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# Food-caching mountain chickadees can learn abstract rules to solve a complex spatial-temporal pattern

## Highlights

- Abstract rules are based on relations between items, not physical features
- Chickadees learned an abstract rule and used it to search for food more efficiently
- Chickadees did not learn the timing of a spatial-temporal task with daily changes
- Spatial tasks provide unique advantages to studying rule-learning

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## In brief

Learning abstract concepts was once considered uniquely human but has recently been shown in nonhuman animal species under laboratory conditions. Benedict et al. show that wild, food-caching mountain chickadees learned an abstract rule from experience with a foraging task set in natural conditions.

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# Food-caching mountain chickadees can learn abstract rules to solve a complex spatial-temporal pattern

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## SUMMARY

The use of abstract rules in behavioral decisions is considered evidence of executive functions associated with higher-level cognition. Laboratory studies across taxa have shown that animals may be capable of learning abstract concepts, such as the relationships between items, but often use simpler cognitive abilities to solve tasks. Little is known about whether or how animals learn and use abstract rules in natural environments. Here, we tested whether wild, food-caching mountain chickadees (*Poecile gambeli*) could learn an abstract rule in a spatial-temporal task in which the location of a food reward rotated daily around an 8-feeder square spatial array for up to 34 days. Chickadees initially searched for the daily food reward by visiting the most recently rewarding locations and then moving backward to visit previously rewarding feeders, using memory of previous locations. But by the end of the task, chickadees were more likely to search forward in the correct direction of rotation, moving away from the previously rewarding feeders. These results suggest that chickadees learned the direction rule for daily feeder rotation and used this to guide their decisions while searching for a food reward. Thus, chickadees appear to use an executive function to make decisions on a foraging-based task in the wild.

## INTRODUCTION

Many species have evolved cognitive strategies to learn and track where resources are located in variable environments.[1,2] As resources often change predictably in both time and space, animals may be able to learn and use rules to forage more efficiently.[3,4] Rules are generalizable concepts that have been learned from previous experiences and can be transferred to new situations,[5,6] such as when to leave a resource patch to maximize foraging efficiency.[4,7] Nonhuman animals are well known to learn rules based on perceptual concepts or generalization from physical characteristics.[6] But rule-learning based on abstract concepts remains controversial,[8] as it involves generalization based on the relationships between and among stimuli, regardless of specific physical characteristics.[6,9] Using abstract concepts to learn and use a rule is associated with executive functions, or higher-level cognitive processes that integrate different types of information for goal-oriented behaviors.[10] The ability to use abstract relational rules may be beneficial in variable environments with repeating conditions but has been considered supposedly unique to humans.[11,12] Recently, studies have found evidence for learning abstract rules in a wide variety of diverse taxa, including nonhuman primates,[9,13] other mammals,[14,15] birds,[16–19] fishes,[20,21] and invertebrates.[22,23] Yet, in other studies, nonhuman animals often fail to fully learn or use abstract concepts.[24–28] As such, how and why abstract learning abilities may vary across taxa or among individuals is still unclear.

Some of the controversy is due to methodologies that do not sufficiently rule out alternative strategies using simpler cognitive processes.[8,9] For example, rule-learning has been commonly tested in laboratory conditions using a classic serial reversal task in which individuals must repeatedly learn reward contingencies associated with two food sources.[29,30] In this task, individuals could improve their performance by learning the "win-stay, lose-shift" rule: return to the rewarding cue; if it stops rewarding, switch to a different cue.[29,31] This rule-based strategy likely involves executive functions to inhibit the previously learned association and shift to the correct rewarding cue.[29,31,32] But because the food reward alternates between the same two cues, an individual could simply learn to search in the order of most recent memory.[29,33] In other words, performance on a serial reversal learning task could demonstrate rule-learning but is often inconclusive when evaluating whether or not the learned rule was abstract.

Failure to learn an abstract rule could also be explained by alternative strategies, depending on the task design.[16,27,34] For

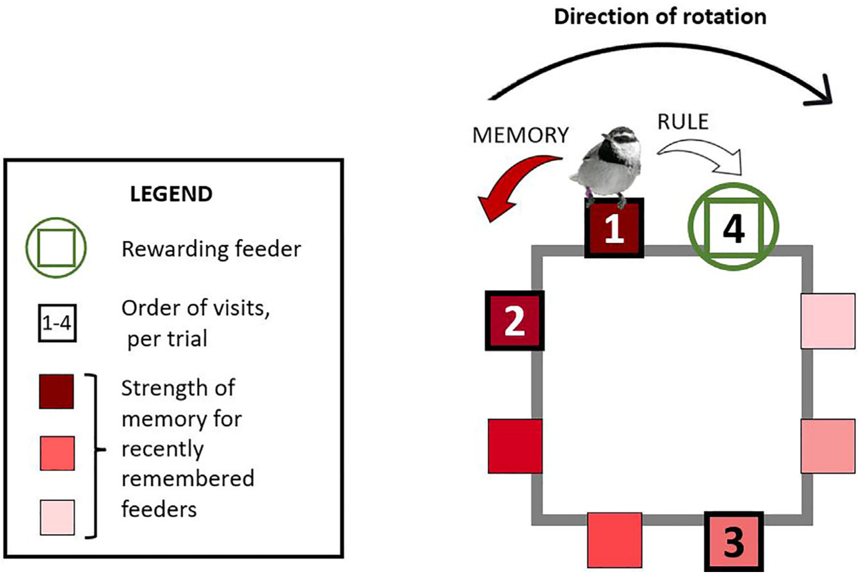

**Figure 1. Spatial-temporal task design**

Each day, the rewarding feeder (green circled square) for each bird is reassigned to the nearest feeder in the direction of rotation (e.g., clockwise). The strength of memory for recently remembered feeders (color of squares) decreases (from dark red to light red) in the opposite direction (e.g., counterclockwise). A bird starts a trial by visiting any feeder at the array and ends the trial by receiving a food reward at the correct rewarding feeder. Visits (numbered boxes) to unrewarding locations before finding the food reward are recorded as location errors. In this example, the bird started a trial by making a location error to the previous rewarding feeder from yesterday, defined as a reversal error (visit #1). After making a reversal error, the bird could search for the rewarding feeder by relying on spatial learning and memory to move in the direction of memory recency or by using the abstract rule to move in the direction of the feeder rotation, toward the correct rewarding feeder. Moving across the array would not provide evidence for either memory recency or rule-learning. In this example, the bird moved away from the correct rewarding feeder and toward the second-most recently remembered feeder (visit #2). The trial ended when it found the correct rewarding feeder on its 4th visit, after making a total of 3 location errors. See also Table S1.

example, a common test of abstract concept learning is the same/different task in which individuals must learn to match or identify pairs of items as “same” or “different” and then apply this relational rule to novel items.[35] Animals fail to learn the rule if they do not categorize the new items as well as the items in the training set.[8,9] However, this failure does not necessarily mean the animal lacks the ability to learn abstract concepts.[27] If the item pairs are repeated or share physical characteristics, then individuals could potentially use simpler perceptual concepts to learn associations with specific characteristics of the items, leading to poor performance.[16,25] An individual might also perform poorly if it has not had previous experience using abstract rules and so has not developed the mental representations needed to learn the rule during the task.[27,36] Similarly, without previous experience, an individual might be biased toward using certain cues, and may need to learn which cues are salient during a same/different task.[27] Testing wild animals with tasks that resemble natural conditions may address these alternatives by increasing the likelihood that individuals have already generated the necessary representations before testing. But because most studies have been conducted under laboratory conditions, it is unclear to what extent wild animals may use abstract rules in natural environments.

Here, we attempted to address these issues by using wild, food-caching mountain chickadees (*Poecile gambeli*) in their natural environment. We designed a novel experimental task to test whether chickadees could learn an abstract rule while making foraging decisions in a complex spatial-temporal task. Chickadees had to learn to track the daily location of a food reward that moved predictably around a square spatial array of eight feeders (Figure 1). Birds could visit any feeder at the array but could only receive a food reward from one feeder per day. We used “smart” feeders[37,38] to reassign each bird to a new rewarding feeder every day for 34 days, always rotating the food reward to the nearest feeder in the same direction (clockwise or counterclockwise; Figure 1). Through experience with the task, birds could learn the spatial pattern (*where* the food reward is located), the temporal pattern (*when* the food reward shifts), and the abstract rule (the relative *direction* that the food reward rotates). By learning all three, birds could also learn to predict where the food reward would be located the next day.

As a food-caching species, mountain chickadees rely on spatial learning and memory to make and retrieve individually cached food items throughout the winter.[39,40] Learning abstract rules may be advantageous because one rule could replace multiple learned associations, reducing overall cognitive load and reducing the possibility of previously learned associations interfering with the formation of new memories (i.e., proactive interference[32]). As chickadees store thousands of memories of caches,[40] any mechanism that reduces cognitive load could be highly beneficial (e.g., forgetting unnecessary cache locations after retrieval[32]). Moreover, chickadees appear to adjust foraging-based search behavior depending on environmental conditions (e.g., harshness) and previous experience.[41] It may be advantageous for chickadees to learn abstract rules that could be used to predict when and where ephemeral resources will be available, especially in harsh winter conditions when caloric requirements may be high.

The design of this spatial-temporal task allowed us to discriminate between two different processes that birds could use to solve the task. The smart feeders recorded all visits from tagged birds, allowing us to count how many incorrect feeder locations (i.e., location errors) were visited before finding a food reward (i.e., completion of a “trial,” Table S1). When a bird makes a location error at the beginning of a trial, it must decide where to search for food next. If the bird remembered the previous day’s reward location, then it likely made this error to that same location and has now learned that the reward contingency has changed. At this point, the chickadee’s next feeder visit

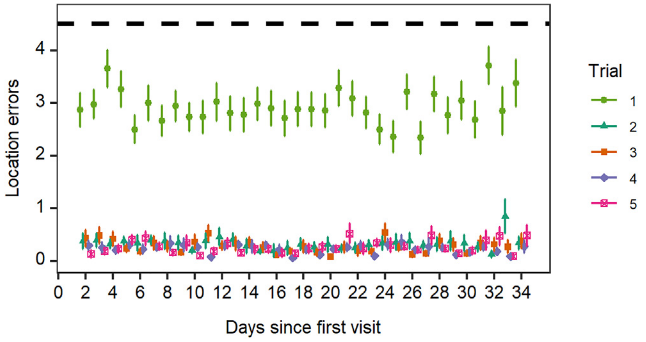

**Figure 2. Performance in the spatial-temporal task improved across trials 1–5 but not across days**

Mean location errors (points) and standard errors (error bars) per trial (color and shape). Heavy dashed line indicates performance based on chance (3.5 out of 7 location errors). See also Tables S1 and S3.

should provide information about which processes influenced its decision-making. First, if the chickadee relied on associative learning and memory recency, we would expect it to search for food by moving backward to visit the locations that most recently provided food. Second, if the chickadee learned the rule of the spatial-temporal rotation, we would expect it to search forward, moving toward the correct rewarding feeder and away from the previously rewarding feeders. This second method demonstrates using an abstract rule: birds must learn that the food reward is located in the feeder, one position to the left (or right) of the most recently rewarding feeder. They must then apply this learned relationship to new feeders, as the rewarding feeder location continues to rotate daily around the feeder array.

Behavior during the first trial completed each day (i.e., "trial 1") should reflect where the bird expected to find food when first visiting the array. Unlike all subsequent trials, trial 1 does not show evidence of learning because the bird does not learn the new rewarding feeder location until it finishes trial 1 and receives a food reward. Instead, trial 1 behavior should show how the bird searches. If chickadees learn to predict the spatial-temporal pattern using the abstract rule, they should search less during trial 1, leading to a reduction in trial 1 location errors as birds learn to go directly to the correct rewarding feeder. If birds learn to use the abstract rule but do not learn to predict the temporal pattern, we do not expect to see perfect performance (i.e., zero trial 1 location errors) but would expect to see fewer location errors to the previous day's rewarding feeder (i.e., a reversal error) throughout the task.

Finally, to assess the role of individual cognitive ability in learning an abstract rule, we used the same spatial feeder arrays to test two spatial cognitive abilities: spatial learning and memory ability,[38,42] as well as spatial reversal learning ability.[32,43] We expected that performance on the spatial-temporal task would correlate with performance on the spatial learning and memory task if birds were using associative memory as an alternative strategy (e.g., learning each rewarding feeder location every day), but would correlate with performance on the spatial reversal learning task if birds learned to use the abstract rule. We expected that the processes involved in reversal learning (i.e., inhibiting the recall of a previous memory and simultaneously learning new, similar information[30,32]) may also be associated with abstract-concept learning. We do not use reversal learning performance to estimate "general intelligence" or to draw conclusions about cognitive flexibility.[44]

## RESULTS

### Performance improved across trials but not across days in the spatial-temporal task

The number of location errors in trial 1 did not change significantly across days (generalized linear mixed model [GLMM] estimate ± SE: $-0.01 \pm 0.02$, $\chi^2_1 = 0.28$, $p = 0.59$) or with the number of trials completed the previous day ($0.002 \pm 0.02$, $\chi^2_1 = 0.12$, $p = 0.91$; $R^2_{GLMM(c)} = 0.13$; $R^2_{GLMM(m)} < 0.001$; $n = 55$; Figure 2). Birds performed better than chance in trial 1 every day, suggesting that search behavior was not random (one-sample t tests, Table S3). As trial 1 performance did not improve across the spatial-temporal task, birds did not appear to learn to predict the daily location of the rewarding feeder across days.

For trials 2–5, the number of location errors per trial was on average less than 1 location error and did not vary significantly across days (GLMM estimate ± SE: $-0.01 \pm 0.04$, $\chi^2_1 = 0.06$, $p = 0.80$) or with the number of trials completed during the previous day ($-0.03 \pm 0.03$, $\chi^2_1 = 0.99$, $p = 0.32$; Figure 2). Location errors per trial varied significantly among individual trials ($\chi^2_3 = 25.59$, $p < 0.001$; Figure 2) and there was a significant interaction effect between trials and days since first visit ($\chi^2_3 = 8.70$, $p = 0.03$). However, differences in the rate of change among trials 2–5 were small, with mean values less than 0.5 location errors across all days (Figure 2). Birds appeared to learn the location of each day's feeder rapidly after trial 1 but did not continue to improve overall performance in trials 2–5 across days.

### Birds did not learn to predict the temporal component of the spatial-temporal task

Birds consistently made a reversal error (i.e., a location error to the previous day's rewarding feeder) in trial 1 throughout the spatial-temporal task. The average probability of making a reversal error in trial 1 did not change significantly with days since first visit (GLMM estimates in log-odds scale ± SE: $0.341 \pm 0.06$, $\chi^2_1 = 0.29$, $p = 0.59$), but birds that completed more trials the previous day were significantly more likely to make a reversal error in the first trial the following day ($0.46 \pm 0.08$, $\chi^2_1 = 30.538$, $p < 0.001$; $R^2_{GLMM(c)} = 0.109$, $R^2_{GLMM(m)} = 0.059$; $n = 55$; Figure 3A). The consistency across days in making a reversal error after the food reward had moved suggests that birds did not learn the temporal component of the task.

The number of location errors made before the reversal error in trial 1 was small and increased significantly across days since first visit (GLMM negative binomial estimate ± SE: $0.18 \pm 0.05$, $\chi^2_1 = 12.29$, $p < 0.001$), but was not significantly associated with the number of trials completed the previous day ($-0.09 \pm 0.06$, $\chi^2_1 = 2.40$, $p = 0.12$; $R^2_{GLMM(c)} = 0.09$, $R^2_{GLMM(m)} = 0.03$, $n = 55$; Figure 3B). Despite this significant increase, birds on average only made ca. 1 location error before making a reversal error, even at the end of the task. This suggests that chickadees typically started a trial by making a reversal error at the beginning of the task, but toward the end of the task more birds were instead making a location error to another feeder first.

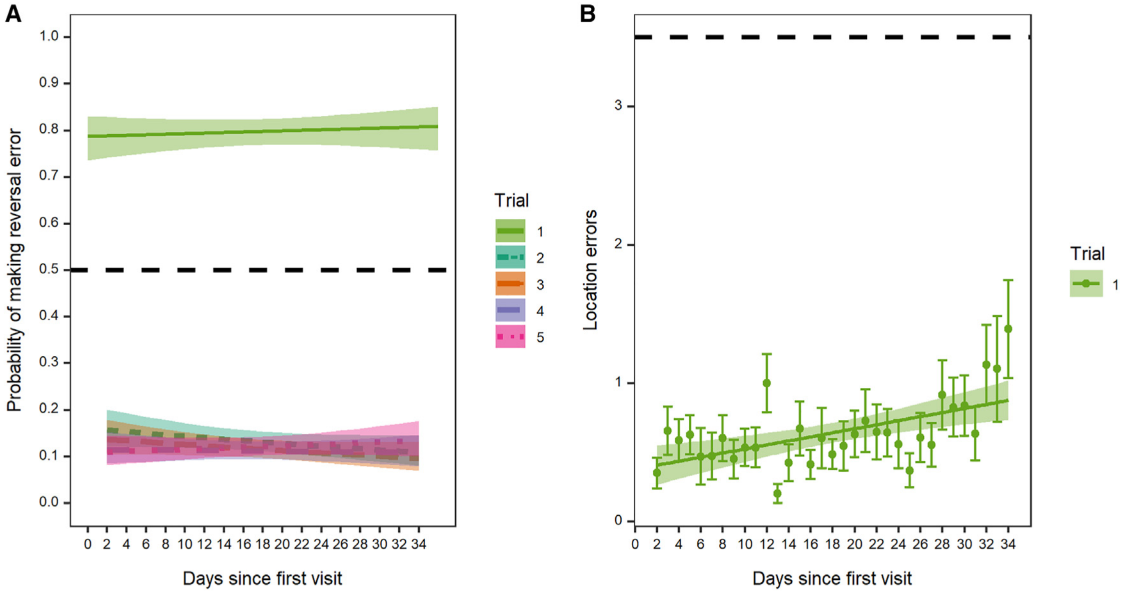

**Figure 3. Birds did not learn to predict the temporal component of the spatial-temporal task**

(A) Probability of making a reversal error (i.e., visit to previously rewarding feeder location) in trials 1–5 across days.

(B) Number of location errors before making a reversal error in trial 1 across days. Regression lines with 95% confidence intervals (shaded) generated from reported GLMMs. For (B), mean location errors (points) and standard errors (error bars) per trial generated from GLMMs, with an interaction of trial by day. Heavy dashed line indicates chance performance for (B), 3.5 out of 7 location errors. See also Table S1.

In trials 2–5, the average probability that a bird made a reversal error also did not vary significantly across days (GLMM estimate in log-odds scale ± SE: $-0.11 \pm 0.07$, $\chi^2_1 = 2.22$, $p = 0.14$), among trials ($\chi^2_3 = 3.50$, $p = 0.32$), with the number of trials completed the previous day ($-0.01 \pm 0.05$, $\chi^2_1 = 0.02$, $p = 0.88$), nor with an interaction between days since first visit and trials ($\chi^2_3 = 3.88$, $p = 0.27$; $R^2_{GLMM(c)} = 0.05$, $R^2_{GLMM(m)} = 0.004$; n = 55; Figure 3A). Unlike in trial 1, birds were unlikely to make a reversal error in trials 2–5 throughout the whole spatial-temporal task.

### Birds learned the abstract direction rule across days in the spatial-temporal task

The probability that a bird moved toward the correct feeder (i.e., in the direction of feeder rotation) after making a reversal error in trial 1 of each day significantly increased across days since the bird's first visit (GLMM estimate in log-odds scale ± SE: $0.30 \pm 0.06$, $\chi^2_1 = 24.55$, $p < 0.001$), but was not significantly associated with the number of trials completed the previous day ($-0.02 \pm 0.07$, $\chi^2_1 = 0.08$, $p = 0.78$; $R^2_{GLMM(c)} = 0.10$, $R^2_{GLMM(m)} = 0.03$; n = 55; Figure 4A). At the same time, the probability that a bird moved backward after making a reversal error (i.e., away from the correct rewarding feeder) significantly decreased across days since the bird's first visit (GLMM estimate in log-odds scale ± SE: $-0.28 \pm 0.06$, $\chi^2_1 = 20.80$, $p < 0.001$; previous day trials: $-0.05 \pm 0.07$, $\chi^2_1 = 0.52$, $p = 0.47$; $R^2_{GLMM(c)} = 0.08$, $R^2_{GLMM(m)} = 0.02$; n = 55; Figure 4B). Birds rarely moved across the array after visiting the previously rewarding feeder (4% of 1,242 trials). Overall, as the task continued, birds were less likely to move backward to the feeders that were rewarding most recently and were more likely to move forward toward the new rewarding feeder.

To address the possibility that birds could be biased to continue moving in a consistent direction around the arrays, we repeated this direction analysis with a conservative subset of only trials that started with a reversal error (825 trials, n = 55 unique birds). This subset excluded 34% of trials in the previous analysis and yielded similar results: the probability of moving toward the correct rewarding feeder increased from below random chance (50%) to above random chance by the end of the task (GLMM estimate in log-odds scale ± SE: $0.21 \pm 0.07$, $\chi^2_1 = 8.10$, $p = 0.004$; previous day trials: $0.13 \pm 0.08$, $\chi^2_1 = 2.54$, $p = 0.11$; $R^2_{GLMM(c)} = 0.09$, $R^2_{GLMM(m)} = 0.02$; n = 55; Figure 4A). The probability to move backward from the previous feeder also decreased significantly throughout the task (GLMM estimate in log-odds scale ± SE: $-0.21 \pm 0.07$, $\chi^2_1 = 8.10$, $p = 0.004$; trials completed the previous day: $-0.20 \pm 0.08$, $\chi^2_1 = 6.09$, $p = 0.01$; $R^2_{GLMM(c)} = 0.09$, $R^2_{GLMM(m)} = 0.02$; n = 55; Figure 4B). Birds rarely moved to the opposite side of the feeder array after visiting the previous feeder (3% of 825 trials). Overall, these results were consistent with previous models: as the task progressed, birds were less likely to move backward to visit recently rewarding feeders and were more likely to move forward toward the correct feeder, after making a reversal error to the previous day's rewarding feeder.

### No effect of spatial learning and memory performance on performance in spatial-temporal task

The number of location errors in trial 1 each day was not significantly associated with spatial learning and memory performance (GLMM estimate ± SE: $-0.11 \pm 0.10$, $\chi^2_1 = 1.10$, $p = 0.29$; days since first visit: $-0.02 \pm 0.06$, $\chi^2_1 = 0.11$, $p = 0.74$; $R^2_{GLMM(c)} = 0.08$; $R^2_{GLMM(m)} = 0.002$; n = 49). The average probability that a bird made a reversal error in trial 1 was also not significantly associated with spatial learning and memory performance (GLMM estimates in log-odds scale ± SE: 0.01 ±

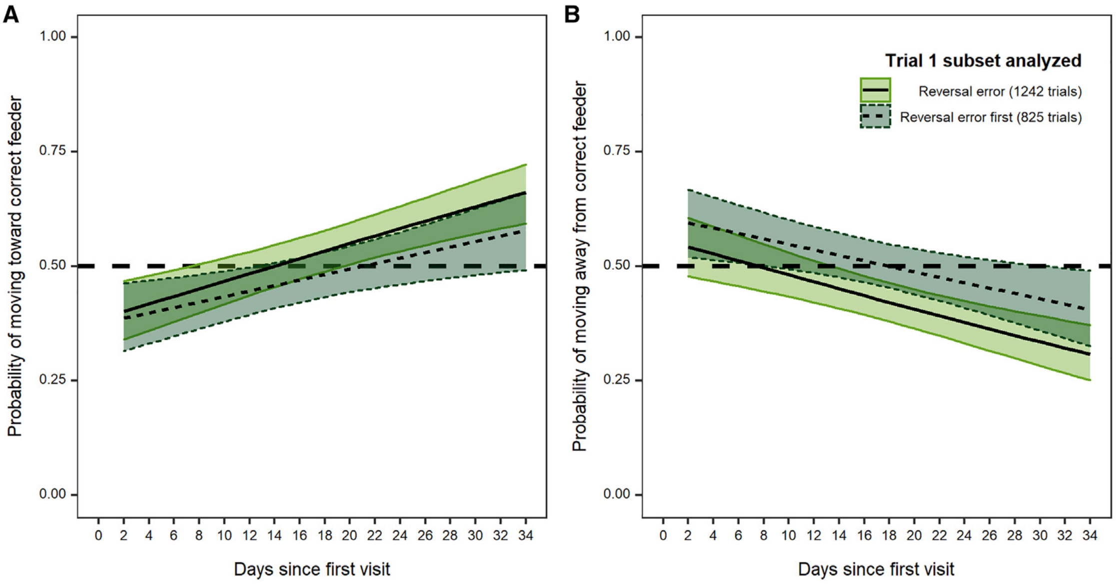

**Figure 4. Birds were more likely to search in the direction of rotation and away from recently rewarding feeders across days**

After making a reversal error in trial 1, the probability of moving (A) toward the correct feeder or (B) away from the correct feeder toward the feeders that were rewarding in the previous few days. Analysis using two subsets of trial 1: all trials with a reversal error (light green, solid line, 1,242 trials) or only trials with a reversal error as the first visit (dark green, dashed line, 825 trials). Linear regression lines and 95% confidence intervals (shaded) calculated from GLMMs (ggeffects). Heavy dashed line indicates chance levels (50%). See also Table S1.

0.09, $\chi_1^2 = 0.02$, p = 0.90; $R^2_{GLMM(c)} = 0.10$, $R^2_{GLMM(m)} = 0.05$; n = 49). The direction birds moved after making a reversal error did not vary with spatial learning and memory for the conservative dataset, either for the probability of moving toward the correct feeder location (GLMM estimate in log-odds scale ± SE: 0.07 ± 0.08, $\chi_1^2 = 0.40$, p = 0.53; $R^2_{GLMM(c)} = 0.08$, $R^2_{GLMM(m)} = 0.01$; n = 49) or away from the correct feeder location (GLMM estimate in log-odds scale ± SE: −0.01 ± 0.10, $\chi_1^2 = 0.01$, p = 0.93; $R^2_{GLMM(c)} = 0.08$, $R^2_{GLMM(m)} = 0.02$; n = 49).

## No effect of spatial reversal learning performance on performance in spatial-temporal task

The number of location errors in trial 1 each day was also not significantly associated with reversal learning performance (GLMM estimate ± SE: 0.03 ± 0.11, $\chi_1^2 = 0.09$, p = 0.77; days since first visit: −0.0247 ±SE = 0.06, $\chi_1^2 = 0.19$, p = 0.66; $R^2_{GLMM(c)} = 0.08$, $R^2_{GLMM(m)} < 0.001$; n = 47). The average probability that a bird made a reversal error in trial 1 was not significantly associated with reversal learning performance (GLMM estimates in log-odds scale ± SE: −0.06 ± 0.09, $\chi_1^2 = 0.49$, p = 0.48; $R^2_{GLMM(c)} = 0.09$, $R^2_{GLMM(m)} = 0.04$; n = 47).

## Birds made almost no location errors in the last 5 trials completed per day

Birds successfully learned the daily rewarding location by the end of each day: every day, birds made fewer than 0.5 mean location errors per trial in the last 5 trials of each day. The sum of location errors in the last 5 trials per day significantly decreased across days (GLMM estimate ± SE: −0.14 ± 0.03, $\chi_1^2 = 17.57$, p < 0.001; $R^2_{GLMM(c)} = 0.13$, $R^2_{GLMM(m)} = 0.02$; n = 55), but the number of errors was close to zero across the entire task (Figure S2).

## DISCUSSION

Overall, our data showed that wild, food-caching chickadees were able to learn an abstract rule for a complex spatial-temporal pattern in a natural setting. To our knowledge, this is the first time that abstract-concept learning has been demonstrated outside of a laboratory setting without using a serial reversal task. As predicted, as birds learned the spatial-temporal task, they appeared to rely less on spatial learning and memory and more on the direction rule to decide where to search next. Although at the beginning chickadees were less likely than chance to search in the correct direction of rotation (and equally likely to search away from the correct feeder), by the end of the task chickadees were significantly more likely to search toward the correct rewarding feeder (and less likely to search away). Due to the setup of the task, the choices were mutually exclusive: a bird could either use memory recency to move backward, searching feeders it likely remembered from previous days, or it could search toward the correct feeder, likely using the direction rule it had learned during the task. It is unlikely that birds could use memory recency or associative learning alone, without a mental representation of direction, to achieve this better-than-chance performance. Moreover, chickadees in this study system do not show directional bias while searching the feeder arrays for a food reward,[45] suggesting that the significant tendency to move in the direction of rotation is not likely due to passive directional biases or laterality in movement.

Although birds appeared to learn the directional rule, they did not learn to predict the temporal part of the task. Chickadees learned to search in the correct direction despite no significant change in trial 1 performance (the number of location errors or the likelihood of making a reversal error). Moreover, there was no significant association between these trial 1 metrics with either spatial learning and memory ability or spatial reversal learning performance. Although the former result supports our prediction that chickadees did not use simple associative learning to solve the spatial-temporal task, the latter was unexpected. One possible explanation is that chickadees at high elevation may rely strongly on spatial learning and memory to survive harsh winter environments,[37,38,46,47] and as such their reversal learning ability may be constrained by strong associations associated with winter caching. We have previously found that chickadees at lower, milder elevations performed better on tasks of reversal learning than chickadees at the higher elevation sites tested in this study.[33,43] Additionally, these low elevation birds were capable of learning to predict the location of a food reward across days in a serial reversal task, unlike high elevation birds,[33] suggesting there may be constraints to flexibility in a spatial context for the birds in this study. Unfortunately, due to low participation, we only analyzed one bird from low elevation and could not test for elevational differences in the present study. We speculate that motivation for low elevation birds to participate may have been low due to abundant natural food sources (i.e., pine nuts).

## Evidence for abstract-concept learning

Learning the direction rule presents evidence for abstract rule-based learning in wild mountain chickadees. The concept of direction in this task likely differs from other uses of direction in navigation. For example, desert ants navigate using path integration, in which individuals use the speed, distance, and direction previously traveled to update their position relative to a starting position.[48] But the representation of direction in path integration may not be abstract because it depends on specific characteristics of the landscape and the previous path that the animal traveled along. In contrast, birds in this study needed to learn the relative direction between previous rewarding feeder locations and then generalize this to new instances (days). By rotating the feeders every day, we prevented birds from learning the rule through simple associations. If a bird associated a given feeder's position with food one day, that bird could not use the same association to find food the next day. Considering that birds did not predict the temporal pattern, they may have learned the rule to search for food in the same direction of rotation. This abstract rule could be summarized as ''win-stay, lose-shift-forward,'' to make a comparison with the optimal strategy to solve a serial reversal task, the win-stay, lose-shift rule. Indeed, there was no correlation between individual spatial learning and memory performance and trial 1 performance on the spatial-temporal task, suggesting that search behavior was not likely determined primarily by associative learning ability. Finally, birds need to inhibit previous memories to learn to move forward, and such inhibition is also part of executive control.[49]

Abstract-concept learning associated with the same vs. different concept has been shown in many bird species, including pigeons,[16,50] corvids,[18,19,49,51] and closely related black-capped chickadees, *Poecile atricapillus*.[17] But reported performance varies widely, and the set sizes needed to train individuals to learn the abstract rules vary from hundreds to thousands.[9] Other types of rule-learning have been documented in birds as well, including ordering rules to recognize auditory sequences[52] and other rules that resemble language or grammar.[53] There has been debate about whether apparent abstract-concept learning could be better explained by other cognitive processes, such as associative learning or feature-based generalization.[8,9,25] A key difficulty in traditional abstract-concept learning tasks is the amount of featural overlap between the learned and transfer stimuli; when the tested stimuli share characteristics with the transfer stimuli, animals may be able to use simple, alternative processes to solve the task instead of a rule.[9] Our spatial-temporal task design limits featural overlap because the feeders were virtually identical in every dimension except for spatial location. The feeder construction ensured that the shape, size, color, material, and reward type for each feeder was the same, and even minor differences in appearance could not be used to find the correct food reward. Moreover, food-caching birds primarily use spatial cues over local cues,[38,39,54] making it less likely that featural overlap could have led birds to learn the rule through simple associative learning. Our spatial-temporal task also differed from previous abstract learning studies because it was conducted with wild, free-living birds in their natural habitat using a foraging task that allowed birds to move freely. Thus, the decisions about where to search during this task likely resembled decisions made during typical foraging behavior. It is well known that chickadees use specialized spatial cognitive abilities to retrieve self-made food caches during the fall and winter; but it has been less studied whether chickadees also use spatial cognition to make foraging decisions. Our spatial-temporal task likely resembles foraging from food sources that vary in accessibility due to harsh storms that prevent access to foraging during the winter. Although spatial tasks have been underutilized for studying abstract-concept learning, such tasks may provide unique advantages.

## Conclusion

Our study presents evidence for abstract rule-learning in wild birds in their natural environments, using a complex spatial-temporal pattern. We conclude that the behavior observed in this foraging task could only be explained by abstract rule-learning, as birds could only learn to search in the correct direction based on transferring learned associations to new feeders in the array. Yet, birds in this study did not learn to predict the spatial-temporal pattern, suggesting that there may be limits to the types of temporal cues or the range of abstraction that is possible for these birds. Using abstract rules could be adaptive in harsh or variable conditions, allowing animals to rapidly adjust their behavior to forage more efficiently. As there was substantial individual variation in abstract learning abilities, the next question is whether natural selection could potentially act on this individual variation in chickadees. Future directions should aim to understand the mechanisms driving this variation and whether it may be associated with heritable, genetic variation or may arise from individual differences in previous experience. We think it is important to conduct tasks that are ecologically relevant, to explore not only whether nonhuman animals can demonstrate executive functions but also whether animals use these higher-level abilities for decision-making with real consequences in the wild.

## STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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## SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2023.06.036.

A video abstract is available at https://doi.org/10.1016/j.cub.2023.06.036#mmc3.

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## AUTHOR CONTRIBUTIONS

Conceptualization, L.M.B. and V.V.P.; methodology, L.M.B., V.K.H., E.S.B., and V.V.P.; investigation, L.M.B., V.K.H., J.F.W., B.R.S., L.E.W., and V.V.P.; data curation, V.K.H. and B.R.S.; formal analysis, L.M.B.; writing – original draft preparation, L.M.B. and V.V.P.; visualization, L.M.B.; writing – reviewing & editing, L.M.B., V.K.H., J.F.W., B.R.S., L.E.W., E.S.B., and V.V.P.; funding acquisition, L.M.B., B.R.S., and V.V.P.; project administration, V.V.P., supervision, V.V.P.

## DECLARATION OF INTERESTS

The authors declare no competing interests.

## INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

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## STAR★METHODS

### KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|---|---|---|
| Deposited data | | |
| Spatial-temporal task data | Benedict | https://doi.org/10.17632/txk2vp6657.1 |
| Experimental models: Organisms/strains | | |
| Mountain chickadee, *Poecile gambeli* | Wild | NA |
| Software and algorithms | | |
| R Statistical Software | R Core Team[55] | RRID:SCR_001905 |
| Contributed R packages | Comprehensive R Archive Network (CRAN) | RRID:SCR_003005 |
| R Code | Benedict | https://doi.org/10.17632/txk2vp6657.1 |

### RESOURCE AVAILABILITY

#### Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Lauren Benedict (lbenedict@nevada.unr.edu).

#### Materials availability

This study did not generate new unique reagents.

#### Data and code availability

- All spatial-temporal task data have been deposited at Mendeley Data Repository and are publicly available as of the date of publication. DOIs are listed in the key resources table.
- All original code has been deposited at Mendeley Data Repository and is publicly available as of the date of publication. DOIs are listed in the key resources table.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

### EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

#### Study subjects and study system

The study was conducted during the winter of 2021-2022 as part of an ongoing, long-term study of Mountain chickadees (Poecile gambeli) in the Sierra Nevada mountains ca. 10 km north of Truckee, CA, USA (started in 2014 at Sagehen Experimental Forest, Sagehen Creek Field Station, University of California Berkeley[37,38,42,43,46]). Wild, free-living birds were trapped and banded during annual banding efforts and breeding surveys using mist nets at feeders or by hand in nestboxes. Trapped birds were banded with unique color bands, including a passive integrated transponder (PIT)-tag with a unique alphanumeric ID (IB Technology, Leicestershire, UK). Banding efforts were concentrated at two elevations (‘high’: ca. 2400m; ‘low’: ca. 1900m). Previous studies in this system found significant elevation-related differences in winter conditions as well as in behavioral, cognitive and morphological traits of chickadees residing at each elevation.[33,42,46,47,56] Although we collected data at two elevations within this study system, we did not explore elevational differences in the present study because our final sample contained only one low elevation bird compared to 54 high elevation birds. We speculate this was due to low participation of low elevation birds during this particular season.

The study was approved by the University of Nevada Reno Institutional Animal Care and Use Committee (Protocol numbers 00818, 00046 and 00603) and was in accordance with California Department of Fish and Wildlife Permit D-0011776516-4. For banding efforts, we followed the U.S. Federal Bird Banding Permit 22878. To the best of our knowledge, no birds were harmed by the collection of these data and wild-caught birds were only handled in the field for a few minutes during banding. We detected no negative effects of using PIT tags and color bands during our study. To reduce stress during handling, banding efforts were not conducted 2903475484326during adverse conditions (i.e., wind, precipitation).

## METHOD DETAILS

### Smart feeders and spatial arrays

Data were collected automatically using four spatial arrays of smart feeders previously established in 2014 (two at high elevation ca. 1.2 km apart, and two at low elevation[37,38,57]). Each array consisted of eight feeders attached equidistantly to a square aluminum frame (1.2x1.2m) that was suspended ca. 3m in the air from four trees in a small clearing (ca. 3m away from foliage on all sides). Each feeder had a perch-mounted antenna connected to a Radio-Frequency Identification (RFID) data logger to detect and record the identity and timestamp of any PIT-tagged bird that landed on the perch to forage.[58,59] Birds could only access black oil sunflower seeds from the perch. A mechanized door controlled individual access to food within each feeder according to three different program modes: (1) 'open' mode: feeder doors were always open so all birds could forage from all eight feeders; (2) 'all' mode: feeder doors were closed until any PIT-tagged bird landed on the perch and triggered the door to open, so all PIT-tagged birds could forage from all eight feeders; and (3) 'target' mode: feeder doors were closed until specific PIT-tagged birds landed on the perch, so only specific PIT-tagged birds could forage from each feeder. In target mode, feeders could be programmed individually for each bird and reassigned depending on the experiment, so that at any given time birds could only access food from one of eight feeders. During all three modes, PIT-tagged birds could forage at the arrays *ad libitum* during daylight hours (ca. 06:00-20:00) until feeders automatically closed and turned off each night. When feeders were off, visits were not recorded, and birds were not able to access their rewarding feeder. However, birds were expected to stop foraging several hours before the feeders turned off.[47]

### Trials during cognitive tasks

During each cognitive task, smart feeders automatically collected visit data from all PIT-tagged birds (bird ID, date, time), regardless of whether the bird received a food reward. Visits could be grouped into 'trials'; a trial began when a bird visited any feeder at an array and ended when the bird received a food reward at its assigned rewarding feeder (Figure 1; Table S1). Chickadees forage for seeds one-at-a-time, leaving the array to consume or cache the seed; thus, each trial resulted in a single food reward. Chickadee motivation to complete trials during each task was not constrained by appetite,[38] as caching drive is unrelated to daily energy requirements[60,61] and likely increases participation in food-rewarded tasks during caching seasons. During each trial, any incorrect feeder location that a bird visited before it found a food reward was counted as a 'location error' (Table S1). Chickadees search the array by landing and inspecting feeders one at a time by moving from feeder to feeder until they discover the rewarding feeder;[41] so birds could make a maximum of 7 location errors per trial, as there were eight total feeder locations in an array and only one provided a food reward per bird. Birds typically arrived at the arrays in small flocks but foraged individually, using both social and asocial information to search for food.[56,58]

### Spatial learning and memory task

To assess individual cognitive ability, we conducted a spatial learning and memory task following our previous work.[37,43] First, all feeders were set to 'open' mode (January 10-26, 2022) and then 'all' mode (January 26-February 2, 2022) to habituate the birds to the feeders at the arrays. Feeders switched to 'target' mode to start the spatial learning and memory task (February 2-6, 2022). For four days, access to the feeders was restricted so that each bird could only forage from one feeder in a given array. Birds were assigned to their rewarding feeder pseudorandomly: tagged birds were equally distributed across all eight feeders and no individual was assigned to the feeder that they had visited most frequently during 'all' mode. Birds rarely visited both arrays, which were spaced ca. 1.2km apart, and so were only assigned a 'target' feeder at one array. Performance was estimated as the mean number of location errors in the first 20 trials of the task, with better performance indicated by lower values. We have previously shown that this metric is a meaningful representation of individual variation and is associated with differences in fitness.[37,42,46,56,62]

### Spatial reversal learning task

Immediately after the spatial learning and memory task, the spatial reversal learning task began by changing the target feeder for each bird to another feeder on a different side of the spatial array (February 6-10, 2022). This was a single reversal task, not a serial reversal task, so there was only one change in reward contingencies. To minimize social learning, birds were reassigned individually.[43] Performance was estimated as the mean number of location errors in the first 20 trials of the task, with better performance indicated by lower values, following our previous work.[33,37,42,43,62]

### Spatial-temporal task

The spatial-temporal task began immediately after the spatial single reversal task (February 10 - March 16, 2022). Birds were reassigned to a new rewarding feeder overnight each day so that the food reward rotated either clockwise or counterclockwise to the next nearest feeder (Figure 1). Importantly, the feeders themselves did not move; instead, the Arduino board within each smart feeder automatically updated the list of specific birds that could access food at that feeder each day.[59] Birds were randomly assigned to either a clockwise or counterclockwise rotation, and the direction of rotation remained consistent for each bird throughout the task. Feeder assignments continued to rotate automatically for 34 days, changing overnight while feeders were closed so that each morning (starting at 06:00) birds could access the new day's rewarding feeder. Performance was estimated as the number of location errors per trial (range: 0-7) as well as whether or not the bird made a reversal error, or a location error made to the previous day's rewarding feeder.

## QUANTIFICATION AND STATISTICAL ANALYSIS

### Data exclusions for spatial-temporal data

In the spatial-temporal task, 165 birds completed at least one trial during the spatial-temporal task (n = 133 from high elevation, n = 32 from low elevation). Participation during the 34-day task varied across birds, both in terms of the number of days (1-34 days) and the number of completed trials per day (0-500 trials per day). We needed to account for this variation in participation because birds could only learn the rule by first learning the sequence of daily rewarding feeders. Each bird's experience should depend on which days it visited the array during the task and whether or not it learned the daily location of the food reward. For example, a bird that participated in 5 consecutive days of the task could learn the feeder sequence '1, 2, 3, 4, 5'. But a bird that participated in 5 nonconsecutive days, missing three days, would experience a different sequence of feeders: '1, 2, 6, 7, 8'. Birds with different perceptions of the daily feeder rotation may not be able to learn the abstract rule that we expected. Birds could fail to learn the daily feeder location due to poor cognitive ability or due to low participation; as such, it was important to exclude data due to low participation before analyses.

To compare birds based on their experience with the task, we created the variable 'days since first visit' to count the number of days since each bird completed its first trial during the spatial-temporal task. We defined a 'missed' day as any day during the spatial-temporal task that a bird was not detected at the array at all or that the bird completed fewer than 20 trials (Table S1). We chose the 20-trial threshold based on our previous work using mean performance scores over the first 20 trials of the two previous spatial cognitive tasks, which have been associated with variation in fitness outcomes.[42,62] Using 20 trials per day provided a conservative estimate to ensure that every bird had sufficient experience with the daily rewarding feeder both to learn and reinforce the spatial memory of the daily food reward. For analyses, data were excluded from days with fewer than 20 trials, as well as each day immediately following a missed day. The 'days since first visit' variable increased by 1 for each day, regardless of whether data were excluded (see Figure S1 for detailed examples).

Next, we made a distinction between missing two or more days in a row and only missing one day at a time. When returning to the feeder arrays after missing one day, a bird could potentially still learn the direction-rule because the next rewarding feeder would be located nearby in the correct direction. But after missing two or more consecutive days, the next rewarding feeder could be located on the opposite side of the array, or further away, and this could provide confusing information to the bird about the spatial-temporal task. As such, we excluded data from all trials after a bird missed two or more days in a row (Table S2; Figure S1). We only used data from *before* a bird missed two or more days in a row to make sure that we only analyzed birds when they attempted the task for the first time; partial experience with the task could affect learning performance.

Finally, we excluded data based on the total number of missed days, so that each bird never exceeded a maximum of four missed days or 15% of the total number of days analyzed in the study. When possible, we excluded data after a bird hit these maximum criteria (i.e., after the 4th missed day) instead of excluding the bird entirely (determined from the 'days since first visit' counter; Table S2; see Figure S1 for detailed examples). We also set a minimum threshold: we excluded birds that did not complete at least 16 days during the spatial-temporal task (including up to 2 missed days). To be conservative, if a bird missed a day within the last 3 days of its last day detected, we excluded all trials after that missed day.

The final dataset (n = 55) only contained one low-elevation bird, so elevational comparisons were dropped from the analysis. Lower participation at low elevation was not completely unexpected, as we have previously recorded low participation during the winters of 2017-2018 and 2018-2019. Overall, these exclusions were important because we could not control participation in the study and so needed another way to ensure that we only analyzed birds that had a reasonable opportunity to learn the task. It is possible that these exclusions may have introduced bias to the analysis by selecting a specific subset of birds. However, we do not think these exclusions substantially affected our interpretations because our conclusions can only be based on birds that completed testing every day. Motivation to participate in the spatial-temporal task every day is likely related to a wide variety of factors and is likely not associated with the individual cognitive abilities we focus on in this study.

### Analyses

The spatial-temporal task dataset consisted of longitudinal data collected from a known set of marked individuals measured repeatedly across time. We analyzed these data primarily through generalized linear mixed effects models (GLMMs) to assess how variation in performance varied throughout the task. All GLMMs included days since first visit as a fixed effect (range: 2-34 days, centered and scaled) and individual bird ID as a random intercept to account for pseudoreplication and temporal autocorrelation. Continuous variables were centered and scaled to compare explanatory variables with widely varying ranges and to improve residual fit and convergence.

We analyzed data from the first trial each bird completed per day ('trial 1'), the first 2-5 trials per day ('trials 2-5) and the last 5 trials per day separately to address different hypotheses. When a bird makes a reversal error during trial 1, the bird should learn that the reward contingency has changed and the direction the bird decides to move next should indicate where the bird expects to find food. This decision happens before receiving any reinforcement and should provide support for whether or not the bird learned the abstract rule. In contrast, behavior during all other trials after trial 1 reflects the bird's ability to overcome proactive interference and learn the new daily feeder location. We performed a specific analysis for the first 2-5 and not subsequent trials because we have previously found that birds learn new rewarding feeder locations extremely quickly[33,43] and we were interested in variation in the initial stages of the learning process. We analyzed data from the last five trials completed by each bird each day to confirm that the bird successfully learned the correct rewarding feeder, and so could be reasonably expected to learn the abstract rule. There was no overlap between the first and last 5 trials analyzed, since all birds completed at least 20 trials per day.

We calculated several metrics to explore our hypotheses: location errors, reversal errors, location errors before a reversal error and direction moved after making a reversal error. Location errors measure an individual's overall ability to learn the rewarding feeder location during the spatial-temporal task, whereas reversal errors measure the ability to learn new reward contingencies while inhibiting a response to the previously learned feeder location.[30,32] While some studies analyze repeated visits to a previously rewarding location to estimate reversal errors, we defined reversal errors as whether or not the bird visited the previous reversal location during a given trial. Birds could make a maximum of one reversal error per trial because there was only one feeder location providing a food reward on the previous day. This allowed us to use logistic regressions to analyze reversal errors across time during the spatial-temporal task. We were also interested in behavior before and after birds made a reversal error. The number of location errors before making a reversal error provided an estimate of whether or not birds went directly to the previous day's rewarding feeder at the beginning of a trial. This metric allowed us to assess to what extent birds were learning to predict or to retain memories of the previous feeder location. The direction a bird moves after making a reversal error provides information about where the bird expects to find food after conditions have changed and what strategy the bird may be using.

### Model fixed effects

To control for variation in reinforcement of the previous day's rewarding feeder, GLMMs that used metrics from the first 5 trials per day also included a fixed effect for the total number of trials completed the previous day ('previous day trials', range: 20-500, centered and scaled; Table S1). In models that included previous day trials as a fixed effect, we excluded the first day of the task, as there were no previous day trials reported. To explore the effects of spatial learning and memory ability and spatial reversal learning ability on performance in the spatial-temporal task, we fit separate GLMMs using the subset of birds that participated in all three cognitive tasks (Table S2). We used the mean location errors per trial in the first 20 trials of the spatial learning and memory task (range: 0.05-1.35 mean location errors per trial, scaled and centered) and for the spatial reversal learning task (range: 0.15-1.05 mean location errors per trial, scaled and centered).

### Overall performance in trial 1 and trials 2-5

To explore how performance on the spatial-temporal task varied across days, we fit a GLMM (Poisson distribution) to the number of location errors in trial 1 each day (range: 0-7 location errors) with fixed effects of days since first visit and previous day trials. To explore the effects of the other two cognitive tasks on trial 1 performance, we fit two additional GLMMs by adding either a fixed effect of spatial learning and memory performance or spatial reversal learning performance.

We compared mean performance in trial 1 (location errors) to chance level using one-sample student t-tests. These tests were aimed to determine whether birds were searching randomly during the first trial each day or whether they appeared to use learning and memory ability to find the correct feeder. Given eight choices, random expectation for location errors in one trial is equal to 4.5 errors.[63] Regarding the assumptions of the student t-test, these data were (a) continuous, (b) normally distributed, (c) represented a moderate sample size of $n = 55$ and passed a simple test for homogeneity of variance. To ensure that data were independent, we ran separate t-tests per day to avoid repeat measures of individuals (test statistics in Table S3). Multiple comparisons may inflate the risk of Type I errors, so caution should be used to analyze these results. The Bonferroni-adjusted threshold for significance is alpha = 0.0015, after dividing the original alpha value (0.05) by the number of tests (34 tests).

### Models for learning to predict the temporal component

To assess whether birds learned to predict the location of the correct rewarding feeder each day, we explored whether the probability of making a reversal error in trial 1 varied across days. If birds learned to predict during the spatial-temporal task, we expected to see an overall decrease in both the number of location errors and the probability of making a reversal error, suggesting that birds went directly to the correct feeder during trial 1 each day. We created a binary categorical response variable for whether or not a bird made a reversal error in trial 1 and fit a GLMM (binomial distribution, "logit link", reported in tables using log-odds scale) with the fixed effects of days since first visit and previous day trials. To explore the effects of the other two cognitive tasks on the probability of making a reversal error in trial 1, we fit two additional GLMMs by adding either a fixed effect of spatial learning and memory performance or spatial reversal learning performance.

To assess whether birds continued to make reversal errors during trials 2-5, we fit another GLMM (binomial distribution, logit link) with the probability of making a reversal error per trial as the response variable. We included fixed effects of days since first visit, trial number (categorical, four levels), previous day trials and an interaction effect between days and trial number. We included trial number as a fixed effect because we were interested in the differences in effect of each trial, as performance should continue to improve across trials.

We fit another model to estimate the number of location errors made before a reversal error in trial 1 each day. This should provide information about whether birds were making a reversal error first during the task, which would suggest they remembered where the previous day's food reward had been located. This only used the subset of trials in which birds made a reversal error, so this does not represent performance or likelihood of making a reversal error. We fit a GLMM (negative binomial distribution, using the MASS package[64]) to these location errors with fixed effects of days since first visit and previous day trials.

### Models for learning the direction rule

To assess whether the birds learned the abstract rule of feeder rotation, we scored each trial for the direction the bird moved after making a reversal error in trial 1. A trial was scored "toward" if the bird moved toward the correct feeder location, in the same direction as the daily feeder rotation and was scored "away" if the bird moved away from the correct feeder, toward the most recently rewarding feeders during the task. For example, consider that the feeders are numbered 1-8, increasing in the direction of rotation, and a bird was assigned to rotate clockwise around the arrays, starting with feeder 1 on day 1. In the first trial completed on day 2, this bird makes a reversal error by visiting feeder 1, the previous day's rewarding feeder. The direction for this trial would be scored depending on the next feeder that the bird visited: "away" for moving backwards to feeders 8 and 7; "toward" for moving forward in the correct direction of rotation to feeders 2, 3, or 4; and "unscored" for feeders across the array (feeders 6 and 5). We scored direction for two subsets of the data: a more conservative subset, in which a bird made a reversal error in trial 1 for their first visit of the trial, and a less conservative subset, in which a bird made a reversal error in trial 1 at any point during the trial. We tested the less conservative subset because if birds learned the direction-rule, then we would expect them to learn to move in the correct direction regardless of whether they remembered to go to the previous day's rewarding feeder first.

We used the direction data to make two binary category variables, one to indicate whether or not the bird went toward and one to indicate whether the bird went away from the correct rewarding feeder. We then fit GLMMs (binomial, logit link) with fixed effects of days since first visit and the number of trials completed the previous day, one for the toward and one for the away response variables. We fit two models using each data subset.

#### *Model for the last 5 trials per day*

To assess whether individuals learned each day's rewarding feeder location and assess how this performance varied across days, we calculated the sum of location errors in the last 5 trials completed each day. We fit a GLMM (Poisson distribution) to the sum of location errors in the last 5 trials with a fixed effect of days since first visit (see also Figure S2).

### Statistical software

All analyses were performed using R version 4.1.0.[55] (G)LMMs were fit using *lme4*[65] unless otherwise indicated and statistics were reported using Wald Chi-Squared values from analysis of variance (ANOVA) tests fit with *car*.[66] GLMMs with a negative binomial distribution were fit with the *MASS* package.[64] Regression assumptions and goodness-of-fit were evaluated using *DHARMa*.[67] Residual variance was reported separately for fixed effects and the full model as marginal ($R^2_{GLMM(m)}$) and conditional ($R^2_{GLMM(c)}$) residual variance for GLMMs, respectively, following Nakagawa and Schielzeth[68] and calculated in the *performance* package.[69] Estimated marginal means and associated standard errors were calculated with *emmeans*[70] and *ggeffects*[71] to make within-group comparisons, plot model estimates and report Tukey post hoc analyses. All plots were made with *ggplot2*.[72]