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Food discovery is associated with different reliance on social learning and lower cognitive flexibility across environments in a food-caching bird

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Social learning is a primary mechanism for information acquisition in social species. Despite many benefits, social learning may be disadvantageous when independent learning is more efficient. For example, searching independently may be more advantageous when food sources are ephemeral and unpredictable. Individual differences in cognitive abilities can also be expected to influence social information use. Specifically, better spatial memory can make a given environment more predictable for an individual by allowing it to better track food sources. We investigated how resident food-caching chickadees discovered multiple novel food sources in both harsher, less predictable high elevation and milder, more predictable low elevation winter environments. Chickadees at high elevation were faster at discovering multiple novel food sources and discovered more food sources than birds at low elevation. While birds at both elevations used social information, the contribution of social learning to food discovery was significantly lower at high elevation. At both elevations, chickadees with better spatial cognitive flexibility were slower at discovering food sources, likely because birds with lower spatial cognitive flexibility are worse at tracking natural resources and therefore spend more time exploring. Overall, our study supported the prediction that harsh environments should favour less reliance on social learning.

1. Introduction

Social information, acquired through the observation of other individuals [1,2], is important across a wide array of socially living taxa and in diverse contexts such as habitat choice [3], mate choice [4,5] and food discovery [6–8]. Acquiring new information through individual exploration requires a significant investment of time and energy, and using social information can reduce these costs [9]. However, social information is typically less reliable than nonsocial information [10,11], for example, because it may be outdated [9,12]. Moreover, in the context of resource acquisition, using social information may increase competition and result in locally decreased resource availability [13]. It is thus critical to determine the factors that might influence the usefulness of social learning in different natural conditions to understand why social species may rely on individual learning in certain contexts.

The relative costs and benefits of using social information may vary depending on environmental conditions. When conditions are harsh and the environment is unpredictable, the probability that group members have current

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and relevant information decreases, and social learners risk making errors such as copying their group members' mistakes, failing to detect new resources or learning about changes in the environment too late to exploit them [10,14,15]. Moreover, a simulation study predicted that when food sources are ephemeral and unpredictable, relying on social learning can reduce the ability of individuals to discover alternative food sources [16]. By contrast, more stable environments have been predicted to favour social learning, which allows individuals to quickly converge on the best resources [16,17].

Reliance on social information may also depend on the natural history of the taxa in question. For example, many scatter-hoarding species cache thousands of food items and rely on recovering these caches to survive the winter (e.g. [18,19]). Many such species are highly social, but information about cache locations is usually guarded from group members via behavioural strategies [20,21]. Food caches are not the only food available to these species, as they can continuously forage and even continue to cache throughout the year. It is not well known, however, how these species balance individual and social learning when discovering novel food sources.

Scatter-hoarding species rely on spatial cognition to recover food caches, and better spatial learning and memory abilities are associated with a higher probability of overwinter survival [18,19]. Given this, it could be expected that individuals with better spatial cognitive abilities experience a more predictable environment as they may rely on their own memory of personal food caches and other detected food sources. Such a predictable personal environment may allow them to reduce potentially costly exploration behaviour. However, individuals with worse spatial cognitive abilities are likely to be less successful at remembering their food cache locations, which makes their foraging less predictable. These individuals can be expected to benefit disproportionately from engaging in more food search behaviour, which may be costly (e.g. energy expenditure, predation risk). Therefore, even within a group, individuals may vary in their foraging strategies associated with the discovery of novel food sources.

Here we tested (i) whether differences in environmental harshness are associated with differences in social learning when searching for novel food and (ii) whether variation in spatial cognitive abilities is associated with differences in the rate of discovery of novel food sources. In contrast with previous studies [22] which tested for social transmission using a single-novel food source, we attempted to emulate more realistic conditions by using multiple novel food sources simultaneously. Introducing multiple food sources could better differentiate the effect of social learning from the effects of independent search. When a single source is found, other group members can converge on that source using social information. However, when multiple novel food sources are present, we can gauge relative reliance on each type of learning; greater reliance on social learning should result in the group discovering fewer food sources, as most individuals would be expected to converge on the first discovered source [23]. Lower reliance on social learning should be associated with more independent exploratory behaviour, leading to faster discovery of multiple food sources.

To test these predictions, we studied food-caching mountain chickadees (*Poecile gambeli*) at high and low elevations in the northern Sierra Nevada [24,25]. Both elevation sites are along a continuously distributed coniferous forest with similar tree density that differs only in tree species composition, so the main differences between elevations are associated with the winter environment. Higher elevations are characterized by more severe winter conditions including lower temperatures, higher and more persistent snow cover, and more frequent and severe winter storms [26]. Comparisons of daily foraging routines between chickadees at high and low elevations suggest that chickadees at high elevation face a greater risk of starvation, and that high elevation environments are unpredictable (e.g. foraging interruptions due to snow storms, temporally unpredictable food) during the winter [25]. Overall, we define this high elevation environment as 'harsh', meaning it is both temporally unpredictable and imposes high metabolic costs (e.g. low temperature, short day length). High metabolic costs can be expected to amplify the negative effects of temporal unpredictability by increasing both the need to obtain sufficient energy, and the costs of failing to do so. Previous work in this system found that chickadees at high-elevation cache more food and have better spatial cognition associated with cache retrieval than those at lower elevations [27]. We predicted that chickadees at harsher high elevation should be faster at discovering multiple novel food sources and that they should rely less on social learning compared to birds at low elevation.

We also compared how variation in two cognitive traits, spatial cognitive ability and reversal spatial cognitive ability (flexibility), is associated with the novel food discovery. While both abilities are associated with acquiring spatial information, spatial learning and memory is likely more important in food cache recovery as it is involved in acquiring initial information [18,19], while spatial cognitive flexibility is likely indicative of how well individuals can learn and remember continuously changing food sources [28]. In both cases, better spatial cognitive abilities are associated with how fast individuals can acquire and remember spatial information [28] and should be associated with a more predictable individual-level environment [25]. Individuals with worse spatial cognitive abilities of both types experience a less predictable environment and therefore may be more motivated to take more risks and perform more searching behaviour, potentially resulting in the faster discovery of novel food sources compared to birds with better spatial cognitive abilities.

2. Methods

(a) Study system

This study was based in our long-term mountain chickadee system in the northern Sierra Nevada, north of Truckee, California, USA (Sagehen Experimental Forest, Sagehen Creek Field Station, University of California, Berkeley). Our study system spans from low- (1900 m) to high-elevation (2400 m) sites associated with drastically different overwinter conditions [26,29]. Our study site is located in a remote area of the Tahoe National Forest with limited human activity. As a result, the only supplementary food available to chickadees at our study site is provided by us. Since 2014, we have banded chickadees with unique combinations of passive integrated transponder (PIT) tags (IB Technology, Leicestershire, UK) and colour bands. We trap and band birds annually using mist nets at established feeders across both elevations during fall and winter and in nest-boxes during the breeding season.

Based on observed breeding activity, chickadee density appears similar across low and high elevation [26]. Feeder attendance during the winter is consistent at high elevation, but varies among years at low elevation, ranging from similar attendance to that at high elevation to almost no birds attending the feeders in some years [24,25,29,30]. At high elevation, we estimate that 95% or more of the chickadees in the area are PIT-tagged based on weekly visual observations. At low elevation, the proportion of PIT-tagged birds varies by year, but on average, is lower than that at high elevation (approx. 70–90%).

We classified all birds in this experiment as either juvenile (first year) or adults (older than the first year of life) based on extensive banding data prior to the experiment, as well as on plumage characteristics and state of moult [31].

(b) Data collection

We used radio frequency identification (RFID)-equipped feeders to conduct all experiments in this study (see [29,30,32]). When active, feeders recorded PIT-tag ID, time, date and location of all PIT-tagged birds landing on the feeder perch. Feeders remained active throughout all daylight hours. Additionally, all feeders could be programmed to allow food access only to specific individuals while still recording visits of all individuals landing on the feeder perch.

(i) Spatial feeder arrays

All feeders used to trap and band birds were closed on 16 December 2019 and supplemental food was made available only at four locations, each containing an array of eight feeders. The eight RFID-equipped feeders in each array were equidistantly attached to a square aluminium frame (122 × 122 cm) with two feeders on each side, suspended approximately 4 m above the ground [24]. We used two arrays at low elevation and two at high elevation, with approximately 1.5 km distance between the two arrays within each elevation (electronic supplementary material, figure S1). Initially, all feeders in the array contained food (black oil sunflower seeds) and were deployed in 'open' mode with all doors permanently open and food visible. Arrays were then set to 'all' mode from 30 December 2019 to 20 January 2020 at low elevation and from 27 December 2019 to 20 January 2020 at high elevation. In 'all' mode, all doors remained closed so the food inside could not be seen, but the feeder doors would open for any PIT-tagged bird landing on the perch. This mode was used to habituate birds to the moving doors prior to spatial cognitive testing [24,29]. During this period, we detected 86 chickadees attending the arrays at low elevation and 154 chickadees attending the arrays at high elevation.

(ii) Spatial cognitive testing

Starting 20 January 2020 at low elevation and 3 February 2020 at high elevation, we tested chickadees on two spatial cognitive tasks, first on a spatial learning and memory task for 5 days (ending 24 January 2020 at low elevation and 7 February 2020 at high elevation) and then on a reversal spatial learning task for the next 5 days (ending 29 January 2020 at low elevation and 10 February 2020 at high elevation) following established protocols [19,24,30].

During the spatial learning and memory task, birds were expected 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 feeder, with assignments spread across all eight feeders pseudorandomly so that no birds were assigned to their most visited feeder from the previous 'open' and 'all' periods. During testing, only the bird's assigned feeder door would open when the bird landed on the perch, allowing that bird to take food. All other feeders recorded the ID, time, date and location of each visit, but did not allow access to food. 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 feeders a bird visited before visiting its assigned feeder. We used the mean number of location errors per trial across the first 20 trials to estimate spatial learning and memory ability, following our previous studies [19,24,29,30].

During the reversal spatial task, we reassigned each bird to a new rewarding feeder within the array, meaning the previously assigned feeder no longer provided a food reward. Birds that had been assigned to the same feeder during the previous task were reassigned to different feeders to reduce the possibility of social learning (following [24,30]). When learning the reversal task using these methods, birds make errors to their previously rewarded locations, as would be expected based on individual rather than social learning [30]. 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 [24,29,30].

(c) Social network construction

After cognitive testing was completed, we collected data to determine the social networks of birds at each elevation using the permanent spatial arrays. Starting from 21 February 2020 at high elevation and 28 February 2020 at low elevation, we programmed two feeders on the opposite sides of each array to remain open, allowing all birds to see and access food at any time. The other six array feeders were emptied with the doors left open so birds could see they contained no food. We used data from 4 days (28 February 2020–2 March 2020) to construct one social network for each elevation (1782 visits from 63 chickadees at low elevation and 3631 visits from 142 chickadees, at high elevation; electronic supplementary material, figure S2). The main reason for using two feeders per array (as opposed to 8) was to collect more interpretable network data. Data collection for four days is likely to be sufficient for measuring the existing social network because chickadees are highly resident birds with mostly stable social structure throughout the non-breeding season [33], and all birds visit the arrays almost every day. Prior to data collection, birds had been visiting these arrays for over a month, so the social networks measured represent both spatially and temporally stable supplementary food conditions. This approach allowed us to measure the most recent network immediately prior to the novel feeder introduction. We used a 'gambit of the group' approach [34] which assumes that all individuals observed together were equally connected to each other and infers the strength of connections based on repeated co-occurrences across groups. We used a Gaussian mixture model (GMM; *gmmevents* function from the R package 'asnipe' [35]) in R 4. 0.3 [36] to define grouping events.

The arrays were visited by many birds from multiple social groups in quick succession, resulting in extremely homogeneous networks. To address this issue, we used the 'double GMM' method [37]. We ran an initial GMM with a resolution of 1 min to detect the start and end of large-scale foraging events at each feeder array. Next, we ran a GMM within each broad foraging event at a 1 s resolution, allowing the second GMM to split each flock event into shorter feeding bouts. For both runs, we treated each array as a single-spatial location, as all array feeders are within 2 m of each other and birds from the same social group can visit different array feeders simultaneously. The result was a single group-by-individual matrix for each elevation. We inferred association strengths among individuals from their co-occurrence in feeding bouts using the simple ratio index function in asnipe (function *get_network*), defined as the number of times two individuals appeared in the same foraging event, divided by the number of foraging events containing at least one of the two individuals [38].

(d) Novel feeder discovery experiment

On 2 March 2020, we removed food from all array feeders, leaving the doors open so birds could see that feeders were empty. We then introduced two novel food 'patches', each consisting of three RFID-enabled feeders, per elevation. Novel feeders were identical to those on the array but mounted on a metal pole approximately 2 m above the ground. Within each patch, feeders were spaced approximately 125 m apart from each other and approximately 125 m from the array, and in subsequent replicates, approximately 125 m from any previously used location (high-elevation mean distance: 128 m, s.d. = 40; low-elevation mean distance: 140 m, s.d. = 58; electronic supplementary material, figure S1). Distance between feeders was not significantly different between elevations ($t_{32} = -0.889$, $p = 0.381$). Considering that different feeder spacing can lead to changes in the network structure in closely related species [39], we specifically kept spacing between novel feeders consistent across sites and replicates to minimize any potential effect of spacing on our results. Within each elevation, the two patches were separated by at least 1 km (electronic supplementary material, figure S1). We carried out three replicates, each lasting 5 days, with all feeders removed from old locations and moved to novel locations for each replicate. Considering rugged mountainous winter conditions, feeders had to be moved during daylight hours but were concealed in a closed trailer during transport and deployed when no birds were visible. No locations were re-used over the course of the study.

(e) Analyses of novel feeder discovery

(i) Social learning, spatial cognition and age in discovery of novel feeders

We estimated social learning rates with network-based diffusion analysis (NBDA), using the R NBDA code v. 1.2.15 [40]. NBDA identifies social transmission by assuming that if the social transmission is occurring, the spread of behaviour should follow the social connections between individuals, with a rate of transmission proportional to the strength of association [41–43]. The behaviour of interest in our study was the discovery of a novel feeder, defined as an individual's first recorded visit to that feeder, with each feeder treated as an independent discovery event. We used a time-of-acquisition approach which assesses both the order in which individuals discovered the feeder, and the time it took them to discover it [42], excluding all non-daylight times. Since individuals arriving at the feeder in a group should be considered as learning about the feeder simultaneously rather than transferring information to each other, we added 'ties' between all individuals that arrived at the feeder within 3 min of each other, preventing information transfer between these individuals [42]. We used the social networks constructed from the post-cognitive testing array data, excluding any individuals that discovered novel feeders but were not present in the social networks (10 at high elevation; 7 at low elevation). As some individuals discovered all six feeders at high elevation, indicating that the two patches were not completely independent, we used one network containing all birds at high elevation (i.e. using data from both arrays), and one network containing all birds at low elevation. However, to account for most birds having a strong preference for one area near one of the two arrays at each elevation, we included this preferred location as an individual-level variable.

We used a multimodel inferencing [41,42] approach in which we constructed every NBDA model for all combinations of the following parameters: individuals' spatial learning and memory abilities (mean number of location errors per trial over the first 20 trials), reversal spatial learning and memory abilities (mean number of location errors per trial over the first 20 trials), age class (adult or juvenile), and initial array assignment as individual-level variables assumed to affect individual-level learning. Replicate and feeder ID were included as random effects [40]. We included models in which all birds were assumed to have the same social transmission rate across elevations, in which social transmission differed between elevations, and in which only nonsocial learning was possible. We considered whether the nonsocial learning rate was constant over time, varied linearly over time or varied following a gamma distribution. We included models where social transmission and nonsocial learning were assumed to combine additively, and where they were assumed to combine multiplicatively. Finally, to investigate whether information flow in fact followed the social network, we also considered models which replaced the observed social network with a homogeneous network, which assumes all individuals at each elevation are equally connected to each other [7].

For each model, we obtained its Akaike information criterion, corrected for sample size (AICc). Competing models were compared with ΔAICc values, with all models within six ΔAICc considered as having good evidence of relative fit to the data [44]. We derived 95% confidence intervals for parameters using profile likelihood techniques, based on the best predictive model that included a given parameter [43].

(ii) Rate and extent of discovery of novel feeders

We recorded the amount of daylight time that elapsed between when we placed the feeder at the novel location and when the first PIT-tagged chickadee detected at each feeder; the time between the placement of the feeders and each bird's first visit to each feeder and the number of feeders each bird discovered within each replicate. We compared these metrics between low and high elevations using linear mixed models, using the Kenward-Rogers algorithm to calculate the denominator degrees of freedom (R packages 'lme4' [45] and 'lmertest' [46]).

First, we analysed whether elevations differed in time to the initial discovery of the novel feeders, using the time until the first bird was detected at each feeder as a dependent variable, and elevation and replicate as fixed factors. Next, we tested whether there were differences between elevations in the time to discovery of subsequent feeders within a patch, using the time until the first bird was detected at each feeder as a dependent variable, and elevation, replicate and feeder number (whether the feeder was the first, second or third discovered within its patch) as fixed effects. Third, we tested for elevational differences in the rate of discovery for all birds, not just the first bird at each feeder. In order to meet assumptions of homogeneity of variance, we log-transformed discovery time for this analysis. We used log-transformed time to discover the first, second and third feeder within a patch by each bird as a dependent variable, bird ID as a random factor, and elevation, order of feeder discovery, spatial learning and memory score, reversal spatial learning score and replicate as fixed factors.

To model the number of feeders discovered during each replicate, we created a generalized linear mixed model with a binomial distribution and logit link function, using the proportion of feeders found by each bird as the dependent variable, elevation, replicate, spatial learning and memory score, and reversal spatial learning score as fixed effects, and bird ID as a random effect. We only counted feeders discovered within a bird's most frequently visited patch, which meant that the small number of birds at high elevation that discovered

Table 1. Summary of the three top models for novel feeder discovery (1–3), along with the best model including age and preferred location (4), the best nonsocial model (5) and the best model with a homogeneous social network (6).

	model type	social transmission	random variables	ILVs	ΔAICc	AICc
1	multiplicative, non-constant	varies with elevation	replicate	spatial reversal learning	0	26594.7
2	multiplicative, non-constant	varies with elevation	replicate, feeder ID	none	16.67	26611.35
3	multiplicative, non-constant	the same across elevations	replicate	spatial reversal learning	17.07	26611.77
4	multiplicative, non-constant	varies with elevation	feeder ID	spatial cognition, age, preferred location	230.3	26824.99
5	additive, non-constant	none	feeder ID	none	1646.58	28241.28
6	multiplicative, non-constant, homogeneous network	varies with elevation	none	spatial reversal learning	1698.04	28292.74

Table 2. Posterior parameter estimates and 95% credible intervals for the best-fitting model of novel feeder discovery.

parameter	mean [95% credible interval]
social, high elevation	40.28 [27.22, 52.04]
social, low elevation	71.22 [65.44, 91.38]
spatial reversal learning	0.39 [0.27, 0.56]

more than three feeders were capped at three. Finally, we tested for elevation differences in the probability of discovering all three feeders in a patch during each replicate and whether such probability was associated with differences in cognitive abilities.

(iii) Model simulations

For each replicate, we recorded the order of *k* individuals' arrival, *k* being the total number of birds that discovered each feeder. For each new arriving bird after the first, we calculated the mean association strength to knowledgeable individuals (i.e. all individuals that had previously arrived at the patch). Following Hillemann *et al*. [47], we compared these observed patterns to a null model which simulated individuals arriving at the feeder in random order, generated by randomly selecting *k* individuals from the local network. This null model assumes social learning plays no role in feeder discovery. We also compared our observations to an affiliate model, which simulates simple social discovery of the feeder. For this model, we randomly selected one individual as the first arrival. We then randomly chose the second arrival from the first arrival's associates. Each subsequent arrival was selected from the pool of knowledgeable individuals' associates, continuing until *k* individuals were selected. We ran 2000 repetitions of each model and compared the mean association strength to knowledgeable individuals from each model to our observed values.

3. Results

(a) Network-based diffusion analysis

Using the networks constructed from the post-testing array data (electronic supplementary material, figure S3), we carried out a full model-fitting procedure on all feeder discovery replicates. The most parsimonious model contained social transmission at both elevations (table 1), with a significantly higher rate of social transmission at low elevation than at high elevation (non-overlapping 95% CI parameter estimates; table 2); included spatial reversal learning and memory ability, which was negatively associated with novel feeder discovery rates at both elevations (table 2); and had a non-constant, decreasing rate of acquisition (table 1). There was substantially less support for a model with the same rate of social learning at both elevations, and little or no support for models containing purely asocial learning mechanisms or models fitted with a homogeneous social network (table 1). Neither preferred array location, age (adult versus juvenile), nor spatial learning and memory ability were significantly associated with novel feeder discovery rates, as no models with these parameters were among the three top models or within six ΔAICc of these models (electronic supplementary material, table S1).

(b) Time to novel feeder discovery

At least one novel feeder was found by 152 chickadees at high elevation and 65 chickadees at low elevation (electronic supplementary material, table S2). Of these birds, 132 birds at high (93% of 142) and 49 (78% of 63) at low elevation were present in the social network (electronic supplementary material, figure S2). Birds at high elevation discovered feeders significantly faster than birds at low elevation, approximately 6 h sooner (ANOVA: $F_{1,32} = 6.807$, $p = 0.014$; electronic supplementary material, figure S3). There was also a significant effect of replicate, indicating feeders in later replicates were discovered sooner (ANOVA: $F_{1,32} = 11.228$, $p = 0.002$). There was no significant interaction between replicate and elevation (ANOVA: $F_{1,32} = 0.285$, $p = 0.597$). We found that a single outlier exerted a disproportionate influence on the model; however, the difference between elevations remained significant when this point was removed (ANOVA: $F_{1,31} = 7.287$, $p = 0.011$).

When we included order of feeder discovery within a patch, there was a significant interaction between elevation and whether the feeder was discovered first, second or third (ANOVA: $F_{1,31} = 5.221$, $p = 0.029$), but no significant

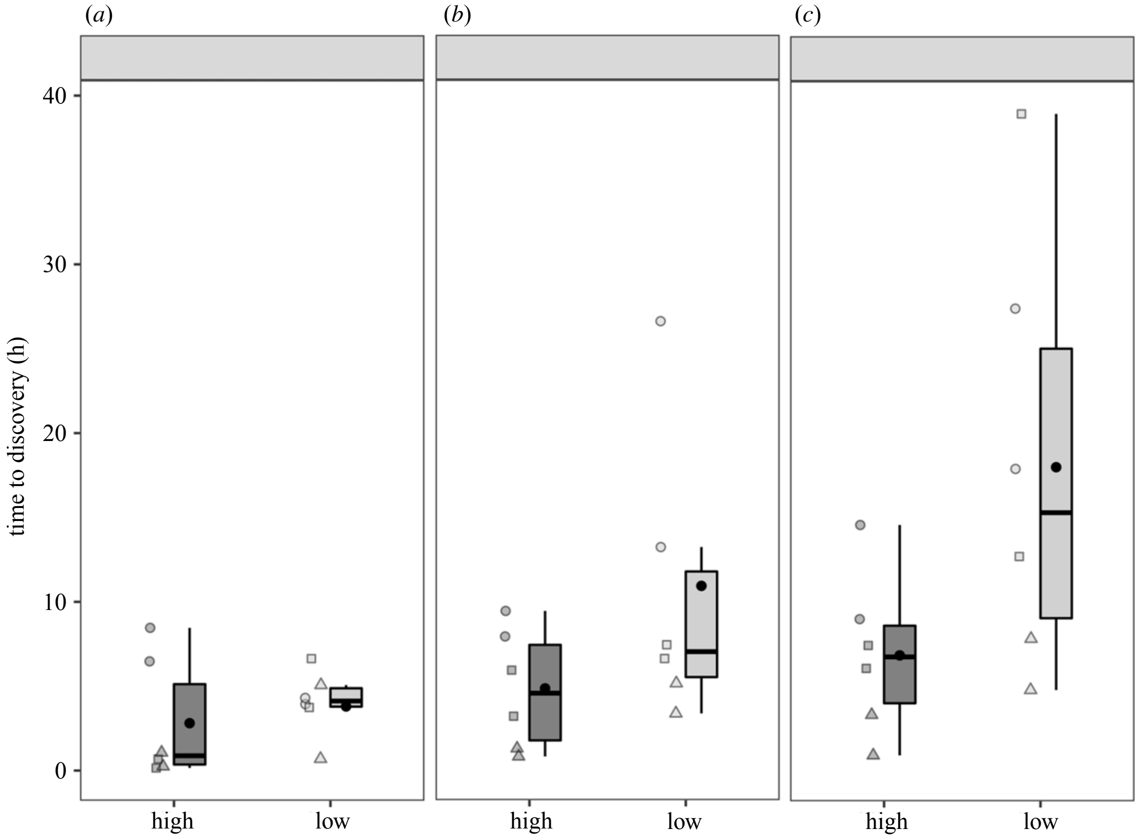

Figure 1. Time elapsed between feeder placement and the first recorded visit at that feeder, separated by whether the feeder was the first (*a*), second (*b*) or third (*c*) feeder discovered within its patch. The horizontal line in the boxplot indicates median time, boxes represent 25% and 75% interquartile ranges and whiskers show the largest and smallest values within 1.5 times the interquartile ranges. Points within the boxplots indicate model means (symbols represent replicates).

main effect of either elevation ($F_{1,30} = 0.724$, $p = 0.401$) or discovery order ($F_{1,30} = 1.66$, $p = 0.207$). There was also a significant main effect of replicate (ANOVA: $F_{1,31} = 18.465$, $p < 0.001$). Tukey post hoc analyses revealed that there were no significant differences between elevations in the time to discovery of the first ($t_{30} = -0.341$, $p = 0.99$) or second ($p = 0.521$) feeders, but birds at high elevation discovered the third ($t_{30} = -3.83$, $p = 0.007$) feeder in each patch significantly faster than low elevation birds (figure 1).

When we analysed the time to feeder discovery for each individual, there was a significant interaction between elevation and discovery order (whether the feeder was the first, second or third discovered by each individual) (GLMM: $F_{1,742.22} = 3.87$, $p < 0.049$). Additionally, we found significant main effects of discovery order (GLMM: $F_{1,742.22} = 63.65$, $p < 0.001$) and replicate ($F_{1815.68} = 60.54$, $p < 0.001$). There were no significant main effects of elevation ($F_{1,728.07} = 0.204$, $p = 0.652$), spatial learning and memory score ($F_{1,136.56} = 0.02$, $p = 0.963$), or spatial reversal score ($F_{1,158.34} = 0.06$, $p = 0.805$), as well as no significant interactions between these terms (all $p > 0.1$). Post hoc analyses showed that there were no significant differences between elevations in the time birds took to discover their first feeder ($p = 0.31$), but chickadees at high elevation were significantly faster than chickadees at low elevation to discover their second ($p = 0.007$) and third feeders ($p = 0.066$; electronic supplementary material, figure S4).

(c) Number of feeders discovered

When we examined the number of feeders found at each elevation, we found a significant interaction between elevation and replicate ($\chi^2_2 = 36.14$, $p < 0.001$), and a significant main effect of replicate ($\chi^2_2 = 70.04$, $p < 0.001$). *Post hoc* comparisons showed that high elevation birds were significantly more likely to discover more feeders during the last replicate ($p < 0.001$). There was no significant association with reversal spatial cognitive ability ($\chi^2_1 = 0.348$, $p = 0.555$) and the interaction between reversal spatial cognitive ability and elevation was not significant ($\chi^2_2 = 2.908$, $p = 0.088$). Finally, when we tested for differences between elevations in the probability of discovering all three feeders during each replicate, high elevation birds were more likely to discover all three feeders (elevation: $\chi^2_1 = 17.370$, $p < 0.001$), and birds were more likely to discover all three feeders in later replicates (replicate: $\chi^2_2 = 22.054$, $p < 0.001$). There was also a significant elevation by replicate interaction ($\chi^2_2 = 20.405$, $p < 0.001$), while the effect of reversal spatial learning ability was not statistically significant ($\chi^2_1 = 0.1263$, $p = 0.722$) and neither were interactions between elevation and reversal spatial learning ability ($\chi^2_1 = 1.886$, $p = 0.167$) or between replicate and reversal spatial learning ability ($\chi^2_2 = 2.826$, $p = 0.243$). Spatial learning and memory ability was not significant in any of these analyses (electronic supplementary material, table S3).

(d) Model simulations

At both high and low elevation, new arrivals to feeders were more connected to knowledgeable individuals than predicted by the null model of random arrival order (electronic supplementary material, figure S5). At low elevation, new arrivals were more connected to knowledgeable individuals than predicted by the affiliate model, which simulated a network-driven order of discovery. By contrast, at high

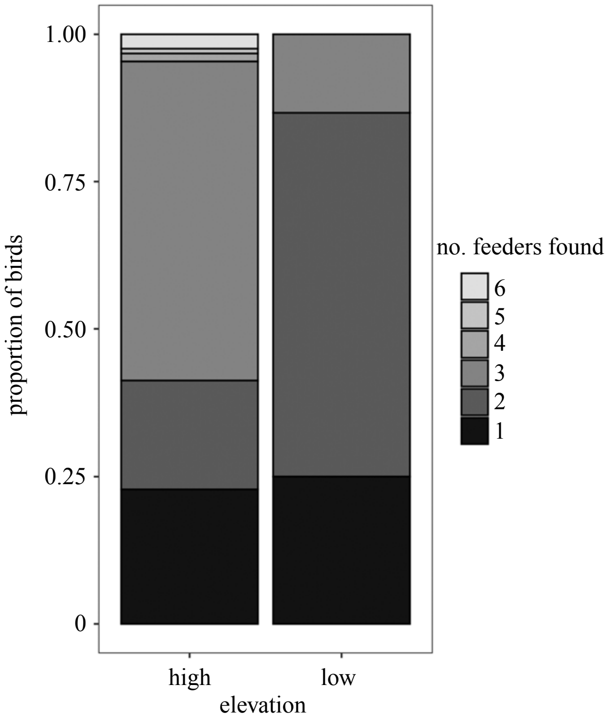

Figure 2. The proportion of individuals that found a given number of the novel feeders at high and low elevations. The majority of the birds at low elevation found two novel feeders per replicate, while more birds at high elevation found three feeders.

elevation, new arrivals were less connected to knowledgeable individuals than predicted by the affiliate model, but slightly more connected than predicted by the random discovery model. At both elevations, standard deviations for the affiliate and random models using existing social networks had substantial overlap, and our observed values fell within the region covered by both models (electronic supplementary material, figure S5).

4. Discussion

Chickadees at harsher high elevation were faster at discovering multiple novel food sources, discovered more novel feeders within each patch and were less reliant on social learning to discover these feeders than birds at low elevation. Our data support social learning along the network edges, as the NBDA with a homogeneous network did not fit the data as well as the observed network. Spatial cognitive flexibility (estimated across both elevations in one model), but not spatial learning and memory ability, was negatively associated with the discovery of multiple novel feeders when controlling for social learning. Thus, birds with worse reversal spatial cognitive performance were faster at discovering novel feeders. Our simulations based on separate high and low elevation networks were aligned with our observed results—at high elevation, observations were less consistent with predictions based on birds using social learning to discover novel feeders suggesting less use of social information.

The rate of initial discovery of the patch was similar at both elevations, suggesting similar motivation to search for feeders, but chickadees at high elevation discovered subsequent feeders in each patch significantly faster. Furthermore, most individuals at low elevation only discovered one or two novel feeders within a patch while most individuals at high elevation discovered all three, and some even discovered all six feeders. These data support our predictions that chickadees at high elevation continued searching for food even after they had already discovered a food source. Combined with our findings that birds rely less on social learning at high elevations, these results suggest that individual learning is more important for birds living in harsher environments. If high-elevation birds relied more on social learning, it might interfere with discovering alternative food sources and gaining new information, which are essential when winter conditions are severe and natural food sources are ephemeral.

Previous work with closely related black-capped chickadees [39] suggested that the distance between feeders may influence aspects of social network measurements, though probably not the overall network structure. Our conclusions rely on the assumption that networks in chickadees remain stable over time [33] following movements of the novel feeders. The network structure we used was measured immediately prior to the introduction of novel feeders at permanent feeder arrays. Even though we only used 4 days prior to novel feeder manipulations to construct the network, these arrays had been consistently used by chickadees for over a month prior to our measurements and so we think our network measurements provided a reliable snapshot of the birds' network. Considering that (i) chickadees are highly resident birds with a stable social group structure [33], (ii) we maintained consistent spacing between novel feeders and (iii) the novel feeder treatments were relatively short in duration between replicates (5 days versus 14 days in the black-capped chickadee study [39]), we assume that our novel feeder treatment was unlikely to trigger significant changes in the existing social network. Nevertheless, it remains possible that our manipulation of novel feeders might have resulted in some network changes, and these potential changes could differ between elevations, which could have affected our results in later replicates.

While chickadees at low elevation seemed to reduce feeder use in some years, which we hypothesize is due to pine seed production, in other years, including the year of this study, they consistently visit the feeders throughout the winter. Hypothetically, lower reliance on feeders at low elevation may also explain our differences between elevations, but we think it is unlikely because (i) time to discover the first feeder in all replicates was similar between elevations, suggesting similar motivation to search for food; (ii) compared to high elevation, adults at low elevation show higher overwinter mortality [48]. Higher adult survival but lower juvenile survival at high elevations is likely associated with stronger selection pressures on spatial cognition associated with food caching, so only the juveniles with the best cognitive abilities survive their first winter [49]. While we predicted that both spatial learning and memory ability and reversal spatial ability should be associated with the rate of novel food discovery, we only detected a significant relationship with spatial cognitive flexibility. Better spatial cognitive flexibility performance was associated with slower novel food discovery. Unlike spatial learning and memory ability, which is likely involved in relatively stable memory associated with food caching and cache recovery [28,30], reversal spatial ability reflects how well birds can learn and remember rapidly changing spatial information—knowing when older spatial associations should be forgotten while simultaneously learning new associations. In some cases, these two abilities appear to show a tradeoff [28]. Our result suggests that birds that are better at learning and remembering rapidly changing locations of ephemeral food can afford to be more conservative in searching for new food sources. Separate independent analyses showed no significant effects of reversal spatial ability on the time to discover new feeders or on the number of feeders discovered. This result is not surprising as these models could not control for the effect of social learning on novel feeder discovery. If social learning and cognitive flexibility are confounded, analyses that only use one of these measurements cannot distinguish between them. Birds that are worse at tracking changing spatial locations of food sources may benefit from relying on social learning and continuous exploration instead, allowing them to quickly discover new food sources.

We think that social learning did not affect our initial measurement of reversal spatial ability because birds were assigned to their initial feeders randomly rather than as existing social groups. Later, we reassigned birds previously assigned to the same feeder to different feeders, further removing opportunities for social information [19,24,30]. In fact, we previously found that if birds were reassigned between initial and reversal feeders as a group, their performance was no different from birds reassigned to different feeders (B.R.S. & V.V.P. 2019, unpublished data). Most importantly, the analyses of errors made during the reversal task showed that poorer performers made errors to the previously rewarded location [30], suggesting that birds indeed rely on their individual cognitive abilities in this task.

We detected no significant effect of age on novel feeder discovery even though it may be expected that juvenile birds, which are always socially subordinate, should experience a more unpredictable environment. A recent meta-analysis also reported no significant association between age and social learning [50]. While Penndorf & Aplin [50] identified some environmental and life-history features associated with social learning, our experiment points to another critical variable—environmental unpredictability and severity. We found that even in the same species on a small spatial scale, individuals experiencing harsher winter conditions had lower reliance on social learning. This is likely a direct behavioural response to immediate environmental conditions [10], but it remains possible that elevation-related differences in social learning may be affected by selection, similar to selection on spatial cognitive abilities, as chickadees do not move across elevations [19,27]. Social dominance status is also known to be associated with novel food discovery in black-capped chickadees [51], but, unfortunately, we were not able to measure dominance status in this experiment. Most importantly, while adding dominance status would have provided more refined results in relation to individual characteristics, it is unlikely to affect our overall conclusions associated with elevations and spatial cognition.

Overall, our study supported our predictions that reliance on social learning is associated with environmental harshness and unpredictability. Greater reliance on social learning in harsher environments may be detrimental by reducing the probability of discovering numerous and ephemeral food sources. Variation in reversal spatial cognitive ability adds another component associated with individual environmental uncertainty, such that individuals with worse reversal spatial cognitive abilities seem to benefit from more active searching associated with the discovery of novel food sources.

Ethics. All research was approved by the University of Nevada Reno IACUC (protocol00818) and followed local and federal guidelines (California Department of Fish and Wildlife Permit D-0011776516-4).

Data accessibility. All data supporting this article are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.s1rn8pk74 [52]. Analysis code has been made available as part of the electronic supplementary material.

NBDA V1.2.15 code is available in the electronic supplementary material for [40]. All other codes supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. V.K.H.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing-original draft and writing-review and editing; A.M.P.: conceptualization, funding acquisition, investigation, methodology and writing-review and editing; B.R.S.: conceptualization, investigation, methodology and writing-review and editing; L.M.B.: conceptualization, investigation, methodology and writing-review and editing; E.S.B.: resources, software and writing-review and editing; D.R.F.: conceptualization, data curation, formal analysis, funding acquisition, methodology, validation and writing-review and editing; V.V.P.: conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, supervision, validation, visualization, writing-original draft and writing-review and editing

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Competing interests. We declare we have no competing interests.

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References

1. Heyes C. 1994 Social learning in animals: categories and mechanisms. *Biol. Rev. Camb. Phil. Soc.* **69**, 207–231. (doi:10.1111/j.1469-185X.1994.tb01506.x)
2. Dall SRX, Giraldeau LA, Olsson O, McNamara JM, Stephens DW. 2005 Information and its use by animals in evolutionary ecology. *Trends Ecol. Evol.* **20**, 187–193. (doi:10.1016/j.tree.2005.01.010)
3. Szymkowiak J, Thomson RL, Kuczynski L. 2017 Interspecific social information use in habitat selection decisions among migrant songbirds. *Behav. Ecol.* **28**, 767–775. (doi:10.1093/beheco/arx029)
4. White DJ. 2004 Influences of social learning on mate-choice decisions. *Learn. Behav.* **32**, 105–113. (doi:10.3758/BF03196011)
5. Jones BC, DuVal EH. 2019 Mechanisms of social influence: a meta-analysis of the effects of social information on female mate choice decisions. *Front. Ecol. Evol.* **7**, 1–14. (doi:10.3389/fevo.2019.00390)
6. Tóth Z, Tuliozi B, Baldan D, Hoi H, Griggio M. 2017 The effect of social connections on the discovery of multiple hidden food patches in a bird species. *Sci. Rep.* **7**, 1–9. (doi:10.1038/s41598-016-0028-x)
7. Webster MM, Atton N, Hoppitt WJE, Laland KN. 2013 Environmental complexity influences association network structure and network-based diffusion of foraging information in fish shoals. *Am. Nat.* **181**, 235–244. (doi:10.1086/668825)
8. Aplin LM, Farine DR, Morand-Ferron J, Sheldon BC. 2012 Social networks predict patch discovery in a wild population of songbirds. *Proc. R. Soc. B* **279**, 4199–4205. (doi:10.1098/rspb.2012.1591)

9. Giraldeau L-AL-A, Valone TJ, Templeton JJ. 2002 Potential disadvantages of using socially acquired information. *Phil. Trans. R. Soc. Lond. B* **357**, 1559–1566. (doi:10.1098/rstb.2002.1065)
10. Kendal RL, Coolen I, van Bergen Y, Laland KN. 2005 Trade-offs in the adaptive use of social and asocial learning. *Adv. Study Behav.* **35**, 333–379. (doi:10.1016/S0065-3454(05)35008-X)
11. Galef BG. 2009 Strategies for social learning: testing predictions from formal theory. In *Advances in the study of behavior*, pp. 117–151. Amsterdam, The Netherlands: Elsevier.
12. Laland KN. 2004 Social learning strategies. *Learn. Behav. Psych. Soc. Publ.* **32**, 4–14.
13. Smolla M, Tucker Gilman R, Galla T, Shultz S. 2015 Competition for resources can explain patterns of social and individual learning in nature. *Proc. R. Soc. B* **282**, 1815. (doi:10.1098/rspb.2015.1405)
14. Boyd R, Richerson PJ. 1988 An evolutionary model of social learning: the effects of spatial and temporal variation. In *Social learning: psychological and biological perspectives* (eds TR Zentall, BG Galef), pp. 29–48. Hillsdale, NJ: Lawrence Erlbaum.
15. Aoki K, Feldman MW. 2014 Evolution of learning strategies in temporally and spatially variable environments: a review of theory. *Theor. Pop. Biol.* **91**, 3–19. (doi:10.1016/j.tpb.2013.10.004)
16. Sasaki T, Janssen MA, Shaffer Z, Pratt SC. 2016 Exploration of unpredictable environments by networked groups. *Curr. Zool.* **62**, 207–214. (doi:10.1093/cz/zow052)
17. Schürch R, Gruťer C. 2014 Dancing bees improve colony foraging success as long-term benefits outweigh short-term costs. *PLoS ONE* **9**, e104660. (doi:10.1371/journal.pone.0104660)
18. Pravosudov VV, Roth TC. 2013 Cognitive ecology of food hoarding: the evolution of spatial memory and the hippocampus. *Ann. Rev. Ecol. Evol. Syst.* **44**, 173–193. (doi:10.1146/annurev-ecolsys-110512-135904)
19. Sonnenberg BR, Branch CL, Pitera AM, Bridge E, Pravosudov VV. 2019 Natural selection and spatial cognition in wild food-caching mountain chickadees. *Curr. Biol.* **29**, 670–676. (doi:10.1016/j.cub.2019.01.006)
20. Dally JM, Clayton NS, Emery NJ. 2006 The behaviour and evolution of cache protection and pilferage. *Anim. Behav.* **72**, 13–23. (doi:10.1016/j.anbehav.2005.08.020)
21. Pravosudov VV. 2008 Mountain chickadees discriminate between potential cache pilferers and non-pilferers. *Proc. R. Soc. B* **275**, 55–61. (doi:10.1098/rspb.2007.1281)
22. Jones TB, Aplin LM, Devost I, Morand-Ferron J. 2017 Individual and ecological determinants of social information transmission in the wild. *Anim. Behav.* **129**, 93–101. (doi:10.1016/j.anbehav.2017.05.011)
23. Farine DR, Aplin LM, Garroway CJ, Mann RP, Sheldon BC. 2014 Collective decision making and social interaction rules in mixed-species flocks of songbirds. *Anim. Behav.* **95**, 173–182. (doi:10.1016/j.anbehav.2014.07.008)
24. Croston R *et al.* 2017 Predictably harsh environment is associated with reduced cognitive flexibility in wild food-caching mountain chickadees. *Anim. Behav.* **123**, 139–149. (doi:10.1016/j.anbehav.2016.10.004)
25. Pitera AM, Branch CL, Bridge ES, Pravosudov VV. 2018 Daily foraging routines in food-caching mountain chickadees are associated with variation in environmental harshness. *Anim. Behav.* **143**, 93–104. (doi:10.1016/j.anbehav.2018.07.011)
26. Kozlovsky DY, Branch CL, Pitera AM, Pravosudov VV. 2018 Fluctuations in annual climatic extremes are associated with reproductive variation in resident mountain chickadees. *R. Soc. Open Sci.* **5**, 171604.
27. Freas CA, LaDage LD, Roth TC, Pravosudov VV. 2012 Elevation-related differences in memory and the hippocampus in mountain chickadees, *Poecile gambeli*. *Anim. Behav.* **84**, 121–127. (doi:10.1016/j.anbehav.2012.04.018)
28. Tello-Ramos MC, Branch CL, Kozlovsky DY, Pitera AM, Pravosudov VV. 2019 Spatial memory and cognitive flexibility trade-offs: to be or not to be flexible, that is the question. *Anim. Behav.* **147**, 129–136. (doi:10.1016/j.anbehav.2018.02.019)
29. Croston R, Kozlovsky DY, Branch CL, Parchman TL, Bridge ES, Pravosudov VV. 2015 Individual variation in spatial memory performance in wild mountain chickadees from different elevations. *Anim. Behav.* **111**, 225–234. (doi:10.1016/j.anbehav.2015.10.015)
30. Tello-Ramos MC, Branch CL, Pitera AM, Kozlovsky DY, Bridge ES, Pravosudov VV. 2018 Memory in wild mountain chickadees from different elevations: comparing first-year birds with older survivors. *Anim. Behav.* **137**, 149–160. (doi:10.1016/j.anbehav.2017.12.019)
31. Pyle P. 1997 *Identification guide to North American birds, part I: Columbidae to Ploceidae*. Point Reyes Station, CA: Slate Creek Press.
32. Bridge ES *et al.* 2019 An arduino-based RFID platform for animal research. *Front. Ecol. Evol.* **7**, 1–10. (doi:10.3389/fevo.2019.00257)
33. Ekman J. 1989 Ecology of non-breeding social systems of Parus. *Wilson Bull.* **101**, 263–288.
34. Franks DW, Ruxton GD, James R. 2010 Sampling animal association networks with the gambit of the group. *Beh. Ecol. Sociobiol.* **64**, 493–503. (doi:10.1007/s00265-009-0865-8)
35. Farine DR. 2013 Animal social network inference and permutations for ecologists in R using asnipe. *Methods Ecol. Evol.* **4**, 1187–1194. (doi:10.1111/2041-210X.12121)
36. R Core Team. 2020 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See https://www.r-project.org/.
37. Ferreira AC *et al*. 2020 How to make methodological decisions when inferring social networks. *Ecol. Evol.* **10**, 9132–9143. (doi:10.1002/ece3.6568)
38. Hoppitt WJE, Farine DR. 2018 Association indices for quantifying social relationships: how to deal with missing observations of individuals or groups. *Anim. Behav.* **136**, 227–238. (doi:10.1016/j.anbehav.2017.08.029)
39. Evans JC, Morand-Ferron J. 2019 The importance of preferential associations and group cohesion: constraint or optimality. *Beh. Ecol. Sociobiol.* **73**, 1–10. (doi:10.1007/s00265-019-2723-7)
40. Wild S, Hoppitt W. 2019 Choosing a sensible cut-off point: assessing the impact of uncertainty in a social network on the performance of NBDA. *Primates* **60**, 307–315. (doi:10.1007/s10329-018-0693-4)
41. Franz M, Nunn CL. 2009 Network-based diffusion analysis: a new method for detecting social learning. *Proc. R. Soc. B* **276**, 1829–1836. (doi:10.1098/rspb.2008.1824)
42. Hoppitt W, Boogert NJ, Laland KN. 2010 Detecting social transmission in networks. *J. Theor. Biol.* **263**, 544–555. (doi:10.1016/j.jtbi.2010.01.004)
43. Hoppitt W. 2017 The conceptual foundations of network-based diffusion analysis: choosing networks and interpreting results. *Phil. Trans. R. Soc. B* **372**, 20160418. (doi:10.1098/rstb.2016.0418)
44. Harrison XA *et al.* 2018 A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ* **2018**, 1–32. (doi:10.7287/peerj.preprints.3113v2)
45. Bates D, Mächler M, Bolker B, Walker S. 2015 Fitting linear mixed-effects models using {lme4}. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss.v067.i01)
46. Kuznetsova A, Brockhoff PB, Christensen RHB. 2017 {lmerTest} Package: tests in linear mixed effects models. *J. Stat. Softw.* **82**, 1–26. (doi:10.18637/jss.v082.i13)
47. Hillemann F, Cole EF, Sheldon BC, Farine DR. 2020 Information use in foraging flocks of songbirds: no evidence for social transmission of patch quality. *Anim. Behav.* **165**, 35–41. (doi:10.1016/j.anbehav.2020.04.024)
48. Benedict LM *et al.* 2020 Elevation-related differences in annual survival of adult food-caching mountain chickadees are consistent with natural selection on spatial cognition. *Behav. Ecol. Sociobiol.* **74**, 40. (doi:10.1007/s00265-020-2817-2)
49. Firth JA, Sheldon BC, Farine DR. 2016 Pathways of information transmission among wild songbirds follow experimentally imposed changes in social foraging structure. *Biol. Lett.* **12**, 20160144. (doi:10.1098/rsbl.2016.0144)
50. Penndorf J, Aplin L. 2020 Environmental and life history factors, but not age, influence social learning about food: a meta-analysis. *Anim. Behav.* **167**, 161–176. (doi:10.1016/j.anbehav.2020.07.001)
51. Evans JC, Jones TB, Morand-Ferron J. 2018 Dominance and the initiation of group feeding events: the modifying effect of sociality. *Behav. Ecol.* **29**, 448–458. (doi:10.1093/beheco/arx194)
52. Heinen VK, Pitera AM, Sonnenberg BR, Benedict LM, Bridge ES, Farine DR, Pravosudov VV. 2021 Data from: Food discovery is associated with different reliance on social learning and lower cognitive flexibility across environments in a food-caching bird. Dryad Digital Repository. (doi:10.5061/dryad.s1rn8pk74)