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Effects of fine-scale changes in resource access and social stability on the sociality of foraging flocks of wild birds

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Social structure arises from individual behaviours and can impact a wide variety of behavioural and ecological processes. Although changes in the physical and social environment shape sociality, how perturbations govern sociality at a fine spatial scale remains poorly understood in wild populations. By applying automated experimental treatments to radio frequency identification tracked wild great tits, *Parus major*, in a field experiment, we examined changes in individual social network metrics in response to manipulated changes in two factors: (1) the distribution of food resources; and (2) the stability of the composition of individuals that had access to the same feeders, a subtreatment that was applied during one of the resource treatment levels. Repeatability analyses revealed consistent differences among individuals in their social network metrics at feeders across the various treatments. As expected, the average flock size and social network metrics increased when the distribution of food changed from two single feeders spaced 50 m apart (dispersed) to one location with an array of five feeders 1 m apart (clustered). However, some social network metrics changed further when individuals were restricted to feeding from only one of the five clustered feeders, even though all five feeders remained active. We also show how experimentally imposed group membership stability can impact social network metrics. Most changes in social network metrics were maintained when the food distribution returned to the dispersed pattern with two feeders 50 m apart, although dyadic associations between individuals of known identity were largely maintained. Our results show that perturbations in access to resources and social group stability at a surprisingly fine spatial scale can change connections in social networks during foraging. Fine-scale effects can arise through assortative positioning within groups and can have important consequences for social processes at larger scales, yet are typically overlooked.

Social network analysis has become a key tool for understanding social interactions, often revealing important effects that would otherwise go undetected in studies of individual behaviour (Godfrey et al., 2009). Social networks and individual social connections are often stable over time (Farine & Sheldon, 2019; Fisher et al., 2016; Shizuka et al., 2014; Stanley et al., 2018) and contexts (Firth & Sheldon, 2015, 2016; Lehmann & Ross, 2011). However, individual social behaviours and interactions are also highly plastic (Heinen et al., 2022; Proops et al., 2021), especially in fission–fusion systems.

Most evidence for the stability or plasticity of social interactions comes from observational studies or large-scale manipulations (e.g. over kilometres, between groups) (but see Borgeaud et al., 2021; Gareta García et al., 2021; Heinen et al., 2022). Individual social interactions can also take place at fine spatial scales within the broader social group (Wolf et al., 2007). Indeed, fine-scale

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interactions during foraging, roosting and under predation threats can impact broader collective motion patterns (Dibnah et al., 2022; Jolles et al., 2017; Papadopoulou et al., 2023). Similarly, broad effects on social group structure can influence individual social interactions (Cantor et al., 2021; Firth et al., 2016). Thus, it is important to consider the interactions between fine-scale environmental change and broader emerging social patterns. Using a natural study population, we experimentally manipulated i) resource distribution at a fine spatial scale (within a group) and ii) social group stability and examined their effects on individual social interactions within a flock.

Resource distribution is a major driver of social network structure (Beck et al., 2011; Foster et al., 2012; Heinen et al., 2022; Tavares et al., 2017). For instance, more clustered food resources can increase recurring aggregation, provide an opportunity to interact with individuals from other groups, and may be linked to stronger social bonds between individuals (Tavares et al., 2017). However, more clustered food resources may require individuals to invest more time in finding food, reducing the overall opportunity for social interactions (Foster et al., 2012). Resource distribution is highly variable over time, affecting individual social behaviours and social network stability (Cantor et al., 2021; He et al., 2019). All of these effects are likely scale-dependent (Levin, 1992; Wiens, 1989), and although they have been investigated from centimetres in captivity (Tanner & Jackson, 2011) to hundreds of kilometres in the wild (Beck et al., 2011; Cortés-Avizanda et al., 2011; Foster et al., 2012; Tavares et al., 2017), less is known about how fine-scale variation in resource distribution affects individual social dynamics during foraging under natural conditions.

Group membership is the main driver of sociality. It follows that changes in group membership are likely to lead to changes in individual social network metrics and social structure (Shizuka & Johnson, 2020), and these changes may be long-lasting. For instance, in macaques, the absence of policing after the loss of key male individuals led the remaining members of the group to have smaller, less diverse and less integrated networks (Flack et al., 2006). Such changes in group membership can also impact functional behaviours, such as food sharing, alloparental care, group hunting or foraging efficiency (Carter & Wilkinson, 2015; Ebensperger et al., 2016, 2017; Gazda et al., 2005; Maldonado-Chaparro et al., 2018). However, there are also cases in which individual social network positions can remain remarkably stable across years even with population turnover (Aplin et al., 2015; Farine & Sheldon, 2019; Shizuka et al., 2014) and when individuals lose close associates (Boucherie et al., 2017; Firth et al., 2017b; Madsen et al., 2023; Siracusa et al., 2021). Studies that manipulate key variables that may affect social structure are needed to determine under what conditions social networks are stable or plastic.

Typically, experimental studies on group membership and sociality involve removing or adding individuals to the group, which arguably makes changes in individual social behaviour inevitable (Boucherie et al., 2017; Firth et al., 2017b; Maldonado-Chaparro et al., 2018). However, even when group membership itself is constant, behavioural changes within the group could lead to changes in an individual's social relationships. For example, an individual that develops a new innovative behaviour (Kulahci & Quinn, 2019; Wascher et al., 2018) can become more central to the group (Kulahci et al., 2018). In addition, the development of persistent assortative interactions among individuals within groups can change individual social network metrics and social structure. Persistent assortative interactions among individuals can arise because of similarities among individuals in their preferences for different resource patches (Caillaud & Via, 2000; Crook, 1999; Martin, 2013; Snowberg & Bolnick, 2008) or in their preferred positions within groups linked to predation risk (Heathcote et al., 2017; Lambert et al., 2021). However, to date, the effects of resource use on the development and stability of persistent social interactions have not been tested experimentally.

Great tits, *Parus major*, form fission–fusion flocks during the non-breeding season in woodland habitats and readily come to feeders where their behaviour can be automatically detected using passive integrated transponders (Aplin et al., 2013; Cauchoix et al., 2022; Cooke, 2021; Reichert et al., 2020). In this study, we manipulated fine-scale resource distribution and social stability in flocks of foraging great tits and examined how these manipulations changed individual social network metrics during the experiment when foraging. Resource distribution varied with treatment and consisted of either two (50 m apart) or 5 feeders (1 m apart in a linear array), although access to food in individual feeders in the five-feeder array also varied depending on the specific treatment (or phase; see below). Social networks based on membership in flocking events were built at our feeder arrays during each level or phase of the experiment and used to estimate the following social network metrics during foraging for each individual: (1) average flock size, a basic metric of sociality (Dunbar, 1998); (2) two measures of individual social centrality: weighted degree and weighted eigenvector centrality; and (3) individual associations between all possible pairs of individuals (dyadic associations) detected during treatment or phase. Weighted degree or node strength, is the sum of all the individual's weighted associations, i.e. the number of times each association between two individuals was observed and summed across all associations. Weighted eigenvector centrality is a measure of the total number of social associations, including those of an individual's associates, i.e. an individual that associates with highly sociable individuals would have relatively high weighted eigenvector centrality. Thus, weighted degree measures the strength of associations with close associates, whereas weighted eigenvector centrality measures the strength of connections with all individuals in the network, including indirect connections via close associates.

Initially, we described patterns of feeder visitation over time and used repeatability analyses (Stoffel et al., 2017) to test whether our social network metrics captured consistent behaviour, i.e. intrinsic differences among individuals in their social connections across treatments and phases. We then explored four main questions. First, we asked how moving from ‘initial dispersed’ to ‘open clustered’ resource distribution levels affected the number, strength and identity of an individual's social interactions during foraging (Q1). We expected that flock sizes and both social centrality measures would increase as feeders move closer together and then explored whether this also disrupted previous dyadic associations. Second, we asked whether the number, strength and identity of individuals' social interactions during foraging were also modified by restricting different groups of individuals to using different, single feeders in the five-feeder array (Q2); we refer to this as the ‘assortative clustered’ treatment because it intended to mimic assortative patch use within flocks. We predicted that forcing individuals to forage at a specific feeder would disrupt the connections formed previously, and as such, their flock sizes and individual social connectedness would decrease; again, we explored whether this manipulation also disrupted previous dyadic associations. Third, we asked whether manipulated social stability during several consecutive phases of the clustered treatment further influenced the number, strength and identity of individuals' social interactions further (Q3). For this test, groups of individuals were re-allocated to one of the five feeders for two additional phases, such that individuals in the stable subtreatment always accessed feeders with the same individuals across phases, whereas individuals in the unstable subtreatment always accessed feeders with different individuals across phases. We predicted that, at the end of the three phases, individuals in the stable subtreatment would have lower centrality in smaller flocks because they were restricted in the individuals they interacted with across phases, whereas unstable individuals would have the opposite because they interacted with more individuals across phases. We also expected previous dyadic associations to be more disrupted by the stable subtreatment. Finally, we asked whether the effects of our manipulations were transient or persisted in a different context by returning the feeders to the original dispersed distribution (Q4). On the one hand, because great tits live in a fission–fusion society and are adapted to regular changes in their physical and social environment, any effects observed during the manipulations should be transient, i.e. individual social network metrics should revert to their initial value, and individuals should associate with the same individuals at the start and end of the experiment. On the other hand, when prolonged associations between individuals have longer-term carryover effects, we predicted that the manipulated effects observed during the treatments should be persistent in the context of foraging at feeders, and especially so in the stable subtreatment, where individuals had more opportunity to interact with the same individuals and create stronger new bonds.

METHODS

Study Site and Species

The study was conducted in Wytham Woods, Oxford, U.K. Great tits and Eurasian blue tits, *Cyanistes caeruleus*, were caught/recaught using mist nets in winter (from September to February) and nest boxes during spring (when chicks were 15 days old), following longstanding procedures of the Wytham tit study (see Ethical Note). Unringed individuals were fitted with a unique metal leg ring from the British Trust of Ornithology and a plastic leg ring with an inbuilt unique passive integrated transponder (PIT) tag, following Reichert et al. (2020) and the British Trust for Ornithology guidelines. Nets were placed next to established feeders to maximize capture efficiency. During winter, these birds form fission–fusion foraging flocks and to some extent move around the woodland (Farine et al., 2015; Firth & Sheldon, 2016). Data were collected during the winter from November 2017 to February 2018. Despite movement within the woods, there was limited overlap in the individuals that used distinct sites within our study area; thus, to maximise the number of individuals in our sample and reduce the likely impact of local site effects, we ran our treatments (see below) at four sites early in the season (November–December 2017) and at another four sites later in the same season (January–February 2018). Only birds ringed before the start of the experiment and those with certain identification records were included in the data. Only data from great tits were used in this study because a very high proportion of the population was tagged. Approximately 80%–90% of great tits were tagged at this time based on previous studies with similar trapping efforts (Aplin et al., 2013; Matechou et al., 2015), and 258 individuals used our feeders (check Table A1 for age and sex profiles following the STRANGE recommendations; Webster & Rutz, 2020).

Treatments

The experiment was performed on a population of great tits that had been using different types of automatic feeders for more than a decade. We assumed this previous experience had no bearing on the hypotheses tested and noted that extant birds had never participated in an experiment in which they had to choose between more than two feeders. Feeders containing sunflower seeds and equipped with a radio frequency identification antenna were active each day during daylight hours from 0700 to 1630, and PIT-tagged birds had ad libitum access to food at some or all of these feeders during those times (Reichert et al., 2020 for details). At each of the eight separate sites, feeders were arranged according to four sequential resource treatments as follows: initial dispersed, open clustered, assortative clustering and final dispersed (check Fig. 1a; the social stability subtreatment is described later). The purpose of

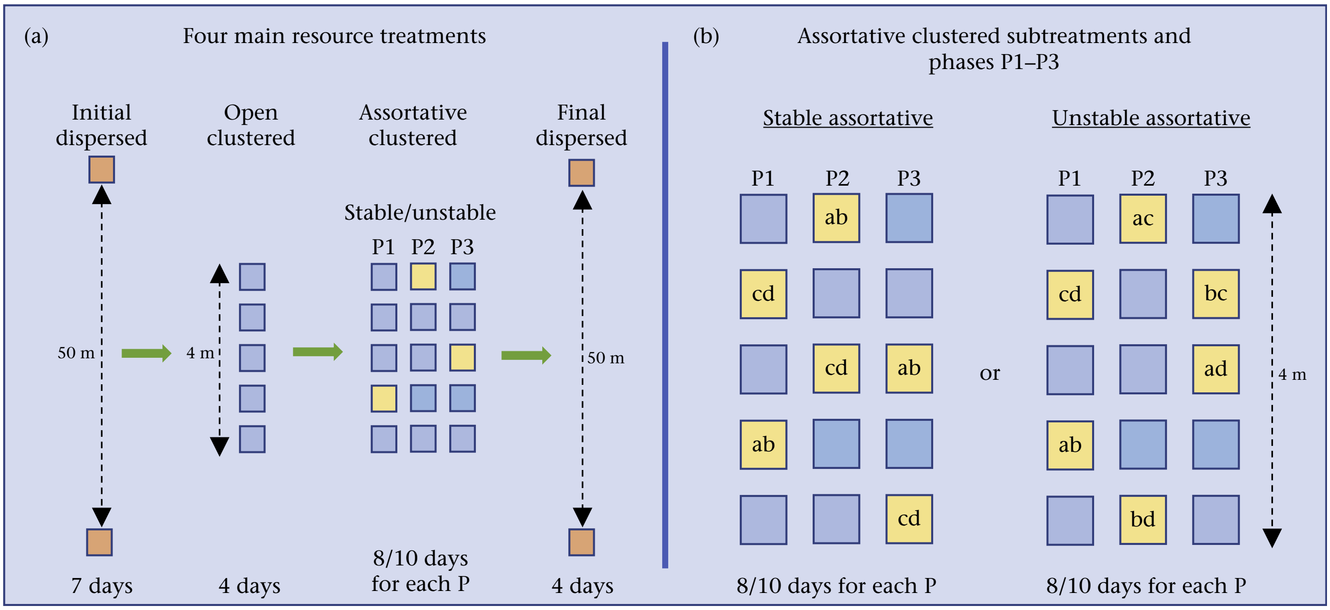


Figure 1. (a) Layout of the experiment showing the food distribution across the four treatments where food distribution was manipulated (initial dispersed; open clustered; assortative clustered; final dispersed). (b) The assortative treatment was further split into stable and unstable subtreatments, each of which ran over three phases (P1; P2; P3). The duration of each treatment is noted at the bottom. In the assortative clustered treatment, letters a, b, c and d correspond to hypothetical individual birds: in the stable subtreatment, birds a and b always feed together across phases, and so do birds c and d; in the unstable subtreatment, bird a can feed on the same feeder as bird b in the first phase (P1), bird c in the second phase (P2), and bird d in the third phase (P3). Note that for the unstable subtreatment, the specific birds assigned to each feeder during each phase were randomly chosen.

these four treatments was to manipulate the distribution of resources, which were dispersed in the first and last treatments and clustered in the other two levels. The durations of these treatments differed, primarily because of time constraints and because some treatments required learning. However, this had no bearing on our analyses because we controlled for the number of flocking events in which individuals participated and network size during each treatment (see the section on data analysis below).

The initial dispersed treatment lasted for 7 days and consisted of one feeder at each of two locations 50 m apart, during which all birds could feed from either feeder. Five days before the experiment began, all individuals could access food from the two feeders to habituate birds, regardless of whether they had a PIT tag, but the feeders were only open to PIT-tagged birds when the treatment began and during all subsequent treatments. In the open clustered treatment, which consisted of a linear array of five feeders 1 m apart placed midway between the two original feeders, PIT-tagged birds could obtain food from any of the five feeders for four days. Food availability may have been higher in the clustered treatment, but we assume that resource distribution was the main change because seeds were always available from all allocated feeders, and delivery of the single seed reward was effectively instantaneous, notwithstanding any queuing that took place around the feeders.

In the assortative clustered treatment, which occurred in three sequential phases (P1—P3), each lasting 8—10 days (see below; 8 days in 2017 and 10 days owing to operational differences in 2018), birds could only access one feeder to which they initially were randomly allocated, based on which birds had been visiting the feeder in the preceding stage. Note that we use the word ‘assortative’ in the sense that restricting individual access to individual feeders in effect placed them into groups of individuals that shared a feeder, even though they had not been grouped based on any a priori shared characteristic. When birds landed on their assigned feeder, the feeder would open and they had access to the food; when they landed on any of the four other feeders, the feeder would remain closed, and the bird would not have access to the food, but its visit would still be recorded and used in generating social network metrics. Great tits quickly learned which feeder they were allocated to, usually within the first day and usually after less than 30 visits (more details in Reichert et al., 2020, which used the same data).

When the first 8 to 10 day phase (P1) of the assortative clustered treatment ended, we manipulated social stability by randomly allocating birds to a different feeder (P2). This was either with the same individuals as in their feeder assignment during P1 (the stable subtreatment) or with a random selection of predominantly different individuals (the unstable subtreatment; Fig. 1b). The stable and unstable subtreatments were each run at four separate sites, two for each subtreatment from November to December 2017, and the other two for each subtreatment from January to February 2018. After another 8—10 days, we repeated the feeder reassignment procedure (P3); birds in the stable subtreatment were again reassigned along with the same individuals from their original feeder assignment, and birds in the unstable subtreatment were again reassigned with a new randomly selected group of individuals. Therefore, for individuals in the stable subtreatment, the identity of individuals that had access to the same feeders was always the same throughout the three phases of the assortative clustered treatment level; for those in the unstable subtreatment, the identity of individuals that had access to the same feeders changed across the three phases of the assortative clustered treatment level.

We finished the experiment with the final dispersed treatment, reverting to two feeders 50 m apart, during which all birds could feed from either feeder, similar to the initial dispersed treatment. This phase lasted for four days.

Individual Social Network Metrics

The raw data set consisted of rows containing the date, time and PIT tag for each detected visit at each feeder. We considered consecutive detections of the same bird to the same feeder within 2 s of each other to be a single visit (following Evans et al., 2018; Reichert et al., 2020). Using the spatiotemporal data of visits to feeders, ‘flocks’ (or ‘flocking events’) were identified at each location using a machine learning algorithm (Psorakis et al., 2012, 2015). This algorithm detects periods of increased feeder activity in the data and clusters those periods into nonoverlapping ‘flocking’ events; a Gaussian Mixture Model (GMM) then assigns each visit from each bird to the flocking event for which it had the highest probability of belonging, without imposing assumptions about the temporal boundaries of flocks (Psorakis et al., 2012). This allowed us to separately calculate the average flock size for each individual at each location during each treatment or each phase of the clustered treatment. From these grouping events, we also created social networks for each location (social network metrics were calculated at the feeder array level, including visits by all individuals to all feeders) during each phase of the treatment, following previous work (Psorakis et al., 2012, 2015). By taking the group-by-individual matrix generated from the GMM, social networks were generated by taking all possible dyads and summing the number of flocking events in which both individuals were present. We used these data to quantify the association strength for each dyad as a ‘simple-ratio index’: the number of times both individuals were seen in the same flocking events ÷ (the number of times individual A was seen in a flocking event without B + the number of times individual B was seen in a flocking event without A + the number of times individuals A and B were both seen in the same flocking event) (Cairns & Schwager, 1987; Whitehead, 2008).

From these social networks, we also separately calculated two commonly used social network centrality metrics, for every individual at each location, during each treatment or each phase of the clustered treatment: (1) weighted degree, the weighted sum of all the focal individual's social associations i.e. the sum of their simple-ratio index scores with all other individuals (also known as node ‘strength’); and (2) weighted eigenvector centrality, a social centrality metric measuring of the total amount of social associations of an individual's associates (i.e. the centrality of their flockmates). For instance, an individual that associates with highly sociable individuals would have high eigenvector centrality, whereas an individual that associates with peripheral individuals would have low eigenvector centrality. These network metrics represent a range of measures of individual centrality (Albery et al., 2021).

Along with the individual-level metrics (described above), we also included a dyadic-level metric: the strength of the associations between pairs of individuals directly from the social network metrics (i.e. each dyad's simple-ratio index score).

Ethical Note

We conducted our experiments following the Association for the Study of Animal Behaviour ethical guidelines. The present study was approved by the Animal Experimental Ethics Committee of University College Cork and the Health Products Regulatory Authority (licence number E19130/P017) in Ireland. Feeder deployment was approved by the ethics review committee Animal Welfare and Ethical Review Board at the Department of Biology, University of Oxford. Before the start of trials at each site, birds were caught in the wild using mist nests in the winter (from September to February) and nest boxes during spring (when chicks were 15 days old) using spring traps that block the entrance when birds return to the nest after foraging, following longstanding procedures of the Wytham tit study. Mist nests and nest boxes were checked approximately every 10 to 15 min and birds were retrieved to ensure trapping time was minimised. All bird ringing and tagging was carried out under standard licensing permissions from the British Trust for Ornithology. Captured birds were handled by trained ringers following techniques of the British Trust of Ornithology and released immediately back into the wild after the necessary measurements were taken. The PIT tags were approximately 0.13 g, which is smaller than the natural diurnal variations in great tits' weight (1.1 ± 0.02 g) (Macleod et al., 2005). The added weight was found to have no significant adverse effects on survival or body condition (Nicolaus et al., 2008).

Data Analysis

All analyses were conducted using R version 4.0.2 (R Core Team, 2020). Linear mixed models were used in all cases with the lme4 and lmerTest packages (Bates et al., 2015; Kuznetsova et al., 2017), and the package *ggplot2* was used for plotting graphs (Wickham, 2016). Initially, we tested whether our measures of individual social behaviour captured intrinsic differences among individuals. We first calculated the mean values across all flocking events for each individual in each treatment or phase separately (of which there were six across the experiment: four resource treatments and three phases within one of the resource treatments) (Fig. 1), thus resulting in six means per individual per sociality measure; note this could not be done for dyadic associations. We then used the *rptR* package (Stoffel et al., 2017) to calculate the repeatability of each sociality measure. We included only birds that appeared in all four resource treatments and all three phases of the assortative clustered resource treatment ($N = 70$; 68 individuals, with two individuals present at two sites). To understand whether temporal variation in feeder usage throughout the experiment might influence our main questions, we examined whether the following three measures varied across all six treatment or phase levels: (1) the number of individuals detected at a site per treatment or phase; (2) the average number of visits per individual per day per treatment or phase; and (3) the average number of flocks an individual was in per day, per treatment or phase. Linear mixed models were used, with the first specifying a Poisson distribution and the remaining two with Gaussian distributions. For the number of individuals per treatment (1), we included experimental treatment as a fixed factor and site as a random effect. For the other two analyses (2 and 3), we included sex, age (adult versus juvenile) and experimental treatment as fixed factors, as well as individual identity and site as random effects ($N = 238$).

Four questions (Q1–Q4; see below in the detailed analysis section) were examined using different subsets of the data from the six treatments or phases. For each question, separate linear mixed models were constructed for each social network metric. Unless otherwise stated, model structures were similar in all analyses: random effects included individual and site effects, whereas fixed effects included sex, age, the number of flocking events individuals participated in and the number of individuals at that site during that treatment or phase. The latter two fixed effects ensured that any observed treatment effects were not simply because of changes in general activity or the total number of individuals present over time. Each model also included two treatment or phase levels, depending on the question being asked (see below in the detailed analysis section, for each question). We used a Gaussian error distribution for all models.

The experiment was conducted in one winter season (November 2017 to February 2018), and the treatments and sites were randomized concerning time. Therefore, for the sake of parsimony and to limit the number of random effects, we did not model time within a season in any of our analyses. Temporal effects should be captured by the random effects of the site, and trends will have no bearing on the hypotheses. Furthermore, there was no difference in the number of visits in the November–December 2017 period compared with the January–February 2018 period (mean number of visits per individual was 1618 and 1502, respectively; $P = 0.997$; generalised linear model with a negative binomial family distribution).

Social network metrics necessarily violate the assumption of independence, as one individual's connection influences another individual's connections; thus, along with the standard statistical models, in all cases we additionally compared the model estimates to those calculated from null models using node-based permutations, where the networks (and individual network metrics) have the same distribution as the observed data (Whitehead, 2008). Additionally, we report P values showing where the observed estimates fall within the distribution of estimates from the 1000 permutations for each model, i.e. if $P < 0.05$, then the observed estimate falls outside the 95% range of the null expectation (Whitehead, 2008). A small number of birds (usually 1–3 in any one analysis) were present at several of our eight sites (as four sites were used early in the season and four sites later in the season), and this was accounted for using individuals as a random effect in all analyses. When they were present at two sites, they were only ever allocated to a feeder at one site during the assortative clustered treatments. For each question, we also modelled dyadic associations using the 'simple-ratio index' during one treatment against the simple-ratio index during the previous treatment, the exact treatments used depending on the question. In these analyses, we did not model the effect of sex; therefore, we included birds of unknown sex and included the identity of both individuals of each dyad and site as random effects. This analysis tested whether the association strength in the prior treatment predicted that of the subsequent treatment, with significant effects suggesting that the same associations between specific individuals were maintained despite the treatment.

Q1: changing from dispersed to clustered resources

We asked whether changing from dispersed to clustered resources influenced social behaviour during foraging. We modelled the three main social network metrics against resource treatment for the initial dispersed and open clustered treatments. Birds of known sex present in both treatments were included ($N = 121$ individuals; $N = 3$ individuals appeared > 1 site; Table A1). For the analysis of the dyadic associations, we used the simple-ratio index during the open clustered treatment as the response variable and the simple-ratio index during the initial dispersed treatment as a fixed effect ($N = 131$ individuals; $N = 3$ individuals appeared at > 1 site).

Q2: assortative feeding after fine-scale spatial change

We asked whether assortative feeding on a fine spatial scale changed social behaviour during foraging. We modelled the three main social network metrics against resource treatment for the open- and associative-clustered treatment (P1 only) levels. Birds of known sex were included in these analyses only if they were present in both treatments ($N = 100$ unique individuals; $N = 2$ individuals appeared at > 1 site; Table A1). We then tested whether dyadic associations during the open clustered phase predicted those observed in the assortative clustered P1 phase in the same manner as described in Q1 ($N = 107$ individuals; $N = 2$ individuals appeared at >1 site).

Q3: effect of social stability

We investigated whether social stability influenced the effect of assortative feeding on social behaviour during foraging. We modelled the three main social network metrics against resource treatment for the assortative clustered P1 and P3 phase treatments and tested their interaction with social stability (stable versus unstable). Birds of known sex were included in these analyses only if they were present during P1 and P3 ($N = 91$ unique individuals; $N = 3$ individuals appeared at > 1 site; Table A1). We ran post hoc tests using the *emmeans* package (Lenth, 2019) to compare the changes across the phases for birds in each social subtreatment. We also examined whether dyadic associations in P1 predicted those in P3 and whether this interacted with social stability ($N = 94$ individuals; $N = 3$ individuals appeared at > 1 site). Note that the main effect of social stability in the dyadic analysis (here and in Q4) is not relevant and is driven by differences in network size among sites and treatments.

Q4: Persistence of observed changes

We investigated whether observed changes in sociality persisted when dispersed food treatment was restored and whether this was the same for both social stability subtreatments. In this analysis, we modelled the three main social network metrics against resource treatment for the initial dispersed and final dispersed treatments to see whether there was a persistent change over time. Additionally, the interaction with social stability was tested. We included only individuals of known sex that were present at all six stages of the experiment ($N = 67$ unique individuals; $N = 2$ individuals appeared at > 1 site; Table A1). Post hoc tests of the interaction were performed. We also tested whether the correlation between the dyadic association score in the final dispersed treatment and the dyadic association score in the initial dispersed treatment interacted with the social stability subtreatment ($N = 68$ individuals; $N = 2$ individuals appeared at > 1 site).

RESULTS

All individual social metrics showed low-moderate repeatability, and our measures therefore captured intrinsic among-individual differences in their sociality (flock size: R = 0.353, 95% confidence interval (CI) 0.232–0.459, $P < 0.001$; weighted degree, R = 0.256, 95% CI = 0.150–0.359; $P < 0.001$; weighted eigenvector centrality, R = 0.104, 95% CI = 0.023–0.190, $P = 0.002$). The number of individuals at each site, the number of visits per individual per day, and the rate of flocking events per individual per day varied throughout the experiment (Table A2; Fig. A1). Thus, in all further analyses, we controlled for the number of individuals at sites and the number of flocks in which individuals participated for each treatment or phase level. We did not control the number of visits each bird made, which was strongly colinear with the number of flocking events ($R = 0.911$).

Q1: Changing from Dispersed to Clustered Resources

All measures of sociality were significantly higher in the open clustered treatment than in the preceding initial dispersed treatment (Table A3, Fig. A2; null model tests Table A4). Dyadic associations in the initial dispersed treatment predicted associations in the open clustered treatment ($B = 0.43$ (95% CI =0.358–0.497); intercept $B = 0.073$ (95% CI = 0.046–0.099); Fig. 2a).

Q2: Assortative Feeding after Fine-Scale Spatial Change

Restricting individuals from accessing food from only one of the five feeders in the array led to a significant increase in flock size and a significant decrease in weighted degree and weighted eigenvector centrality (open clustered versus assortative clustered P1 treatment; Table 1, Fig. 3; null model tests Table A5). Once again, dyadic associations during the open clustered treatment predicted those in the assortative clustered P1 treatment ($B = 0.139$ (95% CI = 0.092–0.187); Intercept: $B = 0.151$ (95% CI = 0.117–0.188); Fig. 2b, Fig. A3).

Q3: Effects of Social Stability

Flock size significantly increased from the first to the third assortative clustered phases (P1–P3), especially in the stable social groups (resource × social stability; Tables 2, A6, Fig. 4; null model tests Table A7). The weighted degree also significantly increased from the first to the third assortative clustered phases, which was similar for both social stability subtreatments (i.e. there was no significant resource × social stability effect; Tables 2, A6, Fig. 4). Weighted eigenvector centrality decreased from the first to the third assortative clustered phases, and there was weak (nonsignificant) support for a more pronounced decrease in the stable groups (resource × social stability; Tables 2, A6, Fig. 4c). Dyadic associations during the assortative clustered P1 treatment predicted the associations during the assortative clustered P3 treatment, and there was weak (nonsignificant) support for this correlation being stronger in the stable than in the unstable subtreatment (resource × social stability, $B \pm SE = -0.101 \pm 0.065$, $P = 0.121$; Table A8, Fig. 2c).

Q4: Persistence of observed changes

All three social network metrics were higher in the final dispersed treatment than in the initial dispersed treatment, even after controlling for changes in network membership and increases in visit rates (main effects of treatment in Table A9 for mixed models and Table A10 for null models; Fig. 5). The increase in flock size was significantly greater for the unstable than for the stable subtreatment; there was no evidence that social stability significantly affected the change in weighted degree or weighted eigenvector centrality from the initial to final dispersed stages (resource × stability; Tables A9, A11; Fig. 5).

Dyadic associations during the initial dispersed treatment predicted those during the final dispersed treatment ($B = 0.228$ (95% CI = 0.125–0.335); Intercept $B = 0.157$ (95% CI = 0.120–0.196); Fig. 2d). There was no evidence that the social stability subtreatment significantly influenced the relationship between dyadic associations at the two time points (association initial dispersed × social stability, $B \pm SE = 0.132 \pm 0.109$, $P = 0.229$; Table A12, Fig. 2d).

DISCUSSION

Using a field experiment conducted on individual-tracked wild great tits, we examined how fine-scale changes in social foraging shape the overall social network structure, as well as individual-level network positions and dyadic associations. The repeatability estimates we observed for the individual social network metrics suggest that the behavioural variation we captured reflects intrinsic differences among individuals in their social tendencies (Bell et al., 2009). Nevertheless, we also found that changes in both resource distribution and social stability influenced individual-level social network metrics (check Fig. 6 for a summary of the social network metrics results). Some of these effects lasted even when food distribution and social groupings reverted to their original structures. Although there was some variation in the social network metrics, the strength of the dyadic associations between individuals was largely consistent across the experiment.

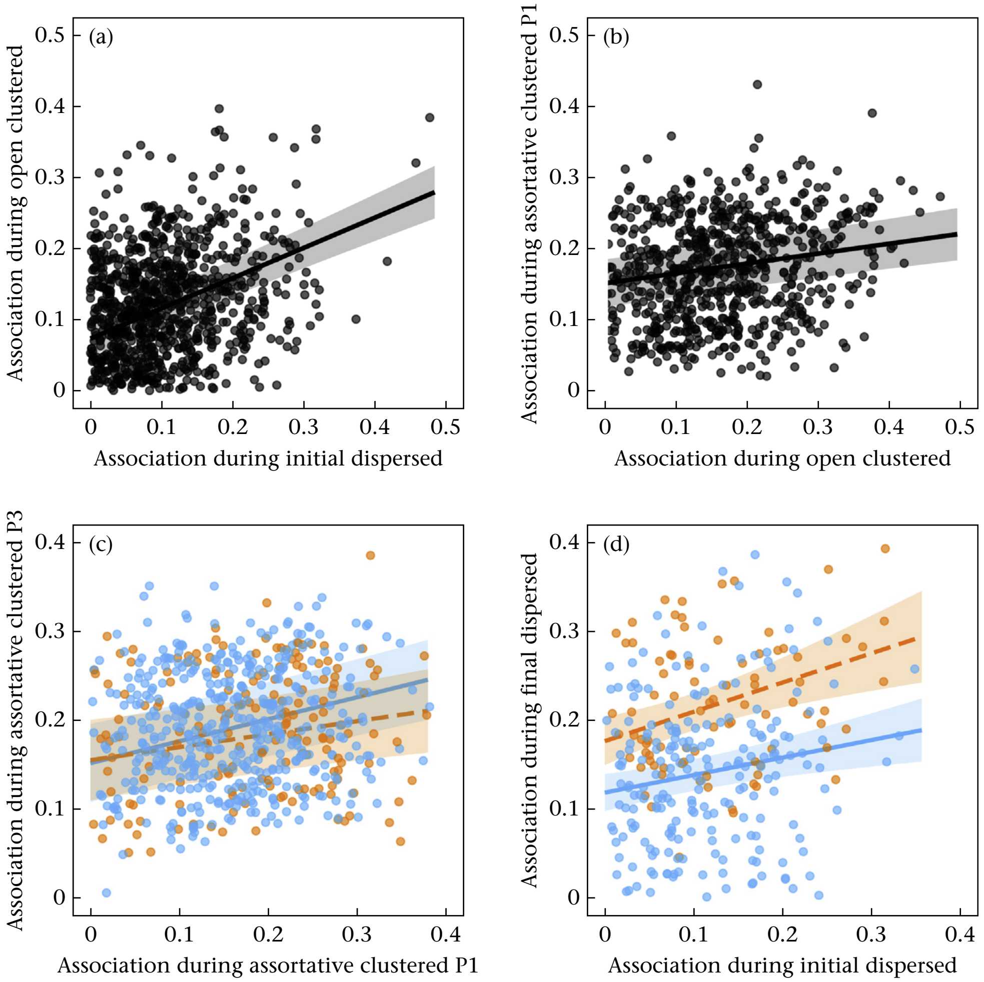


Figure 2. Partial residual plots showing how pairwise associations (measured as the simple-ratio index) in one treatment predicted these in the next for (a) the initial dispersed treatment and the open clustered treatment; b) the open clustered treatment and the assortative clustered treatment (P1) (two outliers are excluded from the graphical representation, to allow for more clarity, see Figure A3 for the graphical representation including the outliers); (c) the assortative clustered P1 treatment and P3 treatment; and (d) the initial dispersed and final dispersed treatments. For (c) and (d), separate lines are shown for birds in the stable (blue) and unstable (orange) social stability subtreatments. The interaction was nonsignificant (ns) for (c) and (d). Shaded areas are the 95% confidence intervals from corresponding models in the main text and in Tables A7 and A10. We added random effects for the identity of both individuals of each dyad and site.

Table 1
Linear mixed models of how each of the three individual social network metrics changed from the open clustered to the assortative clustered treatments

Dependent variable	Independent variables	Estimate (SE)	95% CI	*P* value
Flock size	Intercept	1.35 (0.504)	0.391; 2.30	0.011
	Flocking events	0.001 (0.002)	−0.002; 0.004	0.565
	Individuals in the local network	0.180 (0.018)	0.145; 0.216	<0.001
	Sex (male)[1]	−0.089 (0.115)	−0.313; 0.135	0.441
	Age (juveniles)[2]	−0.030 (0.125)	−0.273; 0.212	0.808
	Resource (assortative clustered P1)[3]	0.765 (0.217)	0.346; 1.18	<0.001
Weighted degree	Intercept	−0.318 (0.310)	−0.917; 0.279	0.311
	Flocking events	0.018 (0.001)	0.016; 0.020	<0.001
	Individuals in the local network	0.085 (0.012)	0.063; 0.107	<0.001
	Sex (male)[1]	0.010 (0.071)	−0.129; 0.148	0.891
	Age (juveniles)[2]	−0.069 (0.077)	−0.219; 0.081	0.374
	Resource (assortative clustered P1)[3]	−1.02 (0.134)	−1.28; −0.762	<0.001
WEVC	Intercept	0.567 (0.071)	0.433; 0.702	<0.001
	Flocking events	0.005 (0.0003)	0.005; 0.006	<0.001
	Individuals in the local network	−0.004 (0.003)	−0.009; 0.002	0.190
	Sex (male)[1]	0.001 (0.022)	−0.043; 0.043	0.955
	Age (y, juveniles)[2]	−0.053 (0.024)	−0.100; −0.006	0.031
	Resource (assortative clustered P1)[3]	−0.371 (0.039)	−0.445; −0.295	<0.001

Fixed effects included the number of flocking events, the number of individuals in the local network, the sex of the individual, the age of the individual, and the resource treatment. The site and individual identity were included as random effects. CI; confidence interval. WEVC: weighted eigenvector centrality.

[1] Baseline = female.

[2] Baseline = adult.

[3] Baseline = open clustered.

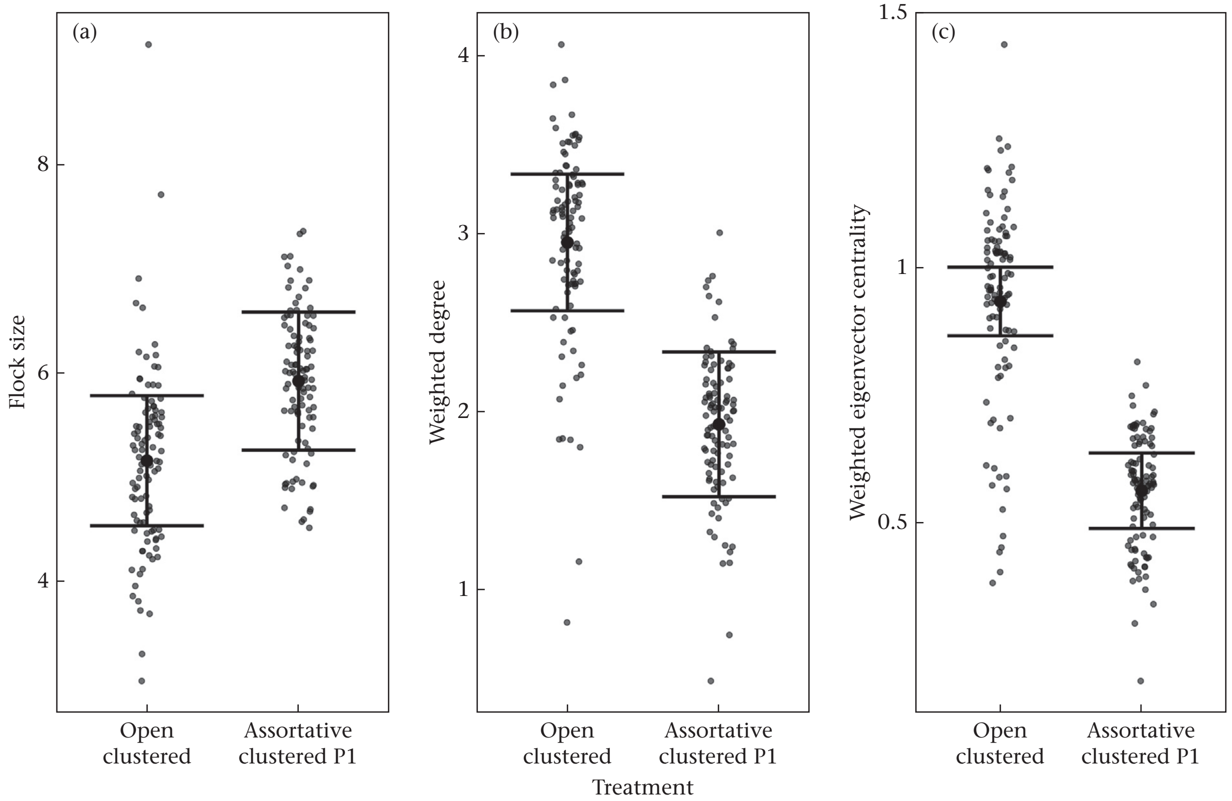


Figure 3. Partial residual plots showing changes in (a) flock size, (b) weighted degree and (c) weighted eigenvector centrality across the open clustered and assortative clustered P1 treatment. Error bars are 95% confidence intervals based on the linear mixed models in Table 1.

Table 2
Linear mixed models of changes in each of three individual social network metrics, from the start (P1) to the end (P3) of the assortative clustered resource treatment

Dependent variable	Independent variables	Estimate (SE)	95% CI	*P* value
Flock size	Intercept	0.946 (0.507)	0.006; 1.88	0.082
	Flocking events	−0.0005 (0.001)	−0.002; 0.001	0.530
	Individuals in the local network	0.255 (0.021)	0.216; 0.293	<0.001
	Sex (male)[1]	−0.017 (0075)	−0.158; 0.125	0.811
	Age (juveniles)[2]	0.040 (0.089)	−0.158; 0.125	0.626
	Resource (assortative clustered P3)[3]	1.02 (0.097)	0.830;1.21	<0.001
	Social stability (unstable)[4]	0.199 (0.548)	−0.844; 1.25	0.731
	Resource (assortative clustered P3) × social stability (unstable)	−0.596 (0.153)	−0.885; −0.305	<0.001
Weighted degree	Intercept	0.124 (0.302)	−0.465; 0.696	0.690
	Flocking events	0.012 (0.0004)	0.011; 0.013	<0.001
	Individuals in the local network	0.042 (0.012)	0.019; 0.069	0.001
	Sex (male)[1]	0.039 (0.0423	−0.043; 0.122	0.361
	Age (juveniles)[2]	0.044 (0.047)	−0.048; 0.135	0.354
	Resource (assortative clustered P3)[3]	0.232 (0.057)	0.120; 0.341	<0.001
	Social stability (unstable)[4]	−0.350 (0.334)	−0.976; 0.260	0.346
	Resource (assortative clustered P3) × social stability (unstable)	−0.007 (0.087)	−0.173; 0.165	0.934
WEVC	Intercept	1.09 (0.123)	0.859; 1.33	<0.001
	Flocking events	0.004 (0.0001)	0.003; 0.004	<0.001
	Individuals in the local network	−0.042 (0.004)	−0.050; −0.032	<0.001
	Sex (male)[1]	0.063 (0.015)	−0.022; 0.035	0.672
	Age (juveniles)[2]	−0.007 (0.016)	−0.039; 0.025	0.683
	Resource (assortative clustered P3)[3]	−0.099 (0.020)	−0.138; −0.061	<0.001
	Social stability (unstable)[4]	−0.184 (0.145)	−0.460; 0.087	0.262
	Resource (assortative clustered P3) × social stability (unstable)	0.049 (0.030)	−0.009; 0.108	0.108

Fixed effects included the number of flocking events, the number of individuals in the local network, the sex of the individual, the age of the individual, the resource treatment, the social stability sub-treatment, and the interaction between the resource treatment and the social stability sub-treatment. The site and individual identity were included as random effects. CI: confidence interval; WEVC: weighted eigenvector centrality.

[1] Baseline = female.

[2] Baseline = adult.

[3] Baseline = assortative clustered P1.

[4] Baseline = stable.

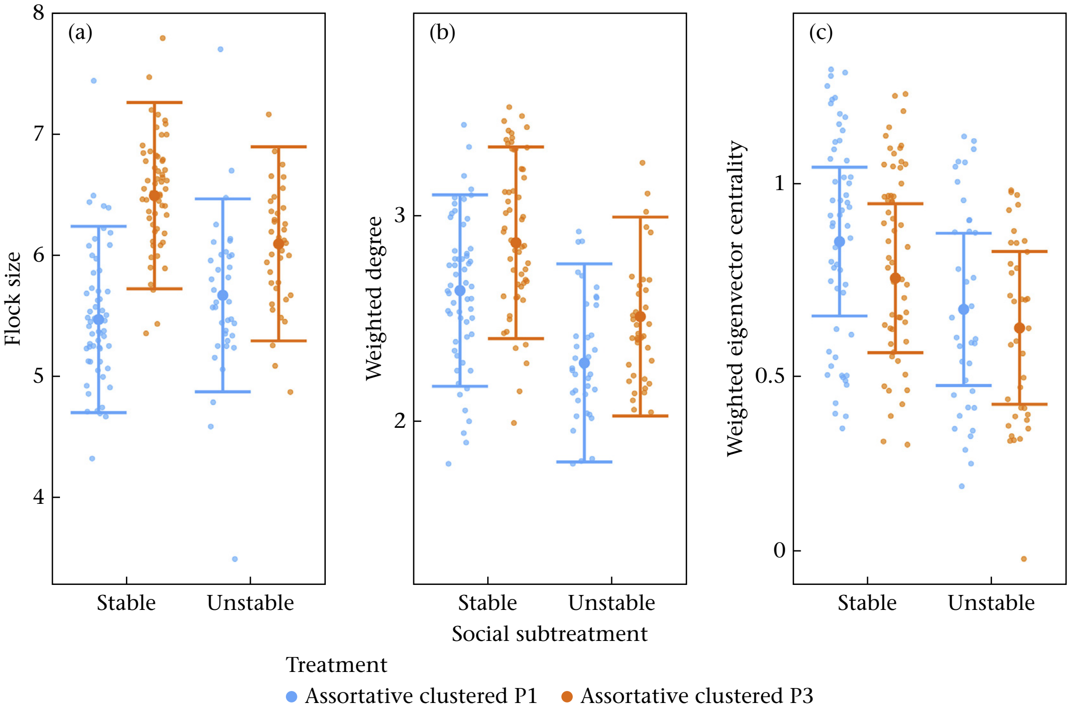


Figure 4. Plots showing the partial residuals for (a) flock size, (b) weighted degree and (c) weighted eigenvector centrality, and how these changed across the assortative clustered P1 and assortative clustered P3 treatment for each social stability subtreatment. Error bars are 95% confidence intervals based on models in Table 2.

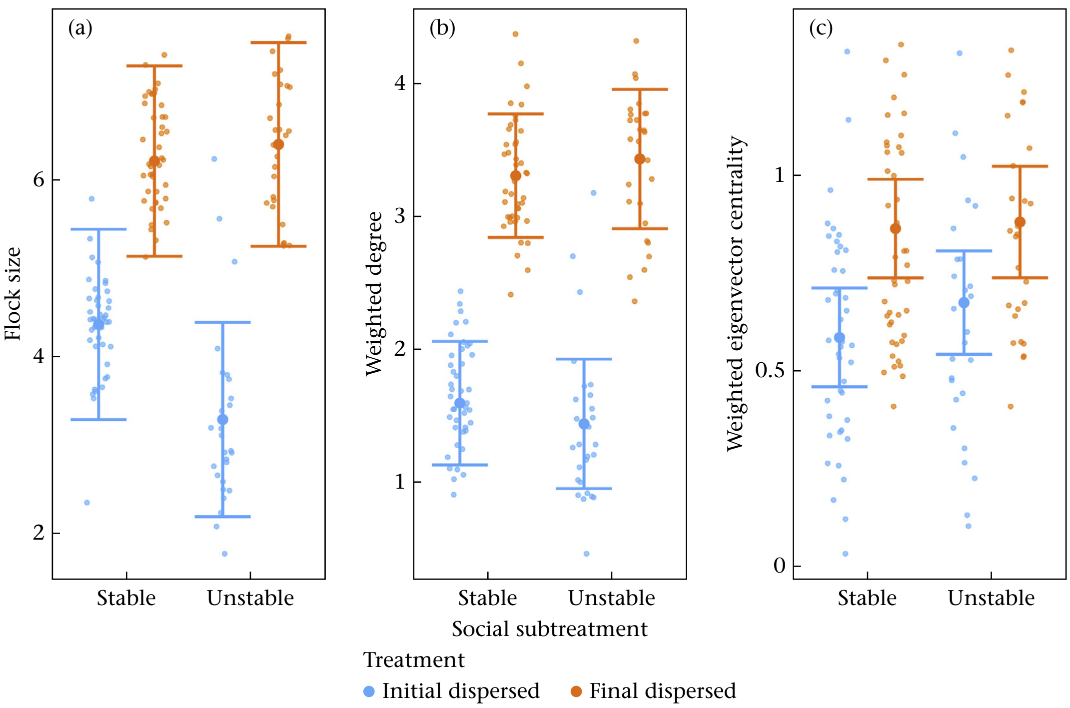
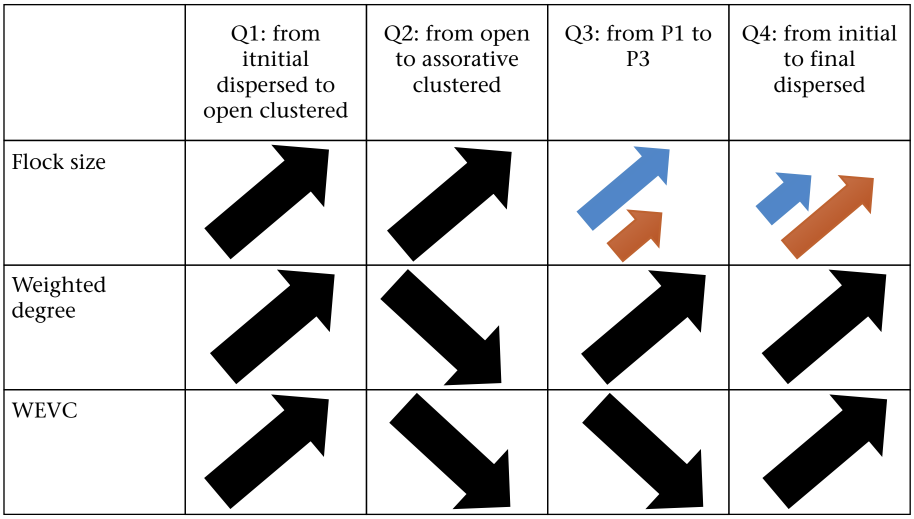


Figure 5. Plots showing the partial residuals for (a) flock size, (b) weighted degree and (c) weighted eigenvector centrality, across the initial dispersed and final dispersed treatment, for each social stability subtreatment. Error bars are 95% confidence intervals based on models in Table A8.

Resource Distribution and Individual Social Behaviour (Q1 & Q2)

Manipulating resource distribution from two feeders 50 m apart (dispersed) to a clustered array of five feeders only 1 m apart led to an immediate increase in individual social connections for all metrics, in line with previous studies (Tanner & Jackson, 2011; Tavares et al., 2017; Zahavi, 1971). This is unsurprising and likely occurred simply because the total number of birds at the site only declined by approximately 20% after the shift in distribution, and yet suddenly the remaining birds were feeding on additional food



	Q1: from itnitial dispersed to open clustered	Q2: from open to assorative clustered	Q3: from P1 to P3	Q4: from initial to final dispersed
Flock size	↗	↗	↗ ↗	↗ ↗
Weighted degree	↗	↘	↗	↗
WEVC	↗	↘	↘	↗

Figure 6. Summary of the main treatment effects on the individual social network metrics flock size, weighted degree and weighted eigenvector centrality (WEVC). Arrows pointing towards the top indicate a significant increase, while arrows pointing towards the bottom indicate a significant decrease. Two boxes have two arrows to show the difference between the stable and the unstable social subtreatment. Arrows in black represent both social treatment groups, arrows in blue represent the stable social group; and arrows in orange represent the unstable social group. When the blue arrow is longer than the orange arrow, this indicates that the increase in the stable group was stronger than that of the unstable group. When the blue arrow is shorter than the orange arrow, this indicates that the increase in the stable group was smaller than that of the unstable group.

resources at one location instead of two, providing more opportunity for social interaction. The observed response indicates that when birds have to find new foraging patches, they ultimately converge on similar feeding locations, likely through a variety of mechanisms linked to shared information (Ward & Webster, 2016).

Our finding was that sociality at the feeders changed considerably when individuals were restricted to one of five feeders 1 m apart within a single foraging location (the assortative clustered treatment). This observation is notable given that the location of the five feeders remained unchanged; each of those feeders could detect all individuals, but the food inside could only be accessed by some individuals, and the social network metrics were calculated using data from all feeders in that treatment. Flock sizes increased, likely caused by reduced feeder access, forcing individuals to spend more time at the location to get the food (presumably being forced to queue for longer and/or taking some time to learn which feeder provides food). As predicted, the same manipulation reduced the strength of connections, as indicated by declines in weighted degree and in individuals' overall social connectedness at feeders (weighted eigenvector centrality). In other words, individuals occurred in larger but less-connected flocks. To our knowledge, this is the first experimental demonstration that restricting where individuals feed within a location the size of a small foraging patch a few metres long and occupied by a small group of individuals can change sociality when feeding, demonstrating the importance of scale in understanding the effects of resource use on social interactions (Cortés-Avizanda et al., 2011; Johnson et al., 2002). Constraints on where individuals feed within group foraging locations can arise through a variety of mechanisms, for example, because of competitive ability when patch quality varies, risk-taking behaviour when risk varies, and personality (Quinn et al., 2012; Webster & Ward, 2011). Our experimental manipulation supports the hypothesis that these constraints may have implications for individual social behaviour even on a very fine spatial scale.

Effect of Social Stability on Social Behaviour (Q3)

We found that sociality changed over the three phases of the assortative clustered treatment, irrespective of the social stability subtreatments. Birds occurred in larger flock sizes; their weighted degrees (the strength of connections with direct associates) increased, and their weighted eigenvector centrality (the strength of connections with associates, direct and indirect) decreased. Although not part of our predictions, this is not surprising given that each of the three phases lasted 8–10 days, and individuals presumably formed stronger connections in larger flocks simply because they spent more time together. Although we might also expect weighted eigenvector centrality to have also increased, the opposite occurred, presumably because connections to formerly peripheral individuals were lost as members of increasingly tighter flocks became more associated during their visits to feeders.

However, our main hypothesis concerned manipulating social stability, and there was mixed support for our predictions. Against our prediction that the stable treatment would lead to lower centrality in smaller flocks because they were restricted in the individuals they interacted with across phases, the increase in flock size mentioned above was greater in the stable than in the unstable subtreatment. One possible explanation for this is that there may have been greater synchrony in arrival times among birds in flocks in the stable subtreatment because, for example, information should be more reliable for stable flock mates (Croft et al., 2009; Kulahci et al., 2018). In contrast, birds in the unstable treatment group may have perceived that their flock mates were less reliable and were therefore unable or less driven to synchronize arrival at the feeders. Previous work on this system has shown that birds that are allowed to access the same selective feeders as one another are also more likely to learn about new food resources from one another (Firth et al., 2016). Thus, the stability we enforced in one subtreatment may have led to greater synchrony and larger flock sizes because of the shared information benefits.

We also predicted that individuals in the stable social group would have lower centrality because they were restricted in the individuals they interacted with across the three phases and that the dyadic correlation across the phase would be more disrupted. However, against predictions, the weighted degree increased equally in both stability subtreatments, and the correlation between the dyadic associations from P1 to P3 was stronger in the stable group, not weaker, than in the unstable group. In support of our predictions; however, the overall connectedness (weighted eigenvector centrality) decreased for both subtreatments, but it decreased more for the stable than the unstable group. Together, these two results suggest that stability may have affected centrality primarily by effects on indirect connections with individuals in the network, not by effects on close associates. This is perhaps in line with expectations from previous simulation studies showing that measures of centrality that capture indirect associations rather than those that rely on direct connections between associates, which is true for both weighted degree and dyadic associations, are likely to be more reflective of underlying social behaviour, especially in complex, noisy social systems such as wild animal populations (Firth et al., 2017a).

Persistence of Observed Changes (Q4)

During the final dispersed phase at the end of the experiment, individuals came to the feeders in larger flocks, had stronger associations with other individuals, and had more central associates, compared to the same dispersed configuration at the beginning of the experiment. This persistence may have spatial and temporal explanations. First, the clustered treatment had a high density of feeders, forcing individuals to interact at close range, increasing opportunities for social bond formation. Indeed, we observed an increase in social connectedness during this period. Once these social associations were formed, they may have been transferred to new contexts. For instance, Firth and Sheldon (2015) found that controlling access to feeders changed the social network in a foraging context, not only at those feeders, but also at unrestricted feeders, and even while prospecting for nests in the context of breeding. Second, the clustered phase of the experiment had a relatively longer duration than the other phases. This afforded individuals increased opportunities to interact and form stable relationships. Once solidified, these were then likely to continue for some time after the distribution of resources changed. However, Heinen et al. (2022), who used a timeline similar to our experiment, found that no significant assortment persisted beyond the initial manipulation. Time spent together does not necessarily influence the strength of the relationship (Boucherie et al., 2017; 2018; Proops et al., 2021), as relationships are dynamic and change overtime. However, a threshold of time spent together may be necessary to create strong and stable associations between individuals. This raises important questions for the study of social networks: over what time scale are strong and stable associations formed, and how does this association interact with the duration of continued social ties following an environmental disturbance?

Given the temporal setup of our experiment, it is difficult to determine which specific treatment led to those persistent effects. Flock size increased through resource and social manipulations throughout the experiment, suggesting that the higher flock size observed at the end is due to either additive or nonadditive effects that were carried over from the different manipulations to affect sociality in the final dispersed phase. Weighted degree and eigenvector centrality increased or decreased throughout our experiment, depending on the treatment applied. Therefore, it is difficult to disentangle the effect of each manipulation. However, effect sizes were larger for the dispersed to clustered manipulation (Q1), than for the manipulation restricting access to feeders (Q2) and the manipulation of social stability (Q3). The direction and size of the effect during Q1 are similar to those comparing the final to the initial dispersed phase (Q4), suggesting that this initial manipulation of food distribution may have had the strongest effect of any of our manipulations in the long term. Along the same line, by the end of the experiment, we did not find any significant effects of the social stability subtreatment on our social network metrics, except for group size, but the group size effect could be explained entirely by the fact that groups that were later assigned to the unstable social treatment had smaller flock sizes at the start of the experiment, although the difference between stable and unstable groups in flock size was not statistically significant. This suggests that while changes caused by manipulating resources were persistent, our social stability manipulation only influenced changes in the social network during the manipulation. Similarly, Heinen et al. (2022), unlike Firth and Sheldon (2015), found that after assorting individuals at food patches in a similar manner to our social stability subtreatment, the assortment did not persist into a new feeding context.

We provide evidence that changes in sociality at feeders persisted over time, but we do not know whether they persisted away from feeders. In the same great tit population, Firth and Sheldon (2015) found that controlling access to feeders changed the social network at unrestricted feeders, and even when prospecting for nests during breeding. Moreover, multiple studies on this population have found that foraging associations at feeders in winter carry through to territorial boundaries and pair bonding in the spring (Firth et al., 2018; Firth & Sheldon, 2016). However, the scale of these manipulations was considerably larger, and we suggest that further research to examine whether manipulated fine-scale changes persist could be valuable.

Dyadic Associations

The majority of the discussion above concerns individual-level social network metrics, but the dyadic associations deserve further mention because they focus on connections between specific individuals. Despite physical and social experimental changes in their environment and the substantial changes in social network metrics at the individual level, the social bonds that individual great tits formed with conspecifics were partially preserved at every stage of the experiment (the imperfect correlations show they were not completely preserved). This finding is in line with other studies that show great tits are highly consistent in their social associations over seasons and years (Aplin et al., 2015; Farine & Sheldon, 2019; Firth et al., 2017a; Firth & Sheldon, 2015, 2016). Such consistency is not observed in all species. For instance, work in gannets, *Morus serrator*, found that the identity of associates was not consistent across different foraging contexts (Jones et al., 2020), and experimental manipulation showed that chickadees, *Poecile gambeli*, restructured their network by assorting mostly with birds assigned to the same resource (Heinen et al., 2022). In general, living in fission–fusion flocks is likely to be selected as a strategy that allows some buffering against the effects of perturbation on maintaining connections with the same conspecifics. For instance, in our experiment, some individuals may have scrounged from known individuals using feeders to which they did not have access (Regan et al., 2022; Reichert et al., 2021). Further work to better understand the mechanisms from which such social stability emerges and is maintained will be important in understanding the evolutionary forces acting on social structure (Farine & Sheldon, 2019).

Conclusion

We show that even in the face of direct fine-scale manipulations of the physical and social environment, consistent individual differences in social behaviour (flock size and social network centralities) are observed in a wild population of birds. We also found that dyadic social associations remained consistent under these perturbations because individuals were consistently associated with the same individuals. Such consistency is in line with previous studies and suggests personality differences in social behaviour during foraging and the resilience of social associations to environmental change. However, the environment also drives plasticity in social network metrics. We found that manipulating a combination of habitat-based and social factors can have persistent effects (i.e. beyond the initial manipulation) on social network structure. Even fine-scale changes in food distribution and interactions at a feeder can affect network metrics, showing that social connections are highly dynamic. Our results provide a novel insight into how fine-scale manipulations of socio-environmental factors have persistent effects on group structure and stability and that relative social differences among individuals may be robust to such perturbations.

Author Contributions

Camille A. Troisi: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Gabrielle L. Davidson:** Writing – review & editing, Methodology, Conceptualization. **Josh A. Firth:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **John L. Quinn:** Writing – review & editing, Writing – original draft, Visualization, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Michael S. Reichert:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Sam J. Crofts:** Writing – review & editing, Investigation.

Data Availability

Following the PREPARE guidelines, the data and code are available on OSF, allowing for both increased reproducibility and reuse of data to reduce waste at https://osf.io/vygw3/?view_only=9fae8017dcad4f3884b3cd7209a15eeb.

Declaration of Interest

The authors declare there are no conflicts of interest.

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Appendix

Table A1

Summary data of unique individuals at each step of the experiment, including the number of males, females, adults and juveniles

Resource treatment	Total	Adult female	Adult male	Adult unknown sex	Juvenile female	Juvenile male	Juvenile unknown sex
Initial dispersed	198	60	71	4	23	30	10
Open clustered	167	52	58	3	18	25	11
Assortative clustered							
Phase I	117	33	40	1	18	18	7
Phase II	116	33	39	0	18	21	5
Phase III	114	34	39	0	18	19	4
Final dispersed	148	43	53	1	21	25	5
Total	258	77	85	5	33	43	15
Birds that took part in the initial dispersed and open clustered treatment	131	42	48	2	13	18	8
Birds that took part in the open clustered and assortative clustered P1 treatment	107	29	40	1	15	16	6
Birds that took part in all 3 assortative clustered treatments	94	29	32	0	16	14	3
Birds that took part in all 6 treatments or phases	68	19	28	0	8	12	1

Table A2

Linear mixed models showing the effect of treatment on each of four dependent variables linked to bird usage of feeders during stages or phases throughout the experiment

Dependent variable	Independent variables	Estimate (SE)	95% CI	*P* value
Number of individuals	Intercept	3.23 (0.143)	2.91; 3.53	<0.001
	Resource (open clustered)^1	−0.214 (0.102)	−0.416; −0.013	0.037
	Resource (assortative clustered P1)^1	0.028 (0.096)	−0.161; 0.217	0.772
	Resource (assortative clustered P2)^1	−0.009 (0.097)	−0.200; 0.181	0.923
	Resource (assortative clustered P3)^1	−0.088 (0.099)	−0.283; 0.106	0.372
	Resource (final dispersed)^1	−0.280 (0.104)	−0.486; −0.076	0.007
Visit count/number of days in treatment	Intercept	43.9 (6.89)	30.1; 57.6	<0.001
	Sex (male)^2	2.56 (4.37)	−5.96; 11.2	0.558
	Age (juveniles)^3	0.435 (4.82)	−9.03; 9.84	0.928
	Resource (open clustered)^1	−6.37 (4.48)	−15.1; 2.49	0.156
	Resource (assortative clustered P1)^1	29.8 (4.98)	20.0; 40.0	<0.001
	Resource (assortative clustered P2)^1	49.8 (5.00)	30.9; 51.0	<0.001
	Resource (assortative clustered P3)^1	55.1 (5.01)	45.2; 65.2	<0.001
	Resource (final dispersed)^1	34.9 (4.61)	25.9; 44.0	<0.001
Number of flock individuals that came to the feeders/ number of days in treatment	Intercept	8.39 (1.51)	5.33; 11.4	<0.001
	Sex (male)^2	0.045 (0.730)	−1.38; 1.49	0.951
	Age (juveniles)^3	−0.805 (0.807)	−2.39; 0.775	0.320
	Resource (open clustered)^1	−1.33 (0.714)	−2.73; 0.079	0.062
	Resource (assortative clustered P1)^1	3.34 (0.792)	1.77; 4.96	<0.001
	Resource (assortative clustered P2)^1	3.58 (0.797)	2.00; 5.20	<0.001
	Resource (assortative clustered P3)^1	6.50 (0.798)	4.92; 8.12	<0.001
	Resource (final dispersed)^1	7.99 (0.735)	6.56; 9.44	<0.001

Fixed effects included the number of individuals present, the number of visits per day, and the number of flock individuals came to the feeders with. For the site level analysis (number of individuals per stage), we included the site as a random effect ($N = 8$ sites). For the individual level analysis (number of visits per individual and number of flock individuals that came in), we included site and individual identity as random effects ($N = 238$ unique individuals). CI; confidence interval. ^{1} baseline = initial dispersed; ^{2} baseline = female; ^{3} baseline = adult.

Table A3

Linear mixed models of how each of the four individual social network metrics changed from the initial dispersed to the open clustered treatments.

Dependent variable	Independent variables	Estimate (SE)	95% CI	*P* value
Flock size	Intercept	2.24 (0.831)	0.609; 3.90	0.012
	Flocking events	−0.002 (0.002)	−0.005; 0.001	0.257
	Individuals in the local network	0.072 (0.026)	0.020; 0.123	0.008
	Sex (male)[1]	−0.092 (0.136)	−0.356; 0.173	0.499
	Age (juveniles)[2]	−0.046 (0.158)	−0.352; 0.263	0.772
	Resource (open clustered)[3]	1.67 (0.224)	1.23; 2.12	<0.001
Weighted degree	Intercept	−1.020 (0.449)	−2.14; −0.313	0.015
	Flocking events	0.013 (0.001)	0.011; 0.016	<0.001
	Individuals in the local network	0.054 (0.014)	0.025; 0.085	0.002
	Sex (male)[1]	−0.003 (0.099)	−0.196; 0.191	0.977
	Age (juveniles)[2]	0.014 (0.115)	−0.209; 0.239	0.905
	Resource (open clustered)[3]	1.66 (0.143)	1.38; 1.94	<0.001
WEVC	Intercept	−0.162 (0.137)	−0.445; 0.118	0.252
	Flocking events	0.005 (0.0003)	0.004; 0.006	<0.001
	Individuals in the local network	0.010 (0.004)	0.001; 0.019	0.037
	Sex (male)[1]	−0.0005 (0.026)	−0.053; 0.050	0.985
	Age (juveniles)[2]	−0.034 (0.031)	−0.062; 0.058	0.912
	Resource (open clustered)[3]	0.356 (0.041)	0.271; 0.435	<0.001

Fixed effects included the number of flocking events, the number of individuals in the local network, the sex of the individual, the age of the individual, and the resource treatment. The site and individual identity were included as random effects. CI: confidence interval; WEVC: weighted eigenvector centrality.

[1] Baseline = female.
[2] Baseline = adult.
[3] Baseline = initial dispersed.

Table A4

Permutation analyses of models in Table A3, which examined the changes in each of the four individual social network metrics, from the initial dispersed to the open clustered resource treatment

Dependent variable	Intercept	Nb flocking events	Nb individuals in the local network	Sex (male)[1]	Age (juvenile)[2]	Initial dispersed vs open clustered resources
Flock size	0.000	0.242	0.004	0.494	0.774	0.000
Weighted degree	0.000	0.000	0.000	0.982	0.878	0.000
WEVC	0.000	0.000	0.016	0.946	0.960	0.000

P values show where the observed estimates fall within the distribution of estimates from the permutations. WEVC: weighted eigenvector centrality.

[1] Baseline = female.
[2] Baseline = adult.

Table A5

Permutation analyses of models in Table 1, which examined the changes in each of the four individual social network metrics, from the open clustered to the assortative clustered P1 resource treatment

Dependent variable	Intercept	Nb flocking events	Nb individuals in the local network	Sex (male)[1]	Age (juvenile)[2]	Open clustered versus assortative clustered
Flock size	0.000	0.594	0.000	0.400	0.818	0.000
Weighted degree	0.000	0.000	0.000	0.866	0.390	0.000
WEVC	0.584	0.000	0.164	0.944	0.044	0.000

Fixed effects included the number of flocking events, the number of individuals in the local network, the sex of the individual, the age of the individual, and the resource treatment. *P* values show where the observed estimates fall within the distribution of estimates from the permutations. WEVC: weighted eigenvector centrality.

[1] Baseline = female.
[2] Baseline = adult.

Table A6

Post hoc analysis of the interaction between resource and social stability subtreatment from the model in Table 2, showing the pairwise difference between the assortative clustered P1 and P3 phases

Dependent variable	Social subtreatment	Estimate	SE	95% CI	*P* value
Flock size	Stable	−1.02	0.097	−1.21; −0.830	<0.001
	Unstable	−0.424	0.114	−0.647; −0.201	<0.001
Weighted degree	Stable	−0.232	0.057	−0.343; −0;121	<0.001
	Unstable	−0.225	0.066	−0.355; −0.095	0.001
WEVC	Stable	0.099	0.020	0.061; 0.138	<0.001
	Unstable	0.050	0.023	0.005; 0.095	0.031

CI: confidence interval; WEVC: weighted eigenvector centrality.

Table A7
Permutation analyses of models in Table 2, which examined changes in each of the four individual social network metrics, from the start (P1) to the end (P3) of the assortative clustered resource treatment level

Dependent variable	Intercept	Nb flocking events	Nb individuals in the local network	Sex (male)[1]	Age (juvenile)[2]	Resource (P3)[3]	Social stability (unstable)[4]	Interaction
Flock size	0.000	0.522	0.000	0.836	0.634	0.000	0.648	0.000
Weighted degree	0.000	0.000	0.002	0.348	0.356	0.000	0.282	0.948
WEVC	0.092	0.000	0.000	0.654	0.642	0.000	0.186	0.118

Fixed effects included the number of flocking events, the number of individuals in the local network, the sex of the individual, the age of the individual, the resource treatment, the social stability stub treatment, and the interaction between the resource treatment and the social stability subtreatment. *P* values show where the observed estimates fall within the distribution of estimates from the permutations.

[1] Baseline = female.
[2] Baseline = adult.
[3] Baseline = P1.
[4] Baseline = stable.

Table A8
Model examining the relationship between dyadic associations during the third phase (P3) and the first phase (P1) of the assortative clustered treatment level

Factor	Estimate (SE)	95% CI	*P* value
Intercept	0.152 (0.022)	0.109; 0.194	<0.001
Dyadic association during P1	0.248 (0.042)	0.166; 0.330	<0.001
Social stability (unstable)[1]	0.003 (0.032)	−0.057; 0.065	0.919
Dyadic association during P1 × social stability (unstable)[1]	−0.101 (0.065)	−0.228; 0.031	0.121

Fixed effects included the dyadic interaction during P1, the social stability subtreatment, and their interaction. The site and individual identity of both individuals of each dyad were included as random effects. CI: confidence interval.

[1] Baseline = stable.

Table A9
Linear mixed models that examined changes in each of the four individual social network metrics, from the initial dispersed to the final dispersed resource treatment.

Dependent variable	Independent variables	Estimate (SE)	95% CI	*P* value
Flock size	Intercept	1.48 (0.695)	0.187; 2.77	0.050
	Flocking events	0.00002 (0.001)	−0.003; 0.003	0.990
	Individuals in the local network	0.107 (0.017)	0.074; 0.139	<0.001
	Sex (male)[1]	−0.028 (0.128)	−0.274; 0.222	0.831
	Age (juveniles)[2]	0.121 (0.140)	−0.146; 0.394	0.391
	Resource (final dispersed)[3]	1.85 (0.162)	1.54; 2.16	<0.001
	Social stability (unstable)[4]	−1.08 (0.774)	−2.54; 0.395	0.209
	Resource (final dispersed)[3] × social stability (unstable)[4]	1.26 (0.344)	0.606; 1.93	<0.001
Weighted degree	Intercept	−0.852 (0.353)	−1.50; −0.192	0.023
	Flocking events	0.010 (0.001)	0.009; 0.012	<0.001
	Individuals in the local network	0.051 (0.010)	0.031; 0.070	<0.001
	Sex (male)[1]	−0.009 (0.080)	−0.163; 0.146	0.908
	Age (juveniles)[2]	0.015 (0.087)	−0.151; 0.185	0.861
	Resource (final dispersed)[3]	1.71 (0.101)	1.52; 1.91	<0.001
	Social stability (unstable)[4]	−0.156 (0.336)	−0.788; 0.471	0.657
	Resource (final dispersed)[3] × social stability (unstable)[4]	0.281 (0.210)	−0.139; 0.672	0.184
WEVC	Intercept	0.241 (0.096)	0.062; 0.418	0.020
	Flocking events	0.004 (0.0002)	0.004; 0.005	<0.001
	Individuals in the local network	−0.004 (0.003)	−0.009; 0.002	0.190
	Sex (male)[1]	−0.007 (0.022)	−0.050; 0.035	0.757
	Age (juveniles)[2]	0.016 (0.024)	−0.031; 0.062	0.500
	Resource (final dispersed)[3]	0.278 (0.028)	0.224; 0.332	<0.001
	Social stability (unstable)[4]	0.089 (0.091)	−0.084; 0.257	0.365
	Resource (final dispersed)[3] × social stability (unstable)[4]	−0.072 (0.058)	−0.180; 0.041	0.213

Fixed effects included the number of flocking events, the number of individuals in the local network, the sex of the individual, the age of the individual, the resource treatment, the social stability stub treatment, and the interaction between the resource treatment and the social stability subtreatment. The site and individual identity were included as random effects. CI: confidence interval; WEVC: weighted eigenvector centrality.

[1] Baseline = female.
[2] Baseline = adult.
[3] Baseline = initial dispersed.
[4] Baseline = stable.

Table A10
Permutation analyses of models in Table A8, which examined how changes in each of the four individual social network metrics, from the initial dispersed to the final dispersed treatments

Dependent variable	Intercept	Nb flocking events	Nb individuals in the local network	Sex (male)[1]	Age (juvenile)[2]	Resource (final dispersed)[3]	Social stability (unstable)[4]	Resource (final dispersed)[3] × Social stability (unstable)[4]
Flock size	0.000	0.978	0.000	0.824	0.392	0.000	0.144	0.000
Weighted degree	0.000	0.000	0.000	0.886	0.854	0.000	0.690	0.230
WEVC	0.002	0.000	0.178	0.728	0.490	0.000	0.296	0.204

Fixed effects included the number of flocking events, the number of individuals in the local network, the sex of the individual, the age of the individual, the resource treatment, the social stability stub treatment, and the interaction between the resource treatment and the social stability subtreatment. *P* values show where the observed estimates fall within the distribution of estimates from the permutations. WEVC: weighted eigenvector centrality.

[1] Baseline = female.
[2] Baseline = adult.
[3] Baseline = initial dispersed.
[4] Baseline = stable.

Table A11
Post hoc analysis of the interaction between resource and social stability subtreatments from the model in Table A8, shows the pairwise difference between the initial and final dispersed treatment

Dependent variable	Social treatment	Estimate	SE	95% CI	*P* value
Flock size	Stable	−1.85	0.163	−2.16; −1.53	<0.001
	Unstable	−3.11	0.317	−3.73; −2.49	<0.001
Weighted degree	Stable	−1.71	0.102	−1.91; −1.51	<0.001
	Unstable	−1.99	0.193	−2.36; −1.61	<0.001
WEVC	Stable	−0.278	0.028	−0.333; −0.223	<0.001
	Unstable	−0.206	0.053	−0.310; −0.102	<0.001

CI: confidence interval; WEVC: weighted eigenvector centrality.

Table A12
A mixed model examining the relationship between dyadic associations during the final dispersed phase and the initial dispersed phase of the resource treatment and whether this varied depending on social stability subtreatment

Factor	Estimate (SE)	95% CI	*P* value
Intercept	0.125 (0.011)	0.104; 0.146	<0.001
Dyadic associations during initial dispersed	0.197 (0.059)	0.081; 0.321	0.001
Social stability (unstable)[1]	0.061 (0.018)	0.027; 0.094	0.007
Dyadic associations during initial dispersed × social stability (unstable)[1]	0.132 (0.109)	−0.078; 0.349	0.229

Fixed effects included the dyadic interaction during the initial dispersed treatment, the social stability subtreatment, and their interaction. The site and individual identity of both individuals of each dyad were included as random effects. CI: confidence interval.

[1] Baseline = stable.

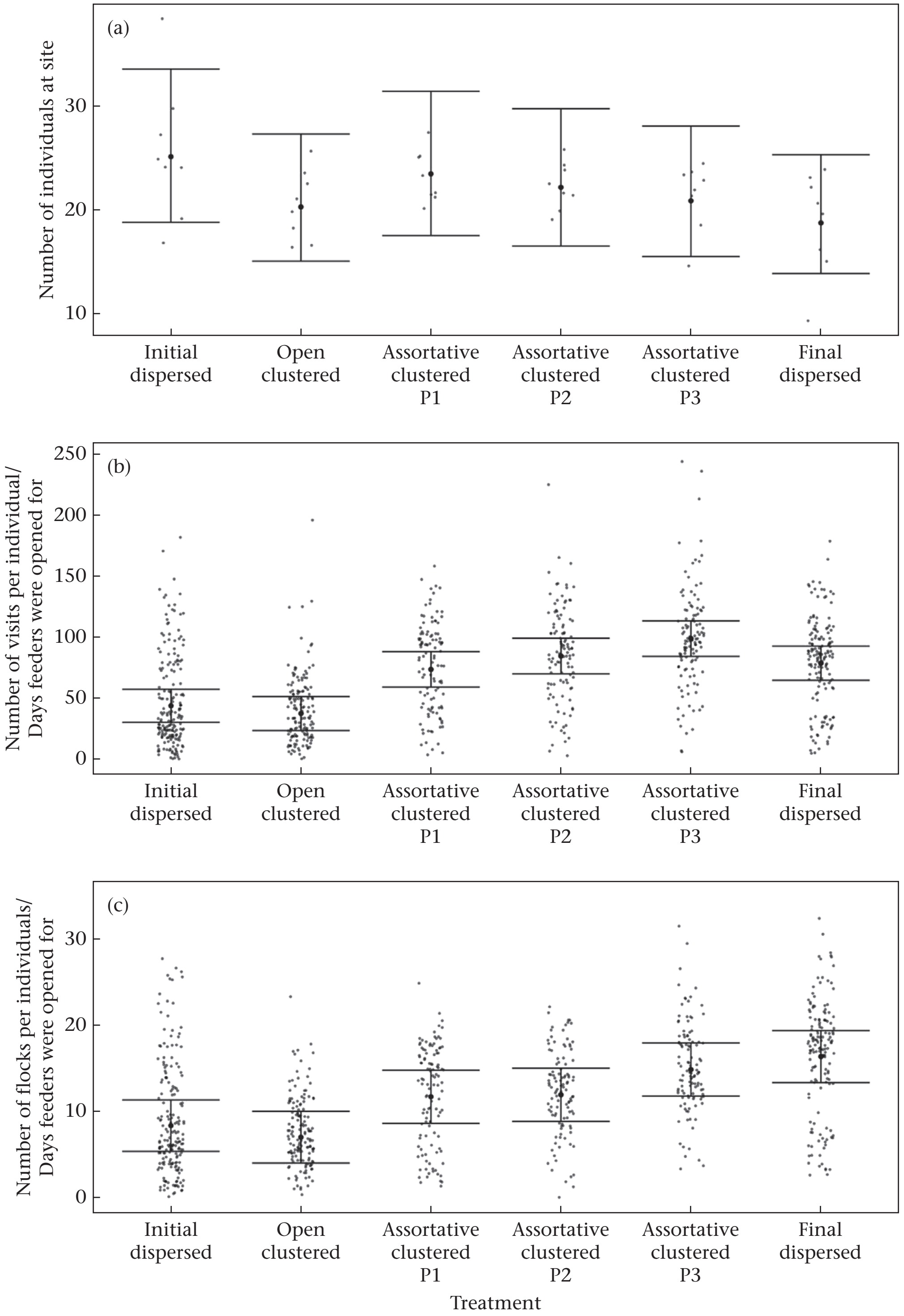

Figure A1. Partial residual plots showing the relationship between the experimental stage and (a) the number of individuals at sites, (b) the number of visits per individual per day, and (c) the number of flocking events per individual per day, across the initial dispersed, open clustered, assortative clustered P3, and final dispersed treatment levels. Error bars are 95% confidence intervals.

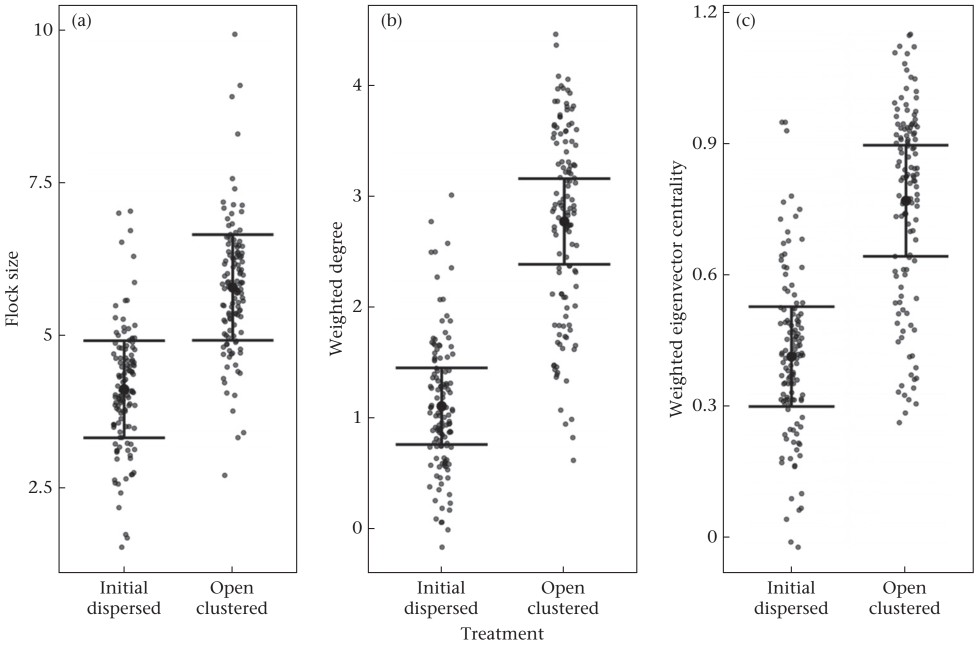

Figure A2. Partial residual plots showing changes in (a) flock size, (b) weighted degree and (c) weighted eigenvector centrality when food first changed from dispersed to clustered treatments. Error bars are 95% confidence intervals based on a model from Table 1.

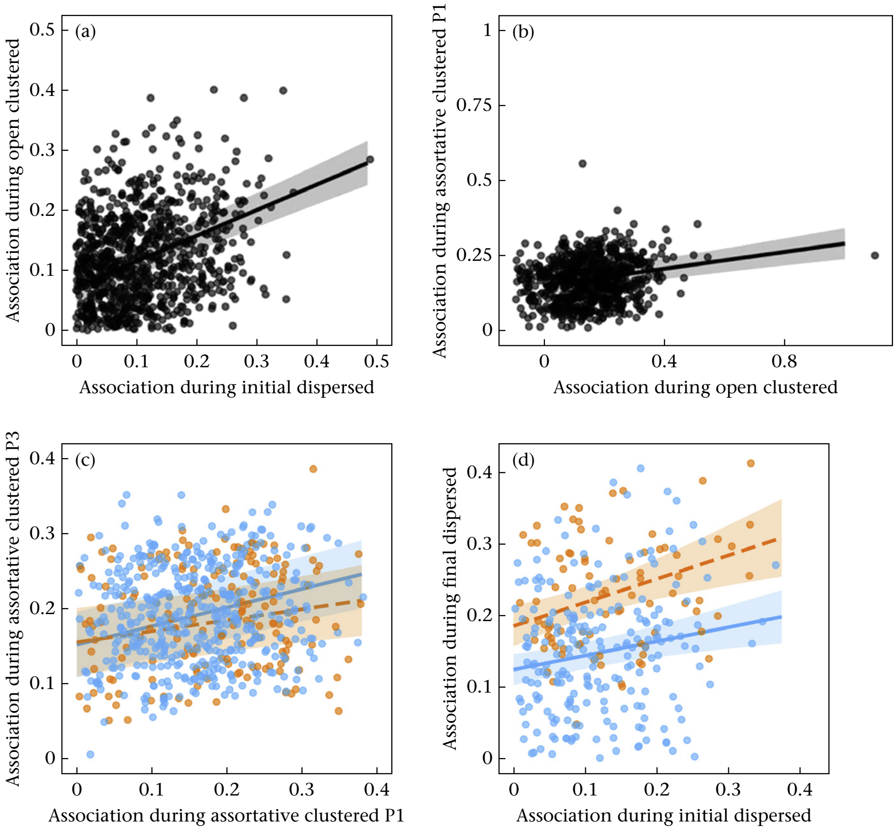

Figure A3. Partial residual plots showing how pairwise associations in one treatment predicted these in the next for (a) the initial dispersed treatment and the open clustered treatment; (b) the open clustered treatment and the assortative clustered treatment (P1); (c) the assortative clustered P1 treatment and P3 treatment; and d) the initial dispersed and final dispersed treatments. For (c) and (d), separate lines are shown for birds in the stable (blue) and unstable (orange) social stability subtreatments. The interaction was nonsignificant for (c) and (d). Shaded areas are the 95% confidence intervals from corresponding models in the main text and in Tables A7 and A10. We added random effects for the identity of both individuals of each dyad and site.