.016

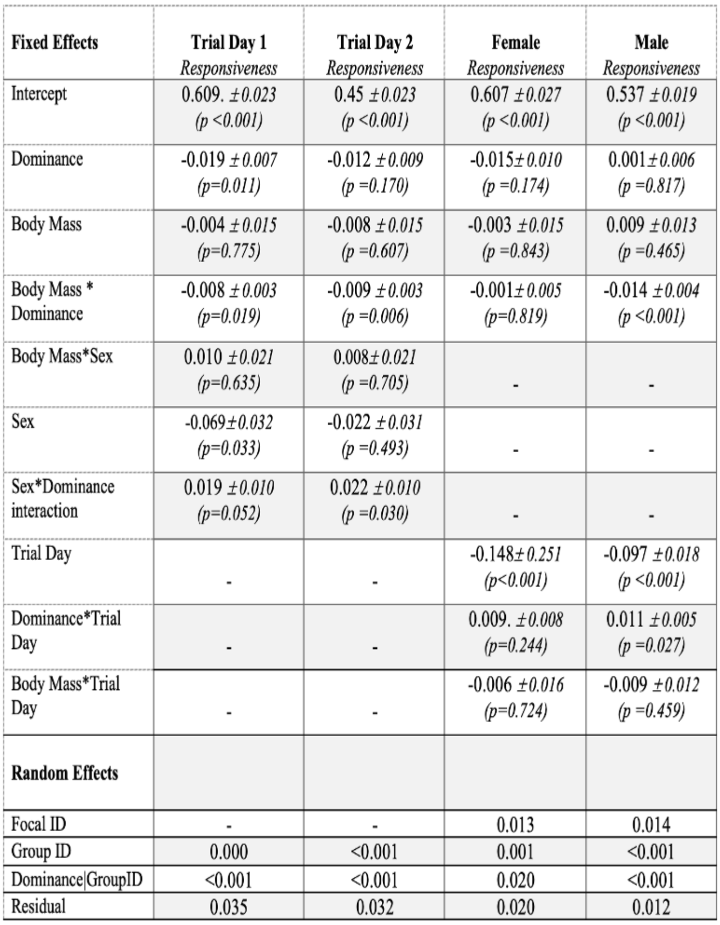
***Table A3:** Output from mixed-effect models explaining individual proportion scrounging for males versus females and first versus second trial day. The data used in the model has been divided to include datapoints for only females or males, or only trial day 1 or 2. The fixed effects for the sex models include dominance (based on video aggressions), body mass, trial day and all their two-way interactions. The fixed effects for the trial day models include dominance (based on RFID scrounging), body mass, sex and all their two-way interactions. Fixed effects are reported with standard errors and p-values, and on log odds scale as the model follows a binomial distribution. Random effects are reported as variance explained.*

Fixed Effects	**Trial Day 1** *Prop. Scrounging*	**Trial Day 2** *Prop. Scrounging*	**Female** *Prop. Scrounging*	**Male** *Prop. Scrounging*
Intercept	-1.654 ± *0.117* *(p <0.001)*	-2.005± *0.135* *(p <0.001)*	-1.535±*0.267* *(p <0.001)*	-1.815±*0.261* *(p <0.001)*
Dominance	-0.194± *0.134* *(p= 0.147)*	0.137±*0.161* *(p =0.395)*	-0.340± *0.393* *(p =0.387)*	-0.885±*0.243* *(p <0.001)*
Body Mass	-0.216±*0.07* *(p=0.002)*	-0.283±*0.079* *(p <0.001)*	-0.220±*0.164* *(p =0.180)*	0.504±*0.176* *(p = 0.004)*
Body Mass * Dominance	-0.007±*0.053* *(p=0.901)*	-0.024±*0.058* *(p =0.682)*	0.226±*0.082* *(p=0.006)*	0.160±*0.060* *(p = 0.007)*
Body Mass*Sex	0.254±*0.104* *(p=0.015)*	0.031±*0.114* *(p =0.786)*	-	-
Sex	-0.297±*0.171* *(p=0.083)*	-0.106±*0.187* *(p =0.572)*	-	-
Sex*Dominance	-0.104±*0.145* *(p=0.474)*	-0.087±*0.154* *(p =0.573)*	-	-
Trial Day	-	-	-0.300±*0.170* *(p=0.078)*	-0.136±*0.163* *(p =0.403)*
Dominance*Trial Day	-	-	-0.295. ±*0.138* *(p=0.033)*	-0.540±*0.138* *(p <0.001)*
Body Mass*Trial Day	-	-	-0.072±*0.104* *(p=0.492)*	-0.320±*0.108* *(p = 0.003)*
Random Effects				
Focal ID	0.000	0.031	0.000	0.033
Group ID	0.011	0.009	0.000	<0.001
Dominance|GroupID	0.218	0.337	2.577	0.138

Table A4: *Output from mixed-effect models explaining individual mean total and proportion scrounging for dominants versus subordinates (based on RFID scrounging dominance). The data used in the model has been divided to include data for only dominants or subordinates. The fixed effects for each of the models includes sex, body mass, trial day and all their two-way interactions. Fixed effects are reported with standard errors and p-values, and as the exponent of the original output for mean scrounging, and on log odds scale as for proportion scrounging. Random effects are reported as variance explained.*

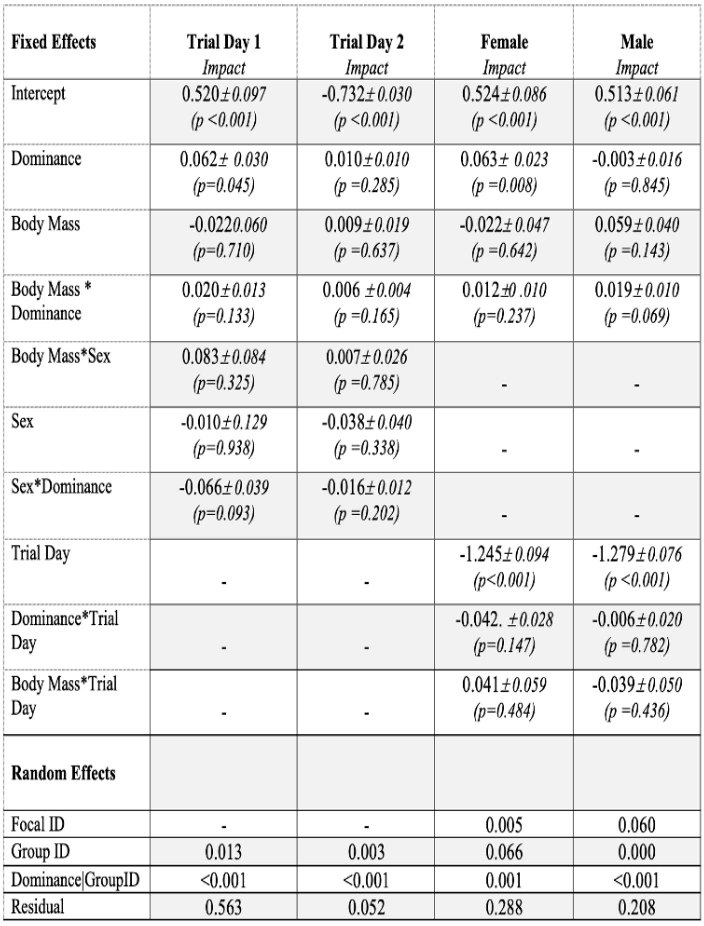
Fixed Effects	**Dominants** *Mean scrounging*	**Subordinates** *Mean scrounging*	**Dominants** *Prop. scrounging*	**Subordinates** *Prop. scrounging*
Intercept	7.999. ±*1.102* *(p <0.001)*	10.309±*1.112* *(p <0.001)*	-1.751 ±*0.383* *(p <0.001)*	-0.907±*0.333* *(p =0.007)*
Body Mass	0.927±*1.057* *(p=0.177)*	0.965±*1.049* *(p =0.463)*	-0.294 ±*0.181* *(p =0.104)*	0.155 ±*0.162* *(p =0.338)*
Sex	0.944±*1.128* *(p=0.634)*	0.798± *1.121* *(p =0.052)*	-0.339 ±*0.522* *(p =0.516)*	-0.570 ±*0.490* *(p =0.245)*
Trial Day	0.829±*1.076* *(p=0.012)*	0.687±*1.076* *(p <0.001)*	-0.140 ±*0.238* *(p =0.557)*	-0.481 ±*0.214* *(p =0.025)*
Body Mass*Sex	0.997±*1.074* *(p=0.961)*	1.112±*1.068* *(p =0.113)*	0.156 ±*0.120* *(p =0.191)*	0.302 ±*0.121* *(p =0.012)*
Sex*Trial Day	1.003±*1.106* *(p =0.973)*	1.183± *1.107* *(p =0.101)*	0.190±*0.322* *(p=554)*	0.164±*0.311* *(p =560)*
Body Mass*Trial Day	1.019±*1.034* *(p =0.579)*	0.989± *1.033* *(p =0.727)*	-0.006 ±*0.107* *(p=0.953)*	-0.231 ±*0.098* *(p =0.018)*
Random Effects				
Focal ID	0.137	0.111	0.122	0.277
Group ID	0.053	0.137	0.000	0.000
Residual	0.091	0.098	-	-

Table A5: *Output from mixed-effect models explaining individual impact for males versus females and first versus second trial day. The data used in the model has been divided to include data for only females or males, or only trial day 1 or 2. The fixed effects for the different sex models include dominance (based on RFID scrounging), body mass, trial day and all their two-way interactions. The fixed effects for the trial day models include dominance (based on RFID scrounging), body mass, sex and all their two-way interactions. Fixed effects are reported with standard errors and p-values. Random effects are reported as variance explained.*



Fixed Effects	**Trial Day 1** *Responsiveness*	**Trial Day 2** *Responsiveness*	**Female** *Responsiveness*	**Male** *Responsiveness*
Intercept	0.609. ±*0.023* *(p <0.001)*	0.45 ±*0.023* *(p <0.001)*	0.607 ±*0.027* *(p <0.001)*	0.537 ±*0.019* *(p <0.001)*
Dominance	-0.019 ±*0.007* *(p=0.011)*	-0.012 ±*0.009* *(p =0.170)*	-0.015±*0.010* *(p =0.174)*	0.001±*0.006* *(p =0.817)*
Body Mass	-0.004 ±*0.015* *(p=0.775)*	-0.008 ±*0.015* *(p =0.607)*	-0.003 ±*0.015* *(p =0.843)*	0.009 ±*0.013* *(p =0.465)*
Body Mass * Dominance	-0.008 ±*0.003* *(p=0.019)*	-0.009 ±*0.003* *(p =0.006)*	-0.001±*0.005* *(p=0.819)*	-0.014 ±*0.004* *(p <0.001)*
Body Mass*Sex	0.010 ±*0.021* *(p=0.635)*	0.008±*0.021* *(p =0.705)*	-	-
Sex	-0.069±*0.032* *(p=0.033)*	-0.022 ±*0.031* *(p =0.493)*	-	-
Sex*Dominance interaction	0.019 ±*0.010* *(p=0.052)*	0.022 ±*0.010* *(p =0.030)*	-	-
Trial Day	-	-	-0.148±*0.251* *(p<0.001)*	-0.097 ±*0.018* *(p <0.001)*
Dominance*Trial Day	-	-	0.009. ±*0.008* *(p=0.244)*	0.011 ±*0.005* *(p =0.027)*
Body Mass*Trial Day	-	-	-0.006 ±*0.016* *(p=0.724)*	-0.009 ±*0.012* *(p =0.459)*
Random Effects				
Focal ID	-	-	0.013	0.014
Group ID	0.000	<0.001	0.001	<0.001
Dominance|GroupID	<0.001	<0.001	0.020	<0.001
Residual	0.035	0.032	0.020	0.012

Table A6: *Output from mixed-effect models explaining individual responsiveness for males versus females and first versus second trial day. The data used in the model has been divided to include data for only females or males, or only trial day 1 or 2. The fixed effects for the sex models include dominance (based on RFID scrounging), body mass, trial day and all their two-way interactions. The fixed effects for the trial day models include dominance (based on RFID scrounging), body mass, sex and all their two-way interactions. Fixed effects are reported with standard errors and p-values. Random effects are reported as variance explained.*



Fixed Effects	**Trial Day 1** *Impact*	**Trial Day 2** *Impact*	**Female** *Impact*	**Male** *Impact*
Intercept	0.520±*0.097* *(p <0.001)*	-0.732±*0.030* *(p <0.001)*	0.524±*0.086* *(p <0.001)*	0.513±*0.061* *(p <0.001)*
Dominance	0.062± *0.030* *(p=0.045)*	0.010±*0.010* *(p =0.285)*	0.063± *0.023* *(p =0.008)*	-0.003±*0.016* *(p =0.845)*
Body Mass	-0.022*0.060* *(p=0.710)*	0.009±*0.019* *(p =0.637)*	-0.022±*0.047* *(p =0.642)*	0.059±*0.040* *(p =0.143)*
Body Mass * Dominance	0.020±*0.013* *(p=0.133)*	0.006 ±*0.004* *(p =0.165)*	0.012±*0 .010* *(p=0.237)*	0.019±*0.010* *(p =0.069)*
Body Mass*Sex	0.083±*0.084* *(p=0.325)*	0.007±*0.026* *(p =0.785)*	-	-
Sex	-0.010±*0.129* *(p=0.938)*	-0.038±*0.040* *(p =0.338)*	-	-
Sex*Dominance	-0.066±*0.039* *(p=0.093)*	-0.016±*0.012* *(p =0.202)*	-	-
Trial Day	-	-	-1.245±*0.094* *(p<0.001)*	-1.279±*0.076* *(p <0.001)*
Dominance*Trial Day	-	-	-0.042. ±*0.028* *(p=0.147)*	-0.006±*0.020* *(p =0.782)*
Body Mass*Trial Day	-	-	0.041±*0.059* *(p=0.484)*	-0.039±*0.050* *(p =0.436)*
Random Effects				
Focal ID	-	-	0.005	0.060
Group ID	0.013	0.003	0.066	0.000
Dominance|GroupID	<0.001	<0.001	0.001	<0.001
Residual	0.563	0.052	0.288	0.208

Table A7: *Output from mixed-effect models explaining individual responsiveness and impact for dominants versus subordinates (Based on RFID scrounging dominance). The data used in each model has been divided to include data for only dominants or subordinates. The fixed effects for each model include sex, body mass, trial day and all their two-way interactions. Fixed effects are reported with standard errors and p-values. Random effects are reported as variance explained.*

Fixed Effects	**Dominants** *Responsiveness*	**Subordinates** *Responsiveness*	**Dominants** *Impact*	**Subordinates** *Impact*
Intercept	0.555 ±0.031 (p <0.001)	0.524±0.036 (p <0.001)	0.721±0.108 (p <0.001)	0.380±0.097 (p <0.001)
Body Mass	-0.006±0.019 (p=0.745)	-0.003±0.020 (p =0.871)	0.055±0.061 (p = 0.372)	-0.053±0.052 (p =0.312)
Sex	-0.039± 0.041 (p=0.351)	-0.097± 0.050 (p =0.056)	-0.202±0.136 (p =0.140)	0.145±0.135 (p =0.286)
Trial Day	-0.136±0.026 (p<0.001)	-0.170±0.036 (p <0.001)	-1.431±0.124 (p <0.001)	-1.133±0.120 (p <0.001)
Body Mass*Sex	-0.017± 0.024 (p=0.489)	0.033±0.028 (p =0.240)	0.076±0.072 (p =0.293)	0.024±0.066 (p =0.718)
Sex*Trial Day	0.085±0.035 (p =0.019)	0.032± 0.050 (p =0.524)	0.107±0.169 (p=0.530)	-0.144±0.167 (p =0.392)
Body Mass*Trial Day	-0.010±0.012 (p = 0.381)	<0.001± 0.016 (p =0.992)	-0.062± 0.056 (p=0.270)	0.036±0.053 (p =0.500)
Random Effects				
Focal ID	0.018	0.022	0.043	0.065
Group ID	0.000	0.000	0.038	0.000
Residual	0.011	0.021	0.242	0.244

Appendix 2 – *Correlations*

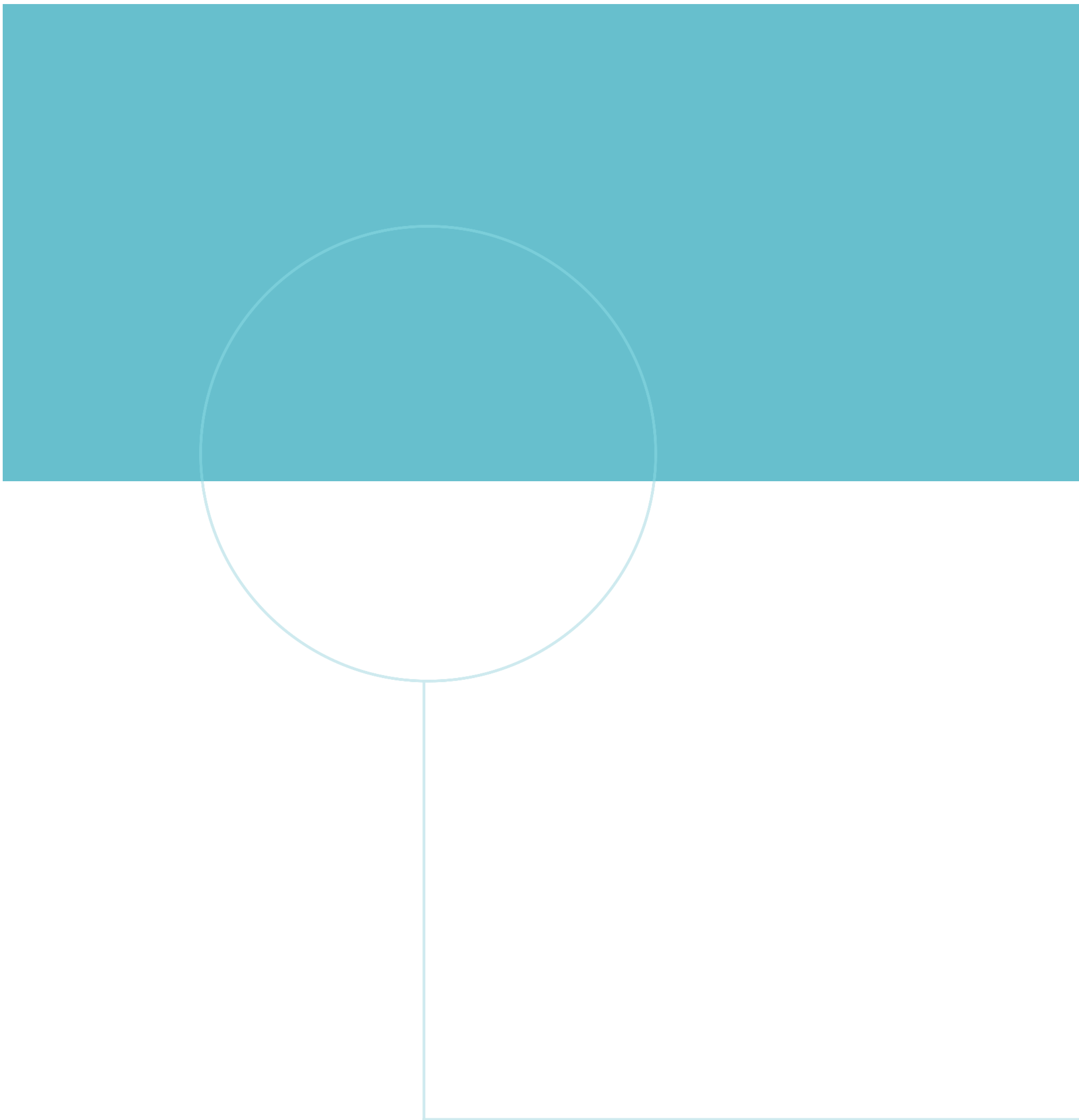
Output from correlation analysis, assessing the interdependence between variables of interest.

Table A8: *Pearson correlations between the main phenotypic traits of interest. In correlations concerning sex, positive values are indicative of a positive correlation between the trait and being male.*

	Sex	David Score	Body Mass
Sex	-	0.027	0.200
David Score	0.027	-	-0.063
Body Mass	0.200	-0.063	-

Table A9: *Among-individual Pearson correlation between responsiveness and impact.*

	Impact
Responsiveness	-0.580



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