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Physiology and Consistent Individual Differences in Social Behavior in *Passer domesticus*: the Role of Hemoglobin Concentrations and Wing Loading.

Master's thesis in Physiology

Supervisor: Jonathan Wright

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Abstract

Foraging in large social groups presents animals with a complex decision: whether to search for food independently (producing) or to exploit resources found by others (scrounging). In this study, I aimed to determine if physiological factors such as hemoglobin (Hb) or morphological factors such as sex and wing loading could predict whether individuals would adopt a producer or a scrounger strategy. To investigate this, we conducted behavioral assays with four populations of house sparrows (*Passer domesticus*), observing their behavior in the producer-scrounger game. We measured the Hb levels and wing loading of each individual and compared these measurements to the number of producing or scrounging visits. I found differences between the sexes, specifically females having lower Hb and wing loading; however, these parameters did not significantly affect producer-scrounger behavior. While changes in Hb and body mass were considered, the repeatability of both Hb and wing area and therefore wing loading was moderate, but too low for subsequent analyses. These findings suggest that while Hb and wing loading may not have predictive power in determining producer-scrounger behavior, perhaps with improved methodology and repeatability of Hb and wing area, future studies would find different results.

Sammendrag

Å søke etter føde i store sosiale grupper presenterer dyr med en kompleks beslutning: om de skal lete etter mat uavhengig, vente og dele, eller stjele fra andre gruppe medlemmer. I denne studien ønsket jeg å bestemme om fysiologiske faktorer som hemoglobin (Hb) eller morfologiske faktorer som kjønn og vingelasting kunne forutsi om individer ville adoptere en producer- eller en scrounger-strategi. For å undersøke dette gjennomførte vi atferdsanalyser med fire populasjoner av gråspurv (*Passer domesticus*), hvor vi observerte deres atferd i producer-scrounger-spillet. Vi målte Hb-nivåene og vingelastingen til hvert individ og sammenlignet disse målingene med antall producer eller scrounger besøk. Resultatene viste noen betydelige forskjeller mellom kjønnene i Hb og vingelasting; imidlertid påvirket ikke disse parameterne producer-scrounger-atferden signifikant. Mens endringer i Hb og kroppsmasse ble vurdert, var gjentakbarheten av både Hb og vingeeareal, dermed vingelasting, skuffende lav. Disse funnene antyder at selv om Hb og vingelasting kanskje ikke har prediktiv kraft i å bestemme producer-scrounger-atferd, ville kanskje fremtidige studier finne forskjellige resultater med forbedret metodikk og gjentakbarhet av Hb og vingeeareal.

Acknowledgements

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My heartfelt appreciation goes to Corné de Groot and Rori Wijnhorst, who not only guided me through the practical challenges of fieldwork but also introduced me to the intricacies of statistical analyses with R. Their mentorship was fundamental in overcoming the various hurdles encountered during my research. I also cannot thank my fellow master's student and field partner, Rok Movh, enough for being an exceptional field partner. Despite the challenges, including the filling of several hundred food wells that tested our patience, your camaraderie and resilience made the demanding work enjoyable and memorable.

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1. Introduction

1.1 Background and Rationale

In order to understand behavioral variation, we need to understand the physiological/morphological mechanisms that mediate behaviors. To fully comprehend behavior, factors such as animal personality, individual plasticity, dominance, and social information must be considered alongside other disciplines such as physiology and morphology. In this thesis I aim to find how a small part of physiology and morphology can play a role in determining animal behavior at an individual level.

One key aspect of this is the concept of 'animal personality', which refers to consistent behavioral differences over time. Like humans, animals exhibit distinct personalities that impact various ecological and evolutionary aspects, including life history strategies, sexual selection, and social behaviors. Réale et al. (2010) signifies that studies investigating such personality traits often examine coping behaviors in social isolation in captivity and might therefore not fully capture the complexity of these traits under natural conditions. Further research in more dynamic environments with phenotypically plastic traits, as described by Dingemans et al. (2010), use the conceptual framework of behavioral reaction norms to provide deeper insights into how personality and behavioral flexibility influences individual fitness and social interactions. A behavioral reaction norm refers to the set of behavioral phenotypes that a single individual/genotype produces in response to environmental variation and is a useful tool in understanding how animals can alter their behavior to cope with changing environments (Dingemans et al., 2010). By comprehending these aspects of individual behavior, we provide a deeper knowledge of the causes and consequences of the variation seen among individuals, considering that each individual does not plastically express the full range of behaviors seen in the entire population.

The extent to which individuals can modify their behavior (plasticity), can have profound implications for their survival and overall reproductive success as well. Bell et al. (2009) highlights that these individual differences in behavior are not only noticeable but also highly repeatable, one of their main findings was that repeatability declines with time between measures suggesting gradual phenotypic changes or plasticity based on state. Understanding the drivers of this behavioral variation, including genetic, environmental, and social factors, is essential for a comprehensive view of animal ecology. Individual differences that drive this behavioral variation could arise due to a variety of factors including not only genes, but environmental and social effects during development. Optimal foraging theory suggests that individuals should adaptively switch between tactics (Barta and Giraldeau, 2000; Giraldeau and Beauchamp, 1999), but we do also see individuals are consistent/repeatable (Bell et al., 2009). It is therefore important to be able to understand which factors could explain this among-individual variation. Physiology also plays an active part in driving and co-varying with behavioral differences, particularly in individuals. In a recent review by Careau et al. (2012), they discuss the links between aspects of behavior, such as producing/scrounging, dominant/subordinate, and individual personality, and physiological measures such as energetics, Basal Metabolic Rate (BMR), blood hemoglobin, and metabolic rate. Knowing which physiological factors can be linked to commonly studied,

individually consistent, and more plastic behavioral traits could provide a better understanding of personality and performance.

Dominance is another significant factor that shapes animal behavior, particularly in social species. It is a social convention concerning the priority of access to resources (subordinates allow dominants to be dominant and vice versa) and is always a property of a social group (Lendvai et al., 2006). Dominant individuals often have preferential access not only to resources such as food but also mates, which can significantly influence their behavior and survival strategies. In social foraging, individuals can choose one of two strategies: "producer," where they search for food themselves, or "scrounger," which involves waiting until another member has already found a resource, and then joining them. For example, Tóth et al., (2009) demonstrated that in house sparrows (*Passer domesticus*), dominant (male) individuals were more likely to engage in scrounging behaviors, exploiting the efforts of others rather than foraging independently. They also found that this effect, sex/dominance, when combined with relatedness of individual also affected foraging strategy. These relationships underscore the complexity of social hierarchies and their direct impact on individual behavior. Considering that male sparrows tend to be more dominant than the females, and females have generally lower Hb than the males do, this physiological variable must also have some impact on how individuals act (Kalinski et al., 2011; Lendvai et al., a 2006; Myrcha et al. 1980).

Hemoglobin levels offer insights into an animal's aerobic capacity and overall energy status, directly influencing their behavioral choices, especially in energy-intensive activities such as foraging. By integrating physiological measures such as this with behavioral data, we gain a more comprehensive understanding of how animals manage their energy in response to environmental and social pressures. This knowledge not only enhances our understanding of animal physiology but also improves our ability to predict how animals might adapt to changing environmental conditions, effectively bridging the gap between physiological ecology and behavioral science.

This integration of physiology and morphology into behavioral analyses proves essential in studying small passerine birds like house sparrows. Research, such as the study by Davies and Deviche (2014) demonstrates that variations in food availability throughout the year can trigger specific behaviors. This ecological approach to studying food availability has revealed that traits related to reproductive timing in females and developmental processes in males are influenced by more than mere survival needs, showing how unrestricted access to food can lead to complex behavioral outcomes (Dufva et al., 1996; Jensen et al., 2004). This thesis will look at a variety of morphological and physiological parameters in the context of the producer-scrounger model in an attempt to provide a comprehensive understanding of the driving factors behind individual variation in foraging tactic-use.

1.1.1 The Producer-Scrounger Model

Acquisition of food resources is key to the survival of all animals. Different species employ a variety of tactics to search for and find food. These strategies can vary depending on several factors, such as the distribution of resources (whether prey or other food sources) (Scharf et al., 2012). This may also influence whether animals share information about resources and whether it is more beneficial to use social or personal information (Dubois et

al., 2012). In the case of highly social animals, principles apply, giving rise to a unique dynamic known as the producer-scrounger game.

The producer-scrounger model, initially proposed by Barnard and Sibly (1981), employs game theory to elucidate foraging decisions, such as joining, made by social animals in group foraging settings (Giraldeau et al., 1999). This model delineates two distinct foraging tactics: producers and scroungers. Producers are individuals that actively search for their own food, whereas scroungers are individuals who exploit producers by joining them at an already discovered food source. Fig. 1.1 shows how the dynamic between the two strategies can be maintained in a population. When the proportion of scroungers is higher, it is better to be a producer and *vice versa*, i.e., *negative frequency dependency*. The choice of strategy depends on various factors including the individual, food availability, and the cost associated with each tactic.

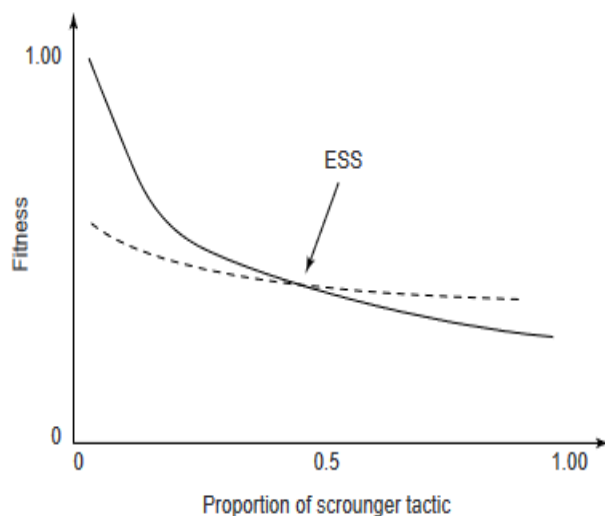


Figure 1.1: Figure from Giraldeau and Beauchamp 1999. The fitness payoff for producers (dashed) and scroungers (solid) as the proportions of scroungers increases. The functions cross when the payoffs for each strategy are equal, (Evolutionarily Stable Strategy).

Choosing the right foraging strategy depends on several factors, such as social information, patch size/quality, producer bonus and chances of finding food, body size, dominance, and energetic state (Barta & Giraldeau 2000; Tóth et al., 2009). Dubois et al., (2012) showed that the timing of arrival of individuals at a patch often resulted in those individuals relying on social information and choosing the producer tactic, but they could change their mind based on unsuccessful attempts, indicating a dependence on the availability and quality of the food patches. However, this is only one of many variables affecting this choice. For instance, body size, and thus dominance and sex, in house sparrows can influence and individual's ability to be a scrounger versus a producer (Tóth et al., 2009).

A study with bald eagles (*Haliaeetus leucocephalus*) showed that larger individuals were more successful when scrounging than when protecting a food source, which indicates the influence of morphology (Hansen et al., 1986). But, hungrier eagles also won more when joining which is consistent with hungry house sparrows also scrounging more, which is more state-dependent (Lendvai et al., 2004). This contrasts however, with findings in the semi-aquatic bug, *Velia capari* that showed hungrier bugs attacked prey first rather than waiting to join once the prey had already been killed (Erlandsson et al., 1988). The importance of body size in choosing a foraging tactic spans a variety of species, not just birds. In social spiders (*Stegodyphus mimosarum*), smaller individuals are more likely to produce (Ward et al., 1986), and the same pattern is observed in striped parrotfish (*Scarus iserti*), where larger females were shown to be more efficient producers than smaller ones (Clifton et al., 1991).

In two of the previously mentioned studies Clifton et al. (1991 and Hansen et al. (1986), larger individuals were more often female, indicating that an individual's sex could also play a role in the producer-scrounger game. Many examples where females are larger than males of the same species have been observed in birds (McDonald et al., 2005; Hansen et al., 1986), mammals (Tombak et al., 2024), and fish as well (Parker et al., 1992). However, it is not always necessarily a result of sexual selection, as previously thought (Isaac et al., 2005). This sexual dimorphism is hypothesized to be due to factors such as increased parental investment and territorial competition. Nonetheless, few studies have considered the combined effects of body mass and sex on the proportion of producer-scrounger activity.

In every social group, there will be a ranking of the members. This dominance order is established based wins/losses which are mediated by other traits such as sex, age, and size. The establishment of these dominant and subordinate individuals often influences individual behavior in foraging situations (Lendvai et al., 2006). Krams et al. (2002) showed that dominant individuals in wintering great tits (*Parus major*) had fewer fat reserves than subordinates, and that males were often the more dominant sex. Dominant individuals have been shown to scrounge more often when foraging, but the ranking of dominance within a flock can influence a change in strategy (Lendvai et al., 2006; Zeiner-Henriksen, 2023). However, Wiley et al., (1991) found that novel food sources were found approximately equally by high and low ranked white-throated sparrows (*Zonotrichia albicollis*), but once food was discovered then the dominant individuals shifted to the scrounging tactic.

The differences found among high-ranking dominants are generally due to differences in individual energetic states, along with the time of day and predation hazard, which also play vital roles in foraging tactic choice. A state-dependent model developed by Barta and Giraldeau (2000) predicts that lower energy reserves earlier in the day would promote the use of the scrounger strategy, while higher energy reserves later in the day would promote using the producer strategy. This is because the state is influenced by several factors, such as body size (larger individuals require more food), physiological regulation, and it is also sex dependent. This model suggests that an individual's energy reserves influence its foraging choice, indicating that overall body condition and potentially physiological factors such as aerobic capacity also possibly influence which strategy an individual is more or less likely to choose.

1.1.2 Hemoglobin and its Role

Aerobic capacity, or VO_{2max} , refers to the maximum oxygen consumption during physical activity (Verzár et al., 1912) and is often considered an indicator of physical condition. It is one of the most studied components of animal physiology (Chappell and Bachman, 1995; Hammond et al., 2000; Hoppeler and Weibel, 2000). However, it has been consistently observed that the aerobic capacity of an animal is not determined by one physiological parameter alone, but rather by a combination of many traits, such as the animal's metabolism (Scott et al., 2011) or its ability to transfer vital substrates to skeletal muscles (Hoppeler and Weibel, 1998). Although several factors contribute to aerobic capacity, two key components include the heart and the lungs.

In a study on red jungle fowl (*Gallus gallus*) (Hammond et al., 2000), a higher aerobic capacity was associated with larger, more dominant males. Some key characteristics associated with these males included larger hearts and lungs, capable of supplying more oxygen and distributing it more efficiently throughout the body. Carey and Morton (1976) found that birds living at higher elevations had larger hearts and lungs. However, they found no morphological variation in animals that migrate between altitudes. Meanwhile, Vágási et al. (2016) found that migratory birds with longer routes had relatively smaller hearts, which decreased mass and, therefore, wing loading, thus improving flight performance.

Aerobic capacity is often measured by recording oxygen concentrations with respirometers during exercise and has been tested in a wide range of species (Hammond et al., 2000; Chappell and Dlugosz, 2009). It can also vary among species, age groups, sexes, and even habitats (Scott et al., 2011). During intense exercise, animals increase their breathing rate to meet the body's increased demand for oxygen to power the muscles (Hoppeler and Weibel, 2000). The oxygen is then bound to the hemoglobin of erythrocytes and circulates throughout the body. Hemoglobin (Hb), an oxygen-carrying protein found in red blood cells (Perutz et al., 1964), is widely considered one of the most important determinants of oxygen-carrying capacity in vertebrates (Minias et al., 2015; Kostelecka-Myrcha et al., 2002). However, this may not always be the case in birds as seen in (Kostelecka-Myrcha et al., 1997; Minias et al., 2015), and warrants further investigation. Hemoglobin is also closely associated with hematocrit (Hct), which represents the percentage of erythrocytes in the total blood volume (Gallaughner and Farrell, 1998), this is important to consider when understanding aerobic capacity as well since one parameter alone is not enough.

Due to the unique aerial lifestyle that many birds have adapted to, their physiology has evolved accordingly. Particularly in birds that fly at higher elevations or over long distances, certain characteristics have developed to help them sustain the exceptional metabolism and body condition required for these demanding flights (Scott et al., 2011). In various species of wading birds, a higher Hb has been associated with long-distance migration over short-distance migration (Minias et al., 2013). Additionally, Yap et al. (2019) found that both Hct and Hb levels are higher in full migrants than in partial or non-migrants, and that birds living at higher altitudes have higher Hb levels but not Hct. This improved oxygen-carrying capacity can be associated with a wide range of environmental and physical parameters.

Considering the vitality of Hb in association with the energetic costs of being a bird, it clearly plays an important role as well even in the non-high flying non-migratory bird such as a sparrow. Several studies have considered the importance of hematological factors to health and body condition of passerine birds (Kaliński et al., 2009; Kilgas et al., 2006; Lobato et al., 2011; Norte et al., 2009; Ots et al., 1998)

1.1.3 Wing Area, Wing Loading and Flight

Bird wings come in many shapes and sizes, specifically adapted to their unique lifestyles. Species that migrate long distances require longer, more pointed wings (with long distal and short primary feathers) and a high aspect ratio, while resident birds may have shorter, more rounded wings (Bowlin and Wikelski, 2008; Mönkkönen, 1995). Migration is an

energetically expensive endeavor, and birds must optimize aerodynamics to be energetically efficient. Wing loading (mass/total wing area) and aspect ratio (proportion of the wing's length to its width) trade-offs are common in many migratory species. A higher aspect ratio allows a bird to fly faster, but it requires a smaller wing area, increasing wing loading and thus the energy needed to maintain flight (Vágási et al., 2016). However, differences in aspect ratios and wing loading are based on other ecological factors for resident birds.

Species living in cluttered habitats may also have rounded wings for better maneuverability but less speed than those living in more open habitats, allowing them to navigate better (Beauchamp et al., 2023). Despite the wide range of shapes and sizes in wing morphology, birds are still able to maintain flight because wing size (referring to both the area and the length) varies allometrically with body size. Larger birds often have wings bigger than what would be predicted (Greenewalt et al., 1962; Rayner et al., 1988). A bird's maneuverability is not only important for its ability to fly around its habitat, but it also plays an important role in foraging and predator avoidance.

Beauchamp et al. (2023) investigated the connection between life history and sociality and found that more solitary species had lower wing loading and aspect ratio to better escape predators. This was less of a concern in highly social species, as individuals can rely on other group members to alert them to the presence of predators. Many passerine species are very social and will forage in groups, and whether to avoid a predator, or a fight with other group members, the ability to take-off quickly is crucial. In a study on wintering great tits (*Parus major*), Krams et al. (2002) found that a smaller wing loading resulted in faster take-offs. Wing area is unlikely to change once a bird has reached maturity, except during periods of moult, but body mass often changes on a daily basis, and sometimes throughout the day in small passerine birds (Lima et al., 1986; Krams et al., 2010). This will change the wing loading and therefore also the energetic cost of flight. Witter and Cuthill (1993) describes this as well in their analysis of the costs and benefits of avian fat storage.

1.2 Research Questions

This project aims to further explain individual differences in social behavior in house sparrows, specifically regarding the physical and physiological basis of social behavior. It focuses on expected patterns of statistical covariance of behavioral, physiological, and morphological data within a captive experimental context. This project also addresses several hypotheses related to sex, flight physiology, differences in producer/scrounger social behaviors, and the specific roles of individual measures of hemoglobin concentration and wing-loading.

To understand this, I have two main research questions outlined below:

Is wing loading a better measure than body mass for determining flight physiology?

Hypothesis for question 1: Wing loading is a better measure of flight physiology as it encapsulates body mass and should therefore be able to be used to predict behavior.

Predictions:

1(a) As body mass decreases over the duration of the experiment, wing loading should also decrease as there would be less mass for a given area. The wing area should not change, unless the bird loses feathers.

1(b) Wing loading should predict the Hb, as Hb is a measure of aerobic capacity and as the wing loading decreases the need to maintain high aerobic capacity should also decrease. This is because the individual would expend less energy to keep itself airborne.

1(c) Individuals with overall larger wings relative to body mass should have lower hemoglobin levels in response to a more energetically efficient body plan.

How does morphology (wing loading) and physiology (body mass and Hb) influence behavior, specifically foraging tactic choice in the Producer-Scrounger model?

Hypothesis for question 2: Individuals with higher wing loading (larger body mass with proportionally smaller wings) should spend more of their time scrounging to make up for the energetic cost of flight. Additionally, individuals with higher Hb would be producers.

Predictions:

2(a) If smaller (female) individuals spend more time producing than larger (male) individuals, which is more energetically costly, their hemoglobin levels should be higher to make up for the energetic cost difference of their foraging strategy.

2(b) Hemoglobin levels should vary according to energy expenditure, but also according to morphology (body mass and moult) and environment (time of year and temperature).

In order to better understand these big questions, I broke them down into some smaller steps. The goal was to narrow down the number of variables into the most descriptive ones in the context of this project. Below are two more questions to help build a clearer picture of the main ideas:

Is wing length a good proxy for wing area?

Hypothesis for question 3: The wing length should be proportionate to the body size of the sparrow and therefore should be able to predict the wing area relatively accurately.

Predictions:

3(a) Individuals with longer wings should have proportionally larger wing areas while individuals with shorter wings should have proportionally smaller wing areas.

3(b) The length of both wings (left + right) should proportionally predict the total wing area for the individuals, also giving us a proxy for calculating wing loading.

3(c) Left- and right-wing areas will vary slightly in everyone.

What are the relationships between Hb and Body mass?

Hypothesis for question 4: Hemoglobin and body mass should have similar effects throughout the experiment as they covary.

Predictions:

4(a) Sparrows will show repeatable individual differences in hemoglobin and body mass.

4(b) Body mass and hemoglobin will decrease over the duration of the experiment.

4(c) Hemoglobin and body mass should covary positively among and within individuals.

2. Methods

2.1 Fieldwork

2.1.1 Study Site and Background

This project involved a natural meta-population of house sparrows in the Åfjord area of mid-Norway. The house sparrow (*Passer domesticus*) is a small, relatively unassuming passerine bird. It is, however, one of the more prolific species on the planet (Anderson et al., 2006). They are often used as a model species in research projects, because they are highly social, very common, and closely associated with humans (e.g. Jensen et al., 2004, 2007, 2013; Araya-Ajoy et al., 2019; Fischer et al., 2018; Guldvik, 2023; Zeiner-Henriksen, 2023). House sparrows are also sexually dimorphic, which makes the sexes easy to differentiate

between in social experiments (Anderson et al., 2006). Norwegian house sparrows are highly associated with dairy farms, and their group-living and social foraging habits make them an excellent candidate for study. The

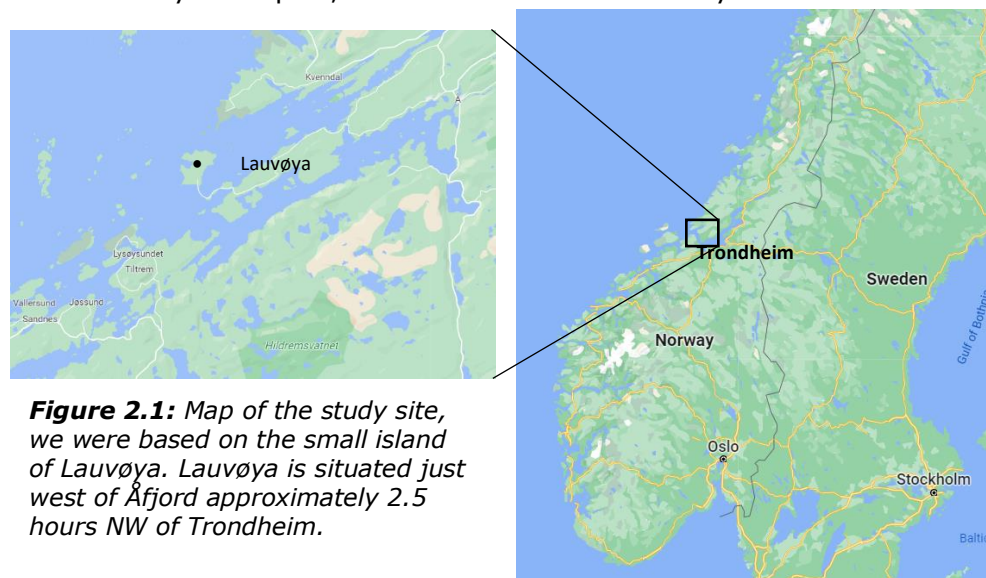


Figure 2.1: Map of the study site, we were based on the small island of Lauvøya. Lauvøya is situated just west of Åfjord approximately 2.5 hours NW of Trondheim.

populations used

in this study are part of a longitudinal project under the Centre of Biodiversity Dynamics (CBD), which has been collecting data in genetics, demographics, morphology, and physiology for nearly 30 years (Guldvik, 2023; Jensen et al., 2004; Nafstad et al., 2023; Zeiner-Henriksen, 2023).

Lauvøya, an island off the coast of central Norway in the Trøndelag region, is primarily used for farming and has a resident house sparrow population, consisting of approximately 170-180 individuals that have been individually marked and tagged, and utilized in previous experimental research. This study adds to these data of the existing sparrow project using the meta-population on and around Lauvøya. One flock was situated on the island, and three other flocks were located on the mainland. In winter 2023, we captured and measured 143 individuals. A number of these birds were also captured in previous years.

2.1.2 Sample Collection and Preparation

Upon capture using mist-nets, we recorded the ring number (if they had one already), sex, age, weight, wing length, tarsus length, beak size (length and depth), beak color (in males), category of mask and badge (also in males), DNA, and Hb for each bird. The beak color and category of mask and badge in the males was measured on a scale rating the color as well as measured with calipers. Morphometric data was collected with protocol outlined in (Jensen et al., 2004; Ringsby et al., 2002, 1999). If an individual had not already been ringed and tagged, they were fitted with an individual-specific metal identification ring, color-rings, and a radio frequency identification (RFID) tag ring.

The final measurement taken was a blood sample to analyze the DNA of everyone, as well as a Hb sample. Blood samples were taken via brachial venipuncture (approximately 25 μ L). During intake the first drop of blood was collected with a microcuvette and stored for DNA analysis. The second drop was then collected using a different microcuvette via capillary action. The samples were processed using the HemoCue system by placing the blood into the provided cuvettes where it mixed with the included reagents (sodium deoxycholate, sodium nitrite, and sodium azide) (Hudson-Thomas et al., 1994). Once the device was turned on it calibrated itself against the international reference method for hemoglobin determination (Clark et al., 2008). For this study, the device was calibrated externally before the start of the experiments and the cuvettes were given 3 minutes to allow the reaction to complete before it was then analyzed by the HemoCue. According (Clark et al., 2008; Andrewartha et al., 2015), the device has a tendency to overestimate the Hb values in fish blood, but is known to be relatively accurate in birds (Harter et al., 2015). Hb is generally measured most efficiently in a laboratory setting which is impractical for field work. The field station in Lauvøya was ill-equipped for such analysis and because of this, the relatively easy-to-use and portable device, the HemoCue, was utilized. This also prevented the need to mix the blood samples with anticoagulants and store them for later analysis.

After the behavioral experiment was complete, the birds were bled again for Hb analysis before release into the recovery aviary. This had the same procedure except no DNA sample was taken.

2.1.3 Behavioral Data Collection

The study took place in an unused, centralized barn on Lauvøya with a relatively temperature-controlled captive environment (approx. 10-12 °C) for the sparrows, with *ad libitum* food access before and after the trials. Daylight was also artificially controlled, with lights being turned on at 08:00 and off again at 22:00. The birds were captured via mist-netting and assigned to a group of six birds with roughly equal sex ratios (ideally groups of three females and three males). The birds stayed in these groups for the duration of the study. They were kept for a period of 5-14 nights. During this time, specific days were allocated to particular tasks: habituation (minimum one night), training (two days), behavioral assays (two or three days), followed by recovery and release. During the training phase, birds experienced checkerboard feeders. On the first day of training, the food was left exposed in the wells, and on the second day the food was covered with sand. Individuals were then weighed using a Pesola spring balance (to the nearest 0.1g) and moved into the experimental aviary. After experimentation, before the individuals were

released, they were monitored in a specified recovery aviary to confirm that they continued to be healthy, and that release would be a success.

For the behavioral assessment portion of this study, individuals were assayed against each other in specifically designed feeders seen in *Fig. 2.2*. Two groups of six were tested in parallel on three feeders, where three birds were tested against one another. *Table 2.1* in *Appendix 7.1* shows all possible combinations of the six birds in each group, so that everyone played against everyone, and *Table 2.2* shows an example of the testing schedule used. Each bird was assayed 10 times a day and twice (two consecutive days) for each



Figure 2.2: Feeders used in the behavioral assays. The feeder plates are 1x1.2 meters and have 36 evenly spaced wells.

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

Table 2.2: Example schedule from the triadic testing. The two different groups of six individuals (A-F in blue, and G-L in green). Developed by Rori Wijnhorst and Corné de Groot.

group for a total of 40 assays per group (20 per individual).

The assays were conducted for 15 minutes in specialized checkerboard feeders outfitted with an RFID system.

Approximately 10 minutes were allocated to cleaning and resetting the feeder wells between each trial. The layout of which wells had food was determined randomly using an online dice simulator. Two six-sided dice were rolled to determine the pattern number, and the orientation of that pattern.

Each feeder had food wells that were evenly spaced in a 6x6 grid. 22 wells were filled with only sand, and 14 will be filled with seeds and sand. Each trial used 12g of millet, the remaining food was weighed after each trial. This setup induced the sparrows to actively search for food within

the feeder. Each of the wells was surrounded by RFID antennae, seen in *Fig. 2.3*, that detected which individuals arrived at wells, and the time spent at the well. Each of the feeders was enclosed by a cage with three small openings for the capture/release of birds via small wooden nest boxes, one small opening for a top-down view offered by the ceiling-mounted camera, and a large opening in the front for resetting of the feeder boards. The three feeders allowed three assays to be run simultaneously. As well as these triadic trials, for a subset of groups a day of group trials were

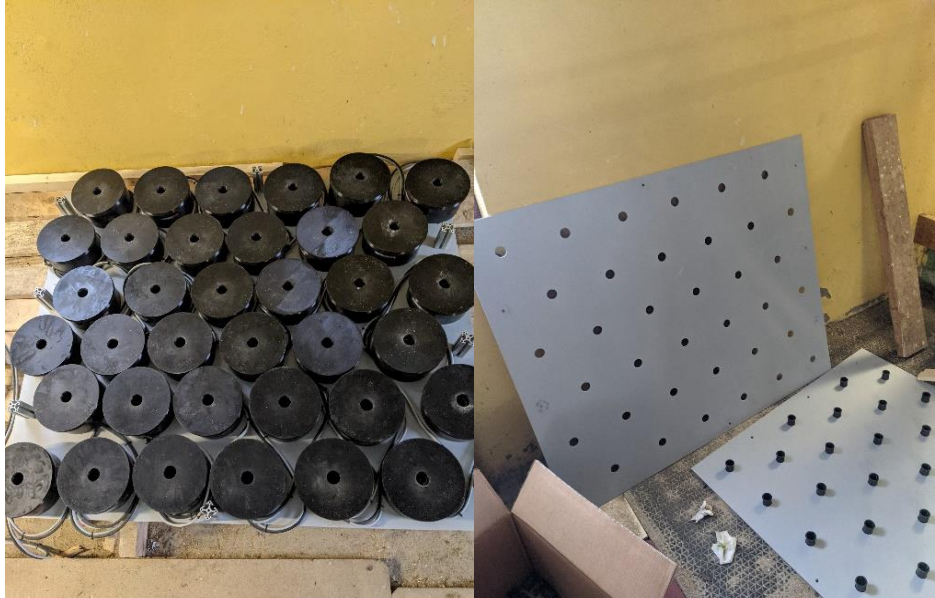


Figure 2.3: The inner workings of the checkerboard feeders. Illustrating the RFID system housed around each food well.

performed where all six individuals were tested together. This was performed twice throughout the experimental period.

Each bird was also fitted with a small identifying barcode on their backs (*Fig. 2.4*). This provided additional identification visually and with potential integration with video tracking software (Alarcón-Nieto et al., 2018). Levels of producing, scrounging, and aggressive encounters were recorded throughout the duration of the video recordings. Levels of producing were measured by noting the frequency at which an individual visits a well with food. In contrast, the level of scrounging was the frequency at which an individual visits a well at which a bird is actively producing.

2.1.4 Wing Area Data Collection

Upon capture and before release, photographs of wings were taken as a new addition to the previously mentioned measurements. A study by Blem et al. (1975) on house sparrows previously assessed wing area, but unfortunately the procedure involved removing the wing from birds. Other problems with this earlier study included, but were not limited to, shrinkage due to drying out of the removed wings. In accordance with modern ethical practices, we adjusted our methods to cause as little stress as possible to the birds, hence the use of a camera and a short handling time. Then, after the course of the behavioral experiments (5-14 days), blood samples were retaken from each bird and wing photos were



Figure 2.4: QR "Backpack" worn by individuals during the behavioral studies. This individual was known as "Yoga."

taken before final release. Birds were placed along the edge of a table in the traditional ringer's grip (*Appendix 7.1, Fig. 7.2*) with a single wing spread out along a grid. In the space between the pointer finger and thumb, we allowed one wing out of the grip (this being the right wing when using the left hand and the left wing when using the right hand). While gripping the bird securely, we rotated the legs to be more comfortable between the pinky and ring fingers while also providing a better angle to flatten the wing against the grid. We then placed the wing, spread out, on top of the grid, each square of the grid measuring 2x2cm.

The wing was spread with the shoulder positioned 2cm away from the edge of the sheet at the marked location with the bird's body flush with the edge of the grid. The feathers were positioned one of two different ways. The first (extended) where the tenth primary feather (P10), (see *Appendix 7.1*) was positioned along a horizontal line, stretched to a second mark on the grid seen in *Fig.2.5*, and a second (relaxed), with the shoulder gently pushed flush, using the thumb from the securing hand, with the surface for a more natural shape. A top-down view of the difference in wing positions can also be seen in *Appendix 7.1*.

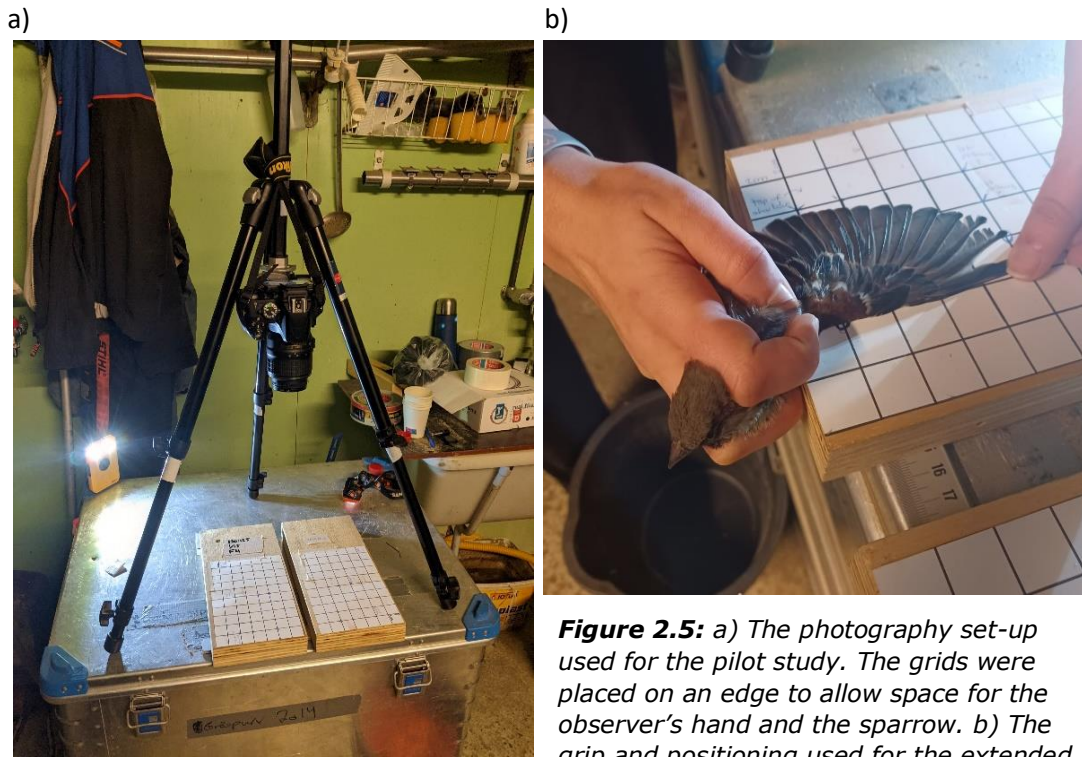


Figure 2.5: a) The photography set-up used for the pilot study. The grids were placed on an edge to allow space for the observer's hand and the sparrow. b) The grip and positioning used for the extended wing photos.

Then a photo was taken from directly above each wing, with in total two photos per wing (four photos per bird total). This process was repeated 2-3 times per individual. Any variation in the wing area due to different stages of moulting was also noted and accounted for. The camera was set directly above the photo surface using a tripod. Each photo was then taken at the baseline settings of 1/15 shutter speed, F4 aperture, and an ISO of 125. The height of the tripod was left the same for the duration of the pilot study as were the

camera settings as seen in *Fig. 2.5*. Each photo was then taken with an RFID remote to avoid moving the camera set-up and because we need both hands for handling the bird.

The height and settings of the camera could be adjusted according to lighting and space available. We took measures to avoid any unnecessary shadows by having multiple light sources, and to collect crisp and easy to interpret photos by setting proper shutter speed and ISO. The grid remained the same for all photos, as it provides a scale for the analysis in ImageJ.

All the photos were then sorted and edited in Adobe Lightroom Classic. Editing was essential to fix any strange lighting effects caused due to natural lighting. Each of the photos was then assessed using ImageJ to set the scale with one grid square (2x2cm). Then, using the trace option, each wing was traced, excluding the observers' fingers.

Once all the data was recorded, and the statistics were run, it was determined which method, "extended" or "relaxed", was the more accurate approach. The average of each wing, left and right, was then calculated for each individual. Using this data along with the initial body mass and the final body mass, the wing loading was calculated in R.

2.1.5 Video Analysis

The video analysis conducted this year served as an extension of the work initiated in 2022, which utilized an RFID system to infer behavioral data based on variables such as position, duration of visit, and the relative position of opponents. Despite the insights gained from the RFID system, the need to validate the accuracy of the inferred data remained paramount. This validation was achieved through manual analysis of the video recordings. Out of the 1,080 videos captured, six observers were tasked with analyzing a total of 68 videos that manually scored this year. The assignment of videos to observers was randomized, taking into consideration the day of recording and the group number, to ensure a representative sample.

Prior to beginning the analysis, observers underwent rigorous training designed to calibrate their observation and scoring capabilities. This training involved watching and scoring three 3-minute videos, each viewed three times for a comprehensive nine viewings per observer. To ensure uniformity in training, all observers were exposed to the same videos, albeit in a randomly assigned order, spread over approximately one week. It was advised that observers limit their viewing to one or two videos daily to optimize attention and retention. Following the initial training phase, the reliability of each observer's scoring was evaluated. Observers achieving a reliability score higher than 0.8 were deemed competent to proceed with the analysis of the experimental videos. Observers failing to meet this benchmark were required to undergo additional training, involving a series of 5-minute videos, to enhance their observational accuracy. This structured approach to training and validation underscores the meticulous efforts undertaken to ensure the integrity and reliability of the manual video analysis, complementing the data obtained from the RFID system.

These analyses were done using BORIS (Behavioral Observation Research Interactive Software; (Friard et al., 2016)). An ethogram (*Table 2.3*) was created in the previous year by Rori Wijnhorst and Corné de Groot to characterize all behaviors of interest.

Event	Type	Description
Testtag	Point	Moment testtag is tapped on the feeder.
Release	Point	Moment the first bird is released, which indicates the start time of the 15min trial.
Board	State	The bird is standing on the board.
Search	State	The bird is sieving through sand or its beak touches and at a well.
Secondary search	State	Same criteria as search, but the well has clear visual cues for seeds.
Join	State	The bird joins at a well or feeds from seeds around the well (<2cm) that another individual is sampling from. Latent joining when the partner has left no longer that 3s ago.
Revisit	State	The bird leaves the well and returns to the same well withing 10s or when it stops feeding for longer than 5s but stays at the well.
Feed	Point	Subject consumes one seed either from the board or a well.
Attack	Point	A short peck or attack launched but not directly reciprocated.
Display	Point	Wing display or flapping, count each individual display or flap.
Aggression	Point	Fighting or a directly reciprocated attack initiated by the focal.
Stop event	Point	Used for stopping a state event

Table 2.3: Ethogram used containing all behavioral events observed during the video analyses. Used with BORIS observation software.

Each of the behaviors were assigned a keyboard shortcut for efficiency. The events were divided into either point or state events which were differentiated based on if the behavior was over a duration of time or a singular occurrence. State events included the feeding events which had a start and an end point and were defined by "search" or "join", which were synonymous with "Producing" and "Scrounging". These were characterized as such due to being behavioral states during which no other behavioral state could occur. Point

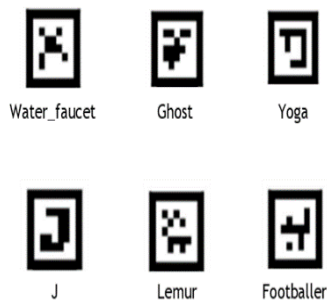


Figure 2.6: Barcode variations used for identification in the video analyses.

events included behaviors such as eating a seed (feed), landing/leaving the feeder board, displays, and attacks. These events are not mutually exclusive and can occur simultaneously with state events.

At the beginning of each trial, before the release of the birds, a PIT tag was tapped near a well to ensure functionality of the RFID system. This also aided in synchronizing all the videos. Analysis began when the first bird was released and then ran for 15min after that point event, marked by pressing "release". The first individual to land on the feeder board became the focal of that watch through of the video. Each 15 min video was watched three times with a different individual being the focal of that watch through. This was done to ensure

that all behaviors for everyone were recorded. Each focal was distinguished by their unique QR backpack (*Fig. 2.6*). Upon landing on the board, the focal individual was noted, and the corresponding key, "board", was pressed and then once the focal left the board it was pressed again to indicate that the individual had left the feeder. This state event is the only exception to only one state event happening at a time since being on the feeder board is a prerequisite to all other state events. Feeding events were scored according to the ethogram, e.g., search was scored by pressing "search" when an individual's beak touched sand at an unoccupied well. If the well had clear visual indications of seeds, it was scored as a secondary search instead of a search. The state event was then stopped using the point event "stop" if the individual left the well or stopped sampling for a minimum of 5s. If the focal sampled or tried to sample from a well from which another individual was already sampling (within 2cm) it was scored as a join. Once "join" was pressed, the user would be prompted to include more information, such as which individual the focal was joining and what the outcome of the event. These outcomes included if the resident, the focal, or both were displaced (focal leaves within 5s, resident leaves within 5s, both leave within 5s, or both stay longer than 5s). If an individual was displaced it needed to be within 5s of the beginning of the event. If the resident of a well left no more than 3s prior to the focal joining at the well, then it was scored as a latent join. When an individual returned to a well within 10s without sampling from another well, then it was recorded as a revisit. Point events could be recorded during state events when these behaviors occurred at a single point in time. Feed was recorded whenever the focal visibly ate a seed or sieved through sand at a well that had visual cues for seeds. A head bobbing motion was associated with the sieving, feeding behavior. Attack was used whenever a focal exhibited a lunge or short peck towards another individual, but the behavior is not reciprocated by the recipient. If the behavior was reciprocated it was then considered an aggression state event. When "aggression" was pressed, the observer was prompted to record the duration of the event and the individuals involved. Whenever the focal flapped its wings or held them out towards another bird this was recorded as a display. This point event was recorded at every occurrence of a display event.

2.2 Statistics and Models

All statistical analyses were conducted using R version 4.2.3 (R Core Team, 2023). The objectives of these analyses were to determine first, the repeatability of the body mass, Hb, and wing area parameters using rptR (Stoffel, 2017), followed by comparing wing length to wing area using the lme4 package (Bates, 2015) for linear regressions. Correlations between Hb and body mass, body mass and wing area, and wing loading and Hb were examined. This was done using bivariate Bayesian models with the brms package (Bürkner, 2017). Finally, the effects of Hb and/or wing loading on the number of primary producing and direct scrounging visits were analyzed using several Bayesian models again with the brms package and then later plotted using the ggplot2 package (Wickham, 2016). All plots in this thesis were created using ggplot2.

2.2.1 Repeatability

In this study, the repeatability of body mass, hemoglobin concentration, and wing area measurements was assessed using the rptR package in R, employing a repeatability model

tailored for each parameter. Specifically, separate models were constructed to analyze the repeatability of body mass and Hb. However, the evaluation of wing area repeatability necessitated the use of several distinct models.

Initially, to assess wing area repeatability, comparative analyses were conducted between the left and right wings for each bird, using sets of measurements taken in both extended and relaxed wing positions. This approach enabled the measurement of repeatability between the left and right wings across multiple instances, incorporating individual ID (ring number) as a random effect to derive the variation associated to differences among individuals and observer as a fixed effect in the analysis. Subsequently, for each wing position, repeatability was further examined by investigating the variance of the same wing's measurements, determining any potential discrepancies in repeatability across the different sets of photographs.

This process resulted in the development of four models, corresponding to the comparisons of right extended (set 1 vs. set 2), right relaxed (set 1 vs. set 2), left extended (set 1 vs. set 2), and left relaxed (set 1 vs. set 2) wing positions. Only the same wings were compared to each other as there was too much of a difference in area between the extended and the relaxed positions. It is noteworthy that each bird contributed at least two sets of photographs for analysis, although not all could provide three or four sets. In a subsequent phase of the analysis, all wing area models were re-evaluated after recalibrating the scale and remeasuring the wings to ensure accuracy and reliability in the repeatability assessments.

Following the establishment of repeatability across the various measurements, the next step involved calculating the mean area for each wing. This calculation was performed for both the right and left wings in their extended positions. The derived mean values combined to for the total mean wing area of each bird and were then compiled into a separate column of the data frame, forming the basis for subsequent statistical analyses. These mean area calculations provided a standardized metric to which to compare further correlations and associations with other physiological and morphological parameters such as calculating the wing loading per individual. Two simple equations were used as seen below to calculate the wing loading at the initial and final mass. The difference of these two was used for the change in wing loading (Δ wing loading).

$$1) \frac{\text{Mass at intake (g)}}{\text{Total wing area cm}^2}$$

$$2) \frac{\text{Mass before release (g)}}{\text{Total wing area cm}^2}$$

2.2.2 Analysis

The analysis of the dataset was structured in sequential steps, as outlined in a schematic path diagram (*Fig. 2.7*), to ensure clarity and ease of interpretation in addressing the primary research questions. The initial phase involved calculating the repeatability of hemoglobin (Hb) concentration, body mass, and wing area measurements. This foundational step was critical for establishing the reliability of these measurements before proceeding to some of the more complex analyses.

Following this, a) in Fig.2.7, a detailed regression analysis was conducted to explore the connection between wing length and wing area. This analysis was performed utilizing a linear regression model in R with the lme4 package, deploying a total of four models to examine the similarities across different conditions: 1) right-wing length with right-wing extended area, 2) right-wing length with right-wing relaxed area, 3) left-wing length with left-wing extended area, and 4) left-wing length with left-wing relaxed area. Although already determined by the wing area repeatability analysis at this point that the extended wing position was decidedly more accurate, the analysis was performed on the relaxed wing position as well for a better overview of the differences in wing positions.

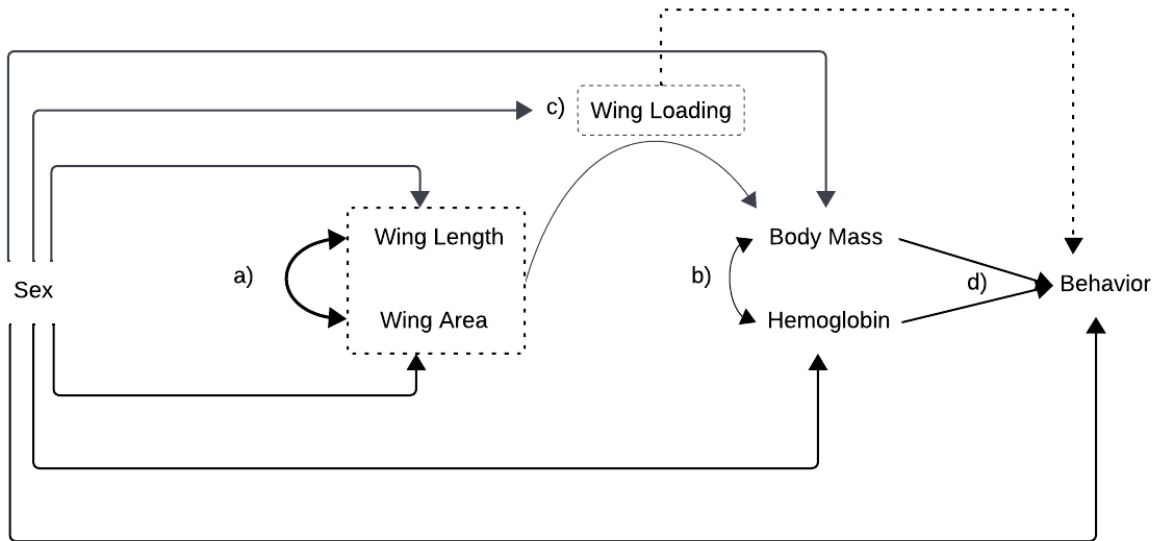


Figure 2.7: Schematic path diagram outlining the flow of the analysis, beginning with a) to determine the functionality of wing length as a proxy for wing area, then moving to b) which looks at the relationship between body mass and hemoglobin, to then c) which looks at the interaction of either length or area (previously determined in a)), with mass or Hb, final to d) which links everything to behavior based on the best measures. Dashed lines indicate a combined measure.

The subsequent analytical phase, b) in Fig.2.7, employed a series of bivariate models with two response variables (brms package) to investigate whether Hb concentration could be considered approximately equivalent to body mass for the purposes of understanding physiological parameters. This investigation was conducted by first estimating the interaction between body mass and Hb, which was intended to improve the understanding of the relationship between these two variables and their uses in further analyses. A series of models then compared following pairs of variables: initial Hb x body mass, Δ Hb x Δ body mass, initial Hb x Δ Hb, and initial body mass x Δ body mass. Both of the parameters were treated as response variables to understand the correlation between them. Once completed, a correlation between wing area and body mass was fitted separately to determine the relationship between the two and decide if wing loading could then be used as a variable as it encompasses the mass as well as the wing area. The total wing area of each wing was compared, still using bivariate Bayesian models, to the body mass at intake, at the end of the study, and to the Δ body mass.

Then part c), in Fig.2.7, was done using the wing loading calculated with the intake mass, as it was determined that that value would be most reflective of natural conditions. The

correlations run for this step were as follows: initial body mass x wing area, Δ body mass x wing area, initial Hb x wing loading, Δ Hb x wing loading, and Δ Hb x Δ wing loading. These were all run using bivariate models with both variables being treated as response variables.

Model	Producing					Scrounging				
	1	2	3	4	5	6	7	8	9	10
Fixed Effects										
Sex		X	X	X	X		X	X	X	X
Intake Hb		X		X			X		X	
Δ Hb			X		X			X		X
Initial WL		X		X			X		X	
Δ WL			X		X			X		X
Trial_day				X	X				X	X
TrialNR_Ind				X	X				X	X
Grp_Tr_b4				X	X				X	X
Initial Hb x Initial WL		X		X			X		X	
Δ Hb x Δ WL			X		X			X		X
Trial_day:				X	X				X	X
TrialNR_Ind										
Trial_day:				X	X				X	X
Grp_Tr_b4										
TrialNR_Ind:				X	X				X	X
Grp_Tr_b4										
Trial_day:				X	X				X	X
TrialNR_Ind:										
Grp_Tr_b4										
Random Effects										
Trial ID	X	X	X	X	X	X	X	X	X	X
Ring Nr	X	X	X	X	X	X	X	X	X	X
Group ID	X	X	X	X	X	X	X	X	X	X

Table 2.4: All models used in the model selection process. Shows which fixed effects were included or excluded per model. All models were run at 3 chains and 5000 iterations, 1000 of those being warmup iterations, using the brms (Paul-Christian Bürkner 2017). package for Bayesian models.

After building a comprehensive understanding of the correlation between these values a series of Gaussian, Bayesian models (Table 2.4) were created to analyze the effect of sex, Hb, wing loading, Δ Hb, and Δ wing loading on the number of primary producing and direct scrounging visits. The first step was creating a model which only included the random effects, ring number (the individual identifier based on the alphanumeric ring), the group ID (the ID of the group of 6 individuals), and the trial ID (the unique trial identifier). This was done separately for producing (Model 1) and scrounging (Model 6). These were then compared to models containing all fixed effects related to habituation and their interactions as well as the parameters in question (sex, Hb, wing loading, Δ Hb, and Δ wing loading). Habituation effects included: Trial_day (the trial day for the triadic trials), TrialNR_Ind (the i-th trial on a given individual within a day), and Grp_tr_b4 (whether individuals had a group trial before the triadic trials). Models 4 and 5 compare the initial values against the Δ

values with all the habituation effects for producing activity while models 9 and 10 compare the same for scrounging activity.

I then compared the variance of the random effects in the models without any fixed effects (Models 1 and 6) to those with habituation effects and the effects in question (Models 4, 5, 9, and 10). This was done with the aim of understanding the effect of habituation and if the variance of these effects could be covered by the random effects. Based on the results of this comparison, I built four simplified final models that excluded the habituation effects and focused solely on the impact of sex, Hb, and wing loading on the number of producing/scrounging visits (Models 2 and 3 for producing and Models 7 and 8 for scrounging). A comprehensive list of R packages used can be found in *Appendix 7.2, Table 7.8*.

3. Results:

3.1 Repeatability

3.1.1 Hemoglobin

Within-subject comparisons of initial versus subsequent hemoglobin (Hb) measurements revealed a significant decrease in Hb concentrations over the observed period ($p < 0.001$). Notably, certain individuals were identified as statistical outliers, but ultimately left in the data, with Hb levels ranging from as low as 7.6 g/dL to as high as 21.1 g/dL, though the average estimated Hb was 17.65 g/dL. A comprehensive analysis indicated that 59.8% of the subjects experienced an estimated decrease of 0.728 g/dL in Hb concentration from the initial to the final measurement.

Differences between males and females were also noted across the measurements. Females exhibited significantly lower initial Hb values than males ($p < 0.001$), although males showed a slightly, non-significant, lower final value. A significant difference in the change in Hb values (Δ Hb) between sexes was also observed ($p < 0.001$), with females experiencing a slight increase, whereas males saw a decrease.

All statistical outputs of these T-tests can be found in *Table 7.2, Appendix 7.2*. The variation between the first and second measurements is depicted in *Fig.3.1*. Furthermore, the repeatability model of the Hb measurements, where the 1st vs. 2nd

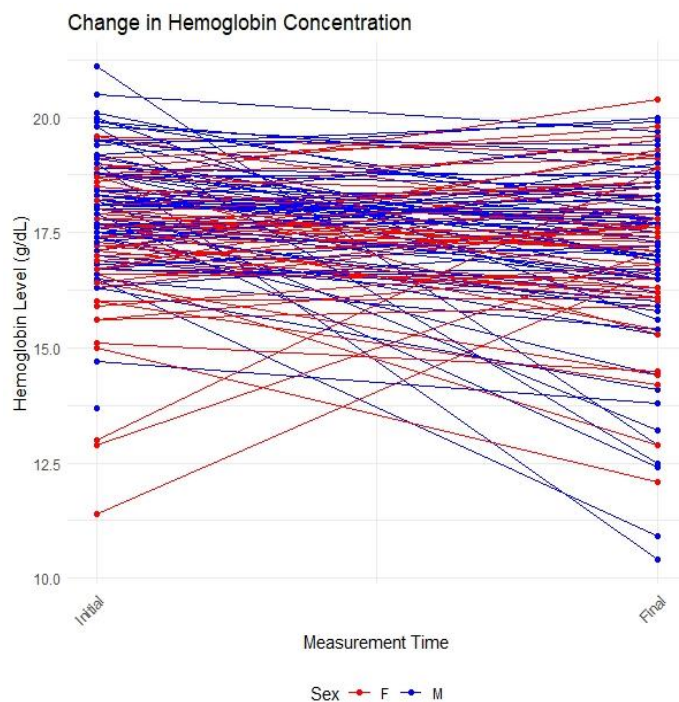


Figure 3.1: Difference in the Hb concentration (g/dL) between males (blue) and females (red) from the initial (upon capture), to the final (before release). Females had a significantly ($p < 0.001$) lower starting Hb than the males.

measures were treated as fixed effects, yielded a coefficient of 0.233, indicating a low degree of repeatability, suggesting significant variability between individuals ($p = 0.008$).

3.1.2 Body Mass

Analysis of the three body mass measurements per individual revealed a significant decrease from intake body mass to the final ($p < 0.001$). Individuals experience an estimated 1.112g decrease in weight between the intake and the pre-experiment measurements and an estimated 3.158g decrease between the intake and the post-experiment measurements. The average estimated body mass of the sparrows was 31.55g.

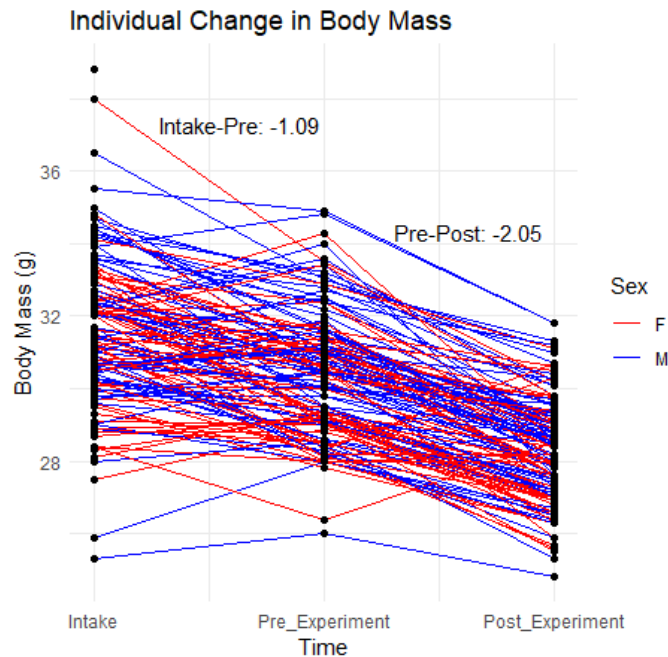


Figure 3.2: Difference in individual weight between measurement times of females (red) and males (blue). Average decrease in mass between the initial measure and the second measure, (Pre_Experiment) was 1.09g while the average decrease from the second measure (Pre_Experiment) to the final measure (Post_Experiment) was 2.05g. Overall average change in mass was 3.15g. Females had a significantly lower Post_Experiment mass than the males ($p = 0.030$)

indicated a generally significant decrease in body mass.

Male sparrows began the experiments with a lower mean intake weight than the females. For the final weight measured however, the females ended with a slightly lower weight than the males ($p = 0.030$). Despite this lower weight for females, both sexes changed their weight in a similar manner over the duration of their

As depicted in Fig.3.2 the body mass of each individual exhibited a decline from the intake phase to the pre-experiment phase, with a more pronounced decrease observed between the pre-experiment and post-experiment phases. While there was variability in weight changes among individual birds—with some losing more or less weight than the average, and a few even gaining weight—the overall trend

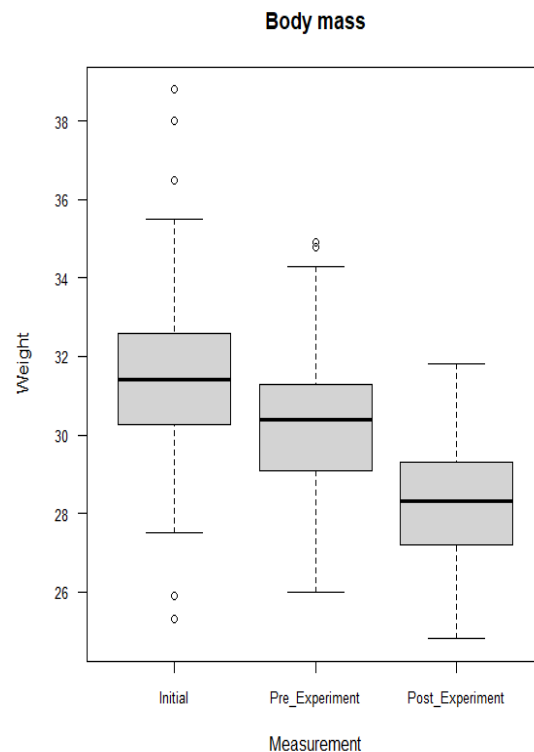


Figure 3.3: Some outliers are indicated above and below the quartile ranges for both the Initial and the Pre-Experiment measure. The differences in averages are consistent with Fig. 3.2

captivity ($p = 0.213$). *Table 7.2* in *Appendix 7.2* further explores these sex differences among variables.

The repeatability model for body mass, treating the measurement type (intake, pre-, post-experiment) as a fixed effect and the individual sparrow as a random effect, yielded a repeatability coefficient of 0.661. This indicates consistency in the body mass measurements within individuals. The observed repeatability proved to highly significant as well ($p < 0.001$).

3.1.3 Wing Area

Initially each of the wing areas were compared for the left vs. right in both the extended and the relaxed positions. These proved to have relatively low repeatability coefficients. However, when the same wings for each position were compared between set 1 and set 2 the repeatability improved somewhat. These R coefficients for the repeatability of each measurement set, where each set indicates a group of four photos taken at different times (some, but not all, by different observers), can be seen in *Table 3.1*.

In the case of right compared to left in the same set as well as the same wings being compared to each other, the observer was the fixed effect (there were 3 different observers). *Fig.3.4* presents a comparative analysis of the repeatability coefficients for the right vs. right and left vs. left wing measurements for the first and the second extended measurements taken, offering a visual representation of these findings. Additional data and plots for the left vs. right analyses (*Table 7.3*) and the relaxed wing positions (*Fig. 7.4*) are provided in *Appendix 7.1* and *7.2* for a comprehensive overview.

Measurement	Repeatability Coefficient	P-value
<i>RE vs. LE Set 1</i>	0.392	< 0.001
<i>RR vs. LR Set 1</i>	0.465	< 0.001
<i>RE vs. LE Set 2</i>	0.387	< 0.001
<i>RR vs. LR Set 2</i>	0.455	< 0.001
<i>RE vs. LE Set 3</i>	0.244	0.091
<i>RR vs. LR Set 3</i>	0.022	0.468
<i>RE Set 1 vs. Set 2</i>	0.625	< 0.001
<i>RR Set 1 vs. Set 2</i>	0.608	< 0.001
<i>LE Set 1 vs. Set 2</i>	0.654	< 0.001
<i>LR Set 1 vs. Set 2</i>	0.512	< 0.001

Table 3.1: Repeatability values for each of the measurement types. RE represents Right Extended, RR represents Right Relaxed, LE represents Left Extended, and LR represents Left Relaxed. Sets are differentiated by when the measurements were taken and indicate a group of four photos.



Figure 3.4: a) Comparison between the first left extended wing photos vs. the second measured in cm^2 ($R^2 = 0.46$). Colored points indicate when the observations between the first and second sets were made by different observers. b) The comparison between the first right extended wing photos vs. the second set, measured in cm^2 ($R^2 = 0.41$).

3.4 Wing Length vs Wing Area

For each individual, the average area of each wing in both extended and relaxed positions (right-wing extended, right-wing relaxed, left-wing extended, and left-wing relaxed) was calculated. This approach was informed by preliminary findings suggesting the extended wing position offers a more reliable measure, with the relaxed position included in *Appendix 7.2, Table 7.3*, for comparative purposes. There is evidence of a linear relationship between length and area as seen in *Table 3.2*. Despite this, the R^2 values indicate that there is a relatively weak correlation between wing length and wing area.

Measurement	<i>Estimate</i>	<i>Std. Error</i>	<i>df</i>	<i>t-value</i>	<i>P</i>	R^2
<i>Right Extended</i>	0.695	0.135	137	5.106	< 0.001	0.160
<i>Right Relaxed</i>	0.769	0.160	137	4.807	< 0.001	0.144
<i>Left Extended</i>	0.697	0.124	137	5.648	< 0.001	0.189
<i>Left Relaxed</i>	0.577	0.148	137	3.915	< 0.001	0.101

Table 3.2: Statistical results for the models when comparing the length (chord) of a wing to its area. This was done for both left and right wings and each wing position, extended and relaxed. The models were run using the average area of each wing between the two measurement sets.

Fig.3.5 visually represents the results with the line of best fit going through the majority of the data with many points scattered relatively far from the line. Also represented in *Fig. 3.5* is the difference between wing size in males and females. There is a clear division between the two with relatively minimal overlap.

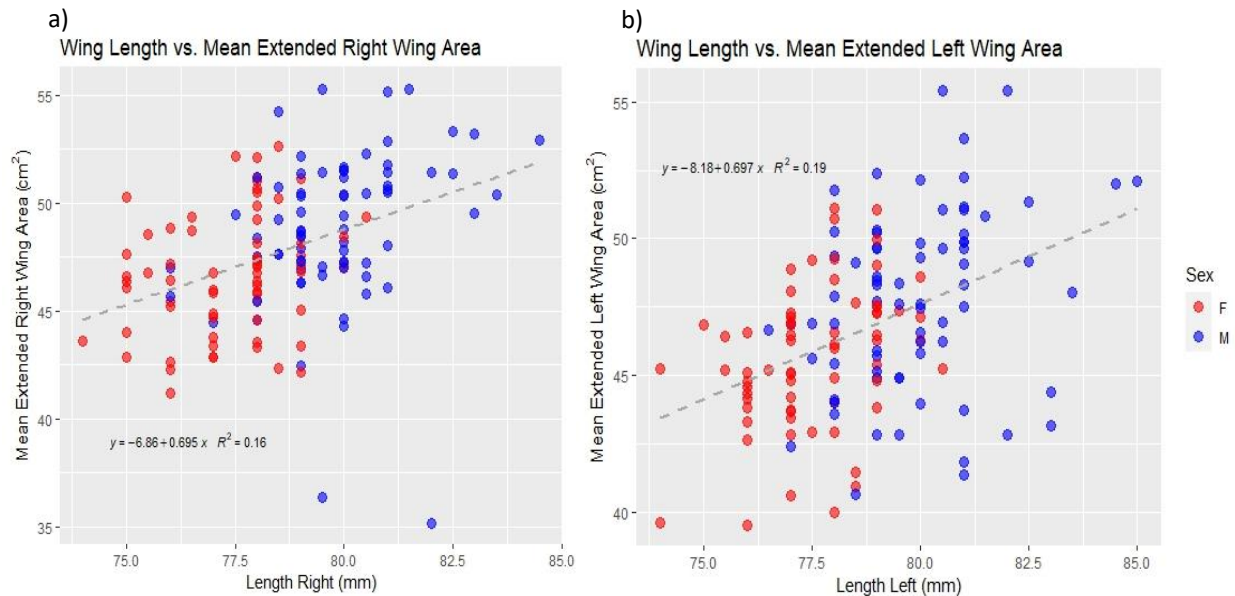


Figure 3.5: a) Mean extended area (cm²) of the left wing of every bird plotted against the length (mm), where the females (red) and males (blue) are differentiated. $R = 0.16$. b) The mean area (cm²) of the right wing of individuals plotted against the length (mm), with the same sex differentiation. $R = 0.19$. Females showed significantly shorter wings ($p < 0.001$) with significantly smaller wing areas ($p < 0.001$) for both left and right wings.

3.5 Hemoglobin and Body Mass

The relationships between initial and final values, as well as the change (Δ) in hemoglobin (Hb) and body mass, were explored through a series of models to assess the correlation between two variables. Specifically, the analyses revealed that a 1g increase in initial weight was associated with a 0.537g reduction in mass change during the experimental period. This model suggests a strong negative correlation (-0.69 , $CI = -0.77$ to -0.59), between the initial mass of an individual and subsequent changes in mass. Similarly, when comparing the Δ Hb to the initial Hb, we see a moderate correlation (-0.43) between the two variables indicating an inverse relationship between Δ Hb and the initial Hb. As the initial Hb becomes larger, we can expect a decrease in Δ Hb and vice versa ($CI = -0.57$ to -0.28). This relationship is statistically significant as indicated by the confidence interval.

No significant correlations were found when comparing the initial and Δ (change) in Hb and mass; the estimate between weight at intake and Hb at intake was -0.12 , indicating a low correlation between Hb and mass upon initial measurement, with little to no statistical significance based on the confidence interval ($CI = -0.29$ to 0.05). When considering the relationship between Δ Hb and Δ mass the estimate is -0.08 with a confidence interval that overlaps zero ($CI = -0.25$ to 0.11) indicating no significant correlation between the two. These relationships are depicted in *Fig. 3.6*, with a model output table provided in *Appendix 7.2, Table 7.4*.

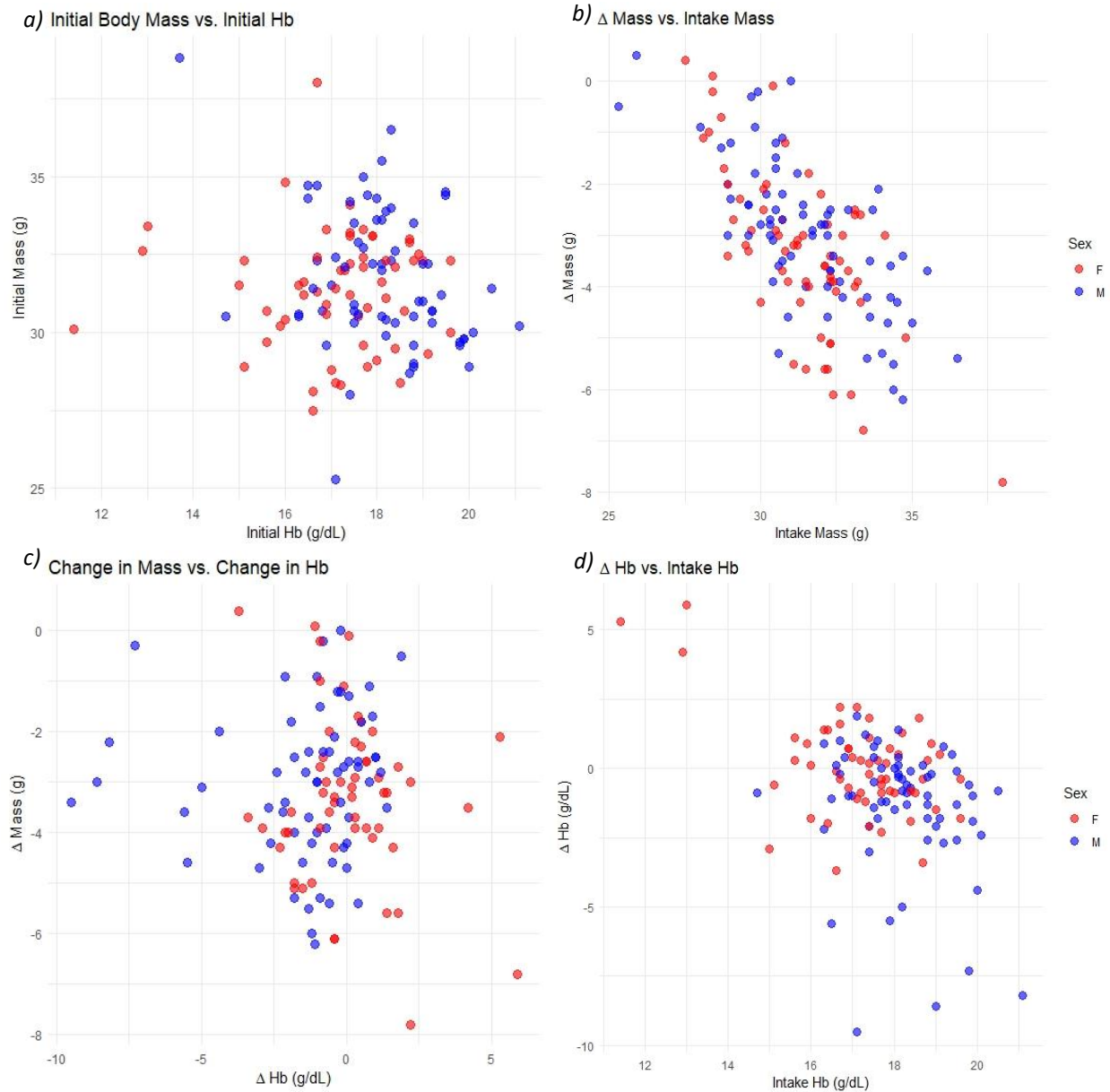


Figure 3.6: a) Correlation between the body mass and Hb levels at the time of intake, correlation = -0.12 (CI = -0.29 to 0.05). b) Between the initial body mass of the subjects and the observed change in their Δ mass, correlation = -0.69 (CI = -0.77 to -0.59). c) Interaction between Δ Hb and Δ mass throughout the experimental period, correlation = -0.08 (CI = -0.25 to 0.11). d) the relationship between the initial Hb concentrations at intake and Δ Hb, correlation = -0.43 (CI = -0.57 to -0.28).

In the subsequent phase, body mass was compared against wing area to determine if employing wing loading as an alternative variable could be a feasible option. The model revealed a significant positive correlation between the two variables, indicating a 0.626 cm^2 increase in wing area per gram of body mass at intake. With a correlation coefficient of 0.21 and a confidence interval from 0.05 to 0.37 , it is implied that wing area tends to slightly increase with weight and *vice versa*. Interestingly, female sparrows tended to have

significantly smaller wings than the males ($p < 0.001$). The results of the T-test for wing area showed that the females had on average, 2.53-6.04 cm² smaller wings than the males. This difference as well as the connection between the initial mass of the sparrows and their wing areas is depicted in *Fig.3.7*.

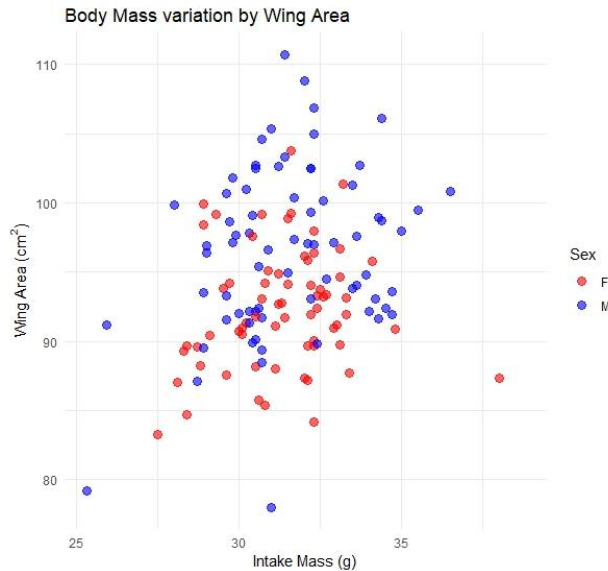
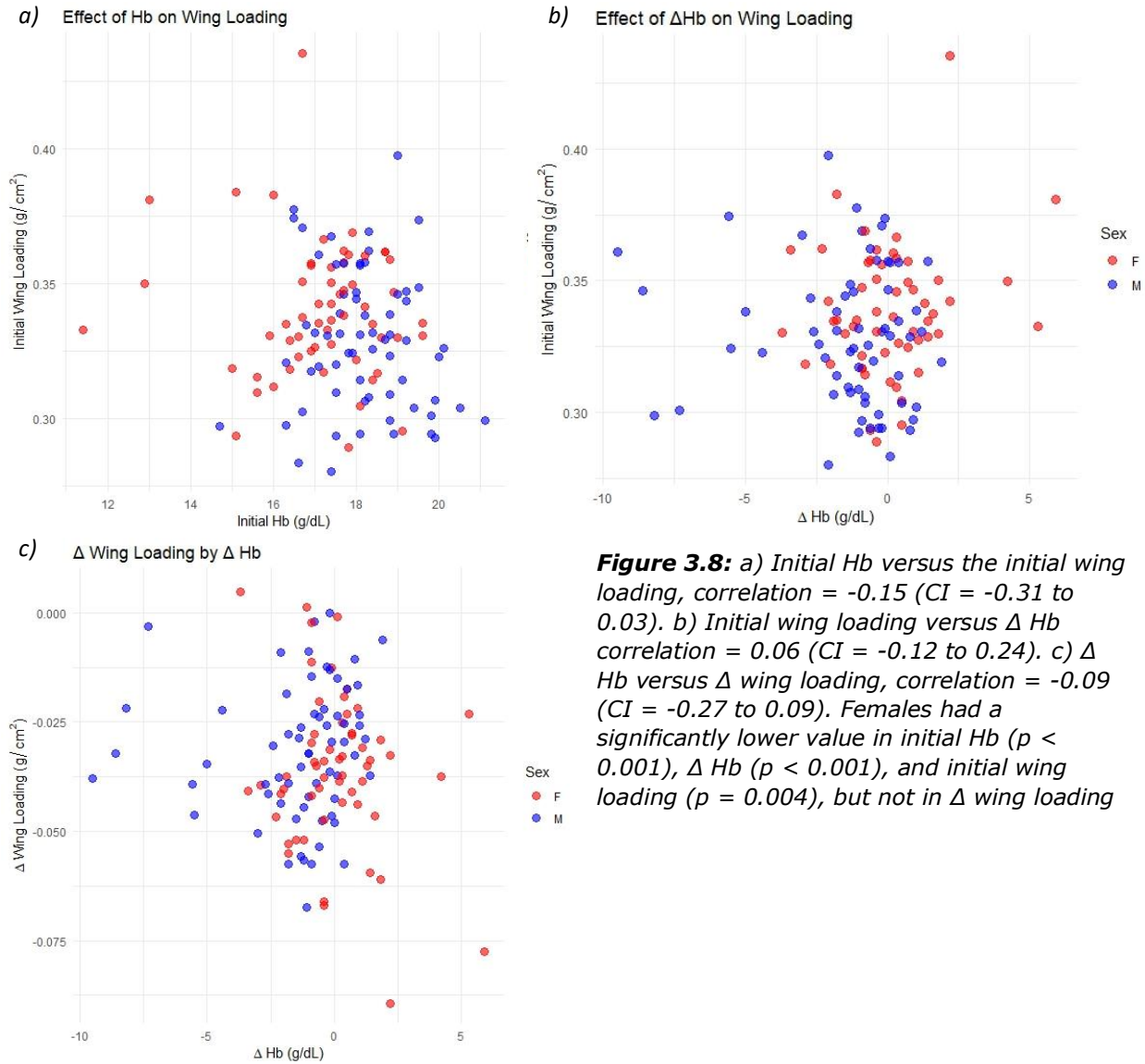


Figure 3.7: Body mass at intake against total wing area per individual, the correlation = 0.21 (CI = 0.05 to 0.37). Individuals are separated by sex. There is no significant difference between males and females in the intake mass ($p = 0.378$), but there is in wing area ($p < 0.001$).

3.6 Wing Loading vs. Hemoglobin

After establishing a significant relationship between wing area and intake body mass, further analyses were conducted to explore the relationships between wing loading and hemoglobin (Hb) concentrations (*Fig. 3.8*). In the first model between the initial Hb and the wing loading at intake, the correlation coefficient was -0.15 with a confidence interval from -0.31 to 0.03. This relationship is therefore not significant, suggesting that changes in the initial Hb and wing loading occur independently of each other.

The correlation coefficient for initial wing loading compared to Δ Hb was 0.06 with a confidence interval from -0.12 to 0.24 indicating that the initial wing loading and the Δ Hb analysis did not show a significant correlation. The analysis of Δ wing loading and Δ Hb similarly presented a non-significant correlation coefficient of -0.09 and a confidence interval from -0.27 to 0.09. Therefore, there is also no relationship between Δ wing loading and Δ Hb. For additional details, refer to *Table 7.5* in *Appendix 7.1*.



3.7 Physiology, Morphology, and Behavior

Based on the above analyses, the final parameters selected for inclusion in the models were intake hemoglobin concentration (Hb) and wing loading, calculated using the mean total wing area and the individual's mass at the start of the experiment, along with the changes (Δ) in these parameters over the full duration of the study. The initial diagnostic models, as described in the Methods section, indicated no significant change in the variance of the random effects when habituation effects were included vs. when they were not.

Due to this finding, all fixed effects associated with habituation were retained in the model to account for all observed variances and to understand their effects. The interaction effects were also considered necessary and provided interesting insights into the results. *Table 3.4* presents the statistical outputs for models 4 and 5 which are concerning producing events, while *Table 3.5* shows scrounging events (models 9 and 10).

	Intake Hb/WL (Model 4)				Δ Hb/WL (Model 5)			
	Estimate	Error	<i>l</i> -95% CI	<i>u</i> -95% CI	Estimate	Error	<i>l</i> -95% CI	<i>u</i> -95% CI
Regression Coefficients								
Intercept	0.06	0.07	-0.08	0.20	0.18	0.11	-0.03	0.39
Sex	0.00	0.10	-0.19	0.19	-0.14	0.09	-0.32	0.05
Intake/ Δ Hb	-0.05	0.03	-0.11	0.02	-0.04	0.04	-0.11	0.03
Initial/ Δ WL	-1.47	1.75	-4.93	1.93	2.11	2.16	-2.21	6.39
Trial_day	0.09	0.04	0.01	0.17	0.10	0.04	0.02	0.17
TrialNR_Ind	0.02	0.01	0.00	0.04	0.02	0.01	0.00	0.09
Grp_Tr_b4	-0.07	0.12	-0.31	0.17	-0.04	0.12	-0.28	0.20
Initial/ Δ Hb x Initial/ Δ WL	0.87	1.10	-1.27	3.04	0.27	0.84	-1.39	1.92
Trial_day: TrialNR_Ind	-0.04	0.01	-0.06	-0.01	-0.04	0.01	-0.06	-0.01
Trial_day: Grp_Tr_b4	-0.23	0.09	-0.40	-0.06	-0.24	0.09	-0.41	-0.06
TrialNR_Ind: Grp_Tr_b4	-0.03	0.02	-0.70	0.02	-0.03	0.02	-0.08	0.02
Trial_day: TrialNR_Ind: Grp_Tr_b4	0.06	0.03	0.00	0.12	0.06	0.03	0.00	0.12
Random Effects								
Group ID	0.09	0.06	0.00	0.22	0.10	0.06	0.01	0.23
Ring Nr	0.43	0.04	0.35	0.51	0.41	0.04	0.34	0.49
Trial ID	0.04	0.03	0.00	0.11	0.04	0.03	0.00	0.11

Table 3.4: Results from both the producer models, on the left, initial/intake values and on the right, the Δ values. Both models were fit to Poisson function in a Bayesian model with the data mean centered and included Trial ID, Ring number and Group ID as random effects. The fixed effects for both models were: Sex, Hb upon intake (Intake Hb)/ Δ Hb, Initial WL/ Δ WL, the trial day, the trial number per individual on a given day (TrialNR_Ind), whether or not an individual had a group trial (Grp_Tr_b4), and several interaction terms (Initial/ Δ Hb x Initial/ Δ WL, Trial_day: TrialNR_Ind, Trial_day: Grp_Tr_b4, TrialNR_Ind: Grp_Tr_b4, and Trial_day: TrialNR_Ind: Grp_Tr_b4).

	Intake Hb/WL (Model 9)				Δ Hb/WL (Model 10)			
	Estimate	Error	<i>l</i> -95% CI	<i>u</i> -95% CI	Estimate	Error	<i>l</i> -95% CI	<i>u</i> -95% CI
Regression Coefficients								
Intercept	-0.80	0.10	-0.99	-0.62	-0.89	0.13	-1.15	-0.64
Sex	0.09	0.11	-0.12	0.31	0.14	0.11	-0.07	0.35
Intake/ Δ Hb	-0.03	0.04	-0.10	0.05	0.05	0.04	-0.03	0.13
Initial/ Δ WL	2.87	2.05	-1.16	6.90	-2.24	2.39	-7.00	2.39
Trial_day	0.13	0.06	0.01	0.25	0.14	0.06	0.02	0.26
TrialNR_Ind	0.02	0.01	0.00	0.05	0.02	0.01	0.00	0.05
Grp_Tr_b4	0.24	0.17	-0.10	0.57	0.26	0.17	-0.08	0.60
Initial/ Δ Hb x Initial/ Δ WL	1.21	1.23	-1.17	3.65	0.48	0.93	-1.34	2.32
Trial_day: TrialNR_Ind	-0.05	0.02	-0.09	-0.01	-0.05	0.02	-0.09	-0.01
Trial_day: Grp_Tr_b4	-0.23	0.13	-0.49	0.01	-0.25	0.13	-0.50	0.01
TrialNR_Ind: Grp_Tr_b4	-0.07	0.03	-0.14	0.00	-0.07	0.03	-0.14	-0.01
Trial_day: TrialNR_Ind: Grp_Tr_b4	0.14	0.04	0.05	0.23	0.14	0.04	0.05	0.23
Random Effects								
Group ID	0.21	0.09	0.09	0.39	0.23	0.08	0.06	0.40
Ring Nr	0.42	0.05	0.32	0.53	0.39	0.05	0.29	0.50
Trial ID	0.20	0.09	0.01	0.36	0.24	0.08	0.05	0.39

Table 3.5: Results from both the scrounger models, on the left, initial/intake values and on the right, the Δ values. Both models were fit to Poisson function in a Bayesian model with the data mean centered and included Trial ID, Ring number and Group ID as random effects. The fixed effects for both models were: Sex, Hb upon intake (Intake Hb)/ Δ Hb, Initial WL/ Δ WL, the trial day, the trial number per individual on a given day (TrialNR_Ind), whether or not an individual had a group trial (Grp_Tr_b4), and several interaction terms (Initial/ Δ Hb x Initial/ Δ WL, Trial_day: TrialNR_Ind, Trial_day: Grp_Tr_b4, TrialNR_Ind: Grp_Tr_b4, and Trial_day: TrialNR_Ind: Grp_Tr_b4).

When assessing the impact of hemoglobin (Hb) on the number of producing and scrounging visits, the confidence intervals for the effect of intake Hb on producing (-0.11 to 0.02) and scrounging (-0.10 to 0.05) included zero, indicating that any observed effects were not statistically significant. These effects are depicted in Fig. 3.9 and Fig. 3.10 where the Hb and wing loading were plotted against the BLUPs (Best Linear Unbiased Predictors) to show the propensity to produce/scrounge based on an individual's Hb or wing loading.

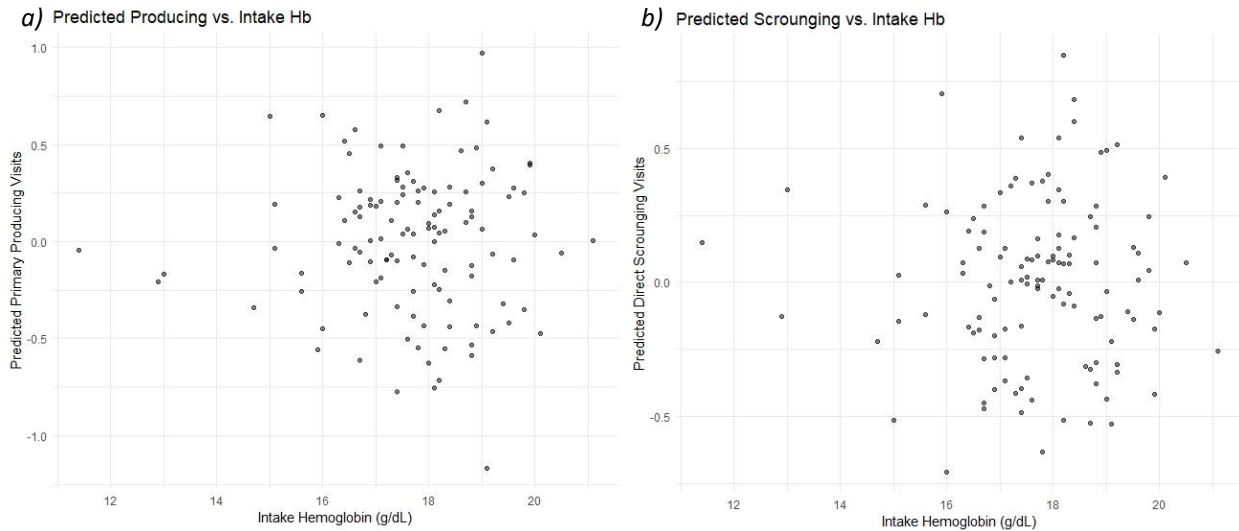


Figure 3.9: Intake Hb concentrations in g/dL against the BLUPs associated with the random effects of individual differences (Ring Number), in the number of predicted visits. Panel a) shows the predicted primary producing visits based on individual effects, while b) shows the predicted number of direct scrounging visits based on the Hb at intake.

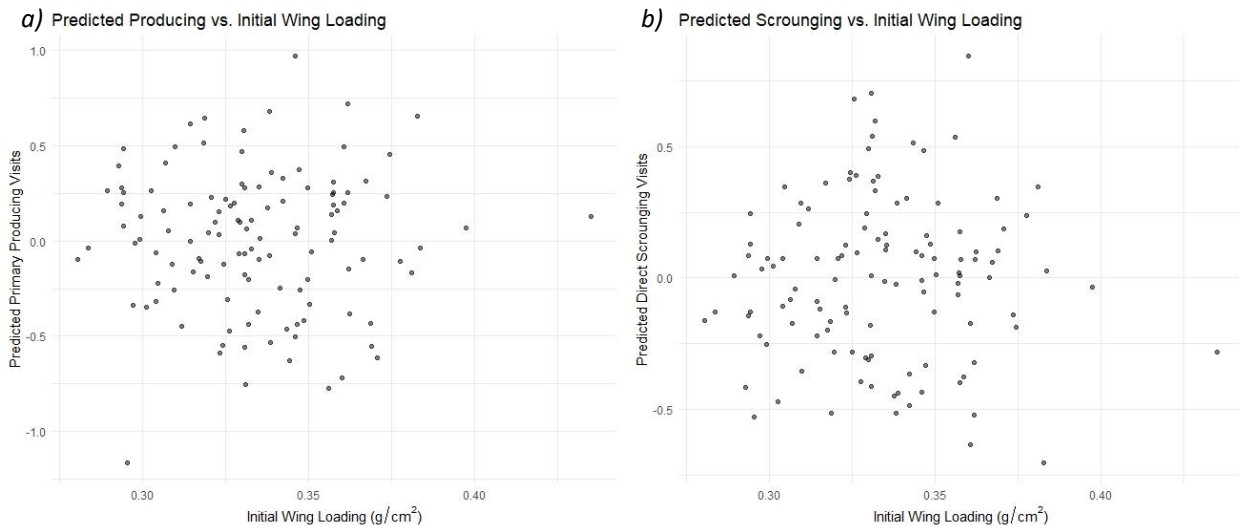


Figure 3.10: Initial wing loading (WL) in g/cm² against the BLUPs associated with the random effects of individual differences (Ring Number), in the number of predicted visits. Panel a) shows the predicted primary producing visits based on individual effects, while b) shows the predicted number of direct scrounging visits based on the WL at intake.

The models were then rerun with Δ Hb values to determine if changes in Hb over the duration of the study could influence an individual's foraging tactics. In the producing model, Δ Hb also showed a slight negative impact, while in the scrounging model, Δ Hb showed a slight positive impact. However, these estimates were very small, and their confidence intervals also included zero (-0.11 to 0.03 for producing and -0.03 to 0.13 for scrounging), suggesting minimal likelihood that changes in Hb significantly influenced the birds' behaviors. The effect of Δ Hb on producing and scrounging behaviors is illustrated in Appendix 7.1, Figure 7.5.

Wing loading demonstrated larger differences in the estimates than hemoglobin (Hb) between the producer and scrounger models. For the intake values, wing loading had a negative estimate in producing but a positive estimate in scrounging, with values of -1.47 and 2.87, respectively. However, the confidence intervals for both estimates included zero (-4.93 to 1.93 for producing and -1.16 to 6.90 for scrounging).

The Δ wing loading values had opposite estimates, with a slight positive estimate in producing and a slight negative estimate in scrounging, with values of 2.11 and -2.24 respectively (CI = -2.21 to 6.93 for producing and -7.00 to 2.39 for scrounging). The confidence intervals for these values also included zero and were very wide, indicating that it is not possible to confirm any significant effect of Δ Hb or Δ wing loading on the number of producing or scrounging visits. *Figure 7.6 in Appendix 7.2* displays Δ wing loading plotted against the predicted number of primary producing visits and direct scrounging visits. Furthermore, there was no significant effect from the interaction between intake Hb and initial wing loading or Δ Hb and Δ wing loading on the number of either producing or scrounging visits.

The estimates for male sparrows showed no clear differences in the number of primary producing visits or direct scrounging visits between sexes, with initial values at 0.00 and changes (Δ values) at -0.14 in the producing model, and initial values at 0.09 and Δ values at 0.14 in the scrounging model. The data also indicate that only the trial day and interactions between the trial day and the trial number per individual, as well as between the trial day and whether the sparrows had a group trial or not, had any significant effect on the number of visits. In both producing and scrounging the majority of habituation effects had confidence intervals that included zero as seen in *Table 3.4* and *3.5*, as well as the interaction between trial day and group indicating that, despite a small effect size, these interactions were significant. The results from models 1-10 indicated that there was only a very small interaction between the random effects and the habituation effects (only a slight increase in the estimates when the habituation effects were removed as fixed effects), and no interaction between the physiological and morphological effects. Model outputs for models 1 and 6 which give the results for the random effects only can be found in *Appendix 7.2, Table 7.1*, and model outputs for models 2, 3, 7 and 8 that show the results without habituation effects can be found in *Appendix 7.2, Tables 7.6* and *7.7*.

In the models concerning the effect of intake Hb/ Δ Hb and initial wing loading/ Δ wing loading on primary producing visits (models 4 and 5), individual differences (ring number) in model 4 explained 24% of the total variance, while group ID accounted for 5%, and trial ID for 2.2%. The residual variance was 68.8%. This slightly differs from model 5, which focused on the effect of changes in Hb and wing loading on primary producing visits, where individual differences accounted for 23% of the variance, group ID for 5.6%, and trial ID for 2.2%, with 69.2% remaining as residual variance. Both model 4 and model 5 are very similar showing now significant difference between initial and Δ values

In the models examining the effect of intake Hb/ Δ Hb and initial wing loading/ Δ wing loading on direct scrounging visits (models 9 and 10), individual differences accounted for 20% of the total variance, group ID for 10%, and trial ID for 9.7%, with a residual variance of 60.3% in model 9. Meanwhile, in model 10, 19% of the variance was explained by

individual ID, 11% by group ID, 12% by trial ID, and 58% by residual variance. These findings highlight the complexity of the factors influencing foraging behavior in sparrows.

The final models used to determine the effect of either Hb or wing loading on foraging behavior were narrowed down from the path diagram seen in *Fig. 2.7* in the methods to a simplified version as seen below in *Fig 3.11*.

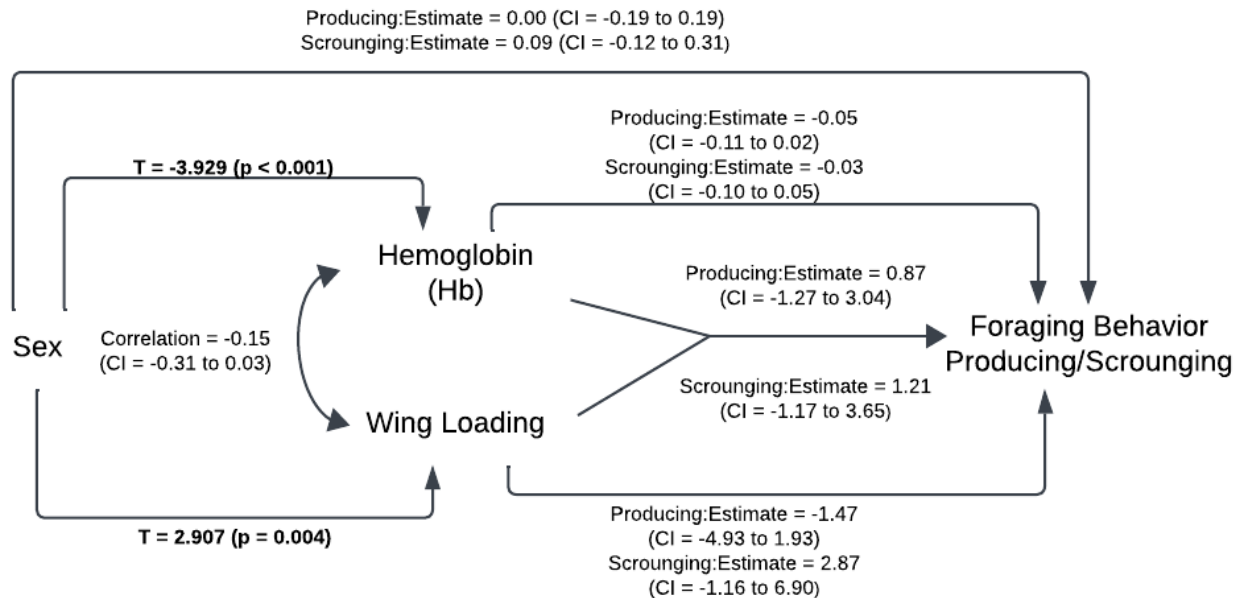


Figure 3.11: The variables chosen for the final comparisons between individual physiology, morphology, and behavior. The schematic path diagram outlines the flow of model selection used to determine the effect of sex on Hb, wing loading, and behavior, Hb and wing loading on each other, Hb and wing loading separately on behavior, and the interaction effect of Hb and wing loading on behavior. The two significant effects here are indicated by bold font.

4. Discussion:

The main objective of this project was to explain individual differences in social behaviors, specifically producer/scrounger foraging strategies, using physiological traits such as Hb and morphological traits such as wing loading. Additionally, we aimed to develop methods for repeatedly measuring Hb and wing area in the field and to analyze strategies to improve these methods.

We found that, from a biological standpoint, Hb and body mass measurements showed acceptable repeatability, while wing area measurements did not. Our analysis suggests that further scrutiny and refinement of the measurement methods could be highly beneficial. Definite differences between sexes were observed in traits such as Hb and wing loading, but not in body mass or producer/scrounger activity. Although there were evident correlations between parameters such as initial and Δ body mass/Hb, and body mass and wing area, there were no prominent correlations between Hb and body mass or Hb and wing loading. Furthermore, while habituation effects played a clear role in increasing the number of primary producing/direct scrounging visits, there was no discernible connection between either Hb or wing loading and producing/scrounging behaviors.

4.1 Interpretation of Results

4.1.1 Repeatability

Hemoglobin

With the majority of approximately 140 individual house sparrows having both a Hb measurement at intake and after the end of the experimental period, we gained useful insights into the use of Hb concentration as a predictive variable. With a repeatability coefficient of 0.233, we understand that, as predicted, this is a generally plastic trait that will vary over time based on external factors, such as weather and food availability (Kaliński et al., 2009), hormones (Puerta et al., 1995), and altitude (Clemens 1990) to name a few. Although the repeatability of Hb was low, the measured values were within an acceptable range from a biological standpoint, as Hb can also vary with a number of physiological conditions such as moult, nutritional state, and breeding status (Minias 2015). None of the individuals in our experiments exhibited any deficiencies in these conditions however, and moult and breeding status were observed. A few individuals had lost some tail feathers during the study and of all subjects, only one had anything resembling a brood patch, so it is highly unlikely that either of these things affected the results.

There was some concern in the beginning phases of analysis whether any of the values that were statistical outliers were also biological outliers, and while the range of Hb concentrations in altricial nestlings tend to be narrow (Kaliński et al., 2015), other studies found a healthy amount of variation in passerine birds (Bańbura et al., 2007; Kaliński et al., 2009). This indicated that the outlier values, the lowest being 7.6 g/dL and the highest at 21.1 g/dL, were within range for adult birds. The individuals under our care were also monitored for signs of stress that could have affected the data, and in general, the birds adapted well to the stress of captivity with *Passer domesticus* being a resilient species (Fischer et al., 2018). The extreme values we saw could also potentially be attributed to errors in the collection of the blood samples, specifically, to access the brachial vein on the bird's wing, it was necessary to move the downy feathers aside. This task proved challenging when the feathers were dry, and a solution was to use a slightly damp finger to gently smooth the feathers away. However, there were some concerns that the additional moisture might have diluted the blood sample loaded into the HemoCue device, potentially affecting the Hb concentration measurement. Unfortunately, it was impossible to determine the effect of this potential dilution, as the instances of added water were not systematically noted, and not all individuals underwent the same procedure used to move the feathers aside.

The HemoCue device, while very useful in fieldwork and proven to be consistent and accurate with humans (Hudson-Thomas, et al., 1994), has run into some issues when working with animal specimens. In Clark et al. (2008) it was shown that the HemoCue device overestimated the Hb concentration in fish blood, but could then be calibrated using the Drabkin method (*Appendix 7.3*). Harter et al. (2015), however, found that many of the issues using the HemoCue device in exotherms (fish in this instance) could be related to the differences body temperatures and the O₂-binding properties between cold vs. warm-blooded organisms. Although the O₂-binding properties differ between humans and birds, Harter et al. (2015) found that the HemoCue device could be used as a reliable tool to

assess Hb in bar-headed geese (*Anser indicus*) as long as the results were corrected using a simple linear equation. In this study, the only calibration done with the HemoCue device was the machine's initial self-calibration on startup and to let the blood sit in the cuvette for at least a minute to allow it to mix with the reagents. No equation was applied to the collected data, but since the relationship here is linear this would have simply shifted all absolute data values in parallel with no changes in relative values, and so would not have affected the results of this thesis, and because the HemoCue data in this experiment is being compared to itself, this is less of a concern. If this data were to be compared to Hb data measured another way, the accuracy would be questionable at best.

Body Mass

The repeatability of body mass was 0.661, indicating a decent consistency of measurements within individuals. While this coefficient does not suggest high repeatability, it reflects the expected variability of body mass as a dynamic trait susceptible to fluctuations over time and across individuals. As expected, a significant proportion of the birds lost mass over the duration of the experiments, approximately 4.270g, with males and females having similar mass at intake and losing similar amounts. This observation aligns with the optimal body mass hypothesis, which considers the trade-off between the risks of starvation and predation (Krause et al., 2010; Lima et al., 1986; Witter and Cuthill, 1993). Since our experiments ran from mid-January to the end of February, we transitioned the birds from harsh winter conditions with scarce food to a temperature-controlled environment (10°C) with *ad libitum* food. The measured weight loss here was consistent with several previous findings of the effects of increases in temperature and food availability and reductions in variance in both of these as well (Lima, 1986; Krams et al., 2010). The only potential perceived risk of predation for the birds, however, could have been the researchers themselves, as entering the aviaries and the experiment room to catch individuals and set up new trials was necessary. This interaction while potentially contributing to the observed weight loss, cannot be the only change in predation risk. It should also be considered that the birds may have felt safer being in a group away from natural predators and therefore we cannot confidently say what sort of a role this may have played in their adaptive mass loss.

Although dominance data was not measured for the 2023 experiments, it was analyzed in 2022 and the more dominant individuals would have been predicted to have lower body mass, leaving the often-larger subordinate individuals susceptible to predation. Additionally, because the social environment and resources are less stable for subordinates, dominants can more easily monopolize resources. According to a master's project last year (Zeiner-Henriksen 2023), on the same population of sparrows and with the experimental methods, the larger more dominant males were more likely to be scroungers, while the heavier more dominant females were more likely to be producers. Consistent with Krams et al. (2010), Zeiner-Henriksen (2023) found larger individuals tended more toward producing behavior than scrounging. This implies that dominance is different across sexes, and body mass and dominance influence the foraging tactics of individuals. It would be interesting in the future to analyze the dominance data in addition to the Hb to see if there is any influence on dominance from Hb or *vice versa*.

Wing Area

The wing area measurements were not repeatable enough according to our predefined threshold and so, do not seem to give a reliable estimate of the true value. Given that not all birds had four sets of wing photos (everyone had at least two), with one set representing a single point in time when four photos were taken, it was more practical to compare wing areas between sets 1 and 2 only. Initially, I attempted to compare the right wing to the left wing for each position (extended or relaxed), but the highest repeatability coefficient recorded was 0.465 for the right versus left wing in the relaxed position. This low repeatability indicated significant variation between measurements of the left and right wings. One possible explanation for this could be the manner in which the birds were held by the observers, which might cause a bird to retract its wing, making accurate measurement challenging. The variation might also stem from the fact that wing area measurements were recorded by three different observers (SL, RW, and CdG). Including the observer as a fixed effect in the model did significantly improved its accuracy, accounting for the possibility that observers might have a preferred hand for holding the bird or use slightly different execution of the same protocol when measuring, which could lead to variations in area measurements.

Another potential issue could arise from the photos themselves. Despite checking the camera and its settings before and during each of the photo sessions, some photos turned out blurry, making them difficult to analyze later using ImageJ. These issues were only identified after the sparrows had been released, preventing any possibility of retaking the photos, and no model was run excluding the blurry photos. This likely contributed to a lower repeatability between the first and second set of photos. When measuring the areas of the wings there were also several methodological concerns. Initially, the repeatability of these measurements was very low, which I determined was due to the scale settings in ImageJ. In the first attempt of calculating the area, the scale was set using the first photo for each set of four images, which did not account for variations among individual photos or any potential camera movement. In subsequent measurements, the scale was set for each individual photo, which significantly improved the repeatability of the data. A final potential factor influencing specifically the repeatability of left-right wing comparisons is fluctuating asymmetry (Balmford et al., 1993), which refers to minor variations in bilateral symmetry that may be influenced by natural selection for aerodynamic efficiency. Given that sparrows are a non-migratory species, the importance of wing symmetry may be limited, possibly leading to slight differences between the left and right wings. The results indicated that there was a higher repeatability when comparing the same wings rather than left to right.

When comparing the same wings to each other across sets, the repeatability coefficients increased significantly, with the highest values being 0.625 and 0.654 for the right and left extended wings, respectively. Although these improvements did not reach the 0.8-0.9 values indicative of high repeatability, they marked a substantial improvement over the coefficients for right versus left wing comparisons. The higher values for the extended wing position also suggested that holding the wings in this position allows for more repeatable and accurate measurements. The chosen methodology was perhaps not the most efficient and should be reconsidered. A recent study by Fu et al. (2023) suggests a new method of

using a wing length and width measurement from a folded wing rather than the total wingspan from a spread-wing method. While the study proved that this method showed greater precision, it would have been impractical for my study as it would have required dead specimens where the wing can be more easily measured and manipulated.

4.1.2 Wing Length vs. Wing Area

Once it was determined that the wing area methods were acceptable, the next step was to see if there was potential to calculate the total wing area using the wing length. Wing area is not a routine measurement for the majority of studies, so the aim was to find either, methods that were simple enough to include in morphometric data collection, or to find a way to use already recorded data to potentially calculate the total area. In Blem (1975), wing area was measured by removing the wing from the bird entirely. The results of this study, comparing the average wing chord to the total wing area, showed a similar linear relationship to the data to my study. However, I compared the length of one wing to the average area of that wing and still obtained similar results. In Fu et al. (2023), different wing shapes across various birds were considered, and fitted to one of three geometric models (ellipse, triangle, or ellipse-triangle), potentially allowing for more precise calculation of wing area for sparrows. It should be noted that there is a difference between wing length and wing chord, and the difference in the terminology has led to confusion between ornithologists, and physiologists or physicists when working with avian aerodynamics (Stiles et al., 2004). In aerodynamics, the wing length should be measured on an extended wing in a natural position, while the wing chord (commonly what is measured by biologists during field work) is measured on a folded wing and is the straight-line distance between the leading and trailing edges of a wing. It is possible that the difference between these two measurements could affect the outcome of trying to predict the area of a wing using the length.

In this study, the extended wing areas proved to have a better fit of the data when comparing the area to the length with about 19% of the area of the left wing being explained by the length, and 16% of the right wing. I hypothesized that the wing length should be proportionate to the body size of the sparrow, and it should therefore be able to predict the wing area, and although the length cannot fully encapsulate the area of a wing, the results did show that there is a linear relationship and generally the larger birds did have proportionally larger wings.

Notably, female sparrows had shorter wings, as well as smaller overall wing areas than the males. Similar results were found in Araya-Ajoy et al. (2019), where females also had significantly shorter wings than the males. They did not, however, have much variation in body mass, indicating that female sparrows experience a higher wing loading initially that then decreased by the end of the study.

4.1.3 Hemoglobin and Body Mass

As predicted, the Hb and body mass of individual sparrows did significantly decrease over the duration of the study, and they did so in a similar manner. I had originally hypothesized that the effects of Hb and body mass should be similar as they are traits that positively covary with one another. Almost all birds lost mass, and this was roughly in proportion with

intake mass meaning heavier individuals lost proportionally the same amount of mass as lighter individuals. This suggests adaptive mass loss down to a lower and less variable value by all birds, due to more stable conditions, as compared with the colder and more variable natural temperatures, food availabilities, etc. So, it is interesting to see who was heavier or lighter at intake, and thus also who was losing most mass, within each the producer-scrounger groups and whether it was linked. This has been looked at in Guldvik, (2023) and Zeiner-Henriksen, (2023) but not much on the specific topic was discovered.

It has been noted that, particularly in migratory birds, a higher Hb was necessary to account for the extra energetic cost of higher fat loads that many birds accumulate in preparation for migration (Minias 2015). Several other studies have also shown a positive correlation between Hb and body mass both for uncorrected (Piersma et al., 1996; Dufva et al., 1996; Lobato et al., 2011), and corrected (Landys-Ciannelli et al., 2002; Minias et al., 2013) body mass. In Yap et al. (2019), it was seen however, that Hb does not scale with body mass at the interspecific level and a higher body mass could rather be indicative of body condition. Still, the wintering sparrows were predicted to have higher body masses and Hb levels at the beginning of the study, as their body condition reflected the harsher winter environment. Then as they acclimated to a warmer environment, they would lose weight and the Hb would decrease in a meaningful way. According to the results of this study, however, there was only a slight, non-significant, negative relationship between Hb and body mass (higher Hb resulted in a lower initial mass and a greater Δ Hb resulted in a slightly greater Δ mass) for both the intake values and the change in these measures over the duration of the experiment. Hanssen et al. (2003), indicated no relationship between hematocrit and body mass in their study of immune response of the common Eider (*Sturnus vulgaris*) which indicates there would have also been no relationship between body mass and Hb as hemoglobin and hematocrit covary (Landys-Ciannelli et al., 2002; Puerta et al., 1995) This could be due missing other parameters such as hematocrit in the models and not fully covering the scope of the interactions or potentially that they are not correlated with one another. This seems unlikely however when considering much of the aforementioned literature.

4.1.4 Wing Loading vs. Hb

When evaluating whether wing loading is a more effective parameter for assessing the impact of morphology on behavior than just body mass alone, it was determined that wing loading could serve as a comprehensive measure, encapsulating both wing area and mass. Because females had smaller wings (both in length and total area), but similar mass when compared to the males, they had significantly higher wing loading at both intake and post-study assessments. Given that Hb is a measure of aerobic capacity, it was hypothesized that Hb levels would covary with the energy required to compensate for differences in wing morphology. Therefore, the higher wing loading associated with female birds could suggest that females had higher Hb levels to compensate for a less energetically efficient body plan. However, contrary to expectations and findings in other species such as the blue tit (*Cyanistes caeruleus*) and seven Antarctic bird species as reported by Kaliński et al. (2012) and Myrcha et al. (1980), the data showed that females had significantly lower Hb at intake than males. This discrepancy could also be influenced by the presence of high outlier values predominantly among males and low outlier values among females. It could also be due to

other physiological factors, such as hormones or age, or environmental factors such as season. In a variety of animals including several mammal species (Sealander et al., 1965) and several bird species (Fair et al., 2007), pregnant or lactating females and juveniles had significantly lower Hb values as well as other blood parameters such as hematocrit and erythrocyte diameters. Juvenile birds specifically were also shown to have lower Hb values than adults (Cornell et al., 2017), which could have also affected the results of this study as all individuals were identified as adults but could have potentially still be rather young. Finally, there is the possibility that the slight inaccuracies of the wing area measurements could have also contributed, not only to this, but to the behavioral analyses as well.

A study by Bowlin et al. (2008) analyzing wing shape found that differences in wing loading due to wing shape correlate with heart rate. Specifically, birds with rounder wingtips, and thus higher wing loading, exhibited higher heart rates, indicating greater energy expenditure. Furthermore, research by Minias et al. (2013) suggested that birds could increase their Hb levels in preparation for winter or migration, anticipating higher energy expenditures. Considering that higher wing loading is associated with increased workload and the corresponding baseline Hb levels needed to support this workload, it was expected that this relationship would be reflected in the study results. However, the findings indicated a slight decrease in wing loading associated with higher Hb at intake, which contradicts the literature. This decrease was not statistically significant and warrants further consideration of improving the repeatability of Hb and wing area to improve our confidence in the measurements.

4.2 Link Between Physiology and Behavior

When attempting to determine how morphology and physiology could influence behavior, I initially hypothesized that individuals with higher hemoglobin (Hb) concentrations would be more likely to opt to produce rather than to scrounge, and that individuals with higher wing loading (larger body mass with proportionally smaller wings) would tend to spend more time scrounging. Based on the results of this study, I was able to accept the null hypothesis since my results showed no effect of the parameters in question. Although Hb cannot definitively indicate the body condition of a bird, it can provide some information such as food availability seen in studies of nestling great tits (*Parus major*) by Kaliński et al. (2009) and Norte et al. (2009). Because Hb alone cannot fully account for body condition, it is important to take external factors such as environmental changes into account. The idea of linking Hb concentrations with foraging strategies was intriguing to me, and there would be merit in including overall body condition, not just Hb, in future studies to further explore these relationships.

In the producer-scrounger models of this study, neither Hb nor the change in Hb (Δ Hb) significantly influenced the number of primary producing or direct scrounging events. However, this does not necessarily imply that Hb played no role, as both foraging strategies entail different energetic costs. Barta and Giraldeau (2000) discuss how an individual's available energy influences their choice of strategy in a state-dependent dynamic model of the producer-scrounger game. Their study examined variations in energetic state at different times of the day, as well as the amount and quality of available food. In contrast, our study provided constant food availability and of consistent quality, which should therefore, have not affected the outcome. The Hb concentrations, measured at the

beginning of the experiments before any habituation, may have reflected the sparrows' state at capture but could have changed by the first day of experimentation after two days of habituation, leading to potentially inaccurate assessments. Nevertheless, observing how much Hb changed from the first to the final measurement should have offered insights into how the sparrows' state changed. In future research, it would be interesting to monitor how Hb levels fluctuate over the course of a day under stable conditions and then compare those findings to a producer/scrounger game conducted under the same conditions.

In Lendvai et al. (2004), researchers manipulated the energy reserves of sparrows to determine if this influenced their choice of foraging strategy. They confirmed the predictions of Barta & Giraldaeu (2000) that sparrows with unexpectedly low energy reserves (indicating hunger) at the very start of the day would opt for the scrounging strategy as it is a safer, more risk averse tactic. In this study the most risk adverse strategy was for birds to wait until others have had their fill and then scrounge from a vacant food source. This potentially led to a lower payoff as there would be less food, but no energy would be expended in searching. While there was no risk of starvation in my study, this does prompt consideration of the effect of energetic state on foraging tactics and the role of Hb. Since Hb is a single measure of aerobic capacity (there are many other physiological measures that attribute to aerobic capacity) and can give a slight indication the energetic capabilities of an individual, it could be suggested that individuals with higher baseline Hb levels start each day in a higher energetic state. This enhanced state could lead an individual to opt for the more energetically costly foraging strategy, i.e., producing. This reasoning aligns with my original hypothesis that individuals that do not need to expend more energy due to wing loading should be producers; however, the lack of significant findings warrants further investigation.

Similar to Hb, neither the wing loading at intake nor the Δ wing loading significantly influenced the number of producing or scrounging visits. I had hypothesized that individuals with higher wing loading might favor scrounging, based on the assumption that heavier bodies with smaller wings to support their weight would necessitate higher energy output for flight, thus making them more likely to choose a less energetically demanding foraging tactic. Wing morphology, however, varies across bird species, and wing loading, and aspect ratios can change based on several factors, including whether the bird is migratory. These characteristics can also be influenced by a bird's life history and sociality.

According to Beauchamp et al. (2023), less social bird species and those with faster pace-of-life histories—those emphasizing reproduction over adult survival—tend to have lower wing loading and aspect ratios, which enhance maneuverability depending on wing length. In contrast, sparrows, being highly social, typically have rounder, shorter wings, and therefore generally higher wing loading, as they can rely on other flock members to alert them to predators. Across and among populations, house sparrows exhibit distinct life histories, potentially leading to variations in wing morphology to suit different ecological needs. These pace of life syndromes (POLS) are seen as a continuum between fast and slow life history strategies (Royauté et al., 2018). For instance Martin et al. (2006) observed that a population of sparrows in Panama exhibited a slower life history compared to a population in New Jersey with a faster life history. Additionally, a study by Araya-Ajoy et al. (2021) on a metapopulation of house sparrows in northern Norway revealed that life histories are

density-dependent and can change relatively quickly. Given the similarities with our study population, I would like to be able to compare life histories and wing loading across global populations in to see if there is more of a difference across populations than among.

But, as previously mentioned, wing loading may be correlated with other traits that could affect available energy even though the birds did not have as much space to fly in the relatively small experimental cages and aviaries. In this study, there was variation between the level of activity between individuals when on the checkerboard feeders in the experimental cages. The aspect ratio was not considered at all, but since the wing area data was collected in the form of photos, but it could be calculated in a future study. Nonetheless, the ability to take off quickly, which heavily relies on an individual's wing loading, could influence whether a producer stays to defend a food source from a scrounger. This aspect of wing morphology remains an intriguing factor in understanding avian behavioral strategies and warrants further exploration in future studies.

Consistent with the findings of Zeiner-Henriksen (2023), heavier, male (and presumably more dominant) sparrows were more often scroungers, implying that these individuals should have a lower wing loading and lesser fat reserves since they are choosing the more risk averse foraging strategy. Part of the strategy in choosing a foraging tactic may have to do with predator avoidance and an individual's ability to escape, but in general individuals should adopt the strategy that maximizes benefit and minimizes losses/risk. This is partly dependent on social partners but also on individual traits such as Hb or wing loading. In great tits (*Parus major*), males were shown to have faster take-offs than females due to larger wings and less mass (Krams 2002) suggesting that the females, typically having larger fat reserves, would also have a higher wing loading. My results are relatively consistent with this as I saw that females did have a higher wing loading than the males but similar masses, but this similarity in mass could be due to the season as mentioned previously. I also saw no evidence that sex influenced the number of either producing or scrounging visits. Zeiner-Henriksen (2023) saw that heavier females produced more while heavier males scrounged more, but in this study the interaction between body mass and sex was not investigated. The lack of significance in the producer-scrounger models, however, may be because of the sheer complexity of interactions and lack of including social factors.

All four models—analyzing the effects of intake hemoglobin (Hb) and initial wing loading on producing and scrounging, as well as the changes in Hb and wing loading over time—incorporated variables that addressed the impact of habituation throughout the trial and how these factors influenced the number of visits. The data revealed a significant influence of the trial day and inclusion in group trials on the number of producing and scrounging visits, indicating substantial habituation effects that were accounted for by the model, as the birds still had to fully habituate to the experimental setup. Therefore, individuals who participated in a group trial gained more experience with the game compared to those who did not and were more habituated to the set-up.

Initially, I ran a series of models (1-3 for producing and 7-8 for scrounging) to determine if the variance attributed to the habituation effects could be explained by the random effects (Group ID and Trial ID). However, since the variation showed minimal change across the models, it was more practical to retain all fixed effects. While understanding habituation effects was not the primary focus of this study, as the main interest lay in the count data of

producing/scrounging visits, it is noteworthy that the number of visits increased over the duration of the experiment, whereas Hb, body mass, and wing loading all decreased. Different individuals and groups all habituated at different rates and because of this the habituation and the experimental setup had a large impact on the results. Individuals that had group trials for example, had more habituation time and learned the producer-scrounger game better, leading to an increase in the number of visits over time. Longer habituation and training could have accounted for this variation in the number of visits, but it would have been impractical given the timeframe and ethical concerns of keeping wild birds longer than strictly necessary. This discrepancy invites further exploration into the potential effects of habituation on the physiology of the birds, which could yield fascinating insights.

5. Conclusions:

This thesis explores the physiology and morphology of house sparrows to assess their impact on social foraging tactics within the producer/scrounger model framework. Both the Hb concentrations and the body masses of the birds significantly decreased over time with some notable sex differences; females had lower initial Hb while males showed a greater overall decline, and both males and females had similar mass and lost it in a similar manner. This change in mass affected the wing loading of the individuals as well, with females experiencing a greater change since they were shown to have considerably smaller wings with less area than the males. There were several concerns with the repeatability and therefore the consistency in the wing area measurements which warrants further exploration of improved methodologies. Future studies could continue to refine these methods and potentially develop a method to simply calculate the wing area using its length. It would be interesting to see the impact of wing loading on behavior both in sparrows and potentially in other species that rely more on flight.

The relationship analysis between Hb and body mass throughout the experimental period indicated that initial body mass significantly predicted subsequent weight changes. While the correlations between changes in Hb and body mass were not statistically significant, the positive correlation between mass and wing area suggests that larger birds generally have larger wing areas, endorsing the potential use of wing loading as a morphological indicator. However, no significant relationships were found between wing loading and Hb in the tested models. One could speculate that this lack of a significant relationship may be due to unmeasured environmental or genetic factors that independently affect these variables, or perhaps the current study's sample size was insufficient to detect more subtle effects despite having 2000+ observations for 140 individuals. Additionally, the dynamic and potentially multifaceted nature of these physiological traits could be influenced by a variety of factors not fully captured in this study, such as micro-climatic conditions, diet variations, or even social stress, which were not controlled for or measured.

Finally, when comparing wing loading and Hb to the number of producer scrounger visits, we saw no significant effects. According to this study, the role that Hb and wing loading play on the predictive power of foraging strategy choice is minimal, so we cannot make any assumptions based on these parameters. However, it would be interesting to look at other aspects of behavior, perhaps some broad and some specific, to see the impact of

physiological factors. Moving forward, it would be fascinating to compare the dominance data from previous years' work with the sparrow project to see if Hb and/or wing loading correlate with dominance. Then we could see how the interaction between dominance, Hb, wing loading, and sex could potentially influence foraging behavior.

Overall, this research sets the stage for future studies aimed at refining methodologies and broadening the scope beyond avian species to enhance the integration of physiological and behavioral ecology. Ongoing tracking of Hb and body mass, alongside the investigation of how various experimental manipulations impact these traits, will further explore the role of physiological changes in survival, reproduction, and longevity, contributing significantly to the field of wildlife research. Potential avenues for study could involve looking at how multivariate traits evolve and better understanding pace of life syndromes.

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7. Appendices:

7.1 Additional Figures

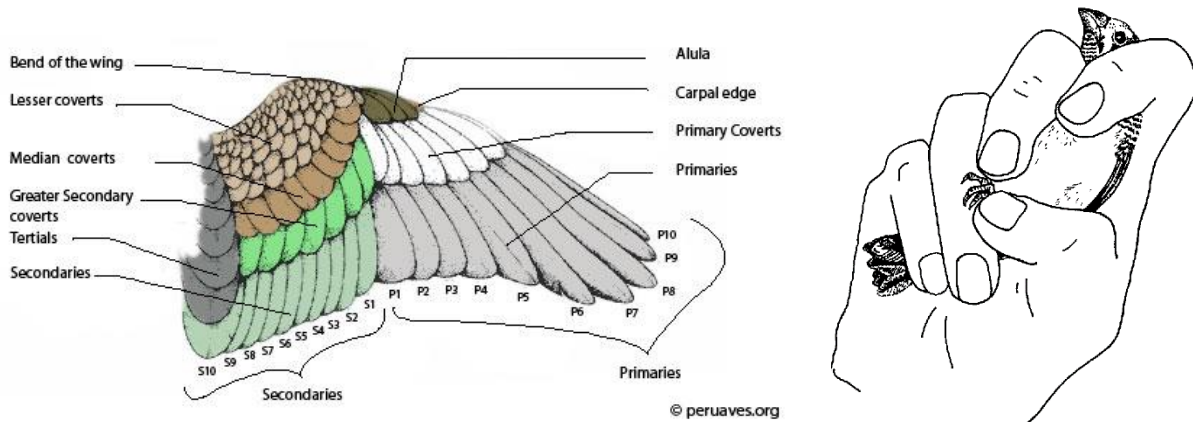


Figure 7.1: The structure of a bird's wing including the numbering of the feathers.

Figure 7.2: The 'ringer's grip' Hold the bird with the neck between the ring and middle fingers. Use the ring and pinky fingers to hold the legs at the tibiotarsal joint.

a)



b)



Figure 7.3: Top-down view of the a) extended vs. b) relaxed wing position of the left wing. The body of the bird was held as closely as possible to the edge of the grid in order to get a scope of the full area. In the extended position a), the 10th primary feather was extended to approximately the same point and then promptly after releasing the feather, another photo was taken of the relaxed position b).

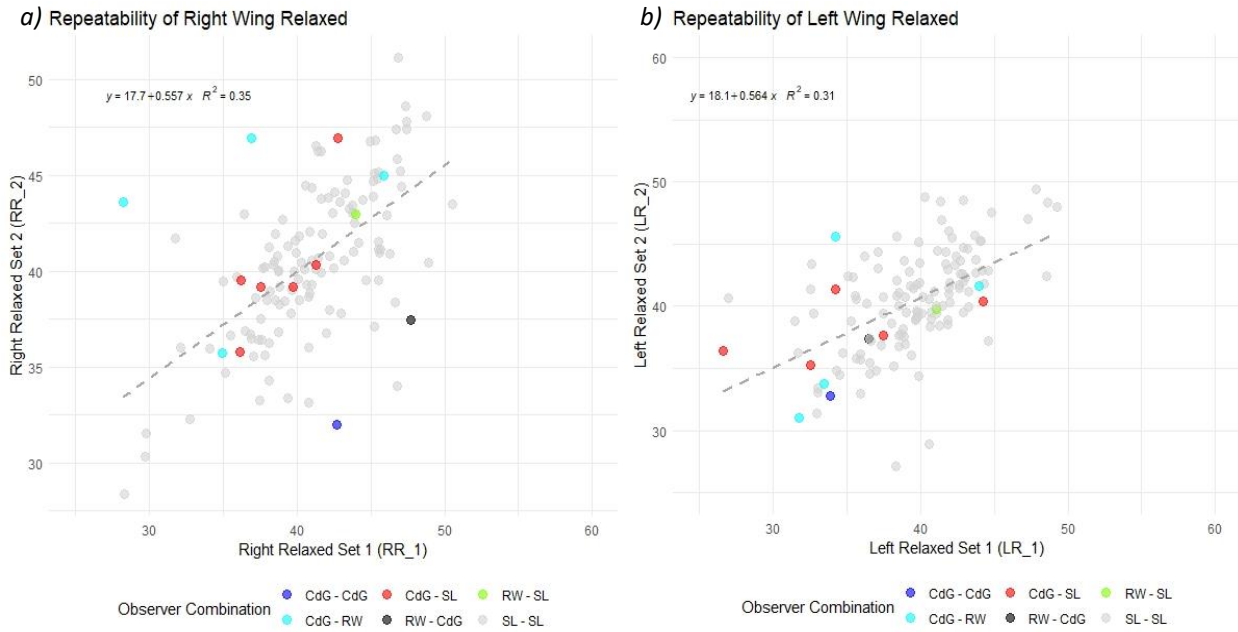


Figure 7.4: Comparison between the first left relaxed wing photos vs. the second measured in cm^2 . Colored points indicate when the observations between the first and second sets were made by different observers. b) The comparison between the first right relaxed wing photos vs. the second set, measured in cm^2 .

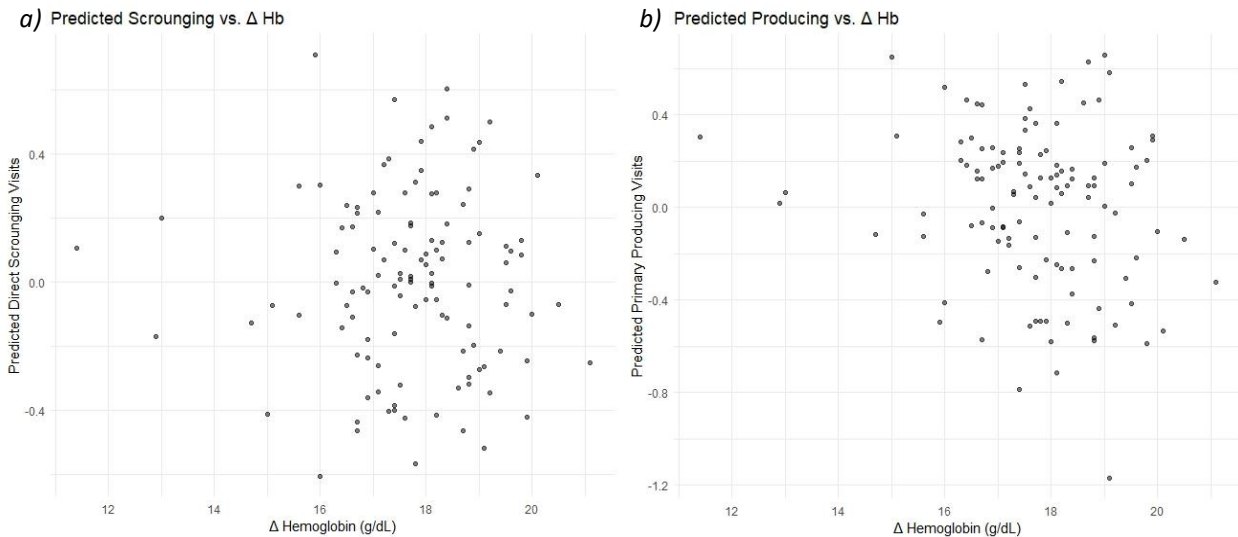


Figure 7.5: Δ Hb concentrations in g/dL on the x plotted against the BLUPs associated with the random effects associated with individual differences (Ring Number), in the number of predicted visits. a) predicted primary producing visits based on individual effects. b) predicted number of direct scrounging visits based on the change in Hb over the duration of the study.

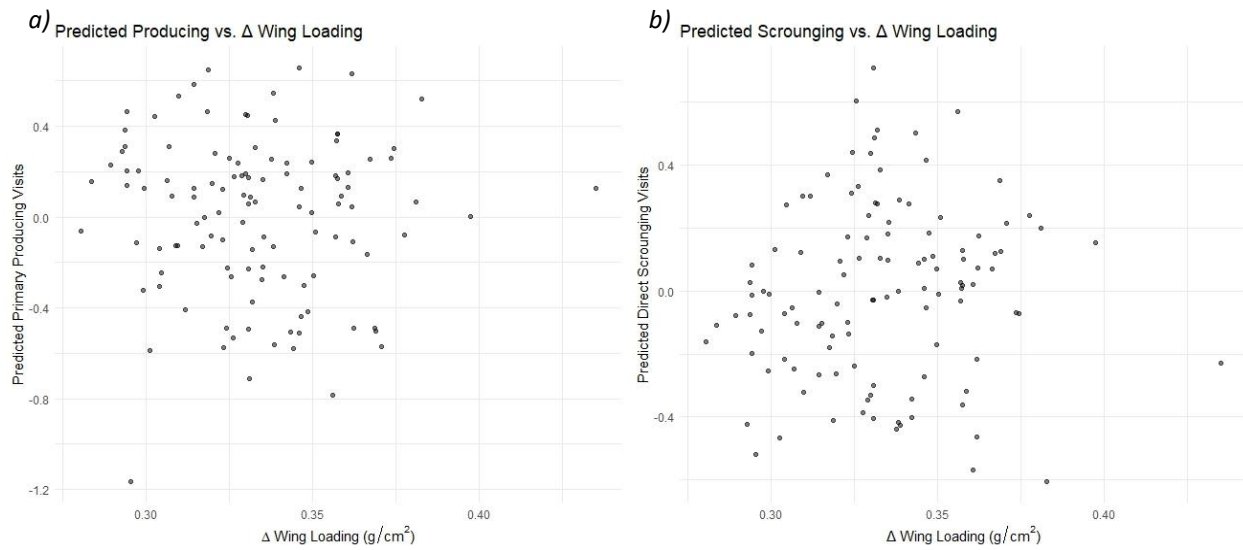


Figure 7.6: Δ wing loading (WL) in g/cm^2 on the x plotted against the BLUPs associated with the random effects associated with individual differences (Ring Number), in the number of predicted visits. a) predicted primary producing visits based on individual effects. b) predicted number of direct scrounging visits based on the change WL over the duration of the study.

Comparative Analysis of Hemoglobin and Wing Loading on Visits

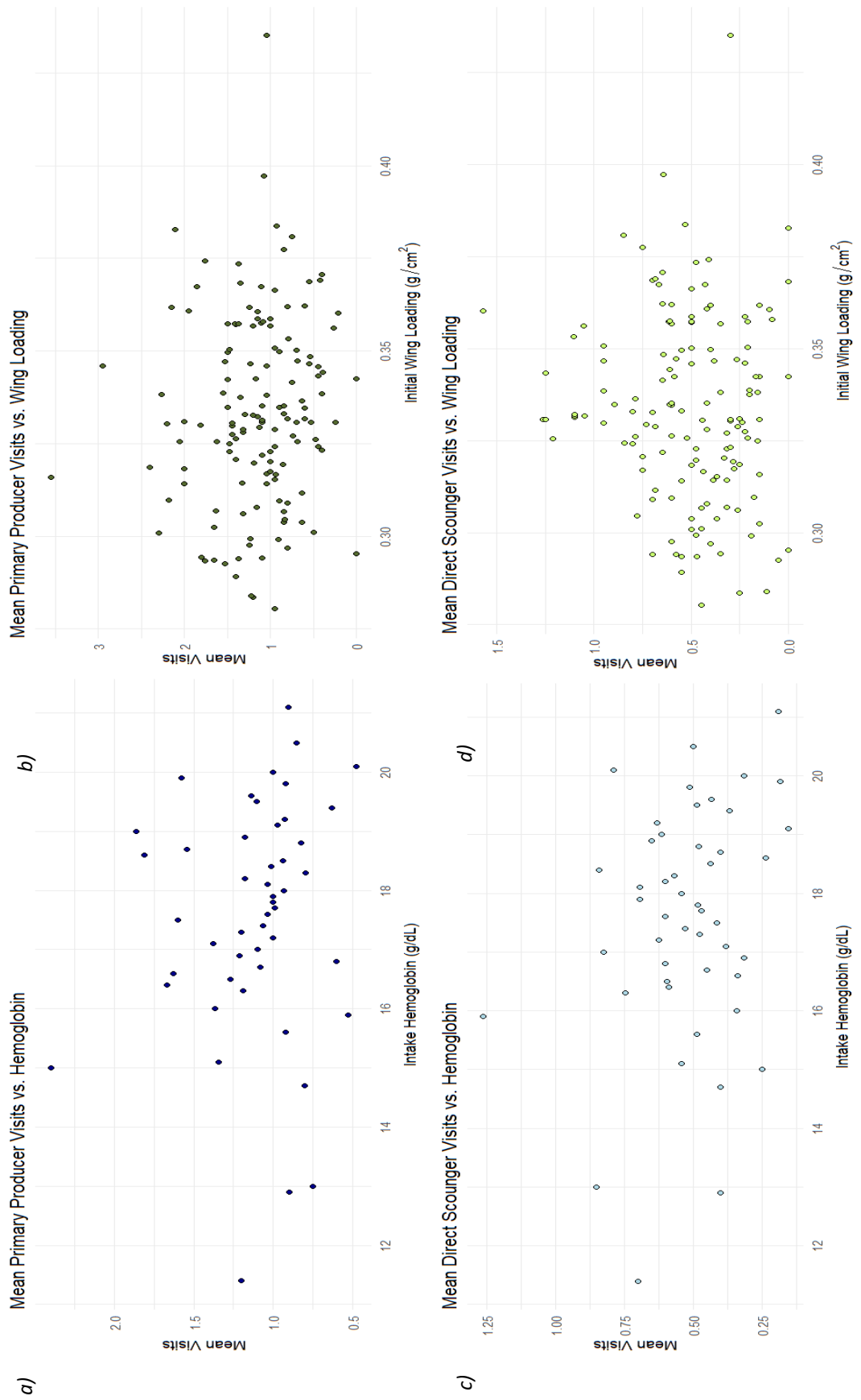


Figure 7.7: The mean number of either primary producing visits plotted against a) intake Hb or b) initial wing loading, or the direct scouring visits plotted against the c) intake Hb or d) wing loading.

7.2 Additional Tables

Bayesian Output for Random Effects Only

	<i>Producing (Model 1)</i>				<i>Scrounging (Model 6)</i>			
	Estimate	Error	<i>l-95% CI</i>	<i>u-95% CI</i>	Estimate	Error	<i>l-95% CI</i>	<i>u-95% CI</i>
Random Effects								
Trial ID	0.05	0.03	0.00	0.12	0.30	0.07	0.15	0.41
Ring Nr	0.43	0.04	0.37	0.51	0.47	0.05	0.38	0.57
Group ID	0.06	0.05	0.00	0.17	0.19	0.09	0.02	0.36

Table 7.1: Bayesian model output of just the effect of the random effects (trial ID, ring number, and group ID) on primary producing visits and direct scrounging visits.

Sex Differences Across Variables

Variable	Type	<i>t</i>	<i>df</i>	<i>p-value</i>	<i>Lower CI</i>	<i>Upper CI</i>	<i>Mean (F)</i>	<i>Mean (M)</i>
Hb (g/dL)	<i>Intake</i>	-3.929	111.42	< 0.001	-1.529	-0.504	17.124	18.140
	<i>Final</i>	0.680	132.99	0.498	-0.473	0.969	17.075	16.826
	Δ	3.876	117.47	< 0.001	0.720	2.225	0.057	-1.415
Body Mass (g)	<i>Intake</i>	-0.885	134.93	0.378	-0.999	0.382	31.319	31.639
	<i>Final</i>	-2.188	135.81	0.030	-1.007	-0.051	28.011	28.540
	Δ	-1.252	129.13	0.213	-0.858	0.193	-3.322	-2.989
Tarsus (mm)	<i>Left</i>	-1.822	128.03	0.071	-0.621	0.026	19.295	19.592
	<i>Right</i>	-1.767	128.72	0.071	-0.616	0.035	19.288	19.579
Wing Length (mm)	<i>Left</i>	-9.106	137.40	< 0.001	-2.926	-1.882	77.515	79.919
	<i>Right</i>	-9.773	137.88	< 0.001	-2.968	-1.969	77.356	79.824
Wing Area (cm ²)	<i>Both</i>	-4.834	130.87	< 0.001	-6.043	-2.533	92.339	96.629
Wing Loading (g/cm ²)	<i>Intake</i>	2.907	134.91	0.004	0.004	0.021	0.339	0.328
	<i>Final</i>	2.347	132.66	0.020	0.001	0.014	0.304	0.296
	Δ	-1.701	126.02	0.092	-0.011	0.001	-0.036	-0.031

Table 7.2: Sex differences across variables. The differences were measured for the initial and final measurements as well as the difference between the two for Hb, Body Mass, and wing loading. The left and right measurements for tarsus and wing length were analyzed separately while the sex difference was measured for only the combined wing area of both wings across individuals.

Fixed Effects	Left vs. Right			Right vs. Right			Left vs. Left				
	E1	R1		E2	R2		E	R			
Intercept	46.626 ± 0.331 (p < 0.001)	39.261 ± 0.375 (p < 0.001)		47.183 ± 0.299 (p < 0.001)	40.268 ± 0.358 (p < 0.001)		48.051 ± 0.320 (p < 0.001)	40.374 ± 0.375 (p < 0.001)		46.626 ± 0.306 (p < 0.001)	39.235 ± 0.356 (p < 0.001)
RE_1 ± SE	1.425 ± 0.361 (p < 0.001)										
RR_1 ± SE		1.334 ± 0.382 (p < 0.001)									
RE_2 ± SE				0.360 ± 0.333 (p < 0.001)			-0.535 ± 0.276 (p = 0.055)				
RR_2 ± SE					0.072 ± 0.371 (p = 0.846)			-0.315 ± 0.336 (p = 0.351)			
LE_2 ± SE									0.492 ± 0.253 (p = 0.053)		
LR_2 ± SE										0.983 ± 0.337 (p = 0.004)	
Random Effects											
Ring Number	6.158	9.323		4.588	8.026		9.065	11.815		8.689	9.779
Residual	9.066	9.973		7.425	9.284		5.179	7.589		4.298	7.636
Repeatability	0.392 (p < 0.001)	0.434 (p < 0.001)		0.387 (p < 0.001)	0.458 (p = 1.728)		0.625 (p < 0.001)	0.608 (p < 0.001)		0.654 (p < 0.001)	0.512 (p < 0.001)

Table 7.3: Outputs from repeatability models for wing area measurements were analyzed. The left wings were compared to the right wings in two sets (E1 and R1 for set one; E2 and R2 for set two). Additionally, each wing was compared against itself (E and R indicating extended or relaxed for right or left wings). Estimates, standard errors, and p-values are provided for fixed effects, while variances are provided for random effects. Repeatability for each model and its p-value are also included.

Body Mass and Hemoglobin

	Estimate	l-95% CI	u-95% CI	Correlation	l-95% CI	u-95% CI
<i>Relationships</i>						
Initial Hb x Initial Mass	17.65	17.38	17.92	-0.12	-1.29	0.05
Δ Hb x Δ Mass	-0.71	-1.11	-0.30	-0.08	-0.25	0.11
Δ Mass x Initial Mass	-3.14	-3.40	-2.88	-0.69	-0.77	-0.59
Δ Hb x Initial Hb	31.43	31.10	31.78	-0.43	-0.57	-0.28
	17.71	17.45	17.97			

Table 7.4: Outputs from the statistical models: initial mass and initial Hb, Δ Hb and initial Hb, Δ mass and Δ Hb, and Δ mass and initial mass. Only the relationships between initial mass and Δ mass and initial Hb and Δ Hb showed any significance.

Hb Concentration and Wing Loading

	Estimate	l-95% CI	u-95% CI	Correlation	l-95% CI	u-95% CI
<i>Relationships</i>						
Initial Wing Loading x Initial Hb	0.33	0.33	0.34	-0.15	-0.31	0.03
Initial Wing Loading x Δ Hb	17.69	17.43	17.95	0.06	-0.12	-0.24
Δ Wing Loading x Δ Hb	-0.72	-1.13	-0.30	-0.09	-0.27	0.09
	-0.03	-0.04	-0.03			
	-0.71	-1.12	-0.31			

Table 7.5: Outputs from the statistical models: initial wing loading and initial Hb, initial wing loading and Δ Hb, and Δ wing loading and Δ Hb. None of these models had statistical significance. Shown here are the estimates, the correlation coefficients, and the confidence intervals for each.

Simple Bayesian Models (Producing)

	Intake Hb/WL (Model 7)				Δ Hb/WL (Model 8)			
	Estimate	Error	<i>l</i> -95% CI	<i>u</i> -95% CI	Estimate	Error	<i>l</i> -95% CI	<i>u</i> -95% CI
Regression Coefficients								
Intercept	-0.84	0.10	-1.04	-0.66	-0.95	0.13	-1.22	-0.70
Sex	0.11	0.11	-0.10	0.33	0.15	0.11	-0.06	0.36
Intake/ Δ Hb	-0.03	0.04	-0.11	0.04	0.05	0.04	-0.03	0.13
Initial/ Δ WL	2.90	2.11	-1.25	7.10	-3.02	2.47	-7.87	1.76
Initial/ Δ Hb x Initial/ Δ WL	1.32	1.24	-1.08	3.71	0.26	0.95	-1.59	2.14
Random Effects								
Group ID	0.23	0.09	0.05	0.40	0.30	0.07	0.13	0.42
Ring Nr	0.43	0.05	0.33	0.54	0.39	0.05	0.29	0.50
Trial ID	0.23	0.09	0.05	0.40	0.26	0.08	0.11	0.42

Table 7.6: Results from both the producer models, on the left, initial/intake values and on the right, the Δ values. Both models were fit to Poisson function in a Bayesian model with the data mean centered and included Trial ID, Ring number and Group ID as random effects. The fixed effects for both models were Sex, Hb upon intake (Intake Hb)/ Δ Hb, Initial WL/ Δ WL and the interaction between Hb and wing loading (Initial/ Δ Hb x Initial/ Δ WL).

Simple Bayesian Models (Scrounging)

	Intake Hb/WL (Model 2)				Δ Hb/WL (Model 3)			
	Estimate	Error	<i>l</i> -95% CI	<i>u</i> -95% CI	Estimate	Error	<i>l</i> -95% CI	<i>u</i> -95% CI
Regression Coefficients								
Intercept	0.03	0.07	-0.11	0.17	0.16	0.11	-0.05	0.36
Sex	0.0	0.10	-0.20	0.19	-0.13	0.09	-0.32	0.05
Intake/ Δ Hb	-0.04	0.03	-0.10	0.02	-0.03	0.03	-0.10	0.04
Initial/ Δ WL	-1.39	1.78	-4.92	2.16	2.41	2.16	-1.87	6.75
Initial/ Δ Hb x Initial/ Δ WL	0.82	1.09	-1.34	2.97	0.38	0.84	-1.27	2.05
Random Effects								
Group ID	0.05	0.03	0.00	0.12	0.05	0.03	0.00	0.13
Ring Nr	0.43	0.04	0.36	0.51	0.41	0.04	0.34	0.49
Trial ID	0.08	0.06	0.00	0.21	0.08	0.06	0.00	0.20

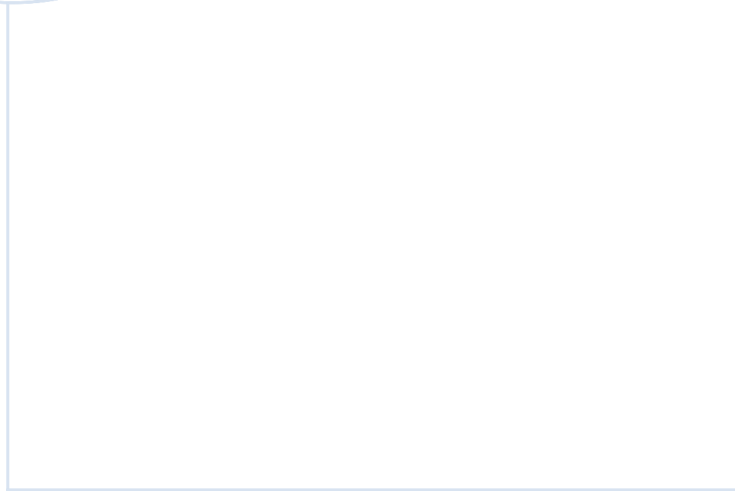
Table 7.7: Results from both the scrounger models, on the left, initial/intake values and on the right, the Δ values. Both models were fit to Poisson function in a Bayesian model with the data mean centered and included Trial ID, Ring number and Group ID as random effects. The fixed effects for both models were Sex, Hb upon intake (Intake Hb)/ Δ Hb, Initial WL/ Δ WL and the interaction between Hb and wing loading (Initial/ Δ Hb x Initial/ Δ WL).

Package	Citation
<i>lme4</i>	Douglas Bates, Martin Maechler, Ben Bolker, Steve Walker (2015). Fitting Linear Mixed-Effects Models Using lme4. <i>Journal of Statistical Software</i> , 67(1), 1-48. doi:10.18637/jss.v067.i01.
<i>Dplyr</i>	Wickham H, François R, Henry L, Müller K, Vaughan D (2023). <i>_dplyr: A Grammar of Data Manipulation_</i> . R package version 1.1.2, < https://CRAN.R-project.org/package=dplyr >.
<i>emmeans</i>	Lenth R (2023). <i>_emmeans: Estimated Marginal Means, aka Least-Squares Means_</i> . R package version 1.8.9, < https://CRAN.R-project.org/package=emmeans >.
<i>lmerTest</i>	Kuznetsova A, Brockhoff PB, Christensen RHB (2017). "lmerTest Package: Tests in Linear Mixed Effects Models." <i>_Journal of Statistical Software_</i> , *82*(13), 1-26. doi:10.18637/jss.v082.i13 < https://doi.org/10.18637/jss.v082.i13 >.
<i>rptR</i>	Stoffel, M. A., Nakagawa, S. and Schielzeth, H. (2017), rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. <i>Methods Ecol Evol</i> , 8: 1639-1644. doi:10.1111/2041-210X.12797
<i>tidyr</i>	Wickham H, Vaughan D, Girlich M (2023). <i>_tidyr: Tidy Messy Data_</i> . R package version 1.3.0, < https://CRAN.R-project.org/package=tidyr >.
<i>ggplot2</i>	H. Wickham. <i>ggplot2: Elegant Graphics for Data Analysis</i> . Springer-Verlag New York, 2016.
<i>ggpmisc</i>	Aphalo P (2023). <i>_ggpmisc: Miscellaneous Extensions to 'ggplot2'_</i> . R package version 0.5.5, < https://CRAN.R-project.org/package=ggpmisc >.
<i>brms</i>	Paul-Christian Bürkner (2017). brms: An R Package for Bayesian Multilevel Models Using Stan. <i>Journal of Statistical Software</i> , 80(1), 1-28. doi:10.18637/jss.v080.i01
<i>bayesplot</i>	Gabry J, Mahr T (2024). "bayesplot: Plotting for Bayesian Models." R package version 1.11.1, < https://mc-stan.org/bayesplot/ >.
<i>rstan</i>	Stan Development Team (2024). RStan: the R interface to Stan. R package version 2.32.6. https://mc-stan.org/ .
<i>glmmTMB</i>	Mollie E. Brooks, Kasper Kristensen, Koen J. van Benthem, Arni Magnusson, Casper W. Berg, Anders Nielsen, Hans J. Skaug, Martin Maechler and Benjamin M. Bolker (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. <i>The R Journal</i> , 9(2), 378-400. doi: 10.32614/RJ-2017-066.
<i>gridExtra</i>	Auguie B (2017). <i>_gridExtra: Miscellaneous Functions for "Grid" Graphics_</i> . R package version 2.3, < https://CRAN.R-project.org/package=gridExtra >.
<i>car</i>	Fox J, Weisberg S (2019). <i>_An R Companion to Applied Regression_</i> , Third edition. Sage, Thousand Oaks CA. < https://socialsciences.mcmaster.ca/jfox/Books/Companion/ >.
<i>reshape2</i>	Hadley Wickham (2007). Reshaping Data with the reshape Package. <i>Journal of Statistical Software</i> , 21(12), 1-20. URL http://www.jstatsoft.org/v21/i12/ .
<i>patchwork</i>	Pedersen T (2024). <i>_patchwork: The Composer of Plots_</i> . R package version 1.2.0, < https://CRAN.R-project.org/package=patchwork >.
<i>ggeffects</i>	Lüdtke D (2018). "ggeffects: Tidy Data Frames of Marginal Effects from Regression Models." <i>_Journal of Open Source Software_</i> , *3*(26), 772. doi:10.21105/joss.00772 < https://doi.org/10.21105/joss.00772 >.

Table 7.8: List of R packages used in statistical analyses.

7.3 Additional Clarifications

The Drabkin Method: The most common and most effective method of measuring hemoglobin concentration, The Drabkin method ("SPECTROPHOTOMETRIC STUDIES | Elsevier Enhanced Reader," n.d.), which uses spectrophotometry and a cyanide derivative (Drabkin's reagent) to hemolyze the erythrocytes and oxidize the hemoglobin derivatives to produce methemoglobin. The methemoglobin and cyanide form a stable cyanmethemoglobin, the absorbance of which can be used to calculate the Hb ("Calibration of the HemoCue Point-of-Care Analyser for Determining Haemoglobin Concentration in a Lizard and a Fish | Conservation Physiology | Oxford Academic," n.d.). This method has, however, proven difficult in field scenarios as it tends to be laborious and would require the transport of cyanide into the field.



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