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COMMENTARY

# Different memory systems in food-hoarding birds: A response to Pravosudov

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## Abstract

We recently showed that food-hoarding birds use familiarity processes more than recollection processes when remembering the spatial location of their caches (Smulders et al., *Animal Cognition* 26:1929–1943, 2023). Pravosudov (*Learning & Behavior*, https://doi.org/https://doi.org/10.3758/s13420-023-00616-x, 2023) called our findings into question, claiming that our method is unable to distinguish between recollection and familiarity, and that associative learning tasks are a better way to study the memory for cache sites. In this response, we argue that our methods would have been more likely to detect recollection than familiarity, if Pravosudov's assertions were correct. We also point out that associative learning mechanisms may be good for building semantic knowledge, but are incompatible with the needs of cache site memory, which requires the unique encoding of caching events.

We recently published a paper in which we claimed that, when food-hoarding birds remember the location of a cache site, they are much more likely to use familiarity than recollection to do so (Smulders et al., 2023). Familiarity is a memory process in which the strength of the feeling of "having encountered this stimulus before" controls the behaviour (i.e., going to that location to check for food). It requires the individual to be exposed to the to-be-remembered stimulus (in this case: a cache site) for the individual to be able to act on this memory. Recollection is closer to being episodic in nature, often includes context of the original learning situation in the memory, and could be activated without exposure to the stimulus in question (Yonelinas et al., 2010). The main implication of our findings is that coal tits would need to be in sight of a cache site to remember it. Food-hoarding birds rely on their hippocampus to retrieve their caches (Sherry & Vaccarino, 1989) and have a larger hippocampus than do nonhoarding birds (Krebs et al., 1989; Sherry et al., 1989). Since the hippocampus in mammals is responsible for recollection, and not familiarity (Yonelinas et al., 2010), ours was a surprising finding. However, the hippocampus is important for spatial information processing as well, and as such can influence familiarity processes based on spatial information (Yonelinas et al., 2010). Additionally, the avian hippocampal formation includes areas believed to be homologous to entorhinal cortex (Striedter, 2016), which is involved in both recollection and familiarity (Yonelinas et al., 2010). For more discussion of how these seemingly contradictory facts might be reconciled, see Smulders et al. (2023). Note that our result does not make us exclude a role for episodic memory in the memory for caches, as there is clear evidence for what-where-when memory in cache memory (Feeney et al., 2009). For a full view of the memory mechanisms involved in cache memory, converging evidence from multiple approaches is necessary (Crystal, 2021).

Soon after we published our results, Pravosudov (2023) wrote a commentary calling our findings into question. His argument had three components to it: (1) all the previous work in this area has provided evidence for recollection as the dominant mechanism; (2) the novel method we developed was inappropriate for distinguishing familiarity from recollection in caching birds; and (3) studying memory in food-hoarding birds using cache-retrieval trials is a flawed approach. We address these points in order below.

First, citing his own review paper (Pravosudov & Roth, 2013), Pravosudov (2023) claims that previous work in this area has provided evidence for recollection as the dominant

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mechanism involved in remembering cache locations. Yet the word "recollection" does not appear anywhere in that paper, nor does the word "recall." He briefly mentions the episodic-like memory in corvids, but the psychological mechanisms involved in the spatial memory component are not discussed. To our knowledge, until we did, nobody had ever asked the question of whether spatial memory performance by food-hoarding birds was driven by familiarity or recollection processes. Indeed, Pravosudov confirms the point we made in the original paper that researchers in the field assume that the process they are looking at is recollection. We too assumed the birds would use recollection and designed our analysis method to confirm this assumption in a novel way. When first we were unable to detect significant levels of recollection in the birds, we assumed our analysis methods were flawed and spent almost 10 years running student projects to validate the analysis method in humans, before returning to the bird data and accepting the finding that familiarity was a stronger contributor than recollection to the memory for cache sites. We therefore strongly dispute the statement that the literature to date provides evidence for spatial memory for cache sites being based on recollection.

Second, Pravosudov (2023) states that laboratory sessions of birds hiding and retrieving multiple items will always underestimate memory performance, because birds will mix in exploration with attempts to retrieve previously hidden food. Captive hoard-and-retrieve sessions have been used for a long time, and nobody would dispute that some "errors" are in fact due to exploration. Nevertheless, this approach has been able to show that memory is involved in cache retrieval (Sherry et al., 1981; Shettleworth, 1983; Smulders et al., 2023), and that this memory declines over time (Hitchcock & Sherry, 1990; Male & Smulders, 2007; Smulders et al., 2023). The question then becomes whether exploration is responsible for our inability to detect recollection as a memory mechanism. Pravosudov (2023) asserts that after one or at most two items have been retrieved (using recollection as the memory process), birds will be satiated, and therefore no longer be motivated to look for more items. This would then predict that their success rate after the first few items should be random (or even below chance, if they actively avoid cache sites, as suggested by Pravosudov).

There are two aspects to this criticism: how quickly birds reach satiety, and whether the pattern of exploration could reduce the detection of recollection in our analyses. The number of items it takes for birds to reach satiety very much depends on how long birds have been food restricted and how large the items are. We used very small pieces of peanut, of which the birds could definitely eat more than two before being satiated. Using small pieces would definitely reduce the danger of loss of motivation due to early satiation. Recollection in the ROC model is conceptualized as the number of correct decisions without any false alarms (Yonelinas, 1994). Pravosudov suggest that birds might retrieve items using recollection until satiated, and then start exploring. Under this scenario, if we assume it takes a fixed number of items to satiate the birds, our estimate of the contribution of recollection would be larger if there were fewer items to be retrieved. After all, the proportion of items retrieved is smaller if the number of items actually retrieved is fixed, but the total number of items is larger. Among the nine birds in our study, the largest estimate of recollection was indeed for the bird that had hidden only four items, but there was no significant correlation between recollection and the number of items retrieved, $r(9) = -.483$, $p = .188$. Our data therefore do not support this explanation for the lack of recollection in our analysis. This scenario also does not explain why we achieve a high estimate of familiarity (similar to that of the human participants, for whom neither satiety nor exploration are an issue). If the birds were satiated for the rest of the trial, we would expect them to forage at random, or even avoid the other cache sites, which would lead to a zero estimate for familiarity. It is possible that a very specific combination of digestive rate (so birds are motivated again to find food) and exploration could lead to the estimates of familiarity we obtained. We would need to model different scenarios (combinations of perfect recollection combined with different rates of satiety, digestion, and exploration) to see if any of those scenarios would match our findings. However, for now, the most parsimonious explanation is that familiarity is the more dominant memory retrieval mechanism, as it seems to be in humans.

Third and finally, Pravosudov's (2023) solution to the problem of exploration in a cache retrieval trial is to propose a different type of memory test altogether: associative learning tasks. In this kind of task, an animal is trained through repeated exposure that a particular location is associated with food. Indeed, after 16 trials in which a mountain chickadee each time found food in the same compartment of a foraging tray, they remembered this information for at least 6 months (Roth et al., 2012). Memory for the (constant) location of a feeder in an array in the field has also been shown to be related to winter survival, and therefore under directional selection in the field (Sonnenberg et al., 2019). While the latter is a beautiful example of cognitive ecology, there is not necessarily a connection between memory for reliable foraging sites and memory for individual cache sites. In fact, Pravosudov's (2023) assertion that studying associative learning is equivalent to studying the memory for cache sites goes against the founding tenets of cognitive ecology. In their seminal paper, Sherry and Schacter (1987) argued that different types of information processing might be incompatible with each other, which would inevitably lead to the evolution of multiple memory systems. One clear example of such an incompatibility is between a memory system for extracting invariances across a number of different experiences (e.g., learning reliable foraging sites), and one for maintaining variance across a number of events (e.g., being able to distinguish different caching events in memory). A memory system that extracts invariances from multiple experiences is building up semantic knowledge. Such a system needs to be resistant to catastrophic interference by contradictory information: If you have found food in the same location 10 times in a row, you should not give up on that location if you don't find food there the 11th time. However, such a memory system will not perform well on a task where unique information of the individual episodes is crucial (as it discards unique information in favour of shared information). On the other hand, a memory system that extracts unique features of individual episodes ("pattern separation" in the jargon) needs to ignore shared information in favour of unique information (O'Reilly et al., 2014). When Pravosudov's birds return to the same location over and over, and find it contains food, they build up semantic knowledge of food location. On the other hand, when they hide food items, each cache site has to be remembered separately and uniquely. The two types of spatial memory therefore likely represent two complementary learning systems as envisioned by McClelland et al. (1995). While we do not believe the two situations engage the same memory systems, the question of whether familiarity or recollection is involved is relevant for both types of memory system. Maybe the same ROC curve approach can be used for the associative learning tasks as well, as long as enough rewarded locations are trained.

In conclusion, Pravosudov's (2023) critique of our analysis method would be a valid concern if we only detected recollection processes and no familiarity. It does not, however, easily explain why we found predominant use of familiarity over recollection. In addition, replacing cache-and-retrieval trials with associative learning paradigms will not give us any meaningful insights into the memory used for cache recovery. Instead, how birds form and retrieve semantic knowledge for efficient foraging and episodic memories of cache sites and their contents should be studied separately to understand the cognitive evolution of food-hoarding (and indeed many other) birds.

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