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Information maintenance of food sources is associated with environment, spatial cognition and age in a food-caching bird

Lauren M. Benedict [a], *, Angela M. Pitera [a], Carrie L. Branch [a, b], Benjamin R. Sonnenberg [a], Virginia K. Heinen [a], Eli S. Bridge [c], Vladimir V. Pravosudov [a]

[a] *Department of Biology, University of Nevada Reno, Reno, NV, USA*
[b] *Cornell Lab of Ornithology, Cornell University, Ithaca, NY, USA*
[c] *University of Oklahoma, Oklahoma Biological Survey, Norman, OK, USA*

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Traditionally, exploration and exploitation of resources have been viewed as mutually exclusive behaviours in which animals can either allocate time to gathering information or to using known resources. But these behaviours can also be viewed as opposite ends of a continuum, with intermediate behaviours that balance exploration and exploitation, such as information maintenance. Updating previously acquired information through information maintenance can allow animals in unpredictable environments to track changing environmental conditions. Theoretical studies predict that the degree of involvement in information maintenance should depend on environmental predictability – when the overall environment is less predictable, animals should update previously acquired information more frequently because such information is less certain and could change quickly. We tested this hypothesis by allowing wild food-caching mountain chickadees, *Poecile gambeli*, to visit and sample multiple feeders with temporarily stable, unlimited food for five consecutive winters. We used an index of feeder use breadth to explore how feeder visits across multiple feeders varied with environmental conditions. Each feeder visit is associated with information updating, and more information maintenance should be associated with distributing more visits across more feeders. While controlling for the total number of visits by each individual, we found that (1) chickadees redistributed feeder use among more feeders when environmental conditions were harsh and unpredictable, (2) juveniles had a higher feeder use breadth than adults, and individuals reduced their feeder use breadth as they aged, (3) better spatial learning and memory ability but not spatial cognitive flexibility was associated with smaller feeder use breadth and (4) learning associated with decreased food availability reduced subsequent feeder use breadth. Our data supported our predictions that factors affecting the predictability of resource information (environmental conditions and individual characteristics such as cognition and age) affect how individuals engage in information maintenance.

Many animals live in variable and heterogeneous environments: weather conditions, predator densities, food sources and mate quality can all vary with space and time and change rapidly. Such environmental variation creates a constantly shifting information landscape in which an individual's certainty in the state of their surroundings progressively diminishes as information becomes outdated (Dall et al., 2005). The consequences of making decisions based on outdated information could range from mild (e.g. wasted energy foraging) to disastrous (e.g. starvation as a result of poor anticipation of future resource distributions; Shettleworth et al., 1988). However, gathering entirely new information can be costly, as many exploratory behaviours take time and energy that cannot be spent exploiting resources (Berger-Tal et al., 2014). To balance the costs of pure exploration and pure exploitation, animals rely on learning and memory abilities as well as information updating behaviours (Berger-Tal et al., 2014; Stephens & Dunlap, 2017).

Information updating behaviours (also known as information or knowledge maintenance) allow an individual to relearn or update part of their existing knowledge. Within the exploration–exploitation continuum, information updating is an intermediate phase in which individuals both exploit resources and keep a constant, optimal level of up-to-date knowledge through directed

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* Corresponding author.
E-mail address: lbenedict@nevada.unr.edu (L. M. Benedict).

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learning behaviours, such as sampling (Berger-Tal et al., 2014). Sampling refers to repeated visits or observations that allow an individual to update information (Dunlap et al., 2017; Krebs et al., 1978; Krebs & Inman, 1992; Shettleworth et al., 1988; Tamm, 1987). For example, females often have incomplete information about the quality of potential mates and will repeatedly visit specific males (i.e. they will sample males) to better assess mate quality before selecting a mate (Luttbeg, 1996). In a foraging context, sampling is often observed when an individual is presented with multiple food sources: first, the animal explores the available sources, then repeatedly visits each source to determine quality and consistency (e.g. Dunlap et al., 2017; Lima, 1984). If an individual stops visiting multiple sources and only forages from one, it has moved from the information updating phase to the pure exploitation phase.

The major conceptual and still debated question is when and how often animals should sample their environment to update previously learned information (Dunlap et al., 2017). Bayesian foraging hypotheses suggest that the decision-making process resembles Bayesian updating (Valone, 2006). Suppose an individual has some previous experience and knowledge of the distribution of resource quality in an area obtained through exploration or knowledge acquisition (the prior distribution). The individual can update specific aspects of this knowledge that may be incomplete or outdated via sampling until it more closely resembles the true distribution of resource quality (posterior distribution). This updated knowledge can then be used to decide whether it is worthwhile to continue foraging in the current area or sample elsewhere (Dall et al., 2005; McNamara et al., 2006; Iwasa et al., 1981; Valone, 2006). The individual should only choose to update that information if the value of the information gained is greater than the cost of sampling to obtain or to maintain the information (Dall et al., 2005). Oversampling could be costly in terms of physical effort and lost opportunities for other activities while undersampling could lead to missing critical environmental changes or making poor choices about which resources to prioritize (Dunlap et al., 2017; Shettleworth et al., 1988).

But how do animals assess the value of updated information and determine how often to sample? During the information maintenance phase, continuous updating of previously acquired information is expected to be strongly affected by temporal unpredictability of the environment (Berger-Tal et al., 2014). When the environment is more predictable, there should be less of a need to constantly maintain fully updated information because the individual's prior knowledge is sufficient to predict the environment; the future value of the updated information would be low. On the other hand, when the environment is relatively unpredictable, maintaining existing information would be extremely beneficial and sampling could allow individuals to maintain the most current information about resources to use (Stephens, 1989). Similarly, we have argued that environmental harshness may also affect the cost–benefit analysis of information maintenance: for example, in harsh environments, the costs of not finding food might be higher due to greater caloric requirements or greater risk of starvation (Heinen et al., 2021; Pitera et al., 2018). Animals would be expected to update information more when conditions are both unpredictable and harsh, as it is more critical to know where food is available in case one food source fails. However, there is little work testing predictions about when animals should shift along the exploration, information maintenance and exploitation continuum. Furthermore, environmental predictability consists of multiple components, including food availability and quality, frequency of storms and weather conditions such as temperature and precipitation patterns. But while some information maintenance studies manipulate environmental predictability via food quality and availability (e.g. Dunlap et al., 2017; Katz & Naug, 2015), few explore how the overall unpredictability and harshness of environmental conditions may affect information updating behaviours.

Here, we tested predictions that information maintenance is a function of the overall environmental uncertainty and harshness in a wild food-caching bird, the mountain chickadee, *Poecile gambeli*. We define a harsh environment as simultaneously unpredictable and metabolically demanding (Croston et al., 2016, 2017; Heinen et al., 2021). High metabolic demands can amplify the negative effects associated with temporal unpredictability by increasing the costs of failing to meet these demands (Heinen et al., 2021). In our study system, winter conditions include lower ambient temperatures (increasing metabolic demands) and more frequent and severe snowstorms that can interrupt foraging (making the environment less predictable; Heinen et al., 2021; Pitera et al., 2018). We thus use snow depth as a proxy for the frequency and severity of winter storms. More severe winter conditions are also usually associated with more unpredictable food supply. Our previous data on daily foraging routines of chickadees during the winter fully supported theoretical predictions based on environmental unpredictability (Pitera et al., 2018). Testing predictions based on the overall environmental conditions in the laboratory presents major logistical challenges, as it is difficult to manipulate the prevailing environmental conditions without altering the testing paradigm (availability and variability of food). We conducted our study in wild birds in their natural environment, keeping the experimental foraging locations temporarily stable while evaluating engagement in information maintenance under different environmental conditions (e.g. climate-related variables). We use the term ‘temporarily stable’ because foraging locations provided consistent quality and amount of food for the duration of the experiment each year (weeks) but not for the entire winter season (months). This approach, however, can only provide correlative support to the hypothesis as it is impossible to experimentally manipulate the overall environment.

Mountain chickadees are an excellent species to explore information maintenance within a foraging context because they forage for food items one at a time. When presented with a supplemental feeder, they will retrieve one food item for each visit to the feeder before leaving to eat or cache the food in a different location. Thus, each visit is associated with information acquisition, updating and exploitation, especially if visual access to the food within each feeder is only available through visits, as it is in our system. Each visit to a previously visited feeder (i.e. after birds first discover the feeders through exploration) is then considered information maintenance because it results in information updating about the food status in that feeder.

We predicted that birds should continue visiting multiple previously visited food sources, even when these sources are temporarily stable, to maintain the most updated information about each in case one fails. More frequent information updating should increase information reliability; the more frequently a bird visits each previously discovered food source, the more certain that bird will be that the food source continues to provide food. Such information maintenance should depend on the overall environmental conditions: if the probability of finding new food sources is low (i.e. in unpredictable environments) or if the consequences of not finding food quickly are high (i.e. starvation in harsh environments; Lima, 1986; Pravosudov & Grubb, 1997; Pitera et al., 2018), then the value of up-to-date information on food sources should be high and birds should engage more in information maintenance (Berger-Tal et al., 2014). Conversely, if the environment is comparatively mild and predictable, the value of constantly updating information will be lower and animals should engage in information maintenance less, as there are fewer missed opportunities to forage (i.e. fewer storms) and such opportunities are less costly (i.e. lower metabolic needs).

Traditional sampling theory predicts that birds should stop sampling when food is stable (Stephens, 1989). However, Stephens (1989) argued that decisions to sample temporarily stable food sources should depend on the future value of the gained information, which is in agreement with Berger-Tal et al. (2014). Considering that the feeders in this study provided stable food only temporarily, individuals could evaluate the stability of their environment based on the overall environmental conditions. Chickadees do not rely on feeders as the only food source and likely use thousands of naturally available food sources. If the overall environmental conditions are unpredictable and harsh, the future value of sampled information even at the temporarily stable food sources would be high and birds should continuously update such information (Berger-Tal et al., 2014; Stephens, 1989). Thus, in our study, we refer to the overall winter environment and not to the local feeder conditions, as we predicted that birds would base their foraging decisions on the overall environment.

Individual characteristics such as cognitive abilities and age-related experience may also affect environmental certainty and hence information updating behaviour. Better learning and memory abilities likely increase environmental predictability, as the individual can rely on these abilities to find previously made food caches and to learn and remember more naturally available food sources (Dunlap & Stephens, 2012; Pitera et al., 2018). Food-caching species, in particular, have evolved food-caching behaviour as a strategy to compensate for environmental harshness and unpredictability, but they rely on spatial cognitive abilities to access their caches (Pravosudov & Roth, 2013). Similarly, age should be associated with more experience and might allow older individuals to fine-tune their responses to environmental cues and better predict changing environmental conditions. This would likely result in less need to keep updating previously acquired information for older, more experienced individuals.

We tested these hypotheses using 5 years of data from our long-term field system of food-caching mountain chickadees in the northern Sierra Nevada. Birds at higher elevations in our system experience harsher and less predictable winter conditions and have better spatial cognitive abilities associated with greater reliance on stored food to survive winter than birds at milder, more predictable lower elevations (Croston et al., 2016, 2017; Freas et al., 2012). There is large variation in winter environment across years. In this system, chickadees use multiple supplemental food sources (arranged in feeder arrays) that are temporarily stable (i.e. food quality and availability are constant within the data collection period, but not within the entire season or year). Visits to multiple feeders within our feeder arrays are highly variable among years and individuals, providing a convenient platform to test the following predictions: (1) individuals should distribute more visits to more feeders in order to maintain the most updated information under more severe winter conditions, whether associated with yearly variation or elevation; (2) adults should distribute visits to fewer feeders than juveniles, and individuals should distribute their visits to fewer feeders with increased age as a result of experience; (3) individuals with better spatial cognitive abilities should distribute their visits to fewer feeders than those with worse spatial cognitive abilities (Fig. 1).

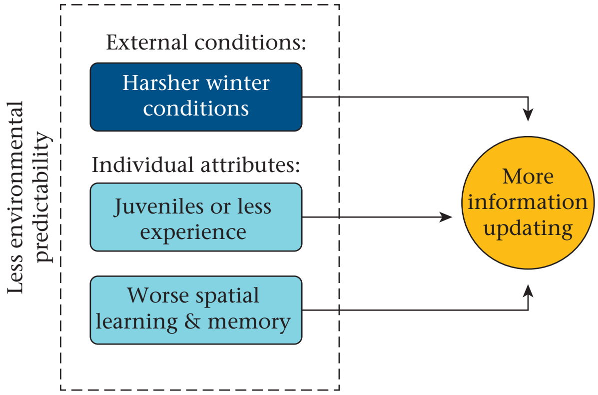

Figure 1. Predictions. Individual attributes (light blue) and environmental factors (dark blue) lead to engagement in more information maintenance/updating sampling (arrows) because they affect how predictable the environment is for each individual.

To estimate breadth of feeder visits (e.g. relative distribution of visits to multiple feeders) across the eight feeders in a given feeder array, we used a measure of niche breadth (Levins' measure; Levins, 1968). This metric provides an estimate of how each bird distributes its visits across all available feeders, from visiting one feeder exclusively (minimum feeder use breadth) to visiting each feeder an equal number of times (maximum feeder use breadth). Unlike simply recording the number of visits per feeder, which cannot describe the overall relative use of all eight feeders, the Levins' measure provides a robust measure of feeder use breadth across all available feeders.

It is important to differentiate between pure exploitation and information maintenance in this system. Exploitation of different feeders could be affected by the social environment (competition) or frequency of visits, as more visits may result in visiting more feeders. Feeders are arranged within a relatively small spatial scale (<2 m), so the costs of visiting multiple feeders are potentially low. We predicted that, if birds engage in more information maintenance rather than in pure exploitation, they should increase or decrease their feeder use breadth based on the overall environment harshness and predictability (as predicted in Berger-Tal et al., 2014) independently of the social context or the total number of visits. Considering that chickadees tend to visit one of the eight feeders more frequently than the rest (a 'preferred' feeder), we expected that birds would not visit the feeders randomly (Croston et al., 2017) and would start using other feeders more frequently when environmental conditions changed.

Theoretical models predict that age associated with life expectancy should affect the value of sampling and information maintenance (Eliassen et al., 2007). According to this hypothesis, older individuals would invest more in exploitation than exploration, as the value of both sampling to acquire new information and to update previously acquired information is less when life expectancy is shorter. We do not think this applies to our system, as the life expectancy of chickadee adults may actually be higher than that of juveniles (Benedict et al., 2020). In our system, experience associated with age is more likely to affect the exploration–exploitation continuum.

During 1 year of the study (2019–2020), we also explored whether learning associated with experimental manipulations of food availability in different feeders affected feeder use for information updating. We looked at feeder use breadth both before and after spatial cognitive testing, during which food was temporarily restricted at the feeders and individuals had to learn that only one feeder provided food while all other feeders provided no food reward. We predicted that after cognitive testing, when food availability was restored at all feeders, individuals that had previously learned that most feeders were not consistently rewarding could be expected to have reduced feeder use breadth. Specifically, better learners should distribute their visits to fewer feeders, as they would have learned that certain feeders had recently not provided food and information gained by sampling these feeders when other feeders provided food should have a lower value. In other words, we predicted individuals should distribute their visits to fewer feeders and have a smaller feeder use breadth in response to this previously learned information, regardless of current feeder status.

METHODS

Study Site

The study was conducted at our long-term mountain chickadee study system in Sagehen Experimental Forest (Sagehen Creek Field Station, University of California Berkeley) in the Sierra Nevada, 10 km north of Truckee, California, U.S.A. (Croston et al., 2016, 2017; Freas et al., 2012; Kozlovsky et al., 2018; Tello-Ramos et al., 2018). Our study system includes two primary areas that we refer to as low (1900 m) and high (2400 m) elevations. These areas differ in winter environmental harshness – at high elevations, winter conditions last longer with lower temperatures, higher and longer-lasting snow cover and more frequent and unpredictable snowfalls compared to lower elevations (Barbour & Minnich, 2000; Kozlovsky et al., 2018). We trapped chickadees annually (2014–2020) using mist nets at multiple established feeders (August–April) and at established nestboxes during the breeding season (May–July). All birds were banded with unique colour band combinations, including a passive integrated transponder (PIT) tag (IB Technology, Leicestershire, U.K.). Sex was determined by breeding status (i.e. presence of cloacal protuberance for males, brood patch for females, or visual observations of behaviour) during the breeding season and by wing length (female wing length $\leq$ 67 mm, male wing length $\geq$ 72 mm) during the nonbreeding season. Age at initial capture (‘juvenile’ or ‘hatch year’ if less than 1 year of age, ‘adult’ if at least 1 year or older) was determined during banding using multiple plumage characteristics (Meigs et al., 1983; Pyle, 1997), breeding status and our records of nestling status at the study site (nestlings banded with metal United States Geological Survey leg bands). Ages at subsequent detections were estimated from previous records.

Environmental harshness was estimated by average temperatures and snow depth (Pitera et al., 2018). Snow depth, a proxy for harshness, additionally provided an estimate of environmental predictability, as snowstorms vary in their harshness, frequency and duration, preventing birds from foraging for unpredictable amounts of time. We obtained climate data from three SNOTEL weather stations (supported by the United States Department of Agriculture's Natural Resources and Conservation USDA Natural Resources Conservation Service, 2020) located within and nearby the study system. High-elevation climate data were sourced from No. 541 – Independence Lake (ca. 2500 m). Low-elevation climate data were sourced from two stations and averaged: No. 540 – Independence Camp (ca. 2100 m) and No. 539 – Independence Creek (ca. 1950 m). We downloaded daily average temperatures and daily snow depth, using the mean values for each annual sampling period in the analyses. Daily maximum and minimum temperatures were also obtained to characterize the two elevation sites used in the study (Appendix, Fig. A1) but were not used in the final analysis. We only used climate data for the specific periods of testing each year (Appendix, Table A1).

Sampling at Feeder Arrays

Data collection for feeder use behaviour

Beginning in 2015, we collected data on feeder visits over five winter seasons (2015–2020) using radiofrequency identification (RFID)-enabled ‘smart’ feeders (Bridge & Bonter, 2011) that allowed automatic detection of all individuals with PIT tags. Feeders were arranged in spatial arrays, each consisting of eight feeders mounted equidistantly to an 122 × 122 cm frame and raised ca. 3 m above the ground using wire rope and pulley system attached to four trees, to avoid damage by squirrels and bears. Four arrays were established at the study area in 2014 (2 arrays per elevation, ca. 1.2 km apart; Croston et al., 2016). Each feeder was equipped with a battery-powered mechanical door that controlled access to the food (black oil sunflower seeds) via a programmable circuit board. Circuit boards could be programmed to one of three settings (‘modes’): (1) ‘open’ mode – feeder doors were always open and any bird could see food inside the feeders; (2) ‘all’ mode – feeder doors were closed so the food inside the feeders was not visible until a PIT-tagged bird landed on the perch (containing an antenna), opening the door and allowing that bird to access the food; (3) ‘target mode’– feeder doors were closed and would only open for specific PIT-tagged birds, such that each bird could only access food at one feeder at an array to assess spatial learning and memory (Croston et al., 2017). ‘Open’ mode was used to habituate birds to the feeders, ‘all’ mode was used to collect sampling data and ‘target’ mode was used to conduct spatial cognitive tests. During each mode, feeders recorded visiting data (bird identity (ID), date, time) for any PIT-tagged bird that landed on the feeder perch (a ‘visit’).

Annual experiments began with a habituation phase, in which feeders were set to ‘open’ mode every autumn (Appendix, Table A1) and continued at least 10 days or until a sufficient number of PIT-tagged chickadees were detected foraging from the arrays (ca. 100 per elevation). Then feeders were switched to ‘all’ mode for at least 8 days to assess relative distribution of feeder use (e.g. feeder use breadth) and collect data for information maintenance behaviour. A key aspect of this mode was that the food was accessible to every PIT-tagged bird but was not visible until a bird visited the feeder, triggering the door to open and providing access to the food. This meant that birds could only update the food status of each feeder by visiting it, allowing the ‘smart’ feeders to record the visit. So, every feeder visit can be considered as information updating. Finally, after the data collection period for information maintenance, feeders were switched to ‘target’ mode for testing spatial cognitive learning and memory and reversal spatial learning and memory (Croston et al., 2017). Food levels were maintained during ‘all’ and ‘target’ mode such that no feeders ran out of seeds during data collection.

During data collection for sampling and information maintenance, all eight feeders contained a stable and predictable food supply. However, when we discuss the harsh and unpredictable environment, we refer to the overall environment and not to the feeder set-up. Prior to the experiment, the feeders were not maintained regularly and did not present stable and predictable food sources. This, combined with the likelihood of hundreds of other natural food sources, makes it infeasible to consider that food was entirely predictable during our study. Thus, our goal was to use stable feeders in order to explore how chickadees maintain information as a function of overall environmental conditions, without the additional manipulation of food predictability.

Criteria for information maintenance behaviour

A bird was considered to be engaged in information updating ‘sampling’ when it visited feeders in an array while food was accessible but not visible (‘all’ mode). Birds had to physically visit the feeder to determine whether food was present by triggering the door to open and reveal access to the seeds. Unlike other birds that sit and eat at feeders (e.g. finches), chickadees visit feeders for no more than a few seconds, select one seed per visit and leave the array to eat or cache the seed elsewhere. This results in significantly reduced social interactions at the feeders. Chickadees are the main species using the feeders in the winter. Nuthatches sometimes visit the feeders but only when they are in the 'open' mode with seeds clearly visible and accessible. Once feeders are in 'all' mode, allowing only PIT-tagged chickadees to access the food, no other species visit the feeders. Given substantial efforts to band as many chickadees as possible, we estimate that most birds near the feeders are PIT-tagged (>90%). The untagged birds stop visiting the feeders during 'all' mode, instead foraging on the ground under the feeders.

Feeder sampling metric

We estimated relative distribution of multiple feeder use or feeder use breadth using the Levins' measure (Levins, 1968), a measure of niche breadth (B) that estimates how uniformly individuals use a given set of resources (also known as the species equivalent of the Simpson's diversity index; Jost, 2006; Simpson, 1949). In this feeder sampling context, feeder use (niche) breadth for each bird was determined from the proportion of visits to each feeder j (equation (1)) at the array.

$$\widehat{B} = \frac{1}{\sum \widehat{p}_j^2} \tag{1}$$

Levins' measures of feeder use breadth ranged from $B = 1$ (all visits to one feeder) to $B = 8$ (visits equally distributed across all 8 feeders at an array); higher values indicate higher feeder use breadth associated with more information updating. This metric was independent of the number of visits by each bird unless the bird made fewer visits than the number of resource states (i.e. fewer than 8 visits per day). Fewer than eight visits would result in an artificially lowered Levins' measure. As such, we set a minimum threshold of 64 visits for birds to be included in the study, allowing for birds to visit at least eight times per day for 8 days (Appendix, Fig. A2). This was important because this study aimed to explore how birds revisit feeders to update previously learned information. Thus, we needed to be sure that birds had the opportunity to initially explore the eight feeders before we considered their visits as information maintenance behaviour. The majority of the excluded birds visited fewer than 10 times (see Appendix, Fig. A3a for exact number of all excluded birds by year, elevation and sex and age) and our exclusions were not biased towards any sex or age group (Fig. A3b, Table A2, Table A3). In summary, the Levins' measure was selected after careful consideration (following Krebs, 2014, pp. 596–653) because it provides a continuous estimate of niche breadth on an intuitive scale, is independent of the total number of visits and it does not need to account for the abundance of resource states, which are constant for all birds in our study (i.e. 8 feeders).

To further control for different levels of participation between birds, the Levins' measure was calculated per bird per day and averaged across the number of days visited during each data collection period. The total number of visits by each bird for each annual data collection period was then included as a covariate in all models.

Low-elevation Data in 2017–2018 and 2018–2019

After setting the minimum visit threshold at 64 visits, we implemented two other exclusions. First, if a bird visited two arrays within the same season, data were excluded from the array that had fewer total visits (this affected $N = 13$ birds). Second, no data were used from 2017–2018 or 2018–2019 at low elevation because few birds visited the feeders before and during the data collection period and visits were inconsistent. This excluded $N = 4$ birds from the data set that otherwise would have fitted our 64 visit criteria.

Postcognitive Testing Data Collection

During 1 year (2019–2020), we collected data for information maintenance behaviour both before and after conducting spatial cognitive tasks, to evaluate both the effect of learning and memory ability on sampling strategies (when all feeders are stable, equal and have reliably provided food before cognitive testing) as well as the direct effect of learning new information on sampling (after some feeders stopped providing stable food for a short period during cognitive testing). To do this, the first 'precognitive testing' sampling period was collected as described above in 2019–2020. Following spatial cognitive testing, feeders were switched from 'target' mode to 'open' mode for 3 days, during which feeder doors were open, allowing birds to see food available at all feeders. Then feeders were switched to 'all' mode, during which we collected 'postcognitive testing' sampling data for 4 days following the same protocol for information maintenance data collection (Appendix, Table A1).

Spatial Cognitive Tests

Two spatial cognitive tasks were conducted annually (Appendix, Table A1). First, individuals were given a spatial learning and memory task in which each bird was assigned to only one rewarding feeder (feeders set to 'target' mode, birds assigned to specific feeders by programming 'smart' feeders to only open doors for specific PIT-tagged birds). Birds were individually and pseudorandomly assigned to a feeder that they had previously visited infrequently during data collection for sampling behaviour. For the second task, birds were given a reversal spatial learning and memory task (a proxy for cognitive flexibility, Croston et al., 2017). Each bird was reassigned to a new rewarding feeder, separating birds that had previously been assigned to the same rewarding feeder to control for the possibility of social learning (Croston et al., 2017; Tello-Ramos et al., 2018). To assess spatial learning and memory in the first task and cognitive flexibility in the second task, we used the number of unrewarding feeders visited prior to visiting the rewarding feeder (location errors) during each trial (Croston et al., 2017). Each trial started with a visit to any feeder in the array and ended with a visit to the assigned rewarding feeder. Following our previous work, we used the mean number of location errors per trial during the first 20 trials of each task separately to assess spatial learning and memory ability and cognitive flexibility (Croston et al., 2017; Sonnenberg et al., 2019; Tello-Ramos et al., 2018).

Statistical Methods

To evaluate individual sampling strategies, we fitted linear mixed effects models in R (R Core Team, 2018) using the R package 'lmerTest' (Kuznetsova et al., 2017). To control for differences in individual participation, the total number of visits per bird per data collection period was included as a fixed effect in all models with mean Levins' measure as the response variable. To evaluate possible social effects on mean Levins' measure due to other conspecifics present at the feeders, models were fitted with and without the total number of birds present at each array during the data collection period (Appendix, Table A4). To better understand the factors affecting how many times individuals visited the feeder, additional models were fitted with total number of visits per bird per data collection period as the response variable (Appendix, Figs A4–A11). All linear effects models held individual ID as a random effect. All numeric fixed effects were scaled. We did not test for every possible interaction between predictor variables, preferring to only consider the interactions that we hypothesized might strongly affect sampling behaviour.

Fixed effects used in models

To control for differences in participation among birds, all models controlled for the total number of visits per bird per year (as a fixed effect). We also controlled for the number of days a bird participated (out of 8 total days of each annual data collection period) in several models. To further ensure that our sampling data were minimally affected by social interactions at the feeders, we controlled for the number of birds present at a feeder array.

We used the same combinations of fixed effects to explore variation in Levins' measures and total number of visits for each bird. To evaluate the effects of environmental harshness, we fitted two models with the following additional fixed effects: (1) year, elevation and year*elevation interaction; (2) mean snow depth and mean daily temperatures for the period of data collection. Year was not included in models with mean environmental conditions. To evaluate the effect of age and experience, two models were fitted with the following fixed effects: (1) year, elevation, age (juvenile versus adult) and interaction effects of year*elevation, year*age, age*elevation and all three together; and (2) year, number of years sampled (first, second, etc.; i.e. increasing age) and cohort (the first year a bird was observed sampling in our system, e.g. 2015–2016, 2016–2017). The second model was fitted to the subset of data that only included birds that had sampled during at least 2 years of the study (Appendix, Table A5). To evaluate whether social dominance might explain age-related differences in sampling breadth, we fitted a model with year, elevation, sex (male versus female), age (juvenile versus adult) and interaction effects of year*elevation and age*sex. There is strong evidence in Paridae species for a linear social hierarchy that follows sex and age (adult male > adult female > juvenile male > juvenile female; Dixon, 1965; Ekman, 1989, 1990; Gentle & Gosler, 2000) and thus support for an age*sex interaction effect would support social dominance as an explanation for variation in sampling breadth. To evaluate spatial cognition, models were fitted with either spatial learning and memory ability or cognitive flexibility (mean errors per trial during the first 20 trials) as fixed effects. Cognition scores were not averaged across years for birds that were observed in multiple years; each year's score was used for that year of sampling data. If a bird did not have both sampling and cognition data for a particular year, those data were excluded from relevant cognition models.

We evaluated feeder use after cognitive testing in 2019–2020 via linear regressions using the ‘stats’ package (R Core Team, 2018). The predictor variables for these linear regressions included total number of visits during the data collection periods for information maintenance (scaled), either spatial or reversal spatial learning and memory ability (scaled) and the total number of visits during the reversal spatial learning and memory task (scaled).

Certain data were not available for every bird; there were individuals for which we did not know sex or were not able to obtain data on cognitive ability. Thus, we ran each model with the maximum number of birds possible (Appendix, Table A5). As models used slightly different data sets, model fit was compared between models using conditional and marginal R^2 values (Nakagawa & Schielzeth, 2013) calculated using the ‘performance’ R package (Ludecke et al., 2020). Within-group comparisons were calculated using estimated marginal means and Tukey post hoc comparisons via ‘emmeans’ (Lenth, 2020). Model assumptions were evaluated by simulating residuals using the R package ‘DHARMa’ (Hartig, 2020). Model output was further evaluated using the ‘stats’ package Type III Analysis of Variance (ANOVA) tests with Satterthwaite's method. Data were visualized using ‘ggplot2’ (Wickham, 2016) and raincloud plots (Allen et al., 2019).

Ethics Note

To the best of our knowledge, no birds were harmed by the collection of these data and birds were only handled for a few minutes during banding. We detected no negative effects of using PIT tags and colour bands during our study. The study was approved by the University of Nevada Reno Institutional Animal Care and Use Committee (Protocol 00818, 00046 and 00603) and

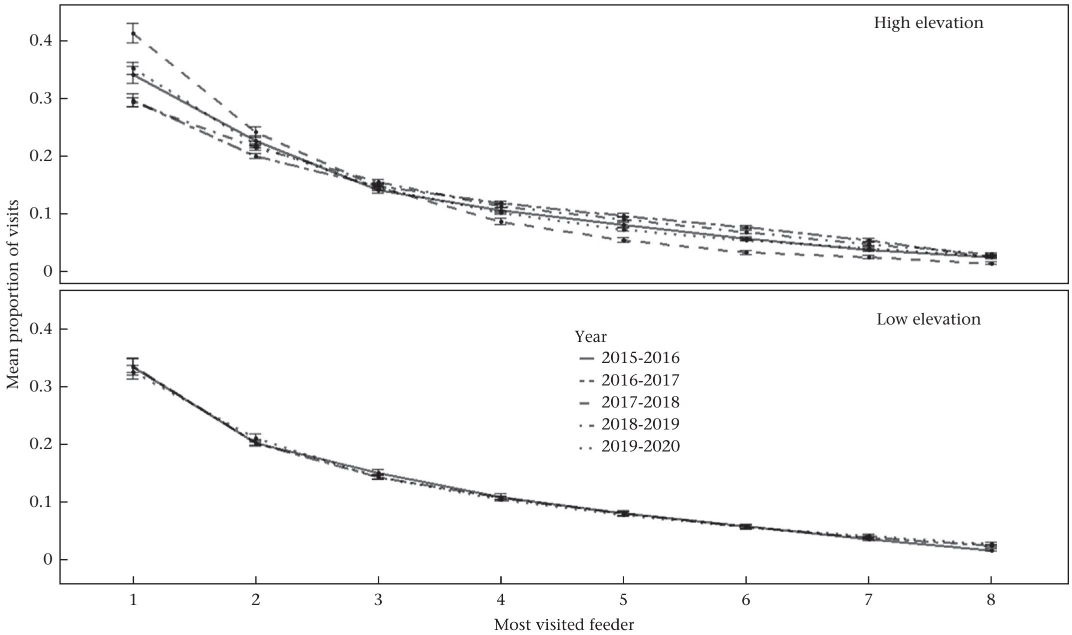

Figure 2. Mean proportion of visits per feeder, ordered from most visited to least visited for each bird (1–8) during the 5 years of study. Note that individuals had different preferred feeders. Error bars indicate standard errors per feeder. $N = 471$.

was in accordance with California Department of Fish and Wildlife Permit D-0011776516-4.

RESULTS

The final data set used to analyse feeder use behaviour included 471 unique chickadees from two elevations ($N = 261$ at high elevation, $N = 210$ at low elevation; Appendix, Fig A4). As some birds were recorded in multiple years ($N = 184$), this resulted in 670 total observations. In accordance with our previous work (Croston et al., 2017), birds showed a preference for one feeder that they visited more than all others at both elevations during all 5 years (high elevation: 0.338 ± 0.05 proportion of total visits; low elevation: 0.329 ± 0.01 proportion of total visits; Fig. 2).

Effects of Environmental Harshness

Mean Levins' measure of feeder use breadth varied significantly among years but not between elevations (linear mixed effects model: year: $F_{4,545.58} = 23.85$, $P < 0.001$; elevation: $F_{1,550.38} = 1.36$, $P = 0.24$; Fig. 3a). There was a significant year*elevation interaction ($F_{2,625.56} = 7.47$, $P < 0.001$): feeder use breadth was significantly higher at low elevation than at high elevation in 1 year (2019–2020) but did not differ significantly between elevations in the other 4 years. Feeder use breadth was positively and significantly associated with the total number of visits ($F_{1,644.63} = 67.60$, $P < 0.001$; R^2 conditional $= 0.35$, R^2 marginal $= 0.20$). When the total number of birds visiting the arrays was added to the model, the number of birds was not statistically significant (Appendix, Tables A4, A6) and did not improve the model fit (R^2 conditional $= 0.34$). When the number of days each bird participated per year was added to the model, it was not statistically significant (Appendix, Table A7) and did not improve the model fit (R^2 conditional $= 0.35$).

At high elevation, feeder use breadth was significantly smaller in 2 out of 5 years (2015–2016 and 2017–2018) compared to the other 3 years (Fig. 3a). These 2 years were characterized by much milder winter conditions compared to 2016–2017 and 2018–2019, which had record snow cover associated with more severe and frequent snowstorms in the overall region. At low elevation, feeder use breadth differed significantly between all 3 years, with the lowest feeder use breadth in 2015–2016 (the mildest year) and the highest in 2019–2020.

Winter environmental conditions (e.g. temperature and snow depth) varied significantly between years and hence these conditions were strongly correlated with year (Appendix, Fig. A1), as there was only one data collection period for feeder use breadth per year. Birds' feeder use breadth was significantly higher when mean snow depth (a proxy for the frequency and severity of snowstorms) was higher and when mean daily temperatures were lower (linear

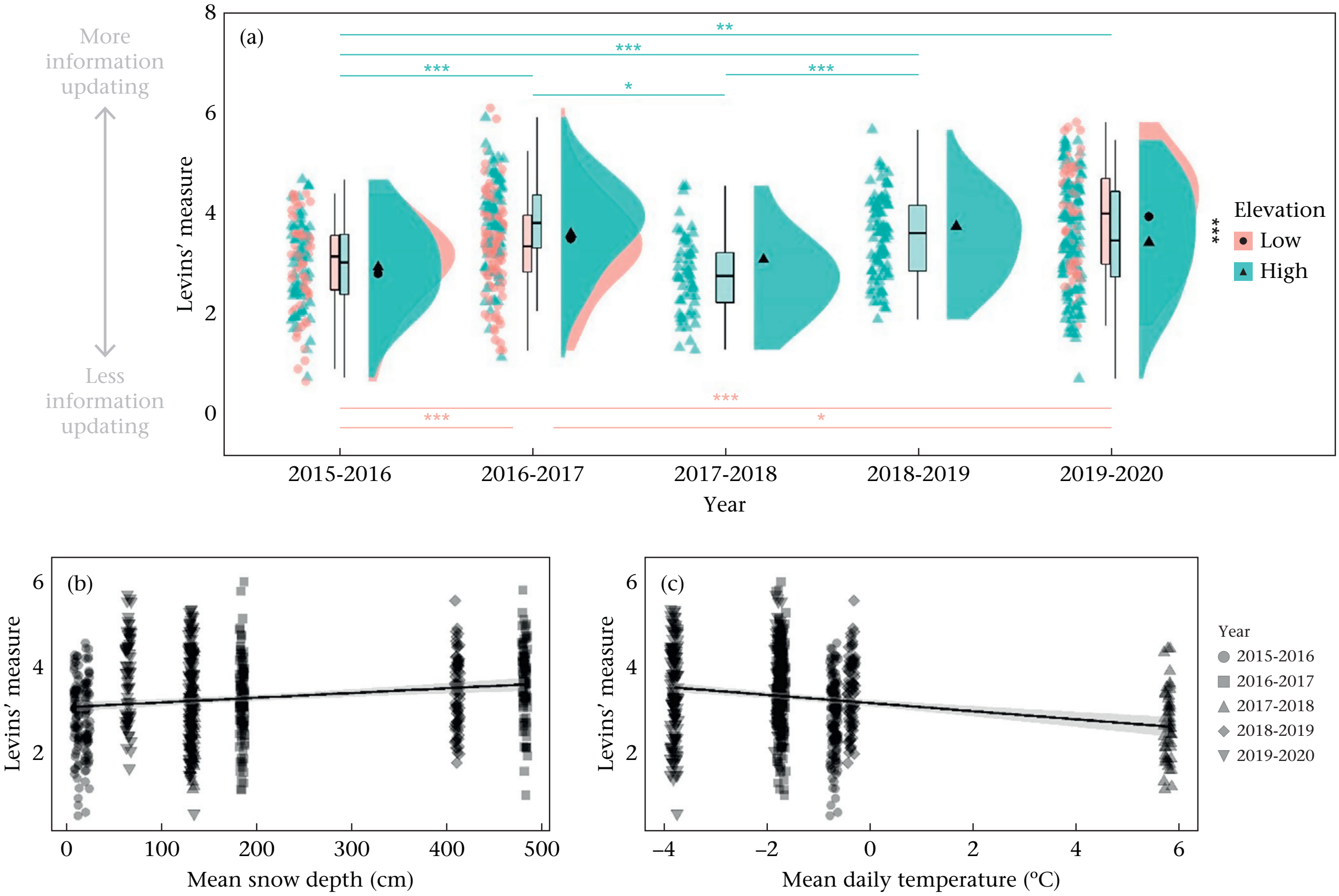

Figure 3. Levins' measure of feeder use breadth during the 5 years of study (a) by year at high and low elevations (blue and pink, respectively), depicted with estimated marginal means from linear mixed effects model (black symbols), (b) by mean snow depth across both elevations and (c) by mean daily temperature across both elevations. Transparent points (jittered for clearer viewing) and density plots represent raw data. In (a), asterisks indicate significance levels from Tukey-adjusted post hoc pairwise comparisons (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$) for within-elevation differences between years (blue lines above plot for high-elevation comparisons and pink lines below plot for low-elevation comparisons) and within-year differences between sites (stacked asterisks: ***$P < 0.001$). Lower and upper box boundaries represent 25th and 75th percentiles, lines inside boxes represent the median, lower and upper error lines indicate 1.5× greater and lesser than the 25th and 75th percentiles, respectively. Outliers not shown. In (b) and (c), linear regression lines are shown by black lines with grey shaded 95% confidence intervals. $N = 471$.

mixed effects model: snow depth: $\beta = 0.21$, $F_{1,528.32} = 29.76$, $P < 0.001$; Fig. 3b; mean temperature: $\beta = -0.16$, $F_{1,594.89} = 9.71$, $P = 0.002$; total number of visits: $F_{1,664.97} = 56.40$, $P < 0.001$; R^2 conditional = 0.31, R^2 marginal = 0.14; Fig. 3c). When the total number of birds visiting the arrays was added to the model, the total number of birds was not statistically significant (Appendix, Tables A4, A6) and did not improve the model fit (R^2 conditional = 0.36).

Age and Sex Differences

The overall effect of age on feeder use breadth approached significance, with juveniles having a higher feeder use breadth than adults (linear mixed effects model: age: $F_{1,670.00} = 3.22$, $P = 0.073$; Fig. 4). There was significant variation in feeder use breadth among years ($F_{4,638.99} = 20.91$, $P < 0.001$), but no significant differences between elevations ($F_{1,585.16} = 0.07$, $P = 0.80$). Notably, there were significant interactions of year*elevation ($F_{1,663.43} = 3.59$, $P = 0.03$) and age*year ($F_{1,662.89} = 4.19$, $P = 0.002$), but not age*elevation ($F_{1,658.89} = 0.004$, $P = 0.95$) or age*year*elevation ($F_{2,668.49} = 2.73$, $P = 0.07$; total visits: $F_{1,655.52} = 57.19$, $P < 0.001$; R^2 conditional = 0.38, R^2 marginal = 0.23). Post hoc pairwise comparisons (Tukey-adjusted for multiple comparisons) revealed that juveniles had significantly higher feeder use breadth than adults at both elevations during 2 of the 5 years (2016–2017 and 2019–2020), the years that were associated with the most severe winter conditions (Appendix, Fig. A1). When the total number of birds visiting the arrays was added to the model, the number of birds was not statistically significant (Appendix, Tables A4, A6) and did not improve the model fit (R^2 conditional = 0.38). When the number of days each bird participated per year was added to the model, it was not statistically significant (Appendix, Table A7) and did not improve the model fit (R^2 conditional = 0.38).

When we included both age and sex in the model, there was no overall significant effect of sex or elevation and the overall effect of age was also not significant (linear mixed effects model: sex: $F_{1,329.71} = 1.15$, $P = 0.28$; elevation: $F_{1,374.96} = 0.81$, $P = 0.37$; age: $F_{1,494.40} = 2.59$, $P = 0.11$). The interaction of age*sex was not statistically significant ($F_{1,445.64} = 0.13$, $P = 0.72$), but there was significant variation among years ($F_{4,400.81} = 17.54$, $P < 0.001$) and a significant year*elevation interaction ($F_{2,456.42} = 6.41$, $P = 0.002$; total number of visits: $F_{1,481.88} = 31.35$, $P < 0.001$; R^2 conditional = 0.36, R^2 marginal = 0.20). As sex was not a significant predictor in this model or other models that included an interaction effect of sex*year, it was dropped from following analyses. When the total number of birds visiting the arrays was added to the model, the number of birds was not statistically significant (Appendix, Tables A4, A6) and it did not improve the model fit (R^2 conditional = 0.36).

To ensure that this nonsignificant interaction between age and sex was not influenced by excluding birds with too few visits, we also ran the model with all birds that visited more than eight times per year (the minimum required visits for using the Levins' measure to describe feeder use breadth in this system). However, the interaction between age and sex remained nonsignificant (linear mixed effects model: total visits: $F_{1,559.98} = 49.89$, $P < 0.001$; year: $F_{4,502.22} = 17.23$, $P < 0.001$; elevation: $F_{1,433.58} = 0.10$, $P = 0.75$; sex: $F_{1,378.52} = 0.34$, $P = 0.56$; age: $F_{1,568.73} = 0.63$, $P = 0.43$; year*elevation: $F_{3,523.67} = 4.40$, $P = 0.005$; sex*age: $F_{1,531.88} = 0.02$, $P = 0.89$; R^2 conditional = 0.41, R^2 marginal = 0.21; $N = 358$).

Increasing Age and Experience

To further explore the association between age and feeder use behaviour, we limited the data set to birds that were recorded repeatedly during multiple years ($N = 184$). Increasing age was estimated by the number of years each bird participated in the study. There was a significant effect of increasing age on feeder use breadth: chickadees gradually, but significantly, reduced their feeder use breadth in subsequent years (linear mixed effects model: increasing age: $\beta = -0.25$, $F_{1,380.89} = 4.77$, $P = 0.03$; Fig. 5). There was also significant variation across years (year:

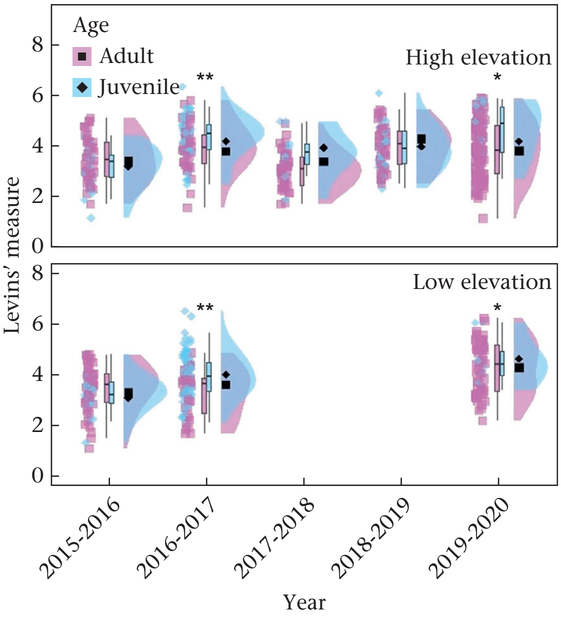

Figure 4. Levins' measure of feeder use breadth by age, year and elevation with estimated marginal means from linear mixed effects model (black symbols). $N = 471$. *$P < 0.05$; **$P < 0.01$. Lower and upper box boundaries represent 25th and 75th percentiles, lines inside boxes represent the median, lower and upper error lines indicate 1.5× greater and lesser than the 25th and 75th percentiles, respectively. Outliers not shown.

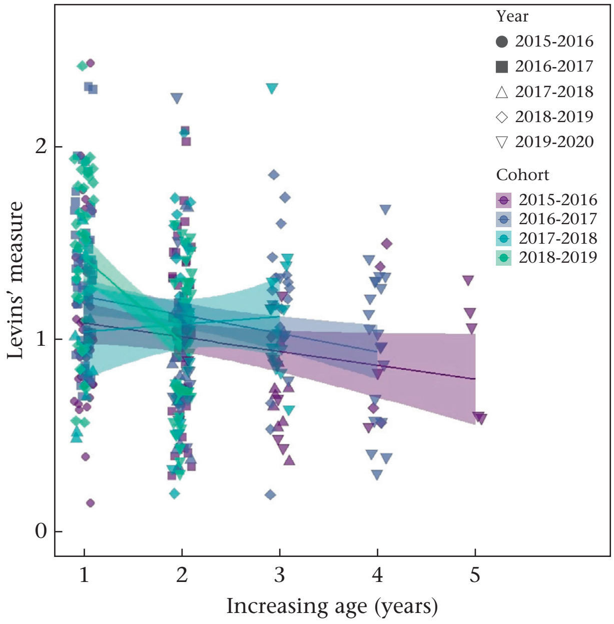

Figure 5. Effect of increasing age (i.e. number of years, first, second, etc.) on mean daily Levins' measure of feeder use breadth. Lines represent simple linear regressions with 95% confidence intervals (shaded). Cohort denotes the first year the birds were recorded sampling at the feeder arrays. $N = 184$.

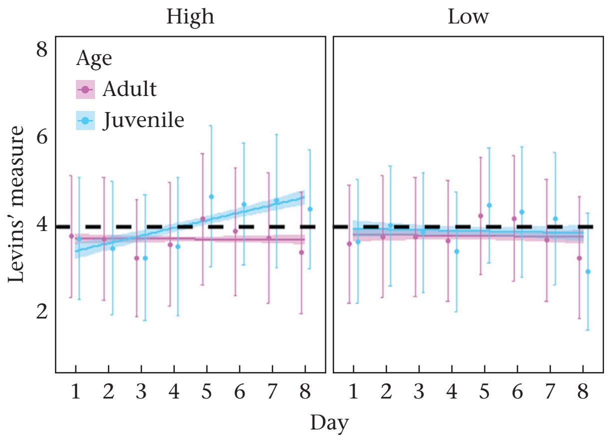

Figure 6. Levins' measure by day of experiment, elevation and age group. Lines are smoothed linear regressions. Points are mean Levins' measures per day for all years by elevation and age group. Bars represent the standard deviation of the daily Levins' measures.

$F_{4,312.67} = 7.41$, $P < 0.001$) and the effect of cohort approached significance (cohort: $F_{3,245.79} = 2.62$, $P = 0.051$; total visits: $F_{1,379.84} = 25.04$, $P < 0.001$; R^2 conditional = 0.33, R^2 marginal = 0.18).

Age Classes in the First Year of Feeder Use

To test whether detected differences between adults and juveniles could have been due to specific previous experience with our experimental arrays, we conducted a post hoc analysis in which we used ANOVA to compare the Levins' measure of feeder use breadth between age classes (juvenile versus adult) within the first year that birds experienced our feeder arrays. We only analysed the 2 years that were associated with significant age class differences in the overall data set (2016–2017 and 2019–2020; $N = 230$). Even among the birds that were exposed to our arrays for the first time, there was a significant difference between juveniles and adults ($F_{1,225} = 7.33$, $P = 0.007$) as well as a significant difference between elevations ($F_{1,225} = 5.32$, $P = 0.02$), a nonsignificant difference between years ($F_{3,225} = 0.08$, $P = 0.8$) and a significant interaction between year and elevation ($F_{1,225} = 6.41$, $P = 0.01$).

Daily Changes in Feeder Use Breadth

As a post hoc analysis, we explored how Levins' measure varied across days within years. Daily feeder use breadth varied significantly across years (linear mixed effects model: $F_{4,2979.8} = 34.16$, $P < 0.001$) and age groups ($F_{1,1441.3} = 4.38$, $P = 0.04$) but not elevations ($F_{1,1141.3} = 1.60$, $P < 0.001$). There were significant main effects of day ($\beta = 0.02$, $F_{1,4527.5} = 20.68$, $P < 0.001$) and daily number of visits ($\beta = 0.40$, $F_{1,4941.6} = 395.02$, $P < 0.001$) as well as significant interactions of year*site ($F_{2,2018.8} = 22.34$, $P = 0.003$), site*age ($F_{1,1427.1} = 9.02$, $P < 0.001$), site*day ($F_{1,4523.5} = 32.16$, $P < 0.001$), age*day ($F_{1,4545.1} = 13.52$, $P < 0.001$) and site*age*day ($F_{1,4533.0} = 28.67$, $P < 0.001$; R^2 conditional = 0.37, R^2 marginal = 0.14). However, the relationship between day and Levins' measure was only significant for juveniles at high elevation (linear mixed effects model: $\beta = 0.40$, $F_{1,858.99} = 96.78$, $P < 0.001$) and was not significant for adults at high elevation (linear mixed effects model: $F_{1,948.7} = 0.55$, $P = 0.46$), juveniles at low elevation (linear mixed effects model: $F_{1,726.70} = 2.43$, $P = 0.12$) or adults at low elevation (linear mixed effects model: $F_{1,940.60} = 0.94$, $P = 0.33$; Fig. 6).

Spatial Cognition and Cognitive Flexibility

The data set was limited to the subset of birds that sampled and participated in subsequent cognitive tests in at least 1 year ($N = 64$ birds excluded with no spatial cognition data; Appendix, Table A5). In a model with age, year, elevation and spatial learning and memory ability, juveniles had significantly higher feeder use breadth than adults in 2016–2017 and 2019–2020 (linear mixed effects model: age: $F_{1,533.21} = 3.02$, $P = 0.083$; age*year: $F_{4,529.03} = 5.95$, $P < 0.001$) and birds with better spatial learning and memory abilities had significantly smaller feeder use breadth than birds with worse spatial learning and memory abilities regardless of elevation (spatial cognition: $\beta = 0.13$, $F_{1,533.96} = 8.28$, $P = 0.004$; year: $F_{4,512.69} = 17.25$, $P < 0.001$; elevation: $F_{1,465.41} = 0.06$, $P = 0.80$; year*elevation: $F_{2,517.83} = 5.78$, $P = 0.003$; total visits: $F_{1,524.16} = 36.15$, $P < 0.001$; R^2 conditional = 0.32, R^2 marginal = 0.24; Fig. 7). When the total number of birds visiting the arrays was added to the model, the total number of birds was not statistically significant (Appendix, Tables A4, A6) and did not improve the model fit (R^2 conditional = 0.28). Also, the interaction between age and cognition was not significant ($F_{1,531.39} = 0.90$, $P = 0.34$) and it was excluded from the analyses.

Spatial learning and memory abilities remained statistically significant in the model when we used mean snow depth and mean daily temperature during the period of data collection on sampling behaviour instead of year and elevation (linear mixed effects model: spatial cognition: $\beta = 0.14$, $F_{1,543.85} = 10.14$, $P = 0.002$; snow depth: $\beta = 0.20$, $F_{1,461.02} = 18.88$, $P < 0.001$; mean temperature:

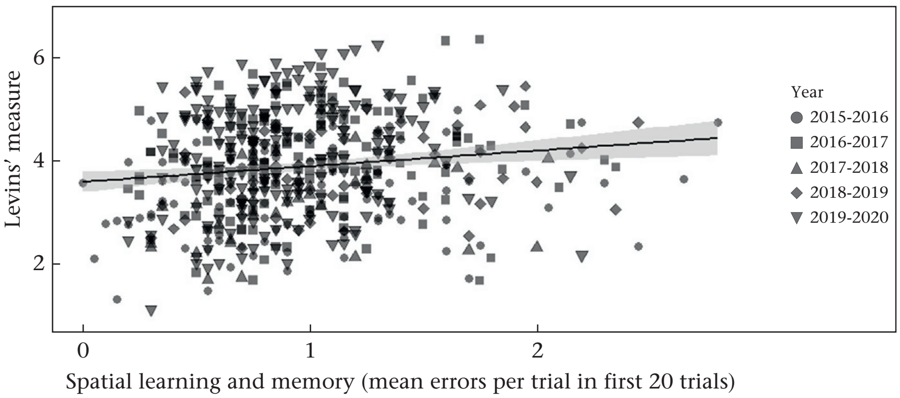

Figure 7. Levins' measure of feeder use breadth and spatial learning and memory ability (mean number of errors per trial in the first 20 trials) for all years of study (2015–2020). Linear regression lines with 95% confidence intervals (grey). $N = 411$.

$\beta = -0.20$, $F_{2,529.58} = 10.93$, $P = 0.001$; total visits: $F_{1,540.81} = 39.94$, $P < 0.001$; R^2 conditional $= 0.25$, R^2 marginal $= 0.15$).

Additional birds were excluded for reversal spatial learning and memory (cognitive flexibility) analyses ($N = 95$ birds did not participate in reversal learning tests directly after the first learning and memory task in the same year; Appendix, Table A5). Performance on the reversal spatial learning and memory task was not a significant predictor of feeder use breadth (reversal learning and memory: $\beta = 0.04$, $F_{1,396.88} = 0.54$, $P = 0.46$; year: $F_{4,341.47} = 10.83$, $P < 0.001$; elevation: $F_{1,370.04} = 1.31$, $P = 0.25$; year*elevation: $F_{2,381.67} = 7.08$, $P < 0.001$; total visits: $F_{1,395.39} = 33.49$, $P < 0.001$; R^2 conditional $= 0.35$, R^2 marginal $= 0.21$). When the total number of birds visiting the arrays was added to the model, the number of birds was not statistically significant (Appendix, Tables A4, A6) and did not substantially improve the model fit (R^2 conditional $= 0.36$).

Effect of Experimental Manipulation of Access to Food (2019–2020)

In 2019–2020, data on feeder use behaviour were collected both before and after spatial cognitive testing. Analyses of pre- and postcognitive testing feeder use data were limited to the subset of birds that participated during both data collection periods and participated in both of the spatial cognitive tasks in 2019–2020 ($N = 156$).

During the regular sampling experiment before cognitive testing, feeder use breadth did not vary significantly with individual's reversal spatial learning and memory ability (linear regression: reversal learning and memory: $\beta = 0.10$, $F_{1,152} = 1.52$, $P = 0.22$; total visits: $\beta = 0.35$, $F_{1,152} = 17.52$, $P < 0.001$; elevation: $F_{1,152} = 6.55$, $P = 0.01$; multiple $R^2 = 0.12$, adjusted $R^2 = 0.11$; $P < 0.001$; Fig. 8).

After the cognitive testing period, there was no significant effect of spatial learning and memory ability (from the first spatial cognitive task) on feeder use breadth (linear regression: spatial learning and memory: $\beta = 0.18$, $F_{1,152} = 2.82$, $P = 0.09$; total visits: $\beta = 0.21$, $F_{1,152} = 6.74$, $P = 0.01$; elevation: $F_{1,152} = 0.001$, $P = 0.98$; multiple $R^2 = 0.06$, adjusted $R^2 = 0.04$). However, after cognitive testing, individuals that performed better (made fewer errors) in the reversal spatial learning and memory task had significantly smaller feeder use breadth compared to individuals that performed worse (linear regression: reversal learning and memory: $\beta = 0.26$, $F_{1,151} = 8.33$, $P = 0.004$; total visits: $\beta = 0.29$, $F_{1,151} = 5.92$, $P = 0.02$; elevation: $F_{1,151} = 0.54$, $P = 0.46$; visits during reversal task: $\beta = -0.03$, $F_{1,151} = 0.07$, $P = 0.8$; multiple $R^2 = 0.10$, adjusted $R^2 = 0.07$).

DISCUSSION

Overall, our findings from 5 years of data generally supported our predictions: chickadees distributed visits more broadly across multiple feeders when the environment was hasher and more unpredictable; juveniles had higher feeder use breadth than adults during the harshest 2 years of the study; and birds with better spatial learning and memory abilities had smaller feeder use breadths than birds with worse abilities. In addition, feeder use breadth was reduced significantly with age, likely due to increased experience. Chickadees had a preferred feeder that they foraged from more than the others, and yet they continued to use other feeders. Our results support the hypothesis that when birds experienced a harsher and less predictable environment, they invested more in maintenance of previously learned information by updating such information more frequently. Having the most updated information may be beneficial in case previously available food sources become unavailable, so birds would be able to quickly find an alternative source.

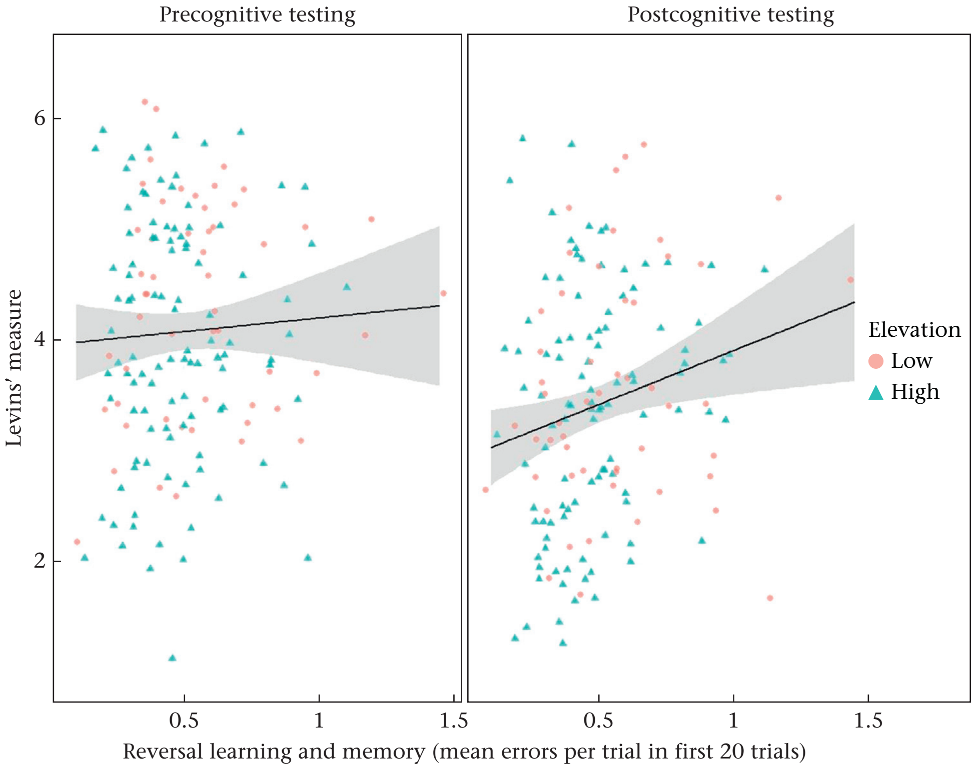

Figure 8. Levins' measure of feeder use breadth and reversal spatial learning and memory ability (mean errors per trial in first 20 trials of cognitive task) before and after cognitive testing in 2019–2020. Linear regression lines with 95% confidence intervals (grey). $N = 157$.

Our data suggest that changes in feeder use breadth are associated with environmental conditions and the need to keep updating information rather than with changes in frequency of visits due to variable energetic needs or potential social factors (e.g. competition for access to the feeders). We think that our data strongly argue against these alternative explanations. First, we found the results discussed above while controlling for variation in the total number of visits per bird in all of our statistical analyses for feeder use breadth and so our results were independent of the total number of visits. Second, if social competition affected our results, we would expect to find differences in feeder use breadth and total number of visits based on social dominance structure; yet there were no differences between males and females and no significant interaction between age and sex, even though females are socially subordinate to males (Dixon, 1965; Ekman, 1989, 1990; Gentle & Gosler, 2001). Third, and most importantly, when the total number of birds present at each array during data collection was added to our models, it was not statistically significant and did not improve model fits (Appendix, Table A6), suggesting that our results were not dependent on variation in social competition. Overall, our data clearly showed that birds changed their feeder visits depending on the environmental conditions and did not exhibit any consistent distribution of feeder use across different conditions (which could be potentially explained by particular permanent environmental features near the arrays). Our results showed that even though food at the feeders was temporarily stable (which might lead to a reduction in information maintenance if birds only used local information to guide their behaviour), chickadees' feeder use was associated with the overall and not with local environmental conditions.

The data supported our prediction that harsher and more unpredictable environments overall should be associated with a greater feeder use breadth even when all available food sources are temporarily stable. Although we did not detect predicted elevational differences in feeder use breadth across all years, we found that chickadees distributed visits across significantly more feeders during years with harsher winter conditions, and when it was colder and there was more snow regardless of elevation. This supports the hypothesis that the value of information maintenance is greater in harsh and unpredictable environments, potentially due to higher costs of searching for food in such conditions (e.g. during unpredictable winter storms characteristic to the Sierra Nevada) and because updated information may be more reliable when the overall environment is less predictable. We must add that even differences in just the harshness of the environment might potentially lead to the same predictions and explanations without added variability. If the environment is harsher and food is limited, discovering and maintaining information about multiple food sources would be beneficial. However, in our system, harsh winters are typically unpredictable as well, due to differences in the frequency, duration and severity of winter snowstorms that can interfere with chickadee foraging.

Juvenile chickadees had significantly greater feeder use breadth compared to adults during the 2 years with the harshest, most unpredictable winter conditions. One potential explanation is that juveniles are socially subordinate to adults, resulting in a more unpredictable environment for younger birds if foraging opportunities at the feeder arrays are limited by losing competitive interactions with more dominant birds. Thus, low social status could be expected to drive juvenile chickadees to engage in more information updating compared to higher-status adults, to compensate for the increased unpredictability from social interactions with higher-status individuals. This effect might be more observable during harsher years when energetic requirements and competition over resources might both be increased. However, if dominance interactions were driving variation in feeder use breadth, we would expect to see an interaction between sex and age that represents the linear dominance hierarchy typically shown in Paridae species (adult males > juvenile males > adult females > juvenile females; Dixon, 1965; Ekman, 1989, 1990; Gentle & Gosler, 2000). Yet, we did not detect significant effects of sex or sex*age interaction, suggesting that juvenile females distributed their visits among multiple feeders similarly to juvenile males, in contrast to the social status explanation.

Another possible explanation for greater feeder use breadth in juveniles compared to adults in the two harshest years is that juveniles are inexperienced during their first winter and as a result overcompensate in their information updating behaviour. As animals age, they gain experience allowing them to better assess conditions and fine-tune their response to environmental cues by minimizing costs associated with overengaging in information maintenance (Dall et al., 2005; McNamara et al., 2006). Our results show evidence for this explanation in two indirect ways: (1) juveniles distributed their visits across more feeders than adults in two of the harshest years in the study; and (2) chickadees reduced feeder use breadth (associated with less information updating) as they aged across the 5 years of our study. Furthermore, Eliassen et al. (2007) suggested that changes in life expectancy should affect information updating behaviour and shorter life expectancy should be associated with less information updating as animals do not have time to obtain the benefits. In this case, age may have an effect on allocation of time between exploration, information maintenance and exploitation directly, regardless of any previous experience. We think this explanation is unlikely in our case as all birds have relatively long life expectancy, which should benefit from more frequent information updating.

However, the effect of age could either be due to age-related experience or to experience specifically with our feeder system. We think it is more likely that this effect is the result of age-related experience for two reasons. First, the difference in feeder use breadth between adults and juveniles remained even when we looked only at birds during their first exposure to the feeders. As birds in both age classes would have had the same experience with the feeders at that point, these results suggest that some other form of experience (perhaps age-related) or characteristic was driving the observed age effect. Second, the feeders were only consistent and predictable during the data collection for this study – throughout the rest of the year, the feeder arrays were at times empty (summer), partially full (i.e. only 2 of 8 feeders filled, early autumn), refilled infrequently (i.e. some feeders ran out while others remained full, early autumn), full with complete visual access to the food ('open' mode before the experiment), or set to 'target' mode during cognitive tests (i.e. each bird can only access food at one feeder). Given the uncertain status of the feeders across an entire year, it would be highly unlikely that the bird would learn that the data collection period for this study provides consistent food every year. Finally, we previously showed that performance in cognitive tasks is not affected by the previous experience with arrays (Sonnenberg et al., 2019).

Our results supported the prediction that cognitive abilities are associated with environmental predictability: individuals with better spatial learning and memory abilities engaged less in information updating, as indicated by smaller feeder use breadth, than birds with worse abilities even when accounting for annual variation and age effects. We have previously shown that birds do not improve spatial cognitive ability with experience – suggesting that the cognitive effect is not driven by specific experience with our feeder set-up (Sonnenberg et al., 2019; Tello-Ramos et al., 2018). In food-caching animals, spatial cognition is needed to retrieve stored food items, decreasing environmental unpredictability by guaranteeing food supply during food-scarce seasons. So, in this case, better spatial learning and memory, but not reversal learning ability, is likely to result in more predictable environments as previously made food caches provide a reliable food source. Accordingly, there were no significant associations between spatial cognitive flexibility (i.e. reversal spatial learning and memory ability) and feeder use breadth across the 5 years of the study. Cognitive flexibility may reflect the ability to track continuously changing information (Tello-Ramos et al., 2018), but it does not seem to be associated with retrieval of food caches in our system (Sonnenberg et al., 2019). Moreover, the ability to better remember more food caches appears to be associated with reduced spatial flexibility (Croston et al., 2018). We do not think that birds with better spatial cognition visit fewer feeders because they remember the last feeder they visited better compared to individuals with worse abilities. If that were the case, cognition would be the only predictor of feeder use breadth yet both environmental conditions and age affect feeder use breadth independently of cognition. In addition, we only detected the effect of spatial learning and memory but not spatial reversal learning, which also argues against this explanation. More research into spatial cognitive flexibility would be necessary to explore how this ability may relate to information updating behaviours.

Finally, we showed that birds changed their relative use of all available feeders in response to learning information about these feeders. When we compared feeder use breadth in the same birds before and after cognitive testing (during which food was limited at certain feeders), we found that birds that had performed better on the reversal spatial learning and memory task (directly preceding) had significantly smaller feeder use breadth during the post-cognitive testing data collection period than birds that performed worse on the task. This is particularly interesting considering that before cognitive testing, feeder use breadth was associated with spatial learning and memory ability, but not with cognitive flexibility. We argue these results make a distinction between the effects of spatial cognitive ability and the direct effect of learned information about food status in different feeders. While spatial learning and memory ability affected feeder use breadth before food availability changed, information learned during the reversal spatial task affected relative use of feeders afterwards. As birds learned the reversal task, they learned both (1) which feeder was rewarding and (2) which feeders did not provide food. These results are consistent with our predictions: when birds learned that some of the previously rewarding feeders no longer provided food, the value of continuing to visit those feeders was lower and thus the birds reduced or stopped updating information for those feeders. We think this reduced feeder use was not only due to the strong learned association with the rewarding feeder, but was also equally related to learning the location of feeders that no longer provided food. Moreover, birds that did not learn which feeders no longer provided food as quickly as other birds continued revisiting more feeders. These birds were still worse learners before and after spatial cognitive testing; their individual abilities did not change due to the cognitive testing, but the way they allocated their visits among available feeders did.

In conclusion, our study provided support to our hypothesis that animals should engage more in maintenance and updating of previously learned information when overall environmental conditions are harsh and unpredictable. Having the most recently updated information about food sources makes the environment more reliable and should increase the predictability of available food sources. Spatial cognitive abilities and age-related experience, which can reduce an individual's environmental unpredictability, also affected animals' decisions to engage in information updating, further supporting our hypothesis.

Data Accessibility

Original data and associated scripts are available from Mendeley Data (https://doi.org/10.17632/csv8nvy7dr.1). SNOTEL climate data are publicly available through the United States Department of Agriculture, Natural Resources Conservation Service, National Water and Climate Center: https://www.wcc.nrcs.usda.gov/snow/

Author Contributions

L.M.B. and V.V.P. designed the study. L.M.B., A.M.P., C.L.B., B.R.S., V.K.H. and V.V.P. collected data. E.S.B. provided continuous support with all RFID issues. L.M.B. conducted all analyses. L.M.B. and V.V.P. wrote the first draft of the manuscript. A.M.P., C.L.B., V.K.H. and B.R.S. contributed to the writing. V.V.P. provided funding.

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Appendix

Table A1
Data collection periods

Year	Elevation	Presampling period ('open' mode)	Data collection period for sampling ('all' mode)	Postcognitive testing ('all' mode)
2015–2016	High	4 Nov 2015–11 Nov 2015	11 Nov 2015–18 Nov 2015	–
2015–2016	Low	4 Nov 2015–11 Nov 2015	11 Nov 2015–18 Nov 2015	–
2016–2017	High	1 Mar 2017–3 Mar 2017	3 Mar 2017–10 Mar 2017	–
2016–2017	Low	22 Feb 2017–1 Mar 2017	1 Mar 2017–8 Mar 2017	–
2017–2018	High	10 Jan 2018–17 Jan 2018	29 Jan 2018–5 Feb 2018	–
2017–2018	Low	–	–	–
2018–2019	High	22 Mar 2019–29 Mar 2019	29 Mar 2019–6 Apr 2019	–
2018–2019	Low	–	–	–
2019–2020	High	20 Dec 2019–27 Dec 2019	13 Jan 2020–20 Jan 2020	19 Feb 2020–22 Feb 2020
2019–2020	Low	20 Dec 2019–27 Dec 2019	13 Jan 2020–20 Jan 2020	5 Feb 2020–8 Feb 2020

Table A2
Birds at high elevation excluded for visiting <64 times, by demographics

Age	Sex	High elevation					
		2015–2016	2016–2017	2017–2018	2018–2019	2019–2020	Total
Adult	Female	3	4	11	9	2	29
Adult	Male	3	2	22	8	7	42
Adult	Unknown	1	0	5	3	4	13
Juvenile	Male	1	0	10	3	0	14
Juvenile	Unknown	5	1	10	6	3	25
Juvenile	Female	0	2	12	2	0	16
Total		13	9	70	31	16	139

Table A3
Birds at low elevation excluded for visiting <64 times, by demographics

Age	Sex	Low elevation					
		2015–2016	2016–2017	2017–2018	2018–2019	2019–2020	Total
Adult	Female	2	0	0	5	3	10
Adult	Male	2	3	0	2	5	12
Adult	Unknown	1	0	0	1	2	4
Juvenile	Male	1	4	0	1	1	7
Juvenile	Unknown	1	5	0	3	0	9
Juvenile	Female	0	6	0	2	0	8
Total		7	18	0	14	11	50

Table A4
Number of birds present at each array each year

Array[a]	Number of birds present				
	2015–2016	2016–2017	2017–2018	2018–2019	2019–2020
High 1	25	45	23	29	74
High 3	43	43	30	50	56
Low 3	37	60	–	–	37
Low 8	38	49	–	14	31

[a] Array names indicate the elevation (high versus low) and each array's position within the field system, not the number of arrays.

Table A5
Data set descriptions and sample sizes used for regression analyses

Data set	*N*	Description	Models used
Full data set	471	Full data set included birds with ≥64 visits during the data collection period for sampling behaviour, no data from low elevation for 2017–2018 or 2018–2019	Elevation and year, temperature, snow, age, variation in mean Levins' measures
Sex data	422	Excluded birds without sex data	Sex
Sex data >8 visits	358	All birds with sex data and >8 visits, including birds from low elevation in 2018–2019	Post hoc sex
Spatial cognition data	411	Birds with spatial cognitive data, excluded birds with >3 errors ($N = 5$)	Spatial cognition analyses
Reversal learning and memory data	316	Birds with spatial cognitive data and reversal learning and memory data	Reversal spatial learning and memory analyses
Repeat birds	184	All birds that were recorded sampling during 2 or more years, 2015–2020	Levins' measures in birds sampling in multiple years
Postcognitive testing 2019–2020	157	Birds that sampled in 2019–2020 during the data collection period for sampling behaviour before and after cognitive testing	Postcognitive testing
First year recorded 2016 and 2019	230	Birds that were recorded for the first time in the feeder array system during 2016–2017 and 2019–2020	Post hoc: age class for first year using feeder arrays
Birds excluded for <64 visits	94	Birds excluded for visiting <64 times (or <8 times/day for 8 days). This included $N = 94$ birds that were excluded from the full data set entirely	None

Table A6
Linear mixed effects models including number of birds present per array

Fixed effects	Statistics	R^2		
		Conditional	Marginal	Change[a]
		0.341	0.206	0.004
Number of birds at array	$B = 0.11$, $F_{1,506.36} = 2.53$, $P = 0.11$			
Total visits	$B = 0.33$, $F_{1,643.85} = 66.95$, $P >$ **0.001**			
Year	$F_{4,543.49} = 13.50$, $P <$ **0.001**			
Elevation	$F_{1,593.54} = 2.86$, $P = 0.09$			
Interaction: year*elevation	$F_{2,594.30} = 6.85$, $P =$ **0.001**			
		0.36	0.227	−0.049
Number of birds at array	$B = -0.02$, $F_{1,603.12} = 0.14$, $P = 0.71$			
Total visits	$B = 0.28$, $F_{1,660.34} = 55.80$, $P <$ **0.001**			
Average temperature	$B = -0.18$, $F_{1,635.06} = 7.28$, $P =$ **0.007**			
Mean snow depth	$B = 0.21$, $F_{1,512.54} = 29.67$, $P <$ **0.001**			
		0.377	0.231	0.004
Number of birds at array	$B = 0.09$, $F_{1,482.11} = 1.55$, $P = 0.21$			
Total visits	$B = 0.31$, $F_{1,638.57} = 55.45$, $P >$ **0.001**			
Year	$F_{4,606.04} = 13.90$, $P <$ **0.001**			
Elevation	$F_{1,607.58} = 0.05$, $P = 0.83$			
Age	$F_{1,652.00} = 3.18$, $P = 0.07$			
Interaction: year*elevation	$F_{2,607.06} = 3.75$, $P =$ **0.024**			
Interaction: year*age	$F_{4,645.23} = 3.93$, $P =$ **0.004**			
Interaction: elevation*age	$F_{1,642.36} = 0.01$, $P = 0.92$			
Interaction: year*elevation*age	$F_{2,650.31} = 2.51$, $P = 0.08$			
		0.358	0.195	0.048
Number of birds at array	$B = 0.02$, $F_{1,356.34} = 0.63$, $P = 0.43$			
Total visits	$B = 0.26$, $F_{1,470.08} = 30.26$, $P <$ **0.001**			
Year	$F_{4,391.19} = 9.56$, $P <$ **0.001**			
Elevation	$F_{1,407.80} = 1.30$, $P = 0.25$			
Age	$F_{1,481.54} = 2.49$, $P = 0.12$			
Sex	$F_{1,324.00} = 1.08$, $P = 0.30$			
Interaction: year*elevation	$F_{2,415.55} = 3.69$, $P =$ **0.03**			
Interaction: age*sex	$F_{1,444.87} = 0.13$, $P = 0.72$			
		0.282	0.209	0.006
Number of birds at array	$B = 0.11$, $F_{1,424.35} = 1.98$, $P = 0.16$			
Total visits	$B = 0.29$, $F_{1,531.21} = 42.73$, $P <$ **0.001**			
Year	$F_{4,477.47} = 9.492$, $P <$ **0.001**			
Elevation	$F_{1,500.36} = 0.24$, $P = 0.63$			
Spatial cognition (scaled)	$B = 0.14$, $F_{1,537.76} = 9.13$, $P =$ **0.003**			
Interaction: year*elevation	$F_{2,490.87} = 5.03$, $P =$ **0.007**			
		0.355	0.207	−0.002
Number of birds at array	$B = -0.04$, $F_{1,308.83} = 0.14$, $P = 0.71$			
Total visits	$B = 0.29$, $F_{1,394.20} = 33.55$ $P <$ **0.001**			
Year	$F_{4,337.05} = 7.39$, $P <$ **0.001**			
Elevation	$F_{1,382.05} = 1.46$, $P = 0.23$			
Reversal spatial cognition (scaled)	$B = 0.04$, $F_{1,395.74} = 0.53$, $P = 0.47$			
Interaction: year*elevation	$F_{2,356.63} = 3.44$, $P =$ **0.03**			

[a] Indicates the difference in R^2 conditional between the model reported in the table and the equivalent model reported in the main text. Bold values denote significant outcomes ($P < 0.05$).

Table A7
Linear mixed effects models including the number of days that each bird participated

Fixed effects	Statistics	R^2		
		Conditional	Marginal	Change[a]
		0.346	0.201	−0.004
Number of days birds participated	$B = -0.04$, $F_{1,658.19} = 1.19$, $P = 0.28$			
Total visits	$B = 0.35$, $F_{1,643.42} = 62.14$, $P >$ **0.001**			
Year	$F_{4,544.35} = 23.60$, $P <$ **0.001**			
Elevation	$F_{1,547.74} = 1.46$, $P = 0.23$			
Interaction: year*elevation	$F_{1,623.35} = 7.54$, $P <$ **0.001**			
		0.381	0.226	0.000
Number of days birds participated	$B = -0.02$, $F_{1,651.00} = 0.39$, $P = 0.53$			
Total visits	$B = 0.32$, $F_{1,639.84} = 59.28$, $P >$ **0.001**			
Year	$F_{4,621.19} = 19.25$, $P <$ **0.001**			
Elevation	$F_{1,570.51} = 0.07$, $P = 0.79$			
Age	$F_{1,650.80} = 2.93$, $P = 0.09$			
Interaction: year*elevation	$F_{2,644.60} = 3.57$, $P =$ **0.029**			
Interaction: year*age	$F_{4,644.07} = 3.89$, $P =$ **0.004**			
Interaction: elevation*age	$F_{1,640.51} = 0.00$, $P = 0.99$			
Interaction: year*elevation*age	$F_{2,649.59} = 2.70$, $P = 0.07$			

[a] Indicates the difference in R^2 conditional between the model reported in the table and the equivalent model reported in the main text. Bold values denote significant outcomes ($P < 0.05$).

Table A8

Tukey post hoc pairwise comparisons of total visits per bird at high and low elevation between years

	2016–2017	2017–2018	2018–2019	2019–2020
High elevation				
2015–2016	$P<0.001$	$P<0.001$	$P<0.001$	$P=0.65$
2016–2017		$P<0.001$	$P<0.001$	$P=0.01$
2017–2018			$P=0.47$	$P<0.001$
2018–2019				$P<0.001$
Low elevation				
2015–2016	$P<0.001$			$P<0.001$
2016–2017				$P=0.085$

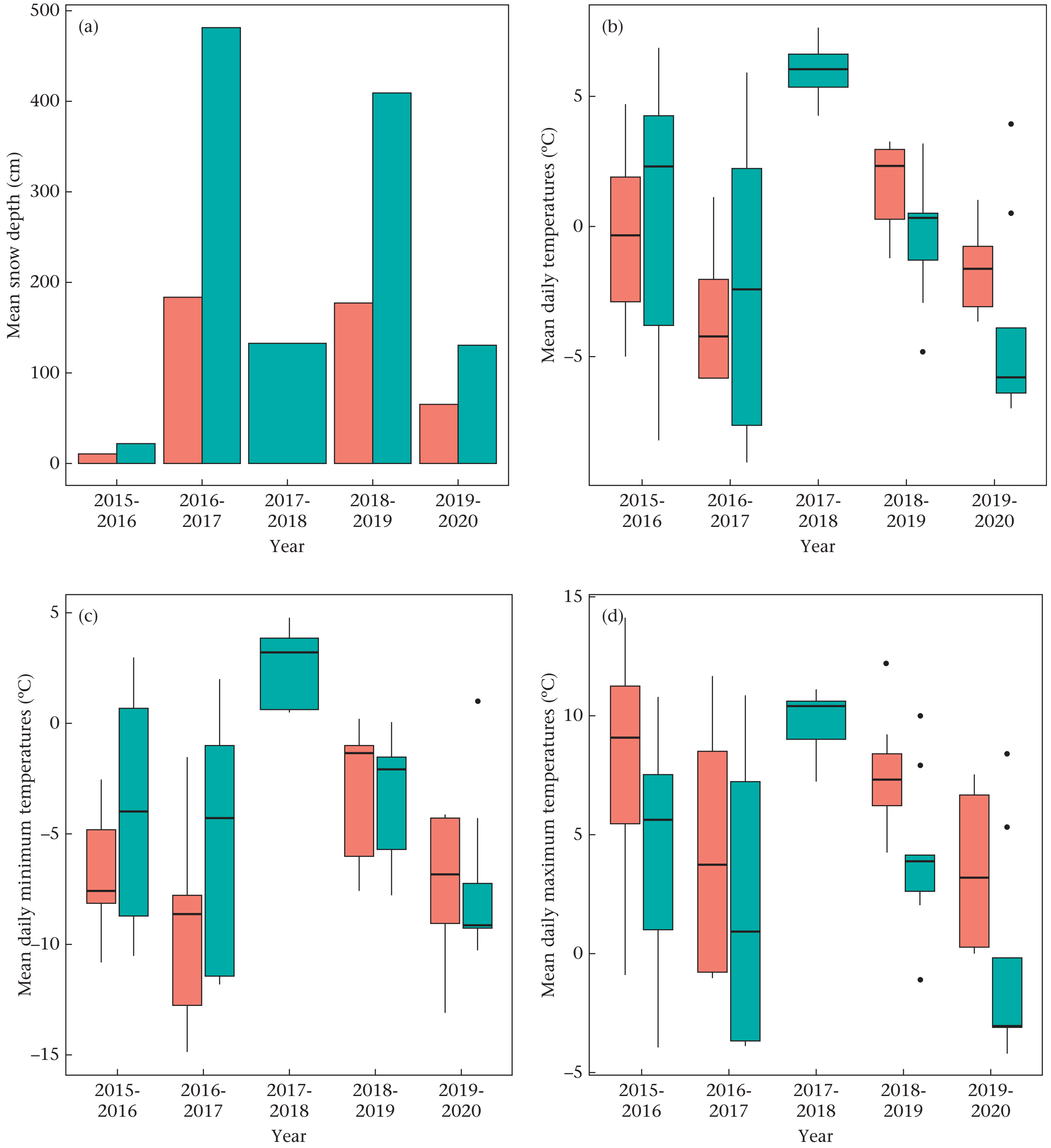

Figure A1. Mean conditions during the data collection periods for sampling behaviour (2015–2020) at high and low elevations. (a) Snow depth, (b) mean daily temperatures, (c) mean daily minimum temperatures and (d) mean daily maximum temperatures. Data from SNOTEL stations 539, 540 and 541.

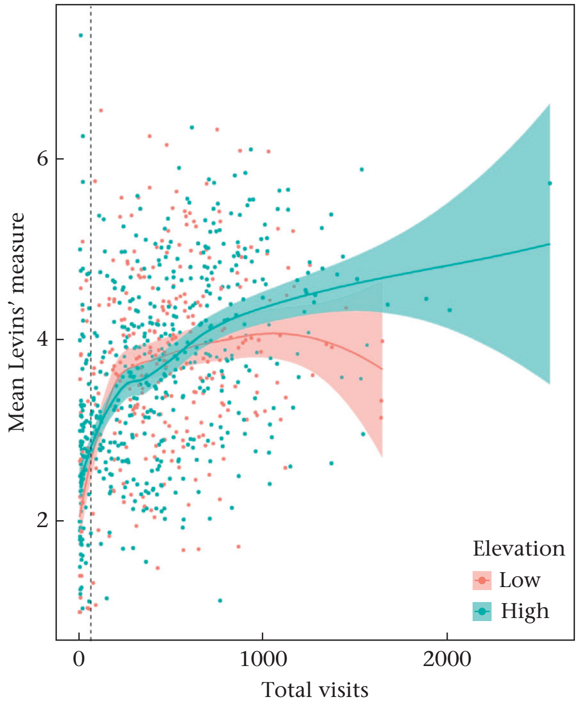

Figure A2. Mean Levins' measure by the total number of annual visits by elevation. Dotted line indicates 64 visits – the criterion for exclusion of some birds due to insufficient number of visits for the analyses. Lines fitted with the 'loess' smoothing function.

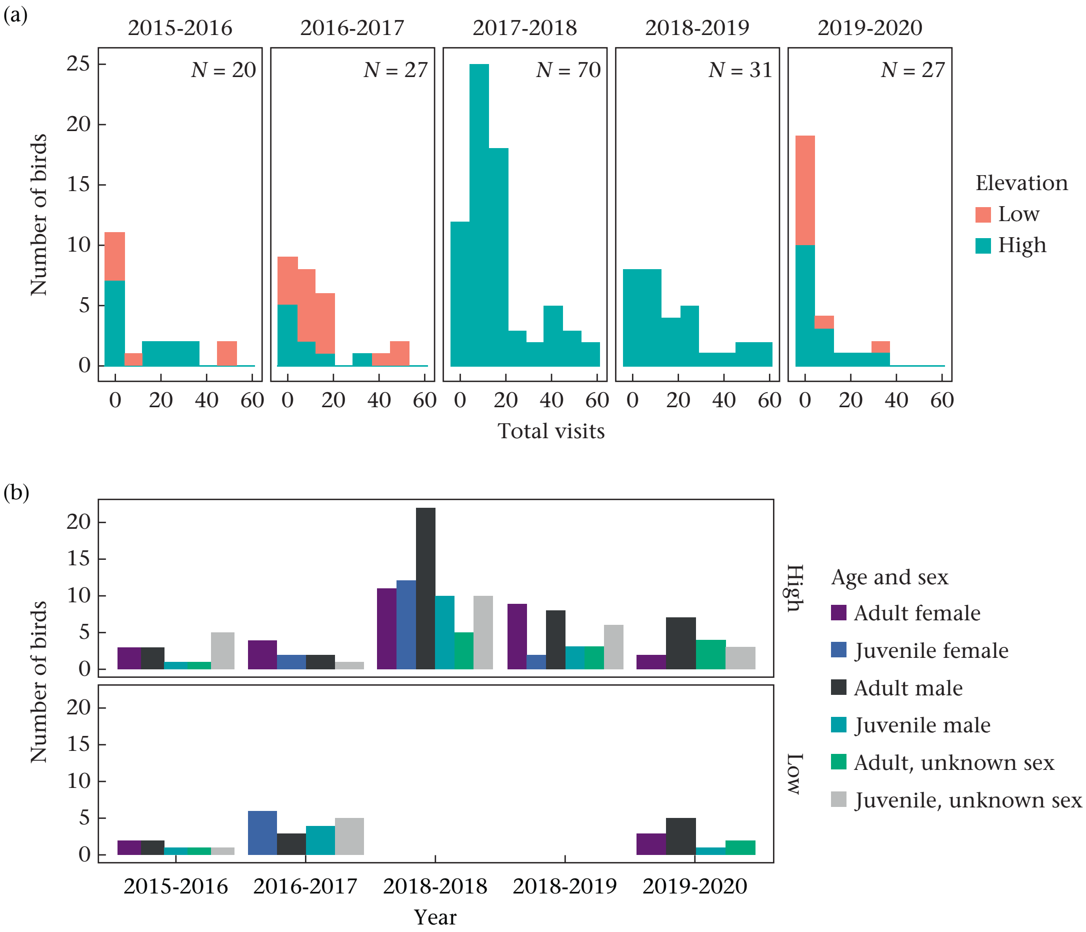

Figure A3. Distribution of excluded birds (with <64 visits) based on (a) the number of visits and (b) the number of birds excluded. s.

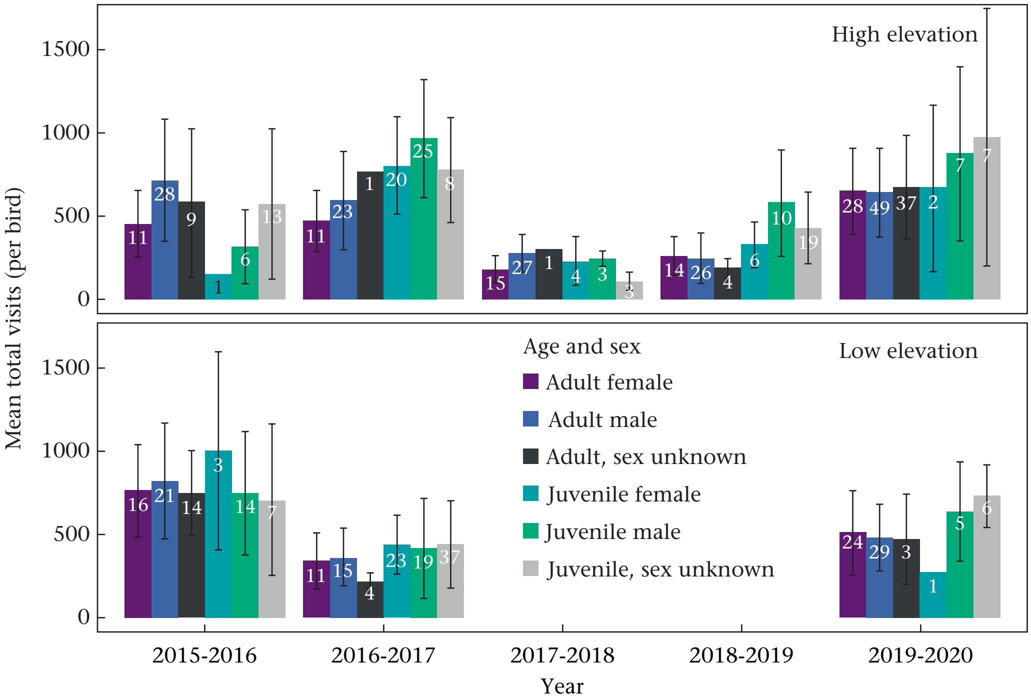

Figure A4. Mean number of visits for each data collection period for sampling behaviour by age and sex. Numbers indicate the number of birds per group. $N = 471$.

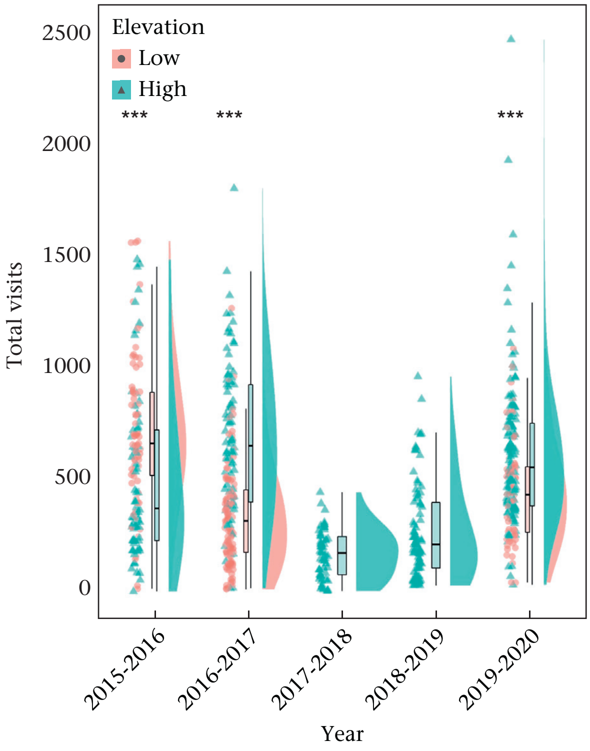

Figure A5. Total visits per bird by year and elevation. Linear mixed effects model (R^2 conditional = 0.66, R^2 marginal = 0.29) with individual bird ID as a random effect (year: $F_{4,354.26} = 66.11$, $P < 0.001$; elevation: $F_{1,486.80} = 17.13$, $P < 0.001$; year*elevation: $F_{2,515.35} = 47.99$, $P < 0.001$). Asterisks indicate significant differences between elevations within the same year (***$P < 0.001$). Lower and upper box boundaries represent 25th and 75th percentiles, lines inside boxes represent the median, lower and upper error lines indicate 1.5× greater and lesser than the 25th and 75th percentiles, respectively. Outliers not shown. $N = 471$. Also see Table A8 for Tukey post hoc pairwise comparisons of total visits per bird at high and low elevation between years.

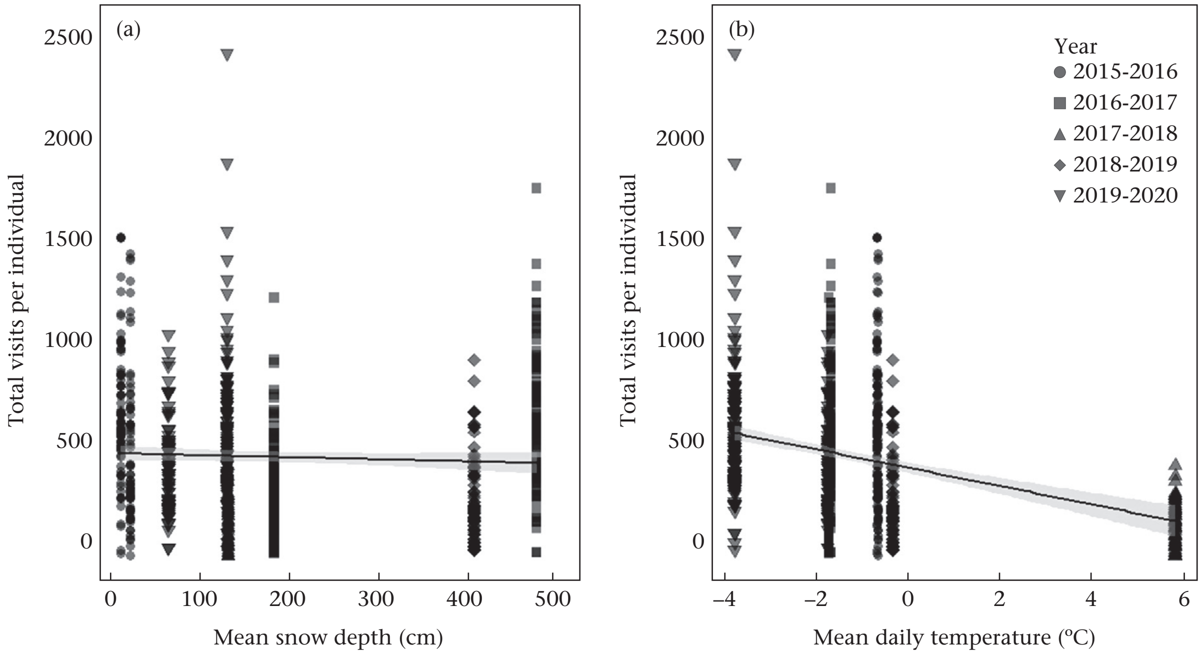

Figure A6. Total visits per bird by (a) mean snow depth and (b) mean daily temperature during the period of data collection for sampling. Linear mixed effects model (R^2 conditional = 0.16, R^2 marginal = 0.11) with individual bird ID as a random effect (mean snow depth: $B = -70.91$, $F_{1,526.20} = 25.65$, $P < 0.001$; mean daily temperature: $B = -145.75$, $F_{1,619.05} = 65.21$, $P < 0.001$). $N = 471$.

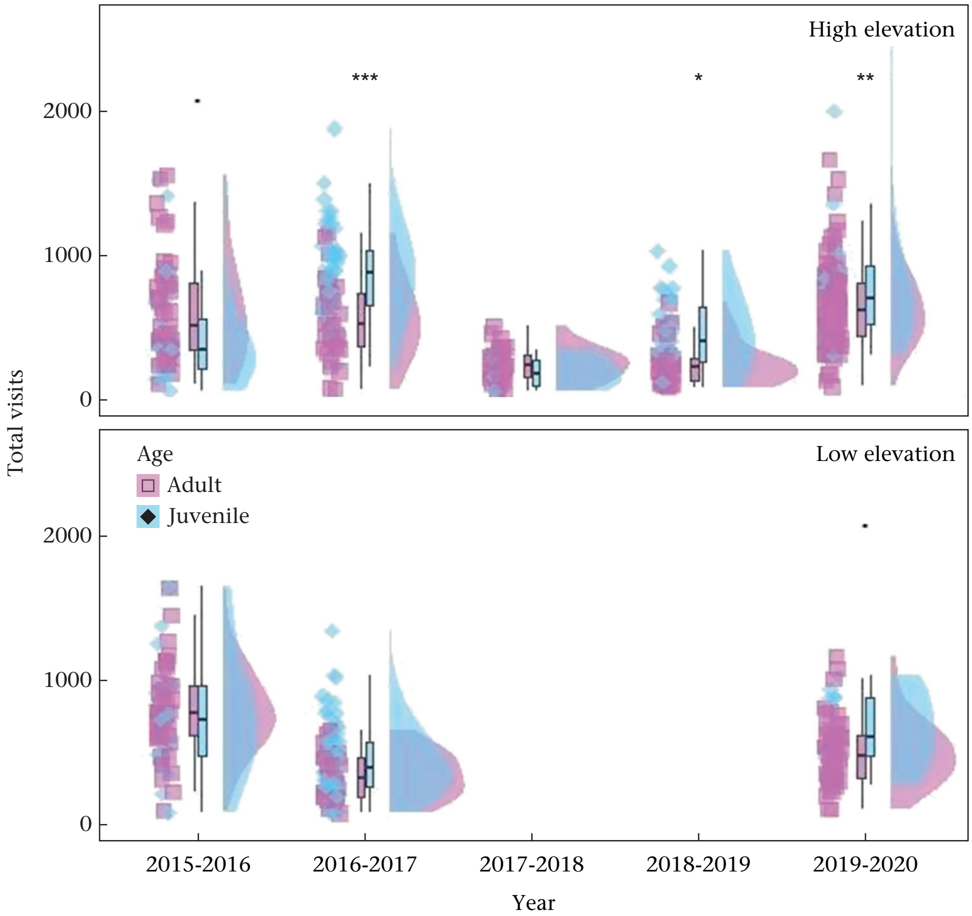

Figure A7. Total visits by age, year and elevation. Linear mixed effects model (R^2 conditional = 0.68, R^2 marginal = 0.33) with individual bird ID as a random effect (year: $F_{4,571.52} = 44.78$, $P < 0.001$; elevation: $F_{1,495.81} = 12.17$, $P < 0.001$; age: $F_{1,646.40} = 10.35$, $P = 0.001$; year*elevation: $F_{2,630.67} = 49.32$, $P < 0.001$; year *age: $F_{4,608.06} = 5.61$, $P < 0.001$; elevation*age: $F_{1,628.18} = 0.27$, $P = 0.60$; year*elevation*age: $F_{2,644.26} = 4.02$, $P = 0.02$). Asterisks denote significance levels from Tukey post hoc pairwise comparisons (within years, between elevations: †$P < 0.06$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). $N = 471$. Lower and upper box boundaries represent 25th and 75th percentiles, lines inside boxes represent the median, lower and upper error lines indicate 1.5× greater and lesser than the 25th and 75th percentiles, respectively. Outliers not shown.

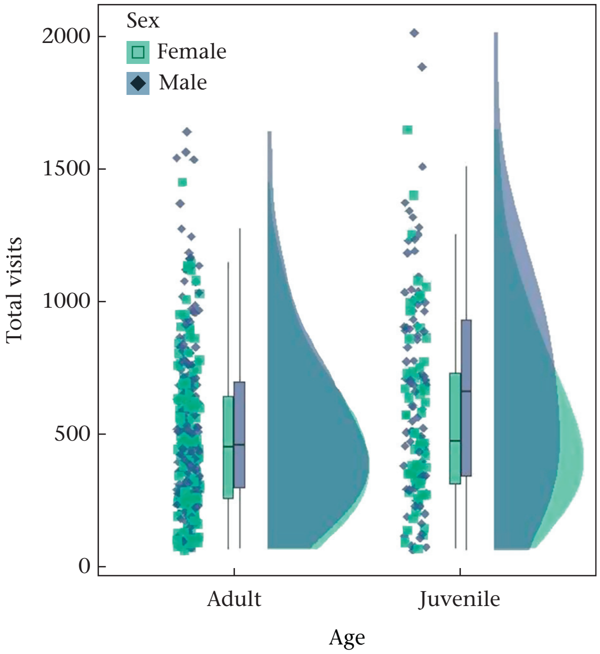

Figure A8. Total visits per individual by age and sex. Linear mixed effects model (R^2 conditional = 0.67, R^2 marginal = 0.35) with individual bird as a random effect (sex: $F_{1,307.71} = 3.07$, $P = 0.08$; age: $F_{1,456.98} = 17.80$, $P < 0.001$; year: $F_{4,291.33} = 57.51$, $P < 0.001$; elevation: $F_{1,329.79} = 14.52$, $P < 0.001$; age*sex: $F_{1,372.98} = 0.08$, $P = 0.78$; year*elevation: $F_{2,383.03} = 37.92$, $P < 0.001$). $N = 321$. Lower and upper box boundaries represent 25th and 75th percentiles, lines inside boxes represent the median, lower and upper error lines indicate 1.5× greater and lesser than the 25th and 75th percentiles, respectively. Outliers not shown.

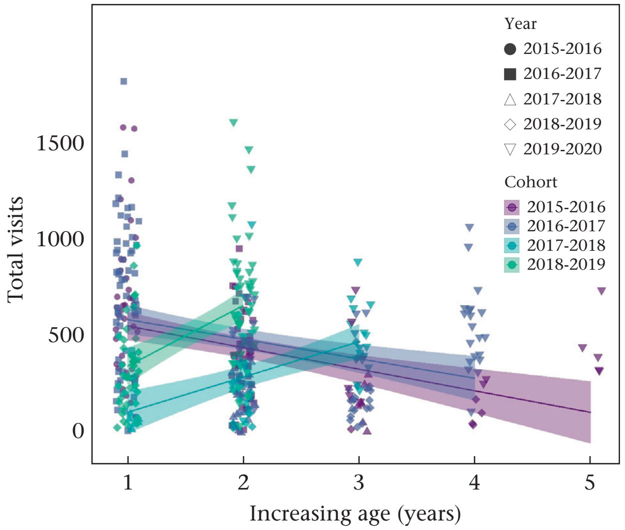

Figure A9. Total visits by increasing age in years. Linear mixed effects model (R^2 conditional = 0.54, R^2 marginal = 0.36) with individual bird as a random effect (years of experience: $F_{1,371.68} = 0.27$, $P = 0.6$; cohort: $F_{3,226.59} = 6.29$, $P < 0.001$; year: $F_{4,262.60} = 56.99$, $P < 0.001$).

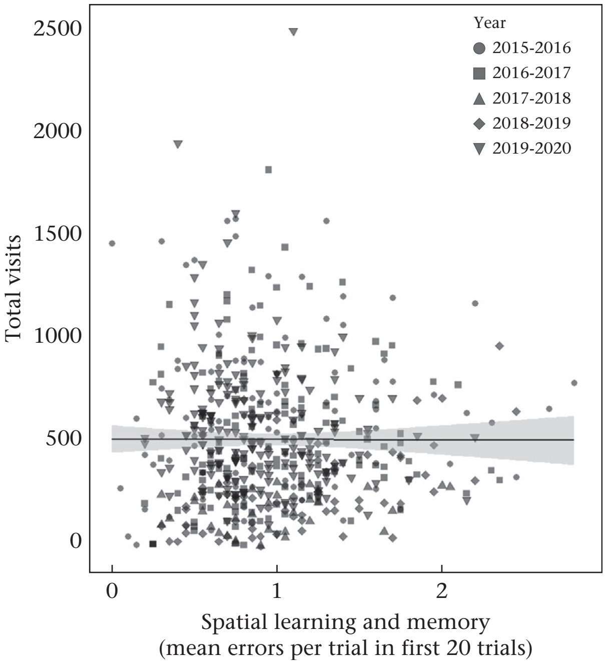

Figure A10. Total visits per individual and spatial learning and memory ability. Linear mixed effects model (R^2 conditional = 0.59, R^2 marginal = 0.28) with individual bird as a random effect (year: $F_{4,310.61} = 48.42$, $P < 0.001$; elevation: $F_{1,426.70} = 16.34$, $P < 0.001$; spatial learning and memory ability: $\beta = 27.39$, $F_{1,518.78} = 3.40$, $P = 0.07$; year*elevation: $F_{2,454.38} = 27.31$, $P < 0.001$). $N = 411$.

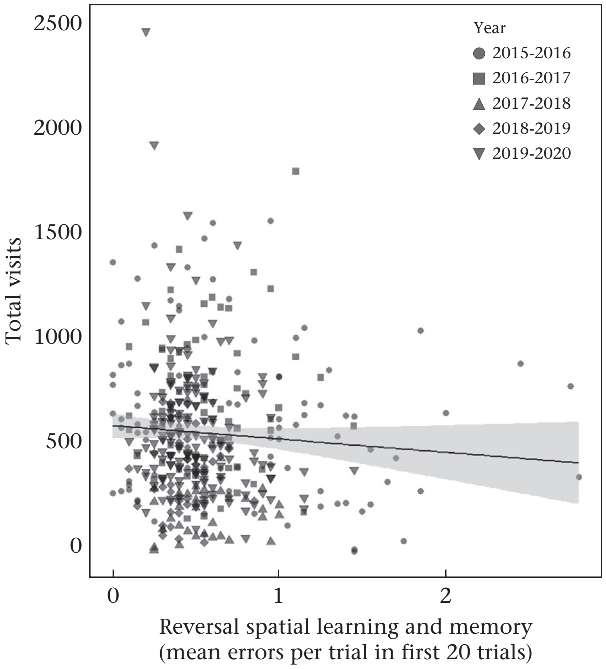

Figure A11. Total visits per individual by reversal spatial learning and memory ability. Linear mixed effects model (R^2 conditional = 0.58, R^2 marginal = 0.26) with individual bird as a random effect (reversal learning and memory: $\beta = -40.08$, $F_{1,386.73} = 3.92$, $P = 0.05$; year: $F_{4,209.87} = 31.36$, $P < 0.001$; elevation: $F_{1,375.18} = 9.82$, $P = 0.002$; year*elevation: $F_{2,316.45} = 15.82$, $P < 0.001$). $N = 316$.