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

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ABSTRACT

The social environment provides both opportunities and challenges for foragers. How multiple components of sociality and foraging interact simultaneously is poorly understood, while experimental manipulation of sociality within wild foraging groups is rare. We tested whether production learning, scrounging, and foraging rate are associated with individual social network metrics and manipulated social stability in mixed species flocks of wild birds. First, individuals were randomly allowed access to, and learned to forage primarily from, one of five feeders. Thereafter, we performed two reversals, manipulating social connections by either assigning birds to a new feeder along with all others assigned to their previous feeder (stable treatment) or reassigning each bird individually (unstable treatment). Most of the effects observed were context dependent but in general we found that: i) Learning was slower in the stable treatment, for individuals with higher weighted degree, and in smaller flocks; ii) Scrounging was higher in the stable treatment, increased with weighted degree, but decreased with flock size; and iii) Foraging rate was predicted only by weighted degree. Our findings demonstrate the complex and dynamic nature of the relationship between sociality and foraging and suggest 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 example, 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 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 of competition (Rieucau and Giraldeau 2009*a*) and the perception of predation risk driven by shared vigilance or the dilution effect (Stevens et al. 2007). Foraging rates can also be improved by the strength of social interactions, which may improve an individual's "sense of security" (Voelkl et al. 2016; Heathcote et al. 2017; Mady and Blumstein 2017). 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; Pitera et al. 2025).

We tested social effects on foraging in wild mixed-species flocks of great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) in the context of an experiment in which birds had to learn which feeder in an array they could access to obtain food (Reichert et al. 2020). First, we tested whether an experimental manipulation of 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. For either scenario, the effects of social instability should increase with each successive reversal. To our knowledge, 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. Second, we tested the relationship between two metrics of individual social network

positioning and foraging. The individual metrics used were the average size of the flocks birds were in when visiting feeders and weighted degree, a measure of the strength of social connections with other individuals in the network. 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 learning tasks because they involve different cognitive traits that have been shown differ in how they interact with the social environment (Lambert and Guillette 2021): learning an initial association versus flexibility in updating behavior in response to environmental change (Izquierdo et al. 2017).

MATERIALS AND METHODS

Study system

In winter, great tits and blue tits form flocks along with several other species and move about woodland areas to forage (Ekman 1989). 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*b*). 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 foraging performance (Aplin et al. 2012; Firth et al. 2015; Beck et al.

2024; McMahon et al. 2024) and for other important traits in these species (Farine and Sheldon 2015; Firth and Sheldon 2016). Furthermore, these social network effects are not limited to conspecifics because heterospecific social interactions also impact foraging (Aplin et al. 2012; Farine et al. 2012, 2014, 2015*a*).

We studied social behavior and foraging in the context of a discrimination learning experiment in a wild mixed species foraging flock focused on great tits and blue 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 and blue 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 British Trust for Ornithology licenses as part of ongoing research in this population.

Prior to the learning experiments that contributed the data analyzed here, the experimental feeders were placed in the area to attract birds and allow them to become accustomed to obtaining food from them (for details see Reichert et al. 2020; Troisi et al. 2025). We initially placed two feeders 50 m apart

178 in an ‘initial dispersed’ stage to attract birds to the area. We then removed those feeders and placed five
179 feeders in a linear array, in the same position as they were used in the learning experiment. During this
180 ‘open clustered’ stage, any tagged bird could feed from any feeder. During the learning experiments, the
181 focus of this study, each bird was assigned to one of the five feeders in the array, and it could only get
182 food from its assigned feeder. If it landed on the assigned feeder, a solenoid would activate, allowing the
183 bird to push open a door to gain access to the seeds inside. If it landed on any of the other feeders, its
184 visit would be recorded but the solenoid would not activate, so it would not be able to access the food.
185 The monitoring of the visits and activation of the solenoid was controlled by a custom program on a
186 ‘Darwin Board’ (Stickman Technologies Inc., UK). The learning experiment was carried out in three
187 stages. The first was an initial learning stage in which each individual was randomly assigned to one of
188 the five feeders in the array and then we monitored their visits over eight days to determine if and when
189 they learned which feeder they were assigned to (see below). Second, in the first reversal stage, we
190 reassigned birds to a new feeder in the array and monitored their visits for another eight-ten days. In
191 contrast to the initial learning stage, in the reversal stage we applied two different ‘social stability
192 treatments’ that determined how birds were reassigned to new feeders. At four of the eight sites (two
193 in each year), we applied the ‘stable’ social treatment, in which the entire set of birds assigned to the
194 same feeder during the initial learning stage were reassigned to the same (randomly chosen) new
195 feeder. Thus, these birds would experience consistency in which other individuals in the flock would be
196 feeding from the same rewarded feeder. At the other four sites, we applied the ‘unstable’ social
197 treatment. In this treatment, each individual was randomly reassigned to a new feeder independently,
198 and thus was not always consistently feeding from the same rewarded feeder with the same other
199 individuals and may therefore have experienced disruptions in their social connections. Third, in the
200 second reversal stage, we again reassigned birds to new feeders, applied the stable and unstable
201 treatments as above, and monitored visits for eight to ten days.

In our previous analyses of this dataset, we provided an extensive description of demographic factors affecting variation in participation, likelihood of learning, and learning speed in this system (Reichert et al. 2020). We found both species- and individual-level variation in learning speed (Reichert et al. 2020), and in the propensity to scrounge (Reichert et al. 2021). In an analysis focused on great tits, we also found that the social stability treatment had lasting effects on the social network that carried over across contexts (Troisi et al. 2025). Here, we extend this work by asking whether an experimental manipulation of flock stability, and individuals' social network positions, affected individual foraging behavior (learning, scrounging, foraging rate), and if so, which components were affected.

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,

226 quantified as the number of visits to their rewarded feeder on the day after it had met the learning
227 criterion.
228
229 We note that individuals of both great tits and blue tits foraged in the same mixed species flocks, and so
230 the social networks were constructed and social network metrics calculated using data from all detected
231 individuals, regardless of species. Monitoring at the study population also involves giving RFID tags to
232 any captured marsh tit (*Poecile palustris*) and nuthatch (*Sitta europaea*), thus social networks also
233 include these individuals when detected. We restrict our analyses to great tits and blue tits because only
234 these two species interacted with the learning apparatus in large numbers. The number of individuals of
235 each species included in the social network varied slightly between experimental stages (Table S1).
236
237 We built social networks by assigning birds' visits to discrete flocking events using a Gaussian mixture
238 model (Psorakis et al. 2012, 2015). We defined edges in the social network between each individual that
239 was detected in a flocking event (Troisi et al. 2025). We then quantified the association strength
240 between each possible pair of individuals using a simple ratio index calculated as the number of times
241 both individuals were seen in the same flocking event divided by the total number of flocking events in
242 which either (or both) individual was present (Cairns and Schwager 1987; Whitehead 2008). From these
243 data we calculated the two social metrics used in analyses for each individual: 1) its average flock size
244 (i.e. the mean number of individuals it was observed with in flocking events) and 2) weighted degree as
245 the weighted sum of its association strengths with all other individuals in the network. These metrics
246 were calculated separately for each of the three experimental stages.
247
248 *Statistical analyses*
249

250 All statistical analyses were conducted in R version 4.5.0 (R Development Core Team 2024). Our dataset
251 included 68 individual great tits and 115 individual blue tits that met the learning criterion in all three
252 experimental stages. Other individuals that were detected during the experiments but did not meet the
253 learning criteria were excluded, because the majority of these individuals made very few visits to the
254 feeders (Reichert et al. 2020), and because we were interested in the effects of the social stability
255 treatment on reversal learning performance, which could not be assessed in a meaningful way if birds
256 did not meet the initial learning criterion prior to the reversal. We used separate statistical models for
257 each of the three foraging strategy variables to determine how these were affected by the social
258 stability treatment and an individual's social network metrics. All models were run with the lme4 version
259 1.1-35.5 package (Bates et al. 2015). Where significant interactions were identified we used Tukey post-
260 hoc tests to determine which groups were different from one another. For interactions involving
261 categorical variables (experimental stage, species and social stability), we did post-hoc testing using the
262 emmeans function from the emmeans version 1.10.4 package in R (Lenth 2022), which calculates
263 estimated marginal means for each combination of factors. For interactions involving a continuous
264 variable (average flock size or weighted degree), we did post-hoc testing using the emtrends function in
265 the emmeans package, which tests for differences in slopes of the relationship between the continuous
266 predictor and the foraging variable between the levels of the categorical variables (experimental stage,
267 species). We checked model assumptions of normality or uniformity of residuals and non-collinearity of
268 variables using the check_model function in the performance version 0.14.0 package (Lüdecke et al.
269 2021). Learning speed (natural log-transformed) was modeled as a Gaussian variable in a linear mixed
270 model. Proportion scrounged was modeled as a binomial variable in a generalized linear mixed model.
271 Foraging rate was modeled as a Gaussian variable in a linear mixed model. Raw data and code are
272 available at https://figshare.com/s/8ddfb55d391138371d36.
273

For each of the three foraging variables, results for which we present in separate sections, we tested for the effects of our social stability manipulation and social variables. First, we tested for effects of the social stability treatment. For these models, we only included data from the two reversal learning stages, because the social stability treatment was applied after the initial learning stage. We included individual identity as a random effect and included the three-way interaction between species, experimental stage and social stability treatment as the main factors of interest, expecting that the effects of the social stability treatment could vary by species or between the two reversal stages. Specifically, for the reversal stages, we expected that relationships between social metrics and foraging should become stronger by the second reversal as the relationships become more established in the stable group and the difference with the unstable group more pronounced. Without specifying any specific a priori predictions, we expected that relationships between sociality and foraging could vary among species because of differences in factors like body size, dominance, and predation risk, all of which influence foraging behavior. We included three additional variables as fixed effects to control for factors that were identified in previous analyses to affect learning performance: whether or not the feeder was located at the edge of the array, and the amounts of time that an individual's assigned and non-assigned feeders were inoperable due to equipment malfunction (Reichert et al. 2020). In our previous study we found that birds assigned to edge feeders learned more quickly in all three experimental stages (Reichert et al. 2020). Some feeders malfunctioned during the course of the experiment because of power loss or antenna failure and did not open for any of the birds or record any visits until they were repaired (further details and data on these occurrences are given in Reichert et al. 2020). We still include data from birds in such arrays, and our statistical approach aims to minimize these disruptions; we acknowledge that feeder malfunctions could have affected individual learning performance and are a source of noise for the other variables, which we assume was random with respect to the hypotheses tested.

Second, we tested for effects of the two social network position variables, average flock size and weighted degree. These models included data from all three experimental stages. Each model included individual identity as a random effect and two three-way interaction terms: species, experimental stage and average flock size, and species, experimental stage and weighted degree. Social stability treatment was not included as a factor in this model because it was not applied during the initial learning stage and because for these tests we were interested in the effects of the social network position itself, which would have been obscured by including a factor that affects social network position, as we demonstrated in a previous analysis of this dataset (Troisi et al. 2025). We again included additional fixed effects of whether or not the feeder was located at the edge of the array, and the amounts of time that an individual's assigned and non-assigned feeders were inoperable due to equipment malfunction.

310 RESULTS

311

312 There were 262530 records of the 183 focal individuals across the three experimental stages (great tits:
313 95818 visits, N = 68 individuals; blue tits: 166712 visits, N = 115 individuals). Across these stages, the
314 average flock size was (mean ± SE) 13.74 ± 0.26 for great tits and 12.59 ± 0.21 for blue tits, and the
315 average weighted degree was 6.65 ± 0.14 for great tits and 6.13 ± 0.12 for blue tits. Learning speed
316 averaged 62.4 ± 6.9 and 63.8 ± 4.62 visits until the learning criterion was met for great tits and blue tits,
317 respectively. For scrounging, great tits had 2347 total scrounging events (mean ± SE = 11.5 ± 1.8), and
318 blue tits had 6552 scrounges (mean ± SE = 19.0 ± 1.3). Foraging rate averaged 51.9 ± 1.4 and 46.0 ± 0.9
319 visits on the day after the learning criterion was met for great tits and blue tits, respectively.

320

321 *Effects of sociality on learning speed*

322 There was no significant three-way interaction between social stability treatment, experimental stage
323 and species (Table 1). However, there was a significant interaction between social stability treatment
324 and experimental stage (Table 1, Figure 1A, 1B). For both species, there was no difference between the
325 unstable and stable groups in learning speeds in the first reversal, but in the second reversal, individuals
326 in the unstable treatment learned more quickly (Table S2, Figure 1A). Learning speeds were not
327 significantly different in the two social stability treatment groups in the initial learning stage, confirming
328 that there were no differences prior to the treatment being applied (Table S3).

329

330 There were significant three-way interactions between species, experimental stage and both average
331 flock size and weighted degree on learning speed (Table 2). For blue tits, individuals in larger flocks
332 learned faster in the initial and first reversal stages, but this pattern was reversed in the second reversal
333 stage where individuals in smaller flocks learned faster (Table S4, Figure 1B). For great tits, individuals

generally learned faster in larger flocks, but, unlike in blue tits, the relationship between flock size and learning speed did not differ across experimental stages (Table S4, Figure 1B). Blue tits were relatively unaffected by weighted degree and showed no significant variation in the relationship between weighted degree and learning speed across the three experimental stages, while great tits showed a significantly different relationship between these two variables in the second reversal compared to initial learning (Table S5, Figure 1C). Specifically, great tits' learning speeds were relatively independent of weighted degree in the initial learning stage, but by the second reversal individuals with lower weighted degrees learned more quickly than individuals with higher weighted degrees (Table S5, Figure 1C).

Effects of sociality on scrounging

There was a significant three-way interaction between species, experimental stage and social stability treatment on the proportion scrounged (Table 1). Post-hoc tests indicated that scrounging levels were significantly higher in the stable treatment compared to the unstable treatment for both species in the second reversal (Table S6, Figure 2A). However, in the first reversal there was no effect of social stability treatment on scrounging for great tits, and for blue tits there was a marginal effect, where again scrounging levels were higher in the stable compared to the unstable treatment groups (Table S6, Figure 2A). However, we noticed that in the initial learning stage, there was a main effect of social stability treatment: individuals at the sites that would be assigned to the stable treatment had higher significantly scrounging levels than individuals in the unstable treatment, indicating that there may have been a pre-existing difference between these groups for this trait, and this difference applied to both species (Table S3). However, because we found no significant effect of social stability treatment in the first reversal and then significant differences in the second reversal, the treatment had an effect over and above any differences in the populations prior to treatment.

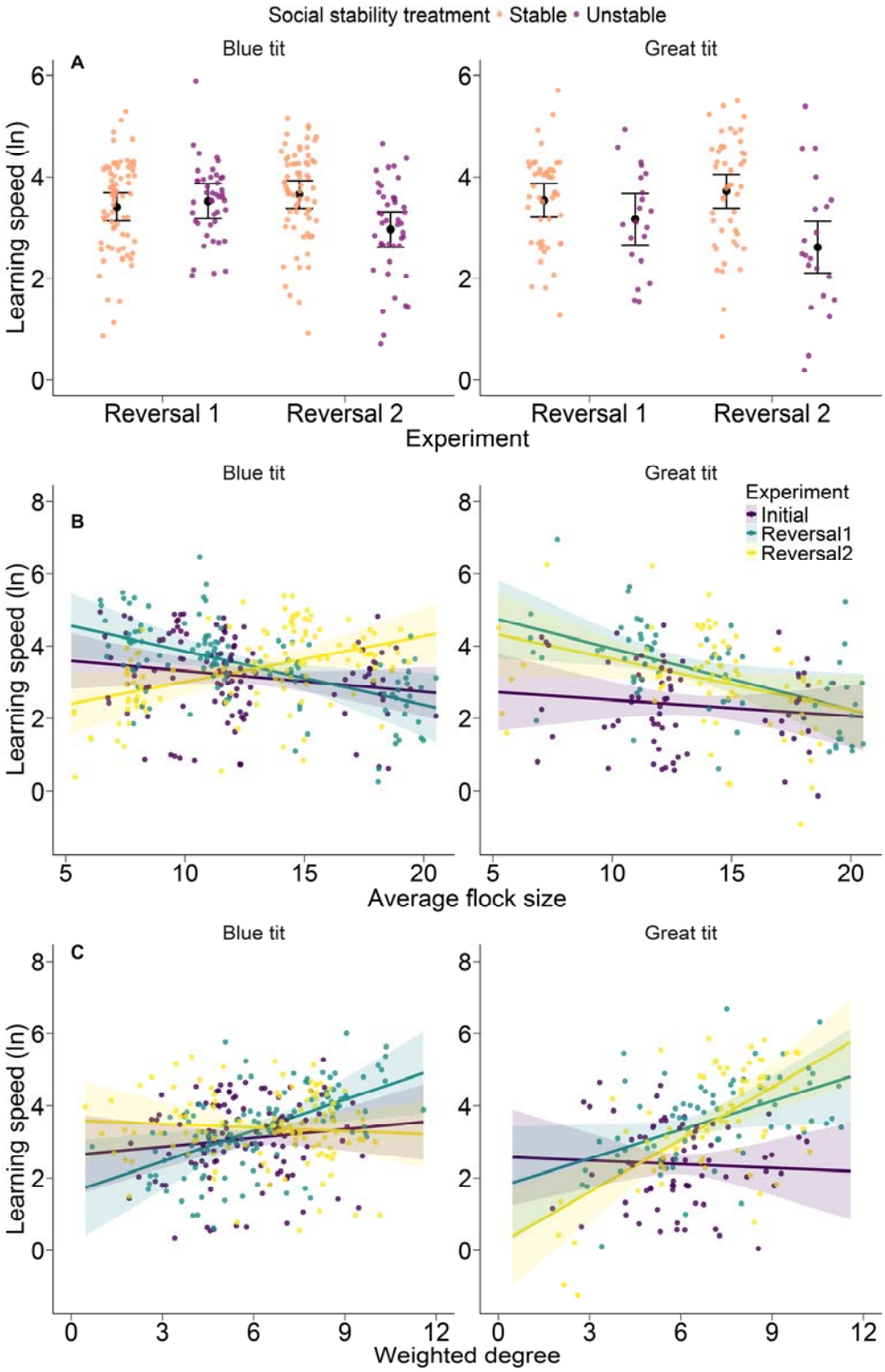
There were significant three-way interactions between species, experimental stage and both average flock size and weighted degree on proportion scrounged (Table 2). For great tits, individuals in larger flocks scrounged less often but this effect was much stronger in the reversal stages than in the initial learning stage (Table S7, Figure 2B). There was also a significant difference between the two reversal stages, with a stronger negative relationship in the first reversal than in the second reversal (Table S7, Figure 2B). For blue tits, the relationship between flock size and proportion scrounged was overall much weaker, but both reversal stages showed a more negative relationship between flock size and proportion scrounged compared to the initial learning stage (Table S7, Figure 2B). In both species there was an increasingly positive relationship between weighted degree and proportion scrounged as the experiment proceeded from the initial learning stage through the reversals (Figure 2C): individuals with higher weighted degree scrounged more often. For blue tits, the relationship became significantly stronger and more positive in comparisons between each successive experimental stage (Table S8, Figure 2C). For great tits, both reversal stages showed significantly stronger positive relationships between weighted degree and proportion scrounged compared to the initial learning stage, but there was no difference between the two reversal stages (Table S8, Figure 2C).

Effects of sociality on foraging rate

There was no effect of the social stability treatment on foraging rate (Figure 3A). This was the case both for the full model including interactions with species and experimental stage (Table 1) and for a reduced model that did not include the interactions (Table S9). In the reduced model, there was a statistically significant effect of species, with great tits having a higher foraging rate than blue tits, and an effect of feeder location, with higher foraging rates for feeders on the edge of the array (Table S9). Foraging rates

were not significantly different in the two social stability treatment groups in the initial learning stage, confirming that there were no differences prior to the treatment being applied (Table S3).

There were no interactions between species, experimental stage and either average flock size or weighted degree (Table 2). There was, however, a main effect of weighted degree: individuals with a higher weighted degree had a higher foraging rate (Figure 3C). This effect was present in both the full model (Table 2) and in a reduced model that did not include interaction effects (Table S10). In the full model there was a marginal effect of average flock size (Table 2), although this effect was reduced and not statistically significant in the reduced model without interactions (Table S10). Foraging rates generally remained relatively constant or decreased slightly with increasing flock sizes (Figure 3B).



391

392 Figure 1. Effects of sociality on learning speed. A. Effects of social stability treatment and experimental

393 stage on learning speed (ln-transformed) for blue tits (left) and great tits (right). Black points represent

394 estimated marginal means (± 95% CI) from the model. Small colored points represent partial residuals
395 from the model for each individual. B. Relationship between average flock size and learning speed for
396 each species. Lines represent predicted estimate (± 95% CI) from the model, with separate colors for
397 each experimental stage, and points represent partial residuals from the model for each individual. C.
398 Relationship between weighted degree and learning speed for each species. Interpretation as in B.
399

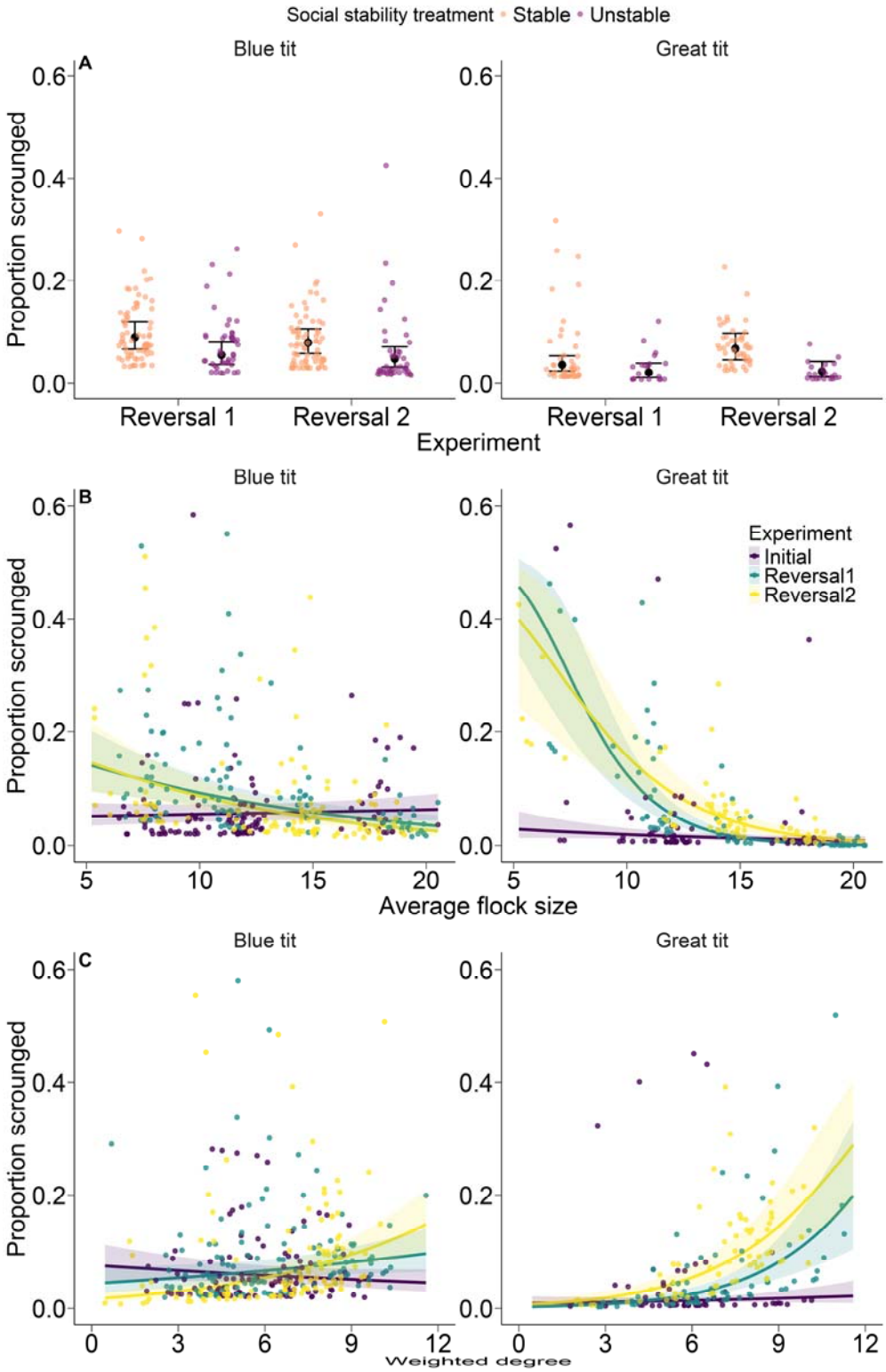
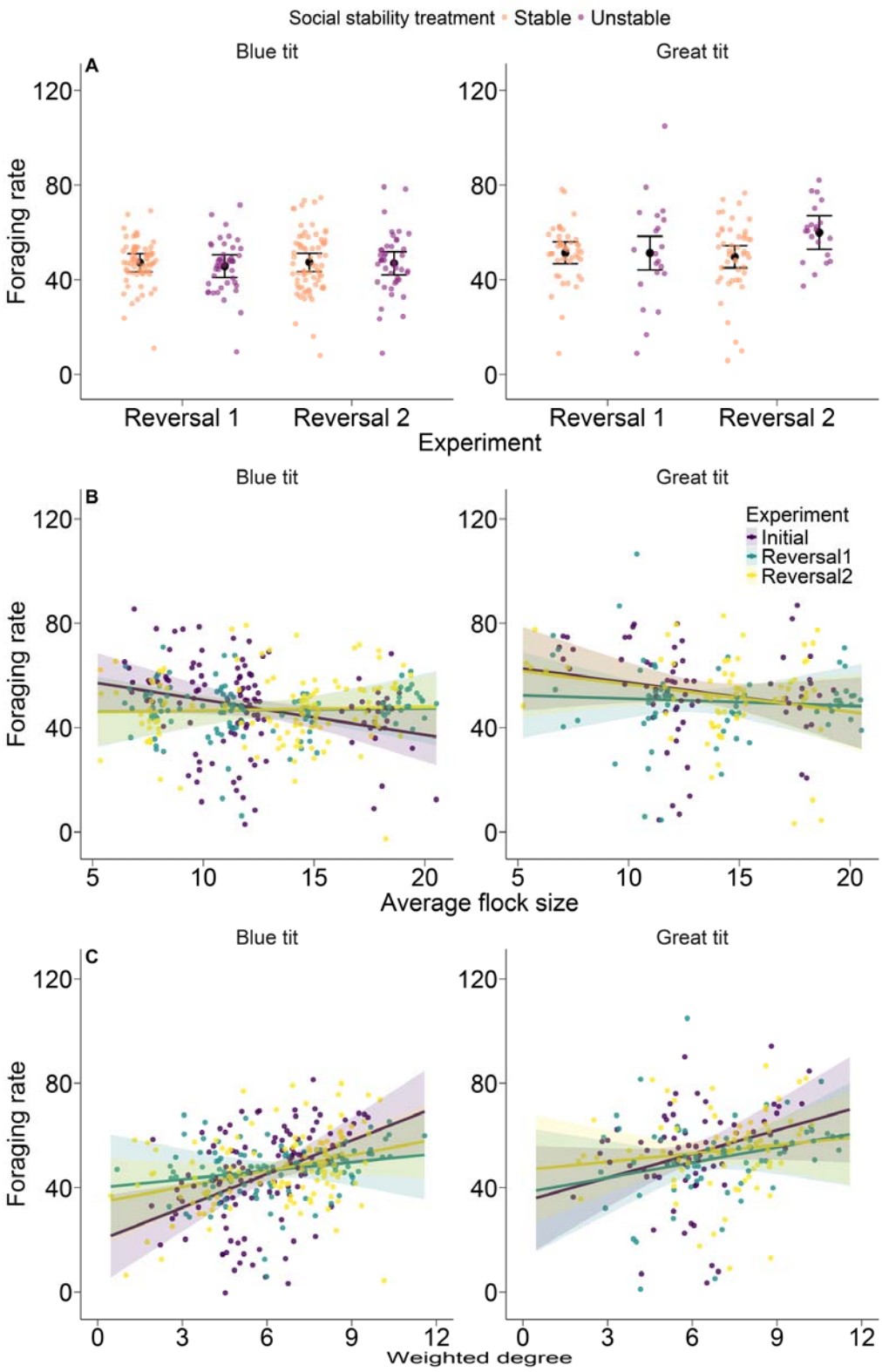


Figure 2. Effects of sociality on scrounging. A. Effects of social stability treatment and experimental stage on the proportion of feeds that were scrounges for blue tits (left) and great tits (right). Black points

403 represent estimated marginal means (± 95% CI) from the model. Small colored points represent partial
404 residuals from the model for each individual. B. Relationship between average flock size and scrounging
405 for each species. Lines represent predicted estimate (± 95% CI) from the model, with separate colors for
406 each experimental stage, and points represent partial residuals from the model for each individual. C.
407 Relationship between weighted degree and scrounging for each species. Interpretation as in B. The y-
408 axis is cut off at 0.6 for visualization purposes, there are 1, 13, and 13 outlying points not depicted in A,
409 B, and C, respectively. Figure S1 presents the same graphs but with all data points included.
410



411

412 Figure 3. Effects of sociality on foraging rate. A. Effects of social stability treatment and experimental

413 stage on foraging rate (number of rewarded visits on the day after the learning criterion was met) for

blue tits (left) and great tits (right). Black points represent estimated marginal means (± 95% CI) from the model. Small colored points represent partial residuals from the model for each individual. B. Relationship between average flock size and foraging rate for each species. 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 for each species. Interpretation as in B.

420 Table 1. Effects of social stability on foraging traits

Foraging trait	Effect	Estimate	SE	t	P
Learning speed	Intercept	3.407	0.145	23.553	
	Social stability treatment (unstable)	0.111	0.226	0.491	0.623
	Experiment (second reversal)	0.244	0.175	1.395	0.165
	Species (great tit)	0.127	0.218	0.583	0.560
	Own feeder malfunction time (hrs)	0.107	0.019	5.532	< 0.001
	Other feeder malfunction time (hrs)	0.061	0.012	5.018	< 0.001
	Feeder location (edge)	−0.46	0.12	−3.827	< 0.001
	Social stability treatment (unstable) X Experiment (second reversal)	−0.8	0.284	−2.819	0.005
	Social stability treatment (unstable) X Species (great tit)	−0.484	0.377	−1.283	0.201
	Experiment (second reversal) X Species (great tit)	−0.062	0.277	−0.224	0.823
	Social stability treatment (unstable) X Experiment (second reversal) X Species (great tit)	0.068	0.483	0.141	0.888
Scrounging	Intercept	−3.469	0.169	−20.535	
	Social stability treatment (unstable)	−0.532	0.273	−1.951	0.051
	Experiment (second reversal)	−0.142	0.038	−3.768	< 0.001
	Species (great tit)	−0.973	0.269	−3.615	< 0.001

	Own feeder malfunction time (hrs)	0.113	0.007	16.235	< 0.001
	Other feeder malfunction time (hrs)	0.065	0.005	12.411	< 0.001
	Feeder location (edge)	−0.016	0.035	−0.446	0.655
	Social stability treatment (unstable) X Experiment (second reversal)	−0.007	0.070	−0.095	0.924
	Social stability treatment (unstable) X Species (great tit)	−0.011	0.470	−0.023	0.982
	Experiment (second reversal) X Species (great tit)	0.800	0.069	11.56	< 0.001
	Social stability treatment (unstable) X Experiment (second reversal) X Species (great tit)	−0.564	0.149	−3.777	< 0.001
Foraging rate	Intercept	46.079	2.03	22.701	
	Social stability treatment (unstable)	-1.457	3.172	-0.459	0.646
	Experiment (second reversal)	0.142	2.418	0.059	0.953
	Species (great tit)	4.149	3.061	1.355	0.176
	Own feeder malfunction time (hrs)	-0.219	0.271	-0.807	0.42
	Other feeder malfunction time (hrs)	-0.233	0.17	-1.375	0.17
	Feeder location (edge)	3.79	1.67	2.269	0.024
	Social stability treatment (unstable) X Experiment (second reversal)	1.05	3.918	0.268	0.789
	Social stability treatment (unstable) X Species (great tit)	1.391	5.295	0.263	0.793
	Experiment (second reversal) X Species (great tit)	-1.817	3.829	-0.475	0.636

Social stability treatment (unstable) X Experiment (second reversal) X Species (great tit)	9.248	6.666	1.387	0.167

Fixed effects from mixed models with individual identity as a random effect and ln−transformed learning speed (Gaussian), proportion scrounged (binary) or foraging rate (Gaussian) as the dependent variable. The reference category for social stability treatment is the stable treatment, for experimental stage is the first reversal stage, for species is blue tits, and for the feeder location is center.

426 Table 2. Effects of social characteristics on foraging traits

Foraging trait	Effect	Estimate	SE	t	P
Learning speed	Intercept	3.53	0.429	8.234	
	Experiment (first reversal)	0.144	0.518	0.279	0.781
	Experiment (second reversal)	−1.432	0.549	−2.607	0.009
	Species (great tit)	−0.214	0.715	−0.300	0.764
	Own feeder malfunction time (hrs)	0.086	0.014	6.244	< 0.001
	Other feeder malfunction time (hrs)	0.065	0.009	7.073	< 0.001
	Feeder location (edge)	−0.831	0.100	−8.271	< 0.001
	Flock size	−0.058	0.047	−1.222	0.222
	Weighted degree	0.080	0.095	0.842	0.400
	Flock size X Experiment (first reversal)	−0.090	0.074	−1.216	0.225
	Flock size X Experiment (second reversal)	0.184	0.071	2.604	0.010
	Flock size X Species (great tit)	0.013	0.080	0.167	0.868
	Experiment (first reversal) X Species (great tit)	0.638	0.909	0.702	0.483
	Experiment (second reversal) X Species (great tit)	0.253	1.001	0.252	0.801
	Weighted degree X Experiment (first reversal)	0.206	0.143	1.437	0.151

	Weighted degree X Experiment (second reversal)	−0.113	0.128	−0.880	0.380
	Weighted degree X Species (great tit)	−0.114	0.153	−0.746	0.456
	Flock size X Experiment (first reversal) X Species (great tit)	−0.035	0.119	−0.293	0.770
	Flock size X Experiment (second reversal) X Species (great tit)	−0.280	0.115	−2.442	0.015
	Weighted degree X Experiment (first reversal) X Species (great tit)	0.093	0.224	0.417	0.677
	Weighted degree X Experiment (second reversal) X Species (great tit)	0.631	0.204	3.096	0.002
Scrounging	Intercept	−3.725	0.25	−14.891	
	Experiment (first reversal)	0.936	0.132	7.076	< 0.001
	Experiment (second reversal)	0.252	0.152	1.656	0.098
	Species (great tit)	−0.959	0.510	−1.878	0.060
	Own feeder malfunction time (hrs)	0.093	0.005	18.612	< 0.001
	Other feeder malfunction time (hrs)	0.054	0.003	17.47	< 0.001
	Feeder location (edge)	−0.214	0.029	−7.381	< 0.001
	Flock size	0.015	0.019	0.752	0.452
	Weighted degree	−0.048	0.033	−1.461	0.144
	Flock size X Experiment (first reversal)	−0.116	0.018	−6.483	< 0.001
	Flock size X Experiment (second reversal)	−0.140	0.02	−7.151	< 0.001

	Flock size X Species (great tit)	−0.098	0.047	−2.081	0.037
	Experiment (first reversal) X Species (great tit)	2.736	0.381	7.173	< 0.001
	Experiment (second reversal) X Species (great tit)	2.446	0.427	5.731	< 0.001
	Weighted degree X Experiment (first reversal)	0.122	0.037	3.283	0.001
	Weighted degree X Experiment (second reversal)	0.251	0.039	6.387	< 0.001
	Weighted degree X Species (great tit)	0.129	0.079	1.632	0.103
	Flock size X Experiment (first reversal) X Species (great tit)	−0.266	0.052	−5.121	< 0.001
	Flock size X Experiment (second reversal) X Species (great tit)	−0.089	0.044	−2.008	0.045
	Weighted degree X Experiment (first reversal) X Species (great tit)	0.206	0.098	2.112	0.035
	Weighted degree X Experiment (second reversal) X Species (great tit)	0.034	0.083	0.412	0.680
Foraging rate	Intercept	35.602	6.486	5.489	
	Experiment (first reversal)	1.722	7.4	0.233	0.816
	Experiment (second reversal)	-4.579	7.864	-0.582	0.561
	Species (great tit)	12.105	10.808	1.12	0.263
	Own feeder malfunction time (hrs)	-0.363	0.205	-1.766	0.078
	Other feeder malfunction time (hrs)	-0.112	0.137	-0.816	0.415
	Feeder location (edge)	4.239	1.448	2.927	0.004

Flock size	-1.349	0.711	-1.896	0.058
Weighted degree	4.285	1.418	3.021	0.003
Flock size X Experiment (first reversal)	1.438	1.068	1.347	0.179
Flock size X Experiment (second reversal)	1.483	1.024	1.448	0.148
Flock size X Species (great tit)	0.235	1.208	0.194	0.846
Experiment (first reversal) X Species (great tit)	-9.344	12.995	-0.719	0.473
Experiment (second reversal) X Species (great tit)	15.762	14.338	1.099	0.272
Weighted degree X Experiment (first reversal)	-3.196	2.065	-1.547	0.123
Weighted degree X Experiment (second reversal)	-2.258	1.872	-1.206	0.228
Weighted degree X Species (great tit)	-1.242	2.295	-0.541	0.589
Flock size X Experiment (first reversal) X Species (great tit)	-0.598	1.715	-0.348	0.728
Flock size X Experiment (second reversal) X Species (great tit)	-1.415	1.657	-0.854	0.394
Weighted degree X Experiment (first reversal) X Species (great tit)	2.096	3.245	0.646	0.519
Weighted degree X Experiment (second reversal) X Species (great tit)	0.281	2.963	0.095	0.925

Fixed effects from mixed models with individual identity as a random effect and ln−transformed learning speed (Gaussian), proportion scrounged (binary) or foraging rate (Gaussian) as the dependent variable. The reference category for experimental stage is the initial learning stage, for species is blue tits, and for the feeder location is center.

432 Table 3. Summary of results and potential mechanisms

433

Social trait	Foraging trait	Effect	Potential mechanism
Social stability	Learning speed	Negative	Social instability disrupts dominance hierarchies, facilitating learning
	Scrounging	Positive	More competition in stable groups, or trade-off with learning speed
	Foraging rate	None	Individual variation in hunger, motivation or competitive ability
Flock size	Learning speed	Mostly positive	Learning is facilitated by shared vigilance, reduced risk of predation
	Scrounging	Negative	Trade-off with learning speed
	Foraging rate	None	Individual variation in hunger, motivation or competitive ability
Weighted degree	Learning speed	Negative	Individuals with strong social ties visit non-rewarded feeders with social partners
	Scrounging	Positive	Stronger connections facilitate learning to scrounge, or trade-off with learning speed
	Foraging rate	Positive	Increased sense of security and shared vigilance with strong social connections

434

435 For each combination of social and foraging trait measured, we give the direction for the general trend in the relationship between the two
436 traits, but note that all of these effects showed additional variation across species and experimental stages that in some cases resulted in a
437 qualitatively different relationship. Potential mechanisms for the effect are given, but these are speculative and our experiments were not
438 designed to isolate specific mechanisms.

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. In a previous analysis of this dataset focused on great tits, we 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 in both great tits and blue tits, 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. Although there were multiple differences in effects on the two study species, these were often in the magnitude rather than the direction of the effect, which also underscores the robustness of our findings. 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 (reviewed in Table 3). 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, but we found no effect of treatment for the first reversal and a significant effect in the opposite direction for the second reversal. For both species, individuals in the unstable group were faster to learn in the second reversal. We note that a previous analysis on this study system focused on the dynamics of the learning process, and therefore including many other

variables not analyzed here, found no effects of social stability treatment on reversal learning speed (Reichert et al. 2020). The difference between our current study and these previous results can be explained by our more focused analysis and including both experimental stages in the same model, which increases power and allows the contrast between the first and second reversal to be identified. Both species were affected similarly by the treatment, suggesting that the consequences of social stability have general effects on learning in a foraging context despite species differences in competitive ability and learning performance (Reichert et al. 2020, 2021). One explanation for our finding that learning performance was not better in stable social groups is that most individuals learned the task relatively quickly, potentially limiting the utility of social learning in this system (Reichert et al. 2020).

The somewhat improved learning performance in the unstable treatment in our study could have occurred because this treatment disrupted social competition and dominance relationships that built up among individuals attempting to access the same feeder. Our social network metrics do not capture such relationships because they are based on flock membership, but they are plausible, because high levels of competition and low dominance ranks are associated with reduced learning performance in many species (Chalmeau and Gallo 1993; Pravosudov et al. 2003; Langley et al. 2018). Similarly, there is evidence from multiple species, including great tits, that better problem solvers are poor competitors at feeders (Cole and Quinn 2012), so the unstable treatment may have enabled those better at problem solving to realize greater cognitive performance when otherwise negative hierarchical interactions with known individuals were reduced. However, other studies of learning in wild systems found limited effects of dominance and social stability (Heinen et al. 2021*a*, 2021*b*; Pitera et al. 2025), and other social processes caused by our manipulation could also be responsible.

For great tits, we found limited evidence for effects of average flock size on learning speed, but in general individuals with larger average flock sizes learned more quickly. For blue tits, individuals with larger average flock size also learned more quickly in the first reversal, but more slowly in the second reversal. In a previous study of great tits from the same population, rates of innovative problem solving also increased with flock size (Morand-Ferron and Quinn 2011). Thus, the costs of being in larger groups, such as increased competition, may be outweighed by other benefits, such as dilution of risk, in addition to other more subtle benefits including better cognitive performance, at least for some contexts and cognitive tasks. When we examined the effects of weighted degree, the strength of an individual's social connections, we found that, at least for the second reversal, great tits 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. Blue tits were less affected by this variable, perhaps because their cognitive performance is more strongly affected by general social competition to access feeders.

Effects of sociality on scrounging

Scrounging rates were higher in the stable treatment during the second reversal stage for both species and, for blue tits, also in the first reversal. These results ran counter to our expectation that individuals in the unstable treatment would scrounge more because if individuals primarily scrounge from close social associates (King et al. 2009; Harten et al. 2018), the unstable treatment would have broken up those associations. However, we previously found that the across-stage correlation between the dyadic associations between individuals in the social network did not differ between the stable and unstable treatments (Troisi et al. 2025), so disruption of scrounging associations was probably not responsible for

our findings of more scrounging in the stable treatment. The most likely explanation for higher scrounging in the stable treatment is that individuals in the unstable treatment were faster to learn to produce, and therefore spent less time using the scrounging tactic, given the general trade-off between producing and scrounging (Barnard and Sibly 1981).

For both great tits and blue tits, scrounging rates were lower for birds with larger average flock size in both reversal stages. These results were surprising both because we had expected larger groups to provide more opportunities to scrounge, and because individuals in larger groups generally learned more quickly, which should have provided more opportunity for scroungers. However, in a previous analysis of this dataset, we found that scrounging and production learning trade-off such that individuals that learn quickly scrounge less often (Reichert et al. 2021). As we argued above for the effects of the social stability treatment, the faster learning speed for birds in larger flocks therefore could have corresponded with reduced benefits of scrounging relative to producing. Thus, the social factors affecting production learning, in this case potentially beneficial effects of being in large groups, could have indirectly negatively influenced the expression of an alternative foraging tactic. This explanation could also apply to the positive relationship between scrounging and weighted degree in the reversals. Particularly for the second reversal, great tits with higher weighted degree were slower to learn, which could have induced more scrounging. However, determining the direction of causation is difficult. Indeed, an alternative explanation is that because effective scrounging is a learned behavior in this system (Reichert et al. 2021), birds with stronger connections may have had more opportunities to learn effective scrounging techniques or could have developed more stable producer-scrounger relationships. This would be consistent with a previous study of great tits in which birds with especially strong connections were found to forgo production to stay with their mating partner, from whom they obtained food by scrounging (Firth et al. 2015).

534

535 *Effects of sociality on foraging rate*

536

537 Individuals' foraging rates after learning the location of their rewarded feeder were not affected by the
538 social stability treatment for either species. Foraging rate at feeders is a repeatable trait in this system
539 (Crates et al. 2016). This individual consistency in behavior may have contributed to our findings that the
540 overall amount of foraging activity remained relatively stable despite any changes that the social
541 stability treatments caused to social relationships, overall social structure, and subsequent effects on
542 interactions at the feeders. Our findings suggest that the effects of living in groups on individual foraging
543 rates are not influenced by the ability to feed near specific individuals, which are unnecessary for
544 general benefits of social foraging like shared vigilance and the dilution effect, though we acknowledge
545 that these effects may have been limited by the relative ease with which food could be obtained post
546 learning.

547

548 Foraging rates were also unaffected by average flock size. A previous study found a similar pattern in
549 which overall visit lengths and inter-visit intervals were not affected by an experimental manipulation of
550 density at the feeder (Regan et al. 2022). However, it also found that individuals with stronger social ties
551 were more likely to visit feeders and that these effects interacted with social group density for some
552 foraging behaviors (Regan et al. 2022), pointing to the importance of weighted degree in foraging.
553 Indeed, we found that individuals had a higher foraging rate at our feeders when they had a higher
554 weighted degree. This effect was somewhat stronger for the initial learning stage, perhaps because at
555 this early stage scrounging levels were low and the social stability treatment had not yet affected social
556 connections. One important consideration is that our measure of foraging rate only includes visits to our
557 experimental feeders. Although feeders are important food sources, great tits have a broad diet in the

558 winter even when supplemental food is available (Coomes et al. 2025), and this is likely to be the case
559 for blue tits as well. Thus, individuals may vary in their tendency to visit feeders in the first place, and
560 this may be related to the strength of their social relationships, which could explain our findings.
561
562 *Differences across stages and species*
563
564 A clear outcome of our study is that effects of sociality on foraging varied across the experimental
565 stages, an initial associative learning task and two subsequent reversal learning tasks. However, this was
566 only the case for the two cognitively demanding foraging traits, learning speed and scrounging rate
567 (which is cognitively demanding because individuals learn to scrounge in our system; (Reichert et al.
568 2021)), but not for foraging rate. This implies that the effects of sociality may be especially pronounced
569 in cognitively challenging situations. The main difference between the experimental stages was in the
570 learning task required of the birds, from an initial association to two successive reversals. Therefore, one
571 explanation for variation across stages is that sociality interacted differently with the cognitive
572 challenges associated with each task. Initial learning is driven by an associative process between a
573 feeder and the reward, while reversal learning requires additional cognitive flexibility so that individuals
574 inhibit their response to the previously rewarded feeder and instead make an association with the new
575 rewarded feeder (Morand-Ferron et al. 2022). At the same time, some individuals were learning to
576 become increasingly proficient at scrounging and there were opportunities to socially learn from other
577 individuals visiting the feeders (Reichert et al. 2021). Some previous studies showed that the effects of
578 the social environment on cognition depend on the cognitive task (Kogan et al. 2000; Schrijver et al.
579 2004), and our results may indicate that these findings extend to foraging behaviors involving different
580 cognitive mechanisms in a wild population. Although further study is needed, our results point to an
581 effect of sociality on the opportunity to learn alternative foraging tactics, adding to the evidence that

582 cognition is shaped by social structure (Hoppitt and Laland 2013; Seyfarth and Cheney 2015; Kulahci and
583 Quinn 2019).
584
585 Another potential explanation for our finding of variation in the effects of sociality across stages is that
586 the overall structural properties of the global social network itself changed. Indeed, we previously
587 showed in this dataset that average flock size and weighted degree both increased from the initial
588 learning to the second reversal stages, and the increase in flock size was stronger for the stable
589 treatment (Troisi et al. 2025). Where we found significant interactions between experimental stage and
590 social network metrics on foraging behavior, the relationships between sociality and behavior were
591 generally stronger during the reversal stages, indicating that the increased strength of social
592 connections led to emergent impacts on foraging. At the same time, we found support for our
593 prediction that the effects of the social stability treatment on foraging would be stronger in the second
594 reversal than the first reversal, which indicates that multiple social disruptions have increasingly large
595 effects on foraging. The current study and the analyses in Troisi et al. (2025) clearly show that the
596 foraging and social processes were highly dynamic within groups during this experiment. We note that
597 some of these social processes were likely already in flux prior to the initial learning stage. Our
598 experimental design involved manipulating feeder placement and access to food to attract birds to the
599 area and acclimate them to the experimental devices before we began the learning experiments. Social
600 network traits and flock size varied even across these early stages, indicating that all individuals would
601 have been experiencing some social instability before our social stability manipulation (Troisi et al.
602 2025). Indeed, some baseline level of social instability is the norm in these foraging flocks, which are
603 characterized by a fission-fusion structure (Farine et al. 2015*b*). Our social stability manipulation
604 therefore aimed to add additional instability to the social group, and our results indicate that this did
605 have effects on foraging traits. Nevertheless, social instability can occur at different scales (e.g., at a fine

606 scale of accessing food at different areas in a plot to a large scale of flock membership), and further
607 work is needed to determine if social processes operating at different scales have different effects on
608 foraging.
609
610 We calculated the social network based on social ties across species, which is appropriate given the
611 strong tendency of great tits and blue tits to forage together. Although some social processes like mate
612 selection will be more strongly affected by within-species social ties (Firth et al. 2018), social foraging
613 tactics like scrounging and competition at feeders are likely to be affected by all network members, even
614 heterospecifics. Indeed, we found that the social stability treatment had qualitatively, if not
615 quantitatively, similar effects on both blue tits and great tits, and the impact of weighted degree and
616 flock size was also broadly similar on most measures of foraging in both species. These common effects
617 not only indicate real social ties that extend to heterospecifics but also give evidence for the
618 effectiveness of our experimental manipulation and the robustness of our results. Our findings also raise
619 important questions for future work, including whether social effects on foraging fundamentally differ
620 between single-species and mixed-species flocks and whether the nature of among-species interactions
621 plays a role.
622
623 *Conclusions*
624
625 Both social network position and foraging emerge from a complex interplay of factors including
626 competition, cognition, individual personality, levels of predation and other environmental
627 characteristics, yet disentangling these factors in the wild has been difficult due to the lack of
628 experiments. Our findings that sociality affects multiple aspects of foraging success in a wild system
629 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 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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