PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research

Cite this article: Heinen VK, Pitera AM, Sonnenberg BR, Branch CL, Benedict LM, Welklin JF, Whitenack LE, Bridge ES, Pravosudov VV. 2023 Food-caching chickadees with specialized spatial cognition do not use scrounging as a stable strategy when learning a spatial task. *Proc. R. Soc. B* **290**: 20230900. https://doi.org/10.1098/rspb.2023.0900

Received: 19 January 2023
Accepted: 9 June 2023

Subject Category:
Behaviour

Subject Areas:
behaviour, cognition

Keywords:
producer–scrounger, spatial cognition, mountain chickadees, foraging

Author for correspondence:
Virginia K. Heinen
e-mail: heinenvi@gmail.com

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.6700193.

THE ROYAL SOCIETY
PUBLISHING

Food-caching chickadees with specialized spatial cognition do not use scrounging as a stable strategy when learning a spatial task

Virginia K. Heinen[1], Angela M. Pitera[1], Benjamin R. Sonnenberg[1], Carrie L. Branch[1,2], Lauren M. Benedict[1], Joseph F. Welklin[1], Lauren E. Whitenack[1], Eli S. Bridge[3] and Vladimir V. Pravosudov[1]

[1]Department of Biology and Evolution, University of Nevada, Ecology Evolution and Conservation Biology Graduate Program, Reno, NV 89557, USA
[2]Department of Psychology, The University of Western Ontario, London, Ontario, Canada, N6A 5C2
[3]University of Oklahoma, OK 73019, USA

VKH, 0000-0003-1804-3589; AMP, 0000-0002-6166-3639; BRS, 0000-0003-4496-4269; CLB, 0000-0002-4671-2420; LMB, 0000-0003-1540-6663; JFW, 0000-0002-7534-8795; LEW, 0000-0002-3031-5244; ESB, 0000-0003-3453-2008; VVP, 0000-0003-1117-7875

Social animals may use alternative strategies when foraging, with producer–scrounger being one stable dichotomy of strategies. While ‘producers’ search and discover new food sources, ‘scroungers’ obtain food discovered by producers. Previous work suggests that differences in cognitive abilities may influence tendencies toward being either a producer or a scrounger, but scrounging behaviour in the context of specialized cognitive abilities is less understood. We investigated whether food-caching mountain chickadees, which rely on spatial cognition to retrieve food caches, engage in scrounging when learning a spatial task. We analysed data from seven seasons of spatial cognition testing, using arrays of radio frequency identification-enabled bird feeders, to identify and quantify potential scrounging behaviour. Chickadees rarely engaged in scrounging, scrounging was not repeatable within individuals and nearly all scrounging events occurred before the bird learned the ‘producer’ strategy. Scrounging was less frequent in harsher winters, but adults scrounged more than juveniles, and birds at higher elevations scrounged more than chickadees at lower elevations. There was no clear association between spatial cognitive abilities and scrounging frequency. Overall, our study suggests that food-caching species with specialized spatial cognition do not use scrounging as a stable strategy when learning a spatial task, instead relying on learning abilities.

1. Introduction

Animals foraging in groups can choose between multiple strategies to obtain food. Under the theory of producer–scrounger dynamics, individuals can act as ‘producers’ by discovering or obtaining food directly, or as ‘scroungers’ by using food sources others have discovered [1]. Scrounging can take many forms, ranging from joining food patches discovered by others [2] to directly stealing food (kleptoparasitism) [3], and can be a beneficial alternative to producing as it allows individuals to avoid the time and energy costs of locating resources on their own [4]. Producer and scrounger social foraging strategies are well established as negatively frequency-dependent and occur at stable equilibrium frequencies [1,5,6]. As the proportion of individuals playing the scrounger tactic increases, the proportion of producers decreases. Scroungers must compete against a larger number of other scroungers for reduced scrounging opportunities, leading the group to settle at a stable equilibrium where the payoffs of producing and scrounging are equal [1,2,7]. This equilibrium can be obtained via all individuals in the group playing the same mixture of producer and scrounger tactics, or by different individuals specializing in either producing or scrounging [5].

Previous research suggests that individuals tend to differ consistently in their propensity to produce or scrounge, relative to other factors affecting the payoff of producer or scrounger behaviours for that individual [4]. For example, dominant individuals are more likely to scrounge if scrounging requires displacing another individual [8,9], while individuals in poor body condition may prefer scrounging if it is less energy intensive than producing [10,11]. Individuals with superior learning abilities may be more likely to use producer strategies, which are thought to rely more on learning, memory or problem-solving abilities [12]. Most research on producer–scrounger dynamics has been based on modelling (e.g. [1,13]) or studies of captive animals (e.g. [8,14,15]), while less is known about how these strategies are expressed in natural environments (though see [16–18]).

One exception to the modelling and captive studies is a study on wild great tits (*Parus major*) [19] that looked at producer–scrounger strategies in the context of learning the solution to a novel problem using automated recordings. This study found that the speed at which birds learned to solve a novel problem was an important predictor of scrounging behaviour, with slower learners being more likely to adopt scrounging tactics. Individuals were also consistent in their tactic specialization, leading to a stable distribution of producers and scroungers. A second study [20] looked at producer–scrounger strategies using an associative learning paradigm in the same species and reported that individuals that performed worse on the associative learning task were more likely to scrounge. These results, however, are more difficult to interpret: the linear feeder set-up was asymmetric, with feeders in the centre of the line both more difficult to learn and riskier to forage at, so it is unclear whether individuals assigned to learn to use the centre feeders scrounged due to individual differences in cognitive capacity, structural differences in task difficulty or as a risk avoidance tactic [21].

In studies of cognition, cognitive ability is often measured through producer-like behaviours (e.g. locating a food reward or completing a novel task); alternative foraging tactics such as scrounging, and their associated cognitive processes, have received much less focus [20]. If the cognitive task permits the use of alternative tactics, there is a risk of misestimating the cognitive abilities of individuals that employ these tactics [15,22,23]. While individuals with poorer cognition may use scrounging tactics [12], scrounging could still be a learned behaviour, as individuals could learn to scrounge more effectively or efficiently with experience [20,24,25]. If scrounging is a possible tactic in a cognitive task, identifying the frequency and distribution of scrounging behaviour is important to ensure the accuracy of cognitive measurements. Previous studies of producer–scrounger tactics in wild animals primarily investigated non-caching species such as great tits [19,20]. What is unknown is whether species with specialized foraging strategies and cognitive abilities, such as food-caching species, also engage in producer–scrounger behaviour whether individual differences in cognitive abilities affect individual tendencies towards producer or scrounger tactics in such species. Considering that learning abilities in these species are critical for survival [26], we hypothesize that they should rely preferentially on their own learning abilities rather than use scrounging as a stable strategy, especially when learning a new task.

Here, we used previously collected data on spatial learning and memory and reversal spatial learning over seven seasons to investigate whether wild food-caching mountain chickadees (*Poecile gambeli*) with specialized spatial cognition engaged in scrounger tactics specifically when solving a spatial cognitive task, and whether the frequency of inferred scrounging events was related to individual differences in spatial cognitive abilities. In our experiments, birds are expected to learn a single spatial location in an eight-feeder spatial array, which most birds successfully accomplish in *ca* 20 trials [27,28]. Selective feeding was accomplished using feeders that integrated a motorized door with a radio frequency identification (RFID) reader that could detect uniquely programmed leg bands on each bird [29]. Since only one feeder in the array will provide food to each bird, learning the location of this feeder encourages birds to stop visiting all other non-rewarding feeders.

While discovering and learning to use the rewarding feeder can be considered a producer strategy, it is possible for birds to obtain food without learning the location of their rewarding feeder by simply following successful individuals and obtaining food after these individuals open the feeder door. Such direct following can lead to successful feeding, so it is possible that some individuals can learn and follow such a scrounging strategy instead of learning the location of their own rewarding feeder. Although the feeder doors only open for specific ‘assigned’ individuals, the doors may take up to 2 s to close following an assigned individual’s departure, providing an opportunity for an unassigned individual to land and obtain food before the door fully closes. An unassigned bird can also actively displace the assigned individual. Because chickadees only spend a few seconds at the feeder—they remove a single seed and immediately leave the feeder to cache—this time window is sufficient for their normal foraging behaviour. Hence, using this testing paradigm, two strategies are available: (i) a producer learns the location of their assigned feeder over multiple trials and relies on spatial memory to use that feeder; or (ii) a scrounger follows the birds that open their assigned feeders and obtains food before the feeder doors close again. This scrounger strategy can also be learned, as if an individual attempts to scrounge and is successful, this could reinforce continued scrounging instead of learning the spatial task.

To detect potential scrounging events we recorded all visits by birds not assigned to each feeder within 5 s and, more conservatively, within 3 s after an assigned bird opened that feeder. We did not record scrounging visually (which would severely limit the scope of the study); instead, we relied on automated recordings of visits from the RFID feeders. We assume that a bird landing at the feeder within this time interval would arrive before the feeder door closed, allowing it to obtain food (a sunflower seed). We have also regularly observed such scrounging events and our visual observations corroborate our assumptions (see electronic supplementary material, video). Since we obtained data from a task specifically designed to evaluate spatial cognitive abilities, there were some limitations, mainly because we could not manipulate the costs or benefits of scrounging. However, considering that Reichert *et al.* [20] suggested that field studies of learning can be confounded by potential scrounging, our experimental design presented an ideal opportunity to directly test whether scrounging impacted our system.

Using 7 years of testing data from our long-term study of spatial cognition, we asked: (i) how frequently food-caching chickadees engaged in potential scrounging (e.g. landed on the feeder within 3–5 s of the producer's arrival), (ii) whether the frequency of potential scrounging varied among seasons and between two montane elevation sites with different environmental conditions and (iii) whether birds that performed worse on spatial learning and memory tasks or spatial reversal learning tasks performed potential scrounges more frequently than those with better performance. Chickadees rely on thousands of individual caches that they locate using their specialized spatial cognitive abilities to survive the winter [26], therefore we predicted that scrounging from a public resource such as our feeders is not a stable alternative strategy compared to reliance on individual cognitive abilities. Accordingly, we predicted that chickadees would engage in scrounging rarely and opportunistically when learning a new spatial task, instead mostly relying on individual cognitive abilities. While it is hypothetically possible that chickadees would engage in scrounging of food caches by following cachers, such a strategy seems unlikely as chickadees cache only one food item per cache location (so there is nothing to scrounge after the cacher has recovered a cache). They also engage in cache protection behaviour when caching to avoid pilferage [30,31] and pilfer rates in the wild appear to be low [32]. Our study specifically investigated scrounging when birds were learning a spatial task, and our study does not cover all possible foraging conditions when scrounging can occur. Considering the natural history of food-caching chickadees, our design presents an ecologically relevant scenario when birds naturally forage using scattered food sources.

2. Materials and methods

(a) Study system

We investigated scrounging behaviour during annual spatial cognitive testing in a population of mountain chickadees at Sagehen Experimental Forest (Sagehen Creek Field Station, University of California, Berkeley) in the Sierra Nevada Mountains, California. We tested birds during the winter at two elevational sites (low: *ca* 1900 m, high: *ca* 2400 m) from 2015 to 2021. Compared to low elevation, winters at high elevation are associated with harsher and more unpredictable environmental conditions such as lower air temperature, deeper and longer lasting snow cover, and stronger and more frequent snowstorms [27,28,33]. In all years, we trapped birds using mist nets at established feeders during the non-breeding months (end of August–December) or by hand at nest-boxes during the breeding season (May–August). Birds were banded with unique combinations of coloured leg bands and passive-integrated transponder (PIT) tag leg bands (IB Technology, Leicestershire, UK). Nestlings received a metal United States Geological Survey leg band at 16-day post-hatch and were given a second coloured leg band and a PIT-tag if they were captured post-fledging. We classified birds as either juvenile (first year) or adult (older than first year of life) based on hatch date if the bird had previously been banded as a nestling, or using multiple age-related plumage characteristics [34]. Birds were sexed when possible based on observed physiological and behavioural indicators during the breeding months (e.g. females incubate eggs and males produce more song) or by wing length (measured to the nearest 0.5 mm using wing cord), as males tend to be larger than females.

Using spatial arrays with RFID-enabled feeders, we conducted two cognitive tests every winter: a spatial learning and memory test and a reversal spatial learning test [26,28,35]. Each array consisted of 8 RFID feeders positioned equidistantly on a square frame (122 × 122 cm) and suspended *ca* 4 m above the ground (electronic supplementary material, figure S1a). An antenna embedded in the feeder perch allowed PIT-tagged birds to be recorded as they landed at the feeder. Feeders were filled with black oil sunflower seeds and could be programmed to open the door only to specific PIT-tagged individuals [27–29]. During cognitive tests, each bird was 'assigned' to a single feeder within an array so that only that feeder would open its door and allow access to food, while all other feeders would only record the time and ID of all visiting birds without providing food. When the bird left the antenna, the door closed automatically, taking up to 2 s to fully close. Therefore, during these cognitive tests, a bird could obtain food from its assigned feeder (producing) or could attempt to obtain food from another feeder after a different bird opened it (scrounging). When foraging at the feeders, birds take a single seed and immediately depart to cache it, only spending a few seconds at the feeder at most.

Since 2015, we have maintained two spatial arrays *ca* 1.5 km apart at each elevation. Prior to cognitive testing, feeders were initially set to 'open' mode, in which all feeder doors were open and any bird could obtain food at any feeder, for a minimum of two weeks. Feeders were then set to 'all' mode, in which feeder doors were closed by default and opened for any PIT-tagged bird, for a minimum of one week. This mode was used to habituate birds to the moving feeder doors before cognitive testing (see [26,27] for detailed methods).

(b) Spatial cognitive testing

During the spatial learning and memory task (spatial learning task), birds were required to learn and remember the spatial location of a single rewarding feeder in the array, a metric associated with differences in overwinter survival [26,27]. Each bird attending the array was assigned to a single-array feeder for a set period (typically 4 days; see electronic supplementary material, table S1). Assignments were pseudo-randomly spread across all eight feeders within an array, so that no birds were assigned to their most visited feeder from the previous habituation period. Spatial learning performance was measured as the number of location errors (unrewarding feeders visited prior to visiting the correct rewarding feeder) that each bird made within a trial (electronic supplementary material, figure S1b). A trial began when an individual visited any feeder in the array and ended when the individual visited 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 [26–28].

The reversal spatial learning task (reversal learning task) took place immediately following the spatial learning task. This task was designed to estimate cognitive flexibility [28,35,36]. We pseudo-randomly reassigned each bird to a new rewarding feeder, meaning that the previously rewarding feeder no longer provided food. Birds were not assigned to the feeder immediately adjacent to the one they had been assigned in the spatial learning task. To avoid the influence of social learning, birds that had been previously assigned to the same feeder were reassigned to different feeders in the array. As in the spatial learning task, we used the mean number of location errors per trial over the first 20 trials to evaluate reversal spatial cognitive ability [26,28,36]. The reversal learning task also typically lasted 4 days (electronic supplementary material, table S1).

(c) Identifying scrounging events

We specifically identified potential scrounging events (e.g. visits to the non-assigned feeders within 3 and 5 s after the producer opened the feeder) only at the beginning of both cognitive tasks (e.g. the first 20 trials) before birds had fully learned these tasks, so individuals had an opportunity to learn either the spatial task or the scrounging tactic. During both cognitive tests, when an individual visited its assigned feeder, the door opened, allowing that bird to obtain food. Chickadees obtain one sunflower seed during each visit and fly away to consume or cache that seed in nearby trees. When an individual leaves the feeder with a seed, the door begins closing after a 0.2 s delay. The total elapsed time between a bird's departure and the door closing completely depended on the speed of the motor powering the door and varied slightly with temperature, but in general was up to 2 s. Before the 2019–2020 season, the time from bird's departure to the door closing completely was approximately 2 s or less; from the 2019–2020 season onwards, the feeders had faster motors, reducing this time to 1 s or less. Therefore, out of the 7 years of data, the first 4 years were associated with twice the amount of time available for scrounging. The time for the door to close allows a different individual to scrounge by quickly landing on the feeder's perch and obtaining a seed before the door closes completely. We have directly observed birds successfully obtaining seeds in this manner regardless of differences in door closing time (electronic supplementary material, video).

We defined a scrounging event as a visit from a bird that was not assigned to the feeder within 5 s of an assigned bird's last recorded tag read at that feeder. This 5 s interval was determined based on our observations of target birds, which can spend several seconds on the perch before departing the feeder and because the feeders were programmed not to record any repeat reads of a tag within 5 s of its first detection. Our feeders do not record individuals' departure times, nor the timing of door closing; therefore, we can infer that an individual has departed at some point within 5 s of its last tag read. Observations suggest that individuals typically spend 2–3 s at the feeder before departing, but occasionally take longer. We selected this 5 s window to account for all possible departure times in our main analysis. In addition, we repeated our analyses using a more conservative 3 s window, which almost guarantees that the potential scrounger landed while the feeder door was still open, at the cost of potentially excluding some scrounging behaviour.

It is possible that some visits identified in this way were not attempts to scrounge, but simply errors made while the bird was attempting to find its own rewarding feeder. However, most visits had intervals of more than 5 s between them (electronic supplementary material, figure S3). The elapsed time between one bird's last tag read and the next bird's arrival also differs between visits to rewarding feeders (feeders the bird could open) and non-rewarding feeders (feeders the bird could not open, but could potentially scrounge from), with a sharper peak in the 3–5 s range for visits to non-rewarding feeders (electronic supplementary material, figure S3). This indicates that birds visiting their rewarding feeder do not typically visit immediately after the previous bird's departure, while birds visiting a non-rewarding feeder are more likely to do so—a potential signature of scrounging behaviour [20]. Our automated visit recordings also do not directly record scrounging *per se*; that is, we could only record when a bird was present, but not whether it actually obtained a seed before the door closed. However, birds should be able to retrieve a seed when landing on a feeder with the door still open and seeds easily available, which is likely under the 5 s and especially under the 3 s window. Our visual observations confirm that these landings right after the target bird departed are typically successful. Considering that such events were recorded specifically at the start of the spatial learning task, successful scrounging prior to learning the spatial task can be expected to reinforce scrounging and allow learning of this strategy [20].

(d) Data analysis

For each year of data, we restricted our analysis to birds that completed 20 or more trials in both the spatial learning task and the reversal learning task (electronic supplementary material, table S2). Birds that failed to meet this criterion did so not because they were making large numbers of scrounging visits or errors, but because they simply did not make many visits to the array. Analyses were conducted in R v.4.1.2 [37].

For each task, we calculated each bird's proportion of visits (all landings on all feeders) that were scrounges during their first 20 trials of each task. Specifically, this was defined as the number of scrounging visits divided by the total number of visits (scrounges, location errors, and rewarded visits) each bird made through to its 20th visit to its rewarding feeder. We counted all scrounges an individual performed, including scrounges made on birds that were otherwise excluded from the analysis because they did not meet criterion for total trials completed (20 total trials). We combined the initial and reversal tasks to calculate a 'total proportion scrounged' for each bird within each year.

For analyses comparing scrounging and cognition, we adjusted cognitive scores to exclude scrounging visits, under the assumption that a scrounging visit represents an alternative foraging strategy, not an error made while searching for the rewarding feeder. That is, if a bird visited a given non-rewarding feeder only once during a trial and this visit was a potential scrounging event, then this bird made one fewer location error and its cognitive score improved. However, if a bird visited the same non-rewarding feeder more than once during a trial, and some of these visits were not potential scrounges, the total number of location errors made was not affected and its cognitive score was unchanged. These adjustments did not substantially alter our overall estimates of cognitive performance (electronic supplementary material, figure S4).

(e) Repeatability of scrounging

To determine if scrounging behaviour was repeatable within individuals, we calculated repeatability of the proportion of visits that were scrounging events between the spatial learning task and the reversal learning task within each year using the *rptR* R package [38]. We modelled the proportion of scrounging visits within each test (spatial learning or reversal learning) as a binomial dependent variable and included test type (spatial cognition or reversal learning), elevation, season, age and sex as fixed factors, and individual identity as a random factor. Season, elevation and age were included because of previously identified relationships with performance on, and engagement in, the cognitive testing tasks ([28,39]). Age and sex are also associated with dominance status [40], which could potentially influence a bird's willingness to approach or displace another individual.

For birds that participated in cognitive testing in more than 1 year, we calculated repeatability across years, using proportion scrounged during both experiments in a year as a binomial dependent variable, and year, age and sex as fixed factors. This and the previous analysis were also repeated without sex to use a larger sample of birds, as we could not determine the sex of all tested birds.

(f) Effect of cognition on scrounging frequency

We performed separate mixed-effects model analyses in the R package *lme4* [41] to assess the relationship between spatial learning performance and scrounging behaviour, and between reversal learning performance and scrounging behaviour, using cognitive scores adjusted for scrounging events as described above.

Both models used proportion of visits scrounged during both the spatial learning and reversal learning tasks combined as the dependent variable. For each bird, relevant cognitive score (either spatial learning score or reversal learning score—mean number of locations errors per trial over the first 20 trials) from the given year, testing season, elevation, age, sex and their first-level interactions were included as fixed effects, and individual identity was included as a random effect. These variables were chosen because of previously identified relationships with cognitive performance (season, elevation and age; [28,35]), and/or because they influence chickadees' dominance status, which could potentially affect a bird's willingness to approach an occupied feeder (sex and age; [40]). We also constructed a model including all fixed effects above, but without any cognitive measurements. We selected our final structure of fixed effects by using all predicted variables, but eliminating non-significant interactions and testing for significant differences in model fit using likelihood ratio tests. Partial R^2 values for each level of each fixed effect were estimated using the 'r2beta' function from the *r2glmm* package [42].

These analyses and all following were run with sex as a fixed effect, but because not all birds in our dataset could be conclusively sexed, this reduced the sample size. Thus, the same analyses were also run excluding sex but including all birds.

(g) Relationship between producer and scrounger cognition

To test whether there was a relationship between producer and scrounger cognitive performance—for example, whether individuals preferentially scrounge from birds with better cognition than themselves—we analysed the subset of scrounging events where both producer and scrounger had completed at least 20 trials in both the spatial learning task and the reversal learning task. As in the previous analyses, we used adjusted cognitive scores that excluded scrounging events from the error calculations. We performed separate mixed-effects model analyses for spatial learning scores and for reversal learning scores. Both models used the producer's cognitive score (spatial learning or reversal learning) from the given season as the dependent variable. Scrounger score (spatial learning or reversal learning) from the same year, testing season, elevation and their interactions were used as fixed effects, and scrounger identity was included as a random variable.

3. Results

(a) Data summary

Over the 7 years of data collection, 327 unique chickadees completed both cognitive tests at high elevation, and 174 at low elevation. Of these birds, 195 birds at high elevation (59.6%) and 109 birds at low elevation (62.6%) could be conclusively sexed (electronic supplementary material, table S2). Using a 5 s threshold for scrounging classification, 309 birds at high elevation (94.5%) and 162 birds at low elevation (93.1%) scrounged at least once. Under the more conservative 3 s threshold, 234 birds at high elevation (71.5%) and 105 birds at low elevation (60.3%) scrounged at least once.

(b) Individual repeatability of potential scrounging

Overall, chickadees rarely engaged in scrounging, with a mean frequency of scrounging during the first 20 trials of both cognitive tasks of just 0.048 ± 0.037 scrounges per trial, ranging from zero to just slightly above 15% of all feeder visits. Within each year, frequency of scrounging was not repeatable between the spatial learning and reversal learning tasks of the experiment ($R = 0.002$, 95% CI = [0–0.004]). 134 birds at high elevation (41.0%) and 40 birds at low elevation (23.0%) completed cognitive testing in more than one season. These birds were also not consistent between seasons in their frequency of scrounging ($R = 0.001$, 95% CI = [0–0.003]).

(c) Timing of potential scrounging

When examining the proportion of scrounging visits per trial over the first 10 trials, there was a significant effect of trial number on the proportion of visits that were scrounging events ($F_{9,\ 17944} = 55.27$, $p < 0.001$), as well as significant interactions between trial and elevation ($F_{9,\ 17944} = 16.71$, $p < 0.001$) and trial and year ($F_{54,\ 17944} = 4.90$, $p < 0.001$). *Post hoc* tests revealed that birds scrounged significantly more during their first trial—before they had identified their rewarding feeder—than in any subsequent trial ($p < 0.05$ for all pairwise comparisons; see electronic supplementary material, table S3). There were no significant differences between any of the other trials, starting with trial two (figure 1). Moreover, the proportion of scrounging after the first trial was close to zero (figure 1), suggesting that birds only engaged in scrounging before they discovered their rewarding feeder and stopped scrounging almost entirely after they discovered it. A more conservative analysis using a 3 s time window produced similar results (electronic supplementary material, table S4).

(d) Individual-level determinants of potential scrounging frequency

There were significant effects of elevation, season and age on the frequency of scrounging over the first 20 trials of both cognitive tasks (table 1). Birds at high elevation scrounged significantly more than birds at low elevation: 4.26 ± 0.16% of visits within the first 20 trials made at high elevation were scrounges, compared to 3.54 ± 0.25% of visits at low elevation. Adults also scrounged significantly more than juveniles; 4.08 ± 0.18% of visits during the first 20 trials made by adults were identified as scrounging events, compared to 3.61 ± 0.23% of visits made by juveniles. Finally, the frequency of scrounging varied significantly across years, with less frequent scrounging in the 2015–2016 and 2016–2017 seasons, and more frequent scrounging in the 2019–2020 and 2020–2021 seasons (figure 2). (See electronic supplementary material, table S5 for full pairwise comparisons.) There was no significant interaction between elevation and year. A more conservative analysis using a 3 s time window produced similar results for elevation and season, but age was not significant in this analysis (electronic supplementary material, table S6).

(e) Spatial learning performance and potential scrounging

When sex was not included in the model, allowing us to analyse the proportion of visits that were potential scrounges using the full sample size, there was no significant overall effect of cognition on scrounging (electronic supplementary material, figure S5a), but there were significant interactions between spatial learning performance and elevation, as well as between spatial learning performance and age (table 2). At low elevation, birds with worse spatial learning performance (both adults and juveniles) scrounged more frequently. However, at high elevation, this relationship was influenced by age: adults that made more cognitive errors scrounged more, while juveniles that made more cognitive errors scrounged less.

When sex was included in the analysis, reducing the sample size, these interactions were not present. There were

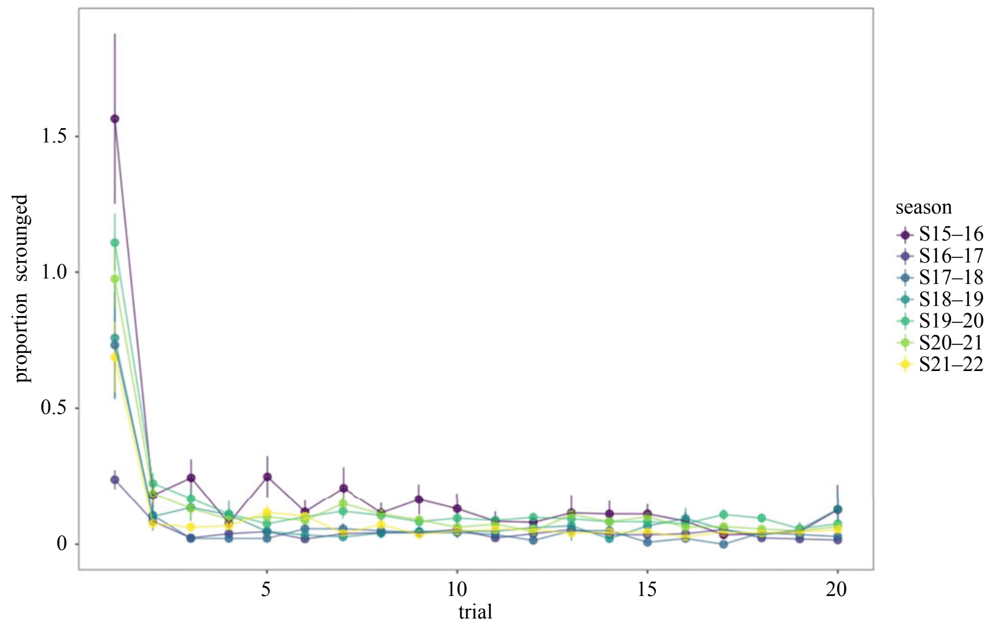

Figure 1. Proportion of visits classified as potential scrounging events during each of the first 20 trials of the two cognitive tasks (spatial learning task and reversal spatial learning task). Visits from the two tests are combined for this figure. Potential scrounging events were identified using the 5 s threshold. Colour indicates season and error bars indicate s.e. For both tests, birds scrounged significantly more during the first trial than in any subsequent trial.

Table 1. Mixed-effects model output with coefficient estimates and partial R^2 estimates for fixed effects. Frequency of scrounging (the number of visits classified as scrounging attempts divided by the total number of visits) was the dependent variable.

variable	d.f.	F	p	coefficient	s.e.	partial R^2	model partial R^2
elevation (high/low)	**1, 587.97**	**6.458**	**0.011**	**−0.007**	**0.003**	**0.009**	0.225
age (juv/adult)	**1, 710.52**	**33.725**	**<0.001**	**0.005**	**0.003**	**0.004**	
season: S16–17	6, 784	2.899	0.090	−0.015	0.005	0.011	
season: S17–18				−0.008	0.005	0.003	
season: S18–19				0.002	0.009	0	
season: S19–20				0.034	0.004	0.082	
season: S20–21				0.027	0.004	0.056	
season: S21–22				0.010	0.005	0.006	

significant effects of elevation, season and age on scrounging frequency, but no significant effects of sex or of spatial cognitive performance (table 3).

We repeated this analysis using the more conservative 3 s window for identifying scrounging events. When sex was not included in the model, results were similar to those from the 5 s window model, with significant main effects of elevation, age and season. However, the interaction between spatial learning score and age was not significant ($F_{1,\ 778.91} = 3.262$, $p = 0.071$; electronic supplementary material, table S7). When sex was included, we found the same trends with significant main effects of elevation and season, but no significant main effects of age, sex or spatial learning score, and no significant interactions (electronic supplementary material, table S8).

(f) Spatial reversal learning performance and potential scrounging

When sex was not included in the analysis, there was no significant effect of reversal learning performance (mean number of location errors per trial over the first 20 trials) on frequency of scrounging (electronic supplementary material, figure S5b), although there were significant effects of elevation and season (table 4). However, when sex was introduced, there was a significant interaction between reversal performance and sex, as well as a significant main effect of sex (table 5). In this subset of birds, females scrounged slightly more than males, with 3.84 ± 0.27% of visits during the first 20 trials by females classified as scrounging events, compared to 3.65 ± 0.24% of visits made by males. Additionally, frequency of scrounging was positively correlated with reversal errors (worse reversal learning performance) in males (slope = 0.016 ± 0.007), but negatively correlated in females (slope = −0.017 ± 0 0.009).

An analysis with the more conservative 3 s window produced similar results. When sex was not included in the model, we found significant main effects of elevation, age and season, but no significant main effect of reversal cognition score, and no significant interactions (electronic supplementary material, table S9). When sex was included, the interaction between reversal spatial cognition and sex was not significant ($F_{1,\ 549.93} = 1.036$, $p = 0.309$). This model found significant main

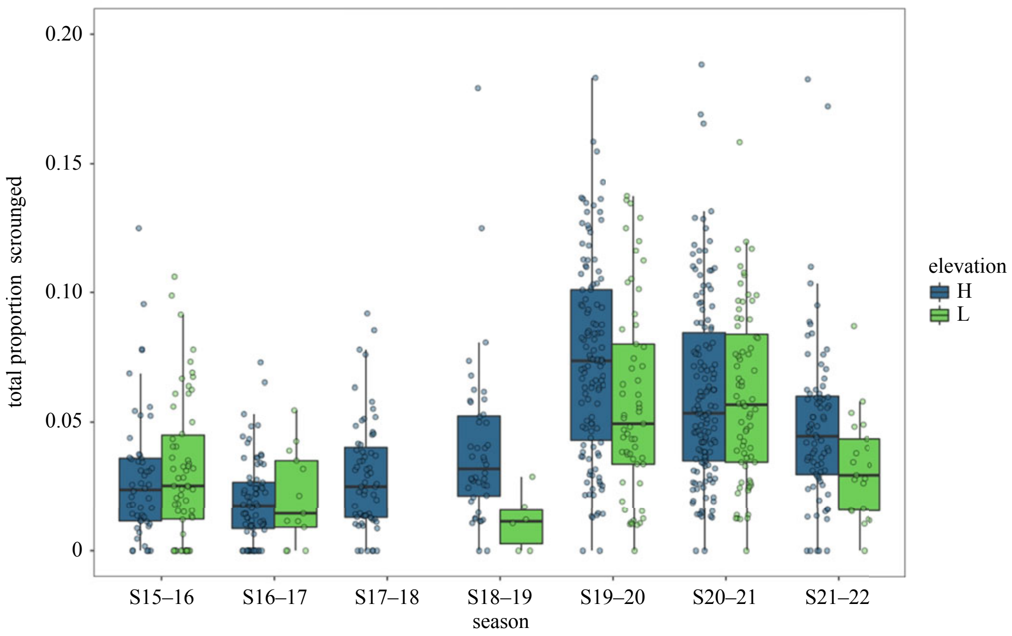

Figure 2. Proportion of visits classified as potential scrounging events during the first 20 trials of the two cognitive tasks (spatial learning task and reversal spatial learning task), separated by testing season. Visits from the two tests are combined for this figure. Colour indicates elevation.

Table 2. Mixed-effects model output with coefficient estimates and partial R^2 estimates for fixed effects. Frequency of scrounging (the number of visits classified as scrounging attempts divided by the total number of visits) was the dependent variable. Spatial learning score was defined as the total number of non-rewarding feeders visited per trial during the first 20 trials of the spatial learning task, adjusted to exclude scrounging attempts from being counted as errors. Sex was not included in this model.

variable	d.f.	F	p	coefficient	s.e.	partial R^2	model partial R^2
spatial learning score	1, 776.67	0.543	0.461	0.003	0.005	0	0.234
elevation (high/low)	**1, 759.48**	**9.467**	**0.002**	**−0.022**	**0.007**	**0.012**	
age (juv/adult)	**1, 779.43**	**8.491**	**0.004**	**0.019**	**0.006**	**0.010**	
season: S16–17	**6, 713.08**	**33.662**	**<0.001**	**−0.015**	**0.005**	**0.012**	
season: S17–18				**−0.009**	**0.005**	**0.003**	
season: S18–19				**0.002**	**0.006**	**0**	
season: S19–20				**0.034**	**0.004**	**0.080**	
season: S20–21				**0.026**	**0.005**	**0.052**	
season: S21–22				**0.008**	**0.005**	**0.004**	
spatial learning score * elevation	**1, 779.45**	**5.111**	**0.024**	**0.015**	**0.007**	**0.006**	
spatial learning score * age	**1, 774.73**	**6.119**	**0.014**	**−0.015**	**0.006**	**0.008**	

effects of elevation and season, but no significant main effects of sex, age or reversal spatial learning score (electronic supplementary material, table S10).

(g) Relationship between producer and scrounger cognition

There was no significant relationship between scrounger and producer cognitive performance in either spatial learning scores (electronic supplementary material, figure S6) or reversal learning scores (electronic supplementary material, figure S7). When examining producer spatial learning scores alone, we found significant interactions between season and elevation ($F_{5,\ 2537} = 2537$, $p < 0.001$), as well as a significant main effect of season ($F_{6,\ 2537} = 19.524$, $p < 0.001$; table 6), indicating that producer spatial learning performance varied significantly between seasons, and between elevations in some seasons. When examining producer reversal spatial learning scores alone, we also found a significant interaction between season and elevation ($F_{5,\ 1458.67} = 2.5277$, $p = 0.027$) and a significant main effect of season ($F_{6,\ 1489.37} = 8.309$, $p < 0.001$; table 7).

4. Discussion

Overall, our study suggests that scrounging behaviour is conditional, and not a common and stable foraging strategy in food-caching mountain chickadees when learning a new spatial task. The proportion of scrounging events was very low across all individuals (mean of 4.8% ranging from 0% to 15% of all visits within the first 20 trials), and most critically,

Table 3. Mixed-effects model output with coefficient estimates and partial R^2 estimates for fixed effects. Frequency of scrounging (the number of visits classified as scrounging attempts divided by the total number of visits) was the dependent variable. Spatial learning score was defined as the total number of non-rewarding feeders visited per trial during the first 20 trials of the spatial learning task, adjusted to exclude scrounging attempts from being counted as errors. Sex was included in this model as a binomial factor; birds of unknown sex were excluded from this analysis.

variable	d.f.	*F*	*p*	coefficient	s.e.	partial R^2	model partial R^2
spatial learning score	1, 543.38	0.210	0.647	−0.002	0.007	0	0.256
elevation (high/low)	**1, 374.00**	**11.926**	**<0.001**	**−0.012**	**0.004**	**0.023**	
age (juv/adult)	1, 549.71	3.276	0.071	0.007	0.004	0.006	
season: S16–17	**6, 503.42**	**24.6702**	**<0.0001**	**−0.017**	**0.006**	**0.016**	
season: S17–18				**−0.010**	**0.006**	**0.005**	
season: S18–19				**−0.001**	**0.007**	**0**	
season: S19–20				**0.034**	**0.005**	**0.076**	
season: S20–21				**0.025**	**0.005**	**0.040**	
season: S21–22				**0.010**	**0.006**	**0.005**	
sex (F/M)	1, 292.04	0.349	0.349	−0.002	0.003	0.001	

Table 4. Mixed-effects model output with coefficient estimates and partial R^2 estimates for fixed effects. Frequency of scrounging (the number of visits classified as scrounging attempts divided by the total number of visits) was the dependent variable. Reversal spatial learning score was defined as the total number of non-rewarding feeders visited per trial during the first 20 trials of the reversal spatial learning and experiment, adjusted to exclude scrounging attempts from being counted as errors. Sex was not included in this model.

variable	d.f.	*F*	*p*	coefficient	s.e.	partial R^2	model partial R^2
reversal spatial learning score	1, 781.07	1.306	0.254	0.006	0.005	0.002	0.227
elevation (high/low)	**1, 587.74**	**6.089**	**0.014**	**−0.007**	**0.003**	**0.008**	
age (juv/adult)	1, 783	3.054	0.081	0.005	0.004	0.004	
season: S16–17	**6, 710.02**	**33.935**	**<0.001**	**−0.015**	**0.005**	**0.012**	
season: S17–18				**−0.008**	**0.005**	**0.003**	
season: S18–19				**0.002**	**0.006**	**0**	
season: S19–20				**0.035**	**0.004**	**0.084**	
season: S20–21				**0.027**	**0.004**	**0.056**	
season: S21–22				**0.010**	**0.005**	**0.006**	

almost all scrounging events occurred during the first trial of each cognitive task when birds had not yet discovered their rewarding feeder. Once birds discovered their rewarding feeder, even if they had scrounged before, they rarely scrounged in subsequent trials and instead relied on their own learning and memory abilities to locate their rewarding feeder. In addition, scrounging was not repeatable across learning tasks or years in the same individuals, suggesting that it is an opportunistic behaviour rather than a stable alternative strategy in this species. Importantly, despite having double the amount of time available to scrounge during the first 4 years due to the slower pace of the closing doors, two of these years were associated with less scrounging than in the years when less time was available to scrounge. Our results are specific to spatial learning task conditions and do not extend to all possible foraging scenarios—it remains possible that food-caching species engage in scrounging when learning spatial locations is not needed.

We also found that scrounging behaviour was unrelated to both spatial cognition and memory performance and reversal spatial cognition performance; birds with worse performance did not scrounge more frequently. While we observed interactions between age and spatial cognition and memory performance, and between sex and reversal spatial cognition performance, these interactions were only present when we defined potential scrounging with a 5 s threshold and were not seen when we used the more stringent 3s threshold, making it difficult to draw conclusions about these observations. We also saw no relationship between producer performance and scrounger performance on either cognitive metric: birds did not preferentially 'scrounge up' from better performers.

Despite the low frequency of detected scrounging, we still observed differences between elevations, sexes, ages and among years with different winter conditions. Birds appear to scrounge less in years with harsh winter conditions. For instance, 2016–2017, a year where scrounging was infrequent, was one of the snowiest years on record, as was 2018–2019; meanwhile, 2019–2020, 2020–2021 and 2021–2022 were very mild years associated with less snow and drought (electronic supplementary material, figure S8), and these were years when scrounging was significantly higher (figure 2). These results suggest that when winters

Table 5. Mixed-effects model output with coefficient estimates and partial R^2 estimates for fixed effects. Frequency of scrounging (the number of visits classified as scrounging attempts divided by the total number of visits) was the dependent variable. Reversal spatial learning score was defined as the total number of non-rewarding feeders visited per trial during the first 20 trials of the reversal spatial learning experiment, adjusted to exclude scrounging attempts from being counted as errors. Sex was included in this model as a binomial factor; birds of unknown sex were excluded from this analysis.

variable	d.f.	*F*	*p*	coefficient	s.e.	partial R^2	model partial R^2
reversal spatial learning score	1, 561.85	0.0217	0.883	−0.017	0.007	0.007	0.271
sex (F/M)	**1, 528.55**	**8.1843**	**0.004**	**−0.018**	**0.009**	**0.015**	
elevation (high/low)	**1, 381.01**	**13.4460**	**<0.001**	**−0.013**	**0.006**	**0.026**	
age (juv/adult)	**1, 560.53**	**4.4249**	**<0.001**	**0.008**	**0.004**	**0.008**	
season: S16–17	**6, 509.50**	**25.7927**	**<0.001**	**−0.017**	**0.006**	**0.015**	
season: S17–18				**−0.010**	**0.006**	**0.005**	
season: S18–19				**−0.001**	**0.007**	**0**	
season: S19–20				**0.034**	**0.005**	**0.081**	
season: S20–21				**0.026**	**0.005**	**0.046**	
season: S21–22				**0.011**	**0.006**	**0.007**	
reversal score * sex	**1, 561.88**	**8.7344**	**0.003**	**0.033**	**0.011**	**0.015**	

Table 6. Model output for the relationship between producer and scrounger cognition during the spatial learning and memory task. Spatial learning score was defined as the total number of non-rewarding feeders visited per trial during the first 20 trials of the spatial learning task, adjusted to exclude scrounging attempts from being counted as errors.

variable	d.f.	*F*	*p*
scrounger spatial learning score	1, 2537	1.712	0.191
elevation	1, 2537	1.729	0.189
season	**6, 2537**	**19.524**	**<0.001**
elevation * season	**5, 2537**	**2.537**	**<0.001**

Table 7. Model output for the relationship between producer and scrounger cognition during the reversal spatial learning task. Reversal spatial learning score was defined as the total number of non-rewarding feeders visited per trial during the first 20 trials of the reversal spatial learning experiment, adjusted to exclude scrounging attempts from being counted as errors.

variable	d.f.	*F*	*p*
scrounger reversal spatial learning score	1, 533.26	0.191	0.662
elevation	1, 2462.68	0.286	0.593
season	**6, 1489.37**	**8.309**	**<0.001**
elevation * season	**5, 1458.67**	**2.528**	**0.027**

are extremely harsh, producer strategies may be favoured, but when winters are milder, scrounging may provide more benefits. However, scrounging was also low in 2015–2016, a relatively mild year.

In contrast with the previous explanation, birds at high elevations, with a harsher winter climate, scrounged more than birds at low, milder elevations, suggesting that the association between winter climate and scrounging is not a simple one. One potential explanation for these seemingly contradictory results is that the differences in scrounging between elevations are due to differences in the number of birds visiting the arrays, and the frequency and timing of those visits. In all years, more chickadees visited arrays at high elevation than at low elevation. Furthermore, birds at high elevation forage in a more time-limited way than at low elevation, concentrating feeder visits to specific times of day [43]. It is likely that greater numbers of birds visiting the arrays at high elevation, and the increased overlap in timing of foraging, presented more opportunities for individuals who had not found their rewarding feeder to scrounge. At the same time, we found no significant interaction between elevation and year, so year-to-year differences in scrounging were similar across high and low elevation. These results support the idea that harsher winters were associated with less frequent scrounging at both elevations, while birds at high elevation likely scrounged more frequently overall than those at low elevation because they had more opportunities to do so.

Adult birds also engaged in more scrounging than juveniles, which could be due to differences in social dominance status. Adults are socially dominant over juveniles [40] and more likely to displace other birds. Juveniles, on the other hand, may avoid scrounging if it requires displacing an adult. Higher dominance rank has been associated with increased scrounging in other bird species [9,44], although this pattern is not universal, particularly if scrounging does not require displacement [8,45].

Our findings contrast with those reported in non-caching but closely related parid species, such as great tits, which appear to regularly engage in scrounging as a stable strategy [39] and demonstrate consistent individual differences in scrounging frequency [15,19,20] when solving a novel problem or learning an associative learning task. Moreover, great tits appear to scrounge regularly when learning a task similar to the one in our study [20]. Food-caching birds rely on spatial cognitive abilities to retrieve thousands of cached food items, and their survival during winter is directly connected to their spatial cognitive abilities [30]. Therefore, learning can be strongly preferred as a more reliable strategy compared to scrounging, at least when presented with a novel spatial learning task. As food caches in chickadees consist of single food items [46], cache pilfering has limited potential benefits compared to cache retrieval. Furthermore, previous work has demonstrated that chickadees engage in cache protection behavioural strategies directed at both conspecific and heterospecific potential pilferers [30,31] and that cache pilferage in Parids is rare [32], suggesting that cache pilferage is unlikely to be a stable alternative form of scrounging in this system. While cache pilfering can likely occur, considering that each cache contains a single food item and that cachers actively avoid being observed when caching, it is likely opportunistic, and it is unlikely that some individuals can use cache pilfering as a stable alternative strategy for finding food.

There are several potential limitations to our study design. Given the relatively short time window during which scrounging is possible, the scrounging task we studied (which requires waiting for a producer to arrive and responding quickly when it departs) may be potentially more difficult than the producing task—learning the location of the rewarding feeder. However, birds in the first 4 years of the study had double the amount of time available to scrounge due to the slower door-closing rate during those years, yet scrounging patterns were similar across all years, suggesting that birds had sufficient time to scrounge. In addition, a few unbanded individuals were observed to scrounge regularly rather than leave the arrays completely, suggesting that scrounging in our system was sustainable.

Birds also have a second foraging strategy available, which could not be measured in this study: producers occasionally drop seeds during their visits to the feeder and other birds can retrieve these seeds from the ground. While there is competition for these fallen seeds from unbanded chickadees or other species, searching for a seed on the ground may be a less complex foraging strategy than visiting a feeder while the door is closing. Any bird without a PIT-tag could also be scrounging at the feeder and this would not be recorded in our data, but untagged birds cannot activate the feeders, so they do not have the option to ‘produce’ as defined in this study. However, for banded individuals, it seems likely that between their enhanced spatial learning and memory abilities (birds make very few errors after their initial 20 trials) and the other options available, even when individuals experienced successful scrounging at the beginning of spatial tasks, they did not continue scrounging but instead relied on their learning abilities to obtain food.

Finally, our automated feeders only recorded visits by potential scroungers when the feeder was still open but not the actual act of feeding. As a result, it is possible that some birds did not actually take food during these visits, but merely made a memory error shortly after another bird fed successfully, in which case such visits would not be scrounging. This appears unlikely because, under the conservative 3 s threshold, potential scroungers almost certainly arrived while the door was still open, and there is no reason to think that such a bird would not take food. Furthermore, birds that did not arrive in time to extract a seed from the feeder, but witnessed the door closing, could still make an association between arriving quickly and having an opportunity to obtain food, which could reinforce scrounging behaviour. In this case, such visits could be more accurately considered ‘scrounging attempts’ or ‘scrounging opportunities’ [20]. It is also possible that birds followed a producer to the feeder quickly not in an attempt to take seeds, but simply because the two were foraging in a group; however, as all birds had habituated to the feeder arrays at this time, and birds made independent visits to other non-rewarding feeders both before and after potential scrounges, this possibility does not fully account for the observed behaviour.

It would be interesting to investigate whether our conclusions would change if we allowed even more time for the feeder door to stay open after a visit by a producer, making scrounging simpler to execute, but such an approach would bring other complications to any interpretations because if the doors were to stay open for longer, this would increase the likelihood of birds simply detecting food visually rather than by following producers. In addition, considering that there are multiple birds accessing the arrays simultaneously, increasing the time for door opening would result in multiple feeders having open doors at the same time, so birds could simply search at random instead of learning the task, and such random search may be more efficient than learning while being unrelated to scrounging. Yet we did not detect any differences in scrounging patterns between the years when birds had double the amount of time for scrounging. In addition, significantly reducing the costs of scrounging by providing unlimited time would provide ecologically unnatural conditions, at least for food-caching chickadees. Our experimental design, on the other hand, tests for scrounging in ecologically relevant settings when birds obtain food one item at a time and when the time available for scrounging is short as chickadees move rapidly from location to location when foraging.

Overall, we found little evidence for scrounging when birds were learning a novel spatial task, suggesting that it may not be a common or stable strategy in this food-caching species with specialized spatial cognitive abilities. While it is possible that these species engage in scrounging in some foraging conditions, especially when obtaining food does not require spatial learning, our data suggest that when spatial learning can be used, such as in a spatial cognitive tasks, individuals rely on their cognitive abilities rather than engaging in scrounging. In caching species, food stores are essential for winter survival and spatial cognitive abilities are critical for finding these food items. Moreover, individual variation in spatial cognitive abilities is associated with differences in overwinter survival ([30,47]), suggesting that individuals with inferior spatial cognitive abilities have no alternative strategy that provides equivalent survival benefits to cognition-based cache retrieval. Our results also showed that scrounging had no effect on our measurements of cognition.

Ethics. All animal procedures were in accordance with University of Nevada Reno Institutional Animal Care and Use protocols 20-11-1103-1, 20-06-104 and 20-08-1062; California Department of Fish and Wildlife Scientific Permit D-0011776516-4 and US Federal Bird Banding Permit 22878.

Data accessibility. Data and code are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.nvx0k6dww [48].

Additional information is provided in the electronic supplementary material [49].

Authors’ contributions. V.K.H.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft and writing—review and editing; A.M.P.: data curation and writing—review and editing; B.R.S.: investigation and writing—review and editing; C.L.B.: investigation and writing—review and editing; L.M.B.: investigation and writing—review and editing; J.F.W.: investigation and writing—review and editing; L.E.W.: investigation and writing—review and editing; E.S.B.: resources, software and writing—review and editing; V.V.P.: conceptualization, funding

acquisition, investigation, methodology, resources, supervision, writing—original draft and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This study was funded by NSF grants (IOS-1856181 and IOS2119824) to V.V.P.

Acknowledgements. All animal procedures were in accordance with University of Nevada Reno Institutional Animal Care and Use protocols 20-11-1103-1, 20-06-104 and 20-08-1062; California Department of Fish and Wildlife Scientific Permit D-0011776516-4 and US Federal Bird Banding Permit 22878. Critical and constructive criticisms from two anonymous reviewers significantly improved the manuscript.

References

1. Barnard CJ, Sibly RM. 1981 Producers and scroungers—a general model and its application to captive flocks of house sparrows. *Anim. Behav.* **29**, 543–550. (doi:10.1016/S0003-3472(81)80117-0)
2. Giraldeau LA, Dubois F. 2008 Social foraging and the study of exploitative behavior. *Adv. Study Behav.* **38**, 59–104. (doi:10.1016/S0065-3454(08)00002-8)
3. Spencer R, Broom MA. 2018 A game-theoretical model of kleptoparasitic behavior in an urban gull (Laridae) population. *Behav. Ecol.* **29**, 60–78. (doi:10.1093/beheco/arx125)
4. Reader S. 2015 Causes of individual differences in animal exploration and search. *Top. Cogn. Sci.* **7**, 451–468. (doi:10.1111/tops.12148)
5. Giraldeau LA, Caraco T. 2000 *Social foraging theory*. Princeton, NJ: Princeton University Press.
6. Giraldeau LA, Soos C, Beauchamp G. 1994 A test of the producer-scrounger foraging game in captive flocks of spice finches, *Loncbura punctulata*. *Behav. Ecol. Sociobiol.* **34**, 251–256. (doi:10.1007/BF00183475)
7. Mottley K, Giraldeau LA. 2000 Experimental evidence that group foragers can converge on predicted producer–scrounger equilibria. *Anim. Behav.* **3**, 341–350. (doi:10.1006/anbe.2000.1474)
8. Beauchamp G. 2006 Phenotypic correlates of scrounging behavior in zebra finches: role of foraging efficiency and dominance. *J. Ethol.* **112**, 873–878. (doi:10.1111/j.1439-0310.2006.01241.x)
9. Liker A, Barta Z. 2002 The effects of dominance on social foraging tactic use in house sparrows. *Behaviour* **139**, 1061–1076. (doi:10.1163/15685390260337903)
10. Mathot KJ, Giraldeau LA. 2008 Increasing vulnerability to predation increases preference for the scrounger foraging tactic. *Behav. Ecol.* **19**, 131–138. (doi:10.1093/beheco/arm114)
11. Mathot KJ, Wright J, Kempenaers B, Dingemanse NJ. 2012 Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity. *Oikos* **121**, 1009–1020. (doi:10.1111/j.1600-0706.2012.20339.x)
12. Katsnelson E, Motro U, Feldman MW, Lotem A. 2011 Individual-learning ability predicts social-foraging strategy in house sparrows. *Proc. R. Soc. B* **278**, 582–589. (doi:10.1098/rspb.2010.1151)
13. Vickery W, Giraldeau LA, Templeton J, Kramer D, Colin C. 1991 Producers, scroungers, and group foraging. *Am. Nat.* **137**, 847–863. (doi:10.1086/285197)
14. Beauchamp G, Kacelnik A. 1991 Effects of the knowledge of partners on learning rates in zebra finches *Taeniopygia guttata*. *Anim. Behav.* **41**, 247–253. (doi:10.1016/S0003-3472(05)80476-2)
15. Zandberg L, Quinn JL, Naguib M, van Oers K. 2017 Personality-dependent differences in problem-solving performance in a social context reflect foraging strategies. *Behav. Processes* **134**, 95–102. (doi:10.1016/j.beproc.2016.09.007)
16. Morand-Ferron J, Giraldeau LA, Lefebvre L. 2007 Wild Carib grackles play a producer–scrounger game. *Behav. Ecol.* **18**, 916–992. (doi:10.1093/beheco/arm058)
17. King A, Nick I, Guy C. 2009 Ecological, social, and reproductive factors shape producer–scrounger dynamics in baboons. *Behav. Ecol.* **20**, 1039–1049. (doi:10.1093/beheco/arp095)
18. Harten L, Matalon Y, Galli N, Navon H, Dor R, Yovel Y. 2018 Persistent producer-scrounger relationships in bats. *Sci. Adv.* **4**, 1–11. (doi:10.1126/sciadv.1603293)
19. Aplin LM, Morand-Ferron J. 2017 Stable producer–scrounger dynamics in wild birds: sociability and learning speed covary with scrounging behaviour. *Proc. R. Soc. B* **284**, 20162872. (doi:10.1098/rspb.2016.2872)
20. Reichert MS, Morand-Ferron J, Kulahci IG, Firth JA, Davidson GL, Crofts SJ, Quinn JL. 2021 Cognition and covariance in the producer–scrounger game. *J. Anim. Ecol.* **90**, 2497–2509. (doi:10.1111/1365-2656.13551)
21. Pravosudov VV. 2022 Cognitive ecology in the wild — advances and challenges in avian cognition research. *Curr. Opin. Behav. Sci.* **45**, 101138. (doi:10.1016/j.cobeha.2022.101138)
22. Lefebvre L, Helder R. 1997 Scrounger numbers and the inhibition of social learning in pigeons. *Behav. Process.* **40**, 201–207. (doi:10.1016/s0376-6357(97)00783-3)
23. Morand-Ferron J, Cole E, Quinn J. 2015 Studying the evolutionary ecology of cognition in the wild: a review of practical and conceptual challenges. *Biol. Rev.* **91**, 367–389. (doi:10.1111/brv.12174)
24. Katsnelson E, Motro U, Feldman MW, Lotem A. 2008 Early experience affects producer–scrounger foraging tendencies in the house sparrow. *Anim. Behav.* **75**, 1465–1472. (doi:10.1016/j.anbehav.2007.09.020)
25. Morand-Ferron J, Giraldeau LA. 2010 Learning behaviorally stable solutions to producer–scrounger games. *Behav. Ecol.* **21**, 343–348. (doi:10.1093/beheco/arp195)
26. 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)
27. Croston R, Kozlovsky DY, Branch CL, Parchman TL, Bridge ES, Pravosudov VV. 2016 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)
28. Croston R, Branch CL, Pitera AM, Kozlovsky DY, Bridge ES, Parchman TL, Pravosudov VV. 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)
29. 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)
30. 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)
31. Pravosudov VV, Roth II TC, LaDage LD. 2010 Chickadees are selfish group members when it comes to food caching. *Anim. Behav.* **80**, 175–180. (doi:10.1016/j.anbehav.2010.04.013)
32. Brodin A, Ekman J. 1994 Benefits of food hoarding. *Nature* **372**, 510. (doi:10.1038/372510a0)
33. Benedict LM, Pitera AM, Branch CL, Kozlovsky DY, Sonnenberg BR, Bridge ES, Pravosudov VV. 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)
34. Pyle P. 1997 Molt limits in North American passerines. *N. Am. Bird Bander* **22**, 49–89.
35. 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)
36. 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)

37. R Core Team. 2021 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
38. Stoffel MA, Nakagawa S, Schielzeth H. 2017 rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods Ecol. Evol.* **8**, 1639–1644. (doi:10.1111/2041-210X.12797)
39. Firth JA, Voelkl B, Farine DR, Sheldon BC. 2015 Experimental evidence that social relationships determine individual foraging behavior. *Curr. Biol.* **25**, 3138–3143. (doi:10.1016/j.cub.2015.09.075)
40. Ekman J. 1989 Ecology of non-breeding social systems of Parus. *Wilson Bull.* **101**, 263–288.
41. Bates D, Maechler 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)
42. Jaeger B. 2017 r2glmm: Computes R Squared for Mixed (Multilevel) Models. R package v. 0.1.2. (See https://CRAN.R-project.org/package=r2glmm.)
43. 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)
44. Bugnyar T, Kotrschal K. 2002 Scrounging tactics in free-ranging ravens, *Corvus corax*. *Ethology* **108**, 993–1009. (doi:10.1046/j.1439-0310.2002.00832.x)
45. Jolles JW, Ostojić L, Clayton NS. 2013 Dominance, pair bonds and boldness determine social-foraging tactics in rooks, *Corvus frugilegus*. *Anim. Behav.* **85**, 1261–1269. (doi:10.1016/j.anbehav.2013.03.013)
46. Pravosudov VV, Roth TC. 2013 Cognitive ecology of food hoarding: the evolution of spatial memory and the hippocampus. *Annu. Rev. Ecol. Evol. Syst.* **44**, 173–193. (doi:10.1146/annurev-ecolsys-110512-135904)
47. Branch CL, Pitera AM, Kozlovsky DY, Sonnenberg BR, Benedict LM, Pravosudov VV. 2019 Elevation-related differences in the age structure of breeding birds suggest stronger selection at harsher elevations. *Behav. Ecol. Sociobiol.* **73**, 143–146. (doi:10.1007/s00265-019-2750-4)
48. Heinen VK, Pitera AM, Sonnenberg BR, Branch CL, Benedict LM, Welklin JF, Whitenack LE, Bridge ES, Pravosudov VV. 2023 Data from: Food-caching chickadees with specialized spatial cognition do not use scrounging as a stable strategy when learning a spatial task. Dryad Digital Repository. (doi:10.5061/dryad.nvx0k6dww)
49. Heinen VK, Pitera AM, Sonnenberg BR, Branch CL, Benedict LM, Welklin JF, Whitenack LE, Bridge ES, Pravosudov VV. 2023 Food-caching chickadees with specialized spatial cognition do not use scrounging as a stable strategy when learning a spatial task. Figshare. (doi:10.6084/m9.figshare.c.6700193)