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ORIGINAL PAPER

Flexible cue use in food-caching birds

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Abstract An animal's memory may be limited in capacity, which may result in competition among available memory cues. If such competition exists, natural selection may favor prioritization of different memory cues based on cue reliability and on associated differences in the environment and life history. Food-caching birds store numerous food items and appear to rely on memory to retrieve caches. Previous studies suggested that caching species should always prioritize spatial cues over non-spatial cues when both are available, because non-spatial cues may be unreliable in a changing environment; however, it remains unclear whether non-spatial cues should always be ignored when spatial cues are available. We tested whether mountain chickadees (*Poecile gambeli*), a food-caching species, prioritize memory for spatial cues over color cues when relocating previously found food in an associative learning task. In training trials, birds were exposed to food in a feeder where both spatial location and color were associated. During subsequent unrewarded test trials, color was dissociated from spatial location. Chickadees showed a significant pattern of inspecting feeders associated with correct color first, prior to visiting correct spatial locations. Our findings argue against the hypothesis that the memory of spatial cues should always take priority over any non-spatial cues, including color cues, in food-caching species, because in our experiment mountain chickadees chose color over spatial cues. Our results thus suggest that caching species may be more flexible in cue use than previously thought, possibly dependent upon the environment and complexity of available cues.

Keywords Spatial memory · Cue use · Food-caching · Mountain chickadees · *Poecile gambeli*

Introduction

Cognitive processes underlying behavior are subject to natural selection and likely have ramifications on fitness. One such process is the use of past representations to guide current behavior, or the use of memory. Memory has been shown to have implications in territoriality, mate choice, navigation, acquisition of food resources and many other ecologically-relevant behaviors (e.g., Brennan et al. 1990; Shettleworth 1990; Godard 1991; Menzel et al. 2000). However, memory capacity may be limited (Dukas 1998) and animals are unlikely to remember and recall all past experiences. Thus, particular cues may potentially compete for priority in the stored and recalled memory. How and which cues are prioritized in memory recall is an important evolutionary and ecological question as it may reveal environment-dependent selection pressures on memory and on cue use, particularly in species that cache food.

Some members of the paridae family (e.g., chickadees, tits and titmice) regularly store numerous food items and retrieve them at a later time. Among these food-caching species, there exists a great diversity in the amount of food stored, from several items to hundreds of thousands of items; similarly, there is great variance in the duration of storage, ranging from hours to months (Vander Wall 1982; Sherry 1989). These food-storing birds have been shown to use spatial memory of the cache sites when retrieving caches, rather than relying on site preference or random search (Shettleworth 1990).

Since survival may depend on accurate cache retrieval, food-storing birds may have an adaptively specialized

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memory when compared with their non-storing relatives (Krebs 1990; Shettleworth 1990), and this memory appears to be based on spatial cues (Krebs 1990). The adaptively specialized memory hypothesis predicts that food-caching birds should perform better on spatial memory tasks compared to non-caching species (Krebs 1990). Multiple tests of this prediction, however, have produced equivocal results (Krebs et al. 1990; Healy and Krebs 1992; Healy 1995; Hampton and Shettleworth 1996a) and have led to criticism of the adaptationist approach to memory (Macphail and Bolhuis 2001; Bolhuis and Macphail 2001). Other studies, however, argued that although spatial memory capacity may be similar between food-caching and non-caching birds, natural selection favored the use of spatial cues in food-caching birds (Shettleworth and Westwood 2002; Shettleworth 2003).

Although spatial cues have been deemed the prioritized cues used in memory recall of cache locations, other cues have also been considered when studying how food-caching birds may retrieve their caches. Studies have attempted to tease apart the relative importance of spatial cues and non-spatial cues such as color and pattern that may guide the recovery of cached food (Healy and Krebs 1992; Brodbeck 1994; Clayton and Krebs 1994; Herz et al. 1994; Watanabe 2005). Results from several of these studies indicate specifically that spatial cues are primarily utilized by food-caching birds when retrieving caches, whereas non-spatial cues are less important. Although other cues are also remembered and may direct retrieval behavior, they do so only when spatial cues are unreliable, suggesting that both spatial and non-spatial cues are remembered and can be utilized (Brodbeck 1994; Clayton and Krebs 1994; Brodbeck and Shettleworth 1995). While several studies have found that spatial cues are always used in the recovery of cached food (Brodbeck 1994; Clayton and Krebs 1994; Hampton and Shettleworth 1996a; Herz et al. 1994; Brodbeck and Shettleworth 1995), overall, the results have been equivocal. Other studies have found little to no difference in cue prioritization in food-caching birds when birds recovered caches using spatial cues versus other cues (Healy and Krebs 1992; Healy 1995; Pravosudov et al. 2005). Further, the primary use of a particular cue may be ontogenetically dependent (Clayton 1995; Pravosudov et al. 2005). Still, the overriding suggestion is that food-caching birds always use spatial cues first when they are available because spatial cues appear to be more reliable and less ephemeral than other cues in a changing environment. Some non-spatial cues such as color may potentially be misleading because colors may change over the long term, and thus, it has been hypothesized that they should always be ignored when spatial cues are present (Bennett 1993; Brodbeck 1994; Clayton and Krebs 1994).

We tested the hypothesis that food-caching species always prioritize spatial cues over non-spatial cues. Specifically, we tested whether mountain chickadees (*Poecile gambeli*) would respond to spatial over color cues in an associative learning paradigm. Previous studies have tested this idea with mixed non-spatial cues (e.g., Brodbeck 1994), where color and pattern were combined and tested against spatial cues. In this study, we attempted to isolate color cues to test against spatial location. We purposefully decreased the complexity of color cues compared with previous studies because if food-caching birds have evolved to prioritize spatial cues over color cues when both are available, birds should always attend to spatial cues first, regardless of their complexity. We predicted that if mountain chickadees always first utilize spatial memory to remember previously found food, birds should respond first to spatially-correct locations rather than to correct color locations in a cue dissociation test. However, if mountain chickadees do not consistently choose spatial cues first, this may suggest that food-caching birds can exhibit flexibility in cue choice rather than adhering to a strict prioritization of spatial cues (Macphail and Bolhuis 2001; Shettleworth and Westwood 2002; Hodgson and Healy 2005).

Methods

Husbandry

Twelve male mountain chickadees were caught near Sagehen Creek in Tahoe National Forest, CA in September of 2007. Birds were individually housed in wire mesh cages (60 × 40 × 60 cm), with only auditory contact with other subjects. Cages contained two perches, a bathing dish and two food dishes. Birds were fed once a day with pine nuts, shelled and unshelled sunflower seeds, crushed peanuts, mealworms, and Roudybush (Roudybush Inc., Woodland, CA). Water was provided ad lib for drinking and bathing. Cages and dishes were cleaned weekly. Subjects were maintained at 20°C on a light cycle that mimicked the natural ambient light schedule.

Testing room

The testing room had two “trees” constructed from wood (8.26 × 8.26 × 238.76 cm), each tree with 20 wooden perches. We hung 16 blocks (8.89 × 14.61 × 3.81 cm), divided among three rows, on one wall of the testing room. Row one had five blocks, row two had six blocks and row three had five blocks. Blocks were staggered between rows. Rows and individual blocks in a row were separated by 20.3 cm. Each block had a hole, a wooden perch and a string with a knot tied in the end. The knot was suspended above the hole so the subjects had to remove the knot from the hole to acquire previously found food items (Fig. 1).

All experimental procedures occurred in the testing room, which was adjacent to the rooms where the birds were housed. Access from the bird's home cage to the testing room was through an opening in the wall connecting each individual bird's cage with the testing room to minimize stress from handling. When testing a subject, the lights in the housing room were extinguished while lights in the testing room remained on. By doing so, the bird was stimulated to fly towards the light and into the testing room without handling by the experimenter. Once the subject had flown into the testing room, the opening between the rooms was closed and the lights were turned on in the housing room. Similarly, this process was reversed to motivate the bird to fly back into its cage at the end of each trial (Pravosudov and Clayton 2001, 2002).

Familiarization period

Each subject was allowed to habituate to the testing room and apparatus for 2 h a day, every other day, for a total of 6 h. During habituation, each bird was familiarized with the testing room and with finding food in the blocks. We randomly baited six blocks per 2-h session so the subjects learned to look for food within the block array (Pravosudov and Clayton 2002). By the final habituation period, all birds had retrieved food from the blocks.

Fig. 1 Experimental apparatus. Sixteen blocks, each with a hole, a wooden perch and a string with a knot tied in the end. The knot was suspended above the hole so the subjects had to remove the knot from the hole to acquire previously found food items. One block was randomly chosen as the focal block and was bordered on the edges of its face by a randomly chosen color of tape. The remaining 15 blocks were bordered on their edges by brown tape, making color the only difference between the focal and remaining blocks

Associative learning task

One block was randomly chosen as the focal block and was bordered on the edges of its face by a randomly chosen color of tape (blue, red, yellow, green, orange, pink or purple). The remaining 15 blocks were bordered on their edges by brown tape, making color the only difference between the focal and remaining blocks (Fig. 1). After we ran all 12 birds through a trial (two training phases and a dissociation phase) in which spatial location and color of the focal block remained the same, we randomly varied the focal block spatial location and tape color without replacement during consequent trials. Each focal block location and tape color was randomly used without replacement during each trial, but in the same random order for all birds per trial. As a result, in each specific trial all birds experienced the same spatial location and color of the focal block, but both spatial location and block color were different between all trials.

Each trial consisted of two training phases and one dissociation phase and all observations of the phases occurred from behind a one-way mirror. The purpose of the first training phase was to allow the bird to locate and associate reward with the focal block. In this phase, the focal block was baited with one pine nut, while the remaining 15 blocks were empty. All 16 caching holes were not covered by the knots and the bird could presumably see the pine nut in the focal block's caching hole. The bird was allowed into the testing room and was given 5 min to locate the pine nut in the focal block. After the bird had located the pine nut, we allowed the bird to peck at the pine nut for 3 s. Therefore, the bird was rewarded for locating the pine nut, but did not eat to satiation. We then extinguished the light and allowed the bird back into its home cage. After a retention interval of 5 min, we allowed the bird back into the testing room for the second training phase. Again, the same focal block in the same location was baited with a pine nut, and the remaining 15 blocks were empty. The second training phase was similar to the first training phase except that all 16 holes of the blocks were now covered by the knots. By doing so, we could assure that the bird was using memory, rather than sight of the food itself, to locate previously found food. Again, we allowed the bird 5 min to locate the pine nut in the focal block. After the bird had located the pine nut, we allowed the bird 3 s to peck at the nut, then extinguished the light and allowed the bird back into its home cage.

After a final 5-min retention interval, the dissociation phase was performed. In this phase, we dissociated the color cue from the spatial cue. We randomly chose a caching block directly adjacent to the focal block and switched the tape colors between the two blocks. By doing so, we could preclude the use of cues from the blocks themselves. Thus, the adjacent block now had the correct color cue but incorrect spatial placement, while the focal block had the correct spatial position but incorrect color cue. All dissociation phases were unrewarded to preclude birds from associating reward with either color or spatial cues. Again, all caching holes were covered by the knots and we allowed the bird five minutes to search the blocks. We considered the bird to have investigated a caching hole if the bird removed the knot in front of the hole in a caching block. For the dissociation phase, we recorded the order in which the birds visited the blocks, whether the spatially-correct or correct color location was chosen first and the number of looks made to, and including, the inspection of the spatially-correct and the correct color location. Although we used a food-finding task, memory performance on food-finding associative learning tests appear to resemble cache retrieval performance (Shettleworth et al. 1990; Brodbeck 1994) and, although previous studies used longer retention intervals than 5 min, our findings might also apply to memory-based cache retrieval behavior (Shettleworth 1990; Shettleworth et al. 1990; Brodbeck 1994).

Each bird was allowed to participate in ten trials; however, if the bird did not perform the second training phase demonstrating the use of memory in relocating previously found food in a particular trial, the bird was not allowed to participate in the final dissociation phase and that trial was not included in the final analysis. All birds participated in at least one trial, but none of the birds successfully completed all ten trials due to lack of participation in the second training phase during some trials. Therefore, only the averages of the trials in which a bird fully completed all three phases were used in the analyses.

Since we tested birds in multiple trials, we first took the averages within each bird for all trials that bird participated in, and then analyzed by bird for all statistical tests. The average number of looks made to investigate the first correct cue and then the second correct cue in the dissociation phase was compared with chance using a one-sample *t* test. Using random sampling without replacement, random chance to find either of the two available correct cues (assuming that both are correct choices) out of 16 blocks was 5.7 looks, while random chance to find a single specific cue was 8.5 looks. Chance to find the second correct cue after the first one was found was based on each bird's individual performance in locating the first correct cue choice, since each bird inspected different number of feeders when finding the first correct cue. For example, a bird may have found the first correct cue on the second look. The chance of finding the second correct cue would then be based on the probability of locating one correct block out of the remaining 14 blocks (7.5 looks). The average number of looks made until investigating the correct color location or the spatially-correct location in the dissociation phase was compared with random chance based on each bird's individual performance in locating each correct cue. Again, random chance was computed by random sampling without replacement.

The number of looks to color versus space and the proportion of looks first made to the correct color location versus random chance (50/50) in the dissociation phase were analyzed with 2-tailed paired *t* tests. Because we ran birds through multiple trials, birds may have learned that the differently colored, or focal block, contained the food. Alternatively, birds may have learned that spatial locations were unstable over trials, thereby switching preference from the unstable spatial cue to a potentially more stable color cue (Biegler and Morris 1993, 1996; Jeffery 1998). Consequently, birds may have started the study with an initial preference for spatial location, but then learned over trials to prefer the differently colored block over the spatial location. Because of this, we also used a binomial test to ascertain the proportion of times color was chosen first versus random chance for the very first trial in which each bird participated. By doing so, we could determine whether birds had an initial preference for the correct spatial location during the first trial with no previous experience with the experimental apparatus. We considered all results to be statistically significant if alpha ≤ 0.05. We also presented data on a by-trial basis in which we plotted proportion of birds that chose color first for each consecutive trial. We only used trials for which at least two birds participated to insure meaningful comparison and as a result we could only compare the first five trials as only one bird participated in an additional three trials.

Results

Chickadees used memory of both color and space when attempting to relocate previously found food during the dissociation phase. When exploring blocks, irrespective of whether color or space was chosen first, birds non-randomly chose a correct cue location ($t_{11} = -30.978$, $P < 0.001$; Fig 1a) and, when applicable, non-randomly chose the other correct cue location ($t_9 = -6.294$, $P < 0.001$; Fig. 2a). Birds chose a cue location (either space or color) within two total looks on average (1.53 ± 0.13 SE) and chose the alternative cue location, when applicable, within two additional looks on average (1.75 ± 0.65 SE) (Fig. 2a), indicating that birds were not choosing either cue location randomly. Choosing the first and second cue location better than expected by random search indicated that the birds were using memory to relocate previously found food, regardless of whether the memory was for color or for space. Further, birds non-randomly choose either color location or space location during trials,

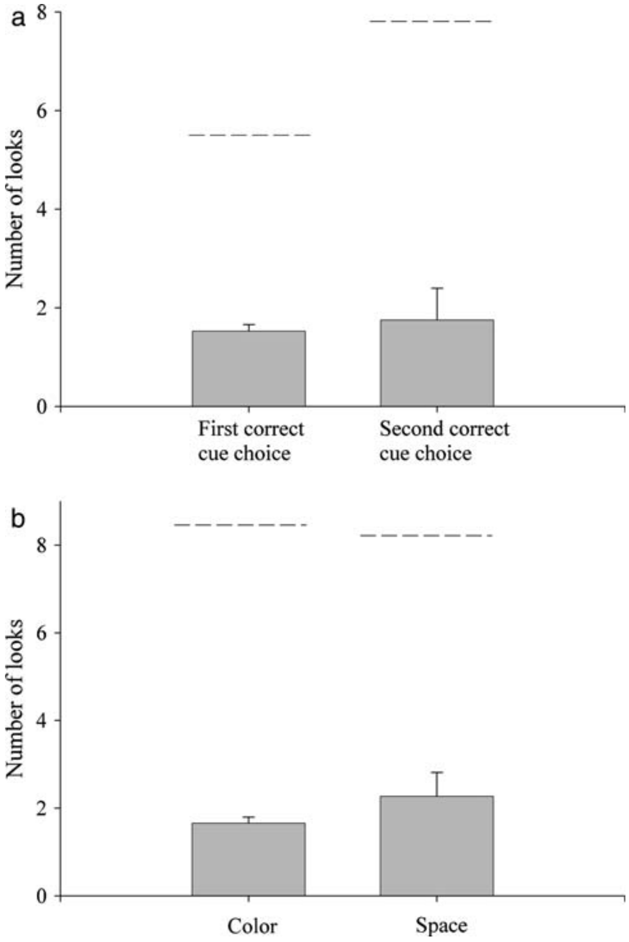

Fig. 2 **a** The mean number of looks (+SE) taken to find the first correct cue choice (either space or color location). The *dashed line* indicates random performance. Random chance to find either of the two available correct cues out of 16 blocks (assuming that both choices are correct) was 5.7 looks, using random sampling without replacement. Random chance to find a single specific cue was based on a probability to locate a single location from all available feeders (8.5). Chance to find the second correct cue was based on each bird's individual performance in locating the first correct cue choice, since each bird inspected different number of feeders when finding the first correct cue. The random chance for the second choice was thus determined using a probability of finding a single correct feeder with non-replacement based on blocks uninspected during discovery of the first correct location. **b** The mean number of looks (+SE) taken to find the correct color location and the correct spatial location. The *dashed line* indicates random performance. Random chance to find either color or space alone was based on random sampling without replacement

regardless of the order of the choice of the cue (color, $t_{11} = -39.913$; $P < 0.001$; space, $t_{10} = -10.517$; $P < 0.001$). Birds investigated the correct color location within two total average looks (1.65 ± 0.14 SE) and the spatially-correct location within three looks on average (2.27 ± 0.54 SE) (Fig. 2b). Choosing space and then color or color and then space at better than chance levels indicated that the memory of one cue does not interfere with the memory for the alternative cue and that chickadees used both spatial and color cues.

Chickadees did not preferentially use spatial cues to guide their retrieval behavior before they used color cues. Birds chose color as their first correct cue choice on average significantly more often than the correct spatial location ($t_{11} = 2.303$, $P = 0.042$; Fig. 3). Eleven out of 12 birds (91.7%; binomial test, $P = 0.006$) chose the correct color as their first choice more often than the correct spatial location (an average of 71% of trials). Similarly, the proportion of first choices to color significantly exceeded random 50/50 chance ($t_{11} = 3.278$, $P = 0.007$). Finally, on the first trial in which each bird participated, birds chose color first significantly more often than expected by chance (83.3%; binomial test, $P = 0.039$; Fig. 4), indicating that birds did not begin the experiment with a spatial location preference. Furthermore, cue preference remained stable throughout all trials (Fig. 4).

Discussion

Mountain chickadees did not primarily use spatial cues over color cues in our associative learning task. We found that when spatial and color cues were dissociated, chickadees chose the dissociated color cue over the correct spatial location. Our results indicate that mountain chickadees do not always prioritize spatial over color cues when given a choice in a particular context and that cue use in food-caching species is likely more flexible than previously reported. This finding is in direct contrast to previous studies suggesting that food-caching birds have evolved to always prioritize spatial cues over local cues such as color when both sets of cues are available (Brodbeck 1994; Clayton and Krebs 1994; Hampton and Shettleworth 1996a; Herz et al.

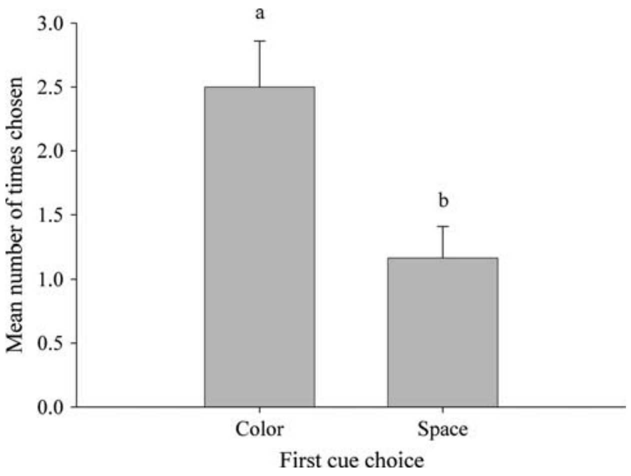

Fig. 3 Of first correct cue choices, the mean number of looks (+SE) made to either color or space

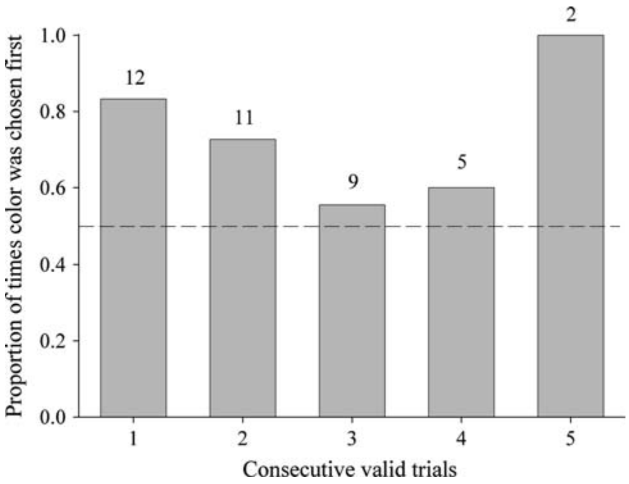

Fig. 4 The mean proportion of times color was chosen first during consecutive valid trials (trials in which a bird completed all three trial phases). Number of birds participating is located above bars. We only used consecutive valid trials for which at least two birds participated to insure meaningful comparison, and as a result we could only compare the first five valid trials, as only one bird participated in valid trials 6, 7 and 8. On the first valid trial in which a bird participated, birds chose color first significantly more often than expected by chance (83.3%; binomial test, $P = 0.039$), indicating that birds did not begin the experiment with a spatial location preference. Furthermore, choice of color remained above 50/50 chance throughout all consecutive valid trials

1994; Brodbeck and Shettleworth 1995). In the previous studies, food-caching birds predominantly used spatial cues when retrieving caches or relocating previously found food. Only when spatial cues were unavailable did birds use local cues to direct cache retrieval behavior (Brodbeck 1994; Clayton and Krebs 1994; Brodbeck and Shettleworth 1995).

The main argument for the prioritization of spatial cue use in food-caching birds has been that spatial cues are less ephemeral than many non-spatial cues in the environment and thus are likely to be more reliable. If spatial cues are more reliable, then they should always take precedence over other cues when given a choice between spatial and other cues (Bennett 1993; Brodbeck 1994; Clayton and Krebs 1994). If this were correct, then we should have never observed the primary selection of color in our study assuming both spatial and non-spatial cues were accessible to the birds. However, we did observe that birds chose color before choosing space. These results cannot be attributed to an initial preference for space, followed by learning through trial experiences to prefer color, as birds chose color significantly more often than expected by chance on their initial trial and preferences did not shift across all trials (Fig. 4). Therefore, chickadees in our experiment initially chose and maintained their preference for color rather then learning it during consecutive trials.

To conclude that chickadees indeed had a choice of spatial cues available to them, it is crucial to demonstrate that the birds utilized spatial cues. We found that individuals selected both the first and second correct cue locations well above chance, regardless of whether the first or second location was the correct color or correct spatial location. These results indicate that mountain chickadees clearly did use both color and spatial cues, and thus the memory of both spatial and color cues could have been used to guide food relocation behavior in our experiment. These results corroborate previous studies indicating that food-caching birds choose locations non-randomly through the use of memory (Healy and Krebs 1992; Brodbeck 1994; Clayton and Krebs 1994; Clayton 1995; Pravosudov and Clayton 2001, 2002; Pravosudov et al. 2005; Watanabe 2005).

Contemporary theories of spatial learning suggest that one cue can block, overshadow or enhance learning of another cue that co-occurs with the first cue (Cheng 2008). We found that the use of one cue did not overshadow learning of the alternative cue, as might be expected (Chamizo 2003). Our results are similar to the findings of Kraemer et al. (1987) that the memory for one cue did not diminish the memory and choice of a second cue and that when one cue was unreliable, the second cue could guide food relocation behavior (Brodbeck 1994; Clayton and Krebs 1994; Brodbeck and Shettleworth 1995; Clayton 1995; Chiandetti et al. 2007; but see Gray et al. 2005). We may account for this by considering a recent model of spatial learning which indicates that co-occurring cues can enhance the learning of one or both of the cues (Miller and Shettleworth 2007). Similarly, cues may be weighted, integrated and reinforce one another if they are not overly discrepant, while large discrepancies may produce reliance on only one cue (Cheng et al. 2007; Gibbs et al. 2007). If our cues had been dissociated to a greater degree (e.g., color cue dissociated from the spatial cue at a greater distance than adjacent), the birds may have only learned one cue, therefore overshadowing and not readily learning the second cue. Taken together, our results indicate that mountain chickadees remembered and utilized memory of both color and space to relocate previously found food and the capacity to remember either spatial or color cues was not overshadowed by the memory or choice of the alternative cue.

Our results are in contrast with several previous studies on food-caching birds, but one possible explanation for differences between this and previous studies is in the relative complexity of cues. Our design differs from that of previous studies in that previous designs appear to use a more complex combination of non-spatial cues, including both color and pattern, each trial used a unique set of colored and patterned blocks and there were usually only four different spatial locations (e.g., Brodbeck 1994; Clayton and Krebs 1994). In this study, we removed the pattern cue and simply focused on space and color. In addition, we purposefully used only two colors during a given trial, thereby changing the context of the distracter blocks compared with previous studies through a potentially simplified design. Therefore, if both spatial and color cues can be remembered, the color cues might have been less complex to the birds than the spatial cues and, as a consequence, the birds might have simply responded to the least complex cues (Macphail and Bolhuis 2001; Shettleworth and Westwood 2002). Thus, if cue complexity is indeed a deciding factor, one might have expected birds to first respond to the spatial locations in the previous studies, while possibly first responding to color cues in this study. If the relative complexity of spatial and non-spatial cues and/or the context of the distracter blocks is more important in guiding retrieval behavior than a strict adherence to the use of one particular cue over another, then this has implications for the design of studies testing cue utilization and prioritization in caching species that utilize memories of more than one cue to guide behavior. Birds may respond differently depending on the design of the study, and the apparatus and our results may be a consequence of our design (Hodgson and Healy 2005). The cue complexity hypothesis then may be a potential alternative to the spatial cue prioritization hypothesis. Although our results do not allow a direct test of the latter hypothesis, they do argue against the hypothesis that food-caching birds should always respond to spatial cues over non-spatial cues.

In more broad terms, our results reflect the possibility that cue use may be flexible and potentially dependent on the ecology across food-caching species. The ecological consideration of a particular species may potentially allow for different or more flexible utilization of different cue types. For example, the duration between caching and cache recovery may affect the perceived reliability of local cues. Within caching species, some species are long-term cachers that do not retrieve caches for up to 6 months, while relatively short-term cachers such as mountain chickadees may recover caches within hours to days during the winter. Within a 6-month time, local cues may be unreliable, thus recovery should be dependent upon fixed spatial cues. However, some cachers may recover their caches within days, during which local color cues may be less likely to change in some habitats. Pravosudov et al. (2005) found that short-term caching Western scrub-jays (*Aphelocoma californica*) also do not preferentially use spatial cues over color cues and that half of the birds used spatial cues first, while the remaining birds used color cues to find food caches. Therefore, it is possible that selection may have allowed for flexibility in cue use within caching species, depending upon, among other variables, the amount of time between caching and recovery. Since previous studies have found differences in cue utilization between caching and non-caching species based on ecological needs (Brodbeck 1994; Clayton and Krebs 1994; Brodbeck and Shettleworth 1995; Clayton 1995; Hampton and Shettleworth 1996b; Shettleworth and Westwood 2002), it may be important to consider that flexibility may exist in cue prioritization within caching species as well based on ecological considerations.

Regardless of the mechanisms underpinning cue use in cache retrieval, this study showed that not all food-caching birds always prioritize spatial cues over local cues when both cues are available. It appears more likely that food-caching birds may select either spatial or local cues depending on the context, environment, and complexity of available cues rather than always relying on spatial cues first as has been hypothesized previously. It would be interesting to know if manipulating the complexity and spatial arrangement of competing cues could alter cue use in food-caching birds, as our study implies. Our findings thus suggest that the relationship between food caching and the prioritization of cue recall in cache retrieval may be more flexible than previously thought and warrants further examination.

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