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Does individual variation in producer-scrounger behavior covary with individual life-histories?

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ABSTRACT

This thesis explores the relationship between animal behavior, personality, physiology, and pace-of-life syndromes (POLSs). Animal personality refers to consistent individual behavior variations. I aimed to examine the correlation between behavioral traits, physiology, and life-history characteristics, specifically within the fast-slow continuum of POLSs. By studying house sparrows (*Passer domesticus*) through experimental producer-scrounger trials against different opponents over two days, I investigated the influence of social environments on individual behavior. Next, I analyzed the relationship between three reproductive life-history traits (which works as a proxy for reproductive effort), body mass and sex, with individual behavioral differences during producer-scrounger trials. The prediction being that larger house sparrows and males will scrounge more, have more impact and less responsiveness during the producer-scrounger trials, and that this will be associated with a faster pace-of-life. Our findings reveal consistent individual differences in scrounging behavior, impact, and responsiveness. Additionally, a greater winter body mass was positively correlated with larger chicks, more chicks, and lay eggs earlier. While trial day and its interaction with body mass or reproductive variables significantly affect behavior, reproductive traits do not significantly impact producer-scrounger behavior on their own. This indicates a strong day effect, and that the sparrows were not habituated to the experimental setup. Next, females tended to scrounge more than males, and the effects of body size on impact differ between sexes, with larger females being less impactful. Larger individuals exhibit more responsiveness and less impact, with varying effects based on sex. These findings suggest that males and females adopt different behavioral and reproductive tactics based on social environments and body mass. To further investigate the interaction between behavior, physiology, reproductive traits, and pace-of-life, future experiments should minimize habituation effects, increase sample sizes, and consider factors such as kinship and friendships in the social environment.

SAMMENDRAG

Denne oppgaven utforsker forholdet mellom dyrs atferd, personlighet, fysiologi og livstempo-syndromer (POLS). Dyrepersonlighet refererer til konsistente individuelle atferdsvariasjoner. Jeg hadde som mål å undersøke sammenhengen mellom atferdstrekk, fysiologi og livshistoriekarakteristikker, spesielt innenfor det raskt-langsomme kontinuumet til POLS. Ved å studere gråspurver (*Passer domesticus*) gjennom eksperimentelle producer-scrounger-forsøk mot forskjellige motstandere over to dager, undersøkte jeg påvirkningen av sosiale miljøer på individuell atferd. Deretter analyserte jeg forholdet mellom tre reproduktive livshistorietrekk (som fungerer som en proxy for reproduktiv innsats), kroppsmasse og kjønn, med individuelle atferdsforskjeller under producer-scrounger-forsøk. Forutsigelsen er at større gråspurver og hanner vil scrounge mer, ha mer påvirkningskraft og vise mindre tilpasningsdyktighet under producer-scrounger-forsøkene, og at dette vil være assosiert med et «raskere» liv. Funnene våre avslører konsistente individuelle forskjeller i scrounging atferd, påvirkningskraft og tilpasningsdyktighet. I tillegg var en større vinterkroppsmasse positivt korrelert med større unger, flere unger og tidligere egglegging. Prøvedag og interaksjonene dens med kroppsmasse og reproduktive variabler hadde en signifikant effekt på producer-scrounger oppførsel, samtidig som reproduktive egenskaper alene ikke hadde signifikant effekt. Dette indikerer en sterk dagseffekt, og at spurvene ikke var habituert til forsøksoppsettet. Videre hadde hunner en tendens til å scrounge mer enn hannene, og effekten av vekt var forskjellig mellom kjønn, hvor større hunner hadde mindre påvirkningskraft. Større individer viser mer tilpasningsdyktighet og mindre påvirkningskraft, med varierende effekter basert på kjønn. Disse funnene tyder på at hanner og hunner bruker forskjellige atferds- og reproduktive taktikker basert på sosiale miljøer og kroppsmasse. For ytterligere å undersøke samspillet mellom atferd, fysiologi, reproduktive egenskaper og hvor raske liv gråspurvene lever, bør fremtidige eksperimenter minimere tilvenningseffekter, øke prøvestørrelsen og vurdere faktorer som slektskap og vennskap i det sosiale miljøet.

TABLE OF CONTENTS

1. INTRODUCTION

The study of animal behavior and the evolution of social behavioral traits has been an important field of research in biology for many years. Behavioral traits are known to exhibit individual repeatability or "animal personality" (Bell et al., 2009), and the suites of correlated behaviors vary between individuals of the same population forming "behavioral syndromes" (Garamszegi et al., 2013). As an example, more active individuals also tend to show more explorative tendencies and aggression compared to their less active counterparts, and such behavioral syndromes can also affect the reproductive success, as is seen in a population of blue tits (*Cyanistes caeruleus)* (Mutzel et al., 2013).

According to a recent hypothesis, personality differences may couple with certain life-history characteristics. This is because certain general combinations of life-history and behavior are superior to others, of pace-of-life syndromes (POLSs), along a fast-slow continuum (Wolf et al., 2007; Dingemanse & Wolf 2010; Réale et al.*,* 2010; Wright et al., 2019). Pace-of-life syndromes suggests that closely related species or populations that experience different ecological conditions should differ in a suite of metabolic, hormonal and immunity traits. Recently, the consistent association between behavioral traits such as boldness and aggressiveness, and its life-history strategy such as the timing and allocation of resources to reproduction, growth and survival has been incorporated into this POLS (Wolf et al., 2007; Réale et al.*,* 2010;). Variation in life histories arises from the interplay of environmental factors, life-history trade-offs, selection pressures, and genetic variation, as different environments pose diverse challenges and shape the optimal life-history strategies, and their theorized associated behavioral and physiological traits.

Niemelä et al., (2011) integrated behavior with life-history events and showed that in field crickets (*Gryllus spp.*) the faster growing individuals tended to mature earlier and invest less in immune defense than their slower growing counterparts. The study of Araya-Ajoy et al. (2020) looked at generation time as a life-history trait that varies within and among populations and found that the favored generation time in a meta-population of house sparrows (*Passer domesticus*) varied with the densities of the populations, such that in more dense populations, a longer generation time was favored. Therefore, trade-offs between investment in survival and behavior could account for the maintenance of variation in personality traits by favoring certain combinations of behavioral and life-history strategies (Niemelä et al., 2011). Wright et al., (2019) presented a novel perspective on animal personality and life-history evolution, combining recent models of fluctuating density-

dependent selection with the notion of POLSs involving phenotypic co-variation in life-history, morphology, physiology, and behavioral traits along a fast-slow continuum. This continuum ranges from the highly fecund, short-lived, bold, aggressive and highly dispersive 'fast' types at one end of the POLS to the less fecund, long-lived, cautious, shy, plastic and socially responsive 'slow' types at the other end. The suggestion being that this POLS is maintained by fluctuating selection and possibly explains why animal populations show animal personality and behavioral syndromes in many behavioral traits which correlates with their individual pace-of-life.

One problem here is in trying to understand the evolution of individual differences in social behavioral traits in the context of this POLS continuum, because the complexity of social evolution makes it difficult to predict patterns of selection. For example, urban great tits (*Parus major)* are found to exhibit a faster pace-of-life, including better stress handling, more exploration, earlier breeding and faster breath rates (Charmantier et al., 2017). Social environments seems to influence behavioral traits along the POLS continuum, with larger subpopulations of birds showing more scrounging behavior and more socially central individuals being scroungers (Aplin & Morran-Ferron, 2017). Additionally, urban birds seem to display increased aggression, boldness, lower neophobia and higher disturbance tolerance compared to rural birds (Minias, 2015; Davies and Sewall, 2016, Tryjanowski et al., 2016; Lowry et al., 2013). They also exhibit shifts in breeding strategies such as earlier lay dates, smaller clutch sizes and lower reproductive success, showing that behavioral and reproductive traits differ across populations in different environments (Peach et al., 2008; Chamberlain et al., 2009; Rebolo-Ifran et al., 2015). Furthermore, individual differences in animal personality in traits such as aggressiveness, boldness and sociability can affect dispersal tendencies and impact population dynamics (Cote et al., 2010; Duckworth & Badyaev, 2007). Still, the existing literature on the covariance between animal behavior and the POLS yields mixed results. For example, an urban lifestyle that leads to a "faster" type behavior, seems to lead to reproductive behavior associated with a "slower" lifestyle, and points out that we do not yet know how behavior, physiology and reproductive traits are connected. Recognizing social behaviors as outcomes of the POLS continuum illuminates the intricate and interconnected nature of individual differences, social environments, and evolutionary processes. With all this considered, it underscores the necessity for continued research in this area.

Game theory (Maynard Smith 1982; Davies et al., 2007) and the use of predictions regarding an evolutionarily stable strategy (ESS) at equilibrium provides one solution in understanding

the evolution of social behaviors. Mixed ESSs involving more than one behavioral tactic and behavioral polymorphisms in cooperative or conflictive tactics can occur in two ways. One is where the ESS involves each socially plastic individual performing the different tactics on different occasions with a strategy that involves a conditional probability (i.e. reversible plasticity). The second mechanism is a stable polymorphic state where one fraction of the population adopts one fixed tactic or unconditional strategy while the remainder adopts the other(s). Such mixed ESSs require negative frequency-dependent selection, which occurs when the selective value of a phenotype is negatively dependent upon its frequency in the population, such that the relative fitness of each tactic or strategy increases when the frequency of the phenotype decreases. Therefore, when the tactic an individual adopts is determined by some aspect of the individual (e.g. life-history traits, energetic or developmental state, age, condition or body size) that changes throughout its lifetime, or by changes in the social environment (e.g. the state, size, or frequency of other individual types), then the mixed strategy is socially plastic or 'conditional'. As an example, in studies on house sparrows, the frequency of scrounging increased gradually with lowered energy reserves during the first feed of the day (Lendvai et al., 2004). Mixed ESSs involving fixed or unconditional strategies are when the strategy that is set is not determined by changes in the state of the individual or his social environment. As an example, hawks and doves play a game where hawks always fight over the resources, and doves always retreat (Smith & Price, 1973). The genetic basis of behavior tends to be poorly understood in most cases, and it is therefore easier as a first step when using game theory to simply assume perfectly heritable phenotypes under simple natural selection (i.e. the 'phenotypic gambit', Grafen., 1984). Different phenotypes can thus be treated as different strategies in any evolutionary game because they will lead to different rewards in terms of fitness when played against the strategies of other individuals (or players). The mathematical modelling of such games, or evolutionary game theory, has become a widely used tool for explaining natural selection for a range of different social behaviors (Davies et al., 2012).

One such game theoretical model of social interactions between animals is the producer-scrounger game (Barnard & Sibly, 1981). Since there is often an uneven distribution of resources in nature, different strategies in behaviors such as foraging may be used by animals when searching and competing for these resources. This is especially apparent in social foraging, where there is relatively large variation in individual contributions towards searching for new sources of food. The producer-scrounger game was first suggested by Barnard & Sibly (1981) to try and explain the exploitation behavior where some individuals

use the resources discovered or generated by other individuals. The tactic of the 'producer' is to search for and discover new resources, while the tactic of the 'scrounger' is to use social information to join others who have already discovered resources. Thus, collectively scroungers may or may not end up taking a larger proportion of the food than the effort they put into locating it, depending on the size of the 'producer' bonus gained by producers before scroungers join them in exploiting the resource patch (Ranta et al., 1996). The producer-scrounger game involves negative frequency dependence, where scroungers do worse, and producers do better, with increasing frequencies of scrounging in the population (Vickery et al., 1991).

One interesting possibility is that a combination of both the conditional and unconditional mixed ESS can occur in the same population, where some individuals act as either (or mostly as) producers or scroungers most the time with little social plasticity, whilst other individuals alternate more quickly between the two tactics due to the condition of the individual and/or the social environment (Vickery et al., 1991; Belmaker et al., 2012). In models by Dubois et al., (2010) and Katsnelson et al., (2011), more plastic individuals appeared to do better than more fixed strategists, at least initially in a producer-scrounger game, because for more of the time they were able to exist in populations at the ESS where fitness is maximized. However, in these models most of the population ended up consisting of fixed strategists, because the more plastic individuals tended to buffer the fitness of the whole population (including the fixed individuals) by keeping the population at the ESS. The selective pressure these latest models predicts on populations might relate directly to animal personality, because an array of coexisting individual strategies seems possible in the same population involving different amounts of producing versus scrounging (on average) and different degrees of conditionality or social responsiveness and impact (Araya-Ajoy & Dingemanse., 2015). To elaborate, socially responsive individuals are described as individuals who adjust their behavior as a function of the previous interactions of their social partner, and social impact is when the focal individual's trait(s) impacts the phenotypes expressed by its social partners (Dingemanse & Araya-Ajoy., 2015; Araya-Ajoy et al., 2020).

Empirical studies, mostly on house sparrows, have shown that individuals tend to use these two strategies flexibly, switching conditionally between producing and scrounging (e.g. Belmaker et al., 2012). How individuals choose to produce or scrounge, and how much they respond conditionally to their social environments and the impact they have on others (e.g. by being stubbornly fixed), and as the relative benefits and costs of producing versus scrounging

behavior affects the fitness consequences for individuals, it shapes the selective pressures acting on these behaviors. Responsiveness and impact can also evolve, further affecting the evolutionary dynamics of social traits (Araya-Ajoy et al., 2020). These studies also indicate that the producer-scrounger game might involve a combination of genetic components and developmental processes in which individuals have evolved to use environmental cues and/or cumulative personal experience (i.e. learning) to conditionally switch between tactics (Katsnelson et al. 2008; Belmaker et al., 2012). In relation to these ideas, in studies on house sparrows, the frequency of scrounging, and success of aggressive scrounging when doing so, increased (gradually) with increasing dominance rank. (Liker & Barta, 2002; Tóth et al., 2009). At the same time, the reaction towards individuals of close kin seems to vary between the sexes (and dominance). Males target close-kin individuals less frequently in non-aggressive scrounging than unrelated flockmates, whereas females show the opposite trend (Tóth et al., 2009). There are many factors coming into play as to which tactic an individual adopts during the producer-scrounger game, and we need to further explore the connections between body mass, sex, kinship, and behavior to fully understand the reasons for these adaptations.

The producer-scrounger paradigm has revealed much about the evolution of a variety of very sophisticated social strategies and stimulated the simultaneous development of game theoretical models and closely related experimental empirical studies (mostly on house sparrows). It would also seem that we are very close to being able to quantify individual variation in such producer-scrounger behavior, and more interestingly individual differences in 'responsiveness' (i.e. the propensity to switch between producing and scrounging, depending upon the social conditions) predicted by the latest producer-scrounger models (Dubois et al., 2010; Katsnelson et al., 2011). To test such individual variation in house sparrow producing versus scrounging tactics, their responsiveness to social cues and their impact on the behavior of others, used a classic 'chequerboard' feeder systems (e.g. Barnard & Sibly, 1981; Vickery et al., 1991; Liker & Barta, 2002; Lendvai et al., 2004; Tóth et al., 2009; Katsnelson et al., 2008; Belmaker et al., 2012) to test each individual house sparrow against two other flockmates in many different combinations. No previous producer-scrounger study has done this, but recent studies of contest competition in crickets have tested every individual against every combination of other individuals (in groups of 4) to separate the effects of the individual versus the opponents (Santostefano et al., 2016). In this case, we simulated more natural 'flock-like' conditions by having three individuals foraging together,

and still be able to extract estimates of individual behavior, impact and responsiveness. We thus recorded data on each individual's repeatable average levels of producing-scrounging behavior and used mixed-effect models to quantify their individual levels of impact and responsiveness. Additionally, we tested whether impact, responsiveness, and producing-scrounging behavior also covary with an individual's pace-of-life, where less responsive, more impactful, and less plastic scrounging types are expected to also have a 'fast' life-history, and the more responsive, less impactful and more plastic producing individual probably is expected to have a 'slow' life-history. This is because there is believed to be a trade-off of responsiveness, where rather than allocating resources to vigilance or rapid responses to changes in environment, 'fast' individuals may invest it towards reproductive effort earlier breeding. Thus, 'fast' individuals are expected to have a faster pace-of-life, in terms of higher reproductive effort and output. To test this, we used long-term reproduction data from five populations of free-living house sparrows along the coast of central Norway, to see if individual life histories covary with their producing-scrounging strategies in feeder trials.

Study objectives

Hypothesis 1: different life-history strategies along a 'slow' to 'fast' axis of pace-of-life should covary with repeatable behavioral difference among individuals in producer-scrounger social foraging tactics.

Prediction 1a: there will be repeatable individual differences in average levels of producer-scrounger behavior, with some of this variation being due to body mass and sex (e.g. large individuals and males should scrounge more on average).

Prediction 1b: that greater average levels of scrounging behavior will be associated with a faster pace-of-life and greater average levels of producer behavior will be associated with a slower pace-of-life.

Hypothesis 2: different life-history strategies of 'slow' and 'fast' pace-of-life should covary with repeatable behavioral difference among individuals in how socially responsive they are between producer-scrounger social foraging tactics.

Prediction 2a: there will be repeatable individual differences in responsiveness and impact in producer-scrounger behavior, with larger individuals and males being less responsive and more impactful on average.

Prediction 2b: that less responsiveness and greater impact in producer-scrounger behavior is associated with a faster pace-of-life, and greater responsiveness and lower impact will be associated with a slower pace-of-life.

Consequently, we predict that individual variation in producer-scrounger behavior, responsiveness, and impact will covary with individual life-histories when compared with life-history data on this population.

2. MATERIALS AND METHODS

2.1 Study population, location and timeframe

Passerine birds have been used in many social and evolutionary studies, and this does not exclude studies regarding producer-scrounger behavior (see Introduction). This is because many passerine species such as house sparrows are easy to observe in captivity and social groups, and individually distinguishable when marked with colored leg-rings (Anderson, 2006). The house sparrow is a small, passerine bird that has proved to be an excellent model species for studying evolutionary and demographic questions, including many of these same behavioral issues. With a preference for feeding in flocks, breeding in colonies, and roosting communally, the sparrow is a very social species and an opportunistic foraging generalist often seen on the ground searching for seeds. (Anderson, 2006). Sparrows are closely associated with human settlements, and in Norway you find them particularly on dairy farms in the countryside (Ringsby et al., 2006).

The house sparrow has been a model species for studies of producer-scrounger and other social foraging behaviors (e.g. Lendvai et al., 2004; Katsnelson et al., 2008; Tóth et al., 2009). This project was a part of an extensive study of the house sparrow by members of the Centre for Biodiversity Dynamics (CBD), involving 30 years of data collection and typing of genetic markers for parentage determination. The Åfjord-system and the Sørdahl farm got introduced in 2012, 3 more farms were introduced in 2018, and the farm of Ressem was introduced only in 2022. Previous studies have focused on for instance spatial and temporal variation in survival and reproduction (Ringsby et al., 1999; Sæther et al., 1999; Ringsby, 2002), selection on heritability and genetic architecture of morphological traits (Jensen et al., 2003, 2004, 2008; Engen et al. 2012, 2014; Aase et al., 2022), genetic and phenotypic population structure (Holand et al., 2011; Hagen et al., 2013; Jensen et al., 2013), effects of inbreeding (Jensen et al., 2007; Billing et al., 2012; Niskanen et al., 2020), effective population sizes (Engen et al., 2007; Baalsrud et al., 2014; Stubberud et al., 2017), the effects of endoparasites on fitness (Holand et al., 2014, 2015), population extinction (Ringsby et al., 2006) and dispersal (Pärn et al., 2009, 2012; Ranke et al., 2021; Saatoglu et al., 2021).

This master's thesis was in collaboration with master's students Tuva Zeiner-Henriksen and Martin Guldvik from NTNU, PhD cand. Ådne Messel Nafstad from NTNU and PhD-students Rori Wijnhorst and Corné de Groot from Ludwig Maximilian University of Munich, Germany, who were the main contributors towards the study design of the methods and

equipment related to this project. Rori and Corné are running a longer-term project spanning over three years at the Åfjord-system, covering five farms and five house sparrow populations in the area, and Ådne was in the last year of collecting data on his PhD project. I have been assisting both these projects during their fieldwork and used some of their data and calculations for this master's thesis.

The study took place in and around Lauvøya (63°55′43″N 09°55′59″E), located at the municipality of Åfjord along the coast of Mid-Norway in the winter (January-March) of 2022. We used the native house sparrow populations at Lauvøya, and four more populations nearby, as our study subjects. The population was estimated to be 180 individuals the winter of 2022, where we caught 168 of these individuals for use in trials. The birds were mostly found at barns on the island and the mainland nearby and were captured by using mist-nets inside these barns.

2.2 Set-up of trials

Once captured, the birds were placed in groups of 6 with an even sex ratio inside holding aviaries in a sealed central barn, where both habituation and producer-scrounger foraging trials took place. We aimed for the temperature being 10-12 degrees Celsius inside the barn, with a 14/8 hour light-dark cycle, which is the normal temperature and light cycles inside barns in Norway during winter. On day 1, they were fed and given water *ad libitum*, and the birds were marked with an individual, unique ring combination (consisting of one numbered metal ring and three colored plastic rings) and a passive integrated responder (PIT-tag) on its tarsi and measured as part of CBD's long-term study. Some of the characters measured were; weight, tarsus length, wing length, beak length and depth, and any difficulties in breathing (i.e. presence of lung parasites). Furthermore, everyone's sex and age were recorded, and a small blood sample (ca. 25µL) was collected by brachial venipuncture to obtain DNA. BMR was measured, and they spent the night in BMR-chambers as a part of another project. Each group of birds was held inside for at least 5 days for habituation and trials during the months of January-March 2022. The first of these trials started on the 22nd of January and the last one ended the 11th of March.

On day 2 and 3, groups of 6 individuals were habituated with a stepwise approach, as they were fed from dummy chequerboard feeders, with millet, general bird seed mix and some sand mixed and filled in wells in their aviaries during the day. Then, between 17:00-18:00, the wells got covered in sand. The holding aviaries were about 2.5x1.5-1.8 meters wide and 2

meters tall. After 2 days habituation to the dummy 'chequerboard' feeders, we captured the birds by flushing them into an adjacent aviary with a mist net. Afterwards, the birds were placed in their experimental cages in a random group of three within their previous group of 6 and spent the night there to habituate. The following day, they were run through a series of triadic producer-scrounger foraging trials. The chequerboards consisted of 36 wells, where 14 of these were manually filled with 12 grams of millet seeds distributed evenly among them, and then covered with a thin layer of sand. The wells were distributed in 6 patterns, up right or upside-down (total of 12 pattern variations) and the pattern was randomly assigned before each trial.

Every trial ran for 15 minutes, and 3 assays were run at the same time using three different feeder cages. The trials were run for all combinations of three individuals within each group. There was a total of 10 assays per individual, per day. Each group was tested for 2 days, where the order they were tested in was randomized, and the whole combination of assays was run for the first day. A repeat was run the second day for the purposes of repeatability. Thus, there were 40 assays per group of birds. There was a total sample size of 29 groups and 1160 assays, where we got 3360 data points from this setup for average level of behavior and plasticity. The dataset we derive the average individual behaviors from consists of 4,6 million datapoints registered during feeding trials (Trovan RFID system). After this, the birds were released into another holding aviary in the barn for a few days, and when judged healthy, released at the site they were captured.

2.3 Data collection during the trials

Each house sparrows PIT-tag registered each time the bird approached a well during the assay through the Trovan PIT-tag system, and thus registered both foraging, potential feeding and when the birds approached each other in the proximity of a well. Each well was equipped with four antennas, and the registration of time and place the bird was there took place each time the PIT-tags was on top of one of the antennas. The birds were additionally equipped with a unique barcode on its back, so that it was easier for observers to keep track of each bird's movement and identity during video analysis. Social foraging behavior was recorded by a Trovan RFID (radio frequency identification) system which reads PIT-tags, and a side- and overhead GoPro hero 8 1080p 24fps with linear view. The social foraging behavior and behaviors recorded include boldness in latency to arrive on the feeder plate, arrival order, latent joining, a join were both individuals stay, join where focal individual leaves, join where focal individual stays (joins are here a proxy of scrounging events), exploration (how many

wells get explored for the first time), activity (how many wells are visited in total), time spent at baited and unbaited wells and number of visits to baited and unbaited wells.
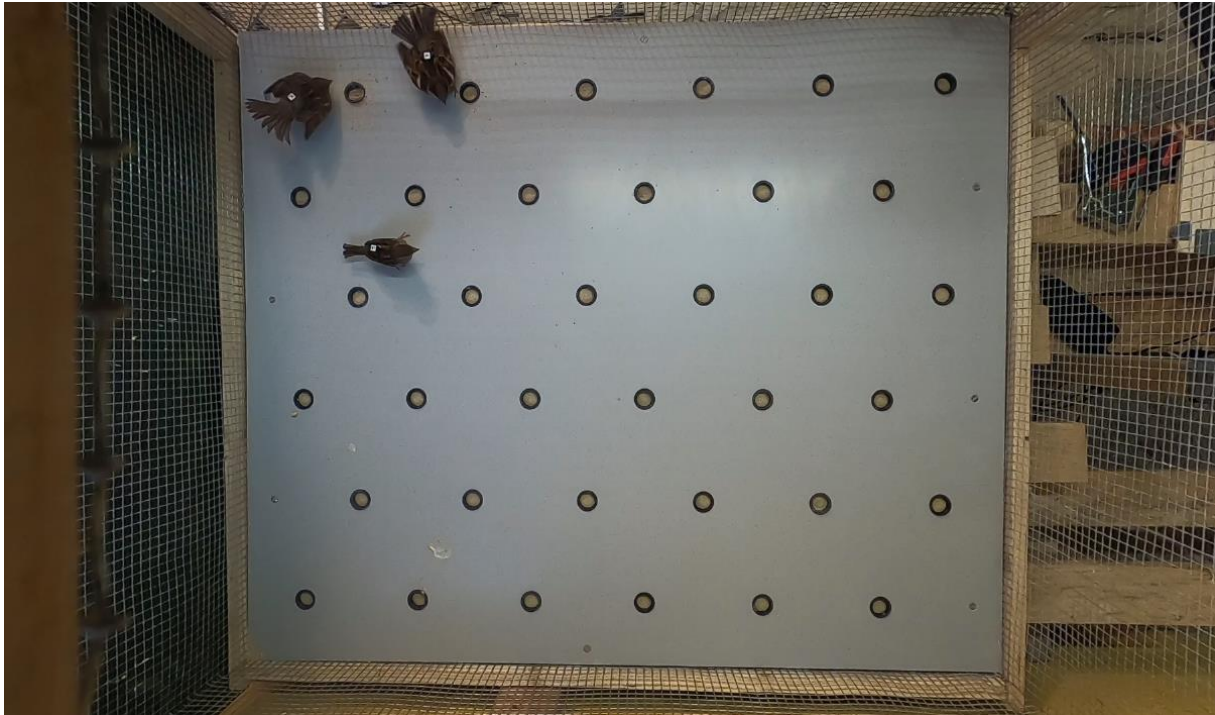
Figure 1: *Picture from an overhead camera, during trial, of the checkerboard used for the three-bird assays. The feeder plates are 1x1.2 meter wide and the cage is 1 meter tall.*

2.4 Collection of life-history data

From May to August 2022, we collected data on house sparrow juveniles from the five populations that we had caught for the producer-scrounger trials during winter in and around Åfjord. This method of data collection is like the previous years of data collection in and around Åfjord, and described in detail in previous studies (Le Pepke et al., 2022). Nest data from May to August of 2021 is additionally used for this study. We visited the area each week and determined the lay date, brood size, clutch size, age and number of hatchlings, consecutively as the breeding season went on by manually checking each nest. The date of hatching and the survival status of each individual was estimated by counting the number of juveniles and dead juveniles, and estimating their age, in each nest, during these weekly visits. The nests and nest boxes had previously been located and marked from previous years in and around the barns where the house sparrows breed. We captured the juveniles while they were still in the nest and unable to fly (5-14 days old, with a median of 10 days old). Once captured, we took a range of measurements of the chicks/jueveniles, including wing length

(measured from the wrist to the tip of the longest primary feather), tarsus length (measured from the back of the tarsus to the base of the toes), and body weight. The juveniles got banded with a alphanumerical ring and a unique set of color rings for future identification, and a small blood sample was taken from everyone for DNA analysis. This DNA analysis is further used to determine the parents and relationship of each juvenile house sparrow, but the DNA-analysis was not completed before the end of this study. Combined with the data when doing the measurements on the birds during winter, we get a good overview of the individual fitness data, such as annual survival, reproductive output and breeding data such as onset of breeding, number of clutches, weight of fledglings and number of fledglings for these populations of house sparrows.

Figure 2: Data collection from a house sparrow nest box.

Figure 3: Juvenile house sparrow on day 6 after hatching.

The number of fledglings and clutch size was measured as indicators of reproductive effort, with larger clutches and more fledglings indicating greater investment in reproduction. Lay date was recorded as an indicator of the age at which parents initiate reproduction. The body weight of chicks was measured as an indicator of growth and development, with faster growth rate indicated by a larger weight. We also collected data on the survival of adults from 2022 until the winter of 2023 based in recaptures and sightings of their unique colorband combinations to assess if this had any correlation with their producer-scrounger behavior. To determine the parents of the chicks, we used RFID-trackers within the nestboxes, that tracked which individuals visited the nests during the rearing of chicks in it. This comes with an assumption that only the biological parents were involved in the rearing of the chicks, which of course does not apply here as house sparrows have an extra pair paternity rate of 20-30%. In total, data from 26 parents was collected (that was examined during the producer-scrounger trials in winter 2022) and 91 of their fledglings, using this method. Nine of the adults tracked were female, 17 males, 2 birds had broods both in 2021 and 2022. Here, 9 nestboxes had data on both a male and female during the rearing of young, while the 8 remaining individuals either had absent partners or partners without an RFID-tag. This data was derived from 19 nestboxes in total.

2.5 Video analysis and further use for calibration

The video analysis was carried out manually, to later compare with, and check the reliability of the RFID-data. The analysis was carried out in the video analysis program BORIS (Friard

& Gamba, 2016), by the various students on this project. We had six observers watching and analyzing videos from the overhead cameras that were filmed during the producer-scrounger trials the past winter. First, every observer ran through the same sample of 9 videos, 3 one-minute,3 three-minute and 3 five-minute videos. These were carried out in a random order and watched through in 3 series, so that we had 3 repeats. Each trial was run through three times, to score each focal individual separately (both for the test run and the main video analysis). When this was done, the repeatability was checked both within and among observers. A threshold of 0.9 was deemed acceptable for most behaviors, and a threshold of 0.8 for joining events, within and among observers. It is important to state that joining events are considered a proxy of scrounging and searches are a proxy of producing events.

Table 1: In this table, we see the behaviors the observers scored and the description they followed when scoring during the behavioral analysis in BORIS.

Aggression/fight	Point event	fighting/directly reciprocated attack initiated by focal.
Attack	Point event	short peck or attack launched and not directly reciprocated
Board	State event	stand on board
Display	Point event	wing display or flapping. Count each display or flap.
Feed	Point event	consuming one seed either from board or from a well.
Join	State event	join at well or feeding from seeds around well (<2cm) that another individual is sampling from. Latent joining when partner has left well no longer than 3s ago....
Release	Point event	moment the first bird is released, which indicates the start time of the 15min trial
Revisit	State event	leaves well and returns to the same well within 10s (only score if subject did not search/join/secondary find at another well) or when it stops feeding for longer than 5s but stays at the well.
Search	State event	sieving through sand or beak touches sand at a well
Secondary find	State event	same as criteria as search, but the visited well already has clear visual cues for seeds
Stop event	Point event	*used for stopping a state event
Testtag	Point event	moment the test tag is tapped on the feeder

When repeatability had been checked for, the main analysis of the BORIS-data started, where each of the 6 observers got randomly assigned 18-19 videos. These were randomly selected from a subset of 112 videos in such a fashion that each individual house sparrow was analyzed at least twice, once on day 1 and once on day 2. The order in which the videos were analyzed was randomized, and the video analysis was done by the start of November 2022.

Further, the BORIS-data was used to assess the accuracy of measures of producing and scrounging derived from the RFID-data, which we had gotten from the Trovan RFID-system. This was done by Rori Wijnhorst and Corné de Groot, where they grouped all observed traits of interest during the BORIS-analysis by observed join per individual per group and compared it to the RFID-data per individual per trial in a correlations analysis. The RFID data was derived by processing the raw data using specific code lines. These code lines filtered out individual sparrows and selected visits to wells with food present, meeting predetermined

conditions. Distinct visits were retained, and measures such as visit duration and the count of baited visits were calculated for further analysis. Joining events were also measured by identifying instances where a focal individual arrived after another individual, and the time gap between their visits was less than 3 seconds. When done, they sent the list of variables, their correlation (which is 0.7 for scrounging events and 0.65 for producing events), and their R-squared so that we could assess the reliability of the RFID variables of interest (which were the producing and scrounging events of individuals). As the variables of interest were quite correlated between the BORIS and RFID dataframes, I decided to use the RFID dataframe for further analysis. There is less human bias and noise from observational analysis on the data, and there are more datapoints to derive the mean behavior between individuals from. A downside is that the RFID-data overestimated the number of producing and scrounging events.

2.6 Statistical analysis

All statistical analyses were carried out in R version 4.1.1 (RStudio Team, 2020). First, to assist later results interpretations, correlations were checked between different predictor variables within the producer-scrounger behavioral data, and within the different explanatory life-history data. A correlation matrix was produced between these variables; lay date (numbered day of year mean-centered across years), age corrected weight in chicks (we age-corrected tarsus length by using the residuals from a regression of tarsus length on age and age squared), number of fledglings and body mass of parents was made using Pearson correlations. For sex of parent, I ran a t-test where I tested the sex of the parent up against all these variables, checked the mean of each sex and its p-value and put it in a table in the results. All the correlations were tested to avoid putting highly correlated explanatory variables into the same linear mixed-effect model in the main models, which can cause multicollinearity and difficulty in separating individual effects of the predictor variables. To assess any covariances with nesting year that could be taken into consideration during the discussion, I ran a t-test where I tested nesting year against all the other life-history variables mentioned above and plotted this too in a table.

Rori Wijnhorst and Corné de Groot calculated the responsiveness, impact and mean level of scrounging in the average social environment of the individuals during trials by mean centering the values of total joins of focal individual during a trial and total amount of scrounges made by its opponents per trial. Next, they implemented a loop to calculate the average trait of the opponent for each trial. This loop iterated 1092 trials in the data set and

calculated the average opponent trait for each individual during trials. Next, they fitted a linear mixed-effects model using the lmer() function from the lme4 package (v1.1-26; Bates et al., 2015). The model included the traits of interest (total scrounges of focal) as the response variable and the opponent trait as a predictor variable. The model also included random intercepts for the individual IDs and ring number, as well as a random for the opponent trait within each ring number. The Best Linear Unbiased Predictors (BLUPs) for the random effects were extracted from the above-mentioned model, which were used to estimate the impact and responsiveness of individuals on the behavior of others in the group. From here they got the values for mean levels of scrounges as the intercept, responsiveness as the slope and impact of the individuals as the average of the residual impacts for the focal on its two opponents. I later split the dataset and reran the code above, to get BLUPs for each separate trial day, getting the average behavior per individual per trial day. All these variables are derived from the average social environment of the focal with this method and, the impact and responsiveness is later used as response variables in the main models.

In this analysis, 'responsiveness' refers to how individual behavior (total scrounges) was influenced by the trait (i.e. number of scrounging/joining events) of their opponents. It thus quantifies social plasticity and the extent to which the focal individual's amount of scrounges changes in response to variation in the opponent's trait, and 'responsiveness' is thus estimated as the slope coefficient in the linear mixed-effect model, indicating the magnitude and direction of the relationship between the focal and the opponent's trait. 'Impact' is the measure of the average effect of an individual's behavior on the behavior of social partners in the group. It reflects the influence of a focal individual's behavior on the behavior of its opponents. In this analysis, the impact is the estimated average of the residual impacts for the focal individual on its two opponents during trials. These capture the unique effect of the focal individual's behavior after accounting for the opponent's trait. And the intercept represents the mean levels of scrounging, which can be interpreted as the mean level behavior of the focal individuals when the opponent's trait is at its reference level. It provides a reference point for comparison and helps assess the relative change in behavior based on the opponent's trait.

Importantly, when using these variables further in the study, we are deriving secondary statistical measures from a primary statistical analysis (statistics on statistics), which should be approached with caution (Houslay & Wilson, 2017). This is because, by using only the mean behavior per individual, we ignore all the within-individual variation. Thus, this is not

considered during the statistical analysis. The original idea was to run a more complex hierarchical analysis, taking into consideration within-individual analysis, but this analysis did not get ready before the end of this project.

Next, the repeatability of the joining behavior, responsiveness, mean levels of scrounges and impact between the two trial days was investigated using the rptR package (Stoffel et al., 2017). Specifically, I estimated the intraclass correlation coefficient (ICC) of the mean proportion of these variables with and without trial day as a fixed effect and ring number as focal ID as random effect under a gaussian distribution.

The main models of the study were three linear mixed-effect models using the lmer() function from the lme4 package and one generalized linear mixed-effect models using the glmer() function, to test whether life-histories were predictive of proportion of scrounges, total mean proportion of scrounges, responsiveness, impact and mean levels of scrounges (in the average social environment). I compared models with different predictor variables from the life-history and behavioral data, with ID of the parents and brood ID (unique number for each brood) as random effect.

For the first main model, I entered number of fledglings, lay date, age corrected body mass of chicks, body mass of parent and trial day as predictor variables. I did a LMER with total mean join as the response variable and a GLMER with proportion joining (which is derived from total amount of scrounging events divided by total amount of scrounging event plus total amount of producing events) as the response variable there. For the second main model, I used the same predictor variables as in the first main model. The response variables were the residual impact and responsiveness (for the focal in its average social environment that day) for the two LMERs in this model. I did no model selection and kept all the two-way interactions in the analysis, as they did not seem to disturb the reliance of the outputs to a significant degree.

3. RESULTS

3.1 Correlations among RFID-data and life-history traits

Figure 4 shows the correlations between explanatory life-history variables. While most of the correlations were statistically significant, the highest correlation was only an R-value of -0.2 between body mass of parents and lay date. While it is significant, it should still be possible to separate the individual effects of these variables in a linear mixed-effect model. Consequently, there was no model selection in further analysis. For the patterns of the variables and their correlation, heavier parents had earlier lay dates, more fledglings, and heavier fledglings. We also found that the more fledglings there are in a brood, the heavier they were.
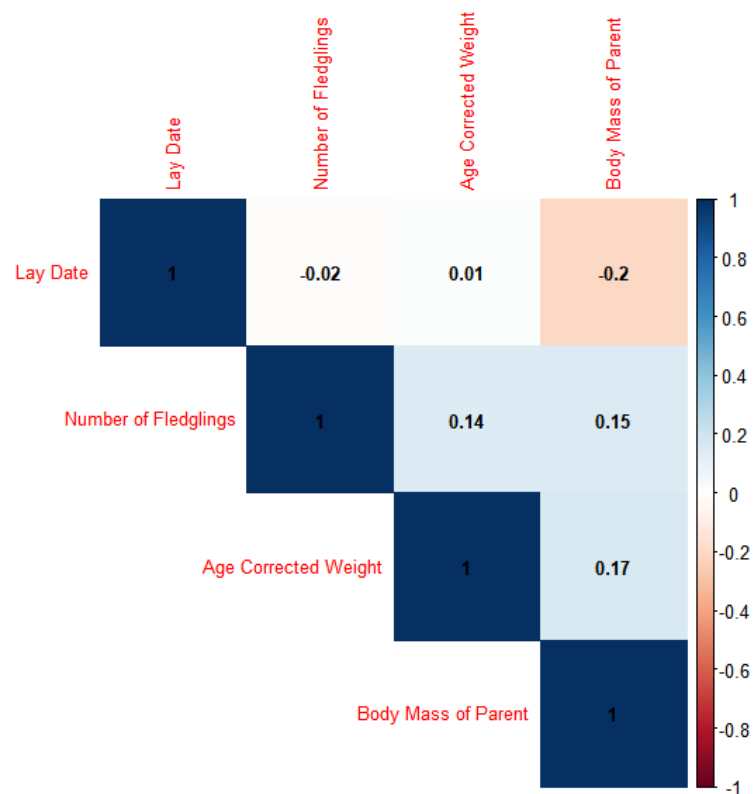
Figure 4: Correlation matrix between mean centered lay date, number of fledglings, age corrected weight of fledglings and body mass of parents. An R-value ± 0.14 indicates a significant correlation, with a p-value < 0.05.

Table 2: *Effects of year on lay date (centered), number of fledglings, age corrected weight of fledglings and body mass of parents.*

Life-history traits	Mean 2021	Mean 2022	T-value	P-value
Lay date (centered)	-2.950	-0.586	-1.798	0.073
Number of Fledglings	3.578	3.280	7.264	< 0.001
Age corrected weight of fledglings	24.138g	24.246g	-0.484	0.629
Body Mass of Parents	30.271	30.603	-3.536	4.18e-04

There were some significant differences in the life-history variables according to the year the breeding event occurred (Table 2). The number of fledglings per brood was significantly lower in 2022 than in 2021, and mean body mass of parents significantly was larger in 2022 compared to 2021.

Table 3: *Effects of sex on lay date (centered), number of fledglings, age corrected weight of fledglings and body mass of parents.*

Life-history traits	Mean Male	Mean Female	T-value	P-value
Lay date (centered)	-0.526	-1.610	0.862	0.389
Number of Fledglings	3.128	3.450	-5.315	< 0.001
Age corrected weight of fledglings	24.096	24.242	-0.549	0.583
Body Mass of Parents	30.611	30.459	1.651	0.099

There is a significant effect of the sex of the parent on the number of fledglings reared per brood in the subset of 26 individuals, with females having more fledglings, while being smaller than males. This will be explored further in the main models and taken into consideration.

3.2 Repeatability of scrounging and responsiveness

Repeatability measures the consistency of predictability of behavior across repeated measurements of in this case individuals. The proportion of scrounging and mean total amount of scrounges, both with and without trial day as a predictor variable, were significantly repeatable (R = 0.645-0.898). This indicates that scrounging is repeatable for

focal individuals, both with and without trial day as a predictor variable, in both the 168 and 26 individual dataframe. Regarding responsiveness, the repeatability estimates were quite similar between datasets (R = 0.661-0.764). For impact, when having trial day as a predictor variable, the repeatability was quite high in both dataframes (R = 0.577-0.591), but low when trial day was not included (R = 0.093-0.161). From Table 4, the pattern seems to be that these behaviors were highly repeatable on an individual level, both for the 168 individuals, and the subset of 26 individuals that life-history data has been collected on. Repeatability even seemed higher for the smaller subset of individuals in all behaviors, except for impact where there was low repeatability in the main data set and even lower in the 26 individual subset, telling us that individual repeatability, when only accounting for individual variation, is quite low for impact (and especially in the subset of 26 individuals). Additionally, the high repeatability in both datasets strengthens the argument that we have enough power in the smaller dataset to spot significant individual differences of life-history trait-effects on producer-scrounger behavior.

Table 4: Individual repeatability of scrounging, impact and responsiveness.

Repeatability estimations	Repeatability with 168 individuals	Repeatability with subset of 26 individuals
Proportion scrounging with trial day as predictor variable	R = 0.697	R = 0.898
Proportion scrounging	R = 0.645	R = 0.861
Mean total scrounging with trial day as predictor variable	R = 0.581	R = 0.736
Mean total scrounging	R = 0.543	R = 0.735
Impact with trial day as predictor variable	R = 0.577	R = 0.591
Impact	R = 0.161	R = 0.093
Responsiveness with trial day as predictor variable	R = 0.746	R = 0.764
Responsiveness	R = 0.661	R = 0.753

All P-values were P < 0.001 and significant for both the subset of 26 and the 168 individuals.

3.3 Effects of life-history variables on proportion scrounging and mean total scrounging

The results show significant interactions between the body mass of adults and trial day, which had a negative effect on proportion scrounging and mean total scrounging, indicating that

larger individuals exhibited lower scrounging proportionally and total scrounging compared on trial day 2 (Figure 5.1 and 5.2), and body mass had a negative effect on proportion scrounging on the second day of trial. Moreover, individuals with heavier fledglings during the breeding season demonstrated decreased scrounging behavior on trial day 2 compared to trial day 1, both in terms of proportion and mean total scrounges (Figure 5.3 and 5.4), with afe corrected weight of fledglings have a negative effect on proportion scrouning on the second trial day. Additionally, individuals with a later lay date engaged in increased scrounging activities on trial day 2, both proportionally and in total, although the relationship between lay date and scrounging was less pronounced on the second day (Figure 5.5). Furthermore, individuals with larger brood sizes exhibited higher total scrounges on trial day 2 (Figure 5.6). Regarding the proportion of scrounges, males tended to scrounge less on day 2, while females showed a higher proportion of scrounging. This pattern was consistent when examining mean total scrounges (Figure 5.7 and 5.8).

The scrounging behavior exhibited interesting interactions between trial day and various factors, including body mass, sex of parent, age-corrected weight of fledglings, lay date, and number of fledglings. This indicates that there was a severe effect of trial day, and that the birds were not habituated to the experimental setup. On the first trial day, the effect of age-corrected weight of fledglings sired by the parent and body mass was positive on the proportion of scrounging, while on the second day, the opposite trend was observed. Males consistently displayed lower levels of total scrounging, both proportionally and in total, while females exhibited higher scrounging on day 2. Moreover, the second day showed variations in mean total scrounging depending on the interaction effects.

These findings challenge the initial expectations that larger individuals investing more in reproduction would exhibit a faster pace-of-life and engage in proportionally higher scrounging. Instead, the results suggest a more complex relationship between trial day, body mass, sex, reproductive factors, and scrounging behavior.

Table 5: Model output of a generalized linear mixed-effect model (left) and a linear mixed-effect model (right): one with proportion scrounging (left) and one with mean total scrounging (right) as response variables. For the fixed effects, estimates, standard errors and p-values are presented. For the random effects, variances explained and standard deviations are presented.

Fixed effects	Proportion scrounging	Mean total scrounging
Intercept	-5.165 ± 9.087 (p = 0.570)	**-3.26e+01 ± 1.30e+01** **(p = 0.018)**
Age Corrected Weight of Fledglings	1.31e-02 ± 0.237 (p = 0.956)	0.103 ± 0.164 (p = 0.530)
Lay Date (centered)	-0.158 ± 2.069 (p = 0.446)	-1.100 ± 2.252 (p = 0.625)
Number of Fledglings	3.37e-02 ± 5.22e-02 (p = 0.519)	4.18e-02 ± 5.60e-02 (p = 0.456)
Body Mass	-0.121 ± 0.305 (p = 0.692)	**1.327 ± 0.428** **(p = 0.004)**
Trial Day	**8.001 ± 1.909** **(p < 0.001)**	**1.72e+01 ± 1.271** **(p < 0.001)**
Sex of Parent (Male)	**5.480 ± 12.655** **(p < 0.001)**	1.543 ± 1.434 (p = 0.302)
Age Corrected Weight of Fledglings x Number of Fledglings	-6.31e-04 ± 1.72e-02 (p = 0.971)	-5.85e-04 ± 1.31e-02 (p = 0.964)
Age Corrected Weight of Fledglings x Lay Date (centered)	3.70e-04 ± 8.82e-04 (p = 0.675)	1.62e-04 ± 6.99e-04 (p = 0.817)
Age Corrected Weight of Fledglings x Body Mass	2.43e-03 ± 8.82e-03 (p = 0.767)	1.71e-04 ± 5.61e-03 (p = 976)

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Age Corrected Weight of Fledglings x Trial Day	**-5.87e-02 ± 2.80e-02** **(p = 3.65e-02)**	**-7.03e-02 ± 2.04e-02** **(p < 0.001)**
Number of Fledglings x Lay Date (centered)	8.27e-04 ± 3.20e-03 (p = 0.796)	1.79e-05 ± 2.59e-03 (p = 0.994)
Number of Fledglings x Body Mass	5.79e-02 ± 6.39e-02 (p = 0.364)	2.17e-02 ± 7.13e-02 (p = 0.761)
Number of Fledglings x Trial Day	-0.184 ± 0.118 (p = 0.118)	**0.273 ± 9.05e-02** **(p = 0.003)**
Lay Date (centered) x Body Mass	-1.51e-03 ± 1.72e-03 (p = 0.379)	-4.48e-04 ± 1.98e-03 (p = 0.821)
Lay Date (centered) x Trial Day	9.18e-04 ± 5.09e-03 (p = 0.857)	**-2.09e-02 ± 3.83e-03** **(p < 0.001)**
Body Mass x Trial Day	**-0.221 ± 6.37e-02** **(p < 0.001)**	**-0.549 ± 4.16e-02** **(p < 0.001)**
Sex of Parent (Male) x Body Mass	-0.176 ± 0.410 (p = 0.668)	-1.012 ± 1.021 (p = 0.340)
Sex of Parent (Male) x Trial Day	**-0.237 ± 6.44e-02** **(p < 0.001)**	**4.553 ± 0.175** **(p < 0.001)**
Sex of Parent (Male) x Age Corrected Weight of Fledglings	-1.25e-02 ± 1.16e-02 (p = 0.803)	-2.23e-03 ± 2.83e-02 (p = 0.937)
Sex of Parent (Male) x Number of Fledglings	-0.228 ± 0.226 (p = 0.313)	-2.22e-02 ± 0.176 (p = 0.900)
Random effects		
Focal ID	0.637 (*SD = 0.798*)	8.150 (*SD = 2.855*)
Group ID	0.463 (*SD = 0.680*)	0 (*SD = 0*)

Brood ID	5.00e-06 (*SD = 2.24e-03*)	0 (*SD = 0*)
Residual	–	2.818 (*SD = 1.679*)

The trial day exerted a significant influence on both response variables, revealing distinct patterns in the scrounging behavior of house sparrows. On the second trial day, individuals exhibited a reduced proportion of scrounging activities, indicating a decreased tendency to engage in this behavior. However, the mean total scrounging across individuals increased on the second day of the trial, suggesting an overall higher level of scrounging activity (Figure 6.7 and 6.8). Mean total scrounges is a variable that could be affected by more variables such as activity and latency to arrive on the feeder plate, which could indicate a higher level of habituation during the second day.

In terms of body mass, a significant positive effect was observed on the total mean scrounging, implying that larger individuals displayed a higher frequency of scrounging behaviors during the trials. This finding suggests that body mass is a contributing factor to the variation in scrounging tendencies among individuals. Additionally, the lack of significance on proportion scrounging suggests that body mass does not have a strong influence on the overall frequency of scrounging behavior on this subset of house sparrows, but that could be explained by the opposite trends we see from trial day on proportion scrounging. Furthermore, it is interesting that there is a significant positive effect of body mass on total mean scrounges, but a non-significant negative effect on mean proportion of scrounges.

Regarding sex differences, males exhibited a lower proportion of scrounging and demonstrated similar levels of total scrounging between trial days. In contrast, females displayed comparable proportions of scrounging activities across trial days but exhibited a slightly higher total scrounging on the second day (Figure 6.7 and 6.8). These results suggest a tendency for males to engage in less scrounging behavior overall, compared to females, but could likely be an effect of the lack of habituation, where females habituated faster.

Overall, the findings indicate that trial day, body mass, and sex significantly influence the scrounging behavior of house sparrows, highlighting the importance of these factors in shaping foraging dynamics within the population.
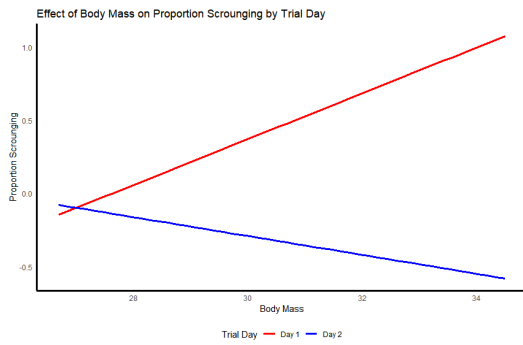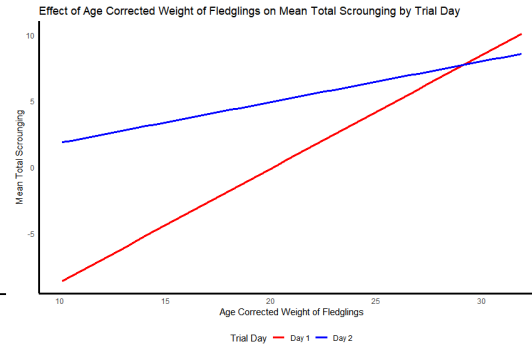
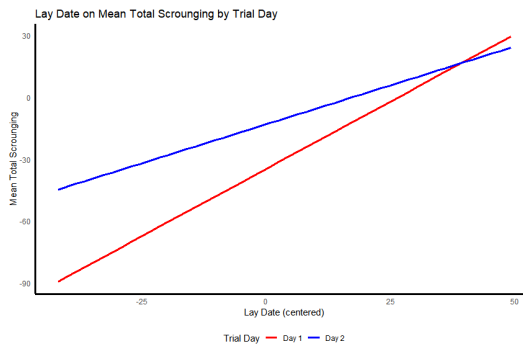**Figure 5.1:** *The estimated effect of body mass and trial day on proportion scrounging.*
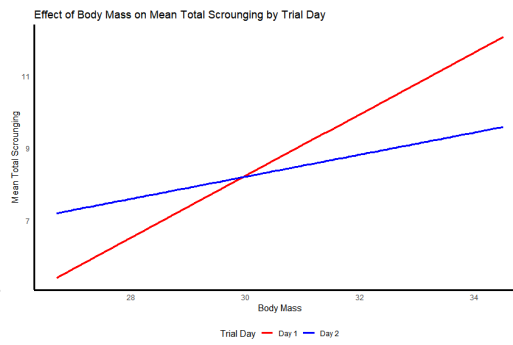
Figure 5.2: *The estimated effect of body mass and trial day on mean total scrounging.*
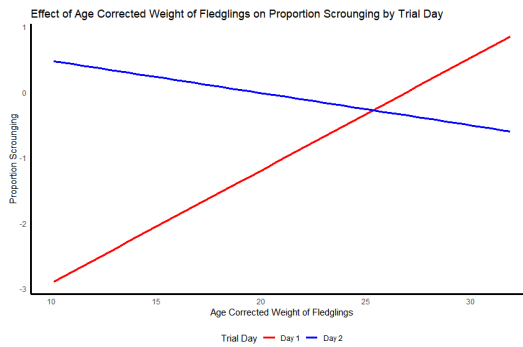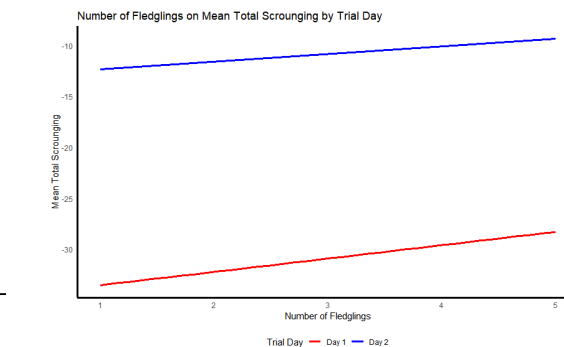

Figure 5.3: *The estimated effect of age corrected weight of fledglings and trial day on proportion scrounging.*
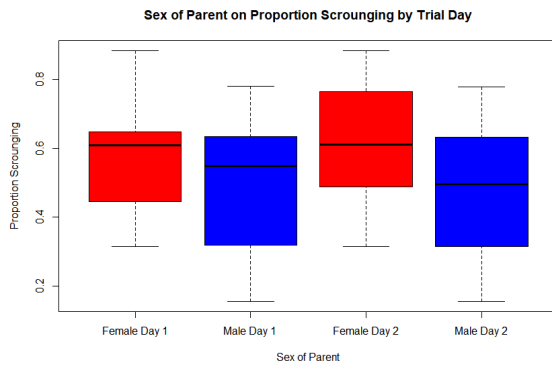

Figure 5.4: *The estimated effect of age corrected weight of fledglings and trial day on total mean scrounging.*
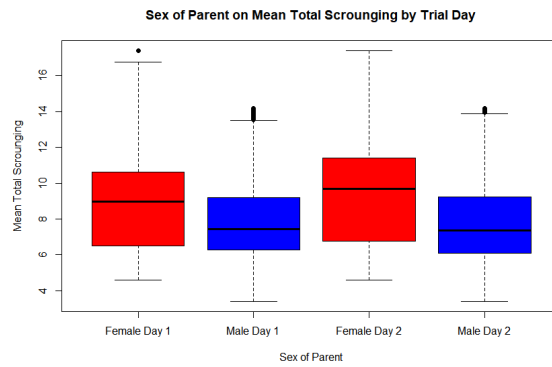

Figure 5.5: *The estimated effect of lay date (centered) and trial day on total mean scrounging.*

Figure 5.6: *The estimated effect of number of fledglings and trial day on total mean scrounging.*

Figure 5.7: *The estimated effect of sex of parent and trial day on proportion scrounging.*

Figure 5.8: *The estimated effect of sex of parent and trial day on mean total scrounging.*

3.4 Effects of life-history variables on impact and responsiveness

The interaction between the body mass of the parents and trial day had a significant and negative effect on impact, while it had a positive effect on responsiveness. Specifically, larger individuals exhibited lower impact and higher responsiveness compared to smaller individuals. Interestingly, the intercept of responsiveness and impact seems lower for the second trial day when accounting for this interaction (Figure 6.1 and 6.2). The number of fledglings and its interaction with trial day significantly affected impact and responsiveness, where more fledglings leads to less impact and more responsiveness, with some different effect from trial day. Individuals that had more fledglings tended to be more responsive and less impactful on the second day of the trial (Figure 6.3 and 6.4). Examining the relationship between age-corrected weight and impact on trial day 2, it was observed that a larger weight was correlated with a shallower slope, but lower intercept regarding impact. Additionally, a more shallow slope in responsiveness on the second day was associated with a larger age-corrected weight (Figure 6.5 and 6.6). Furthermore, a later lay day showed more effect on impact and a restrained slope in responsiveness on the second trial day, but overall less impact and more responsiveness (Figure 6.7 and 6.8). Regarding sex and its interaction with trial day, females exhibited slightly higher impact and responsiveness on the second day, while males showed a slight decrease in these measures (Figure 6.9 and 6.10). The impact of body mass varied with sex, where larger females had less impact compared to smaller females, whereas

larger males had slightly more impact than smaller males (Figure 6.11). Overall, the patterns of impact across trial days showed similar slopes, but with lower impact observed on the second day. Additionally, there was a positive correlation between the reproductive traits and responsiveness on day 1, but this correlation was almost non-existent on day 2. However, there was a higher overall level of responsiveness on day 2.

Table 6: Model output of two mixed-effect models: one with impact (left) and one with responsiveness (right) as response variables. For the fixed effects, estimates, standard errors and p-values are presented. For the random effects, variances explained and standard deviations are presented.

Fixed effects	Impact	Responsiveness
Intercept	**-3.26e+01 ± 1.30e+01** **(p = 0.018)**	-0.987 ± 0.600 (p = 0.111)
Age Corrected Weight of Fledglings	0.103 ± 0.164 (p = 0.531)	6.01e-03 ± 6.64e-03 (p = 0.365)
Lay Date (centered)	-1.100 ± 2.252 (p = 0.625)	-7.10e-02 ± 9.19e-02 (p = 0.440)
Number of Fledglings	4.18e-02 ± 5.602e-02 (p = 0.456)	1.76e-03 ± 2.28e-03 (p = 0.440)
Body Mass	**1.327 ± 0.428** **(p = 0.004)**	**5.33e-02 ± 1.97e-02** **(p = 0.011)**
Trial Day	**1.72e+01 ± 1.271** **(p < 0.001)**	**0.738 ± 5.14e-02** **(p < 0.001)**
Sex of Parent (Male)	1.535 ± 1.433 (p = 0.304)	-3.960 ± 2.082 (p = 0.079)
Age Corrected Weight of Fledglings x Number of Fledglings	-5.85e-04 ± 1.31e-02 (p = 0.964)	3.07e-06 ± 5.30e-04 (p = 0.995)
Age Corrected Weight of Fledglings x Lay Date (centered)	1.62e-04 ± 6.99e-04 (p = 0.817)	6.07e-06 ± 2.83e-05 (p = 0.830)

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Age Corrected Weight of Fledglings x Body Mass	1.71e-04 ± 5.61e-03 (p = 0.976)	7.15e-06 ± 2.27e-04 (p = 0.975)
Age Corrected Weight of Fledglings x Trial Day	**-7.03e-02 ± 2.04e-02 (p < 0.001)**	**-4.19e-03 ± 8.23e-04 (p < 0.001)**
Number of Fledglings x Lay Date (centered)	1.79e-05 ± 2.59e-03 (p = 0.994)	-1.28e-05 ± 1.05e-04 (p = 0.903)
Number of Fledglings x Body Mass	2.17e-02 ± 7.13e-02 (p = 0.761)	3.19e-04 ± 2.91e-03 (p = 0.913)
Number of Fledglings x Trial Day	**0.273 ± 9.05e-02 (p = 0.003)**	**3.92e-02 ± 3.66e-03 (p < 0.001)**
Lay Date (centered) x Body Mass	-4.48e-04 ± 1.98e-03 (p = 0.821)	-7.15e-06 ± 8.05e-05 (p = 0.929)
Lay Date (centered) x Trial Day	**-2.09e-02 ± 3.83e-03 (p < 0.001)**	**-1.07e-03 ± 1.55e-04 (p < 0.001)**
Body Mass x Trial Day	**0.549 ± 4.16e-02 (p < 0.001)**	**-2.66e-02 ± 1.68e-03 (p < 0.001)**
Sex of Parent (Male) x Body Mass	**0.149 ± 6.80e-02 (p = 0.048)**	-6.45e-02 ± 4.68e-02 (p = 0.192)
Sex of Parent (Male) x Trial Day	**-0.302 ± 1.97e-02 (p < 0.001)**	**0.214 ± 6.50e-03 (p < 0.001)**
Sex of Parent (Male) x Age Corrected Weight of Fledglings	-1.90e-04 ± 3.18e-03 (p = 0.952)	-1.86e-04 ± 1.05e-03 (p = 0.860)
Sex of Parent (Male) x Number of Fledglings	7.76e-04 ± 1.95e-02 (p = 0.968)	-7.34e-04 ± 6.55e-03 (p = 0.911)
Sex of Parent (Male) x Lay Date (centered)	1.58e-04 ± 7.51e-04 (p = 0.834)	1.79e-05 ± 2.50e-04 (p = 0.943)

| Random effects		
Focal ID	4.43e-02 (*SD = 0.211*)	1.94e-02 (*SD = 0.139*)
Group ID	0 (*SD = 0*)	9.56e-17 (*SD = 9.78e-09*)
Brood ID	0 (*SD = 0*)	0 (*SD = 0*)
Residual	2.85e-02 (SD= 0.169)	4.60e-03 (*SD = 6.78e-02*)

The body mass of house sparrows had a notable influence on their impact, with larger individuals demonstrating a reduced impact (Figure 6.1 and 6.2). This is interesting as the sex and body mass interaction shows that males were more impactful the more mass they have, while females were less impactful the more mass they had. Additionally, body mass exhibited a significant positive correlation with responsiveness, indicating that larger individuals tended to be more responsive (Figure 6.3 and 6.4). The trial day also played a significant role in shaping both impact and responsiveness. Specifically, impact was observed to be lower on the second day of the trial, while the effects on responsiveness varied depending on the interaction between trial day and life-history traits. However, overall, responsiveness tended to be higher on the second day of the trial (Figure 6.1-6.10).
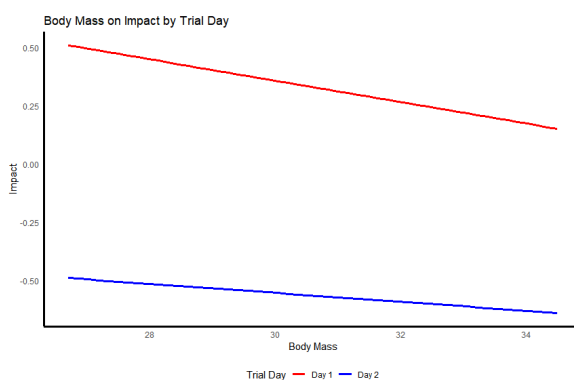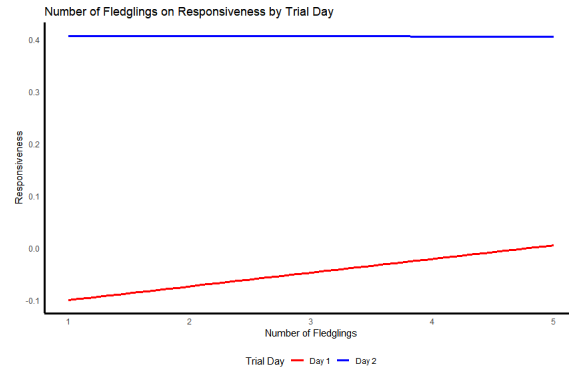

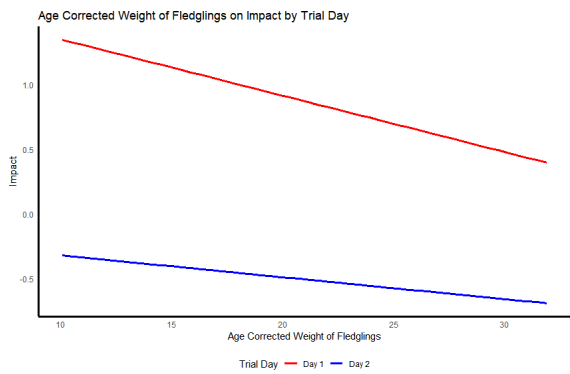*Figure 6.1*: *The estimated effect of body mass and trial day on impact.*
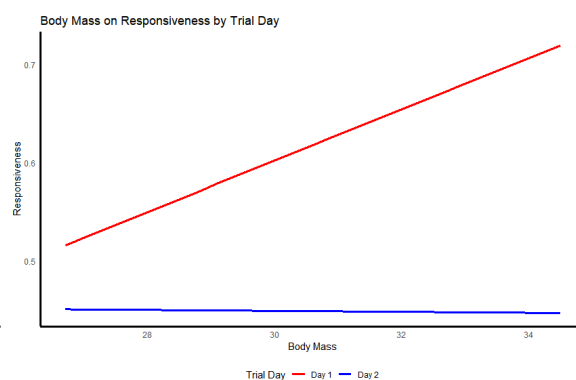
Figure 6.2: *The estimated effect of body mass and trial day on responsiveness.*
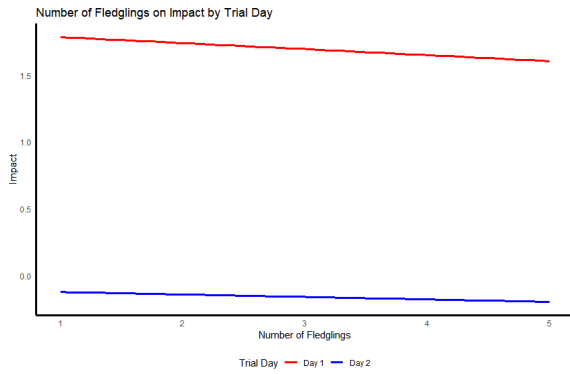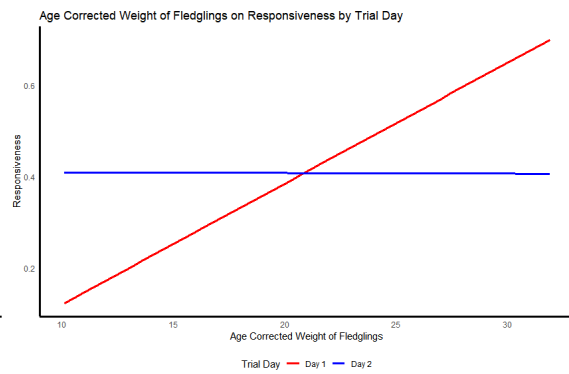
Figure 6.3: *The estimated effect of number of fledglings and trial day on impact.*

Figure 6.4: *The estimated effect of number of fledglings and trial day on responsiveness.*

Figure 6.5: *The estimated effect of age corrected weight of fledglings and trial day on impact.*

Figure 6.6: *The estimated effect of age corrected weight of fledglings and trial day on responsiveness.*
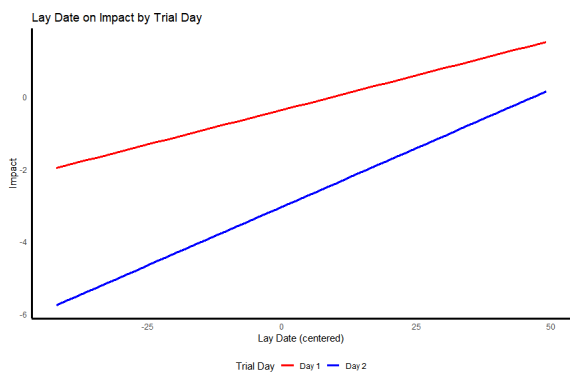
Figure 6.7: *The estimated effect of lay date (centered) and trial day on impact.*
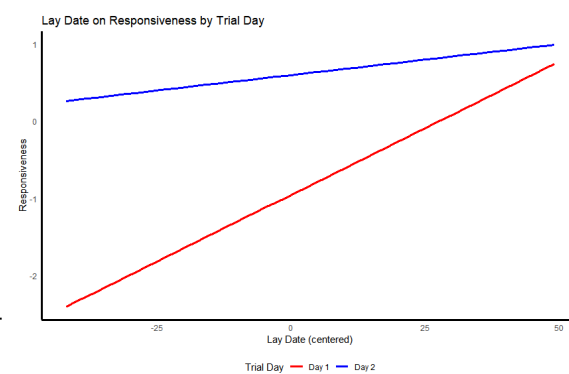
Figure 6.8: *The estimated effect of lay date (centered) and trial day on responsiveness.*
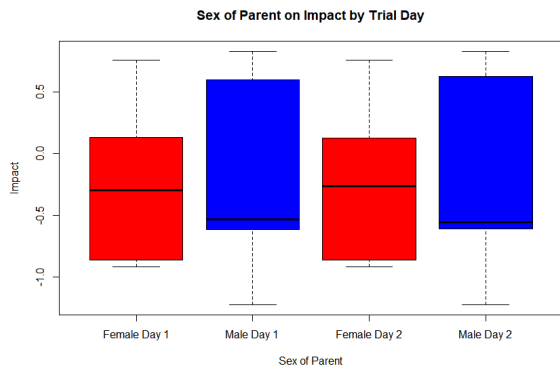
Figure 6.9: *The estimated effect of sex of parent and trial day on impact.*
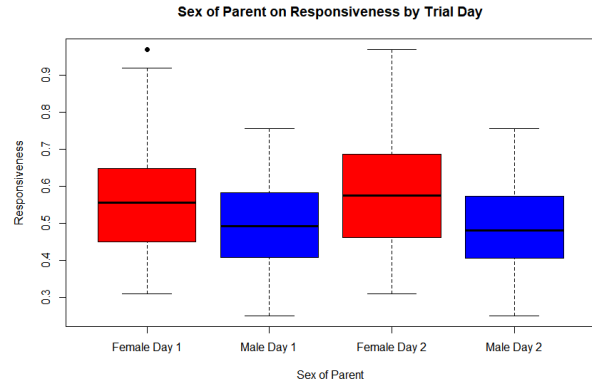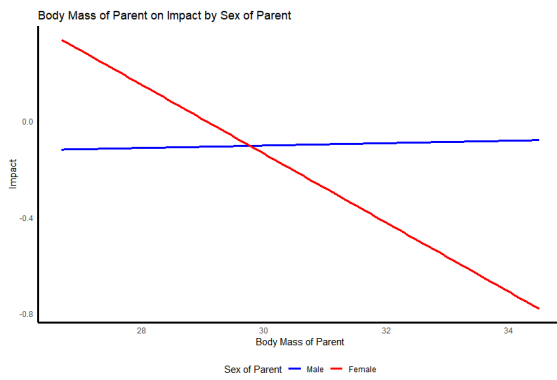

Figure 6.10: *The estimated effect of sex of parent and trial day on impact.*

Figure 6.11: *The estimated effect of body mass of parent and sex of parent on impact.*

4. DISCUSSION

4.1 Body mass, life-history traits and their correlations

The correlations seen in Figure 4, although not part of the main hypotheses under test here, warrant further discussion. The weight of the parent was correlated with an earlier onset of breeding, which suggests that heavier individuals, with presumably higher energy reserves, as indicated by greater winter body weight, may have been more capable of initiating breeding earlier in the season. It is found that in the non-migratory black-capped chickadees *(Poecile atricapillus)* a higher winter fat reserve was associated with an earlier onset of breeding, while higher residual body mass was correlated with a later onset of breeding (Montreuil-Spencer et al., 2019). This indicates that fat stores, and thus energy reserves, can have some effect on onset of breeding in house sparrows.

Furthermore, individuals with a greater winter body weight tended to produce more fledglings and larger fledglings, suggesting increased parental investment and greater allocation towards reproduction. Larger individuals may have had greater energy reserves in the winter going into the spring, enabling them to provide for their offspring more effectively, and thus invest more in total in their reproductive effort. Related to this, Jensen et al. (2004) found that breeding body mass positively correlated with fledgling production in female house sparrows, while Rønning et al. (2015) found that winter body mass did not correlate with fledgling production, but rather had mixed effects on survival chances dependent of sex and environment of adult house sparrows. Body mass includes both a more fixed body size (skeletal and muscular component), plus a more flexible fat reserve. Winter body mass in small passerines is fluctuating, as the fat reserve varies depending on individual and environmental conditions, and is not necessarily and indicator of quality of state, but rather a result of the trade-off between starvation risk, predation, social status and availability of food (Lima, 1986). This indicates that winter body masses, while positively correlated with more and larger fledglings, has some uncertainties following along, and suggests that there could be additional traits correlated with winter body mass that affects number and weight of fledglings.

Wolf et al. (2007) argues that life-history predicts differences in fitness expectations and that they should result in consistent differences in risk-taking behavior such as exploration, boldness and aggressiveness. Individuals with high future expectations (potential to get many offspring) have much to lose, and should be risk averse, while the opposite should be the

trend for individuals with low expectations. It can work as a mechanism to maintain behavior in the population. Resource availability may be an underlying factor that would make us better understand what is happening, but pace-of-life and the behavior of the parents may help shed some light on the relationship between parental weight and reproductive success. Resource availability was the same for everyone, but there could be some difference in acquisition of territory, foraging ability or willingness to risk predation to gain food and breed, that could be correlated with the body mass, lay date, fledgling weight and number of fledglings (e.g., individuals could risk predation by storing energy for later reproductional effort). For example, Moirón et al. (2019) found that body mass positively correlated with risk taking behaviors such as aggressiveness and exploration, Montreuil-Spencer et al. 2019 showed that there were correlations between body mass and lay date and Piper et al. (2000) showed that larger loons held on to their territories for longer than smaller loons.

Interestingly, there were no significant correlations between the lay date and age corrected weight of fledglings and number of fledglings in house sparrows, indicating that an earlier lay date did not affect these characteristics of the fledglings. There was a significant negative correlation between earlier lay date and offspring survival in Ringsby et al. (1998), but they attributed this to cold weather early in the breeding season. Next, the number of fledglings exhibited a positive correlation with the age-corrected weight of fledglings. This is contradictory to the study of Ringsby et al. (1998), where they found that there was no correlation between broods of different sizes and body mass. Higher numbers of fledglings were associated with increased weight, which indicates that some parents are better at producing both more and heavier fledglings (e.g., they are better at provisioning, take more risks when providing for chicks, get better nesting habitats).

These positive correlations between variables relating to offspring productivity might be predicted from a fast pace-of-life, with greater current parental investment. Hence an expectation of a shorter reproductive lifespan for these highly productive parents could explain some of the variation that we do see here in the correlations between life-history traits. This is perhaps further supported when we see that greater winter mass was associated with an earlier onset of breeding, as well as higher number and larger fledglings. If winter mass covaries with later breeding mass, then parental condition, specifically body mass, may play a role in determining reproductive success. This is because such parents can afford to allocate more resources to offspring, but also because they may have had a strategically faster pace-of-life compared to smaller individuals. However, these conclusions are speculative

since these are not measures of breeding parental body mass, but rather mid-winter data that might fluctuate depending on resource availability and temperature within a few days.

4.2 Differences in breeding years

Lay date was two and a half days later during 2022 compared with 2021. Combined with a negative effect of breeding year on fledgling production per brood, this could indicate that 2023 was a less favorable breeding season for the house sparrows in the area. The population of house sparrows was unusually large for the winter of 2022 (estimated 180 individuals), and combined with a cold spring and summer, this could lead to both higher competition of resources and worse individual breeding conditions in some cases. In Ringsby et al. (1998) there was lower recruitment into adult population from nests with earlier lay dates, and this was during a cold spring. Interestingly, age corrected weight of the fledglings did not seem to differ between years, indicating a possible emphasis of quality over quantity during a worse breeding season like 2023. This decline could also be attributed to food availability. The data on food availability is not gathered yet, but looking into this could be interesting. Additionally, winter body mass of parents changed slightly between the years, with parents being heavier during the winter of 2023. This contradicts the theory slightly, as larger parents should have more energy to put into parental investment, but then again, we are not measuring breeding masses but winter body masses, which could account for some of the variation seen here. Furthermore, this could indicate the presences of density dependent selection on the house sparrows, as shown in Araya-Ajoy et al. (2021), where 'faster' types of house sparrows did worse in denser populations. This showcases the factors and complexity a changing social and abiotic environment can inflict on optimal phenotypes and behavior, and if looked further into over several years, could help build up the argument of an existing POLS.

4.3 Repeatability of scrounging behavior, responsiveness, and impact

The predictions from our first and second hypothesis, that there would be individual variation and repeatability between scrounging behavior, responsiveness and impact seems to be consistent with the results of this study, for both the whole population and the 26 individual subset. Except for impact where repeatability was significantly lower when not accounting for trial day. Still, we see distinct individual behavioral profiles within the producer-scrounger foraging game. The repeatability of this suggests that they are not random fluctuation but stable parts of their personalities, potentially shaped by ecological constraints and

evolutionary processes, such as the density-dependent selection proposed by Wright et al. (2019). There could be individual repeatable differences in animal behavior, that undergoes density-dependent selection. If so, this highlight the adaptive alignment of pace-of-life syndromes (Wright et al. 2019). The individual repeatability of behavior observed during the negative frequency-dependent game lays the foundation for further analysis, that certain combinations of behavior, morphology and reproductive traits may be selected for, and selected for at the same time.

4.4 Trial day and significant interactions

The significant interactions observed between trial day and all other predictor variables highlight an important biological phenomenon known as habituation, which influences the variation in behavior among the house sparrows. On the first day of the trial, the birds displayed perhaps more timid and shy foraging behavior, that could be characterized by groups staying closer together and overlapping in the wells they foraged from. As a result, we see higher impact, and higher responsiveness on trial day 1. This shyness suggests that even slight changes in behavior, sounds, or noise during the trial could have a more substantial impact on the opponents compared to habituated birds. The shyness of the birds during the first day of trials likely influenced their arrival time at the feeding board and increased vigilance, leading to a decrease in both the proportion of scrounges and the mean total scrounges. Most of this is in accordance with the results found by Guldvik (2023) and Zeiner-Henriksen (2023) who ran similar analysis on the effects of trial day on proportion scrounging and mean total scrounging on the whole 168 individuals. However, the results seem to differ on scrounging ratio and proportion, as in their models, there were more scrounging in trial day 1 as a result of individuals staying closer together, suggesting that this subset may exhibit different scrounging behavior than the average of the population.

Considerable efforts were made to habituate the birds and minimize stress during the trials. They were perhaps habituated to a non-experiment set-up that were not similar enough to the experimental cages, and they only habituated to the experimental cages for one night before trial day 1. Thus, it is worth noting that running the trials for additional days, or getting habituation aviaries more similar to the experimental setup, could have provided further insights. Nonetheless, as there is a need for manual human handling, the release and catch of the birds during trials, exposure to stress and extended trial durations may impose significant strain on the focal birds, Alternatively, conducting producer-scrounger trials in a natural environment, if feasible and able to yield sufficient data, would provide more accurate

observations of house sparrows' behavior. This could be done with outside automatic feeders, where disturbances from human activity would be minimized. In Aplin & Morran-Ferrond (2017), they conducted their experiments with two kinds of feeders in the birds' natural environment. To access producing and scrounging, they placed and automatic feeder equipped with an RFID-antenna registering type of behavior (producing or scrounging), identity and duration of behavior when birds arrived at the feeder. They also conducted an experiment to assess the spatio-temporal feeding patterns of the flocks, by placing out feeders with accessible feeder holes equipped with RFID-antennas, registering every PIT-tag equipped bird arriving. This approach or an approach similar to this would minimize potential disturbances from human and artificial interactions, which are inevitable in experimental set-ups, while still producing viable data on both producer-scrounger behavior and how social structure and kinship within the flocks affect these types of behaviors.

4.5 Effects of body mass and sex on producer-scrounger behavior

In the studies by Liker and Barta (2002) and Tóth et al. (2009), they found that there was a positive association between body mass in sparrows and dominance and scrounging behavior. This might lead us to expect that larger individuals, particularly males, were engaging in more scrounging behavior. Our findings does not align with this prediction. However, Guldvik (2023) and Zeiner-Henriksen (2023) found a significant interaction between sex and body mass, where larger males scrounged more and larger females less. Of course, the lack of habituation could have some significance in our results, but we could also lack the power or simply have a group of individuals acting differently than the mean of the whole dataset. Additionally, it is possible that the observed relationship between body mass and scrounging behavior was influenced by factors such as exploration and activity levels of the individuals. Larger individuals may not have scrounged more in proportion, contrary to expectations, but rather engaged in other behaviors such as early arrival at feeder plates and visited more wells during trials, resulting in more mean total scrounges, but less in proportion. Interestingly, when we examined the interaction between trial day and sex, we found that females tended to scrounge more than males, both totally and in proportion, on both trial days. This finding challenges the notion that males (which are usually larger) exhibit higher levels of scrounging behavior. The relationship between sex and scrounging behavior observed suggests that factors other than body size may be influencing their foraging strategies. This discrepancy

suggests a need to consider factors beyond body mass and sex when examining scrounging behavior, and rather consider social dynamics within the groups.

One possible explanation for the lack of a proportional increase in scrounging behavior among larger individuals and males could be related to kinship dynamics. During the trials, the birds used were caught from the same barn and placed together without accounting for social structure and kinship. Previous research by Tóth et al. (2009) and Mathot & Giraldeau (2010) suggests that relatedness in social foraging can influence scrounging behavior, depending on the costs and benefits involved. According to Hamilton's rule, individuals are expected to behave in ways that maximize their own benefits and those of their close kin. In the study by Tóth et al. (2009), larger males, who also tend to be larger in size, though not significantly in our subset, engaged in less non-aggressive scrounging behavior with close kin. Captive house sparrows have been shown to recognize kin and adapt their behavior accordingly. Interestingly, for females, the opposite trend was observed, with a tendency to engage in more non-aggressive scrounging behavior with close kin. This theory suggests that larger males may allow close-kin females to scrounge from them while they scrounge from a wider range of opponents. Our study's results, if we got to know the relatedness within trial groups and get rid of habituation effects, could be consistent with this theory.

To gain a more comprehensive understanding of the effects of sex and body mass on scrounging behavior, further research is needed with larger sample sizes, including a greater number of individuals from both sexes. Additionally, examining the influence of kinship and social networks could provide valuable insights into the underlying mechanisms at play. By incorporating these factors into future investigations, we can shed more light on the complex dynamics of scrounging behavior in house sparrows and enhance our understanding of the interplay between sex, body mass, and social interactions.

4.6 Effects of body mass and sex on responsiveness and impact

Surprisingly, larger individuals demonstrated reduced impact and more responsiveness, suggesting that their behavior had a lesser effect on their opponents' decisions and actions, while they themselves adjusted their behaviors. Although this finding contradicts our initial prediction, it may be partially explained by the interaction effects we see between sex and trial day on responsiveness and sex and body mass on impact. Larger males exhibited increased impact, while larger females displayed lower impact. Additionally, females seem to be more responsive on both trial days than males. This observation raises intriguing questions

about the differing tactics employed by males and females based on their body mass, especially when considering the positive link between body mass and dominance (Liker & Barta, 2002). The combination of these factors could indicate that despite of having more mass, female house sparrows possess a heightened awareness of social dynamics and adapt their behavior to a greater degree. It could also be that males are more susceptible to let lesser females of close kin scrounge from them, as larger females can gain access to food themselves from lesser individuals. Though it is worth mentioning, because of the lack of habituation, this could indeed not be the dynamics of a producer-scrounger game. The study conducted by Aplin & Morran-Ferrond (2017), which found a connection between scrounging behavior and sociability in great tits, further underscores the significance of body mass, sex and social interactions. In this context, the fact that females were more responsive, and with a negative effect of body mass on impact, gives a rise to new questions regarding the dymanics of sex, kinship, body mass and behavior. A study taking into consideration spatio-temporal feeding patterns and kinship could possibly account for many of the possible interactions here.

It is important to note that the analyzed data represents a subset of 26 individuals, potentially functioning as an outgroup in certain aspects. Comparing these results to the findings of Guldvik (2023) and Zeiner-Henriksen (2023), which explored the effects of sex, trial day, and body size on social dynamics of the full data set, we observe differences. These studies found no significant interaction effects for sex and trial day or body mass and trial day, and no direct effect of body mass on responsiveness. However, Guldvik (2023) did find that larger individuals, when considering body size and its interaction with BMR, exhibited greater responsiveness. Moreover, the only significant interaction effect observed in impact in their analysis was that of trial day. These comparisons suggest that the subset of 26 individuals differs from the larger population of 168 individuals in several ways, and thus, the validity of these findings is questionable.

Despite this, these analyses have revealed the notable influence of body mass and sex on impact and responsiveness in our trials and could raise some questions of the sex and body mass differences in responsiveness and impact. It would be interesting to look at the effects of kinship, and the effects of body mass on dominance in a natural habitat with automatic feeders. The unexpected finding of reduced impact in larger individuals coupled with the interplay between body mass, dominance, the contrasting effects between males and females and social dynamics could lead to some interesting questions being raised and interesting

answers to them, although these results must be taken with a grain of salt as the sample size is small (only 9 females) and there is evidence of it being a behavioral outgroup of the main population in some ways.

Reproductive traits and effects on scrounging, responsiveness, and impact

The only significant effects seen between age corrected weight of fledglings, number of fledglings and lay date, was the interaction between them and trial day, on the response variables, indicating that the effects of habituation and variation between days was stronger on the behavior of the birds than their reproductive strategies. Meanwhile, there were some interesting patterns from significant interactions in these results. For example, age corrected weight of fledglings and its interaction with trial day followed the same trend for proportion scrounging and mean total scrounging as with the interaction of body mass and trial day on the same response variable (bigger individuals and individuals that got larger offspring have higher mean total scrounges for both days, and higher proportion for the first but lower proportion scrounges for the second day). Some similarities can be seen with a later lay date, more offspring, body mass and their interaction with trial day, with all leading to more scrounging in total. This points to the conclusion that larger parental body mass, larger offspring, more offspring, and a later lay date led to more scrounging in total, but not necessarily in proportion. That larger size, larger offspring and more offspring covary positively with total scrounges are consistent with our predictions, because a greater effort put into reproduction, as indicated by these variables, should be correlated with a faster pace-of-life. Another possibility is that there could be differences in phenotypic quality, with larger and heavier individuals going on to be more effective parents. The fact that we see the correlations from the correlation's matrix furthermore in the main models strengthen the argument that these traits are covarying. And as mentioned earlier, mean total scrounges has the potential to covary with other behavioral factors such as heightened exploration and boldness, where ease proportion scrounging says more about the choice of either producing or scrounging. Next, a later lay date is not expected from the predictions. A reason for a later lay date could be an unusually harsh and wet spring and summer, or the denser population than normal during this year. 'Fast' types in a dense population have been shown to do worse than 'slow' types (Araya-Ajoy et al. 2021) and could compensate by having later lay dates and fewer clutches in total, as they do not have the extra resources to allocate towards reproduction.

For the main effects without interactions, it was no significant effects, but the trends are interesting, although it could all be by chance. More fledglings, larger fledglings and an earlier lay date were all positively associated with higher proportion of scrounging, mean total scrounging, more impact and more responsiveness. This could again reflect an effect of breeding year, as in 2021 the mean mass of the parents was smaller, but still, they got more chicks. This is in the opposite direction of what seems to be the correlation, and it seems plausible that it is rather just a year effect. In addition, we assumed no extra-pair paternity during breeding, which is likely wrong, and adds more noise to the analysis of involving reproductive traits. The effect size of the variables and the power gained from number of individuals seems to be insufficient, and for further study, a larger sample size, with better overview of kinship during trials and genetic parenthood of fledglings could account for much of the noise we see in this sample when considering reproductive traits. In addition, trials over more days or trials in the house sparrow's natural habitat could be beneficial to account for habituation effect and get more accurate scores of repeatability of behaviors.

5. Conclusion

This study aimed to investigate the relationships between body mass, life-history traits, and producer-scrounger behavior in house sparrows. During trials, there seems to have been a strong influence from a lack of habituation on the behaviors of birds during producer-scrounger trials, to such a degree, that the lack of habituation may have created something different than a producer-scrounger dynamic. This is indicated by a positive responsiveness, rather than a negative one on most predictor variables, and higher amounts of impact during the first day of trial. In addition, the subset of 26 individuals seems to differ in some key behaviors to the 168 individuals trialed during the winter of 2022 (Guldvik, 2023; Zeiner-Henriksen, 2023), and brings questions of the validity of the behaviors displayed during trials, and thus, the results of this thesis.

On the other side, although the results are derived from an unhabituated and smaller sample size, there seems to be some interesting patterns of the effects that could need further exploration. The positive covariance between body mass, more fledglings and larger fledglings is in accordance with predictions, and if investigated with a habituated and larger sample size, could yield some interesting results. This aligns with the theory that larger

animals could be more dominant, have access to better breeding grounds, invest more in the present, take risks in relation to reproductive effort and be better parents.

Moreover, larger individuals exhibited reduced impact. The interaction between body mass and impact differed between sexes, with larger males displaying increased impact and larger females exhibiting lower impact. This indicates distinct tactics employed by males and females based on their body mass and associated dominance. Additionally, larger individuals, particularly females, showed heightened responsiveness, indicating a greater awareness of social dynamics and adaptive behavior.

Our results challenge the expected relationship between body mass, sex, and scrounging behavior in sparrows. While previous research and our predictions suggested that larger individuals, particularly males, would exhibit more scrounging behavior, our results did not align with this prediction. Factors such as exploration, activity levels, social dynamics, and kinship relationships may play a significant role in shaping scrounging behavior. Further research should focus on getting larger sample sizes and to consider kinship and social networks. This is needed to gain a more comprehensive understanding of the complex dynamics of scrounging behavior in house sparrows and the interplay between sex, body mass, and social interactions. In addition, it could be beneficial to take measurements of breeding body mass, to control for the variation in winter body mass, and thus get more accurate results.

Individuals with larger winter body mass initiate breeding earlier. Larger parents also produced more and larger fledglings, indicating increased parental investment and allocation towards reproduction. These findings emphasize the importance of considering resource availability and parental behavior and could support the notion that there are some correlated traits with winter body mass that yield more and better offspring. The theory of pace-of-life syndromes and the incorporation of behavior into this could help shed some light on these results. This is what this study tried to do, but with some noise and problems along the way, could not get an accurate comparison between physiology and reproductive traits to the individual differences in producer-scrounger behavior. Additionally, proxies for boldness, exploration and scrounging behavior needs to be found and incorporated during analysis, to see if these correlate with a larger body mass both during winter and breeding body mass, as this could give valuable insights into if a larger body mass could relate to reproductive trade-offs that indicate a fast pace-of-life.

Although our predictions were not fully supported, our study demonstrated the existence of individual behavioral profiles and stable social personality traits in house sparrows but failed to get any significant interactions between reproductive traits and behavioral traits. This could be due to a small effect size, or a small sample size, or could be due to the noise from for example the habituation effect or the bias from assuming no extra-pair paternity. The concept of pace-of-life syndromes does not align with, nor is contradicted by our observations, as there are indications that different reproductive and behavioral strategies can coexist within the population. Again, if this is so, this diversity could contribute to genetic variability and help enhance adaptability in fluctuating environments.

In conclusion, our study tries to shed some light on the interplay between body mass, life-history traits, and producer-scrounger behavior in house sparrows, but suffered from habituation effects and possibly a too small sample size. It would in addition be beneficial to get the genetic parenthood of the fledglings. Further research with larger sample sizes and consideration of social structure, kinship dynamics, and social networks will deepen our understanding of the underlying mechanisms. Finding ways to reduce the effects of habituation is also needed, with non-experimental setups being the best option. Further unraveling the intricacies of individual behavior and social interactions could provide valuable insights into the adaptive strategies of avian populations.

6. REFERENCES

Aase, K., Jensen, H. & Muff, S. (2022). Genomic estimation of quantitative genetic parameters in wild admixed populations. Methods Ecol Evol, 13(5), 1014-26.

Anderson, T. R. (2006). Biology of the ubiquitous house sparrow: from genes to populations. Oxford University Press.

Aplin, L. M., & Morand-Ferron, J. (2017). Stable producer-scrounger dynamics in wild birds: Sociability and learning speed covary with scrounging behaviour. Proceedings of the Royal Society B: Biological Sciences, 284(1852), 20162872.

Araya-Ajoy, Y. G., Niskanen, A. K., Froy, H., Ranke, P. S., Kvalnes, K., Rønning, B., Le Pepke, M., Jensen, H., Ringsby, T. H., Sæther, B. & Wright, J. (2020). Variation in generation time reveals density regulation as an important driver of pace of life in a bird metapopulation. Ecology Letters CNRS Wiley.

Araya-Ajoy, Y.G., Westneat, D.F. & Wright, J. 2020. Pathways to social evolution and their eco-evolutionary feedbacks. Evolution, 74, 1894–1907).

Baalsrud, H. T., Sæther, B. E., Hagen, I. J., Myhre, A. M., Ringsby, T. H., Pärn, H., & Jensen, H. (2014). Effects of population characteristics and structure on estimates of effective population size in a house sparrow metapopulation. Mol Ecol, 23(11), 2653-68.

Barnard, C. J., & Sibly, R. M. (1981). Producers and scroungers: a general model and its application to captive flocks of house sparrows. Animal Behaviour, 29(2), 543-550.

Bates, D., et al. (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67(1), 1-48.

Bell AM, Hankison SJ, Laskowski KL. (2009). The repeatability of behaviour: a meta-analysis. Anim. Behav. 77, 771-783.

Belmaker, A., Motro, U., Feldman, M. W., & Lotem, A. (2012). Learning to choose among social foraging strategies in adult house sparrows (*Passer domesticus*). Ethology, 118(11), 1111-1121.

Billing, A. M., Lee, A. M., Skjelseth, S., Borg, Å. A., Hale, M. C., Slate, J., Pärn, H., Ringsby, T. H., Sæther, B. E. & Jensen, H. (2012). Evidence of inbreeding depression but not inbreeding avoidance in a natural house sparrow population. Mol Ecol, 21(6), 1487-99.

Chamberlain, D. E., Cannon, A. R., Toms, M. P., Leech, D. I., Hatchwell, B. J., & Gaston, K. J. (2009). Avian productivity in urban landscapes: A review and meta-analysis. Ibis, 151(1), 1-18.

Charmantier, A., Demeyrier, V., Lambrechts, M., Perret, S., & Grégoire, A. (2017). Urbanization is associated with divergence in pace-of-life in great tits. Frontiers in Ecology and Evolution, 5, 53.

Côté, J., Clobert, J., Brodin, T., Fogarty, S., & Sih, A. (2010). Personality-dependent dispersal: Characterization, ontogeny, and consequences for spatially structured populations. Philosophical Transactions of the Royal Society B: Biological Sciences, 365(1558), 4065-4076.

Davies, N. B., Krebs, J. R., & West, S. A. (2012). An introduction to behavioural ecology. John Wiley & Sons.

Davies, N. B., & Sewall, K. B. (2016). Ecology of cooperatively breeding animals. Cambridge University Press.

Dingemanse, N. J. & Araya-Ajoy, Y. G. 2015. Interacting personalities: behavioural ecology meets quantitative genetics. Trends Ecol. Evol 30, 88-97.

Dingemanse, N.J. & Wolf, M. (2010) Recent models for adaptive personality differences: a review. Philosophical Transactions of the Royal Society B-Biological Sciences, 365, 3947–3958.

Dubois, F, Morand-Ferron, J and Giraldeau, L. (2010) Learning in a game context: strategy choice by some keeps learning from evolving in others. Proc. R. Soc. B.2773609–3616.

Duckworth, R. A., & Badyaev, A. V. (2007). Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. Proceedings of the National Academy of Sciences, 104(36), 15017-15022.

Engen, S., Kvalnes, T., & Sæther, B. E. (2014). Estimating phenotypic selection in age-structured populations by removing transient fluctuations. Evolution, 68(9), 2509-2523.

Engen, S., Ringsby, T. H., Sæther, B. E., Lande, R., Jensen, H., Lillegard, M., & Ellegren, H. (2007). Effective size of fluctuating populations with two sexes and overlapping generations. Evolution, 61(8), 1873-85.

Engen, S., Sæther, B. E., Kvalnes, T., & Jensen, H. (2012). Estimating fluctuating selection in age-structured populations. Journal of evolutionary biology, 25(8), 1487-1499.

Friard, O., & Gamba, M. (2016). BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. Methods in Ecology and Evolution, 7(11), 1325-1330.

Garamszegi LZ, Markó G & Herczeg G. (2013). A meta-analysis of correlated behaviours with implications for behavioural syndromes: mean effect size, publication bias, phylogenetic effects and the role of mediator variables. Evol. Ecol. 26, 1213–1235

Grafen, A. (1984). Natural selection, kin selection and group selection. Behavioural ecology: an evolutionary approach, 2.

Guldvik, M. (2023). Effects of energetics and social environment on individual foraging strategies in a population of house sparrows, *Passer domesticus* (Master's thesis). Norwegian University of Science and Technology, Norway.

Hagen, I. J., Billing, A. M., Rønning, B., Pedersen, S. A., Pärn, H., Slate, J., & Jensen, H. (2013). The easy road to genome-wide medium density snp screening in a non-model species: development and application of a 10k snp-chip for the house sparrow (*Passer domesticus).* Molecular Ecology Resources, 13(3), 429-439.

Holand, A. M., Jensen, H., Tufto, J., & Moe, R. (2011). Does selection or genetic drift explain geographic differentiation of morphological characters in house sparrows *Passer domesticus*? Genetics Research, 93(05), 367-379.

Holand, H., Jensen, H., Tufto, J., Pärn, H., Sæther, B. E., & Ringsby, T. H. (2015). Endoparasite infection has both short-and long-term negative effects on reproductive success of female house sparrows, as revealed by faecal parasitic egg counts. PLoS One, 10(5).

Holand, H., Jensen, H., Tufto, J., Soliman, M., Pärn, H., Sæther, B. E., & Ringsby, T. H. (2014). Lower survival probability of house sparrows severely infected by the gapeworm parasite. Journal of Avian Biology, 45(4), 365-373.

Houslay, T. M., & Wilson, A. J. (2017). Avoiding the misuse of BLUP in behavioural ecology. Behavioral Ecology, 28(4), 948-952.

Jensen, H., Bremset, E. M., Ringsby, T. H., & Sæther, B. E. (2007). Multilocus heterozygosity and inbreeding depression in an insular house sparrow metapopulation. Molecular Ecology, 16(19), 4066-4078.

Jensen, H., Moe, R., Hagen, I. J., Holand, A. M., Kekkonen, J., Tufto, J., & Sæther, B. E. (2013). Genetic variation and structure of house sparrow populations: is there an island effect? Molecular Ecology, 22(7), 1792-1805.

Jensen, H., Sæther, B. E., Ringsby, T. H., Tufto, J., Griffith, S. C., & Ellegren, H. (2003). Sexual variation in heritability and genetic correlations of morphological traits in house sparrow (*Passer domesticus*). Journal of Evolutionary Biology, 16(6), 1296-1307.

Jensen, H., Steinsland, I., Ringsby, T. H., & Sæther, B. E. (2008). Evolutionary dynamics of a sexual ornament in the house sparrow *(Passer domesticus)*: the role of indirect selection within and between sexes. Evolution, 62(6), 1275-93.

Jensen, H., Sæther, B. E., Ringsby, T. H., Tufto, J., Griffith, S. C., & Ellegren, H. (2004). Lifetime reproductive success in relation to morphology in the house sparrow *Passer domesticus*. Journal of Animal Ecology, 73(4), 599-611.

Katsnelson, E., Motro, U., Feldman, M. W., & Lotem, A. (2008). Early experience affects producer–scrounger foraging tendencies in the house sparrow. Animal Behaviour, 75(4), 1465-1472.

Lendvai, A. Z., Barta, Z., Liker, A., & Bokony, V. (2004). The effect of energy reserves on social foraging: hungry sparrows scrounge more. Proc Biol Sci, 271(1556), 2467-72.

Liker, A., & Barta, Z. (2002). The effects of dominance on social foraging tactic use in house sparrows. *Behaviour*, *139*(8), 1061-1076.

Lima, S. L. (1986). Predation risk and unpredictable feeding conditions: Determinants of body mass in birds. Ecology, 67(2), 377-385.

Maynard Smith, J. (1982). Evolution and the theory of games. Cambridge University Press.

Mathot, K. J., & Giraldeau, L.-A. (2010). Within-group relatedness can lead to higher levels of exploitation: A model and empirical test. Behavioral Ecology, 21(4), 843-850.

Minias, P. (2015). Successful colonization of a novel urban environment is associated with an urban behavioral syndrome in a reed-nesting waterbird. Ethology, 121(12), 1178-1190.

Moiron, M., Araya-Ajoy, Y. G., Mathot, K. J., Mouchet, A., & Dingemanse, N. J. (2019). Functional relations between body mass and risk-taking behavior in wild great tits. Behavioral Ecology, 30(3), 617-623.

Montreuil-Spencer, C., et al. (2019). Winter corticosterone and body condition predict breeding investment in a nonmigratory bird. Behavioral Ecology, 30(6), 1642-1652.

Mutzel, A., Dingemanse, N. J., Araya-Ajoy, Y. G., & Kempenaers, J. (2013) Parental provisioning behaviour plays a key role in linking personality with reproductive success. Proc R Soc B 280: 20131019.

Niemelä, P.T., Vainikka, A., Hedrick, A.V. and Kortet, R. (2012) Integrating behaviour with life history: boldness of the field cricket, Gryllus integer, during ontogeny. Functional Ecology, 26: 450-456.

Niskanen, A. K., Billing, A. M., Holand, H., Hagen, I. J., Araya-Ajoy, Y. G., Husby, A., Rønning, B., Myhre, A. M., Ranke, P. S., Kvalnes, T., Pärn, H., Ringsby, T. H., Lien, S., Sæther, B. E., Muff, S., & Jensen, H. (2020). Consistent scaling of inbreeding depression in space and time in a house sparrow metapopulation. Proceedings of the National Academy of Sciences of the United States of America, 117, 14584– 14592.

Pärn, H., Jensen, H., Ringsby, T. H., & Sæther, B. E. (2009). Sex-specific fitness correlates of dispersal in a house sparrow metapopulation. J Anim Ecol, 78(6), 1216-25.

Pärn, H., Ringsby, T. H., Jensen, H., & Sæther, B. E. (2012). Spatial heterogeneity in the effects of climate and density-dependence on dispersal in a house sparrow metapopulation. Proc Biol Sci, 279(1726), 144-52.

Peach, W. J., Vincent, K. E., Fowler, J. A., & Grice, P. V. (2008). Reproductive success of house sparrows along an urban gradient. Animal Conservation, 11(6), 493-503.

Pepke, M. L., et al. (2022). Genetic architecture and heritability of early-life telomere length in a wild passerine. Molecular Ecology, 31(23), 6360-6381.

Piper, W. H., Tischler, K. B., & Klich, M. (2000). Territory acquisition in loons: The importance of take-over. Animal Behaviour, 59(2), 385-394.

Ranke, P.S., Araya-Ajoy, Y.G., Ringsby, T.H., Pärn, H., Rønning, B., Jensen, H., Wright, J. & Sæther, B. E. (2021) Spatial structure and dispersal dynamics in a house sparrow metapopulation. J Anim Ecol, 90(12), 2767-81.

Ranta, E. S. A., Peuhkuri, N., Laurila, A., Rita, H., & Metcalfe, N. B. (1996). Producers, scroungers and foraging group structure. Animal Behaviour, 51(1), 171-175.

Réale, D., Garant, D., Humbries, M.M., Bergeron, P., Careau, V. & Montiglio, P.-E. (2010) Personality and the emergence of the pace-of-life syndrome concept at the population level. Philosophical Transactions of the Royal Society B-Biological Sciences, 365, 4051–4063.

Rebolo-Ifrán, N., Carrete, M., Sanz-Aguilar, A., Rodriguez-Martinez, S., Cabezas, S., Marchant, T. A., et al. (2015). Links between fear of humans, stress, and survival support a non-random distribution of birds among urban and rural habitats. Scientific Reports, 5, 13723.

Ringsby, T. H., Sæther, B. E., Altwegg, R., & Solberg, E. J. (1999). Temporal and spatial variation in survival rates of a house sparrow, *Passer domesticus*, metapopulation. Oikos, 85(3), 419–425.

Ringsby, T. H., Sæther, B. E., Jensen, H., & Engen, S. (2006). Demographic characteristics of extinction in a small, insular population of house sparrows in northern norway. Conserv Biol, 20(6), 1761-7.

Ringsby, T. H., Sæther, B.-E., & Solberg, E. J. (1998). Factors affecting juvenile survival in house sparrows *Passer domesticus*. Journal of Avian Biology, 29(3), 241-247.

Ringsby, T. H., Sæther, B. E., Tufto, J., Jensen, H., & Solberg, E. J. (2002). Asynchronous Spatiotemporal Demography of a House Sparrow Metapopulation in a Correlated Environment. Ecology, 83(2), 561–569.

RStudio Team. (2020). RStudio: Integrated Development for R. RStudio, PBC.

Rønning, B., et al. (2016). Is basal metabolic rate associated with recruit production and survival in free-living house sparrows? Functional Ecology, 30(7), 1140-1148.

Saatoglu, D., Niskanen, A. K., Kuismin, M. O., Ranke, P. S., Hagen, I. J., Araya-Ajoy, Y. G., Kvalnes, T., Pärn, H., Rønning, B., Ringsby, T. H., Sæther, B. E., Husby, A., Sillanpää, M. J., & Jensen, H. (2021). Dispersal in a house sparrow metapopulation: An integrative case study of genetic assignment calibrated with ecological data and pedigree information. Molecular Ecology, 30(19), 4740– 4756.

Santostefano, F., Wilson, A. J., Araya-Ajoy, Y. G. & Dingemanse, N. J. (2016) Interacting with the enemy: indirect effects of personality on conspecific aggression in field crickets. Behav. Ecol 27, 1235-1246.

Smith, J., & Price, G. (1973). The logic of animal conflict. Nature, 246, 15-18.

Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods in Ecology and Evolution, 8(12), 1639-1644.

Stubberud, M.W., Myhre, A.M., Holand, H., Kvalnes, T., Ringsby, T.H., Sæther, B.E. & Jensen, H. (2017) Sensitivity analysis of effective population size to demographic parameters in house sparrow populations. Mol Ecol, 26(9), 2449–65.

Sæther, B. E., Ringsby, T. H., Bakke, Ø., & Solberg, E. J. (1999). Spatial and temporal variation in demography of a house sparrow metapopulation. Journal of Animal Ecology, 68(3), 628-637.

Tóth, Z., Bókony, V., Lendvai, Z., Szab´o, K., P´enzes, Z., & Liker, A. (2009). Effects of relatedness on social-foraging tactic use in house sparrows. Animal Behaviour, 77(2), 337-342.

Tryjanowski, P., Møller, A. P., Morelli, F., Biaduń, W., Brauze, T., Ciach, M., et al. (2016). Urbanization affects neophilia and risk-taking at bird-feeders. Scientific Reports, 6, 28575.

Vickery, W. L., Giraldeau, L.-A., Templeton, J. J., Kramer, D. L., & Chapman, C. A. (1991). Producers, scroungers, and group foraging. The American Naturalist, 137(6), 847-863.

Wolf, M., van Doorn, G.S., Leimar, O. & Weissing, F.J. (2007) Life-history trade-offs favour the evolution of animal personalities. Nature Letters, 447, 581–584.

Wright, J., Bolstad, G. H., Araya-Ajoy, Y. G. & Dingemans, N. (2019). Life-history evolution under fluctuating density-dependent selection and the adaptive alignment of pace-of-life syndromes. Biological Reviews (2019), 94, pp. 230-247.

Zeiner-Henriksen, T. (2023). Effects of individual variation on social foraging dynamics in the house sparrow, *Passer domesticus* (Master's thesis). Norwegian University of Science and Technology, Norway