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Experimental manipulation of food distribution alters social networks and information transmission across environments in a food-caching bird

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While many animals utilize socially transmitted information, there is still much to understand about how individuals form social networks and how these networks influence social information use. Here, we tested the hypothesis that food distribution and availability can influence social structure and social information transfer when discovering novel food sources. We experimentally manipulated distribution and access to food in wild food-caching mountain chickadees, *Poecile gambeli*, by randomly dividing existing individuals between two feeding locations, with birds only allowed to obtain food at one of the two locations. We carried out such manipulations at multiple sites associated with two montane elevations of different environmental harshness, where birds show differing use of social information. Following 2 weeks of manipulation, we measured social networks and then introduced novel feeders to test how the manipulation affected social information use. The manipulations effectively split the resident chickadees at both elevations into two distinct communities, and when subsequently discovering novel feeders, information transmission about novel food sources followed the new, rather than the premanipulation, network structure at both elevations, although low-elevation birds used social information more than high-elevation birds. Our data show that chickadees can quickly adjust their social associations in response to short-term changes in the distribution of available resources and that these changes influence who they learn from socially when searching for food. Overall, we observed that chickadees are highly flexible in their use of social information despite their rather stable social group structure and that this information use reflects the most current social environment that individuals experience.

While it is widely recognized that animal sociality is beneficial in providing social information about environmental conditions (Galef & Laland, 2005), it is less clear how animals decide when to learn socially and which individuals are valuable sources of social information (Aplin, 2016; Rieucau & Giraldeau, 2011). Animals can use social information in many different contexts, such as mate choice (Jones & DuVal, 2019; White, 2004) or habitat choice (Morinay et al., 2021; Szymkowiak et al., 2017). In a foraging context, an animal may follow knowledgeable individuals to discover food sources instead of, or in addition to, searching for food independently (Tóth et al., 2017; Valone, 2007). Environmental conditions can influence the value of social information when foraging; if food sources are unpredictable and highly ephemeral, using social information may lead to the transmission of outdated information and missed opportunities to discover novel food sources (Boyd & Richerson, 1988; Sasaki et al., 2016; Webster et al., 2013). Many species alter their social information use under different environmental conditions (Afshar et al., 2015; Morand-Ferron et al., 2019). For example, food-caching mountain chickadees, *Poecile gambeli*, at high elevations in the mountains with harsher and less predictable winter conditions use social

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information less when discovering novel food sources than chickadees at lower (milder) elevations and discover novel food sources independently of social associations more often (Heinen et al., 2021).

Social network analyses have suggested that animals use social information from their associates when foraging (Aplin et al., 2012), but that the patterns of associations (i.e. the social network structure itself) can also be sensitive to environmental conditions (Leu et al., 2016; Sosa et al., 2021; Webster et al., 2013). Structural features of the environment, such as the distribution of resources, influence which individuals are likely to encounter each other, affecting the formation of social relationships and determining potential sources of social information (He et al., 2019). However, individuals' use (or disuse) of social information can also affect their interaction patterns and shape social network structure (Cantor et al., 2021). Species with a more modular social structure (e.g. fission–fusion) may also be more flexible in their social information use compared to species with more stable, structured social groups because they have more social connections and more frequently changing social connections (Evans et al., 2021; Kerth et al., 2006). While frequently changing social associations in fission–fusion societies can predispose animals to flexibly change their social preferences in foraging contexts and specifically follow individuals that they have socialized with most recently when successfully discovering novel food sources, it remains unclear whether individuals in more stable social groups can learn socially from individuals in different social groups. The relationships between the environment, social network structure and social information transmission are complex and challenging to tease apart.

Despite recent proliferation of social network research, our understanding of the effects of network structure on social learning remains limited (Cantor et al., 2020; Firth et al., 2016). One challenge is that social network structure is difficult to manipulate experimentally. Many studies are correlational, describing network changes in response to incidental events (Ansmann et al., 2012; Lantz & Karubian, 2017). There are several ways in which a social network could be manipulated. One approach for social network manipulation is the removal of individuals (Firth et al., 2017; Naug, 2009; Piefke et al., 2021). However, this type of manipulation also changes critical aspects of social structure, such as group size and composition, which can impact the network in unpredictable ways. An alternative approach is to modify the environment directly, which allows for network manipulation without altering population membership (He et al., 2019; for examples, see Firth & Sheldon, 2015; Firth et al., 2016; Leu et al., 2016). There is evidence linking network structure to social information transmission pathways associated with finding novel food sources, which have been shown to be sensitive to experimental manipulation (Aplin et al., 2012; Farine et al., 2015). In great tits, *Parus major*, a species characterized by a fission–fusion social structure with frequently changing social associations, manipulation of social network dynamics by experimentally restricting access to food sources to different groups of individuals for an extended period (90 days) affected social information use during discovery of novel food sources, resulting in greater social information transmission rates within the new, experimentally induced social groups compared to the premanipulation network (Firth & Sheldon, 2015). Specifically, birds were more likely to follow the individuals they were associated with following the experimental manipulation rather than the individuals they associated with prior to the manipulation when discovering novel food sources, which resulted in higher social information transmission rates about novel food sources specifically via new manipulation-induced social connections. These results suggest that great tits can change their decisions about who to follow when searching for food based on their recent experiences with these individuals. However, it is unclear whether such experimental restructuring of existing social associations would produce the same results in species with different and more rigid social systems and whether much shorter network restructuring would still result in birds always using the most recent social connections.

Because environmental conditions can change rapidly (e.g. in winter environments), it may be advantageous to respond to changing social connections and social information on a relatively short time scale. In addition, it remains unknown how underlying environmental conditions affect a social group's response to resource manipulation. If individuals in harsh, unpredictable environments use less social information when searching for food, then changes in their social environment induced by changes in food distribution and access may have a reduced impact on both their social network and on how they learn and discover novel food sources.

Beyond stability in social group structure, cognitive abilities of individuals within social groups can also be expected to influence individuals' decisions to use social information. In food-caching species, spatial cognitive abilities are critical for successful retrieval of thousands of previously made food caches (Pravosudov & Roth, 2013) and individual variation in spatial cognitive abilities is associated with differences in overwinter survival (Sonnenberg et al., 2019). In such species, better cognitive abilities may be associated with more predictable foraging conditions. In this case, individuals with better cognitive abilities may find social information less reliable than their personal information and may rely more on their own cognition than on social information to find food (Heinen et al., 2021). Cognitive flexibility, which allows animals to quickly relearn changing associations and keep track of rapidly changing foraging conditions, may also afford highly flexible individuals more reliable personal information compared to socially transmitted information (Heinen et al., 2021). We can therefore expect that individual variation in cognitive abilities and cognitive flexibility can be associated with different reliance on social information use (Heinen et al., 2021).

Here, we tested whether short-term changes in food distribution, and resulting redistribution of individuals, within a naturally existing population of food-caching mountain chickadees directly affects social information transfer when discovering novel food sources. Mountain chickadees form stable social winter groups (Ekman, 1989), making them ideal to understand how these processes work in such social systems. We further tested whether changes in social learning associated with manipulated food distribution differed between birds in harsh, unpredictable (high-elevation) and mild, more predictable (low-elevation) winter environments. If the value of social information changes rapidly, animals should be highly sensitive to short-term changes in social network structure associated with food distribution, which would allow them to follow individuals with the most current information and to find novel food sources faster. In addition, we measured individuals' spatial learning and memory ability and reversal spatial learning ability, which are associated with food discovery, caching and retrieval, and tested whether these cognitive traits influenced social learning of novel food sources. Spatial cognitive abilities could affect the way birds respond to our treatment because better spatial cognition is associated with a more predictable environment and can affect rates of both social and asocial learning (Heinen et al., 2021).

We used customized radiofrequency identification (RFID)-controlled bird feeders capable of selectively provisioning different individuals banded with unique passive integrated transponder (PIT) tags to initially discern social connections among individuals and then manipulate where (and thereby with whom) individuals could forage. Our study proceeded in three stages. After assessing birds' learning and memory abilities at an eight-feeder spatial array (Fig. 1a) (Croston et al., 2016, 2017), we (1) measured the social network at the array, using two of the eight feeders (Fig. 1b) and then (2) split the birds visiting each array pseudorandomly between two new locations, each consisting of two experimental feeders, ca. 100 m apart (Fig. 1c), for 2 weeks while keeping the previous food locations closed. The experimental feeders at these two new locations were programmed such that half of the birds in the existing network were allowed to obtain food at one location and the other half at the other location, similar to Firth et al. (2016). Following this experimental treatment, we (3) removed the experimental feeders and simultaneously introduced novel food patches, each consisting of three novel feeders (which provided food to any visiting bird) spaced ca. 150 m apart (Fig. 1d).

We first predicted that after the manipulation of food availability via the experimental feeders, the existing social network would split into two distinct sets of birds that foraged together (i.e. distinct communities in the social network). We then predicted that chickadees would adjust their social learning decisions when searching for food and discover the novel feeders by following the birds that were allowed to forage together at the same experimental location instead of following their premanipulation social network associations. Such changes should be evident by the patterns of novel feeder discoveries being better reflected by the social associations in the manipulated social network than by the social connections among individuals in the premanipulated network (Firth et al., 2016). While birds from both high and low elevations could be expected to change their social information use, we predicted that birds at the harsher, less predictable high-elevation site should respond less to our manipulations as they rely less on social learning when searching for food compared to birds at the milder, low-elevation site (Heinen et al., 2021).

METHODS

Study System

The study took place at our long-term study system of mountain chickadees in the northern Sierra Nevada, north of Truckee, California, U.S.A. (Sagehen Experimental Forest, Sagehen Creek Field Station, University of California, Berkeley). This system includes low-elevation sites (1900 m) and high-elevation sites (2400 m), which differ in winter climate severity (Croston et al., 2016, 2017; Tello-Ramos et al., 2018). High elevation is associated with harsher winter environments, which are both more unpredictable and metabolically challenging than winter environments at low elevation (Croston et al., 2016; Heinen et al., 2021). Since 2014, we have banded chickadees with unique combinations of PIT tag leg bands (IB Technology, Leicestershire, U.K.) and colour bands. We trap and band birds annually using mist nets at established feeders across both elevations during autumn and winter and in nestboxes during the breeding season. We classified all birds in this experiment as either juvenile (first year) or adults (older than first year of life) based on banding data prior to the experiment, as well as on plumage characteristics (Pyle, 1997). Birds were sexed based on observed physiological indicators during breeding months (when available) or by wing length.

Ethical Note

All animal procedures were conducted in accordance with the Institutional Animal Care and Use Committee (IACUC) of the University of Nevada Reno (IACUC protocols 00818, 00046 and 00603), under California Department of Fish and Wildlife Scientific Collecting Permit D-0011776516-4 and U.S. Federal Bird Banding Permit 22878. Mist nets were monitored continuously in cold conditions, or checked at 15 min intervals during warm weather. Birds were extracted immediately from the net upon detection. After extraction, birds were placed in a cloth bag (one bird per bag) until banding. Birds were released immediately after banding. Typically, the entire process from extraction to release took no more than 10 min. We have detected no detrimental effects of PIT tag banding in this system.

Data Collection

We used RFID-equipped feeders filled with black oil sunflower seeds in all experiments in this study. During daylight hours, feeders recorded the time, date, location and identity of all PIT-tagged birds that landed on the feeder perch. Feeders featured a motorized door controlling access to food and could be programmed to allow access only to specific individuals while recording feeding attempts from all PIT-tagged individuals (Bridge et al., 2019; Croston et al., 2016, 2017).

Spatial feeder arrays

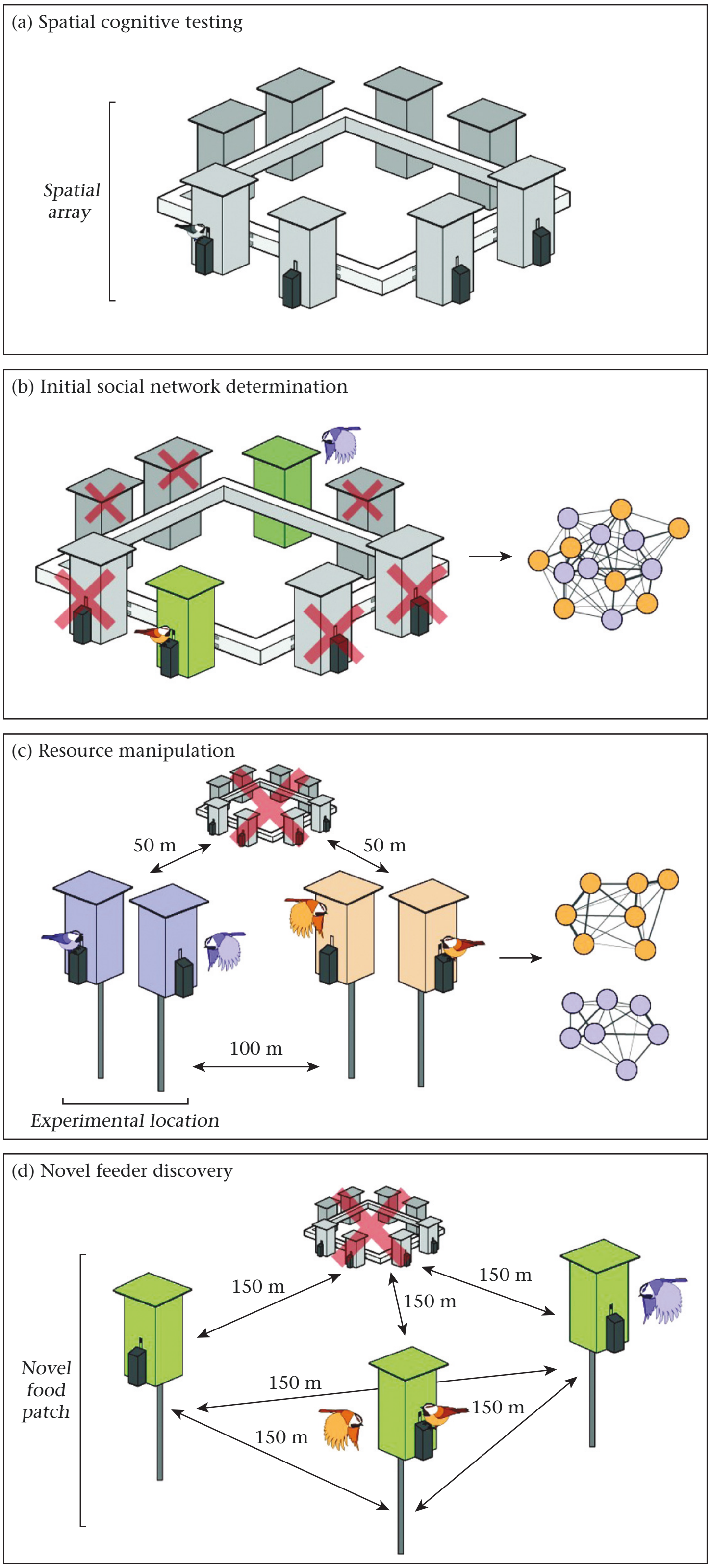
Since 2015, we have maintained four spatial arrays (two per elevation, ca. 1.5 km apart) consisting of eight RFID-based feeders attached equidistantly to a square aluminium frame (122 × 122 cm) suspended 4 m above the ground (Croston et al., 2016, 2017; Tello-Ramos et al., 2018) (Fig. 1a). On 12 December 2020, we made supplemental food available at all array feeders in all four spatial feeder arrays. All array feeders were initially set to ‘open’ mode, in which all feeder doors were open with food visible and all visits from PIT-tagged birds were logged (Croston et al., 2016, 2017; Tello-Ramos et al., 2018). Array feeders were set to ‘all’ mode on 18 December 2020. In all mode, array feeder doors were closed by default, but opened for any PIT-tagged bird landing on the feeder perch. This mode was used to habituate birds to the moving feeder doors (Croston et al., 2017; Tello-Ramos et al., 2018).

Spatial cognitive testing

Using our four spatial arrays, we tested chickadees on two spatial cognitive tasks, first on a spatial learning and memory task for 5 days (13–17 January 2021), then on a reversal spatial learning and memory task for 5 days (17–22 January 2021), following our established protocols (Croston et al., 2017; Heinen et al., 2021; Sonnenberg et al., 2019; Tello-Ramos et al., 2018). We estimated each individual's spatial learning, memory and reversal spatial learning scores and included these values as individual level variables in our NBDA models (see below).

During the spatial learning and memory task, birds were required to learn and remember the spatial location of a single rewarding feeder in the array. Each bird attending the array was assigned to a single array feeder. Only the bird's assigned feeder door would open when the bird landed on the perch, allowing that bird to take food. All other array feeders recorded the identity (ID), time, date and location of each visit but did not allow access to food. Assignments were spread across all eight array feeders pseudorandomly so that no birds were assigned to their most visited feeder from the previous habituation period. Spatial learning and memory performance was measured as the number of location errors each individual made within a trial. A trial began when an individual visited any feeder in the array and ended when the individual visited its assigned feeder. Location errors were defined as the number of unrewarding array feeders a bird visited before visiting its assigned feeder in any given trial. We used the mean number of location errors per trial across the first 20 trials to estimate spatial learning and memory ability (Croston et al., 2017; Heinen et al., 2021).

During the reversal spatial task designed to measure cognitive flexibility (as in Tello-Ramos et al., 2019), we reassigned each bird to a new rewarding array feeder, meaning that the previously rewarding feeder no longer provided food. Birds that had been assigned to the same feeder during the previous task were reassigned to different array feeders to reduce the possibility of social



learning. As in the previous task, we used the mean number of location errors per trial over the first 20 trials of the task to evaluate reversal spatial cognitive ability (Croston et al., 2017; Heinen et al., 2021; Sonnenberg et al., 2019; Tello-Ramos et al., 2018).

Initial social network determination

After completing cognitive testing, we collected data to determine the social networks of birds at each spatial feeder array. From 26 February to 3 March 2021, we programmed two array feeders on the opposite sides of each of the four arrays to remain open, allowing all birds to see and access food (Fig. 1b). The other six feeders in each array were emptied, with the doors left open so birds could see there was no food. We used two feeders per array instead of eight in order to maintain consistency in the number of feeders available per location when determining social networks across the phases of the experiment (Heinen et al., 2021). All RFID-based feeders used in this study were equipped with GPS modules that updated the system clocks at regular intervals to ensure 1 s accuracy of RFID tag detections.

We used a 'gambit of the group' approach, which assumes that all individuals observed together were equally connected to each other and infers the strength of connections based on repeated co-occurrence across groups (Franks et al., 2010). We identified grouping events using a Gaussian mixture model (GMM; 'gmmevents' function from the R package 'asnipe' (Farine, 2013) in R 4.1.0 (R Core Team, 2021)). Following the 'double GMM method' (Ferreira et al., 2020), we ran an initial GMM with a 1 min resolution to detect the start and end of large-scale foraging events at each array. Next, we ran a second GMM with a 1 s resolution within each large-scale foraging event, which split each large flocking event into shorter feeder bouts. For both runs, we treated each array as a single spatial location, as the close spacing of feeders within an array means birds from the same social group can visit different array feeders simultaneously (Heinen et al., 2021). This resulted in a single group-by-individual matrix for each elevation. We inferred association strength between individuals using the simple ratio index (function 'get_network' in 'asnipe'); this calculates association strength between two individuals as the number of times the two appeared in the same foraging event, divided by the number of foraging events containing at least one of the two individuals (Hoppitt & Farine, 2018).

We used data from the last 5 days of data collection (27 February – 3 March 2021) to construct the network, following our previous work (Heinen et al., 2021). Birds that visited the arrays less than four times during this period were excluded from the network; this cutoff was chosen to maximize the statistical power of our planned network-based diffusion analysis and minimize the rate of false positives, based on simulated information diffusions (following Wild & Hoppitt, 2019).

Resource manipulation

To manipulate the feeder-based associations among birds at each of the four spatial array locations, we identified all birds that had visited that array during habituation, testing or social network data collection. Within each array, we sorted birds by the total number of visits they made to the array, then assigned alternate birds to one of two groups. This allowed us to split the population of birds attending each of the four arrays into two pseudorandomly selected, equally sized groups, while controlling for differences in how frequently birds used the supplemental food in the arrays. On 3 March 2021, we emptied all feeders in the spatial arrays, leaving the feeder doors open so birds could see that no food was available. At the same time, we introduced four new experimental feeders, grouped into two experimental locations, with each location consisting of two identical RFID-equipped feeders spaced 2 m apart (Fig. 1c). These experimental feeders were identical to those on the array but were mounted on metal poles ca. 2 m above the ground. Each experimental location was placed ca. 50 m from the array (mean ± SD = 69.53 ± 7.99 m), with ca. 100 m distance between the two locations (mean ± SD = 87.72 ± 6.60 m). The two experimental feeders at each of the two new locations were programmed to allow access only to birds in one of the two experimentally determined groups.

Our manipulation of food locations and differential access to each new location maintained the same number of feeders available to each bird during premanipulation (two feeders in each array) and during manipulation (two experimental feeders per bird), as in Firth et al. (2016). These experimental feeders were active for 14 days (3–17 March 2021).

The final 5 days of data from this manipulation stage were used to construct a second social network at each elevation following the procedures described above. Each pair of experimental feeders at each location was treated as a single location for constructing the social networks, giving us a total of four new locations at each elevation (two per each array).

Novel feeder discovery

On 17 March 2021, we removed all experimental feeders used in the resource manipulation stage and introduced two novel food patches per elevation (each patch 150 m from each array location) (Fig. 1d). Each novel food patch consisted of three novel feeders identical to those in the resource manipulation stage. Unlike in the previous stage, these novel feeders were set so the door remained open, allowing any bird to access food. Following our previous methods (Heinen et al., 2021), novel feeders within each patch were spaced ca. 150 m from each other (mean ± SD = 153.41 ± 15.90 m) and 150 m from the array (mean ± SD = 164.22 ± 17.05 m). The two patches within each elevation were separated by at least 1 km. Feeders were placed so that they were not visible from the array. We also avoided placing novel feeders in locations used in a previous experiment (Heinen et al., 2021). We conducted two replicates of this novel feeder discovery stage, each lasting 5 days. Between the replicates, each of the novel feeders was removed and relocated to a new location, ca. 150 m from the previous replicate and not visible from the previous location (mean ± SD = 151.95 ± 12.81 m). Due to environmental conditions, novel feeders had to be moved during daylight hours, but were moved and placed when no birds were visible.

Figure 1. Diagram illustrating the phases of the experiment. (a) During spatial cognitive testing, chickadees were first required to learn and remember the location of a single rewarding feeder in an eight-feeder spatial array (spatial learning and memory task), and then to learn the location of a different single rewarding feeder, while the first feeder was no longer rewarding (reversal learning task). (b) To determine initial social networks, six of the eight feeders on the array were emptied and two were left open so that any visiting bird could obtain food (indicated by green highlighting). These two feeders recorded the identities and timing of all visiting PIT-tagged birds. (c) During the resource manipulation phase, all feeders at the spatial array were emptied and two experimental locations consisting of two experimental feeders each were placed within 50 m of the array, 100 m apart. All birds that had previously visited the array were randomly assigned to one of the two experimental feeder locations, such that they could only obtain food from those two feeders. (d) During novel feeder discovery, the array remained empty and the four experimental feeders used in the previous stage were removed. We introduced a novel food patch consisting of three novel feeders, which provided food to any visiting bird (indicated by green highlighting). These three feeders were placed at least 150 m from the array and 150 m apart from each other. After two replications of this stage, all novel feeders were removed, and two of the feeders on the array were opened and provided food to all birds (not pictured).

Postmanipulation network measurements

Following the conclusion of the second novel feeder discovery replicate on 26 March 2021, we removed all novel feeders and refilled two feeders at each original spatial array, leaving the feeder doors open so that any bird could access food. We recorded all visits to these array feeders for 6 days (26 March – 2 April 2021) and used the last 5 days of data to construct a third social network as described previously.

Assortment Analysis

We predicted that our experimental manipulation would result in assortment by feeder assignments; that is, birds should associate more with those that could access the same experimental feeders and should associate less with birds that could only access the alternate experimental feeders. We used the 'assortnet' R package (Farine, 2016) to measure the assortativity coefficient in the premanipulation and manipulated networks using weighted associations (Farine, 2014). To determine whether the measured assortment significantly differed from chance, we compared the assortativity coefficients with results calculated from 10 000 randomized networks generated through node permutation (Croft et al., 2011), which randomly swaps individual identities within grouping events. This allowed us to permute experimental feeder assignment, while maintaining original group level associations and the number of observations of each individual.

To further identify whether our manipulation affected network structure, we tested for correlations between the premanipulation and manipulated networks at each location using Mantel tests via the 'vegan' R package (Dixon, 2003) and compared the correlation estimates to those from 10 000 node-permuted networks.

Analysis of Novel Feeder Discovery

We estimated social and asocial learning rates with network-based diffusion analysis (NBDA) using the 'NBDA' R package v.0.9.6 (Hoppitt et al., 2020). NBDA identifies social transmission by assuming that, if a behaviour is socially transmitted, then the spread of that behaviour should follow the pattern of social connections among individuals. The transmission rate (s) indicates the rate of social information transmission per unit of connection to knowledgeable individuals, relative to an estimated baseline rate of asocial learning (Franz & Nunn, 2009; Hoppitt, 2017; Hoppitt et al., 2010). In this study, the behaviour of interest was the discovery of a novel feeder during the novel feeder discovery stage, defined as an individual's first recorded visit to that feeder. The first detection of a bird at each novel feeder within a patch was treated as an independent discovery event. We used a continuous time-of-acquisition approach, which assesses both the order in which individuals discovered a feeder and the amount of time it took for them to discover it since the novel feeders' introduction, defined as the elapsed daylight time between when a novel feeder was placed and when the individual first visited it. Since individuals visiting the novel feeder in a group should be considered to have discovered that feeder simultaneously, we specified 'ties' among all individuals that first visited a novel feeder within 3 min of each other, indicating that no social information transmission between those individuals could be determined.

We used a multi-network NBDA (Hasenjager et al., 2020; Hoppitt, 2017) to test whether social transmission (here the order and time of discovery of novel feeders) was more reflective of the patterns of social connections in the manipulated social network compared to the patterns of connection in the premanipulation network. Multi-network NBDA allows the estimation of the relative contribution of different social networks to observed social transmission events, thereby allowing us to test which set of social connections was likely to be most important for social information spread. Multi-network NBDA can also estimate social transmission rates for each network, and therefore compare these across multiple networks using all possible transmission pathways (Hassenjager et al., 2020). Finally, multi-network NBDA can estimate the proportion of social transmission events via each specific network (Farine et al., 2015; Hasenjager et al., 2020).

We ran a multi-network NBDA (Farine et al., 2015; Hasenjager et al., 2020; Hoppitt et al., 2020) with two social networks: the original premanipulation network derived from the spatial feeder arrays following cognitive testing (Fig. 1a) and the experimentally manipulated network derived from the experimental feeders during the resource manipulation phase (Fig. 1b). For each bird, we included individual level variables that were likely to predict their tendency to discover novel feeder patches. We excluded all individuals that were not present in both social networks (final network size: 200 birds at high elevation, 144 birds at low elevation).

We then used a multimodel inference approach to construct NBDA models that included all combinations of networks and individual level variables. We included all combinations of the following individual level variables: (1) spatial learning and memory score (mean number of location errors per trial over the first 20 trials, standardized to mean = 0, SD = 1); (2) reversal spatial learning and memory ability (mean number of location errors per trial over the first 20 trials, standardized to mean = 0, SD = 1); (3) sex; (4) age class (adult or juvenile); (5) elevation; (6) preferred spatial array; (7) replicate.

We selected these variables to test our predictions that individual differences in cognition could influence both social learning about feeders and independent discovery of these feeders and that information transmission between birds at high elevation would be less sensitive to our resource manipulations. Sex and age class were included because males and females, and adults and juveniles, can exhibit differences in exploratory behaviour (e.g. Benedict et al., 2021). Preferred spatial array was included to control for the fact that birds are much more likely to discover feeders at the novel food patch closest to their preferred array.

Each individual level variable was tested as affecting asocial or social learning only (additive model), both types of learning (social and asocial) at different rates (unconstrained model) and both types of learning at a single fixed rate (multiplicative model). We also compared models that included only the premanipulation networks, only the manipulated networks, or both. For the latter, we included models in which information transmission rates through the premanipulation network (s) was constrained to be equal to that through the manipulated network (restricted to $s1 = s2$) with unrestricted models in which transmission rates were allowed to differ between the networks. We also included models containing a 'null' network with all connections between birds set to 0, which excludes the possibility of social transmission, allowing us to test whether pure asocial learning fit the observed patterns of feeder discovery. We modelled social learning rate as constant over time, varying linearly over time or varying following a gamma distribution. Finally, to investigate whether information flow followed the social network or merely reflected location preferences, we also considered models that replaced the observed social network with a homogenous network, assuming all individuals at each preferred array were equally connected to each other.

We obtained the Akaike's information criterion corrected for small samples (AICc) for each model. Competing models were compared, with all models with ΔAICc values of less than 6 relative to the best model considered as having good evidence of relative fit to the data (Harrison et al., 2018). We then used the top model to generate all presented estimates. We estimated the social transmission parameter *s* separately for the premanipulation network and the manipulation-induced network to test for expected differences in the social information transmission rates between the networks. More specifically, we tested a prediction that social transmission rates should be higher through the manipulation-induced social network representing the most current food distribution and availability. In addition to estimating parameters using the top model, we also used model averaging to estimate parameters using all top five models. Finally, we used the code provided by Hasenjager et al. (2020) to estimate the proportion of discovery events that resulted from information transmission through each network.

As a second approach to test the question whether our manipulations of food distribution and availability resulted in birds using social transmission pathways through the restructured network rather than through the premanipulation network, we used a multi-network NBDA to estimate social transmission rates within matched dyads (birds assigned to the same experimental feeders) and mismatched dyads (birds assigned to different experimental feeders; e.g. Firth et al., 2016). We did this by fitting individuals' discovery times of the novel feeders to the premanipulation (spatial array feeders) and manipulated (two new experimental food locations per array) networks. This model used the same variables as the top model selected previously, but we partitioned each of the networks into two components: matched individuals (those that had been assigned to the same experimental feeders during the network manipulation phase) and mismatched individuals (those that had been assigned to different experimental feeders), as in Firth et al. (2016). This analysis allowed us to calculate social transmission of information about novel feeders separately for transmission between matched and mismatched birds. If individuals preferentially obtained information about novel feeders from other birds they had associated with during the feeder access manipulation, then we expected to see higher rates of information transmission between matched individuals than between mismatched individuals. Comparing relative values of *s* within each network, instead of comparing the two networks directly, as in the previous analysis, eliminates confounding variables such as the temporal difference between the two networks or potential correlations between the networks.

RESULTS

Data Summary

A total of 200 birds at high elevation and 144 birds at low elevation were present in both the social networks determined during the premanipulation stage and during the experimental resource manipulation stage. At high elevation, 193 birds discovered at least one novel feeder; of these, 187 were in the set of 200 birds from the social networks. At low elevation, 147 birds found at least one novel feeder, 139 of which were in the set of 144 birds from the social networks.

Comparing Premanipulation and Manipulation-induced Social Networks

We first tested whether our manipulation of resource ability affected associations between birds. There was a small (maximum $r < 0.19$), albeit statistically significant, correlation between the premanipulation and manipulation-induced social networks at all sites (Table 1). These results suggest that the majority of connections from the premanipulation networks were restructured, with some (likely strong) ties being carried over into the manipulated network.

Table 1
Results of Mantel tests for the correlation between the premanipulation networks and the experimentally manipulated networks at each location

Location	Mantel *r*	*P*
High elevation 1	0.119	<0.001
High elevation 2	0.100	0.009
Low elevation 1	0.086	0.017
Low elevation 2	0.147	0.001

Experimentally Imposed Social Assortment

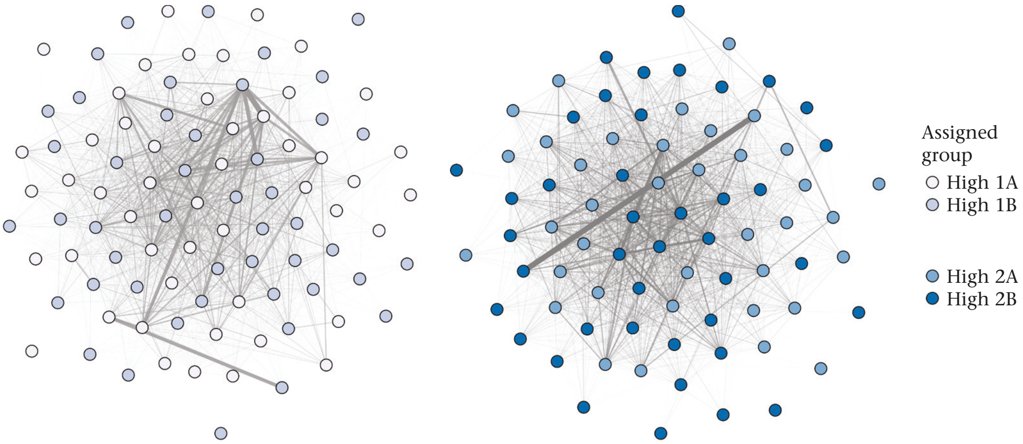
Here we tested whether we successfully randomized assignments of individuals to new social groups. We found that our feeder assignments were indeed random, as no assortment by experimental feeder assignment during the experimental manipulation was detected in any of the networks constructed from data collected at the spatial arrays during the premanipulation period (Fig. 2, Table 2). By contrast, networks constructed using data from the experimental manipulation were strongly assorted by experimental feeder assignment (Fig. 3), indicating that birds became more strongly associated with birds assigned to the same experimental feeder than with birds assigned to the other available experimental feeder at their array site during this time. While birds at both elevations became highly and significantly assorted during the manipulation, birds at low elevation were more strongly associated by experimental feeder assignment than those at high elevation (Table 2). When we tested whether these changes persisted after the novel food discovery period, we detected no significant assortment by experimental feeder assignment at the spatial arrays at either elevation after the novel feeder discovery experiment had concluded (Table 2). These results indicate that birds no longer preferentially associated with their experimentally imposed partners over those that had been assigned to the other experimental feeder and suggest that the novel network structures that formed during the manipulation were no longer present.

Social Transmission of Novel Feeder Locations during the Novel Feeder Discovery Stage

Within the ‘best models’ set (models within 6 ΔAICc of the best-fitting model), all models in this set included social transmission along both the experimentally manipulated and premanipulation baseline networks (Table 3). There was little support for models using either only the premanipulated baseline network, only the manipulated network, a homogenous network where all birds within a location have equal probability of learning from each other, or no social learning at all (Table 3). The constrained models in which social transmission rates were made equal between the two networks also had little support compared to the models in which transmission rates between the networks were different. All models in the ‘best model’ set also included effects of elevation on both asocial and social learning rates. There was variation in whether age, reversal learning performance and sex were included, and spatial learning and memory performance was not included in any of the best models.

The most parsimonious NBDA model included social transmission about novel food sources along both the premanipulation baseline and experimentally manipulated network edges, but with different social transmission rates between the networks (Table 3). Social transmission was estimated to be significantly higher through the manipulated network (nonoverlapping 95% CI

(a) High elevation



(b) Low elevation

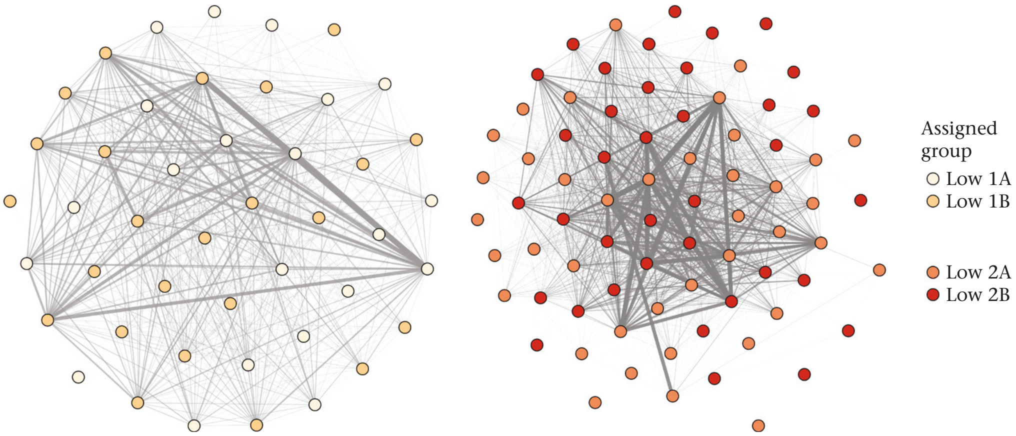


Figure 2. Social networks before the experimental manipulation at (a) high and (b) low elevation. Colours indicate which group individuals would be assigned to during the future resource manipulation. Edge width indicates weighted degree. For visualization purposes, the bottom quartile of edges are not depicted.

Table 2
Weighted assortativity coefficients for assortment by experimental feeder assignment at three stages: before the experimental manipulation began, during the experimental network manipulation and following the conclusion of the novel feeder discovery phase

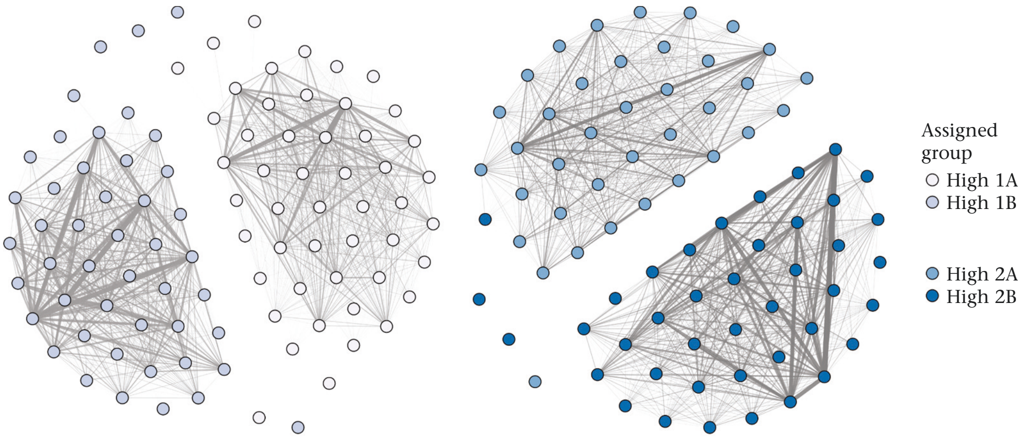
Stage	Location	Assortment coefficient (r)	SE
Premanipulation	High elevation 1	-0.019	0.012
	High elevation 2	-0.025	0.015
	Low elevation 1	-0.028	0.024
	Low elevation 2	-0.021	0.015
Manipulation	High elevation 1	0.858	0.003
	High elevation 2	0.830	0.005
	Low elevation 1	0.909	0.004
	Low elevation 2	0.922	0.002
Post-testing	High elevation 1	-0.018	0.016
	High elevation 2	-0.033	0.022
	Low elevation 1	-0.032	0.038
	Low elevation 2	-0.018	0.020

parameters estimates; Table 4). We estimated that the differences in information resulted in 63.8% of feeder discovery events having occurred via social transmission through the experimentally manipulated network and only 10.8% of discovery events having occurred via social connections captured by the premanipulation network but not present in the manipulated network.

The social transmission rate parameter, *s*, indicates the rate at which an individual acquires information per unit of network connectedness to knowledgeable individuals relative to the rate of asocial learning. In our NBDA analysis, we coded high elevation and adult age as 0, so the values of *s* presented in Table 4 are those of an adult bird at high elevation. The average adult at high elevation discovered novel feeders 4.07 times faster per unit of connection to knowledgeable individuals along edges in the premanipulation social network compared to the rate of asocial learning alone but 25.74 times faster per unit of connection to knowledgeable individuals along edges from the experimentally manipulated network compared to the rate of asocial learning alone.

We also found effects of elevation on both asocial and social learning rates. Since individual level variables are modelled on a log scale in NBDA, the ratio of learning rates can be estimated as e^{ILV} (Hasenjager et al., 2020). The rate of asocial transmission at low elevation was approximately $e^{0.866}$, or 2.38 times greater than that at high elevation, but the rate of social learning at low elevation was also $e^{0.295}$, or 1.34 times faster than that at high elevation. As an alternative method of interpreting differences between elevations, rerunning the model while specifying low elevation as the baseline allowed us to directly extract the social transmission rate *s* for each network at low elevation. In an identical model using an adult bird at low elevation as the baseline, the average adult at low elevation discovered novel feeders 5.07 times faster per unit of connection to knowledgeable individuals along edges from the premanipulations baseline network but 26.74 times faster per unit of connection to knowledgeable individuals along edges from the experimentally manipulated network, relative to asocial learning alone.

(a) High elevation



(b) Low elevation

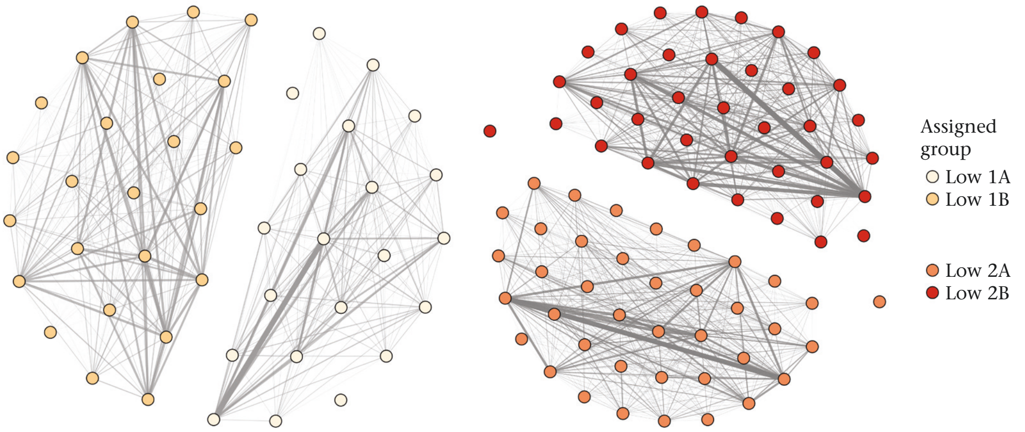


Figure 3. Social networks during the experimental manipulation at (a) high and (b) low elevation. Colours indicate which group individuals were assigned to during the resource manipulation. Edge width indicates weighted degree. For visualization purposes, the bottom quartile of edges are not depicted.

Table 3

Summary of the top five models of novel feeder discovery (1–5), plus the best model using only the experimentally manipulated network (6), the best model using only the premanipulation baseline network (7), the best model using a homogenous network (8) and the best nonsocial model (9)

	Model type	Networks	Social ILVs	Asocial ILVs	AICc	ΔAICc
1	Unconstrained, constant	Baseline, manipulated	Elevation, reversal learning	Elevation, reversal learning, age	41870.306	0
2	Unconstrained, constant	Baseline, manipulated	Elevation, reversal learning	Elevation	41870.432	0.126
3	Unconstrained, constant	Baseline, manipulated	Elevation	Elevation, age, sex	41871.486	1.3066
4	Unconstrained, constant	Baseline, manipulated	Elevation	Elevation, reversal learning	41871.632	1.4524
5	Unconstrained, constant	Baseline, manipulated	Elevation, reversal learning	Elevation, age, sex	41871.668	1.4885
6	Unconstrained, constant	Manipulated only	Elevation, reversal learning	Elevation, age	41898.835	27.1667
7	Additive, constant	Baseline only	None	Age	42121.663	249.9951
8	Unconstrained, constant	Homogenous	Elevation	Elevation, age	43379.880	1508.2121
9	Asocial, constant	None	None	Age	44435.094	2563.4617

The five best models all included both asocial and social learning (unconstrained), constant learning rates and both premanipulation networks and experimentally manipulated networks. Some of the top models also included age and spatial reversal learning, but none of the top models included spatial learning or memory.

There was also a negative, but nonsignificant, association of reversal learning performance with both social and asocial learning (Table 4), suggesting that birds with worse spatial reversal cognitive performance seemed to be slower at discovering novel feeders. None of the top models included spatial learning and memory ability, suggesting that it was not affecting rates of novel feeder discovery (Table 4). Finally, there was a significant effect of age on asocial learning: juvenile birds had a rate of asocial learning when discovering novel feeders approximately $e^{0.142}$, or 1.14 times faster than adults (Table 4).

Social Transmission along Matched and Mismatched Dyads

When we fitted the premanipulation network based on the spatial array data (partitioned into matched and mismatched dyads during the subsequent feeder manipulation stage) to novel feeder discovery times, this analysis showed more social transmission between mismatched birds (39.1%) than between matched birds (25.4%) along edges from this network, although the 95% CI was overlapping between the two (Table 5). In contrast, when we fitted the manipulated network (based on differential assignment of birds

Table 4
Posterior parameter estimates and 95% credible intervals (CI) for the best-fitting model

Parameter	Support	Mean (top model)	95% CI (top model)	Model averaged estimate	Unconditional SE
Social transmission (*s*)					
Original network	1	4.067	[2.94, 5.21]	1.963	0.324
Manipulated network	1	25.745	[21.80, 29.70]	14.92	4.654
Individual level variables					
Effect of elevation on asocial learning	1	0.866	[0.75, 0.99]	0.865	0.014
Effect of elevation on social learning	1	0.295	[0.29, 0.30]	0.295	0.064
Effect of reversal learning performance on social learning	0.414	-0.036	[-1.11, 0.04]	-0.036	0.038
Effect of reversal learning performance on asocial learning	0.142	-0.034	[-0.07, 0.00]	0	0.003
Effect of age on asocial learning	0.858	0.142	[0.02, 0.27]	0.257	0.064

The model was parameterized with high elevation and adult age as baselines; therefore, the value of *s* presented is that of an adult bird at high elevation. The elevation and age parameters indicate how low elevation and juvenile age, respectively, influence learning compared to high elevation and adult age. Model average estimates were estimated using the top five models combined.

Table 5
Posterior parameter estimates and 95% credible intervals (CI) for the social transmission rate parameter (*s*) between matched birds (those assigned to the same feeder during network manipulation) and mismatched birds (those assigned to different feeders during the manipulation), for the premanipulation social networks and the manipulated social networks

Parameter	Mean	95% CI
Premanipulation network		
Social transmission: matched dyads	7.351	[6.194, 8.508]
Social transmission: mismatched dyads	8.489	[7.286, 9.692]
Manipulated network		
Social transmission: matched dyads	15.582	[13.009, 17.307]
Social transmission: mismatched dyads	10.845	[8.996, 12.694]

to one of the two new experimental food locations near each array) to novel feeder discovery times, we found strong support for differing rates of information transfer between matched and mismatched birds along edges from the manipulated network, with matched dyads significantly more likely to transfer information than mismatched dyads (Table 5). We estimated that 59.6% of novel feeder discoveries were made through social transmission between matched birds along the manipulated network edges, while only 13.3% of discovery events occurred through social transmission between mismatched birds within the experimentally manipulated network.

DISCUSSION

Our results show that after a short period of manipulation of resource distribution and access (2 weeks), chickadees restructured their social network by assorting mostly with birds assigned to the same resource (here a feeder) regardless of their pre-existing (premanipulation) social connections. Model selection suggested that models with differential social transmission rates between the premanipulation and manipulation-induced networks had much better fit to the data compared to models that were restricted to the same rates of transmission in both social networks. Chickadees at both elevations preferentially used their new, experimentally induced social connections to acquire social information when searching for novel food sources, and social transmission rates when discovering novel feeders were significantly higher through the connections formed by manipulating the resources that individuals could recently access. When assessing the rate of social transmission between matched or mismatched dyads through the experimentally manipulated network, birds assigned to the same experimental feeders showed significantly faster transfer of social information about novel food sources compared to social information transfer between birds assigned to different experimental feeders around each array.

While birds from both high and low elevations seemed to respond to our manipulations of food distribution and accessibility similarly by preferentially using new, experimentally induced associations when learning novel food locations, birds at the harsher, less predictable high-elevation sites were slightly less strongly assorted during the manipulation and showed an overall lower reliance on social learning to discover novel food sources. These results reinforce our previous findings in the same study system that high-elevation chickadees use less social information when foraging (Heinen et al., 2021) and suggest that these birds show less of a social response to changes in resource availability than birds at low elevation. After the novel feeder discovery stage, birds at both elevations similarly exhibited no preferential assortment with conspecifics that were assigned to the same experimental feeder during the manipulation stage. Overall, these results suggest that chickadees can quickly readjust their social behaviour and social information use when searching for food, following just 2 weeks of using the same feeders together, emphasizing the importance of resource distribution for the social network structure (He et al., 2019). While our manipulation of food distribution and accessibility appeared to directly affect who chickadees decided to follow and who not to follow while searching for food, it did not necessarily affect who they associated with in other contexts. Such a rapid response is likely adaptive in winter environments when food is relatively scarce and the environment is less predictable, as birds pay attention to and preferentially follow the individuals they forage with and the individuals that can successfully obtain food (Seppänen et al., 2011; van Leeuwen et al., 2021).

Our findings on chickadee responses to manipulation of food distribution and availability mirror those obtained in related noncaching great tits, which also preferentially used new, experimentally induced social associations related to differential access to new food sources when searching for novel food sources following 3 months of experimental treatment (Firth et al., 2016). Also, similarly to our chickadees, great tits did not show preferential assortment by experimental assignment after the end of resource manipulation (Firth & Sheldon, 2015). We find these similarities even though great tits differ from mountain chickadees in several ways: they do not cache food and they have a more flexible social structure (fission–fusion, associated with frequently changing social associations) than mountain chickadees, which form stable social groups in the winter (Ekman, 1989). The manipulation of food distribution in the great tit study was rather lengthy (90 days), which might have also provided long-term reinforcement of the manipulation-induced social structure. Our study showed that even a brief period (2 weeks) is sufficient for chickadees to change their social associations and social information use when foraging despite their more rigid social structure. Such results suggest that social animals may benefit from monitoring their social surroundings both within and across social groups, which would allow them to quickly change their social learning preferences based on their most recent social associations. In a foraging context, learning from the most recent foraging partners means that animals would use the most recent social information available, allowing them to discover novel food sources faster.

One remaining question is whether network changes based on changes in food distribution and access impact other subsequent behaviours, and over what timescale. For example, several studies in great tits (Firth & Sheldon, 2016) and blue tits, *Cyanistes caeruleus* (Beck et al., 2020) demonstrated that social associations predicted subsequent breeding pairs and extrapair mating. While our study was not designed to address breeding behaviour, we noted that our random network assignments split 14 pairs of birds that had bred together during the previous season, while reinforcing four pairs. After the experiment, birds from eight of the split pairs were detected during the next breeding season, and seven of the pairs again bred together. Of the four reinforced pairs, three were detected the following breeding season and all three bred together that season. While anecdotal, these observations suggest that any effects of our manipulation on long-term associations were mild.

There were differences in the effects of individual level cognitive and demographic variables on social information transmission between the current study and our previous social learning study in the same system (Heinen et al., 2021). Unlike our previous study (Heinen et al., 2021), we did not detect a significant and consistent effect of reversal spatial learning ability on either social or asocial learning during novel feeder discovery. It is possible that the association between spatial cognitive flexibility and novel food discovery is dependent on specific winter conditions and food availability and hence may vary among years. In addition, unlike our previous study (Heinen et al., 2021), we detected an effect of age on the rate of asocial learning, but not social learning, with juveniles being faster than adults in discovering novel feeders via asocial learning. While a recent meta-analysis reported no significant association between age and social learning (Penndorf & Aplin, 2020), it is likely that juvenile birds in our system experience a more unpredictable environment than adults due to their subordinate social dominance status (Ekman, 1989) and overall inexperience (Benedict et al., 2021). For example, juvenile mountain chickadees show more information-updating behaviour than adults when sampling multiple food sources, especially during harsh winters (Benedict et al., 2021). During this experiment, it appears that juveniles also were relying on asocial learning more than adults by searching for novel food sources independently, which likely allows them to be more successful at discovering novel food sources while avoiding potential competition with adults. Similar to our previous study (Heinen et al., 2021), spatial learning and memory performance were not associated with social or asocial learning during the novel feeder discovery.

Overall, our results suggest that (1) food distribution and availability can have a direct effect on social network structure, (2) chickadees share social information associated with food using social networks along the network edges, (3) despite their rather rigid social structure associated with stable social groups, chickadees appear highly opportunistic and quickly adjust their social information use when searching for food depending on their observations of who can discover and obtain novel food and (4) this social information use varies with elevation and environmental harshness. At the same time, chickadees do not seem to change their social network permanently following experimental manipulation of food distribution and access, as they did not continue to associate preferentially with the birds matched by the feeder assignment after the experiment. Such results show high social flexibility, which is likely adaptive in harsh, unpredictable environments, as chickadees can track the most recent and reliable social information associated with foraging without permanently altering their long-term social associations.

Author Contributions

Virginia Heinen: Methodology, Formal analysis, Investigation, Data curation, Visualization, Writing – original draft. **Lauren Benedict:** Investigation, Writing – review & editing. **Benjamin Sonnenberg:** Investigation, Writing – review & editing. **Eli Bridge:** Resources, Software, Writing – review & editing. **Damien Farine:** Resources, Software, Writing – review & editing. **Vladimir Pravosudov:** Conceptualization, Methodology, Investigation, Supervision, Project administration, Funding acquisition, Writing – original draft.

Data Availability

Data will be made available on request.

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