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Linking variation in personality and behavioural syndromes to social foraging and producer-scrounger effects in house sparrows (*Passer domesticus*)

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MSc in Biology

Submission date: May 2016

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Acknowledgment

First I would like to thank my parents, your unconditional and endless love has helped me through the ups and downs I've experienced during this thesis. You have always supported me, now more than ever, and encouraged me to follow my dreams. I would not have been the person I am today, and I certainly would not have been able to finish this thesis without you. A special thank you to my supervisor, Jonathan Wright, for all the help and guidance. Your dedication to your work and to your many master students has been an inspiration and a source of motivation during these two years. You have introduced me to the exciting field of behavioural ecology and showed me the interesting life of a researcher. I owe my learning outcome and personal development to you. I would also like to thank all the guys in the sparrow group at CBD for letting me be part of their fascinating project, and for all their help during the fieldwork. Thank you Peter Sjolte Ranke and Yimen Araya for always taking the time to help me with my statistics, and Bernt Rønning and Thor Harald Ringsby for reading and commenting on my thesis. Finally, I would like to thank Mette Finnøen and John Hammerås for helping me and standing by my side throughout this incredible journey - it wouldn't have been the same without you. And to all my fellow students, thank you for the good times we have shared during our study in Trondheim.

Abstract

Consistent behavioural differences between individuals across time and situations are referred to as animal personality. Associated with this are ‘behavioural syndromes’, which are suites of correlated behaviours across individuals. When foraging in social groups, individuals can use a ‘producer’ tactic, which involves searching for food independently, or a ‘scrounger’ tactic, which involves joining others who have already discovered food. In this study, wild populations of house sparrows (*Passer domesticus*) were tested in captive communal behavioural assays, trying to link variation in personality and behavioural syndromes to social foraging and producer-scrounger tactics in 8 social flocks. Individual variation and the covariation between the measured behavioural variables was quantified using univariate tests and structural equation modelling (SEM), respectively. There were surprisingly few sex differences in behaviour in these flocks. Nevertheless, clusters of covariance around individual differences in both ‘activity’ (coming and going from the feeder in groups) and ‘joining’ behaviour (rates of scrounging and aggression at the feeder) provided the best model for the individual variation in different behaviours in these sparrow flocks. However, I found little individual consistency in the behavioural traits tested, indicating that there are no personalities, and thus only plasticity, in social foraging behaviours in these house sparrows. The findings here suggests that the birds were acting as a group of almost interchangeable individuals, and that the patterns of social foraging recorded were not driven by individual-specific producer-scrounger tactics or a wider behavioural syndrome.

Sammendrag

I atferdsbiologien omtales ‘animal personality’ som konsekvente forskjeller i adferd mellom individer over tid og situasjoner. I tilknytning til dette begrepet finner vi atferdssyndromer. Dette er korrelert atferd på tvers av individer. Når næringssøk foregår i sosiale grupper kan individer velge en ‘producer’ taktikk, som innebærer å lete etter mat uavhengig av andre, eller en ‘scrounger’ taktikk, hvor individet følger andre som allerede har oppdaget mat. I denne studien ble ville bestander av gråspurv (*Passer domesticus*) i fangenskap testet i en felles atferdsanalyse, hvor vi prøvde å knytte variasjon i ‘personlighet’ og atferdssyndromer til sosialt næringssøk og producer-scrounger taktikker. Dette ble utført i 8 sosiale flokker. Individuell variasjon og kovariansen mellom de målte atferdsvariablene ble undersøkt ved hjelp av henholdsvis univariate tester og structural equation modelling (SEM). Det var overraskende få kjønnsforskjeller i atferd hos disse flokkene. Den beste modellen for den individuelle variasjonen i forskjellig atferd hos disse spurveflokkene viste seg å være klynger av kovarians rundt individuelle forskjeller i både ‘aktivitet’ (komme og gå fra feederen i grupper) og ‘deltagende’ atferd (rater av scrounging og aggresjon ved feederen). Vi fant imidlertid liten individuell konsistens i de atferdstrekkene som ble testet, noe som indikerer at det ikke er noen ‘personlighet’, og dermed kun plastisitet, i sosial næringssøksatferd hos disse gråspurvane. Funnene her tyder på at de registrerte mønstrene i sosialt næringssøk ikke var drevet av individuell-spesifikk producer-scrounger taktikker eller et mer omfattende atferdssyndrom.

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Introduction

In almost all animal species studied so far, individuals have been found to differ consistently in their average level of behaviour. Consistent behavioural differences between individuals across time and situations are commonly referred to as *animal personality* (Reale et al. 2007; Dingemanse et al. 2010a; Reale et al. 2010). An implication of this is that each individual does not express the entire range of a particular behavioural trait present in the population, which leads to individual variation in behaviour both within and between populations and species (Sih et al. 2004; Dingemanse et al. 2010a; Reale et al. 2010). An important point is that animal personalities are a feature of populations, not individuals, which only have behavioural types within personalities. The interesting thing about animal personalities is that we do not expect so much individual variation in behaviour, especially if there has been selection for some optimum level of the behaviour as predicted and demonstrated in much of behavioural ecology (Krebs and Davies 1987).

Associated with the phenomenon of animal personalities are suites of correlated behaviours across individuals, termed *behavioural syndromes*, that have also been identified in an increasing number of cases (Sih et al. 2004; Reale et al. 2007; Dingemanse and Dochtermann 2014). Dingemanse and Dochtermann (2014) define behavioural syndromes as when «an individual's average behaviour in one context is correlated with its average behaviour in another context». These correlated behaviours reflect between-individual consistency in behaviour across different (physical and/or social) environments (Sih et al. 2004). A good example of this is the aggressiveness-boldness syndrome (Garamszegi et al. 2012), where some individuals are more aggressive than others, but also bolder over a range of situations such as during predation threat. Activity, exploratory behaviour, aggressiveness and boldness are, for example, positively correlated across individuals in some populations of three-spined sticklebacks (*Gasterosteus aculeatus*) (Bell 2005; Dingemanse et al. 2007). Also, in a study on male great tits (*Parus major*), Verbeek et al. (1996) found that the more aggressive individuals tended to be more explorative towards novel objects and environments than the less aggressive ones. Based on what is theoretically expected from optimality theory in behavioural ecology, it is surprising to find behavioural syndromes. Adaptive optimality or game theory emphasizes selection towards an optimum mean value separately for each behaviour in isolation (i.e. the evolutionary stable strategy or ESS). This implies that behavioural syndromes, in the same way as animal personalities, are unexpected, as each

behavioural trait should evolve to its own optimum independently of other behaviours (Krebs and Davies 1987).

When living in social groups, the behaviour of one individual will in many situations affect the behaviour of others. This means that an individual and its environment are not the only factors affecting the consequences of the individual's action, it also depends on the behaviour of others (Maynard Smith 1983). This is especially seen in social foraging, where group members vary in their contribution to searching and the discovery of new sources of food. Barnard and Sibly (1981) presented a model of animal interaction, *the producer-scrounger game*, when trying to explain the exploitation behaviour where some individuals use the resources found by other individuals. The tactic of the 'producer' is to search for the food independently, while the 'scrounger' joins others who have already discovered food (Barnard and Sibly 1981). The scroungers use public information and may take a disproportionately larger share of the food compared to their food-searching efforts (Ranta et al. 1996). The producer-scrounger game involves negative frequency dependence, where scroungers do poorly when in the majority, but do better when rare (Vickery et al. 1991). A population may consist of a mix of pure producers and pure scroungers, or it may include individuals playing a mixed strategy of producer some of the time and scrounger the rest of the time (Vickery et al. 1991; Belmaker et al. 2012). Either way, the two strategies are expected to coexist in a stable equilibrium, making it evolutionarily stable (Vickery et al. 1991; Katsnelson et al. 2008; Tóth et al. 2009).

House sparrows (*Passer domesticus*) are one of the best-known producer-scrounger systems and therefore a typical study species for these studies (Barnard and Sibly 1981; Liker and Barta 2002; Tóth et al. 2009). Studies have shown that individuals of numerous other species use these two strategies flexibly, switching between producing and scrounging (Lendvai et al. 2004). This indicates that the producer-scrounger game might «involve a combination of genetic components and a process in which individuals use environmental cues or personal experience to choose among strategies» (Belmaker et al. 2012). There is still an uncertainty whether the producer-scrounger game is under genetic control or not, due to the lack of direct investigations of the genetic basis of the producer-scrounger tendencies (Katsnelson et al. 2008). However, levels of producing and scrounging have been shown to differ in apparently adaptive ways according to group size (i.e. the potential number of producers to scrounge from, Vickery et al. 1991; Coolen 2002), predation risk (i.e. scrounging and anti-predator

vigilance can be done together, Ranta et al. 1998; Barta et al. 2004; Mathot and Giraldeau 2008), and patchiness of resources (i.e. the profitability of searching, Coolen et al 2001; Beauchamp and Giraldeau 1997). Further, Liker and Barta (2002) found that the frequency of scrounging increased gradually with increasing dominance rank. Lendvai et al. (2004) showed in another study that individuals with lowered energy reserves increased their use of scrounging during the first feed of the day. Tóth et al. (2009) used kin selection theory to predict the frequency of scrounging from relatives, and found that the birds used aggressive joining less often and obtained less food by scrounging from their close kin than from unrelated flockmates.

Innovation, or the tendency to invent new behaviours or use existing behaviours in new contexts to solve novel problems, is an important aspect in behavioural flexibility (Reader and Laland 2003). A problem with many behavioural studies is that they do not separate, either conceptually or empirically, between animal personalities and innovation. In addition, since most personality studies are necessarily carried out in novel captive environments they probably include a lot of individual variation in response to coping with artificiality, which might be quite different from personalities expressed in natural context. Given the links between animal personality and innovation, the question now is whether individual differences in things like exploration and neophilia are linked to the types of individual propensities to produce versus scrounge, especially in the types of captive artificial feeder tasks required to experimentally explore producer-scrounger tactics. Producers in artificial feeders could be bold innovators, but little is known about the consistent individual variation in producer-scrounger behaviour (e.g. the propensity to switch between tactics, or the social switch point), or individual variation in innovation within and between populations, because no studies on these topics have provided links to recent work on animal personalities.

In this study, I will link variation in personality and behavioural syndromes to social foraging and producer-scrounger effects in house sparrows, where I predict that there will be consistent individual differences in behaviour when testing individuals at a social feeder (in captivity), including differences in boldness in approaching the feeder first, aggression towards others, number of visits to the feeder and time spent at the feeder. Specifically, I expect certain individuals to act more as producers in finding the clumps of food within the feeder, whilst others should act more like scroungers in joining successful producers when they find food. The null hypothesis is that there will be no consistent individual difference in the levels of

expression of any behavioural traits between individuals and that these traits will not be correlated across contexts at the social feeder.

Method

Study Area

Data were collected on the islands Leka, Lauvøya and Vikna located on the coast of mid-Norway between 02.02.2015 and 09.03.2015. Each island contains a number of spatially distributed sub-populations that live closely associated with farms, which constitutes a meta-population structure.

Study Species

Passerine birds have been used as model species in many behavioural and evolutionary studies, because such species are easy to observe in captivity and social groups, and are individually distinguishable when marked with colored leg-rings (Anderson 2006). The house sparrow is a small, passerine bird that has proved to be an excellent model species for studying evolutionary and demographic questions (Anderson 2006). With a preference for feeding in flocks, breeding in colonies and roosting communally, the sparrow is a very social species, and also an opportunistic and foraging generalist often seen on the ground searching for seeds, etc. (Anderson 2006). This is one of the reasons why the house sparrow is an ideal model system for producer-scrounger studies. Sparrows are closely associated with human settlements, and in Norway you find them particularly on dairy farms in the countryside (Ringsby et al. 2006). Hence, it is a classic example of an invasive bird species, which has spread worldwide due to its behavioural flexibility and innovation in artificial human environments (Anderson 2006).

Behavioural Assays

As part of a wider project, all the individuals were captured using mist nets, and held in a sealed central barn, for a period of 10-14 days, on each island. The birds were marked with an individual, unique ring combination (consisting of one numbered metal ring and three colored plastic rings), and then measured and analyzed as part of the Centre for Biodiversity Dynamics' (CBD) long-term study. Some of the characters measured were: body mass, tarsus length, wing length, and beak length and depth. Furthermore, each individual's sex and age

was recorded, any difficulty in breathing (i.e. presence of lung parasites) was registered and a small blood sample (ca. 25 μ L) was collected by brachial venipuncture to obtain DNA.

During the sparrow's captive period in the central barn we conducted both individual behavioural assays and a communal feeder assay per flock from each farm. All birds that were used in the behavioural assays had previously spent an 8-hour period in a respiratory chamber for measuring basal metabolic rate (BMR), as a part of another study. The BMR measurements ended either at 23:00 the day of capture or at 08:00 the next morning. All birds then spent one full day communally as a flock with *ad libitum* access to food on a dummy communal feeder to habituate them to such feeders, before the food was taken away for the night prior to the behavioural assays the next day. Flocks were kept in separate aviaries within the barns, where the temperature was approximately 10-12°C (the normal temperature within cow sheds on dairy farms during winter). Temperatures in all aviaries were monitored. The behavioural assays started at 08:00 the next morning, and were only performed on birds that had been measured for BMR, because this ensured that individuals were in approximately similar body condition. However, changes in individual body mass, taken upon capture, before and after the BMR measurements and before and after the behavioural assay, were recorded in order to assess any within and between individual differences in state.

All birds were first tested in an individual behavioural assay, as part of another masters project (see master thesis by Mette Finnøen 2016), before testing their foraging behaviour communally. In the communal feeder assay I tested the social foraging behaviour in the presence of familiar conspecifics from the same farm that they were captured. The feeder was a 1.2m x 1.2m panel with 144 small recessed wells, equally distanced from each other, to hold three seeds each (sunflower kernels) and to create a clumped resource (see Fig. 1), based upon similar communal feeders used in previous producer-scrounger foraging studies on this species (Lendvai et al. 2004; Tóth et al. 2009). The feeder was surrounded by a cage with only one entrance, forcing the birds to enter at the same side. By filling only 60 of the 144 wells during the experimental trials, the birds always had to search within the feeder for food (i.e. the 'producer' option). The birds were video recorded from above and from the side of the entrance to identify the individuals by their ring combinations.

A maximum flock size of 16 birds was assayed at the communal feeder per day, due to constraints regarding the catching rate of birds and sample sizes in the BMR study, the number of individual assays and the size of the communal feeder.

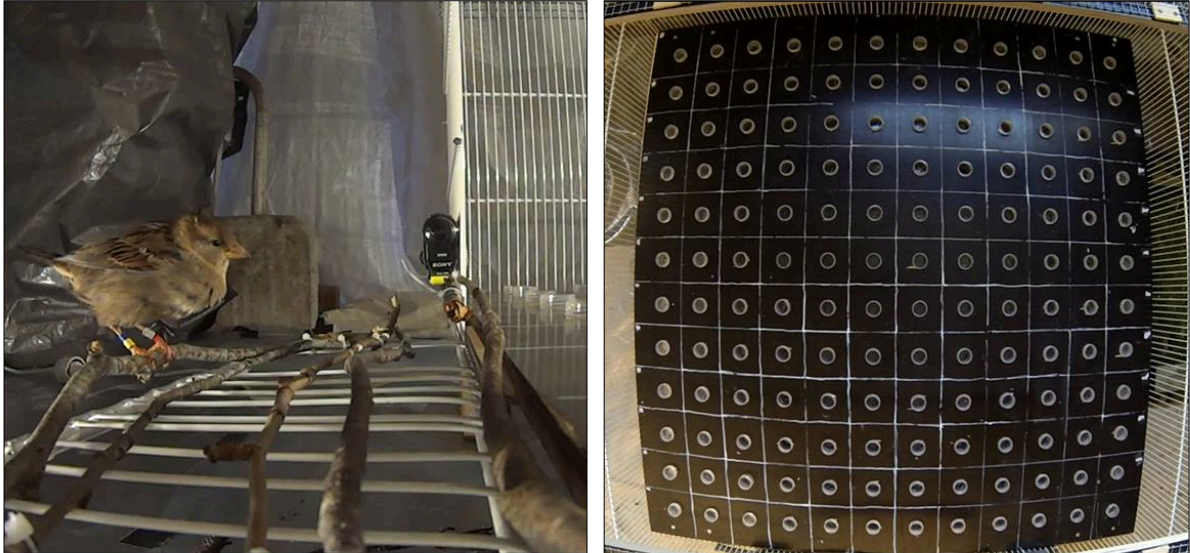


Figure 1. Feeder used for the communal assay. (a) Viewed from right entrance camera, and (b) from the camera above.

Subsets of 44 individuals from three different farms (Leknes at Leka, Sør Dahl at Lauvøya and Valøen at Vikna, see Table 1) were tested in the individual and communal assays a second time in order to measure repeatability in all of the behaviours being scored (see Bell et al. 2009; Dingemanse and Dochtermann 2013).

Video Analyses

The videos from the communal feeder assays were analyzed manually. Due to problems with the operation of some cameras, and therefore problems with identification of individuals from farms on Leka, only trials from Lauvøya and Vikna were used for the communal feeder analyses. Groups that didn't enter the feeder during the trial were also excluded. Therefore, only 8 flocks participated in the communal producer-scrounger trials, and three of these were from the larger single farm community on Lauvøya (Table 1).

Table 1. Date, island, flock and trial time used for the behavioural assays. * Marking repeat dates.

Date	Island	Flock name	Trial time (sec)
19.02.15	Lauvøya	Sørdahl (1)	2780
20.02.15	Lauvøya	Sørdahl (2)	3078
21.02.15	Lauvøya	Sørdahl (3)	4338
22.02.15 *	Lauvøya	Sørdahl (2)	1781
23.02.15	Lauvøya	Ovesen	3960
28.02.15	Vikna	Fjukstadstrand	3700
03.03.15	Vikna	Setneøya	7139
04.03.15	Vikna	Valøen	3736
05.03.15	Vikna	Krystad	4753
06.03.15 *	Vikna	Valøen	4187

The videos from the communal feeder entrance were used to identify individuals as they entered and left the feeder. The individual, unique ring combination, sex and time in and out of the feeder were recorded. Duration of stay and the number of times each individual entered the feeder was therefore known. The videos shot from the ceiling were then used to assess individual foraging by crosschecking the entrance time with the videos from the entrance. Each individual was followed continuously during each visit to the feeder, and the following was recorded: (i) the number of birds in the feeder when the individual entered; (ii) the number of birds in the feeder when the individual left; (iii) which wells the individual visited (only noted if there was a distinct movement of the head into the well); (iv) the number of individuals standing/feeding within one well distance of the focal well; (v) if the individual joined or got joined by other individuals at each well it visited; (vi) any aggressive interactions and their consequences; and (vii) how many seeds the individual ate (both in the well and around).

Statistical Analyses

The essential variables measured in the communal feeder setup involved time of first visit to the feeder, duration of individual visits to the feeder, number of wells visited in the feeder, the number of aggressive events, and the number of producing and scrounging events during the trial. Time for first visit and duration of stay, measured in seconds, were log-transformed to obtain normal distributions. The number of wells visited per second at the feeder was also

log-transformed. Due to the low number of aggressive- and scrounging events per individual these analyses were carried out with Poisson distributed errors. Sample sizes involved 8 flocks and 99 individuals, with varying numbers of visits to the feeder and feeding/aggressive events per individual over the 2hr trial. The statistical analyses were run on one dataset including the whole 2hr trial and one dataset stopping at the time when the food was thought to have run out (i.e. were no seeds were observed eaten, see Table 1). Since the foraging interactions were of interest and there weren't big differences between the two dataset, the results from the shorter dataset are presented here. For the results from the whole dataset see Appendix A.

The behavioural variables were tested using linear mixed-effects models, with individual and/or flock as random effects. Covariance between the different explanatory variables was avoided by checking beforehand using Pearson's correlation coefficients. Univariate ANCOVAs were carried out separately on the behavioural variables to explore any effects of sex, flock or body mass. The within-versus between-individual effects of covariance within the models were assessed using the mean-centering method described by Van de Pol and Wright (2009). Using this method, three different models were compared. In the first model only the original observed variable is used as a covariate, while in the second model this is represented by both the between- and the within-individual effect, to investigate their effect on the response variable. In the third, and last model, the original variable and the between-individual effect are used as explanatory variables to see whether the between- and within-individual effects are significantly different from each other. The within-versus between-flocks effects were also assessed using the Van de Pol and Wright-method. The assumption of a linear effect of all covariates was tested by including second-order terms into models, but was non-significant in all cases (as might be expected given the log-transformation). Thus, second order terms were excluded for simplicity in the further analyses. Individual sex and its interactions had little influence in many of these models (based on non-significant P-values), and sex was therefore excluded from most of the models presented, with an exception for the univariate models of scrounging and aggression, where possible sex effects are of particular interest. All the statistical analyses were carried out in R, version 3.2.2 (R Core Team 2015).

Repeatability is defined as the phenotypic variation explained by differences between individuals (Lessells and Boag 1987) and is calculated by dividing the between individual variance by the total variance:

$$r = \frac{\sigma_{among}^2}{\sigma_{among}^2 + \sigma_{within}^2}$$

Repeatability therefore varies from zero to one, with higher repeatability with less within individual variation. The equation assumes a Gaussian error distribution and that the repeated measures were taken under the same conditions (Dingemanse and Dochtermann 2013). In these analyses, a multivariate generalized linear mixed model in the MCMCglmm package (Hadfield 2010) was used to estimate repeatability with confidence intervals for the normally distributed variables. Order of observations (i.e. familiarity with the feeder, etc.) was added as a fixed effect and individual ID as a random effect. Mean duration of stay per visit to the feeder, first visit times, number of visits, number of wells visited per second, pre-assay mass and number of birds at the feeder were log-transformed to obtain a normal distribution. For the poisson-distributed data, the repeatabilities were calculated from generalized linear mixed-effects models with a binomial error structure and a probit link function (see Nakagawa and Schielzeth 2010).

To further study the structure of the covariances between different variables, structural equation modelling (SEM) was used to examine ten different hypothesized covariance structures (see Table 2 and Fig. 2). This was carried out in the lavaan package in R (Rosseel 2010). In order to evaluate which of the models explained the covariance structure the best, AIC values were used.

Table 2. Descriptions of the ten different models tested in SEM

Hypothesis	Description
H0 – no correlation	No correlation between any of the variables
H1 – all correlates	All variables correlate together into one latent variable
H2a – hunger vs. activity, no correlation	Hunger and activity constitute two different latent variables, where the latent variables do not correlate with each other
H2b – hunger vs. activity, correlation	Hunger and activity constitute two different latent variables, where the latent variables do correlate with each other
H3a – hunger vs. activity, scrounging alone	Hunger and activity constitute two different latent variables, where the latent variables correlate, and scrounging is correlating with aggression
H3b – hunger vs. activity, scrounging with hunger	Hunger and activity constitute two different latent variables, where the two latent variables correlate, and scrounging is part of hunger (and correlating with aggression)
H3c – hunger vs. activity, scrounging with activity	Hunger and activity constitute two different latent variables, where the two latent variables correlate, and scrounging is part of activity (and correlating with aggression)
H4a – joining vs. activity, pre-assay mass and change in duration alone	Joining and activity constitute two different latent variables, where the latent variables correlate, and pre-assay mass is correlating with change in duration
H4b – joining vs. activity, pre-assay mass with joining	Joining and activity constitute two different latent variables, where the two latent variables correlate, and pre-assay mass is part of joining (and correlating with change in duration)
H4c – joining vs. activity, pre-assay mass with activity	Joining and activity constitute two different latent variables, where the two latent variables correlate, and pre-assay mass is part of activity (and correlating with change in duration)

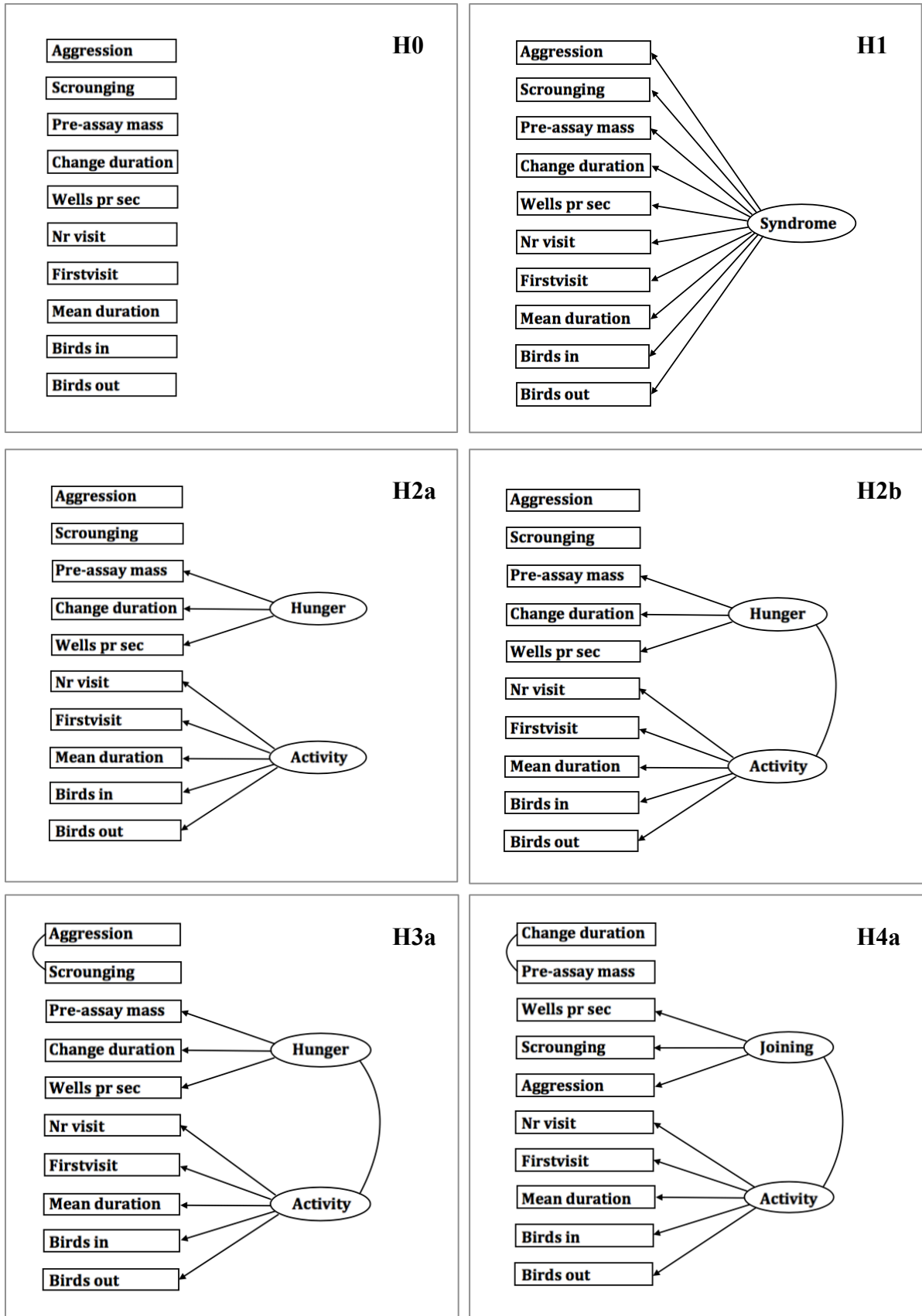


Figure 2. Six of the ten hypothesized covariance structures tested using SEMs. The squares indicate the observed variables and the circles the latent variables. The arrows indicate the error variance explained by the latent variable, the lines indicate correlations.

Results

Body mass and mass change

Individual pre-assay body mass had a negative linear effect on individual mass change during the trial ($\beta = -3.45 \pm 1.74$; $F_{1,96.34} = 3.93$; $P = 0.050$; Fig. 3). To test whether the variation in pre-assay body mass was due to between- versus within-flock changes in behaviour, pre-assay body mass was decomposed in a second model into the mean between-flock effect ($\beta = -10.94 \pm 7.84$; $F_{1,6.09} = 1.95$; $P = 0.212$) and the mean-centered within-flock effect ($\beta = -3.06 \pm 1.78$; $F_{1,90.23} = 2.94$; $P = 0.090$). A third model then showed no significant difference between the two slopes of these within- versus between-flock effects of pre-assay body mass ($F_{1,6.73} = 0.96$; $P = 0.361$). So, there was a non-significant trend for lighter and thus presumably hungrier individuals to gain more mass when foraging at the feeder, and whilst this effect appears to come mostly from a within-flock effect this might just be due to the small number of flocks being tested.

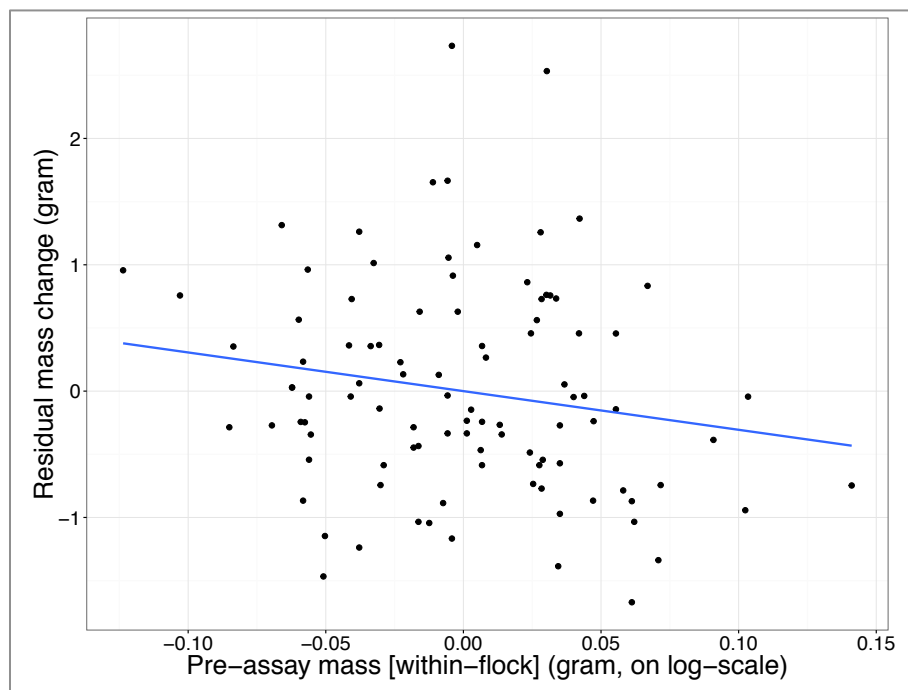


Figure 3. The negative trend of within-flock centered pre-assay body mass (in grams, on log-scale) on residual individual mass change (i.e. controlling for between-flock effects), with the fitted line $y = -3.06x$

Individual pre-assay body mass had no significant effect on individual total duration of time at the feeder ($\beta = 0.25 \pm 1.47$; $F_{1,96.15} = 0.03$; $P = 0.863$). To check that this was not due to

contrasting effects within- versus between-flocks, pre-assay body mass was decomposed in a second model into the mean between-flock effect ($\beta = -8.15 \pm 6.53$; $F_{1,6.17} = 1.56$; $P = 0.257$) and the mean-centered within-flock effect ($\beta = 0.67 \pm 1.50$; $F_{1,90.31} = 0.20$; $P = 0.655$). This showed that lighter (and possibly hungrier) individuals did not spend more total time at the feeder. Given the trend (above) for greater mass gain in these individuals during the trial, this suggests some form of more intensive foraging per unit time at the feeder by lighter and possibly hungrier individuals.

Number of visits and visit duration

As we might expect, the number of visits to the feeder per individual had a significant positive effect on total duration of stay at the feeder ($\beta = 0.63 \pm 0.10$; $F_{1,95.93} = 37.20$; $P < 0.001$). The between-flock effect here was not significant ($\beta = 0.75 \pm 0.35$; $F_{1,6.09} = 4.64$; $P = 0.074$), while the within-flock effect was significantly positive ($\beta = 0.62 \pm 0.11$; $F_{1,89.99} = 32.10$; $P < 0.001$), and these two effects were not significantly different from each other ($F_{1,7.33} = 0.14$ $P = 0.723$). Also as expected, mean duration of stay at the feeder had a significant and positive effect on total visit duration ($\beta = 0.69 \pm 0.09$; $F_{1,96.02} = 63.05$; $P < 0.001$). The between-flock effect was not significant ($\beta = 0.68 \pm 0.44$; $F_{1,5.89} = 2.38$; $P = 0.175$), while the within-flock effect was significantly positive ($\beta = 0.70 \pm 0.09$; $F_{1,89.94} = 60.27$; $P < 0.001$), and the two effects were not significantly different from each other ($F_{1,6.39} = 0.001$; $P = 0.976$). Therefore, both number of visits and mean duration contributed as might be expected to the total foraging time per individual at the feeder, but there might still be individual differences in how this was achieved.

Interestingly, the number of visits to the feeder per individual had a significant negative effect on mean duration of stay at the feeder ($\beta = -0.36 \pm 0.10$; $F_{1,95.90} = 12.13$; $P < 0.001$; Fig. 4). The between-flock effect was not significant ($\beta = -0.25 \pm 0.35$; $F_{1,6.09} = 0.53$; $P = 0.494$), while the within-flock effect was significantly negative ($\beta = -0.37 \pm 0.11$; $F_{1,89.99} = 11.63$; $P = 0.001$), and the two effects were not significantly different from each other ($F_{1,7.33} = 0.10$; $P = 0.757$). This suggests alternative individual strategies of many short visits versus fewer longer visits to the feeder operating mostly at the within-flock level.

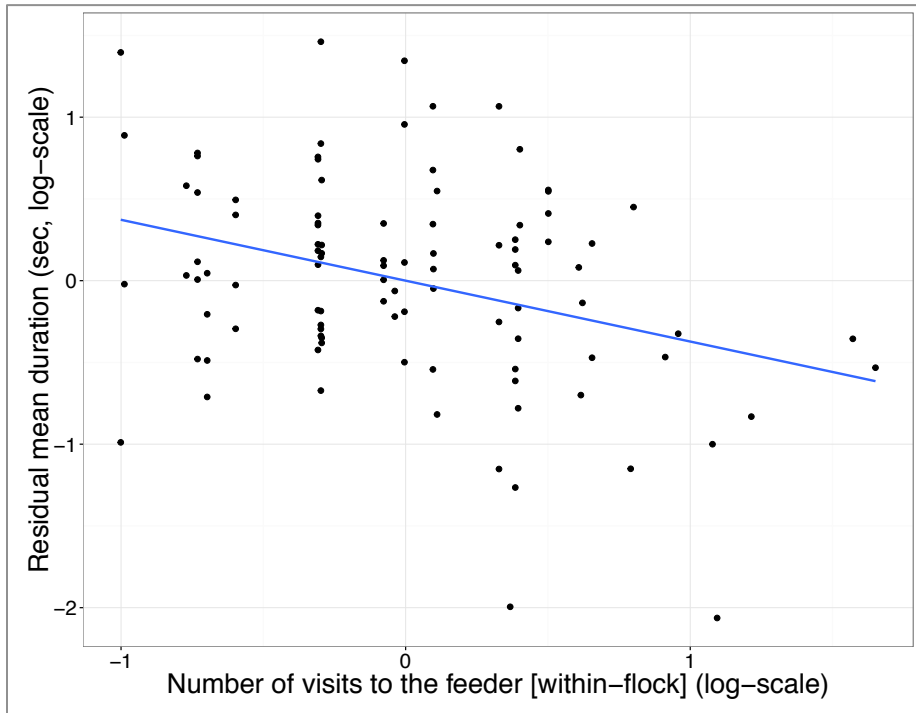


Figure 4. The negative effect of number of visits to the feeder during the trial (within-flock, on log-scale) on residual mean visit duration (i.e. controlling for random between-flock effects, on log-scale), with the fitted line $y = -0.37x$.

First visit times

Individual pre-assay body mass had no significant effect on the timing of the first visit to the feeder per individual ($\beta = 0.37 \pm 0.44$; $F_{1,90.46} = 0.71$; $P = 0.400$). When this effect was decomposed in a second model into the between-flock effect ($\beta = -0.77 \pm 9.46$; $F_{1,66.19} = 0.007$; $P = 0.938$) and the within-flock effect ($\beta = 0.37 \pm 0.44$; $F_{1,90.18} = 0.72$; $P = 0.397$) it was clear that lighter (presumably hungrier) birds did not come down earlier to the feeder.

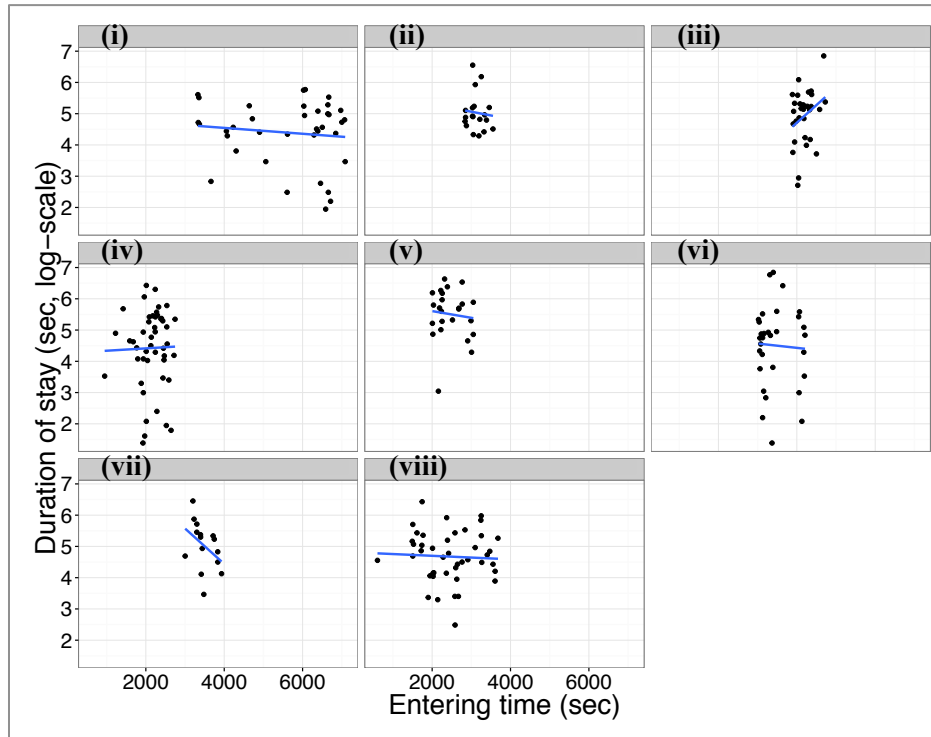
Number of visits during the trial had significantly negative effect on individual first visit time ($\beta = -0.16 \pm 0.03$; $F_{1,90.69} = 23.56$; $P < 0.001$). The between-flock effect had no significant effect ($\beta = -0.63 \pm 0.55$; $F_{1,6.02} = 1.31$; $P = 0.295$), while within-flock effect was the origin of the significant negative effect ($\beta = -0.16 \pm 0.03$; $F_{1,90.01} = 22.95$; $P < 0.001$), although the two models were not significantly different from each other ($F_{1,6.06} = 0.73$; $P = 0.426$). Therefore, individuals that visited the feeder more often within each flock were the ones that visited the feeder earliest in the trial. Mean duration of stay at the feeder had a non-significant effect on first visit time ($\beta = 0.05 \pm 0.03$; $F_{1,90.50} = 2.31$; $P = 0.132$). The between- and within flock

effects also had no significant effects ($\beta = -0.54 \pm 0.64$; $F_{1,6.01} = 0.71$; $P = 0.431$, and $\beta = 0.05 \pm 0.03$; $F_{1,90.02} = 2.46$; $P = 0.120$, respectively), and they were not significantly different from each other ($F_{1,6.04} = 0.85$; $P = 0.391$). Therefore, it appears that first visit times (within-flocks) were driven by the number of visits (above), and there was no (possibly indirect) effect of mean duration of visits on the timing of first visits due to the negative relationship between number of visits and mean duration of visits (see above)

Change in visit duration

The time an individual entered the feeder within the trial had a non-significant effect on the duration of the visit ($\beta = -0.26 \pm 0.21$; $F_{1,26.72} = 1.43$; $P = 0.242$; Fig. 5a). To test whether the variation in entering time was due to between- versus within-individual changes in behaviour, time was decomposed in a second model into the between-individual effect ($\beta = -0.16 \pm 0.24$; $F_{1,69.37} = 0.42$; $P = 0.520$) and the within-individual effect ($\beta = -0.58 \pm 0.38$; $F_{1,175.19} = 2.34$; $P = 0.128$). A third model then showed a non-significant difference between the two slopes of these within- versus between-individual effects of time ($F_{1,237.50} = 0.879$; $P = 0.349$). It is clear from Figure 5a that for many of the flocks there was a limited range of entering times involved in the dataset when there was food and active feeding. When looking at the full dataset including the ends of the trials when food appeared to have depleted, entering time had a negative linear effect on the duration of visit ($\beta = -0.58 \pm 0.11$; $F_{1,76.48} = 29.15$; $P < 0.001$; Fig. 5b). When decomposed into the mean between-individual effect ($\beta = -0.03 \pm 0.28$; $F_{1,153.87} = 0.01$; $P = 0.911$) and the mean-centered within-individual effect ($\beta = -0.64 \pm 0.11$; $F_{1,78.31} = 32.25$; $P < 0.001$), the significant negative linear effect of entering time came almost entirely from a within-individual effect. A third model then showed a marginally significant difference between the two slopes of these within- versus between-individual effects of time ($F_{1,184.14} = 4.21$; $P = 0.042$). Therefore, there was an effect of entering time on the visit duration within each flock (but not between flocks), perhaps reflecting the temporal decrease in the birds' expectation of finding food during each successive visit to the feeder. The continuation of the effect (making it more detectable) after all of the food at the feeders appeared to have been depleted supports this contention that it is the birds' perception of the probability of finding food, rather than the actual declining amount of food, that created this effect.

(a)



(b)

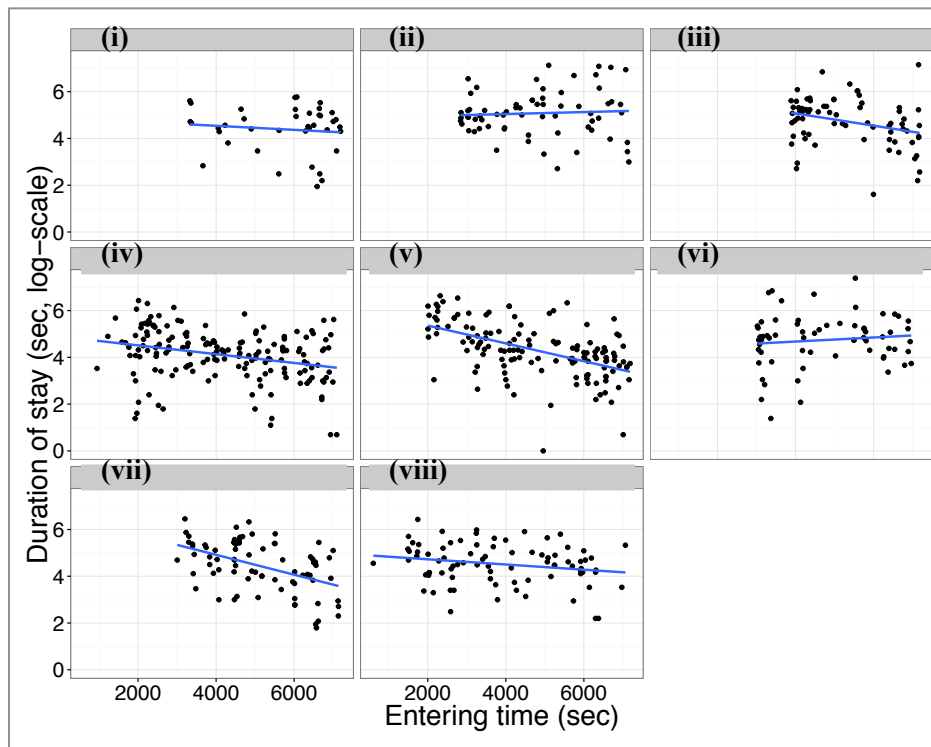


Figure 5. The effect of the time when individuals entered the feeder (in seconds) on the duration of stay on the feeder (in seconds, on log-scale) for each flock separately; (i) Setneøya, (ii) Valøen, (iii) Krystad, (iv) Sør Dahl 1, (v) Sør Dahl 2, (vi) Sør Dahl 3, (vii) Ovesen, and (viii) Fjukstadstrand. In **(a)** for the dataset of when there was food at the feeder, and **(b)** for the full dataset also including the time after food appeared to have been depleted at each feeder. Each point represents a visit to the feeder per individual, and the line shows the overall trend per flock.

Number of wells visited per second at the feeder

The variation among individuals in entering time to the feeder during the trial had no significant effect on the number of wells visited per second ($\beta = 0.16 \pm 0.20$; $F_{1,27.37} = 0.63$; $P = 0.433$). The between-flock effect was not significant ($\beta = 0.11 \pm 0.27$; $F_{1,8.60} = 0.16$; $P = 0.699$), and also the within-flock effect was non-significant ($\beta = 0.21 \pm 0.32$; $F_{1,232.20} = 0.42$; $P = 0.520$), and these two effects were not significantly different from each other ($F_{1,44.21} = 0.05$; $P = 0.821$). When looking at the full dataset including the ends of the trial with no food, entering time had a significant positive effect on the number of wells visited per second ($\beta = 0.57 \pm 0.07$; $F_{1,607.88} = 60.94$; $P < 0.001$; Fig. 6). The between- and within-flock effects were significantly positive ($\beta = 0.64 \pm 0.18$; $F_{1,337.88} = 12.90$; $P < 0.001$, and $\beta = 0.56 \pm 0.08$; $F_{1,603.78} = 49.65$; $P < 0.001$, respectively), and these two effects were not significantly different from each other ($F_{1,398.46} = 0.19$; $P = 0.660$). The non-significant effect of time on number of wells visited per second in the food-in-the-feeder dataset is an effect of the short dataset. The effect of time in the whole dataset suggests that everyone starts to search harder and visits more wells as the food depletes (or is completely depleted), even though the duration of those visits are getting shorter (see above).

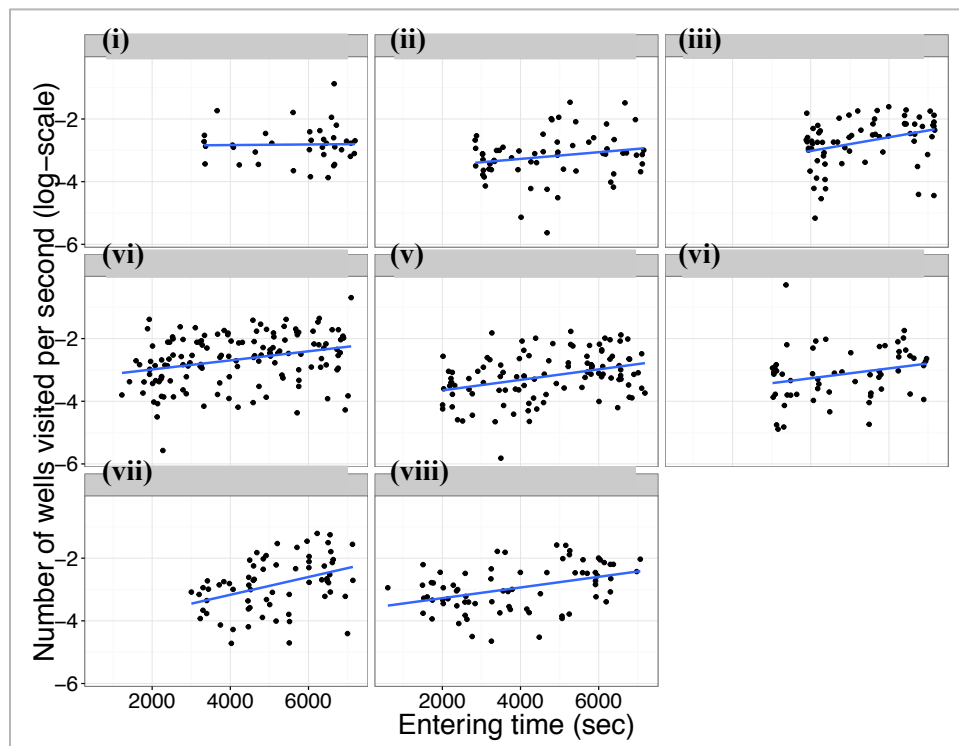


Figure 6. The positive effect of entering time (in seconds) on the number of wells visited per second at the feeder (on log-scale) for each flock separately, for the full dataset including the time after food appeared to have been depleted. Each point represents a visit to the feeder per individual, and the line shows the overall trend per flock. The order of the flocks i-viii is the same as in figure 5.

Number of birds at the feeder

The number of visits to the feeder per individual had a significant positive effect on number of birds at the feeder when the individual entered ($\beta = 2.01 \pm 0.18$; $F_{1,92.51} = 119.67$; $P < 0.001$). The between-flock effect was not significant ($\beta = 1.12 \pm 0.70$; $F_{1,6.07} = 2.55$; $P = 0.161$), while the within-flock effect was significantly positive ($\beta = 0.87 \pm 0.08$; $F_{1,90.04} = 116.88$; $P < 0.001$), and these two effects were not significantly different from each other ($F_{1,6.23} = 0.13$; $P = 0.736$). The number of visits to the feeder per individual also had a significant positive effect on number of birds at the feeder when the individual left ($\beta = 1.72 \pm 0.17$; $F_{1,92.89} = 97.83$; $P < 0.001$). The between-flock effect here was not significant ($\beta = 1.11 \pm 0.59$; $F_{1,6.08} = 3.46$; $P = 0.112$), while the within-flock effect was significantly positive ($\beta = 0.74 \pm 0.08$; $F_{1,90.04} = 94.45$; $P < 0.001$), and these two effects were not significantly different from each other ($F_{1,6.28} = 0.38$; $P = 0.558$). Therefore, birds visiting the feeder frequently did so when there were more birds present at the feeder, both when they entered and when they left. This suggest that birds that came and went to the feeder a lot (and stayed for shorter durations – see above) did this in groups of individuals compared to more solitary birds that came down less frequently but for longer each time. There also seemed to be a significant interaction effect between number of visits and sex ($P = 0.022$).

Scrounging

The time an individual entered the feeder within the trial had a positive effect on the proportion of scrounging ($\beta = 0.51 \pm 0.22$; $P = 0.021$), suggesting that individuals that entered the feeder late to a larger extent were scrounging. The between-individual effect was not significant ($\beta = 0.25 \pm 0.22$; $P = 0.251$), while the within-individual effect was significantly positive ($\beta = 1.46 \pm 0.40$; $P = 0.002$), and these two effects were significantly different from each other ($P = 0.005$). Sex had surprisingly no significant effect on the proportion of scrounging when included in the model alone ($P = 0.934$). However, there seemed to be a weak significant time by sex interaction on the proportion of scrounging, where females increase the proportion of scrounging more than males during the trial ($\beta = 1.23 \pm 0.41$; $P = 0.002$, and $\beta = 0.07 \pm 0.48$; $P = 0.016$, respectively; Fig. 7).

Aggression

The time an individual entered the feeder within the trial had no significant effect on the proportion of aggressive events per visit ($\beta = -0.22 \pm 0.25$; $P = 0.372$). The between-individual effect was also not significant ($\beta = -0.27 \pm 0.25$; $P = 0.286$), as was the within-individual effect

($\beta = 0.16 \pm 0.52$; $P = 0.764$), and these two effects were not significantly different from each other ($P = 0.410$). Sex had surprisingly no significant effect on the proportion of aggression, neither when included alone in the model ($P = 0.934$) nor when added together with time, i.e. the time by sex interaction was non-significant on the proportion of aggression ($P = 0.992$).

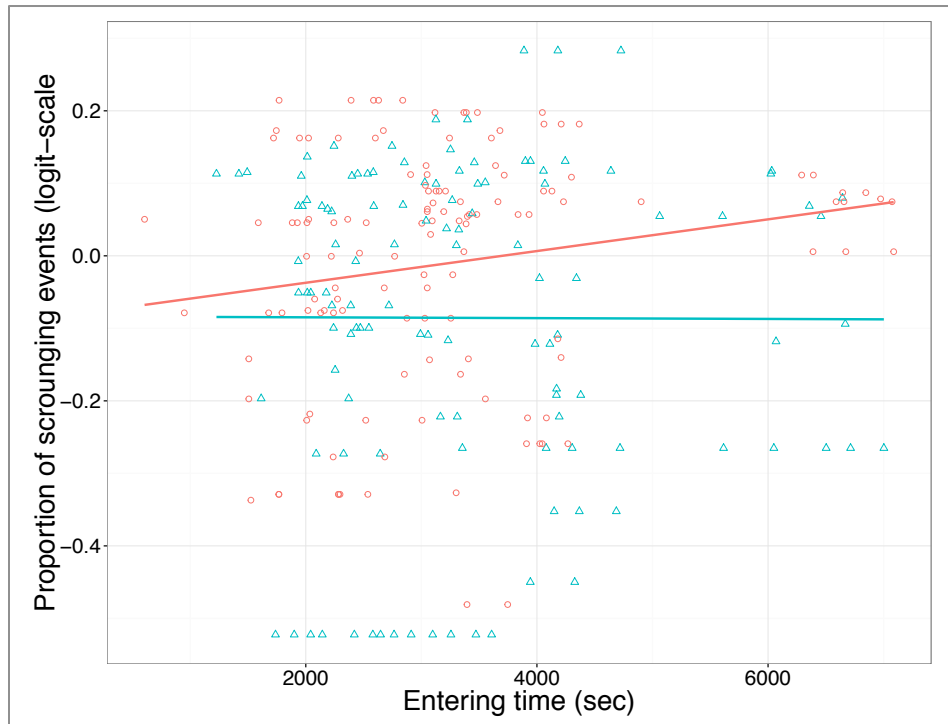


Figure 7. The effect of entering time (in seconds) on the proportion of scrounging events (on probit-scale), for females (red circles) and males (blue triangles).

Repeatability

Neither first visit times, number of visits, mean duration, change in duration, number of wells visited per second, number of birds in the feeder when entering or leaving, mass change, the proportion of scrounging nor the proportion of aggression were repeatable within individuals (see Table 3). Only the pre-assay body mass seemed to be repeatable across the two trials. This means that individual birds did not differ in the number of times and seconds they stayed at the feeder or the interactions they were included in, and that there were no individual consistency in behaviour across the two trials.

Table 3. Repeatability and the corresponding confidence intervals for the different variables measured. For the variables with subscript ⁽¹⁾ the estimated repeatabilities and the confidence intervals were carried out using the MCMCglmm package in R, and fitted with a multivariate generalized linear mixed model with order as fixed effect and individual ID as a random effect. For the variables with subscript ⁽²⁾ the estimated repeatabilities and the confidence intervals were calculated from generalized linear mixed-effects models with binomial error structure and a probit link function. First visit times, mean duration of stay, number of visits, change in duration, number of wells visited per second, number of birds at the feeder when entering and leaving, and pre-assay body mass were log-transformed.

	Repeatability	Confidence intervals
Time of first visit ⁽¹⁾	< 0.001	< 0.001 – 0.095
Nr. of visits ⁽¹⁾	< 0.001	< 0.001 – 0.162
Mean duration of stay ⁽¹⁾	< 0.001	< 0.001 – 0.745
Change in duration of stay ⁽¹⁾	< 0.001	< 0.001 – 0.137
Nr. wells visited per second ⁽¹⁾	< 0.001	< 0.001 – 0.036
Nr. of birds (when arriving) ⁽¹⁾	< 0.001	< 0.001 – 0.001
Nr. of birds (when leaving) ⁽¹⁾	< 0.001	< 0.001 – 0.036
Mass change ⁽¹⁾	< 0.001	< 0.001 – 0.942
Pre-assay body mass ⁽¹⁾	0.841	0.689– 0.944
Proportion of scrounging ⁽²⁾	< 0.001	< 0.001 – 0.001
Proportion of aggression ⁽²⁾	0.031	0.024 – 0.041

Structural Equation Models

The evaluation of the inter-correlation among the various behavioural variables revealed that the number of visits correlated closely with both the time of first visit and mean duration of the visits (Table 4), reflecting the significant results (above) with earlier entrance to the feeder resulting in more visits and also more visits resulting in shorter stays. Further, if an individual visited more wells per second, the predicted proportion of scrounging should increase, which was confirmed by the high correlation between these variables. In addition, increased levels of scrounging resulted in more aggressive events. Since it is hard to interpret the correlation matrix in Table 4 as a whole, it was used in the different SEM models to determine the particular syndrome structure.

Table 4. Pair-wise Pearson correlations between the different behavioural variables. The significant correlations are marked in bold

	Time of first visit	Number of visits	Mean duration of stay	Change in duration	Nr of wells per second
Time of first visit	1	r = -0.35 p < 0.001	r = -0.02 p = 0.84	r = -0.04 p = 0.66	r = 0.11 p = 0.30
Number of visits		1	r = -0.33 p < 0.001	r = -0.05 p = 0.63	r = 0.07 p = 0.49
Mean duration of stay			1	r = 0.08 p = 0.41	r = -0.52 p < 0.001
Change in duration				1	r = -0.03 p = 0.75
Nr of wells per second					1

	Pre-assay body mass	Scrounging	Aggression	Nr of birds when entering	Nr of birds when leaving
Time of first visit	r = 0.02 p = 0.86	r = 0.08 p = 0.42	r = 0.03 p = 0.75	r = -0.36 p < 0.001	r = -0.41 p < 0.001
Number of visits	r = -0.01 p = 0.90	r = -0.08 p = 0.43	r = -0.34 p < 0.001	r = 0.67 p < 0.001	r = 0.66 p < 0.001
Mean duration of stay	r = 0.003 p = 0.97	r = -0.10 p = 0.30	r = 0.53 p < 0.001	r = -0.16 p = 0.11	r = -0.27 p = 0.006
Change in duration	r = 0.15 p = 0.14	r = -0.06 p = 0.56	r = 0.01 p = 0.93	r = 0.05 p = 0.61	r = 0.01 p = 0.91
Nr of wells per second	r = 0.08 p = 0.42	r = 0.39 p < 0.001	r = 0.21 p = 0.03	r = -0.17 p = 0.09	r = -0.02 p = 0.85
Pre-assay body mass	1	r = -0.02 p = 0.82	r = -0.03 p = 0.76	r = -0.03 p = 0.79	r = -0.11 p = 0.30
Scrounging		1	r = 0.44 p < 0.001	r = -0.20 p = 0.05	r = -0.14 p = 0.16
Aggression			1	r = -0.25 p = 0.01	r = -0.26 p = 0.01
Nr of birds when entering				1	r = 0.77 p < 0.001
Nr of birds when leaving					1

In both the raw dataset (Table 5a) and the residual datasets (correcting for flock or sex, Table 5b, and c, respectively) the H0-model was obviously the worst, indicating that there is some form of correlation between the variables, as the correlation matrix in Table 4 suggests. Models H4a, H4b and H4c were the best models according to the AIC values (Table 5; Fig. 8), and although they were not necessarily distinguishable on the basis of AIC values model H4a was perhaps the most parsimonious. It therefore seems that variation in behaviour in these sparrow flocks was driven by clusters of covariance around both ‘activity’ and ‘joining’ behaviour. In these models the number of birds at the feeder when entering and leaving was positive correlated and they also correlated with number of visits. The latent variable ‘activity’ is therefore capturing something about the greater movements of groups of birds versus the slower movements of more solitary individuals that stayed longer at the feeder. The ‘joining’ latent variable captures something about the frequency of individual interactions at wells, because the more wells an individual visited per second the more scrounging and aggressive events they were also involved in. In addition, ‘activity’ and ‘joining’ appeared to negatively covary. Therefore, surprisingly, having more birds at the feeder did not lead to more aggression and/or scrounging.

In the residual models correcting for flock, only model H4a was the best (Table 5b; Fig. 9a), suggesting that the main result was not a product of differences between flocks (or the circumstances of each flocks trial), but reflect true individual differences within and between flocks. Interestingly, in the residual models correcting for sex, both model H3b and model H4a were indistinguishable as the best model (Table 5c; Fig. 9b-c). This perhaps suggest that, contrary to the lack of any sex differences in the univariate tests on scrounging and aggression (above), sex differences were to some extent driving part of the covariances constituting the ‘joining’ latent variable in model H4. However, elsewhere in Table 5 it is not clear that flock or sex were having any great influence in these SEM models. The correlation matrices (see Fig. B1 and Fig. B2 in Appendix B) also suggest that the same was going on in all three datasets.

Table 5. Comparison of the ten SEM models (see Table 3) using AIC values, where df is the degrees of freedom, from (a) the raw dataset, (b) the dataset with residuals correcting for flock, and (c) the dataset with residuals correcting for sex.

Comparison of the ten SEM models				
(a)	Model	df	AIC	Δ AIC
	H4a	20	2610.338	0
	H4c	21	2611.911	1.573
	H4b	21	2612.279	1.941
	H3b	20	2620.488	10.150
	H3a	19	2628.302	17.964
	H3c	20	2630.198	19.860
	H1	20	2640.882	30.544
	H2a	17	2645.878	35.540
	H2b	18	2647.475	37.137
	H0	10	2819.447	209.109
(b)				
	H4a	19	2474.259	0
	H4b	21	2476.674	2.415
	H4c	21	2476.768	2.509
	H3b	20	2484.215	9.956
	H3a	20	2490.798	16.539
	H3c	21	2491.250	16.991
	H1	20	2494.559	20.300
	H2b	19	2507.654	33.395
	H2a	18	2603.143	128.884
	H0	10	2793.833	319.574
(c)				
	H3b	20	2543.195	0
	H4a	19	2544.654	1.459
	H4b	21	2545.445	2.250
	H4c	21	2546.499	3.304
	H3a	20	2549.398	6.203
	H3c	21	2550.235	7.040
	H1	20	2559.590	16.395
	H2b	19	2568.543	25.348
	H2a	17	2634.148	90.953
	H0	10	2819.447	276.252

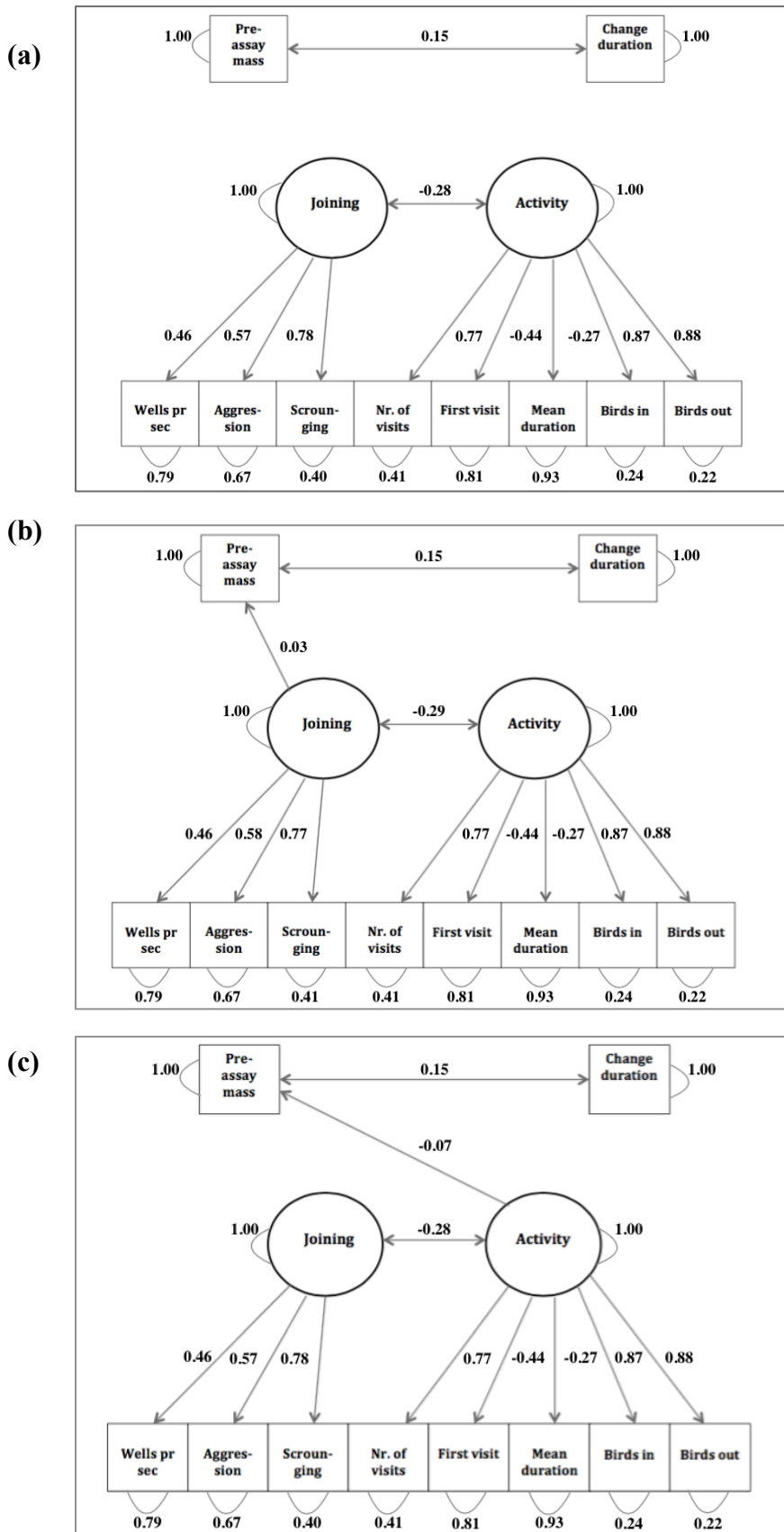


Figure 8. SEM diagrams showing the best hypotheses from Table 3. In (a) model H4a, (b) model H4b, and in (c) model 4Hc. The arrows between the observed variables and the latent variables show the error variance explained by the latent variable. The numbers shown next to the observed variables show the error variance left unexplained by the latent variable, and the double-headed arrow between the variables shows the correlation between them.

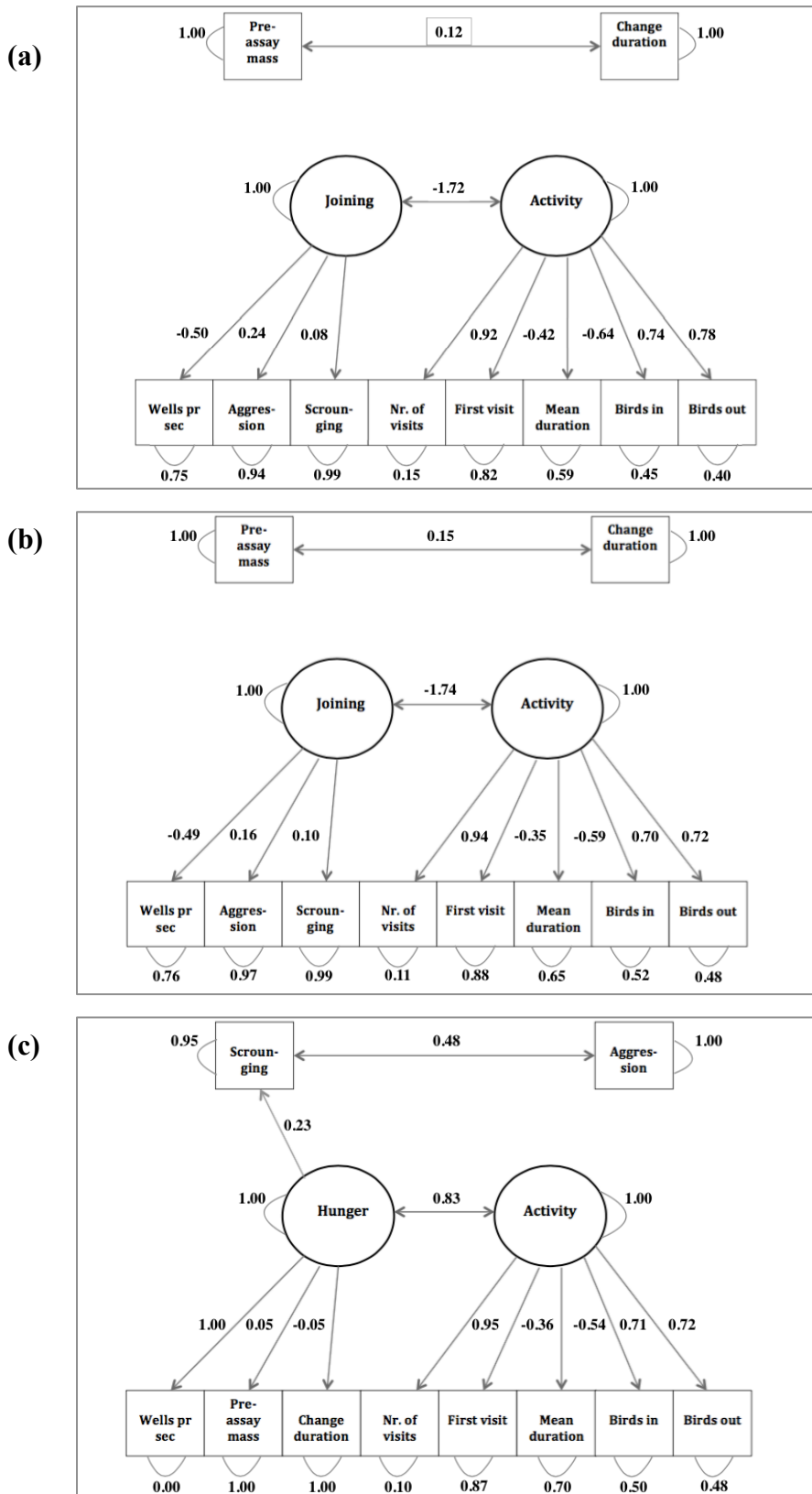


Figure 9. SEM diagrams showing the best hypotheses from Table 3. In (a) model H4a from the flock residuals, (b) model H4a from the sex residuals, and in (c) model 3Hb from the sex residuals. The arrows between the observed variables and the latent variables show the error variance explained by the latent variable. The numbers shown next to the observed variables show the error variance left unexplained by the latent variable, and the double-headed arrow between the variables shows the correlation between them.

Discussion

I have examined the captive foraging behaviour of wild groups of house sparrows and found, as expected, that both number of visits and mean duration of stay at the feeder contributed to the total foraging time per individual at the feeder. More visits and/or longer visits at the feeder contributed to a longer foraging time, but there seemed to be different ways to achieve this. The negative relationship between the number of visits and mean duration of stay at the feeder suggests that individuals used alternative strategies when feeding, where some had many short visits whilst others had fewer longer visits to the feeder. However, there were few repeatable individual differences in both the number of visits or the duration of stay at the feeder, suggesting that these might be chance differences between individuals or flexible responses to the social foraging context. My results also showed that the birds visiting the feeder many times did so when there were many other birds there, both when they arrived and when they left. This therefore suggests that individuals that had many short visits did it together in groups of individuals compared to the more solitary individuals that had fewer and longer visits. However, given the lack of repeatability on number of birds, this again might just reflect temporary patterns in flexible social associations.

Individuals that joined others more often during their stay at the feeder visited more wells per second, scrounged more and were involved in more aggressive events. My results further showed that the number of visits to the feeder was negatively correlated with aggression, and so it was the individuals that stayed in the feeder for longer periods on their own that got into more aggressive events. However, without repeatable individual differences in the number of wells visited, the proportion of scrounging and aggression this could just reflect a flexible response to the social foraging context.

The small differences in the results between the food-only dataset and the full dataset suggest that, somewhat surprisingly, birds behaved largely in the same manner when searching a depleted feeder compared to when they actually were obtaining rewards. This seemed to be true for both the duration of visits and the number of wells visited per second. However, there wasn't much variation in entering time in the dataset while there was food in the feeder, and so these results were relatively weak compared to the full dataset. Nevertheless, the effect of entering time in the full dataset suggests that the individuals started to search harder for longer periods and visited more wells as the food depleted, thus showing that the foraging

intensity increased during the trial as the relatively small amount of food in the feeder failed to satiate these groups of birds. It is interesting that the birds left the feeder sooner after visiting fewer wells per second early on in the trials, presumably because they found food and left for a safer location outside the feeder. This might also indicate that the birds left the feeder to process or digest, or just rest, in between the feeds.

The study also revealed that the time an individual entered the feeder within the trial had a non-significant effect on the proportion of aggression, while it had a significant positive effect of the proportion of scrounging. This is interesting, given that scrounging and aggression positively covaried. Since the proportion of aggression increases with the proportion of scrounging, and scrounging increases with trial time one would expect the proportion of aggression to increase with trial time as well. The results could be due to the decrease in scrounging being a within-individual effect (i.e. all individuals decrease over time), whilst the covariation is a between-individual effect (i.e. some individuals are more aggressive and scrounge more than others). The lack of sex differences in the scrounging analyses was also unexpected, and even though there did seem to be an interaction effect between time and sex on scrounging this effect was only marginally significant. The lack of a sex-effect in aggression is also surprising as one might expect there to be some differences in the aggressive encounters in males compared with females. Males are normally socially dominant over females at food sources in the non-breeding season in many bird species (Senar and Domènech 2011), and since the birds in our study emptied the feeder relatively quickly then one might assume that the availability of resources to the flock members would be low and thereby result in more aggressive encounters, with males trying to monopolize the resources. Other studies have shown that males initiate most of the aggressive interaction, as Senar and Domènech (2011) found in serins (*Serinus serinus*) and siskins (*Carduelis spinus*). However, Liker and Barta (2001) investigated dominance in captive house sparrows and found that both sexes were involved in aggressive encounters, and that the mean dominance rank of females didn't differ from the mean rank of the males. They argued that there might be seasonal differences in sex-specific aggression, with males being more dominant and aggressive during the autumn and first half of winter, when sexual activity is low, but less aggressive during early spring, when pairs form and males reduce their aggression towards females. Anderson (2006) also mentions the possibility of seasonal shifts in dominance relationships between the sexes when describing aggression and dominance hierarchies in house sparrows, with males being dominant to females during the early winter months and females tending to be dominant

during breeding season. It is possible that I conducted the experiment in a transitional phase, with males going from being highly aggressive to less aggressive towards females and this reduction removed the sex-effect normally seen. However, this explanation is less than certain as the trials were conducted in February and March, which is well before any sexual activity. My results may instead depend on the familiarity of the individuals. I deliberately used individuals caught at the same farm and at the same time, to get naturally occurring flocks. The low number of aggressive encounters might therefore be a result of the individuals having the dominance ranks sorted out beforehand.

Liker and Barta (2002) found a strong association between dominance and foraging tactics, with dominants being more aggressive and scrounging more successfully. Subordinates weren't only less successful in their aggressive joinings they were also less likely to attempt the scrounging. Lendvai et al. (2006) found similar results. However, in their study reducing the energy reserves of the sparrows increased the attempts at scrounging, but the subordinates were unable to scrounge effectively because of the increased scrounging of dominants. Dominance status may therefore determine which foraging tactic an individual can use. Thus, the already fixed dominance hierarchy within the groups in my study may also explain the low number of scrounging, i.e. the subordinates didn't attempt to scrounge from the dominants. The problem is, however, to explain the lack of scrounging behaviours by the dominants. Barta and Giraldeau (2000) predicted that individuals should alternate between producing and scrounging depending on both the time of the day and the individuals' state (i.e. energetic reserves). Early in the day, low reserves will result in a preference for scrounging, while the same condition later in the day will favor the producing strategy. Thus, individuals being scroungers should be lighter early in the day and heavier late in the day compared to those being producers. To avoid starvation birds only need small but reliable amounts of food, and according to Barta and Giraldeau (2000) it would be optimal to be a scrounger if you have low reserves, because it gives the opportunity to get some food almost certainly compared to being a searching producer. Dingemanse and Wolf (2010) also expected individuals with lower energy reserves to be bolder in a foraging context than those with higher reserves due to the risk of starvation. This is consistent with the results from a study by Lendvai et al. (2004) looking at the effect of energy reserves on social foraging. Their results showed that flock-feeding house sparrows with lowered energy reserves increased their use of scrounging during the first feed of the day. The lack of state-dependent differences in behaviour between the individuals in the trial may be one explanation of my

results, because not everyone can scrounge at the same time however food-deprived they were. Another possibility is that the birds chose to produce because there is a risk of injury when scrounging, especially perhaps in a covered artificial feeder. House sparrows might fight aggressively for food patches or even defend patches they already have found (Lendvai et al. 2004), but individuals whose energy reserves are far below the critical level can avoid the cost of injury by being producers instead of scroungers.

The lack in scrounging in the current study could also be due to high levels of relatedness in the flocks used, where the individuals tried to avoid scrounging from each other. Tóth et al. (2009) suggested that house sparrows are able to recognize their close kin flock-mates and that they would use aggressive scrounging less often on close kin compared to unrelated flock-mates. However, one of the most important factors influencing the lack of scrounging in my study is most likely the experimental set-up, which didn't quite give me the sustained mix of foraging tactics I had hoped for. I deliberately chose to change the number of seeds used in the feeder compared to Liker and Barta (2002), Lendvai et al. (2004), Tóth et al. (2009), etc. They used a lot of small seeds (i.e. 120 millet seeds) per well to encourage lots of scrounging after the discovery of seeds, because the producers were sitting there feeding for a long time and thus allowing for more scrounging, and also presumably also social interactions and aggression. I wanted to avoid the situation where the individuals stayed too long at one well and thereby resulting in individuals scrounging from scroungers with unclear individual roles. Even though I wanted some aggression, I wasn't interested in provoking too many aggressive encounters and dominance effects. However, by using only 3 seeds, even if they were large sunflower seeds, I seem to have prevented most individuals from scrounging. They essentially never got the opportunity to scrounge from each other, because the producers emptied each well by the time another joined them. The resulting absence of social interactions on the feeder in my study might thus have been reflected in the lack of individual variation in the scrounging and aggression data due to zero-inflation. Aggressive interactions ranging from various types of threats to overt fighting are common in flocks of foraging sparrows (Anderson 2006), and even though fighting is uncommon in winter foraging flocks, attempts to displace other individuals at a feeding station are frequent (Anderson 2006), and such subtle interaction were included in my classifications. A suggestion for later studies is therefore to use smaller seeds in larger amounts, although perhaps not as many as 120, in order to get higher levels of scrounging without provoking too many aggressive interactions.

A prerequisite for a behaviour to be referred to as a personality is consistency, resulting in each individual behaving in the same manner across time and situations. The individuals I tested a second time in the behavioural assay should therefore responded in the same way across the two trials for me to be able to link personality to social foraging. However, neither mean duration of stay per visit, total number of visits to the feeder, first visit times, number of wells visited per second nor mass change was repeatable. The same was true for the proportion of scrounging and the proportion of aggressive events. Therefore, my results did not show any individual consistency across the trials, and by definition, there can be no personality in any of the behaviours in these wild populations of house sparrow. It therefore seems that I only observed plasticity and that the birds only acted flexibly within a group of individuals foraging together in a social group, where individuals behaved differently perhaps by chance or social circumstances that we have no information about (Bergmüller et al. 2010). I might have failed to discover the repeatability due to the few repeated measures made (i.e. I tested the individual behaviour only twice in a minority of individuals). There is a possibility that I would get different results if I had tested the birds several times and for longer periods of time. In addition, only one flock per island was run through the assay a second time. It was assumed that they would represent the individual behavioural consistencies for the rest of the flocks. These repeat-flocks were in addition not randomly chosen, but the second last flocks caught were used for convenience. Finally, since all of these behaviours were collected in a flock then they wouldn't necessarily constitute a reflection of an individual's behaviour (i.e. an individual may behave that way because of others and not because of itself). The individual assays were done immediately prior to the flock assay, to remove the social element, and it would be interesting to compare these results. Nelson et al. (2008) found consistent individual behaviours in male fowl (*Gallus gallus*). However, the signaling of the males were context-specific and the results suggested that the vocal behaviour under naturalistic conditions reflected the operation of social constraints, and that the behaviour of individuals in groups were affected by dominance.

It was clear from the SEMs that the variation in the behaviour in these sparrow flocks were driven by unmeasured latent effects that I have labeled 'activity' and 'joining' behaviours. Even though sex may have been driving part of the covariances constituting the 'joining' latent variable in the residual model H4, there were some methodological issues with specific patterns of covariances in these models, and looking at the correlation matrices in Appendix B there seem to be no evidence for no sex differences. The separate sexes could be tested in

separate SEMs, as recommended by Dingemanse et al. (2010b), but because of the small sample sizes this gave uncertain and unreliable results (i.e. it is recommended to have a sample size >100). I therefore state that the results were confirmed in the residual models correcting for flock and sex, where the main results weren't a product of differences between flocks (or circumstances of each flocks trial) or the different sexes. The latent variable 'activity' showed that larger groups of birds moved more in and out of the feeder while more solitary individuals moved less but therefore stayed longer at the feeder. The 'joining' latent variable reflected the individual interactions. The more wells an individual visited per second the more scrounging and aggression it was involved in. Surprisingly, having more birds at the feeder did not lead to more scrounging or aggressive events. Previous studies have shown the opposite, where scrounging increases with increasing group size due to the increasing number of potential producers to scrounge from (Vickery et al. 1991; Coolen 2002). It would be interesting to test whether the aggression here comes from situations where individuals are joining others or if it comes from situations where they are being joined by others – I have data on this distinction, and so this represents an additional analysis that is possible in the future. One might predict that the covariance with scrounging and number of wells comes from joining aggression (and not being joined by aggression). This could therefore be something to look further into in future analyses and studies.

Conclusion

There was no individual consistency in any of the behavioural traits tested for in the wild populations of house sparrows in this study, and little indication of any sex differences either. There was therefore no indication of animal personalities within these flocks, only plasticity and birds acting as a group of interchangeable individuals foraging together in a social group, and where individuals may well have behaved differently only by chance. However, since all of the behaviours were collected in a flock then they would not necessarily constitute a reflection of an individual's behavior - i.e. an individual may behave a specific way because of others and not because of itself. So, it would be interesting to compare these results with the individual assay data collected immediately prior to the flock assays. The individual variation in the behaviour in the sparrow flocks seemed to be driven by latent variables of 'activity' and 'joining' behaviours. The 'activity' variable showed that larger groups of birds had greater movements while more solitary individuals moved less and stayed longer at the

feeder. The 'joining' variable reflected the individual interactions, where the more wells an individual visited per second the more scrounging and aggression it was involved in. Surprisingly, having more birds at the feeder at one time did not appear to lead to more scrounging or aggressive events. The conclusion here is therefore that producer-scrounger behaviour in natural flocks of familiar individuals (in largely the same nutritional state) is not part of a wider syndrome of individual differences in behaviour.

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Appendix A: Full data set results

Body mass and mass change

Individual pre-assay body mass had a negative linear effect on individual mass change during the trial ($\beta = -3.99 \pm 1.63$; $F_{1,107.96} = 5.96$; $P = 0.016$). This significant effect of pre-assay body mass was decomposed in a second model into the mean between-flock effect ($\beta = -15.32 \pm 8.29$; $F_{1,5.08} = 3.42$; $P = 0.123$) and the mean-centered within-flock effect ($\beta = -4.77 \pm 1.53$; $F_{1,92.14} = 9.74$; $P = 0.002$). A third model then showed no significant difference between the two slopes of these within- versus between-flock effects ($F_{1,5.43} = 1.57$; $P = 0.262$). So, there was a trend for lighter and thus presumably hungrier individuals to gain more mass when foraging at the feeder, but whilst this effect appears to come mostly from a within-flock effect this might just be due to the small number of flocks being tested.

Individual pre-assay body mass had no significant effect on individual total duration of time at the feeder ($\beta = 0.64 \pm 1.33$; $F_{1,105.63} = 0.23$; $P = 0.633$). To check that this was not due to contrasting effects within- versus between-flock, pre-assay body mass was decomposed in a second model into the mean between-flock effect ($\beta = -6.01 \pm 12.90$; $F_{1,4.91} = 0.22$; $P = 0.661$) and the mean-centered within-flock effect ($\beta = 0.30 \pm 1.38$; $F_{1,91.93} = 0.05$; $P = 0.829$). This showed that lighter (and possibly hungrier) individuals did not spend more total time at the feeder. Given the trend (above) for greater mass gain in these individuals during the trial, this suggests some form of more intensive foraging per unit time at the feeder by lighter and possibly hungrier individuals.

Number of visits and visit duration

As we might expect, the number of visits to the feeder per individual had a significant positive effect on total duration of stay at the feeder ($\beta = 0.62 \pm 0.10$; $F_{1,93.89} = 41.01$; $P < 0.001$). The between-flock effect here was positive and slightly significant ($\beta = 0.71 \pm 0.25$; $F_{1,6.04} = 8.05$; $P = 0.029$), the within-flock effect was significantly positive ($\beta = 0.60 \pm 0.11$; $F_{1,105.01} = 32.16$; $P < 0.001$), and these two effects were not significantly different from each other ($F_{1,8.39} = 0.16$; $P = 0.699$). Also as expected, mean duration of stay at the feeder had a significant and positive effect on total visit duration ($\beta = 0.72 \pm 0.10$; $F_{1,109.27} = 52.92$; $P < 0.001$). The between-flock effect was not significant ($\beta = 0.26 \pm 0.67$; $F_{1,5.88} = 0.16$; $P = 0.708$), while the within-flock effect was significantly positive ($\beta = 0.74 \pm 0.10$; $F_{1,104.96} = 53.27$; $P <$

0.001), and the two effects were not significantly different from each other ($F_{1,6.15} = 0.49$; $P = 0.509$). Therefore, both number of visits and mean duration contributed as might be expected to the total foraging time per individual at the feeder, but there might still be individual differences in how this was achieved.

Interestingly, the number of visits to the feeder per individual had a significant negative effect on mean duration of stay at the feeder ($\beta = -0.31 \pm 0.08$; $F_{1,90.34} = 14.83$; $P < 0.001$). The between-flock effect was not significant ($\beta = -0.27 \pm 0.20$; $F_{1,6.04} = 1.77$; $P = 0.231$), while the within-flock effect was significantly negative ($\beta = -0.32 \pm 0.09$; $F_{1,105.01} = 12.84$; $P < 0.001$), and the two effects were not significantly different from each other ($F_{1,8.59} = 0.05$; $P = 0.828$). This suggests alternative individual strategies of many short visits versus fewer longer visits to the feeder.

First visit times

Individual pre-assay body mass had no significant effect on the timing of the first visit to the feeder per individual ($\beta = 0.73 \pm 0.48$; $F_{1,103.37} = 2.24$; $P = 0.137$). When this effect was decomposed in a second model into the between-flock effect ($\beta = -3.80 \pm 9.99$; $F_{1,5.06} = 0.14$; $P = 0.719$) and the within-flock effect ($\beta = 0.84 \pm 0.46$; $F_{1,92.06} = 3.25$; $P = 0.075$) it was clear that it was only *within* flocks that lighter (presumably hungrier) birds came down earlier to the feeder. However, a third model showed that there was no significant difference between the two slopes of the within- versus between-flock effects ($F_{1,5.06} = 0.22$; $P = 0.662$), and so it could be that I just didn't have enough different flocks to detect the between-flock effect here.

Number of visits during the trial had significantly negative effect on individual first visit time ($\beta = -0.16 \pm 0.05$; $F_{1,110.22} = 11.78$; $P < 0.001$). Both the between- and the within-flock effects had significant negative effects ($\beta = -0.67 \pm 0.18$; $F_{1,5.97} = 13.56$; $P = 0.010$, and $\beta = -0.14 \pm 0.05$; $F_{1,104.96} = 9.09$; $P = 0.003$, respectively), and the two models were slightly significantly different from each other ($F_{1,6.79} = 7.93$; $P = 0.027$).

Mean duration of stay at the feeder had a non-significant effect on first visit time ($\beta = -0.03 \pm 0.05$; $F_{1,106.65} = 0.48$; $P = 0.492$). The between-flock effect had a non-significant effect ($\beta = 0.54 \pm 0.53$; $F_{1,5.95} = 1.01$; $P = 0.354$), and also the within-flock effect had no significant effect ($\beta = -0.03 \pm 0.05$; $F_{1,104.98} = 0.61$; $P = 0.435$), and they were not significantly different from each other ($F_{1,6.05} = 1.15$; $P = 0.324$).

Change in visit duration

The time an individual entered the feeder within the trial had a negative linear effect on the duration of its visit ($\beta = -0.60 \pm 0.11$; $F_{1,80.14} = 32.25$; $P < 0.001$). To test whether this effect of time was due to between- versus within-individual changes in behaviour, time was decomposed in a second model into the mean between-individual effect ($\beta = -0.03 \pm 0.27$; $F_{1,157.78} = 0.02$; $P = 0.898$) and the mean-centered within-individual effect ($\beta = -0.68 \pm 0.11$; $F_{1,782.15} = 36.01$; $P < 0.001$). Therefore, the significant negative linear effect of time came almost entirely from a within-individual effect. A third model then showed a marginally significant difference between the two slopes of these within- versus between-individual effects of time ($F_{1,192.26} = 5.03$; $P = 0.026$).

In a separate model, time during the trial, flock ID (i.e. farm), and the interaction between time and flock ID had a significant effect on the duration of stay in the feeder (Table A1a). The effect of sex and all interactions with sex were clearly non-significant, and were therefore excluded. When sex was excluded from the model, the effects of entering time, flock ID, and their interaction remained highly significant (Table A1b). This reduced model turned out to be a better model, with an AIC value of 1993.30, compared with 2008.98 in the full model including sex. Therefore, duration of visits to the feeder decreased over time, but at different rates for the different flocks (Fig. 5b, in Results), with no effect of individual sex in any of this.

Table A1. The effect on the duration of stay in the feeder of (a) the full model of time, flock, sex and their interaction; and (b) a reduced version of the same model excluding the effect of sex. The highly statistical effects ($p < 0.01$) are shown in bold.

a	Duration			
	Error df	Effect df	F	P
Time	1	150.45	27.95	< 0.001
Flock	7	87.93	3.20	0.005
Sex	1	164.59	3.09	0.081
Time:Flock	7	92.18	4.52	< 0.001
Time:Sex	1	150.45	0.92	0.339
Flock:Sex	7	87.93	0.68	0.686
Time:Flock:Sex	7	92.18	0.52	0.817
b				
Time	1	171.91	29.73	< 0.001
Flock	7	96.21	3.41	0.003
Time:Flock	7	101.45	5.10	< 0.001

Appendix B: Correlation matrix for the residual datasets

Table B1. Pair-wise Pearson correlations between the different behavioural variables, for the residual dataset correcting for date. The significant correlations are marked in bold

	Time of first visit	Number of visits	Mean duration of stay	Change in duration	Nr of wells per second
Time of first visit	1	r = -0.45 p < 0.001	r = 0.21 p = 0.03	r = 0.15 p = 0.15	r = -0.37 p < 0.001
Number of visits		1	r = -0.47 p < 0.001	r = -0.12 p = 0.25	r = 0.80 p < 0.001
Mean duration			1	r = 0.12 p = 0.23	r = -0.65 p < 0.001
Change in duration				1	r = -0.15 p = 0.15
Nr of wells per second					1

	Pre-assay body mass	Scrounging	Aggression	Nr of birds when entering	Nr of birds when leaving
Time of first visit	r = 0.09 p = 0.38	r = 0.05 p = 0.62	r = 0.07 p = 0.47	r = -0.21 p = 0.04	r = -0.30 p = 0.003
Number of visits	r = -0.04 p = 0.70	r = -0.06 p = 0.54	r = -0.37 p < 0.001	r = 0.75 p < 0.001	r = 0.72 p < 0.001
Mean duration of stay	r = 0.09 p = 0.37	r = -0.03 p = 0.75	r = 0.52 p < 0.001	r = -0.38 p < 0.001	r = -0.52 p < 0.001
Change in duration	r = 0.12 p = 0.25	r = -0.06 p = 0.58	r = 0.03 p = 0.80	r = -0.08 p = 0.42	r = -0.13 p = 0.20
Nr of wells per second	r = -0.04 p = 0.70	r = 0.18 p = 0.08	r = -0.14 p = 0.18	r = 0.52 p < 0.001	r = 0.61 p < 0.001
Pre-assay body mass	1	r = -0.07 p = 0.49	r = 0.03 p = 0.74	r = 0.02 p = 0.83	r = -0.08 p = 0.40
Scrounging		1	r = 0.42 p < 0.001	r = -0.16 p = 0.11	r = -0.08 p = 0.46
Aggression			1	r = -0.38 p < 0.001	r = -0.40 p < 0.001
Nr of birds when entering				1	r = 0.63 p < 0.001
Nr of birds when leaving					1

Table B2. Pair-wise Pearson correlations between the different behavioural variables, for the residual dataset correcting for sex. The significant correlations are marked in bold

	Time of first visit	Number of visits	Mean duration of stay	Change in duration	Nr of wells per second
Time of first visit	1	r = -0.34 p < 0.001	r = 0.05 p = 0.63	r = -0.05 p = 0.64	r = -0.19 p = 0.05
Number of visits		1	r = -0.48 p < 0.001	r = -0.05 p = 0.64	r = 0.81 p < 0.001
Mean duration of stay			1	r = 0.05 p = 0.60	r = -0.67 p < 0.001
Change in duration				1	r = -0.05 p = 0.64
Nr of wells per second					1

	Pre-assay body mass	Scrounging	Aggression	Nr of birds when entering	Nr of birds when leaving
Time of first visit	r = 0.01 p = 0.93	r = 0.08 p = 0.43	r = 0.03 p = 0.77	r = -0.36 p < 0.001	r = -0.41 p < 0.001
Number of visits	r = -0.01 p = 0.93	r = -0.08 p = 0.44	r = -0.33 p < 0.001	r = 0.67 p < 0.001	r = 0.66 p < 0.001
Mean duration	r = -0.01 p = 0.89	r = -0.07 p = 0.50	r = 0.54 p < 0.001	r = -0.29 p = 0.004	r = -0.40 p < 0.001
Change in duration	r = 0.15 p = 0.15	r = -0.06 p = 0.55	r = 0.01 p = 0.94	r = 0.05 p = 0.59	r = 0.01 p = 0.92
Nr of wells per second	r = 0.05 p = 0.63	r = 0.17 p = 0.10	r = -0.15 p = 0.15	r = 0.44 p < 0.001	r = 0.52 p < 0.001
Pre-assay body mass	1	r = -0.03 p = 0.80	r = 0.03 p = 0.77	r = -0.02 p = 0.83	r = -0.11 p = 0.28
Scrounging		1	r = 0.44 p < 0.001	r = -0.20 p = 0.05	r = -0.14 p = 0.15
Aggression			1	r = -0.24 p = 0.01	r = -0.26 p = 0.01
Nr of birds when entering				1	r = 0.77 p < 0.001
Nr of birds when leaving					1