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Social structure and social stability predict learning, scrounging and feeding rate in foraging flocks of wild songbirds

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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.

DATA AVAILABILITY STATEMENT

Raw data and analysis code are available at https://doi.org/10.6084/m9.figshare.29923118

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ABSTRACT

The social environment provides both opportunities and challenges for foragers but how multiple components of sociality and foraging interact is poorly understood. We tested whether foraging traits were associated with manipulated social stability and individual social network metrics in wild mixed-species bird flocks. First, individuals were required to learn to which feeder in an array of five they were assigned and thus rewarded. Thereafter, fine-scale social connections at the feeders were manipulated during two further stages by either assigning individuals to a new feeder along with all others assigned to their previous feeder (stable treatment), or reassigning individuals with random individuals to another feeder (unstable treatment). We measured the latency to learn to forage from the rewarded feeder at each stage, the rate of scrounging from otherwise non-rewarded feeders, and foraging rate the day after learning. In general we found: i) slower learning and higher scrounging in the stable treatment, and for individuals with higher weighted degree, and in smaller flocks; ii) foraging rate and weighted degree were positively associated. Our findings demonstrate the complex and dynamic nature of the relationship between sociality and foraging, and suggest how selection for group living is likely more nuanced than often 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).

One of the factors that changes most in the environment for many species is sociality, which 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 has received limited attention (Morand-Ferron et al. 2011; Aplin and Morand-Ferron 2017), but is 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 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). Here, we tested how foraging behavior in a wild mixed-species flock is predicted by: i) metrics of individual sociality; and ii) experimentally manipulated social stability at individual feeders within a five-feeder array, each feeder only one meter apart. This fine-scale manipulation of who individuals interact with at feeders within flocks has previously been shown to affect overall social network structure in this system (Troisi et al. 2025).

Foraging traits are likely to vary in how they are influenced by social interactions and yet most studies of the effects of sociality on foraging focus on an isolated foraging trait. An important exception to this is in the context of the producer-scrounger game, where the presence of other individuals is a prerequisite for scrounging, and is impacted by the behavior of individual associates, social network structure and social stability (Firth et al. 2015; Aplin and Morand-Ferron 2017; de Groot et al. 2026). In contrast, other components of foraging do not require, but may nevertheless be affected by, social contact. 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 increase when social connections are stronger, if these reduce an individual's perceived risk (Voelkl et al. 2016; Heathcote et al. 2017; Mady and Blumstein 2017).

Foraging traits also differ in their underlying cognitive mechanisms, and social effects on cognition could therefore drive variation in foraging strategies. Learning about where food can be found and how food can be extracted are two such cognitive mechanisms that can be 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). In the context of the producer-scrounger game, learning is involved in both production and improving scrounging efficiency (Reichert et al. 2021), though it should have limited effects 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 (Chimento et al. 2024). 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 to whom they are connected (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 therefore examined the effects of sociality on multiple foraging traits including production learning, scrounging and overall foraging rate, each of which was measured during three stages of the experiment (initial and two reversal learning stages).

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 a feeder-array they could access to obtain food (Reichert et al. 2020). In our previous analyses of this dataset, we provided an extensive description of demographic factors affecting variation in participation, likelihood of learning, and the latency to learn in this system (Reichert et al. 2020). We found both species- and individual-level variation in the latency to learn and the propensity to scrounge,

and that there is a trade-off between learning and scrounging such that individuals that learned more slowly scrounged more often (Reichert et al. 2020, 2021). In great tits, we also found that an experimental manipulation of fine-scale social stability when interacting at individual feeders in a five-feeder array (henceforth, “social stability”), where feeders were only one meter apart, had lasting effects on the social network at that array, and that these carried over across contexts (Troisi et al. 2025). Our previous work with this dataset was either focused on factors affecting cognitive mechanisms of foraging (Reichert et al. 2020, 2021; Morand-Ferron et al. 2022) or those driving variation in the social network (Troisi et al. 2025). We did not previously test whether the social network affects the different components of foraging explored here, but answering this question is critical for understanding how an ever-changing complex social environment can give rise to variation in foraging strategies in wild populations. Here we extend this previous work by asking whether i) an experimental manipulation of social stability, and ii) individuals’ social network positions, affected multiple components of individual foraging behavior across an initial learning stage and two reversal learning stages.

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 (note that the stability treatment was not applied in the initial learning stage, which was therefore excluded from this analysis). Our social stability treatment manipulated whether groups of individuals were consistently assigned to the same rewarded feeder in the five-feeder array across the two reversal stages. Although the small spatial separation between feeders in the array meant that whole flocks and any associated dominance hierarchy need not necessarily have changed (Troisi et al. 2025), the dyadic interactions taking place on a finer scale at any given feeder by definition did change during the reversal in the treatment where individuals previously assigned to one feeder were

independently reassigned to new feeders. During this treatment, while individuals searched the array for their new rewarded feeder they began visiting it more exclusively along with a new set of individuals as they learned its location. Our principal focus was to test what impact social stability had on foraging, and we suggest several non-mutually exclusive mechanisms that could give rise to these outcomes, though we do not attempt to experimentally distinguish between these. Social instability could lead to slower reversal learning through reduced potential for social learning from known individuals. If social instability disrupts established patterns of visits to feeders associated with turn taking or dominance hierarchies, which then need to be re-established, this could also lead to a pattern of slower reversal learning in the unstable treatment. On the other hand, these same disruptions could benefit learning if competitive hierarchies limit feeder access as they become more established. Similarly, social instability could reduce scrounging if this mainly occurs between established social partners at feeders (Firth et al. 2015), or increase scrounging if producing becomes more challenging (Giraldeau et al. 1994). We expected overall foraging rate post-learning within each stage to be less sensitive to social stability at this level. Regardless of the direction, we expected that the effects of social instability should increase with each successive reversal stage because relationships would become more established in the stable group, and the difference with the unstable group more pronounced as it experienced multiple social disruptions. To our knowledge, no previous study in a wild species has manipulated social stability in the context of fine-scale social interactions within a social network to determine the effects on multiple components of foraging success, although some captive studies have shown effects of immigration on socially learned foraging behaviors (Chimento et al. 2021, 2024).

Second, using data from all three stages of the experiment, we tested the relationship between foraging and two metrics of individual social network positioning: i) the average size of the flocks birds were in when visiting feeders, and ii) 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 can have multiple impacts on foraging, including influencing shared vigilance, levels of competition, opportunities for social learning and the expression of alternative foraging tactics (Dias 2006; Cantor et al. 2020). Because of these complex, sometimes conflicting, effects we did not make directional predictions but in the discussion we speculate on which of these may have been influential in driving the results observed for each foraging trait. We examined these relationships across learning tasks that involve different cognitive traits – learning an initial association followed by two reversal stages requiring flexibility in updating behavior in response to environmental change (Izquierdo et al. 2017). We predicted that the effects of social network position on foraging would be stronger for reversal learning than initial learning because the former is more challenging and has been shown to be especially sensitive to variation in the social environment (Schrijver et al. 2004; Latchem et al. 2025).

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 their foraging behavior and social networks can be readily observed by tagging individuals with passive integrated transponders and monitoring their visits to RFID-equipped feeders (Firth and Sheldon 2015; Milligan et al. 2017; Cauchoix et al. 2022). By programming feeders to allow access to food for only certain individuals, it is possible to 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). 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 wild mixed species foraging flocks 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. At least 90% of the

population was estimated to be tagged (Aplin et al. 2013). 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 site (mean ± SD distance between array sites: 1.35 ± 0.67 km). There were four array sites in each of the two study years spanning one winter season (i.e., four arrays monitored from November-December 2017; another set of four arrays in different sites from January-February 2018) for a total of 8 array sites in the study (Figure S1). 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.

At each array site, we had five individual feeders arranged linearly and spaced 1 m apart. Prior to the learning experiment that was the focus of this study, feeders were programmed so that any tagged individual could feed from any feeder to allow birds to become accustomed to obtaining food. When a pit-tagged bird landed on the feeder platform, a solenoid activated, allowing the bird to push open a door to gain access to the seeds inside. After four days in this configuration, we began the learning experiment. Now, each bird was assigned to one of the five feeders in the array, and it was only rewarded with food from its rewarded feeder. If it landed on any of the other four non-rewarded feeders in the array, its visit would be recorded but the solenoid would not activate, so it would not be rewarded unless it scrounged from a previously rewarded bird (see below). 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: 1) An initial learning stage, in which each individual was randomly assigned to one of the five feeders in the array. We monitored their visits over eight days to determine if, and when, they learned to which feeder they were assigned (see below). 2) In the first reversal stage, we reassigned birds to a new feeder in the array and monitored their visits for another 8 to 10 days. 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' treatment, in which the entire set of birds assigned to the same feeder during the initial learning stage was reassigned to the same (randomly chosen) new feeder in the same array. Thus, these birds experienced consistency in which other individuals in the flock were feeding from the same rewarded feeder. At the other four sites, we applied the 'unstable' treatment. In this treatment, each individual was randomly reassigned to a new feeder in the same array independently, and thus was not always feeding from the same rewarded feeder with the same other individuals as in the preceding stage, potentially disrupting their social connections. 3) In the second reversal stage, we again reassigned birds to new feeders in the same array, continuing the stable and unstable treatments at the same array sites, and monitored visits for eight to ten days.

Foraging and social network measures

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 for each stage (initial and two reversals) by calculating the latency to learn as the number of visits until an individual first met a criterion of 16 correct visits within a window of 20 consecutive visits, which we previously showed to be a robust indication of learning in this system and which follows common procedures in animal learning studies (Gabor and Gerken 2010;

Antzoulatos and Miller 2011; Reichert et al. 2020). Second, we characterized the propensity to scrounge in each stage as the proportion of rewarded visits (i.e. visits in which the bird obtained food, 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 be rewarded with food by "producing") that took place 1 s or less after the departure of a bird that was assigned to that feeder. Although we designed the feeders to prevent access to unassigned birds, there was an inevitable delay of 1 s before the feeder door closed and in such cases, the scrounger could obtain food from that feeder (Reichert et al. 2021). An alternative explanation of visits to feeders very soon after another bird's departure could be that these represent aggressive displacements by the arriving bird rather than scrounges, although these are not mutually exclusive because aggressive displacement could be a mechanism of scrounging behavior. If aggression were the only driver, we would expect the intervals between an individual's arrival and the previous bird's departure to be similar for its rewarded and non-rewarded feeders. However, individuals were much faster to arrive after a previous bird had departed from the arriving bird's non-rewarded feeders than from their rewarded feeder (Figure S2), which rules out aggression independent of scrounging as an explanation for this visit pattern. 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 met the learning criterion (in units of visits per day). We used this criterion rather than the total of all rewarded visits after the criterion was met because birds varied in the number of days before the learning criterion was met, and thus in the number of days remaining in the experimental stage.

We note that individuals of both great tits and blue tits foraged in the same mixed species flocks, and so the social networks were constructed and social network metrics calculated using data from all detected individuals, regardless of species. Monitoring at the study population also involved giving PIT tags to any

captured marsh tit (*Poecile palustris*) and nuthatch (*Sitta europaea*), thus social networks also included these individuals when detected. We restrict our subsequent analyses to great tits and blue tits because only these two species interacted with the learning apparatus in large numbers, although individuals of the other two species were also assigned a feeder and could have visited it. The number of individuals of each species included in the social network and the mean number of flocking events per individual varied slightly between experimental stages (Table S1).

Social networks were calculated separately for each experimental stage using the visit data for that experimental stage across all five feeders in the array. 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 the sum of its association strengths with all other individuals in the network. These metrics were calculated separately for each of the three experimental stages using data from all detected individuals in the flock, regardless of species.

Statistical analyses

All statistical analyses were conducted in R version 4.5.0 (R Development Core Team 2024). Our dataset included 68 individual great tits and 115 individual blue tits that met the learning criterion in all three

experimental stages. Other individuals that were detected during the experiments but did not meet the learning criteria were excluded, because the majority of these individuals made very few visits to the feeders (Reichert et al. 2020), and because we were interested in the effects of the social stability treatment on reversal learning performance, which could not be assessed in a meaningful way if birds did not meet the initial learning criterion prior to the reversal. We used separate statistical models for each of the three foraging strategy variables to determine how these were affected by the social stability treatment and an individual's social network metrics. All models were run with the lme4 version 1.1-35.5 package (Bates et al. 2015). Where significant interactions were identified we used Tukey post-hoc tests to determine which groups differed statistically from one another. For interactions involving categorical variables (experimental stage, species and social stability), we did post-hoc testing using the emmeans function from the emmeans version 1.10.4 package in R (Lenth 2022), which calculates estimated marginal means for each combination of factors. For interactions involving a continuous variable (average flock size or weighted degree), we did post-hoc testing using the emtrends function in the emmeans package, which tests for differences in slopes of the relationship between the continuous predictor and the foraging variable between the levels of the categorical variables (experimental stage, species). We checked model assumptions of normality or uniformity of residuals and non-collinearity of variables using the check_model function in the performance version 0.14.0 package (Lüdecke et al. 2021). Latency to learn (natural log-transformed) and foraging rate were modeled as Gaussian variables in linear mixed models ('lmer' function). Proportion scrounged was modeled as a binomial variable in a generalized linear mixed model ('glmer' function). For latency to learn and foraging rate, we included the total number of observations using the weights argument. Scrounging was modeled as the proportion of scrounges with the weights argument being the number of all rewarded visits. Both of these aimed to control for uncertainty in our estimates by weighting more heavily observations from

individuals that were observed more frequently. Raw data and code are available at https://doi.org/10.6084/m9.figshare.29923118.

First, we tested for effects of the social stability treatment on each of the three foraging variables. 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 main effects, and two- and three-way interactions between species, experimental stage and social stability treatment as the main factors of interest. We do not specify any specific a priori predictions, but expected that relationships between social stability and foraging could vary among species because of differences in factors that affect foraging like body size, dominance, and predation risk, and across experimental stage because the treatment was repeated at each stage. We included three additional fixed effect variables 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 rewarded and non-rewarded feeders were inoperable due to equipment malfunction (Reichert et al. 2020). Previously, we found that birds assigned to edge feeders learned more quickly in both reversal 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. Because these variables were included to control for factors not of direct interest in the study and because their effects have been discussed elsewhere (Reichert et al. 2020), their effects are reported in the tables but not discussed directly in the text.

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, along with all main effects of these variables and the two-way interactions between each set of two variables within the three-way interaction. Social stability treatment was not included as a factor in this model. Including social stability treatment would have changed the interpretation of these variables to be the effect of social network position over and above the effect of the specific social stability treatment, which we previously showed also contributed to variation in the social network (Troisi et al. 2025). We were interested in the effects of the social network position itself. In addition, we had not applied the social stability treatment during the initial learning stage, so including treatment as a factor would complicate interpretation of the social network variable effects in that stage. 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 rewarded and non-rewarded feeders were inoperable due to equipment malfunction.

RESULTS

There were 262530 records of the 183 focal individuals across the three experimental stages (great tits: 95818 visits, N = 68 individuals; blue tits: 166712 visits, N = 115 individuals). Across these stages, individual great tits were in flocks with an average size of (mean ± SE) 13.74 ± 0.26 birds and individual blue tits were in flocks with an average size of 12.59 ± 0.21 birds, and the average weighted degree was 6.65 ± 0.14 for great tits and 6.13 ± 0.12 for blue tits. These metrics were calculated from the entire mixed-species foraging flock and thus include connections to both conspecifics and heterospecifics. Great tits and blue tits averaged 62.4 ± 6.9 and 63.8 ± 4.62 visits, respectively, until the learning criterion was met. For scrounging, great tits had 2347 total scrounging events (mean ± SE = 11.5 ± 1.8), and blue tits had 6552 scrounges (mean ± SE = 19.0 ± 1.3). Foraging rate averaged 51.9 ± 1.4 and 46.0 ± 0.9 visits on the day after the learning criterion was met for great tits and blue tits, respectively.

Effects of sociality on latency to learn

There was no significant three-way interaction between social stability treatment, experimental stage and species on latency to learn (Table 1). However, there was a significant interaction between social stability treatment and experimental stage (Table 1, Figure 1A, 1B). For both species, there was no difference between the unstable and stable groups in the latency to learn in the first reversal, but in the second reversal, individuals in the unstable treatment learned more quickly (Table S2, Figure 1A). Latencies to learn 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 significant three-way interactions between species, experimental stage and both average flock size and weighted degree on latency to learn (Table 2). For blue tits, individuals in larger flocks learned faster in the initial and first reversal stages, but this pattern was reversed in the second reversal 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 latency to learn 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 latency to learn 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' latencies to learn 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). In an analysis of 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-

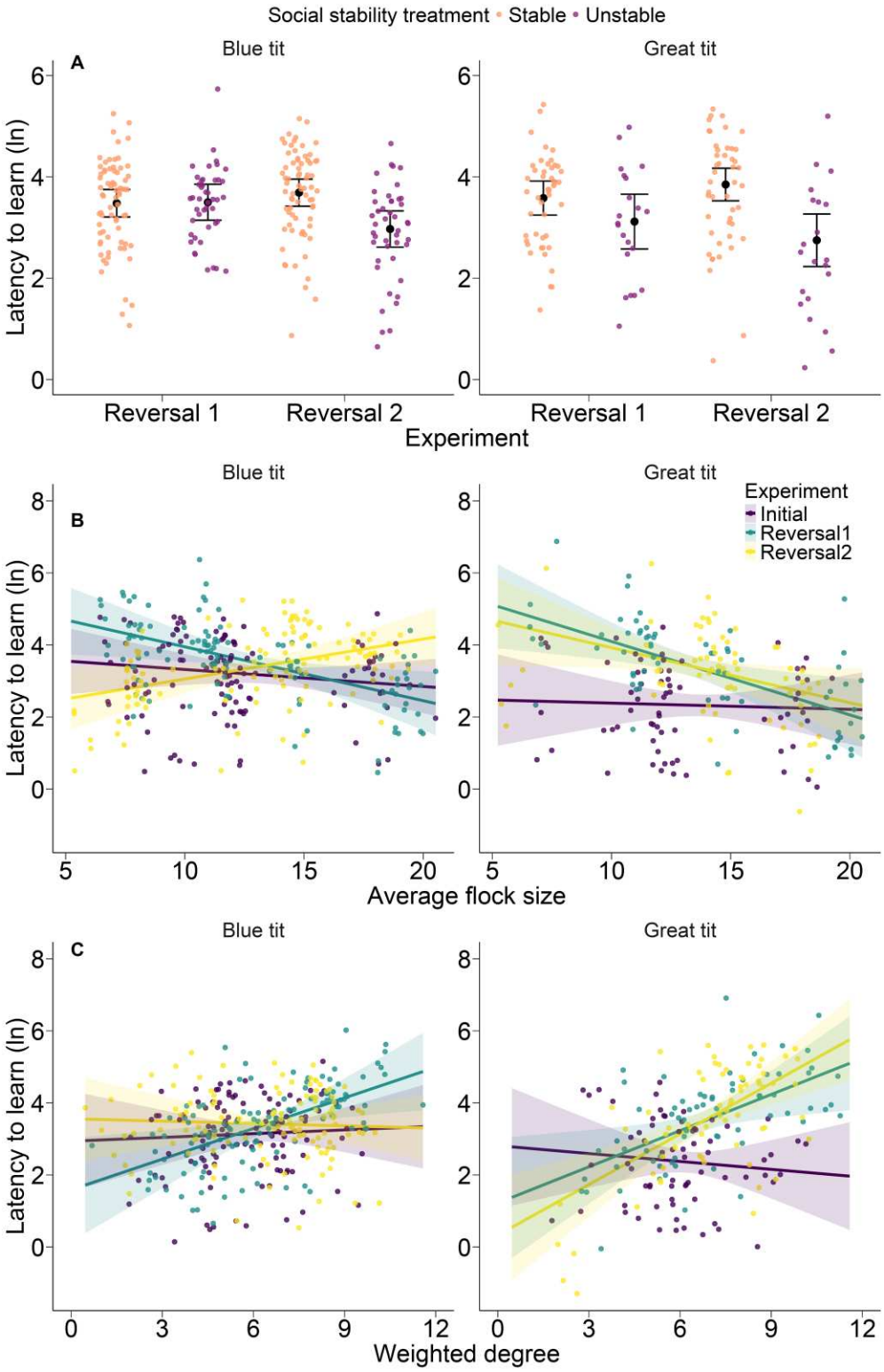
existing difference between these groups for this trait, and this difference applied to both species (Table S3). Because we found no significant effect of social stability treatment in the first reversal and then significant differences in the second reversal, the treatment had an effect over and above 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). Foraging rates were not significantly different in the two social stability treatment groups in the initial learning stage,

confirming that there were no differences before the treatment was applied (Table S3). There were no interactions between species, experimental stage and either average flock size or weighted degree (Table 2). There was a main effect of weighted degree: individuals with a higher weighted degree had a higher foraging rate (Figure 3C). There was also a marginal effect of average flock size (Table 2). Foraging rates generally remained relatively constant or decreased slightly with increasing flock sizes (Figure 3B).

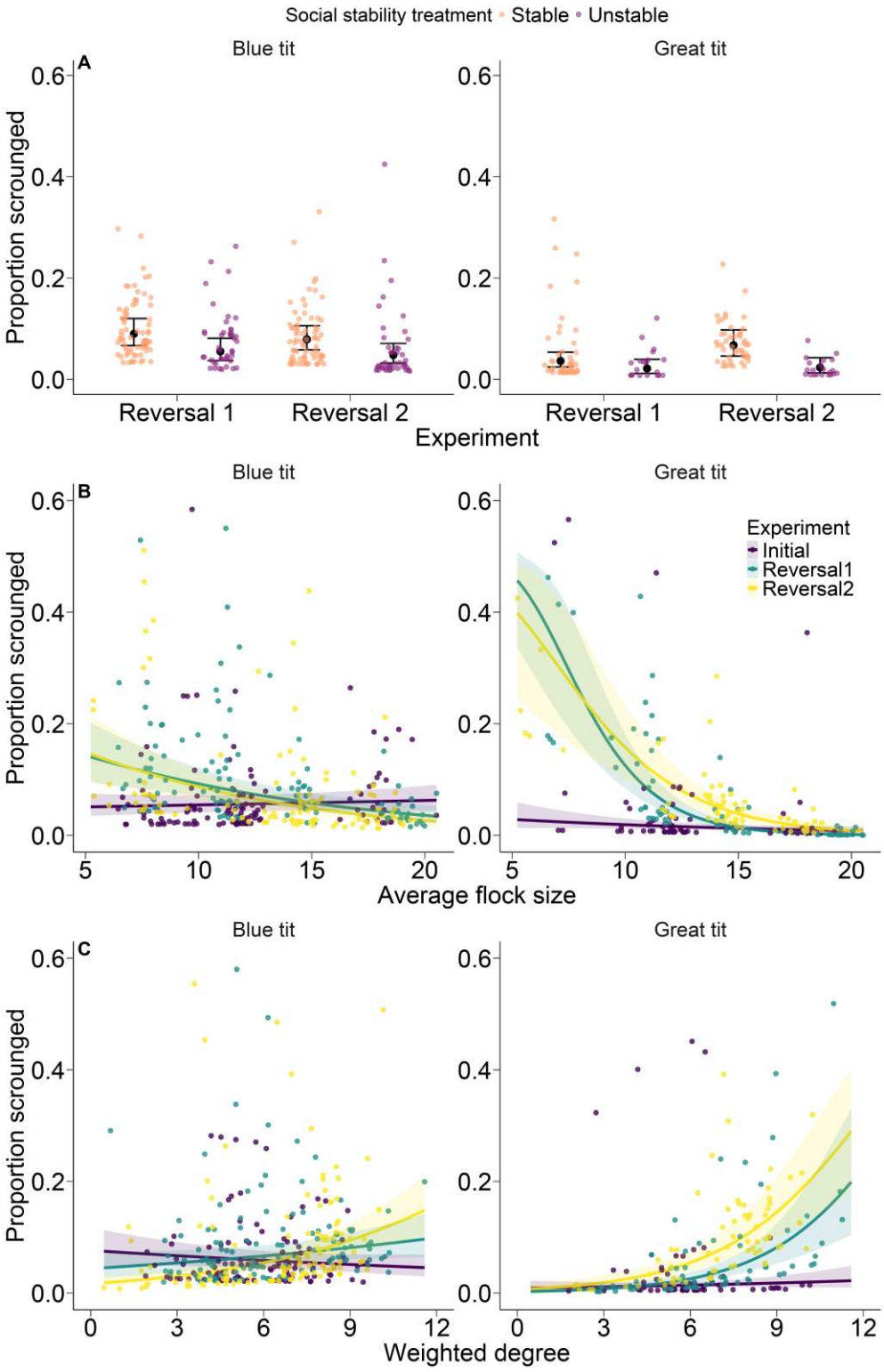


444

445 Figure 1. Effects of sociality on latency to learn. A. Effects of social stability treatment and experimental

446 stage on latency to learn (ln-transformed) for blue tits (left) and great tits (right). Black points represent

447 estimated marginal means (± 95% CI) from the model. Small colored points represent partial residuals
448 from the model for each individual. B. Relationship between average flock size and latency to learn for
449 each species. Lines represent predicted estimate (± 95% CI) from the model, with separate colors for
450 each experimental stage, and points represent partial residuals from the model for each individual. C.
451 Relationship between weighted degree and latency to learn for each species. Interpretation as in B.
452

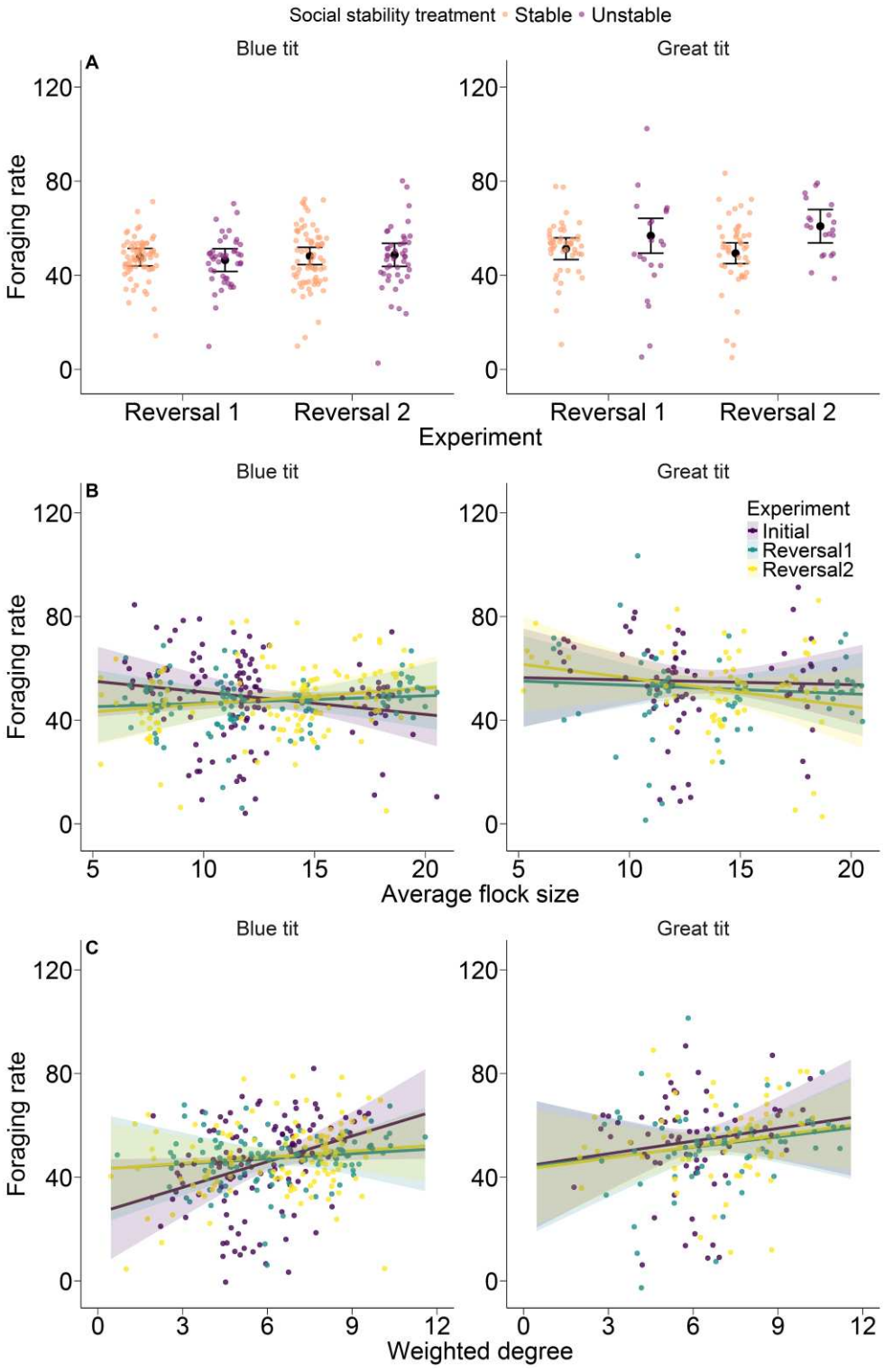


453

454 Figure 2. Effects of sociality on scrounging. A. Effects of social stability treatment and experimental stage

455 on the proportion of feeds that were scrounges 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 scrounging 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 scrounging for each species. Interpretation as in B. The y-axis is cut off at 0.6 for visualization purposes, there are 1, 13, and 13 outlying points not depicted in A, B, and C, respectively. Figure S3 presents the same graphs but with all data points included.



464

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

466 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.

473 Table 1. Effects of social stability on foraging traits

	Latency to learn				Scrounging				Foraging rate			
Effect	**β**	**SE**	**t**	**P**	**β**	**SE**	**t**	**P**	**β**	**SE**	**t**	**P**
Intercept	3.42	0.143	23.98		−3.469	0.169	−20.54		46.65	1.963	23.76	
Social treatment (unstable)	0.019	0.23	0.081	0.935	−0.532	0.273	−1.951	0.051	−1.229	3.158	−0.389	0.697
Expt (2nd reversal)	0.209	0.168	1.245	0.215	−0.142	0.038	−3.768	< 0.001	0.492	2.269	0.217	0.828
Spp (GT)	0.101	0.218	0.466	0.642	−0.973	0.269	−3.615	< 0.001	3.595	2.998	1.199	0.231
Own feeder down time (hrs)	0.129	0.02	6.281	< 0.001	0.113	0.007	16.24	< 0.001	−0.127	0.280	−0.452	0.651
Other feeder down time (hrs)	0.078	0.014	5.699	< 0.001	0.065	0.005	12.41	< 0.001	−0.312	0.188	−1.657	0.098
Feeder location (edge)	−0.411	0.119	−3.438	< 0.001	−0.016	0.035	−0.446	0.655	3.538	1.629	2.172	0.031
Social treatment (unstable): Expt (2nd reversal)	−0.736	0.281	−2.619	0.010	−0.007	0.070	−0.095	0.924	1.732	3.806	0.455	0.650
Social treatment (unstable):Spp (GT)	−0.482	0.392	−1.231	0.219	−0.011	0.470	−0.023	0.982	6.758	5.389	1.254	0.211
Expt (2nd reversal):Spp (GT)	0.059	0.266	0.221	0.826	0.800	0.069	11.56	< 0.001	−2.424	3.608	−0.672	0.503

Social treatment (unstable):Expt (2nd reversal):Spp (GT)	0.100	0.488	0.205	0.838	−0.564	0.149	−3.777	< 0.001	4.256	6.617	0.643	0.521

Fixed effects from mixed models with individual identity as a random effect and ln−transformed latency to learn (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. Abbreviations: 'Expt' – experimental stage, 'Spp' – species, 'GT' – great tit. Down time refers to the amount of time when either the rewarded ('own') or non-rewarded ('other') feeders were not operative due to equipment malfunction prior to the learning criterion being met.

481 Table 2. Effects of social characteristics on foraging traits

	Latency to learn				Scrounging				Foraging rate			
Effect	**β**	**SE**	**t**	**P**	**β**	**SE**	**t**	**P**	**β**	**SE**	**t**	**P**
Intercept	3.66	0.454	8.06		−3.725	0.25	−14.89		36.49	6.836	5.338	
Expt (1st reversal)	0.008	0.525	0.015	0.988	0.936	0.132	7.076	< 0.001	1.922	7.559	0.254	0.799
Expt (2nd reversal)	−1.471	0.565	−2.605	0.010	0.252	0.152	1.656	0.098	−2.495	8.146	−0.306	0.760
Spp (GT)	−0.518	0.752	−0.689	0.491	−0.959	0.510	−1.878	0.060	9.049	11.32	0.799	0.424
Own feeder down time (hrs)	0.105	0.016	6.639	< 0.001	0.093	0.005	18.612	< 0.001	−0.245	0.234	−1.047	0.296
Other feeder down time (hrs)	0.076	0.01	7.398	< 0.001	0.054	0.003	17.47	< 0.001	−0.221	0.151	−1.461	0.145
Feeder location (edge)	−0.758	0.099	−7.637	< 0.001	−0.214	0.029	−7.381	< 0.001	3.589	1.440	2.493	0.013
Flock size	−0.047	0.054	−0.868	0.386	0.015	0.019	0.752	0.452	−0.857	0.810	−1.058	0.291
Weighted degree	0.035	0.111	0.313	0.754	−0.048	0.033	−1.461	0.144	3.303	1.648	2.004	0.046
Flock size X Expt (1st reversal)	−0.102	0.076	−1.342	0.180	−0.116	0.018	−6.483	< 0.001	1.138	1.104	1.031	0.303
Flock size X Expt (2nd reversal)	0.158	0.075	2.119	0.035	−0.140	0.02	−7.151	< 0.001	1.463	1.083	1.351	0.177
Flock size X Spp (GT)	0.030	0.093	0.320	0.749	−0.098	0.047	−2.081	0.037	0.677	1.393	0.486	0.627
Expt (1st reversal):Spp (GT)	0.871	0.916	0.951	0.342	2.736	0.381	7.173	< 0.001	−0.453	13.20	−0.034	0.973
Expt (2nd reversal):Spp (GT)	0.783	1.013	0.773	0.440	2.446	0.427	5.731	< 0.001	13.41	14.56	0.918	0.359

Weighted degree:Expt (1st reversal)	0.249	0.150	1.658	0.098	0.122	0.037	3.283	0.001	−2.649	2.173	−1.219	0.224
Weighted degree:Expt (2nd reversal)	−0.057	0.142	−0.400	0.690	0.251	0.039	6.387	< 0.001	−2.519	2.063	−1.221	0.223
Weighted degree:Spp (GT)	−0.108	0.181	−0.596	0.551	0.129	0.079	1.632	0.103	−1.676	2.695	−0.622	0.534
Flock size:Expt (1st reversal):Spp (GT)	−0.084	0.127	−0.665	0.507	−0.266	0.052	−5.121	< 0.001	−1.289	1.833	−0.703	0.482
Flock size:Expt (2nd reversal):Spp (GT)	−0.294	0.124	−2.364	0.019	−0.089	0.044	−2.008	0.045	−2.381	1.802	−1.321	0.187
Weighted degree:Expt (1st reversal):Spp (GT)	0.159	0.241	0.660	0.509	0.206	0.098	2.112	0.035	2.345	3.495	0.671	0.503
Weighted degree:Expt (2nd reversal):Spp (GT)	0.598	0.226	2.647	0.008	0.034	0.083	0.412	0.680	2.367	3.290	0.719	0.472

Fixed effects from mixed models with individual identity as a random effect and ln−transformed latency to learn (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. Abbreviations as in Table 1.

Table 3. Summary of results and potential mechanisms

Social trait	Foraging trait	Effect	Potential mechanism
Social stability	Latency to learn	Negative	Social instability disrupts competitive relationships, facilitating learning
	Scrounging	Positive	More competition in stable groups, or trade-off with latency to learn
	Foraging rate	None	Individual variation in non-social traits like hunger or motivation
Flock size	Latency to learn	Mostly positive	Learning is facilitated by shared vigilance, reduced risk of predation
	Scrounging	Negative	More opportunities to learn scrounging in large flocks, trade-off with latency to learn
	Foraging rate	None	Individual variation in non-social traits like hunger or motivation
Weighted degree	Latency to learn	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 latency to learn
	Foraging rate	Positive	Increased sense of security and shared vigilance with strong social connections

For each combination of social and foraging trait measured, we give the direction for the general trend in the relationship between the two traits, but note that all of these effects showed additional variation across species and experimental stages that in some cases resulted in a qualitatively different relationship. Potential mechanisms for the effect are given, but these are speculative, non-exhaustive, and our experiments were not 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). We also previously demonstrated consistent among-individual variation in latency to learn and the propensity to scrounge, and that these two foraging traits trade off with one another (Reichert et al. 2020, 2021). Given this variation in foraging behavior and sociality, here we tested whether social position affects multiple components of foraging. We found that flock size and weighted degree are related to variation in multiple foraging behaviors 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 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 underscores the robustness of our findings. Nevertheless, because our social metrics were derived from point estimates of experimentally observed social networks, future work applying generative-network approaches that propagate uncertainty would be valuable for assessing the robustness of these conclusions (Hart et al. 2023; Ross et al. 2024). The links among these traits were context dependent, and suggest interactions with both individual factors like variation in cognitive ability and the various consequences 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 latency to learn

We found no effect of social stability treatment for the first reversal, but reversal learning was faster in the unstable treatment for the second reversal in both species. 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 the latency to reversal learn (Reichert et al. 2020). The difference between our current study and these previous results probably is because here we included 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).

Our findings indicate that social instability did not reduce learning performance by reducing opportunities to socially learn. Most individuals learned the task relatively quickly, potentially limiting the utility of social learning in this system (Reichert et al. 2020). A study of mountain chickadees using a similar design also found no evidence for social learning of rewarded feeder location (Pitera et al. 2025). The somewhat improved learning performance in the unstable treatment in our study could have occurred if this treatment disrupted competitive relationships that built up among individuals attempting to access the same feeder. Our social network metrics do not capture such relationships at the feeder level, which would have necessarily been disrupted due to the treatment, because they are based on flock membership across the feeder array, although in previous work we found weakly supportive evidence that dyadic associations at the flock level were more stable in the stable treatment (Troisi et al. 2025). High levels of competition and subordinate status 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 by disrupting dominance relationships that reduced subordinate individuals' access to the feeder. Because our data are based on feeder visits, we cannot directly assess the extent to which individuals were prevented from attempting to feed, but this is a worthy target for future work. 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 latency to learn, 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 such behavior occurred in our study where birds were similarly restricted in feeder access, then this tendency to remain near close social partners could have slowed down an individual's own learning. Blue tits were

564 less affected by this variable, perhaps because their cognitive performance is more strongly affected by
565 general social competition to access feeders.
566
567 *Effects of sociality on scrounging*
568 Scrounging rates were higher in the stable treatment during the second reversal stage for both species
569 and, for blue tits, also in the first reversal. If individuals primarily scrounge from close social associates
570 (King et al. 2009; Harten et al. 2018), this could explain higher scrounging levels in the stable treatment
571 where, by design, those associations were maintained. As described above, our previous analyses gave
572 weak evidence that dyadic associations were more stable in the stable treatment (Troisi et al. 2025). An
573 alternative explanation is that scrounging was higher in the stable treatment because producing was
574 more difficult (Barnard and Sibly 1981), and indeed reversal learning was slower in the stable treatment.
575
576 For both great tits and blue tits, scrounging rates were lower for birds with larger average flock size in
577 both reversal stages. These results were surprising both because we had expected larger groups to
578 provide more opportunities to scrounge if for no other reason than because there were more birds
579 available to access feeders, and because individuals in larger groups generally learned more quickly,
580 which should have provided more opportunity for scroungers. However, in a previous analysis of this
581 dataset, we found that scrounging and production learning trade-off such that individuals that learn
582 quickly scrounge less often (Reichert et al. 2021). Thus, the social factors facilitating production learning,
583 in this case potentially beneficial effects of being in large groups, could have indirectly negatively
584 influenced the expression of an alternative foraging tactic by reducing the benefits of scrounging relative
585 to producing. This explanation could also apply to the positive relationship between scrounging and
586 weighted degree in the reversals. Particularly for the second reversal, great tits with higher weighted
587 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).

Effects of sociality on foraging rate

Individuals' foraging rates after learning the location of their rewarded feeder were not affected by the social stability treatment for either species. Foraging rate at feeders is a repeatable trait in this system (Crates et al. 2016). This individual consistency in behavior along with the relative ease with which food could be obtained after learning may have contributed to our findings that the overall amount of foraging activity remained relatively stable despite any changes that the social stability treatments caused to social relationships at the level of the individual feeder. In addition, non-social factors like hunger and motivation may be stronger drivers of variation in foraging rate.

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 stage, 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), and this is likely to be the case for blue tits as well. 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.

Differences across stages and species

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, production learning and scrounging rate (which is cognitively demanding because individuals learn to scrounge in our system; (Reichert et al. 2021)), but not for foraging rate. This implies that the effects of sociality may be especially pronounced in cognitively challenging situations. The main difference between the experimental stages was in the learning task required of the birds, from an initial association to two successive reversals. Therefore, one explanation for variation across stages is that sociality interacted differently with the cognitive challenges associated with each task. Initial learning is driven by an associative process between a feeder and the reward, while reversal learning requires additional cognitive flexibility so that individuals inhibit their response to the previously rewarded feeder and instead make an association with the new rewarded feeder (Morand-Ferron et al. 2022). At the same time, some individuals were learning to become increasingly proficient at scrounging and there were opportunities to socially learn from other individuals visiting the feeders (Reichert et al. 2021). Some previous studies showed that the effects of the social environment on cognition depend on the cognitive task (Kogan et al. 2000; Schrijver et al.

2004), and our results suggest that these findings extend to foraging behaviors involving different cognitive mechanisms in a wild population. Although further study is needed, our results point to an effect of sociality on the opportunity to learn alternative foraging tactics, adding to the evidence that cognition is shaped by social structure (Hoppitt and Laland 2013; Seyfarth and Cheney 2015; Kulahci and Quinn 2019).

Another potential explanation for our finding of variation in the effects of sociality across stages is that the structure of the social network itself changed. Indeed, we previously showed in this dataset that average flock size and weighted degree both increased from the initial learning to the second reversal stages, and the increase in flock size was stronger for the stable treatment (Troisi et al. 2025). The effects of the social stability treatment are thus partially reflected in the social network metrics, but the different ways in which they impacted foraging outcomes likely arose because they impacted different behavioral mechanisms. Whereas the social stability treatment likely impacted mechanisms like turn-taking, hierarchical disruptions and perhaps social learning, the social network metrics better quantify an individual's overall sociality and the general social milieu in which it was foraging.

Where we found significant interactions between experimental stage and social network metrics on foraging behavior, the relationships between sociality and behavior were generally stronger during the reversal stages, indicating that sociality may play a stronger role on foraging when environmental conditions change. At the same time, we found support for our prediction that the effects of the social stability treatment on foraging would be stronger in the second reversal than the first reversal, which indicates that multiple social disruptions have increasingly large effects on foraging. The current study and the analyses in Troisi et al. (2025) clearly show that foraging and social processes were highly dynamic within groups during this experiment. We note that some of these social processes were likely

660 already in flux prior to the initial learning stage. Our experimental design involved manipulating feeder
661 placement and access to food to attract birds to the area and acclimate them to the experimental
662 devices before we began the learning experiments. Social network traits and flock size varied even
663 across these early stages, indicating that all individuals would have been experiencing some social
664 instability before our social stability manipulation (Troisi et al. 2025). Indeed, some baseline level of
665 social instability is the norm in these foraging flocks, which are characterized by a fission-fusion
666 structure (Farine et al. 2015*b*), so we suggest that the sort of instability we introduced here reflects
667 similar effects.
668
669 We calculated the social network based on social ties across species, which is appropriate given the
670 strong tendency of great tits and blue tits to forage together. Although some social processes like mate
671 selection will be more strongly affected by within-species social ties (Firth et al. 2018), social foraging
672 tactics like scrounging and competition at feeders are likely to be affected by all network members, even
673 heterospecifics. Indeed, we found that the impacts of weighted degree and flock size were broadly
674 similar on most measures of foraging in both great tits and blue tits. These findings raise important
675 questions for future work, including whether social effects on foraging fundamentally differ between
676 single-species and mixed-species flocks, and whether the nature of among-species interactions plays a
677 role.
678
679 *Conclusions*
680
681 Both social network position and foraging emerge from a complex interplay of factors including
682 competition, cognition, individual personality, levels of predation and other environmental
683 characteristics, yet disentangling these factors in the wild has been difficult due to the lack of

684 experiments. Our findings that sociality affects multiple aspects of foraging success in a wild system
685 expand on our knowledge of social foraging and demonstrate the utility of social network metrics and
686 the manipulation of fine-scale social interactions within groups for explaining variation in key behavioral
687 traits. The results demonstrate a series of costs (slower learning in stable flocks and when weighted
688 degree was higher) and benefits (greater scrounging opportunity with stable and more connected flocks,
689 and higher foraging rates in flocks with stronger relationships) associated with greater sociality.
690 However, there is still much progress to be made in identifying the mechanisms behind these results.
691 Many of our findings suggested a role of competition and so a key next step will be to better
692 characterize competitive interactions, which is challenging from RFID data but increasingly possible with
693 new monitoring technologies, such as machine vision and proximity loggers (Smith and Pinter-Wollman
694 2021). Our findings also raise questions of causation: an individual's social position certainly influences
695 its foraging behavior, but it may also be the case that positive feedback leads to foraging behavior
696 affecting social position (Kulahci and Quinn 2019), for example if some individuals serve as models for
697 social learning or easy targets for scroungers (Harten et al. 2018). Expanded efforts to monitor and
698 manipulate the social dynamics of wild groups of animals are likely to yield exciting new insights into the
699 factors that drive the expression of functional, multi-faceted behaviors like foraging.
700

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Supplementary Files (PDF, Word, TeX, figures)

Supplementary Material for: Social structure and social stability predict learning, scrounging and feeding rate in foraging flocks of wild songbirds

Table S1. Number of individuals used to calculate the social network

Experimental Stage	Species	Number of individuals	Mean number of flocking events (SD)
Initial	Blue tit	152	153.9 (61.1)
	Great tit	117	149.1 (62.0)
	Marsh tit	32	407.5 (208.3)
	Nuthatch	4	280.0 (236.9)
First reversal	Blue tit	155	162.3 (55.7)
	Great tit	117	159.8 (65.4)
	Marsh tit	32	323.2 (173.0)
	Nuthatch	4	163.3 (161.5)
Second reversal	Blue tit	151	174.8 (64.8)
	Great tit	114	174.6 (79.6)
	Marsh tit	33	332.4 (149.3)
	Nuthatch	4	200.8 (128.7)

Social networks were calculated from the record of individual visits to the feeder array. Four species were fitted with RFID tags and could be detected at the feeders, and all of these were included in the social network. Numbers fluctuated slightly across the experimental stage because not all individuals visited the feeders in all experimental stages. We also include the mean (SD) number of flocking events that birds of that species were assigned to. See Methods in the main text for details on the social network calculation.

Table S2. Contrasts for effects of social stability treatment and experimental phase on latency to learn the rewarded feeder

Experiment	Social Treatment	EMM	SE	Lower CI	Upper CI	Contrast Estimate	SE	t	P
First reversal	Stable	3.56	0.11	3.34	3.78	0.22	0.20	1.10	0.27
	Unstable	3.34	0.17	3.01	3.66				
Second reversal	Stable	3.80	0.11	3.58	4.01	0.91	0.20	4.67	< 0.001
	Unstable	2.89	0.16	2.57	3.20				

Estimated marginal means (EMM) are given for each combination of social stability treatment and experimental phase from the linear mixed model for effects on latency to learn (see Table 1). The contrast estimate is for the comparison between the latencies to learn in the stable and unstable social stability 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). Note that results are combined across species because the interaction effect including species was not statistically significant (Table 1).

Table S3. Models comparing foraging traits in the social stability treatment groups during the initial learning stage

Foraging trait	Effect	Estimate	SE	t	P
Latency to learn (ln)	(Intercept)	3.50	0.181	19.28	
	Social stability treatment (unstable)	0.151	0.216	0.697	0.49
	Species (great tit)	−0.850	0.214	−3.98	< 0.001
	Own feeder malfunction time (hrs)	0.096	0.024	3.966	< 0.001
	Other feeder malfunction time (hrs)	0.088	0.015	5.981	< 0.001
	Feeder location (edge)	−1.476	0.178	−8.288	< 0.001
	Social stability treatment (unstable):Species (great tit)	0.319	0.365	0.875	0.38
Scrounging rate	(Intercept)	−2.33	0.24	−9.73	
	Social stability treatment (unstable)	−1.07	0.39	−2.76	0.006
	Species (great tit)	−1.50	0.43	−3.49	< 0.001
	Own feeder malfunction time (hrs)	0.02	0.03	0.59	0.55
	Other feeder malfunction time (hrs)	0.02	0.02	1.03	0.31
	Feeder location (edge)	−1.31	0.34	−3.83	< 0.001
	Social stability treatment (unstable):Species (great tit)	0.56	0.93	0.60	0.55
Foraging rate	(Intercept)	48.3	3.38	14.31	
	Social stability treatment (unstable)	1.36	4.03	0.338	0.736
	Species (great tit)	9.09	3.98	2.29	0.023
	Own feeder malfunction time (hrs)	−0.826	0.449	−1.84	0.067
	Other feeder malfunction time (hrs)	−0.472	0.272	−1.73	0.085
	Feeder location (edge)	1.23	3.32	0.37	0.712
	Social stability treatment (unstable):Species (great tit)	−6.67	6.80	−0.981	0.328

These models were run because the social stability treatment was only applied at the first reversal stage but it is possible that there were pre-existing differences between the treatment groups, which we could test by examining these variables in the initial learning experimental stage. Interpretation as in Table 1 in the main text. Fixed effects from a linear model with the foraging trait of interest as the dependent variable (for proportion scrounged, a general linear model with the dependent variable fit with the quasibinomial family to deal with overdispersion). The reference category for social stability treatment is the stable treatment, and for species is blue tits, and for the feeder location is center.

Table S4. Contrasts for effects of average flock size, experimental phase and species on latency to learn the rewarded feeder

Species	Experiment	Slope	SE	Lower CI	Upper CI	Contrast	Estimate	SE	t	P
Blue tit	Initial	−0.05	0.05	−0.15	0.06	Initial − First reversal	0.10	0.08	1.34	0.37
	First reversal	−0.15	0.06	−0.26	−0.04	Initial − Second reversal	−0.16	0.07	−2.12	0.09
	Second reversal	0.11	0.05	0.01	0.22	First reversal − Second reversal	−0.26	0.08	−3.41	0.002
Great tit	Initial	−0.02	0.07	−0.16	0.13	Initial − First reversal	0.19	0.10	1.86	0.15
	First reversal	−0.20	0.07	−0.35	−0.06	Initial − Second reversal	0.14	0.10	1.37	0.35
	Second reversal	−0.15	0.07	−0.29	−0.01	First reversal − Second reversal	−0.05	0.10	−0.52	0.86

Estimated marginal trends are given for the relationship between average flock size and latency to learn for each experimental phase and species, from the linear mixed model for effects on latency to learn (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 S5. Contrasts for effects of weighted degree, experimental phase and species on latency to learn the rewarded feeder

Species	Experiment	Slope	SE	Lower CI	Upper CI	Contrast	Estimate	SE	t	P
Blue tit	Initial	0.03	0.11	−0.18	0.25	Initial − First reversal	−0.25	0.15	−1.66	0.22
	First reversal	0.28	0.11	0.07	0.50	Initial − Second reversal	0.06	0.14	0.40	0.92
	Second reversal	−0.02	0.09	−0.20	0.16	First reversal − Second reversal	0.31	0.14	2.20	0.07
Great tit	Initial	−0.07	0.14	−0.35	0.20	Initial − First reversal	−0.41	0.19	−2.16	0.08
	First reversal	0.33	0.13	0.07	0.60	Initial − Second reversal	−0.54	0.18	−3.09	0.006
	Second reversal	0.47	0.12	0.24	0.70	First reversal − Second reversal	−0.13	0.17	−0.78	0.72

Estimated marginal trends are given for the relationship between weighted degree and latency to learn for each experimental phase and species, from the linear mixed model for effects on latency to learn (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 social stability treatment and experimental phase on proportion scrounged from non-rewarded feeders

Species	Experiment	Social Treatment	EMM	SE	Lower CI	Upper CI	Contrast Estimate	SE	t	P
Blue tit	First reversal	Stable	−3.23	0.17	−3.56	−2.90	0.53	0.27	1.95	0.051
		Unstable	−3.76	0.21	−4.18	−3.34				
	Second reversal	Stable	−3.37	0.17	−3.70	−3.04	0.54	0.27	1.98	0.048
		Unstable	−3.91	0.21	−4.33	−3.49				
Great tit	First reversal	Stable	−4.20	0.21	−4.62	−3.79	0.54	0.38	1.41	0.16
		Unstable	−4.75	0.32	−5.38	−4.11				
	Second reversal	Stable	−3.55	0.21	−3.95	−3.14	1.11	0.38	2.93	0.003
		Unstable	−4.66	0.32	−5.28	−4.04				

Estimated marginal means are given for each combination of social stability treatment, experimental phase and species, from the generalized linear mixed model for effects on proportion scrounged (see Table 1). The contrast estimate is for the comparison between the proportion scrounged in the stable and unstable social stability 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 S7. Contrasts for effects of average flock size and experimental phase on proportion scrounged from non-rewarded feeders

Species	Experiment	Slope	SE	Lower CI	Upper CI	Contrast	Estimate	SE	t	P
Blue tit	Initial	0.01	0.02	−0.02	0.05	Initial − First reversal	0.12	0.02	6.48	< 0.001
	First reversal	−0.10	0.02	−0.15	−0.05	Initial − Second reversal	0.14	0.02	7.15	< 0.001
	Second reversal	−0.13	0.03	−0.18	−0.07	First reversal − Second reversal	0.02	0.02	1.23	0.43
Great tit	Initial	−0.08	0.04	−0.17	−0.0002	Initial − First reversal	0.38	0.05	7.95	< 0.001
	First reversal	−0.47	0.05	−0.56	−0.37	Initial − Second reversal	0.23	0.04	5.86	< 0.001
	Second reversal	−0.31	0.05	−0.41	−0.22	First reversal − Second reversal	−0.15	0.05	−3.36	0.002

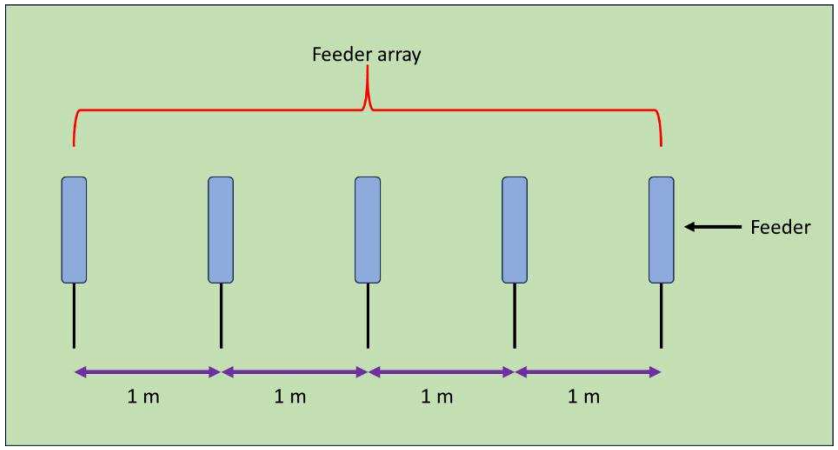
Estimated marginal trends are given for the relationship between average flock size and proportion scrounged for each experimental phase and species, from the generalized linear mixed model for effects on proportion scrounged (see Table 2). The contrast column on the right side of the table compares 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 S8. Contrasts for effects of weighted degree and experimental phase on proportion scrounged from non-rewarded feeders

Species	Experiment	Slope	SE	Lower CI	Upper CI	Contrast	Estimate	SE	t	P
Blue tit	Initial	−0.05	0.03	−0.11	0.02	Initial − First reversal	−0.12	0.04	−3.28	0.003
	First reversal	0.07	0.04	0.002	0.15	Initial − Second reversal	−0.25	0.04	−6.39	< 0.001
	Second reversal	0.20	0.04	0.13	0.27	First reversal − Second reversal	−0.13	0.04	−3.64	< 0.001
Great tit	Initial	0.08	0.07	−0.06	0.22	Initial − First reversal	−0.33	0.09	−3.67	< 0.001
	First reversal	0.41	0.08	0.26	0.56	Initial − Second reversal	−0.28	0.07	−3.97	< 0.001
	Second reversal	0.37	0.05	0.26	0.47	First reversal − Second reversal	0.04	0.07	0.62	0.81

Estimated marginal trends are given for the relationship between weighted degree and proportion scrounged for each experimental phase and species, 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).


Feeder array
Feeder
1 m
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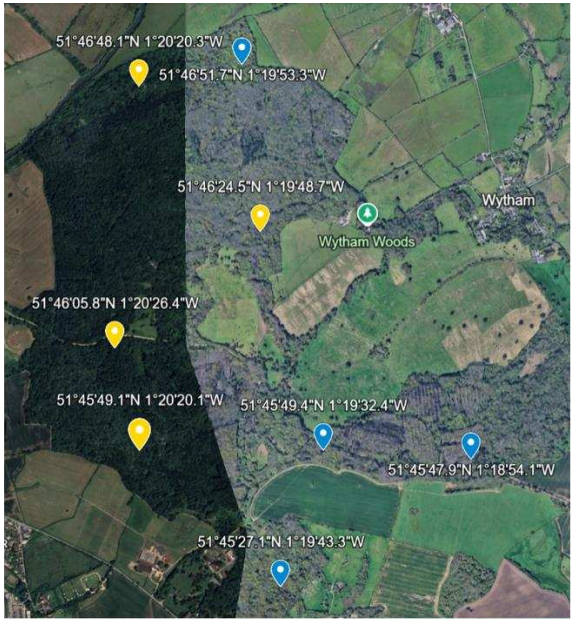
51°46'48.1"N 1°20'20.3"W
51°46'51.7"N 1°19'53.3"W
51°46'24.5"N 1°19'48.7"W
Wytham
Wytham Woods
51°46'05.8"N 1°20'26.4"W
51°45'49.1"N 1°20'20.1"W
51°45'49.4"N 1°19'32.4"W
51°45'47.9"N 1°18'54.1"W
51°45'27.1"N 1°19'43.3"W
1 km

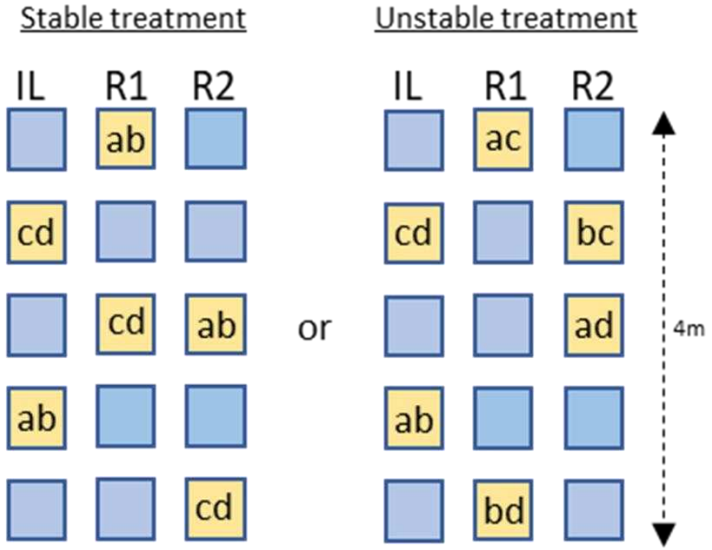
Stable treatment
Unstable treatment
IL
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Figure S1. Illustration of the experimental design and feeder layout at different scales. **Top** l**eft image** shows a single feeder array. During the learning experiment, we monitored visits to an array of five individual RFID-equipped feeders. Each feeder was spaced 1 m apart and feeders were arranged in a line. Each bird was randomly assigned to one rewarded feeder in the array, and this was the only feeder that would open and provide food for it during a given experimental stage (the other four were unrewarded feeders for that bird). We first monitored foraging during an initial learning stage in which birds had to learn which of the feeders in the array would provide them food. Prior to this stage we had the feeders in the same arrangement but all birds could access all feeders, to acclimate them to accessing the food (they had to push open a transparent door in order to access the food once the RFID antenna detected their PIT tag). This stage was termed the open clustered stage. Data from this stage were not analyzed in the present manuscript, which is focused on the learning stages. And before the open clustered stage, we used a different feeder layout (not illustrated) in which only two feeders were spaced 50 m apart (the central point of these two feeders was in the same position as the central feeder in the five-feeder array). This was termed the open dispersed stage, and was mainly used to attract flocks to the general area, acclimate birds to the feeder, and generate data on foraging from feeders in different spatial arrangements that are not relevant to the present manuscript and were discussed in (Troisi et al., 2025). Following the initial learning stage, we reassigned birds to a new feeder in the five-feeder array (see main text for details) during the first reversal stage, and again reassigned them to a new feeder in the second reversal stage. **Top right image** shows the locations of each of the eight five-feeder arrays used in the study. The arrays were located in Wytham Woods, Oxfordshire, UK. Points indicate locations of the arrays, with GPS coordinates provided. Color corresponds to the year of testing. Only four feeder arrays were in place at a time. One set of four (yellow points) was tested in November-December 2017, and another set of four in January-February 2018. Map created using Google Earth. **Bottom image** illustrates the three experimental stages and the social stability treatment. Each column indicates the feeder array during one of the three experimental stages (IL = initial learning, R1 = first reversal learning, R2 = second reversal learning). Each square corresponds to a feeder within the array. The letters illustrate a hypothetical implementation of the social stability treatment, where each letter corresponds to an individual bird assigned to that feeder. In the stable treatment, all birds assigned to one feeder during the initial learning stage are reassigned to a new feeder together during the reversal stages. In the unstable treatment, each individual is randomly reassigned to a new feeder, independently of any other individual that was assigned to that bird's feeder in the previous stage. We show assignments to only two of the five feeders in array for simplicity, but in the experiment all feeders had some birds assigned, and the unstable treatment was independently and randomly reassigned.

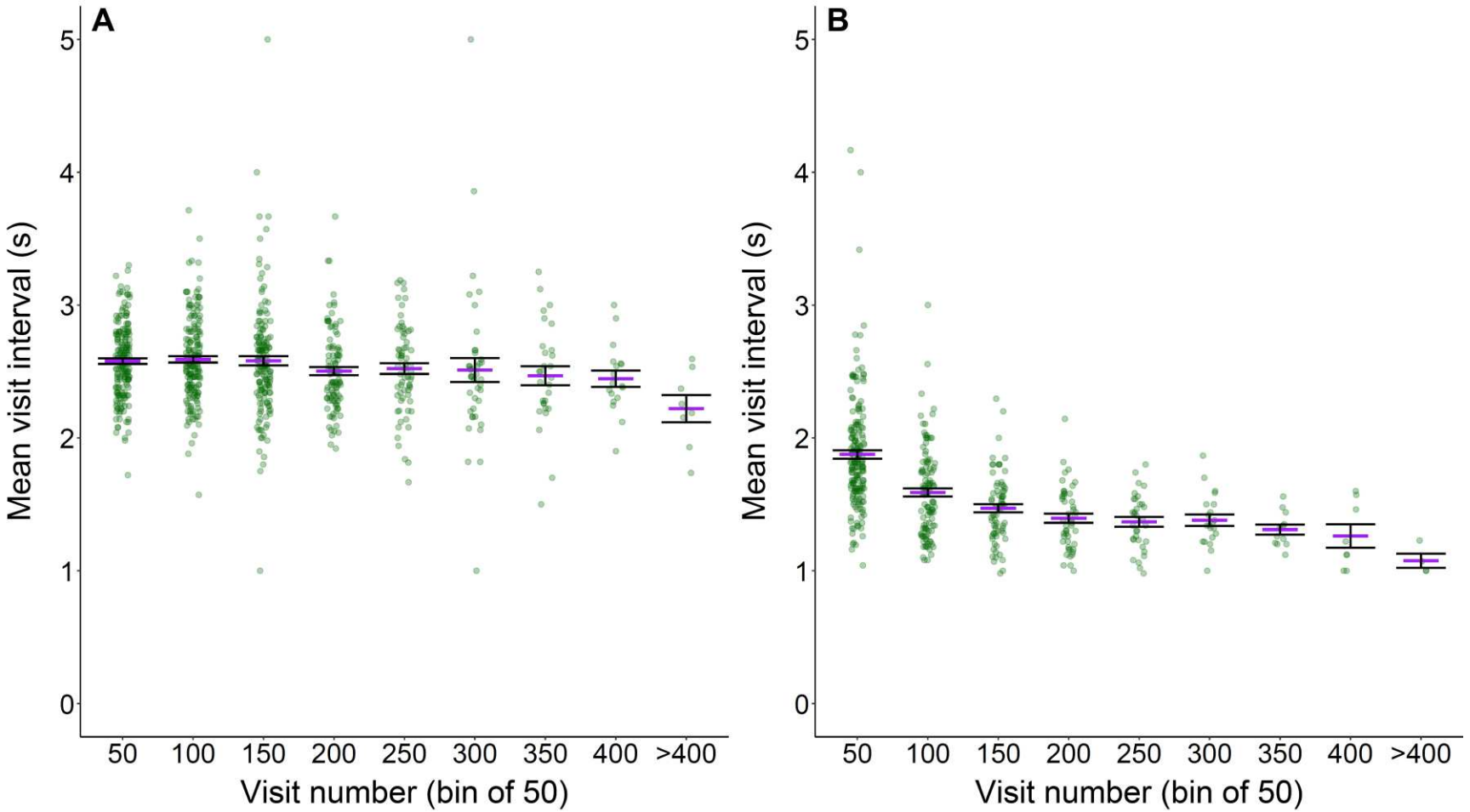

Figure S2. Comparison of visit intervals for (A) visits to the bird's own assigned feeder to (B) visits to the bird's non-assigned feeders (after (Reichert et al., 2021)). For each graph, we calculated the visit interval amount of time between the focal bird's visit to the feeder and the most recent previous feeder visitor (in B, constrained to only previous feeder visitors that had access to the feeder), only including intervals of 5 seconds or less. The x-axis shows, in chronological order, the visit number in bins of 50 consecutive visits (i.e. the first bin corresponds to visits 1–50). Very few birds made more than 400 visits, so these visits were combined into a single bin. Dots correspond to mean values within that visit bin for individual birds, and are jittered along the x-axis and rendered slightly transparent to reduce overlap. Horizontal bars represent mean (±SE) values across all birds within each bin. The graph in (B) was used as evidence that individuals learn to scrounge over repeated visits in

which they had the opportunity to scrounge (i.e., because the focal bird did not have access to the feeder but arrived shortly after a bird that did have access; if they did so within 1 s then they were able to scrounge by obtaining food from the feeder). The graph in (A) was made to test if, rather than being scrounges, the visits in (B) could represent aggressive displacement attempts. If this were the case then we would expect a similar pattern in (A) and (B) (or even lower visit intervals in A) because birds should be expected to aggressively displace others occupying their own rewarded feeder. Instead, the results in A are evidence against short-interval visits as aggressive displacement attempts because: 1) the visit intervals are larger, in some cases twice as large, for a bird's own rewarded feeder compared to non-rewarded feeders, and 2) there is no evidence of a decrease in visit intervals with increasing number of visits. Thus, while (B) shows evidence for a learning process in which individuals improve by decreasing their intervals over time (increasing the likelihood of a successful scrounge), there is no such process evident in (A). If this behavior were explained by aggressive displacements, and individuals becoming more aggressive over time, then we would expect a similar decrease in (A). Thus, we can rule out that aggressive displacements are responsible for the behavior of birds visiting non-rewarding feeders and instead continue to interpret these as attempts to scrounge.

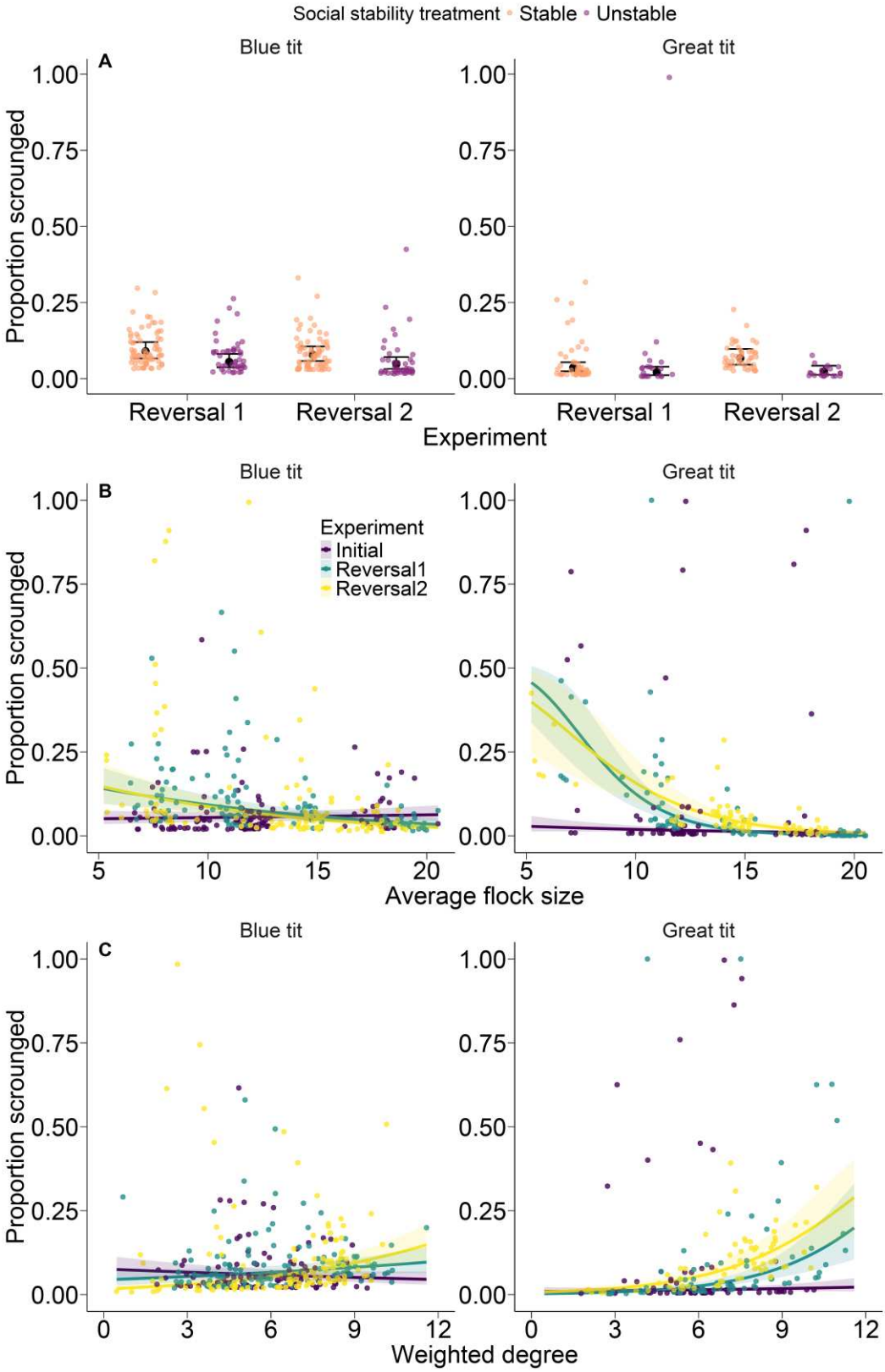

Figure S3. As in Figure 2 in main text, but showing all data points. The y-axis in Figure 2 was cut off at 0.6 to facilitate visualization, here the full dataset including outlying points is depicted.

References

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

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Troisi, C. A., Firth, J. A., Crofts, S. J., Davidson, G. L., Reichert, M. S., & Quinn, J. L. (2025). Effects of fine-scale changes in resource access and social stability on the sociality of foraging flocks of wild birds. *Animal Behaviour*, *221*, 123071. https://doi.org/10.1016/j.anbehav.2024.123071