Social connections, group size and fine-scale manipulations of social stability shape learning, scrounging and foraging rate in wild great tits

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ABSTRACT

The social environment provides both opportunities and challenges for foragers. There is limited information on how sociality affects multiple components of foraging success, while experimental manipulation of sociality within wild foraging groups is rare. We tested whether production learning, scrounging, and foraging rate are associated with individual sociality and manipulated social stability in wild great tits. Individuals were randomly allowed access to, and learned to forage primarily from, one of five feeders. We then performed two reversals, manipulating social connections by either assigning birds to a new feeder with all others assigned to the same previous feeder (stable treatment) or reassigning each bird individually (unstable treatment). Learning was slower in the stable treatment and for individuals with higher weighted degree, suggesting effects of competition, and learning was faster in larger flocks, perhaps from reduced perceived predation risk. Scrounging increased with flock size and weighted degree. Foraging rate increased with weighted degree but was not influenced by social stability or flock size. However, these effects of sociality on foraging were context dependent. Our findings indicate that the consequences of sociality depend on the foraging trait and its cognitive basis, suggesting that selection for group living is more nuanced than usually recognized.

INTRODUCTION

Foraging is the result of a complex set of decisions about when, where and how to obtain food (Stevens et al. 2007). Because foraging provides the energy that is critical for fitness, a diverse set of strategies have evolved to ensure foraging success (Waite and Field 2007). A key challenge for foragers is that this behavior takes place in a constantly changing environment, and this environmental change can drastically affect variables that determine the risks and rewards of any given foraging strategy such as the availability and distribution of food, the technique required to extract it, and the necessary trade-offs with other traits such as reproduction and vigilance against predators (Oom et al. 2004; Monk et al. 2018).

Additionally, for the many species that forage in social groups, sociality can offer both opportunities and challenges to foraging individuals (Clark and Mangel 1986; Krause and Ruxton 2002). Social groups may provide advantages to individual foragers such as increased discovery of food (Pitcher et al. 1982; Snijders et al. 2021), increased efficiency in extracting it (Courchamp and Macdonald 2001; Beauchamp 2005; MacNulty et al. 2014), opportunities to socially learn from other individuals (Hoppitt and Laland 2013) and shared vigilance against predators (Cresswell 1994; Lima et al. 1999; Silk 2007; Sansom et al. 2008). However, foraging in a group also leads to increased competition (Cresswell 1997; Focardi and Pecchioli 2005; Beltrão et al. 2022), as well as other general costs of sociality such as predator attraction and disease spread (Godfrey et al. 2009; Drewe 2010; Weber et al. 2013). Previous studies show mixed results for whether social group characteristics such as group size enhance or detract from foraging success (Beauchamp 1998). In part this may be because foraging itself is a complex trait that is the outcome of multiple functional variables, and individuals differ in how these combine to determine their overall foraging strategy (Nachappa et al. 2010). For instance, some individuals are simply more active

foragers than others (DeLong et al. 2021), and for any given foraging effort some will spend more time as producers and others as scroungers (Morand-Ferron et al. 2007). The interplay between sociality and individual variation in multiple components of foraging is not well understood (Morand-Ferron et al. 2011; Aplin and Morand-Ferron 2017), but critical for a full understanding of the factors that determine foraging success in natural populations.

Understanding the effects of sociality on foraging is further complicated because not all individuals in the same social group experience the same social environment. Animal social network analyses have shown that some individuals have stronger connections, are more central in the network or experience specific types of connections more often than others (Whitehead 2008; Krause et al. 2015). The temporal stability of social networks can also affect individual network position (Ansmann et al. 2012; Murphy et al. 2020). Social network position in turn affects individual foraging behaviors (Giraldeau and Caraco 2000). For instance, individuals that are more central in the network may experience greater levels of foraging competition but also have more opportunities to scrounge from others (Aplin and Morand-Ferron 2017; McMahon et al. 2024). Network density can also affect competition levels, although the direction of this effect is highly variable (Beauchamp 1998; Vásquez and Kacelnik 2000; Grueter et al. 2018; Sheppard et al. 2018). Individuals with close social ties may reduce their own foraging effort in order to maintain those ties (Firth et al. 2015). And individuals that are closely connected to others that act as sources of information — for instance individuals that discover a new food patch or innovate a new foraging technique — may benefit from those connections by being an early recipient of social information (Slagsvold and Wiebe 2011; Aplin et al. 2012; Kulahci et al. 2016; Schakner et al. 2017; McMahon et al. 2024). Likewise, the overall structure of the social network may impact on individual foraging behavior. For instance, networks that are more temporally stable (i.e. in which connections between individuals remain relatively consistent over time) may allow for more

opportunities for social learning (Kulahci and Quinn 2019), but may also affect an individual's competitiveness through the establishment of dominance hierarchies (McDonald and Shizuka 2013).

Different components of foraging success may be differentially impacted by social network structure and position. First, foraging traits differ in how much they rely on or are affected by social interactions. For example, scrounging requires the presence of other individuals, and it is impacted by both social network structure and social stability (Firth et al. 2015; Aplin and Morand-Ferron 2017). In contrast to scrounging, other components of foraging behavior do not require social contact and may or may not be affected by interactions with others in a social group. For instance, individual foraging rates could be a product of individual hunger levels and extraction efficiency, but they can also be affected by social group characteristics such as group size, for example through effects on competition (Rieucau and Giraldeau 2009*a*). Learning about beneficial sources of food and how these can be obtained is another important component of foraging that is not necessarily a social process although it is often modulated by social interactions. Second, the role of cognition, and the associated social environment effects on cognitive performance, varies across foraging traits. Learning about where food can be found and how it can be extracted is a common role for cognition in foraging, and is affected in multiple ways by the social environment, not only via social learning but also through indirect effects of competition, dominance and local enhancement (Pravosudov et al. 2003; Morand-Ferron and Quinn 2011; Avarguès-Weber and Chittka 2014; Ashton et al. 2018, 2019; Langley et al. 2018), although there is variation in these effects (Heinen et al. 2021*a*; Lambert and Guillette 2021). Learning is involved not only in production but also scrounging (Reichert et al. 2021), but learning should have limited effects on foraging performance when feeding on a known, readily accessible food source. The effects of sociality on learning may be especially important when environmental conditions change, and previously learned contingencies are no longer effective for finding food. When this happens, strong connections to other

individuals may be beneficial when there is social learning, such that when any individual accesses a new food source others can quickly do the same (Aplin et al. 2012; Jones et al. 2017). However, strong connections could also be costly when conditions change if social information is outdated or if foraging opportunities available to some individuals are not available for others they are connected to (Beauchamp et al. 1997; Kendal et al. 2005; Hall and Kramer 2008; Rieucau and Giraldeau 2009*b*; Firth et al. 2016). In this case, individuals would be better off using their own private information to learn about new food sources, but some may do so more readily than others (Thornton and Malapert 2009; Kurvers et al. 2010).

Great tits (*Parus major*) are an excellent study system for understanding the effects of sociality on foraging behavior in the wild. In winter, great tits form flocks to forage. These flocks have a fission-fusion structure, in which individuals frequently leave and rejoin the group, resulting in variation in the social bonds among individuals (Aplin et al. 2015; Farine et al. 2015). Multiple aspects of both their foraging behavior and their social networks can be readily observed by tagging individuals with passive integrated transponders and then monitoring their visits to RFID-equipped feeders (Firth and Sheldon 2015; Milligan et al. 2017; Cauchoix et al. 2022). Furthermore, by programming feeders to allow access to the food inside for only certain individuals, it is possible to both measure different components of foraging performance and to manipulate the social structure (Firth and Sheldon 2015). Social structure and social network positioning have important consequences for great tit foraging performance (Aplin et al. 2012; Firth et al. 2015; Beck et al. 2024; McMahon et al. 2024) and other important traits (Farine and Sheldon 2015; Firth and Sheldon 2016). However, no previous study in a wild species has manipulated the structure of the social network to determine the effects on multiple components of foraging success.

Previous work has found that individual great tits vary in the speed at which they learn which feeder in an array is rewarding (Reichert et al. 2020), and also in the extent to which they scrounge from others (Reichert et al. 2021). Experiments manipulating the social network by reassigning birds to new feeders during reversal experiments either completely randomly, potentially disrupting connections formed with others previously assigned to the same feeder, or as a cohort of individuals who were assigned to the same feeder already and therefore maintaining any social connections that formed showed that this manipulation had lasting effects on the social network that carried over across contexts (Troisi et al. 2025). Here, we ask whether social manipulation of flock stability affected individual foraging performance, and if so, which components were affected, and whether these effects were due to specific changes in an individual's social network positioning.

We first tested whether social stability would affect three measures of foraging success: reversal learning of a rewarded feeder location, propensity to scrounge, and overall foraging rate. On the one hand, social instability could lead to disruptions in social relationships and opportunities for social learning, resulting in slower reversal learning, and an increased tendency to scrounge. On the other hand, social instability could facilitate reversal learning through disruptions to competitive hierarchies at feeders while reducing scrounging opportunities. We also tested the effects on foraging of two metrics of individual social network positioning, the average size of the flocks it was in and its weighted degree, a measure of the strength of social connections. Both of these metrics capture aspects of sociality that are likely to have multiple impacts on foraging by influencing shared vigilance, levels of competition, opportunities for social learning and expression of alternative foraging tactics (Dias 2006; Cantor et al. 2020). We examined these relationships across three different learning tasks, an initial production learning and two reversals. We predicted that the effects of sociality on foraging would vary across these foraging tasks because they involve different cognitive traits that could differ in how they interact

with the social environment: learning an initial association versus flexibility in updating behavior in response to environmental change (Izquierdo et al. 2017).

MATERIALS AND METHODS

Study system

We studied social behavior and foraging in the context of a discrimination learning experiment in a wild population of great tits at Wytham Woods, Oxfordshire, UK. The general experimental design and methods are described in detail in our previous publications (Reichert et al. 2020, 2021; Morand-Ferron et al. 2022). Briefly, we used arrays of sunflower-seed feeders with radio frequency identification (RFID) antennas to monitor foraging of great tits that had been fitted with a passive integrative transponder (PIT) tag (IB Technology, Aylesbury, UK). Every bird had a unique RFID code and we could therefore detect each visit by each individual to any of the feeders in the array. Each array consisted of five feeders arranged linearly and spaced 1 m apart. Four arrays were operative in different areas of the wood at any given time, and they were placed far enough apart that birds rarely visited feeders at more than one array. One set of four feeders was monitored from November-December 2017 and another set of four between January-February 2018. All procedures were approved by the Animal Welfare Body at University College Cork (HPRA license number AE19130-P017), and were in accordance with the Association for the Study of Animal Behaviour Guidelines for the Treatment of Animals in Behavioural Research and Teaching. All research was conducted under BTO licenses as part of ongoing research in this population.

During the learning experiments, each bird was assigned to one of the five feeders in the array, and it could only get food from its assigned feeder. If it landed on the assigned feeder, a solenoid would activate, allowing the bird to push open a door to gain access to the seeds inside. If it landed on any of the other feeders, its visit would be recorded but the solenoid would not activate, so it would not be able to access the food. The monitoring of the visits and activation of the solenoid was controlled by a custom program on a 'Darwin Board' (Stickman Technologies Inc., UK). The learning experiment was carried out in three stages. The first was an initial learning stage in which each individual was randomly assigned to one of the five feeders in the array and then we monitored their visits over eight days to determine if and when they learned which feeder they were assigned to (see below). Second, in the first reversal stage, we reassigned birds to a new feeder in the array and monitored their visits for another eight-ten days. In contrast to the initial learning stage, in the reversal stage we applied two different 'social stability treatments' that determined how birds were reassigned to new feeders. At four of the eight sites (two in each year), we applied the 'stable' social treatment, in which the entire set of birds assigned to the same feeder during the initial learning stage were reassigned to the same (randomly chosen) new feeder. Thus, these birds would experience consistency in which other individuals in the flock would be feeding from the same rewarded feeder. At the other four sites, we applied the 'unstable' social treatment. In this treatment, each individual was randomly reassigned to a new feeder independently, and thus was not always consistently feeding from the same rewarded feeder with the same other individuals. Third, in the second reversal stage, we again reassigned birds to new feeders, applied the stable and unstable treatments as above, and monitored visits for eight to ten days.

Social network and foraging measures

In order to capture various aspects of foraging behavior, we calculated variables corresponding to three components of individual foraging strategies. Each of these variables was calculated separately for each individual in each of the three experimental stages. First, we characterized production learning behavior by calculating learning speed as the number of visits until an individual first met a criterion (following previous research) of 16 correct visits within a window of 20 consecutive visits (Reichert et al. 2020). Second, we characterized the propensity to scrounge as the proportion of rewarded visits (i.e. visits in which the bird obtained food, which could happen either by visiting the correct feeder or scrounging) that were scrounges. We defined scrounging as a visit by an individual to a feeder it was not assigned to (and therefore where it could not obtain food by producing) that took place 1 s or less after the departure of a bird that was assigned to that feeder. In such cases, the feeder door had not yet shut and the scrounger could obtain food from that feeder (Reichert et al. 2021). Third, we characterized foraging intake rate as a measure of the rate at which birds obtained food once they had learned the task, quantified as the number of visits to their rewarded feeder on the day after it had met the learning criterion.

We built social networks by assigning birds' visits to discrete flocking events using a Gaussian mixture model (Psorakis et al. 2012, 2015). We defined edges in the social network between each individual that was detected in a flocking event (Troisi et al. 2025). We then quantified the association strength between each possible pair of individuals using a simple ratio index calculated as the number of times both individuals were seen in the same flocking event divided by the total number of flocking events in which either (or both) individual was present (Cairns and Schwager 1987; Whitehead 2008). From these data we calculated the two social metrics used in analyses for each individual: 1) its average flock size (i.e. the mean number of individuals it was observed with in flocking events) and 2) weighted degree as

223 the weighted sum of its association strengths with all other individuals in the network. These metrics
224 were calculated separately for each of the three experimental stages.
225
226 *Statistical analyses*
227
228 All statistical analyses were conducted in R version 4.5.0 (R Development Core Team 2024). Our dataset
229 includes a total of 95818 records of the 68 individuals that met the learning criterion in all three
230 experimental stages. We used separate statistical models for each of the three foraging strategy
231 variables to determine how these were affected by the social stability treatment and an individual's
232 social network metrics. In each case, we included individual identity as a random effect and included
233 fixed effect interactions between experimental stage and i) social stability treatment, ii) average flock
234 size, and iii) weighted degree, expecting that the effects of each of the three social variables on the
235 foraging strategy variables could change across the experimental stages. We included three additional
236 variables as fixed effects to control for factors that were identified in previous analyses to affect learning
237 performance: whether or not the feeder was located at the edge of the array, and the amounts of time
238 that an individual's assigned and non-assigned feeders were inoperable due to equipment malfunction
239 (Reichert et al. 2020). All models were run with the lme4 version 1.1-35.5 package (Bates et al. 2015).
240 Where significant interactions were identified we used Tukey post-hoc tests to determine which groups
241 were different from one another. For interactions involving two categorical variables (experimental
242 stage and social stability), we did post-hoc testing using the emmeans function from the emmeans
243 version 1.10.4 package in R (Lenth 2022), which calculates estimated marginal means for each
244 combination of factors. For interactions involving a continuous variable (experimental stage with
245 average flock size or weighted degree), we did post-hoc testing using the emtrends function in the
246 emmeans package, which tests for differences in slopes of the relationship between the continuous

247 predictor and the foraging variable across experimental stages. We checked model assumptions of
248 normality or uniformity of residuals and non-collinearity of variables using the check_model function in
249 the performance version 0.14.0 package (Lüdecke et al. 2021). Foraging rate was modeled as a Gaussian
250 variable in a linear mixed model. Proportion scrounged was modeled as a binomial variable in a
251 generalized linear mixed model. Learning speed (natural log-transformed) was modeled as a Gaussian
252 variable in a linear mixed model. Raw data and code are available at
253 https://figshare.com/s/8ddfb55d391138371d36.
254
255

256 RESULTS

257

258 We observed 95818 records of the 68 focal individuals across the three experimental stages. Across
259 these stages, the average flock size was (mean±SE) 6.29±0.11, and the average weighted degree was
260 3.06±0.07. Learning speed averaged 62.4±6.9 visits until the learning criterion was met. We observed
261 2347 total scrounging events (mean±SE = 11.5±1.8). Foraging rate averaged 51.9±1.4 visits on the day
262 after the learning criterion was met.

263

264 *Effects of sociality on learning speed*

265

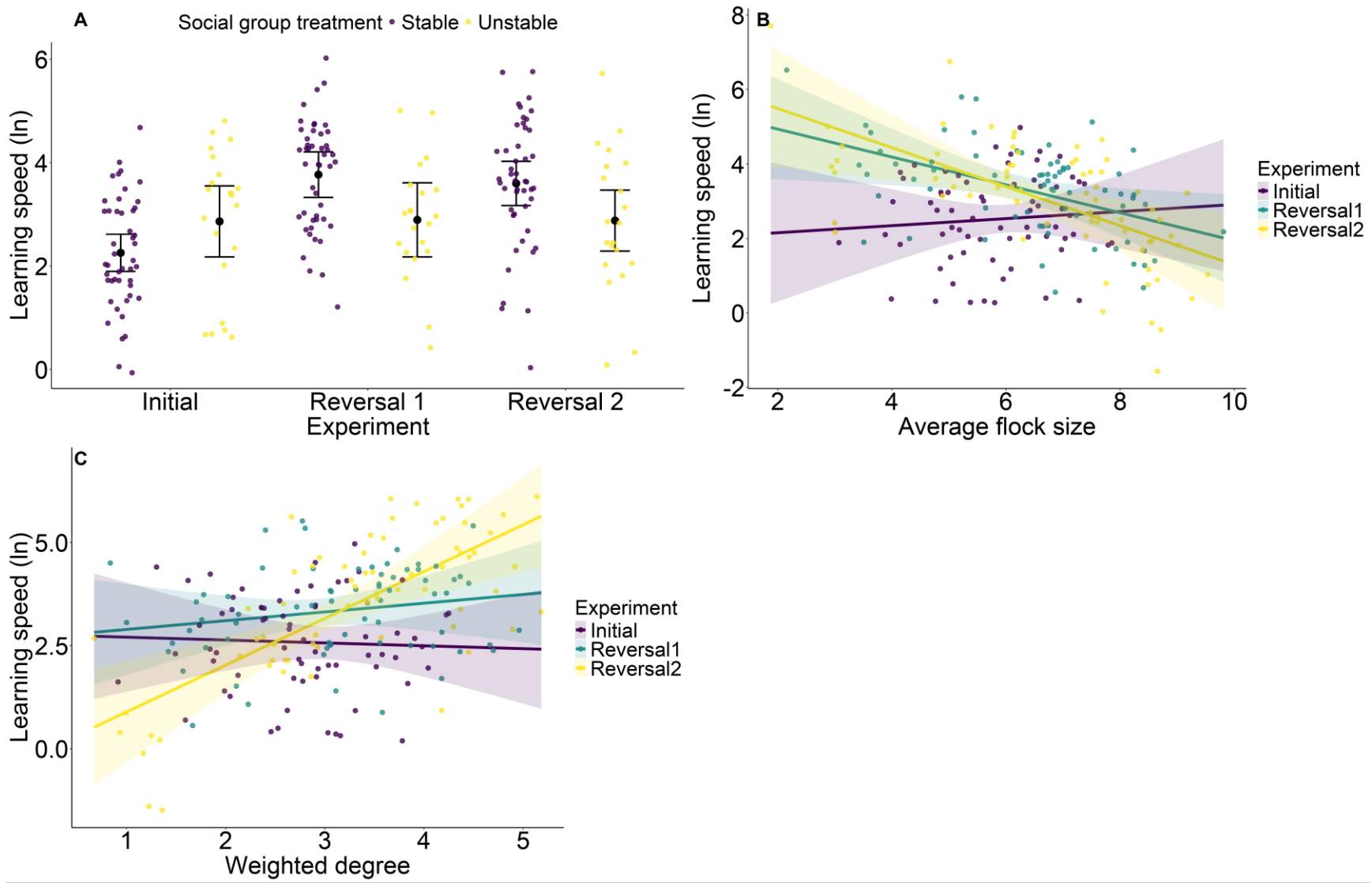
266 There were significant interactions between experimental stage and each of social stability treatment,
267 average flock size and weighted degree on learning speed (Table 1). However, the post-hoc tests
268 indicated that the only significant effect after correction for multiple comparisons was a difference
269 between the initial learning and second reversal stages for the relationship between weighted degree
270 and learning speed (Table S1-S3, Figure 1C). There was little to no relationship between weighted
271 degree and learning speed in the initial learning experiment and in the first reversal, but in the second
272 reversal, individuals with lower weighted degree learned faster (Table S3, Figure 1C). There was weak,
273 but not statistically significant, evidence for effects of the social stability treatment on learning speed in
274 the first and second reversals (individuals in the unstable treatment learned faster than individuals in
275 the stable treatment; Table S1, Figure 1A), for a difference between the initial learning and second
276 reversal stages for the relationship between average flock size and learning speed (individuals in larger
277 flocks learned faster in the second reversal; Table S2, Figure 1B), and for a difference between the first
278 and second reversals for the relationship between weighted degree and learning speed (Table S3, Figure
279 1C).

Effects of sociality on scrounging

There were significant interactions between experimental stage and each of social stability treatment, average flock size and weighted degree on proportion scrounged (Table 2). Individuals in the stable treatment scrounged more than individuals in the unstable treatment for both the initial learning and first reversal stages (Table S4, Figure 2A). In both the initial learning and second reversal experimental stages, scrounging propensity increased slightly with flock size, and there was no difference in the relationship between these two stages (Table S5, Figure 2B). However, for the first reversal, scrounging levels were highest in smaller flocks and decreased with flock size, resulting in a significant difference in the relationship at this stage compared to the other two experimental stages (Table S5, Figure 2B). The relationship between weighted degree and scrounging propensity was significantly different between the initial and both reversal stages, but did not differ significantly between the two reversal stages (Table S6, Figure 2C). For initial learning, individuals with lower weighted degree scrounged more, while for the reversals, individuals with higher weighted degree scrounged more (Figure 2C).

Effects of sociality on foraging rate

There were no significant interactions between experimental stage and any of the sociality variables on foraging rate (Table 3). However, there was a main effect of weighted degree on foraging rate, in which individuals with higher weighted degree had higher foraging rates (Figure 3C). Neither the social stability treatment nor average flock size were related to foraging rate (Table 3, Figure 3). The main effect results were not qualitatively affected by removing the non-significant interaction effects from the model (Table S7).


A
Social group treatment • Stable • Unstable
Learning speed (ln)
Initial
Reversal 1
Reversal 2
Experiment
B
Learning speed (ln)
Average flock size
Experiment
Initial
Reversal1
Reversal2
C
Learning speed (ln)
Weighted degree
Experiment
Initial
Reversal1
Reversal2

306 Figure 1. Effects of sociality on learning speed. A. Effects of social group treatment and experimental stage on learning speed (ln-transformed).

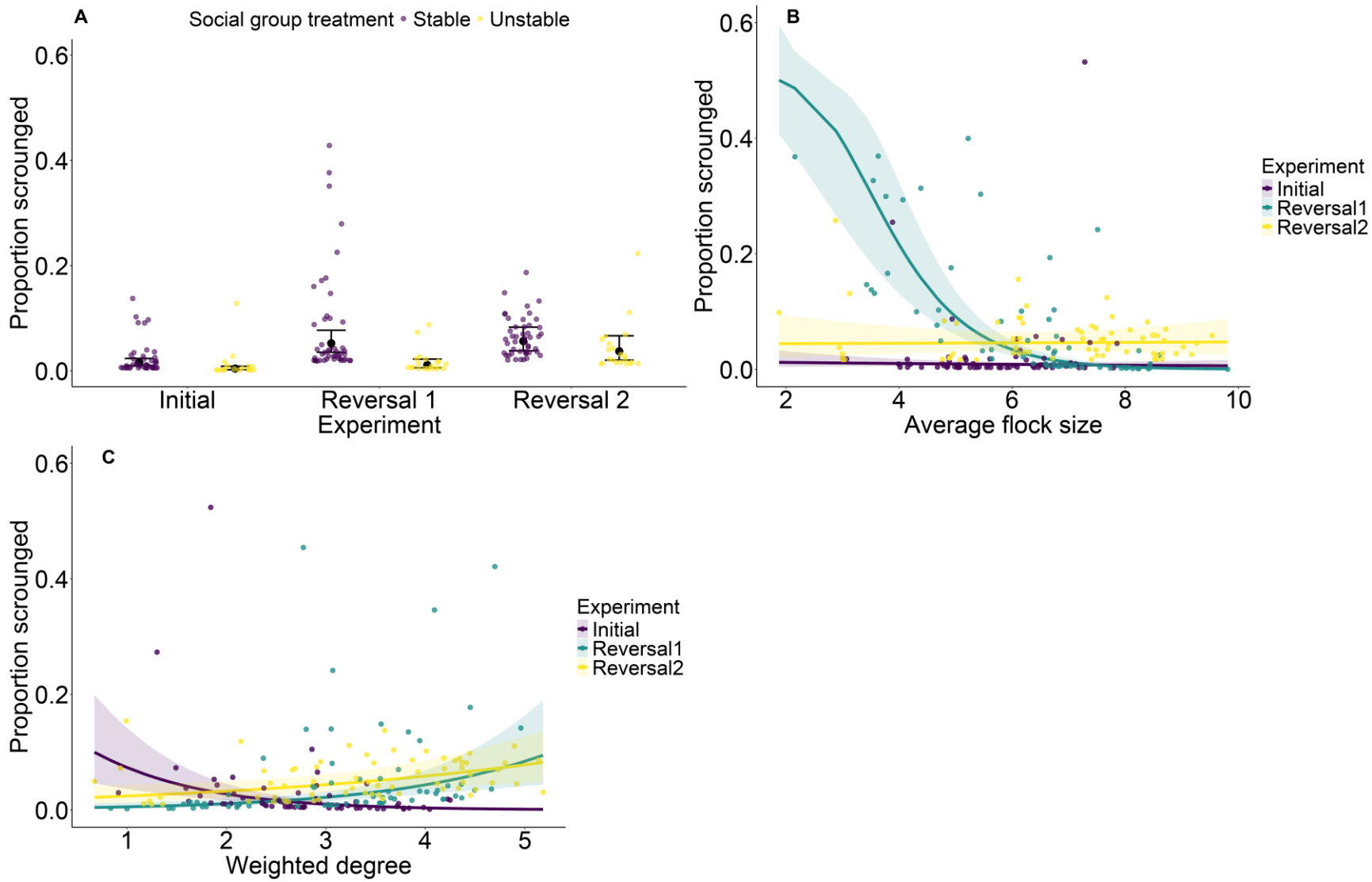
307 Black points represent estimated marginal means (± 95% CI) from the model. Small points represent partial residuals from the model for each

308 individual. B. Relationship between average flock size and learning speed. Lines represent predicted estimate (± 95% CI) from the model, with

309 separate colors for each experimental stage, and points represent partial residuals from the model for each individual. C. Relationship between

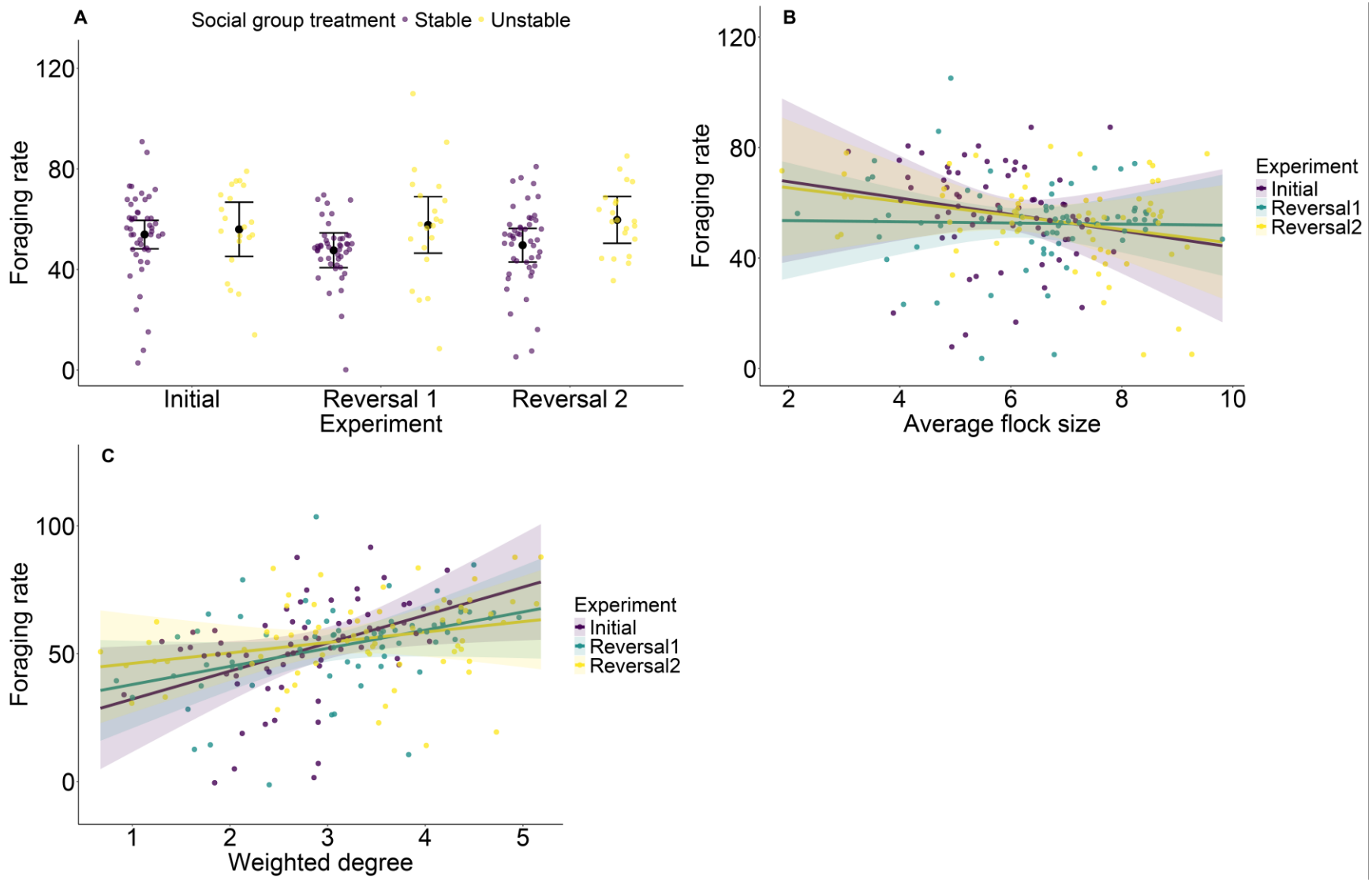
310 weighted degree and learning speed. Interpretation as in B.

311


A
Social group treatment • Stable • Unstable
Proportion scrounged
0.6
0.4
0.2
0.0
Initial
Reversal 1
Reversal 2
Experiment
B
Proportion scrounged
0.6
0.4
0.2
0.0
2
4
6
8
10
Average flock size
Experiment
Initial
Reversal1
Reversal2
C
Proportion scrounged
0.6
0.4
0.2
0.0
1
2
3
4
5
Weighted degree
Experiment
Initial
Reversal1
Reversal2

312

Figure 2. Effects of sociality on scrounging. A. Effects of social group treatment and experimental stage on the proportion of feeds that were scrounges. Black points represent estimated marginal means (± 95% CI) from the model. Small points represent partial residuals from the model for each individual. B. Relationship between average flock size and scrounging. Lines represent predicted estimate (± 95% CI) from the model, with separate colors for each experimental stage, and points represent partial residuals from the model for each individual. C. Relationship between weighted degree and scrounging. Interpretation as in B. The y-axis is cut off at 0.6 for visualization purposes, there are 7, 5 and 6 outlying points not depicted in A, B, and C, respectively. Figure S1 presents the same graphs but with all data points included.


A
Social group treatment • Stable • Unstable
Foraging rate
120
80
40
0
Initial
Reversal 1
Reversal 2
Experiment
B
Foraging rate
120
80
40
0
2
4
6
8
10
Average flock size
Experiment
Initial
Reversal1
Reversal2
C
Foraging rate
100
50
0
1
2
3
4
5
Weighted degree
Experiment
Initial
Reversal1
Reversal2

322

Figure 3. Effects of sociality on foraging rate. A. Effects of social group treatment and experimental stage on foraging rate (number of rewarded visits on the day after the learning criterion was met). Black points represent estimated marginal means (± 95% CI) from the model. Small points represent partial residuals from the model for each individual. B. Relationship between average flock size and foraging rate. Lines represent predicted estimate (± 95% CI) from the model, with separate colors for each experimental stage, and points represent partial residuals from the model for each individual. C. Relationship between weighted degree and foraging rate. Interpretation as in B.

Table 1. Effects of sociality on learning speed

Effect	Estimate	SE	t	P
(Intercept)	1.894	1.05	1.803	
Social group treatment (unstable)	0.607	0.383	1.583	0.115
Experiment (first reversal)	3.596	1.443	2.492	0.014
Experiment (second reversal)	1.539	1.294	1.189	0.236
Own feeder malfunction time (hrs)	0.07	0.02	3.482	< 0.001
Other feeder malfunction time (hrs)	0.069	0.015	4.508	< 0.001
Feeder location (edge)	−0.615	0.182	−3.376	< 0.001
Flock size	0.095	0.231	0.410	0.682
Weighted degree	−0.07	0.323	−0.216	0.830
Social group treatment X Experiment (first reversal)	−1.482	0.629	−2.358	0.020
Social group treatment X Experiment (second reversal)	−1.326	0.567	−2.339	0.021
Average flock size X Experiment (first reversal)	−0.469	0.284	−1.651	0.101
Average flock size X Experiment (second reversal)	−0.619	0.28	−2.214	0.028
Weighted degree X Experiment (first reversal)	0.282	0.421	0.669	0.505
Weighted degree X Experiment (second reversal)	1.204	0.405	2.976	0.003

Fixed effects from a linear mixed model with individual identity as a random effect and ln-transformed learning speed as the dependent variable. The reference category for social group treatment is the stable treatment, for experimental stage is the initial learning stage, and center for the feeder location.

Table 2. Effects of sociality on scrounging

Effect	Estimate	SE	t	P
(Intercept)	−1.283	0.592	−2.168	
Social group treatment (unstable)	−1.266	0.394	−3.211	0.001
Experiment (first reversal)	1.801	0.637	2.827	0.005
Experiment (second reversal)	−3.527	0.551	−6.404	< 0.001
Own feeder malfunction time (hrs)	0.081	0.011	7.329	< 0.001
Other feeder malfunction time (hrs)	0.022	0.006	3.605	< 0.001
Feeder location (edge)	−0.211	0.064	−3.309	< 0.001
Flock size	−0.085	0.116	−0.729	0.466
Weighted degree	−1.036	0.157	−6.589	< 0.001
Social group treatment X Experiment (first reversal)	−0.305	0.264	−1.157	0.247
Social group treatment X Experiment (second reversal)	0.827	0.2	4.144	< 0.001
Average flock size X Experiment (first reversal)	−0.962	0.144	−6.661	< 0.001
Average flock size X Experiment (second reversal)	0.093	0.112	0.83	0.407
Weighted degree X Experiment (first reversal)	1.746	0.217	8.049	< 0.001
Weighted degree X Experiment (second reversal)	1.347	0.165	8.175	< 0.001

Fixed effects from a generalized linear mixed model with individual identity as a random effect and proportion scrounging as the binary dependent variable. Reference categories for factors as in Table 1.

Table 3. Effects of sociality on foraging rate

Effect	Estimate	SE	t	P
(Intercept)	37.64	16.33	2.304	
Social group treatment (unstable)	2.063	6.018	0.343	0.732
Experiment (first reversal)	−11.77	21.23	−0.555	0.580
Experiment (second reversal)	13.96	19.08	0.732	0.465
Own feeder malfunction time (hrs)	−0.413	0.313	−1.319	0.189
Other feeder malfunction time (hrs)	−0.014	0.235	−0.061	0.951
Feeder location (edge)	3.580	2.693	1.329	0.186
Flock size	−2.969	3.616	−0.821	0.413
Weighted degree	10.95	5.056	2.166	0.032
Social group treatment X Experiment (first reversal)	8.001	9.237	0.866	0.388
Social group treatment X Experiment (second reversal)	7.992	8.298	0.963	0.337
Average flock size X Experiment (first reversal)	2.757	4.254	0.648	0.518
Average flock size X Experiment (second reversal)	0.459	4.190	0.110	0.913
Weighted degree X Experiment (first reversal)	−3.856	6.325	−0.610	0.543
Weighted degree X Experiment (second reversal)	−6.868	6.069	−1.132	0.259

Fixed effects from a linear mixed model with individual identity as a random effect and foraging rate as the dependent variable. Reference categories for factors as in Table 1.

DISCUSSION

Sociality had clear effects on all aspects of foraging behavior, indicating that foraging in social groups affects food intake, which could carry over to affect allocation of resources to life history traits. We previously demonstrated that metrics of an individual's social network position in these experiments are repeatable, indicating consistent among-individual variation in sociality (Troisi et al. 2025). Here we show that these same metrics affect foraging behavior, demonstrating an important consequence of individual variation in sociality and also indicating that these summary metrics of social position do indeed capture meaningful biological variation. The links among these traits were context dependent, and suggest interactions with both individual factors like variation in cognitive ability and the positive and negative effects of social grouping. Below, we explore and highlight the novelty in our results, and generate hypotheses for future experimental work to understand the mechanisms by which complex social structure affects different aspects of foraging success simultaneously.

Effects of sociality on learning speed

We had predicted that reversal learning would be faster in the stable treatment because of increased opportunities for social learning for great tits, but our results indicated trends in the opposite direction. We note that previous analysis on this study system, but considering interactions between all individuals of all species involved, found no effects of social stability treatment on learning speed (Reichert et al. 2020); the contrast between our current study and these results can be explained by our focus here on a single species, the great tit, which may indicate that within-species social stability is more relevant than between-species sociality (Firth et al. 2016). Indeed, social stability between conspecific great tits is likely to relate to various aspects of behavior (such as mating, territory acquisition, learning etc.) to

375 which interspecific sociality is less tied (Firth et al. 2018). One explanation for our finding that learning
376 performance was not better in stable social groups is that most individuals learned the task relatively
377 quickly, potentially limiting the utility of social learning in this system (Reichert et al. 2020).
378
379 The somewhat improved learning performance in the unstable treatment in our study could have
380 occurred because this treatment disrupted social competition and dominance relationships that built up
381 among individuals attempting to access the same feeder. Our social network metrics do not capture
382 such relationships because they are based on flock membership, but they are plausible, because high
383 levels of competition and low dominance ranks are associated with reduced learning performance in
384 many species (Chalmeau and Gallo 1993; Pravosudov et al. 2003; Langley et al. 2018). Similarly, there is
385 evidence from multiple species, including great tits, that better problem solvers are poor competitors at
386 feeders (Cole and Quinn 2012), so the unstable treatment may have enabled those better at problem
387 solving to realize greater cognitive performance when otherwise negative hierarchical interactions with
388 known individuals were reduced. However, other studies of learning in wild systems found limited
389 effects of dominance and social stability (Heinen et al. 2021*a*, 2021*b*), and other social processes caused
390 by our manipulation could also be responsible.
391
392 We found limited evidence for effects of average flock size on learning speed, although there was a
393 trend for the second reversal where individuals with larger average flock size learned more quickly,
394 which agrees with another study in the same population in which rates of innovative problem solving
395 also increased with flock size (Morand-Ferron and Quinn 2011). This finding suggests that the costs of
396 being in larger groups, such as increased competition, may be outweighed by other benefits, such as
397 dilution of risk, in addition to other more subtle benefits including better cognitive performance. When
398 we examined the effects of weighted degree, the strength of an individual's social connections, we

found that at least for the second reversal that individuals with higher weighted degrees were slower to learn the task. In a previous study, great tits reduced their own foraging to stay with their mating partner (Firth et al. 2015). Particularly for the challenging second reversal, if similar behavior occurred in our study where birds were similarly restricted in feeder access, then this tendency to remain near strong social partners could have slowed down an individual's own learning.

Effects of sociality on scrounging

Scrounging rates were higher in the stable treatment during both the initial and first reversal stages. Because the stability treatments had not been applied at the initial stage, the most likely explanation for these results is a pre-existing difference between the birds at the sites chosen for each treatment that persisted into the first reversal. Scrounging rates were very low at the initial stage in both groups, so the absolute difference between groups was minimal despite being statistically significant. As scrounging increased across the treatments, in part due to learning (Reichert et al. 2021), levels equalized in both groups. Regardless, these results ran counter to our expectation that individuals in the unstable treatment would scrounge more. Our prediction was based on an expectation of disrupted production ability in the unstable group due to reduced opportunity for social learning, given the general trade-off between producing and scrounging (Barnard and Sibly 1981), and so may not have been realized because individuals in the unstable treatment in fact did not learn to produce more slowly. However, it may also have been predicted that scrounging levels would be lower in the unstable group if individuals primarily scrounge from close social associates (King et al. 2009; Harten et al. 2018).

Scrounging rate was lower for birds with larger average flock size in the first reversal stage, although there were no effects of flock size on scrounging in the other two stages. These results were surprising both because we had expected larger groups to provide more opportunities to scrounge, and because

423 individuals in larger groups learned faster in the first reversal, which despite not being a significant
424 effect should have still provided more opportunity for scroungers. However, we previously
425 demonstrated that scrounging and production learning trade-off such that individuals that learn quickly
426 scrounge less often (Reichert et al. 2021). This fast learning speed therefore could have corresponded
427 with reduced benefits of scrounging relative to producing. Thus, the social factors affecting production
428 learning, in this case potentially beneficial effects of being in large groups, could have indirectly
429 negatively influenced the expression of an alternative foraging tactic. This explanation could also apply
430 to the positive relationship between scrounging and weighted degree in the reversals. Particularly for
431 the second reversal, individuals with higher weighted degree were slower to learn, which could have
432 induced more scrounging. However, determining the direction of causation is difficult. Indeed, an
433 alternative explanation is that because effective scrounging is a learned behavior in this system
434 (Reichert et al. 2021), birds with stronger connections may have had more opportunities to learn
435 effective scrounging techniques or could have developed more stable producer-scrounger relationships.
436 These findings are consistent with those of a previous study of great tits in which birds with especially
437 strong connections will forgo production to stay with their mating partner, from whom they obtained
438 food by scrounging (Firth et al. 2015).
439
440
441 *Effects of sociality on foraging rate*
442
443 Individuals' foraging rates after learning the location of their rewarded feeder were not affected by the
444 social stability treatment. Foraging rate at feeders is a repeatable trait in this system (Crates et al. 2016).
445 This individual consistency in behavior may have contributed to our findings that the overall amount of
446 foraging activity remained relatively stable despite any changes that the social stability treatments

caused to social relationships, overall social structure, and subsequent effects on interactions at the feeders. Our findings suggest that the effects of living in groups on individual foraging rates are not influenced by the ability to feed near specific individuals, which are unnecessary for general benefits of social foraging like shared vigilance and the dilution effect. Foraging rates were also unaffected by average flock size. A previous study found a similar pattern in which overall visit lengths and inter-visit intervals were not affected by an experimental manipulation of density at the feeder (Regan et al. 2022). However, it also found that individuals with stronger social ties were more likely to visit feeders and that these effects interacted with social group density for some foraging behaviors (Regan et al. 2022), pointing to the importance of weighted degree in foraging. Indeed, we found that individuals had a higher foraging rate at our feeders when they had a higher weighted degree. This effect was somewhat stronger for the initial learning experiment, perhaps because at this early stage scrounging levels were low and the social stability treatment had not yet affected social connections. One important consideration is that our measure of foraging rate only includes visits to our experimental feeders. Although feeders are important food sources, great tits have a broad diet in the winter even when supplemental food is available (Coomes et al. 2025). Thus, individuals may vary in their tendency to visit feeders in the first place, and this may be related to the strength of their social relationships, which could explain our findings.

Changes across the experiment

A clear outcome of our study is that effects of sociality on foraging varied across the experimental stages, an initial associative learning task and two subsequent reversal learning tasks. However, this was only the case for the two cognitively demanding foraging traits, learning speed and scrounging rate, but not for foraging rate. This implies that the effects of sociality may be especially pronounced in

471 cognitively challenging situations. The main difference between the experimental stages was in the
472 learning task required of the birds, from an initial association to two successive reversals. Therefore, one
473 explanation for variation across stages is that sociality interacted differently with the cognitive
474 challenges associated with each task. Initial learning is driven by an associative process between a
475 feeder and the reward, while reversal learning requires additional cognitive flexibility so that individuals
476 inhibit their response to the previously rewarded feeder and instead make an association with the new
477 rewarded feeder (Morand-Ferron et al. 2022). At the same time, some individuals were learning to
478 become increasingly proficient at scrounging and there were opportunities to socially learn from other
479 individuals visiting the feeders (Reichert et al. 2021). Some previous studies showed that the effects of
480 the social environment on cognition depend on the cognitive task (Kogan et al. 2000; Schrijver et al.
481 2004), and our results may indicate that these findings extend to foraging behaviors involving different
482 cognitive mechanisms in a wild population. Although further study is needed, our results point to an
483 effect of sociality on the opportunity to learn alternative foraging tactics, adding to the evidence that
484 cognition is shaped by social structure (Hoppitt and Laland 2013; Seyfarth and Cheney 2015; Kulahci and
485 Quinn 2019).
486
487 Another potential explanation for our finding of variation in the effects of sociality across stages is that
488 the overall structural properties of the global social network itself changed. Indeed, we previously
489 demonstrated that average flock size and weighted degree both increased from the initial learning to
490 the second reversal stages, and the increase in flock size was stronger for the stable social group
491 treatment (Troisi et al. 2025). Where we found significant interactions between experimental stage and
492 social network metrics on foraging behavior, these were generally stronger during the reversal stages,
493 indicating that the increased strength of social connections led to emergent impacts on foraging. The
494 current study and Troisi et al. (2025) clearly show that the foraging and social processes were highly

dynamic within groups during this experiment. Further study is needed to disentangle the mechanisms that generate variation and covariation among these traits.

Conclusions

Both social network position and foraging emerge from a complex interplay of factors including competition, cognition, individual personality, levels of predation and other environmental characteristics, yet disentangling these factors in the wild has been difficult due to the lack of experiments. Our findings that sociality affects multiple aspects of foraging success in a wild system expand on our knowledge of social foraging and demonstrate the utility of social network metrics for capturing variation in key behavioral traits. The results demonstrate a series of costs (slower learning in stable flocks and when weighted degree was higher) and benefits (greater scrounging opportunity with stable, larger and more connected flocks, and higher foraging rates in flocks with stronger relationships) associated with greater sociality. However, there is still much progress to be made in identifying the mechanisms behind these results. Many of our findings suggested a role of competition and so a key next step will be to better characterize competitive interactions, which is challenging from RFID data but increasingly possible with new monitoring technologies (Smith and Pinter-Wollman 2021). Our findings also raise questions of causation: an individual's social position certainly influences its foraging behavior, but it may also be the case that foraging behavior affects social position (Kulahci and Quinn 2019), for example if some individuals serve as models for social learning or easy targets for scroungers (Harten et al. 2018). Expanded efforts to monitor and manipulate the social dynamics of wild foraging flocks are likely to yield exciting new insights into the factors that drive the expression of functional behaviors.

AUTHOR CONTRIBUTIONS

Conceptualization: M.R., J.F., J.Q.; Data curation: M.R., C.T., J.F.; Formal analysis: M.R., C.T., J.F.; Funding acquisition: J.Q.; Investigation: M.R.; Methodology: M.R., J.F., J.Q.; Writing – original draft: M.R.; Writing – review & editing: M.R., C.T., J.F., J.Q.

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DECLARATION OF INTEREST

The authors declare there are no conflicts of interest.

REFERENCES

Ansmann, I. C., G. J. Parra, B. L. Chilvers, and J. M. Lanyon. 2012. Dolphins restructure social system after reduction of commercial fisheries. Animal Behaviour 84:575–581.

Aplin, L. M., D. R. Farine, J. Morand-Ferron, and B. C. Sheldon. 2012. Social networks predict patch discovery in a wild population of songbirds. Proceedings of the Royal Society B: Biological Sciences 279:4199–4205.

Aplin, L. M., J. A. Firth, D. R. Farine, B. Voelkl, R. A. Crates, A. Culina, C. J. Garroway, et al. 2015. Consistent individual differences in the social phenotypes of wild great tits, *Parus major*. Animal Behaviour 108:117–127.

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

Ashton, B. J., A. R. Ridley, E. K. Edwards, and A. Thornton. 2018. Cognitive performance is linked to group size and affects fitness in Australian magpies. Nature 554:364–367.

Ashton, B. J., A. Thornton, and A. R. Ridley. 2019. Larger group sizes facilitate the emergence and spread of innovations in a group-living bird. Animal Behaviour 158:1–7.

Avarguès-Weber, A., and L. Chittka. 2014. Local enhancement or stimulus enhancement? Bumblebee social learning results in a specific pattern of flower preference. Animal Behaviour 97:185–191.

Barnard, C. J., and R. M. Sibly. 1981. Producers and scroungers: A general model and its application to captive flocks of house sparrows. Animal Behaviour 29:543–550.

Bates, D., M. Maechler, B. M. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Beauchamp, G. 1998. The effect of group size on mean food intake rate in birds. Biological Reviews 73:449–472.

———. 2005. Does group foraging promote efficient exploitation of resources? Oikos 111:403–407.

Beauchamp, G., M. Belisle, and L.-A. Giraldeau. 1997. Influence of conspecific attraction on the spatial distribution of learning foragers in a patchy habitat. The Journal of Animal Ecology 66:671–682.

Beck, K. B., C. E. Regan, K. McMahon, S. Crofts, E. F. Cole, J. A. Firth, and B. C. Sheldon. 2024. Experimental manipulation of population density in a wild bird alters social structure but not patch discovery rate. Animal Behaviour 209:95–120.

Beltrão, P., A. C. R. Gomes, and G. C. Cardoso. 2022. Collective foraging: Experimentally increased competition decreases group performance exploiting a permanent resource. Functional Ecology 36:1796–1805.

Cairns, S. J., and S. J. Schwager. 1987. A comparison of association indices. Animal Behaviour 35:1454–1469.

Cantor, M., L. M. Aplin, and D. R. Farine. 2020. A primer on the relationship between group size and group performance. Animal Behaviour 166:139–146.

Cauchoix, M., G. B. Jason, A. Biganzoli, J. Briot, V. Guiraud, N. El Ksabi, D. Lieuré, et al. 2022. The OpenFeeder : A flexible automated RFID feeder to measure interspecies and intraspecies differences in cognitive and behavioural performance in wild birds. Methods in Ecology and Evolution 13:1955–1961.

Chalmeau, R., and A. Gallo. 1993. Social constraints determine what is learned in the chimpanzee. Behavioural Processes 28:173–179.

Clark, C. W., and M. Mangel. 1986. The evolutionary advantages of group foraging. Theoretical Population Biology 30:45–75.

Cole, E. F., and J. L. Quinn. 2012. Personality and problem-solving performance explain competitive ability in the wild. Proceedings of the Royal Society B: Biological Sciences 279:1168–1175.

583 Coomes, J. R., J. Cuff, M. Reichert, G. L. Davidson, W. O. C. Symondson, and J. Quinn. 2025. Spatio-
584 temporal variation in diet among age and sex cohorts of a model generalist bird species, the great tit
585 *Parus major*: new insights revealed by DNA metabarcoding. Ecology and Evolution.
586 Courchamp, F., and D. W. Macdonald. 2001. Crucial importance of pack size in the African wild dog
587 *Lycaon pictus*. Animal Conservation 4:169–174.
588 Crates, R. A., J. A. Firth, D. R. Farine, C. J. Garroway, L. R. Kidd, L. M. Aplin, R. Radersma, et al. 2016.
589 Individual variation in winter supplementary food consumption and its consequences for reproduction
590 in wild birds. Journal of Avian Biology 47:678–689.
591 Cresswell, W. 1994. Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*. Animal
592 Behaviour 47:433–442.
593 ———. 1997. Interference competition at low competitor densities in blackbirds *Turdus merula*. The
594 Journal of Animal Ecology 66:461–471.
595 DeLong, J. P., S. F. Uiterwaal, and A. I. Dell. 2021. Trait-based variation in the foraging performance of
596 individuals. Frontiers in Ecology and Evolution 9:649542.
597 Dias, R. I. 2006. Effects of position and flock size on vigilance and foraging behaviour of the scaled dove
598 *Columbina squammata*. Behavioural Processes 73:248–252.
599 Drewe, J. A. 2010. Who infects whom? Social networks and tuberculosis transmission in wild meerkats.
600 Proceedings of the Royal Society B: Biological Sciences 277:633–642.
601 Farine, D. R., L. M. Aplin, B. C. Sheldon, and W. Hoppitt. 2015. Interspecific social networks promote
602 information transmission in wild songbirds. Proceedings of the Royal Society B 282:20142804.
603 Farine, D. R., and B. C. Sheldon. 2015. Selection for territory acquisition is modulated by social network
604 structure in a wild songbird. Journal of Evolutionary Biology 28:547–556.
605 Firth, J. A., E. F. Cole, C. C. Ioannou, J. L. Quinn, L. M. Aplin, A. Culina, K. McMahon, et al. 2018.
606 Personality shapes pair bonding in a wild bird social system. Nature Ecology & Evolution 2:1696–1699.

Firth, J. A., and B. C. Sheldon. 2015. Experimental manipulation of avian social structure reveals segregation is carried over across contexts. Proceedings of the Royal Society B 282:20142350.

———. 2016. Social carry-over effects underpin trans-seasonally linked structure in a wild bird population. Ecology Letters 19:1324–1332.

Firth, J. A., B. C. Sheldon, and D. R. Farine. 2016. Pathways of information transmission among wild songbirds follow experimentally imposed changes in social foraging structure. Biology Letters 12:20160144.

Firth, J. A., B. Voelkl, D. R. Farine, and B. C. Sheldon. 2015. Experimental evidence that social relationships determine individual foraging behavior. Current Biology 25:3138–3143.

Focardi, S., and E. Pecchioli. 2005. Social cohesion and foraging decrease with group size in fallow deer (*Dama dama*). Behavioral Ecology and Sociobiology 59:84–91.

Giraldeau, L. A., and T. Caraco. 2000. Social Foraging Theory. Princeton University Press, Princeton.

Godfrey, S. S., C. M. Bull, R. James, and K. Murray. 2009. Network structure and parasite transmission in a group living lizard, the gidgee skink, *Egernia stokesii*. Behavioral Ecology and Sociobiology 63:1045–1056.

Grueter, C. C., A. M. Robbins, D. Abavandimwe, V. Vecellio, F. Ndagijimana, T. S. Stoinski, and M. M. Robbins. 2018. Quadratic relationships between group size and foraging efficiency in a herbivorous primate. Scientific Reports 8:16718.

Hall, C. L., and D. L. Kramer. 2008. The economics of tracking a changing environment: competition and social information. Animal Behaviour 76:1609–1619.

Harten, L., Y. Matalon, N. Galli, H. Navon, R. Dor, and Y. Yovel. 2018. Persistent producer-scrounger relationships in bats. Science Advances 4:e1603293.

Heinen, V. K., L. M. Benedict, A. M. Pitera, B. R. Sonnenberg, E. S. Bridge, and V. V. Pravosudov. 2021*a*. Social dominance has limited effects on spatial cognition in a wild food-caching bird. Proceedings of the Royal Society B: Biological Sciences 288:20211784.

Heinen, V. K., A. M. Pitera, B. R. Sonnenberg, L. M. Benedict, E. S. Bridge, D. R. Farine, and V. V. Pravosudov. 2021*b*. Food discovery is associated with different reliance on social learning and lower cognitive flexibility across environments in a food-caching bird. Proceedings of the Royal Society B: Biological Sciences 288:20202843.

Hoppitt, W., and K. N. Laland. 2013. Social Learning. Princeton University Press, Princeton.

Izquierdo, A., J. L. Brigman, A. K. Radke, P. H. Rudebeck, and A. Holmes. 2017. The neural basis of reversal learning: An updated perspective. Neuroscience 345:12–26.

Jones, T. B., L. M. Aplin, I. Devost, and J. Morand-Ferron. 2017. Individual and ecological determinants of social information transmission in the wild. Animal Behaviour 129:93–101.

Kendal, R. L., I. Coolen, Y. van Bergen, and K. N. Laland. 2005. Trade-offs in the adaptive use of social and asocial learning. Advances in the Study of Behavior 35:333–379.

King, A. J., N. J. B. Isaac, and G. Cowlishaw. 2009. Ecological, social, and reproductive factors shape producer–scrounger dynamics in baboons. Behavioral Ecology 20:1039–1049.

Kogan, J. H., P. W. Franklandand, and A. J. Silva. 2000. Long-term memory underlying hippocampus-dependent social recognition in mice. Hippocampus 10:47–56.

Krause, J., R. James, D. W. Franks, and D. P. Croft, eds. 2015. Animal Social Networks. Oxford University Press, Oxford.

Krause, J., and G. Ruxton. 2002. Living in Groups. Oxford University Press, Oxford.

Kulahci, I. G., and J. L. Quinn. 2019. Dynamic relationships between information transmission and social connections. Trends in Ecology and Evolution 34:545–554.

Kulahci, I. G., D. I. Rubenstein, T. Bugnyar, W. Hoppitt, N. Mikus, and C. Schwab. 2016. Social networks predict selective observation and information spread in ravens. Royal Society Open Science 3:160256.

Kurvers, R. H. J. M., K. van Oers, B. a Nolet, R. M. Jonker, S. E. van Wieren, H. H. T. Prins, and R. C. Ydenberg. 2010. Personality predicts the use of social information. Ecology letters 13:829–37.

Lambert, C. T., and L. M. Guillette. 2021. The impact of environmental and social factors on learning abilities: a meta-analysis. Biological Reviews 96:2871–2889.

Langley, E. J. G., J. O. van Horik, M. A. Whiteside, and J. R. Madden. 2018. Group social rank is associated with performance on a spatial learning task. Royal Society Open Science 5:171475.

Lenth, R. 2022. emmeans: estimated marginal means, aka least-squares means version 1.8.3.

Lima, S. L., P. A. Zollner, and P. A. Bednekoff. 1999. Predation, scramble competition, and the vigilance group size effect in dark-eyed juncos (*Junco hyemalis*). Behavioral Ecology and Sociobiology 46:110–116.

Lüdecke, D., M. Ben-Shachar, I. Patil, P. Waggoner, and D. Makowski. 2021. performance: An R Package for Assessment, Comparison and Testing of Statistical Models. Journal of Open Source Software 6:3139.

MacNulty, D. R., A. Tallian, D. R. Stahler, and D. W. Smith. 2014. Influence of group size on the success of wolves hunting bison. (C. Sueur, ed.)PLoS ONE 9:e112884.

McDonald, D. B., and D. Shizuka. 2013. Comparative transitive and temporal orderliness in dominance networks. Behavioral Ecology 24:511–520.

McMahon, K., N. M. Marples, L. G. Spurgin, H. M. Rowland, B. C. Sheldon, and J. A. Firth. 2024. Social network centrality predicts dietary decisions in a wild bird population. iScience 27:109581.

Milligan, N. D., R. Radersma, E. F. Cole, and B. C. Sheldon. 2017. To graze or gorge: consistency and flexibility of individual foraging tactics in tits. Journal of Animal Ecology 86:826–836.

Monk, C. T., M. Barbier, P. Romanczuk, J. R. Watson, J. Alós, S. Nakayama, D. I. Rubenstein, et al. 2018. How ecology shapes exploitation: a framework to predict the behavioural response of human and animal foragers along exploration–exploitation trade-offs. (V. Calcagno, ed.)Ecology Letters 21:779–793.

Morand-Ferron, J., L.-A. Giraldeau, and L. Lefebvre. 2007. Wild Carib grackles play a producer scrounger game. Behavioral Ecology 18:916–921.

Morand-Ferron, J., and J. L. Quinn. 2011. Larger groups of passerines are more efficient problem solvers in the wild. Proceedings of the National Academy of Sciences 108:15898–15903.

Morand-Ferron, J., M. S. Reichert, and J. L. Quinn. 2022. Cognitive flexibility in the wild: Individual differences in reversal learning are explained primarily by proactive interference, not by sampling strategies, in two passerine bird species. Learning and Behavior 50:153–166.

Morand-Ferron, J., G. M. Wu, and L. A. Giraldeau. 2011. Persistent individual differences in tactic use in a producer-scrounger game are group dependent. Animal Behaviour 82:811–816.

Murphy, D., H. S. Mumby, and M. D. Henley. 2020. Age differences in the temporal stability of a male African elephant (*Loxodonta africana*) social network. (A. Griffin, ed.)Behavioral Ecology 31:21–31.

Nachappa, P., D. C. Margolies, J. R. Nechols, and T. J. Morgan. 2010. Response of a complex foraging phenotype to artificial selection on its component traits. Evolutionary Ecology 24:631–655.

Oom, S. P., J. A. Beecham, C. J. Legg, and A. J. Hester. 2004. Foraging in a complex environment: from foraging strategies to emergent spatial properties. Ecological Complexity 1:299–327.

Pitcher, T. J., A. E. Magurran, and I. J. Winfield. 1982. Fish in larger shoals find food faster. Behavioral Ecology and Sociobiology 10:149–151.

Pravosudov, V. V., S. P. Mendoza, and N. S. Clayton. 2003. The relationship between dominance, corticosterone, memory, and food caching in mountain chickadees (*Poecile gambeli*). Hormones and Behavior 44:93–102.

Psorakis, I., S. J. Roberts, I. Rezek, and B. C. Sheldon. 2012. Inferring social network structure in ecological systems from spatio-temporal data streams. Journal of the Royal Society Interface 9:3055–3066.

Psorakis, I., B. Voelkl, C. J. Garroway, R. Radersma, L. M. Aplin, R. A. Crates, A. Culina, et al. 2015. Inferring social structure from temporal data. Behavioral Ecology and Sociobiology 69:857–866.

R Development Core Team. 2024. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Regan, C. E., K. B. Beck, K. Mcmahon, S. Crofts, J. A. Firth, and B. C. Sheldon. 2022. Social phenotype-dependent selection of social environment in wild great and blue tits : an experimental study. Proceedings of the Royal Society B 289:20221602.

Reichert, M. S., S. J. Crofts, G. L. Davidson, J. A. Firth, I. G. Kulahci, and J. L. Quinn. 2020. Multiple factors affect discrimination learning performance, but not between-individual variation, in wild mixed-species flocks of birds. Royal Society Open Science 7:192107.

Reichert, M. S., J. Morand-Ferron, I. G. Kulahci, J. A. Firth, G. L. Davidson, S. J. Crofts, and J. L. Quinn. 2021. Cognition and covariance in the producer-scrounger game. Journal of Animal Ecology 90:2497–2509.

Rieucau, G., and L.-A. Giraldeau. 2009*a*. Group size effect caused by food competition in nutmeg mannikins (*Lonchura punctulata*). Behavioral Ecology 20:421–425.

———. 2009*b*. Persuasive companions can be wrong: the use of misleading social information in nutmeg mannikins. Behavioral Ecology 20:1217–1222.

Sansom, A., W. Cresswell, J. Minderman, and J. Lind. 2008. Vigilance benefits and competition costs in groups: do individual redshanks gain an overall foraging benefit? Animal Behaviour 75:1869–1875.

Schakner, Z. A., M. B. Petelle, M. J. Tennis, B. K. Van Der Leeuw, R. T. Stansell, and D. T. Blumstein. 2017. Social associations between California sea lions influence the use of a novel foraging ground. Royal Society Open Science 4:160820.

721 Schrijver, N. C. A., P. N. Pallier, V. J. Brown, and H. Würbel. 2004. Double dissociation of social and
722 environmental stimulation on spatial learning and reversal learning in rats. Behavioural Brain Research
723 152:307–314.
724 Seyfarth, R. M., and D. L. Cheney. 2015. Social cognition. Animal Behaviour 103:191–202.
725 Sheppard, C. E., R. Inger, R. A. McDonald, S. Barker, A. L. Jackson, F. J. Thompson, E. I. K. Vitikainen, et al.
726 2018. Intragroup competition predicts individual foraging specialisation in a group-living mammal.
727 Ecology Letters 21:665–673.
728 Silk, J. B. 2007. The adaptive value of sociality in mammalian groups. Philosophical Transactions of the
729 Royal Society B: Biological Sciences 362:539–559.
730 Slagsvold, T., and K. L. Wiebe. 2011. Social learning in birds and its role in shaping a foraging niche.
731 Philosophical transactions of the Royal Society of London. Series B, Biological sciences 366:969–977.
732 Smith, J. E., and N. Pinter-Wollman. 2021. Observing the unwatchable: Integrating automated sensing,
733 naturalistic observations and animal social network analysis in the age of big data. Journal of Animal
734 Ecology 90:62–75.
735 Snijders, L., S. Krause, A. N. Tump, M. Breuker, C. Ortiz, S. Rizzi, I. W. Ramnarine, et al. 2021. Causal
736 evidence for the adaptive benefits of social foraging in the wild. Communications Biology 4:94.
737 Stevens, D. W., J. S. Brown, and R. C. Ydenberg, eds. 2007. Foraging Behavior and Ecology. University of
738 Chicago Press, Chicago.
739 Thornton, A., and A. Malapert. 2009. Experimental evidence for social transmission of food acquisition
740 techniques in wild meerkats. Animal Behaviour 78:255–264.
741 Troisi, C. A., J. A. Firth, S. J. Crofts, G. L. Davidson, M. S. Reichert, and J. L. Quinn. 2025. Effects of fine-
742 scale changes in resource access and social stability on the sociality of foraging flocks of wild birds.
743 Animal Behaviour 221:123071.

Vásquez, R. A., and A. Kacelnik. 2000. Foraging rate versus sociality in the starling *Sturnus vulgaris*. Proceedings of the Royal Society of London. Series B: Biological Sciences 267:157–164.

Waite, T. A., and K. L. Field. 2007. Foraging with others: Games social foragers play. Pages 331–362 *in* D. W. Stephens, J. S. Brown, and R. C. Ydenberg, eds. Foraging. Behavior and Ecology. University of Chicago Press, Chicago.

Weber, N., S. P. Carter, S. R. X. Dall, R. J. Delahay, J. L. McDonald, S. Bearhop, and R. A. McDonald. 2013. Badger social networks correlate with tuberculosis infection. Current Biology 23:R915–R916.

Whitehead, H. 2008. Analyzing animal societies: Quantitative methods for vertebrate social analysis. The University of Chicago Press.

Supplementary Material for: Social connections, group size and fine-scale manipulations of social stability shape learning, scrounging and foraging rate in wild great tits

Table S1. Contrasts for effects of social stability treatment and experimental phase on learning speed

Experiment	Social Treatment	EMM	SE	Lower CI	Upper CI	Contrast Estimate	SE	z	P
Initial	Stable	2.26	0.18	1.90	2.62	−0.61	0.38	−1.58	0.12
	Unstable	2.86	0.35	2.17	3.56				
First reversal	Stable	3.77	0.23	3.32	4.21	0.88	0.50	1.75	0.08
	Unstable	2.89	0.37	2.17	3.61				
Second reversal	Stable	3.60	0.22	3.17	4.03	0.72	0.41	1.76	0.08
	Unstable	2.88	0.30	2.29	3.47				

Estimated marginal means are given for each combination of social stability treatment and experimental phase from the linear mixed model for effects on learning speed (see Table 1). The contrast estimate is for the comparison between the learning speeds in the stable and unstable social group treatments for each experimental phase, with the P-value calculated using the Tukey adjustment for multiple comparisons. Values were calculated using the emmeans function from the emmeans version 1.10.4 package in R (Lenth, 2022).

Table S2. Contrasts for effects of average flock size and experimental phase on learning speed

Experiment	Slope	SE	Lower CI	Upper CI	Contrast	Estimate	SE	t	P
Initial	0.095	0.23	−0.36	0.55	Initial − First reversal	0.47	0.28	1.65	0.23
First reversal	−0.37	0.16	−0.69	−0.06	Initial − Second reversal	0.62	0.28	2.21	0.07
Second reversal	−0.52	0.18	−0.89	−0.16	First reversal − Second reversal	0.15	0.25	0.60	0.82

Estimated marginal trends are given for the relationship between average flock size and learning speed for each experimental phase, from the linear mixed model for effects on learning speed (see Table 1). The contrast column on the right side of the table compares slopes for each combination of experimental phases, along with P-values testing the statistical difference between slopes calculated using the Tukey adjustment for multiple comparisons. Values were calculated using the emtrends function from the emmeans version 1.10.4 package in R (Lenth, 2022).

Table S3. Contrasts for effects of weighted degree and experimental phase on learning speed

Experiment	Slope	SE	Lower CI	Upper CI	Contrast	Estimate	SE	t	P
Initial	−0.07	0.32	−0.71	0.57	Initial − First reversal	−0.28	0.42	−0.67	0.78
First reversal	0.21	0.28	−0.33	0.76	Initial − Second reversal	−1.2	0.41	−2.98	**0.009**
Second reversal	1.13	0.29	0.56	1.71	First reversal − Second reversal	−0.92	0.40	−2.32	0.056

Estimated marginal trends are given for the relationship between weighted degree and learning speed for each experimental phase, from the linear mixed model for effects on learning speed (see Table 1). The contrast column on the right side of the table compares slopes for each combination of experimental phases, along with P-values testing the statistical difference between slopes calculated using the Tukey adjustment for multiple comparisons. Values were calculated using the emtrends function from the emmeans version 1.10.4 package in R (Lenth, 2022).

Table S4. Contrasts for effects of social stability treatment and experimental phase on proportion scrounged

Experiment	Social Treatment	EMM	SE	Lower CI	Upper CI	Contrast Estimate	SE	z	P
Initial	Stable	−4.95	0.21	−5.37	−4.53	1.27	0.39	3.21	**0.001**
	Unstable	−6.21	0.34	−6.88	−5.54				
First reversal	Stable	−3.84	0.22	−4.26	−3.42	1.57	0.42	3.71	**< 0.001**
	Unstable	−5.41	0.34	−6.08	−4.74				
Second reversal	Stable	−3.75	0.22	−4.18	−3.33	−0.1	0.38	−0.27	0.26
	Unstable	−4.19	0.31	−4.8	−3.58				

Estimated marginal means are given for each combination of social stability treatment and experimental phase from the generalized linear mixed model for effects on proportion scrounged (see Table 2). The contrast estimate is for the comparison between the proportion scrounged in the stable and unstable social group treatments for each experimental phase, with the P-value calculated using the Tukey adjustment for multiple comparisons. Values were calculated using the emmeans function from the emmeans version 1.10.4 package in R (Lenth, 2022).

Table S5. Contrasts for effects of average flock size and experimental phase on proportion scrounged

Experiment	Slope	SE	Lower CI	Upper CI	Contrast	Estimate	SE	z	P
Initial	−0.08	0.12	−0.31	0.14	Initial − First reversal	0.96	0.14	6.66	**< 0.001**
First reversal	−1.05	0.13	−1.29	−0.8	Initial − Second reversal	−0.09	0.11	−0.83	0.68
Second reversal	0.01	0.08	−0.15	0.17	First reversal − Second reversal	−1.06	0.12	−8.51	**< 0.001**

Estimated marginal trends are given for the relationship between average flock size and proportion scrounged for each experimental phase, from the generalized linear mixed model for effects on proportion scrounged (see Table 2). The contrast column on the right side of the table compares slopes for each combination of experimental phases, along with P-values testing the statistical difference between slopes calculated using the Tukey adjustment for multiple comparisons. Values were calculated using the emtrends function from the emmeans version 1.10.4 package in R (Lenth, 2022).

Table S6. Contrasts for effects of weighted degree and experimental phase on proportion scrounged

Experiment	Slope	SE	Lower CI	Upper CI	Contrast	Estimate	SE	z	P
Initial	−1.04	0.16	−1.34	−0.73	Initial − First reversal	−1.75	0.22	−8.05	**< 0.001**
First reversal	0.71	0.19	0.35	1.07	Initial − Second reversal	−1.35	0.17	−8.18	**< 0.001**
Second reversal	0.31	0.12	0.08	0.54	First reversal − Second reversal	0.4	0.19	0.22	0.08

Estimated marginal trends are given for the relationship between weighted degree and proportion scrounged for each experimental phase, from the generalized linear mixed model for effects on proportion scrounged (see Table 2). The contrast column on the right side of the table compares slopes for each combination of experimental phases, along with P-values testing the statistical difference between slopes calculated using the Tukey adjustment for multiple comparisons. Values were calculated using the emtrends function from the emmeans version 1.10.4 package in R (Lenth, 2022).

Table S7. Effects on foraging rate from a model with no interaction terms.

Effect	Estimate	SE	z	P
Intercept	47.22	8.079	5.844	
Social group treatment (unstable)	5.119	4.197	1.220	0.226
Experiment (first reversal)	−2.331	3.171	−0.735	0.463
Experiment (second reversal)	−1.147	3.295	−0.348	0.728
Own feeder malfunction time (hrs)	−0.358	0.304	−1.181	0.239
Other feeder malfunction time (hrs)	−0.074	0.209	−0.355	0.723
Feeder location (edge)	3.630	2.629	1.381	0.169
Flock size	−2.440	1.753	−1.392	0.166
Weighted degree	6.093	2.845	2.141	0.034

Fixed effects from a linear mixed model with individual identity as a random effect and foraging rate as the dependent variable. This model differs from Table 3 in the main text because it does not include the interactions between experimental stage and each of social group treatment, flock size and weighted degree. Reference categories for factors as in Table 1 in the main text.

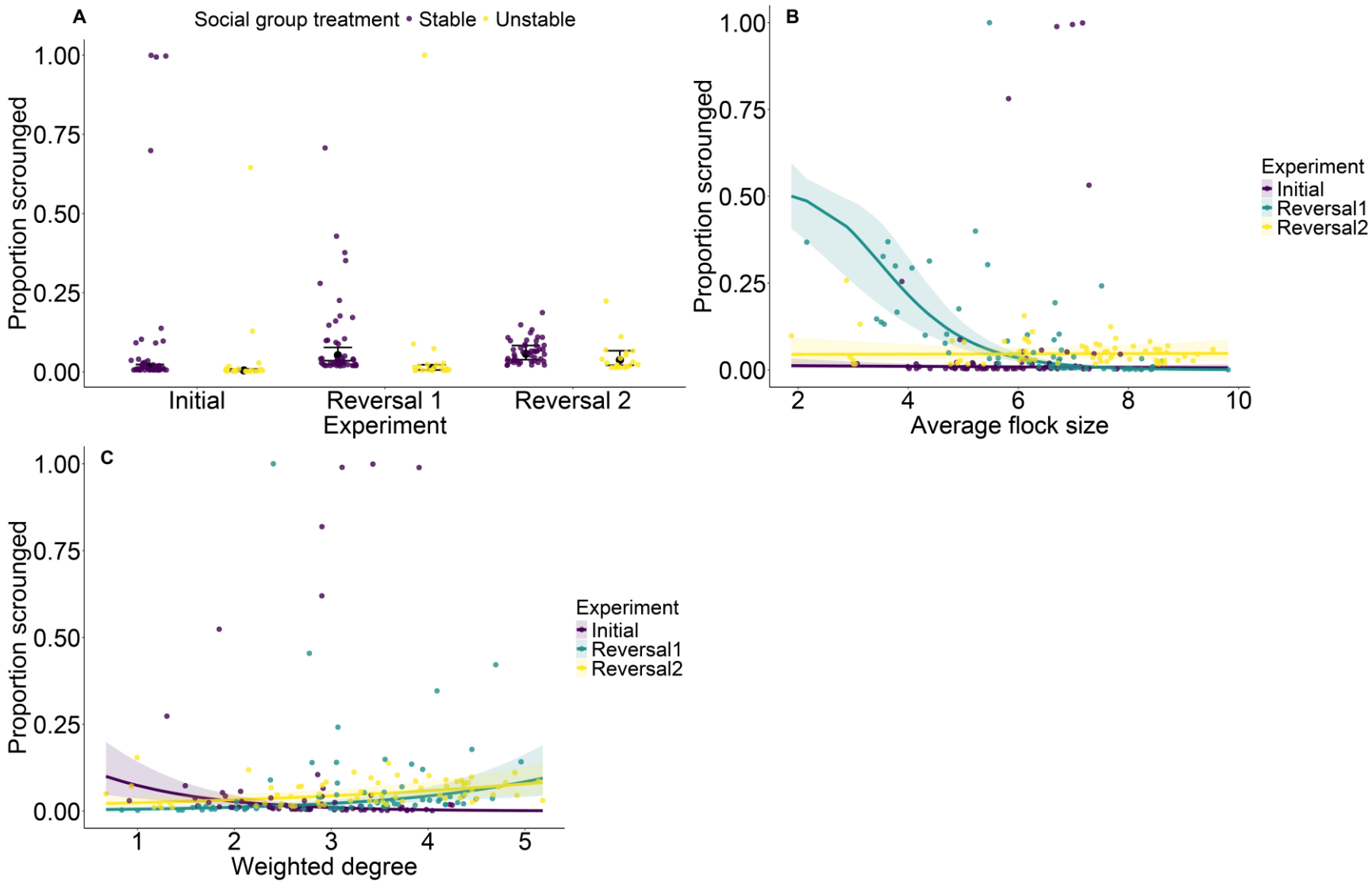

Figure S1. As in Figure 2 in main text, but showing all data points. The y-axis in Figure 2 was cut off at 0.6 to facilitate visualization, here the full dataset including outlying points is depicted.

References

Lenth, R. (2022). *emmeans: Estimated marginal means, aka least-squares means version 1.8.3* [Computer software].