Spatial memory and cognitive flexibility trade-offs: to be or not to be flexible, that is the question

Maria Cristina Tello-Ramos[1], Carrie L Branch[2], Dovid Y Kozlovsky[2], Angela M Pitera[2], and Vladimir V Pravosudov[1]

Department of Biology and Graduate Program in Ecology, Evolution, and Conservation Biology
University of Nevada, Reno
Reno, NV 89557

[1]Corresponding authors
Email: mariatelloramos@gmail.com; vpravosu@unr.edu
[2]Equal contribution

Word count: 5,833

Abstract

Cognitive flexibility allows animals to readily acquire new information even when learning contingencies may rapidly change, as is the case in highly variable, but predictable environments. While cognitive flexibility is broadly thought to be beneficial, animals exhibit inter- and intra-specific variation, with higher levels of flexibility associated with reduced memory retention and vice versa. In this review, we discuss when and why such variation may exist and focus specifically on memory and memory flexibility. We argue that retained memories may negatively affect the acquisition of new information, most likely via proactive interference, and available data suggest that there may be a trade-off between memory retention and acquiring new memories. We discuss neurogenesis-mediated forgetting as the mechanism reducing memory interference, as new neurons enhance learning new information, but also cause forgetting of older memories. Selection may be expected to favor either end of the continuum between memory retention and memory flexibility depending on life history and environment. More stable environments may favor memory retention over flexibility whereas rapidly changing environments may favor flexibility over retention. Higher memory capacity also seems to be associated with higher memory interference, so higher neurogenesis rates associated with forgetting of unnecessary information may be favored when higher capacity is beneficial such as in food-caching species. More research is necessary to understand if inter- and intra-specific differences in the association between memory retention and flexibility are related to some general ecological patterns, whether this association is heritable, and whether developmental conditions and experience have different effects on this association in different species.

Keywords: cognitive flexibility; reversal learning, interference, forgetting, neurogenesis, food caching birds, migratory birds

Introduction

Animals are able to modify their behavior due in part to their ability to learn new information associated with relevant contingencies in their environment. However, relevant contingencies often change and animals must be able to switch their behavioral responses to fit new contingencies and this is usually referred to as cognitive flexibility. Behavioral or cognitive flexibility has been defined by psychologists as the ability to reverse contingencies while learning new information (Badre & Wagner, 2006). More flexible animals can readily learn continuously changing contingencies. Traditionally, within a laboratory context, an animal is thought to be cognitively flexible if it can successfully learn new information while either keeping or forgetting older information. To test cognitive flexibility, the "reversal-learning task" is often used. This task uses an experimental paradigm where contingencies of previously learned associations are changed or reversed (Anderson & Neely, 1996; Strang & Sherry, 2014). For example, in a color association reversal-learning task an animal may be presented with two different color handles, and is first trained that pressing the blue handle will result in reinforcement, while pressing the green handle results in no reinforcement. After the animal has reached a set performance criterion, the relationship is reversed, such that pressing the green handle now results in reinforcement and pressing the blue handle results in no reinforcement. An animal that scores highly on a cognitive flexibility task is one that takes fewer trials to extinguish the previously reinforced behavior and only responds to the new contingency. Similarly, in spatial reversal-learning task, changing the location associated with reward also allows testing for cognitive flexibility. In this case, a flexible individual is expected to learn the new locations and stop visiting the location that no longer provides reward (e.g. Croston et al. 2017). A standard serial reversal task frequently involves just a binary choice that keeps changing between the same two available options with each reversal (two colors or two spatial locations). An alternative version involves non-repeatable choices at each reversal (e.g. different color at each reversal or different spatial location at each reversal).

Behavioral ecologists have greatly expanded the use of the term 'behavioral flexibility' to include any behaviors that allow animals to adjust to changing environments, including behavioral innovations and problem solving. Such diversification of the term has produced confusion as different behaviors used to describe behavioral flexibility often have different underlying neural and physiological mechanisms. This confusion prompted Audet and Lefebvre (2017) to suggest that we should stop using the term flexibility and instead focus on specific behaviors associated with flexibility.

Traditionally, cognitive flexibility has been viewed as a highly adaptive ability (Dukas, 2004; Lefebvre, Reader, & Sol, 2004) that increases survival and reproductive success (Snell-Rood, 2013). However, available data shows both inter- and intra-species variation, with higher levels of flexibility associated with reduced memory retention and vice versa. Throughout this review, we will consider (1) potential trade-offs among memory retention, memory capacity, memory load, and cognitive flexibility, (2) forgetting as a mechanism allowing this trade-off, (3) adult neurogenesis as a mechanism of forgetting, and (4) future directions to investigate the proposed trade-offs. We will specifically focus on memory and memory flexibility, which we define as the ability to successfully learn new information when learning contingencies keep changing.

Why are some animals less flexible?

One of the major questions in understanding the evolution of cognitive flexibility is why there is inter- or intra-specific variation in cognitive flexibility and what are the mechanisms underlying such variation. One of the earliest studies on this subject reported that pigeons (*Columba livia*) were better at learning a reversal task (e.g. more flexible) but showed worse memory retention, while goldfish (*Carassius auratus*) performed worse on the reversal task (e.g. less flexible) but showed better memory retention (Gonzalez, Behrend, & Bitterman, 1967). This study suggested that (a) species differ in memory flexibility and (b) there appears to be a trade-off between cognitive flexibility and memory retention.

Inter-specific variation in cognitive flexibility suggests that there should be a cost to being cognitively flexible. Some of these costs may be energy-related, such that the energy needed to maintain a long-term memory (Plaçais & Preat, 2013) or to process information (Dukas, 1999; Mery & Kawecki, 2003). The physiological costs of cognition can affect other traits like reproduction. For example, fruit fly (*Drosophila melanogaster*) lines selected for enhanced learning abilities also showed a decline in larval competitive ability (Mery & Kawecki, 2003).

Other costs might be related to potential trade-offs associated with cognitive flexibility. While there is a paucity of comparative studies including both aspects of cognitive flexibility (e.g. memory retention and memory flexibility), the few that do exist are consistent with the idea of a trade-off between flexibility and memory retention and suggest that a better ability in one is associated with a worse ability in the other.

Research on food-caching species exemplifies this trade-off. Food-caching black-capped chickadees (*Poecile atricapillus*) with the overall better spatial memory ability than non-caching dark-eyed juncos (*Junco hyemalis*), were less capable at learning a new contingency after reversal, suggesting that older memories interfered with acquiring new memories (Hampton, Shettleworth, & Westwood, 1998). Clark's nutcrackers (*Nucifraga columbiana*), which are known for their extremely long lasting spatial memory, performed significantly worse on a spatial reversal-learning task compared to their performance on an initial spatial learning task (Lewis & Kamil, 2006). Finally, mountain chickadees (*Poecile gambeli*) inhabiting high elevations performed worse on a spatial reversal-learning task compared to low elevation chickadees (Croston et al., 2017; Tello-Ramos et al. 2018). At the same time, our previous studies documented that high elevation chickadees performed significantly better on an initial spatial memory task (both acquisition and retention), had a larger hippocampus with more neurons, and exhibited higher rates of adult hippocampal neurogenesis (Freas, LaDage, Roth, & Pravosudov, 2012). All of these findings are also consistent with the idea of a potential trade-off between the ability to retain older memories and the ability to rapidly acquire new memories.

Memory interference resulting in a major trade-off

The cost of learning new information reflects the fact that the brain and the neural networks that store memory patterns are finite, with networks eventually reaching saturation (i.e., memory load or capacity). Because memory storage or capacity is limited, the acquisition of new memories may interfere with old memories, and vice versa, specifically when new and old memories are similar (Anderson & Neely, 1996; Wixted, 2004). The essential problem associated with interference is that the retrieval cues available at the time of recall fail to access the target memory (Anderson & Neely, 1996). One way to explain this phenomenon is that when a cue is linked to more than one memory, different memories compete for access during the recall processes (Bjork, 1989). Interference should increase with the number of competitors or distractors associated with the same cues. In humans, for example, memory recall performance decreases when the number of memories that are paired with the same cue increases - the cue-overload principle (Watkins & Watkins, 1976). On the other hand, when cues and contexts used to learn are more dissimilar, interference should decrease. For example, in Clark's nutcrackers, memory performance improved in a spatial reversal learning task when given new spatial cues during the reversal phase compared to performance in a reversal task with the same spatial cues as during the initial learning (Lewis, Kamil, & Webbink, 2013). Similarly, lab rats showed significant interference after learning a second task but such interference was significantly reduced when the context, such as light, size of arena, and texture of arena, of each task was made increasingly different from each other (Rodriguez, Borbely, & Garcia, 1993). Interference is thought to occur specifically during memory retrieval (or recall) and depending on whether old memories or the formation of new ones is impaired, interference can be classified as retroactive or proactive interference.

Retroactive interference occurs when previously learned information is affected, or forgotten, by learning new, similar information. For example, honeybees (*Apis mellifera*) that were trained to turn right on a green land mark first and then trained to turn left on a blue landmark, decreased their performance on a later test for the first task (Cheng & Wignall, 2006).

Proactive interference occurs when previously learned information interferes with learning and remembering new information. Proactive interference appears to be one of the main mechanisms affecting cognitive flexibility because it may directly influence learning of new information. Most common tests for proactive interference include learning reversals and serial learning reversal tasks. When serial reversal task is used with just two possible choices (e.g. Cauchloix, Hermer, Chaine, Morand-Ferron, 2017), animals are expected to learn the rule that they need to switch when the previously rewarding choice is no longer rewarding. Such task does not allow testing for memory retention and how memory retention may affect learning of new associations via proactive interference. A more appropriate reversal task (whether single or serial reversal) should require an animal to learn new associations that have not been used before during each reversal stage. Such approach allows direct assessment of both retention of memories of previously rewarded associations and acquisition rates of new associations.

For instance, highly specialized food-caching Clark's nutcrackers that were given either one or two "lists" of rewarded locations performed worse during recall of the second list than during the recall for the first list, demonstrating proactive interference (Lewis & Kamil, 2006). Likewise, Florida scrub-jays (*Aphelocoma coerulescens)* that performed better in an initial learning task did worse in a reversal task and vice versa, again suggesting there may be a trade-off between initial and reversal learning ability (Bebus, Samll, Jones, Elderbrock, & Schoech, 2016). If learning a useful association in the environment interferes with learning a new association in the future, animals would not be able to quickly adjust their behavior in a rapidly changing environment.

Based on human studies, it appears that retroactive interference is stronger when the delay between learning new information and recalling old information is short. When more time has passed between learning new information and recalling the older information, retroactive interference decreases. Conversely, proactive interference increases with more time between learning new information and recalling it – older information is recalled more accurately than the newer information as more time has passed (Postman, Stark, & Fraser, 1968; Storm & Bjork, 2016).

Overall, it appears that the extent of proactive interference is a critical mechanism involved in the trade-off between memory retention and the ability to acquire new memories. Better memory retention seems to be associated with a higher level of proactive interference and hence with less cognitive flexibility while higher cognitive flexibility appears to be associated with less proactive interference and with worse memory retention. As such, the rest of this review will focus on proactive interference.

Forgetting as a mechanism reducing interference and increasing cognitive flexibility

At least one mechanism known to reduce proactive interference is forgetting, as forgetting allows the acquisition of new memories without interference with older memories (Anderson & Neely, 1996). Forgetting, described as the absence of expression for memories that once caused expression, is no longer regarded as memory failure (Kuhl & Wagner, 2009). Instead, given the dynamic nature of the environment, forgetting is likely an essential component of any adaptive memory system that increases behavioral and cognitive flexibility and therefore, remembering and forgetting are intimately related (e.g. Kraemer & Golding 1997). Although forgetting might reflect actual memory loss (decay), it can also be explained as a failure to retrieve existing memories (interference) and can reduce memory load. In humans, deliberate attempts to forget specific information can improve learning new information (Festini & Reuter-Lorenz, 2014). Imagine for example the memory task of a restaurant cook, for whom it would be advantageous to forget an order once it has been completed. The advantage of forgetting a completed order, is that it reduces confusion (proactive interference) when trying to remember other current orders (Bjork, 1970). Work on animals implicated adult neurogenesis as one of the main neural mechanisms that facilitate forgetting (Frankland, Köhler, & Josselyn, 2013).

Neurogenesis as a mechanism of forgetting and reducing proactive interference

Adult neurogenesis is a process of neuronal replacement during adulthood first described by Altman and Das in the 1960´s (Altman & Das, 1965,1967). Adult neurogenesis consists of neuron proliferation, migration, survival, and finally incorporation into the existing neural circuits, usually in the hippocampus, a brain region involved in memory (van Praag, Christie, Sejnowski, & Gage, 1999). Adult hippocampal neurogenesis does not result in increasing the total number of neurons – instead adult neurogenesis and apoptosis, or neuron death, operate simultaneously and result in adult neuron replacement (Barnea & Pravosudov, 2011; Olson, Eadoe, Ernst, & Christie, 2006; van Praag et al., 1999). The majority of new neurons actually die without being recruited into neural circuits, and it is hypothesized that new neurons may form a neurogenic reserve that can provide new neurons when needed (Kempermann, 2008).

Most research on adult neurogenesis has been focused on its role in facilitating new learning and almost all existing hypotheses about the function of neurogenesis suggest that it improves learning (Gould et al. 1999; van Praag et al., 1999; Kempermann 2008). Ecological research, in particular, primarily considers neurogenesis as the neural mechanism that enhances learning of new information (Barnea & Pravosudov, 2011).

More recently, however, it was discovered that adult neurogenesis is also directly involved in forgetting and that enhanced learning of new information associated with neurogenesis appears to be, at least in part, due to forgetting of older information (Akers et al., 2014; Epp et al. 2016). New findings show that new neurons enhance the acquisition of new memories, but at the same time death of old neurons associated with incorporation of new neurons appears to cause forgetting of older memories which decreases proactive interference (Akers et al., 2014; Epp et al. 2016). Interestingly, it seems that apoptosis of old neurons is not random, but rather a targeted replacement of old memories that are no longer useful with new neurons produced by neurogenesis.

Learning and memory, and the decrease in proactive interference are positively associated with adult neurogenesis rates because at least one function of neurogenesis represents a decay process that continually clears out old memories from the hippocampus (Frankland et al., 2013). Newly born cells are different compared to older neurons; they are both more excitable and more sparse, which is why adult neurogenesis seems to promote pattern separation, a process by which overlapping patterns of neural activation are mapped to less overlapping representations, effectively reducing interference (Becker, 2005). Computational models of neural networks also show that neuronal turnover should improve learning of new information specifically by discarding older memories (e.g. forgetting) (Chambers, Potenza, Hoffman, & Miranker, 2004; Crick & Miranker, 2006; Weisz & Argibay, 2012).

It appears that hippocampal neurogenesis directly mediates the continuous process of forgetting older hippocampus-dependent memories by reconfiguring neural circuits and resulting in the dissociation of memory cues with previously stored memories (Akers et al., 2014). Neurogenesis is more active in younger animals, which are also more forgetful (and more flexible), but experimentally reduced hippocampal neurogenesis rates in adulthood result in longer lasting memories (but less flexibility; Akers et al., 2014). For instance, in adult mice, experimentally increasing neurogenesis rates induced forgetting, while in young animals with naturally occurring higher neurogenesis rates, experimental reduction in neurogenesis increased memory retention (Akers et al., 2014; Kitamura et al., 2009). In a different study, increased neurogenesis rates associated with more running resulted in reduced memory retention, but also resulted in better performance in a reversal learning task (Epp et al. 2016). Experimental suppression of adult neurogenesis resulted in better memory retention but also in worse performance in a reversal learning task (Epp et al. 2016). These findings support the idea that increased neurogenesis reduces proactive interference and enhance learning of new information, but at a cost of reduction in memory retention (e.g. forgetting), while reduced neurogenesis enhances memory retention but impedes learning new information because of proactive intereference.

As mentioned earlier, the neurogenic reserve hypothesis (Kempermann, 2008) suggests that new neurons form a pool that may be used when needed. This hypothesis is consistent with the idea of adult neurogenesis aiding forgetting and not just the idea that new neurons are recruited only to increase memory ability (e.g. Johnson et al., 2010). Incorporation of new neurons into the existing circuits should disrupt older memories (e.g. forgetting), therefore, at the time when animals may consistently acquire new memories, such as the case with food-caching animals when they actively store food, they would not benefit from higher neurogenesis as it will result in forgetting existing caches as memories of new caches are being constantly formed.

Overall, there is mounting evidence that adult hippocampal neurogenesis improves the acquisition of new information while at the same time causing forgetting and increasing cognitive flexibility (Akers et al. 2014; Swan et al. 2014; Garthe, Behr, & Kempermann, 2009; Burghardt et al. 2012; Frankland et al. 2013; Weisz & Argibay 2012; Hardt, Nader,

& Nadel, 2013; Kitamura et al. 2009; Guskjolen, Epp, & Frankland, 2017; Feng et al. 2001; Martinez-Canabal 2015; Becker, MacQueen, & Wojtowicz, 2009; Epp, Mera, Kohler,Jesselyn & Frankland, 2016; Yau, Li, & So, 2015).

Need to re-evaluate how we view neurogenesis in many ecologically relevant paradigms

Most of research on forgetting and neurogenesis have been conducted with model systems such as lab rodents and focused directly on the mechanistic relationship between neurogenesis, memory and forgetting. At the same time, there is great historical paucity of research addressing inter- and intra-specific variation in this relationship and how such variation might be associated with different selection pressures despite great interest in inter- and intra-specific variation in adult neurogenesis rates (Barnea & Pravosudov 2011).

Food-caching animals

Recent advances in our understanding of adult neurogenesis involvement in forgetting requires reconsideration of most current ecologically-based hypotheses about role of adult neurogenesis. Previously, adult hippocampal neurogenesis has always been considered only as a mechanism enhancing spatial learning (Barnea & Pravosudov, 2011). Starting with Barnea and Nottebohm’s (1994) study reporting seasonal differences in hippocampal neurogenesis and connecting these differences to variation in food caching activity, all studies of neurogenesis in food-caching birds and mammals attempted to explain any differences in hippocampal neurogenesis rates by memory benefits associated with increased neurogenesis rates (Barnea & Nottebohm, 1994; Hoshooley & Sherry, 2007; Roth et al., 2012; LaDage et al., 2010, 2011; Barker et al., 2005; Johnson et al., 2010). While species/population comparisons did find that animals with higher demands for food caches indeed have higher hippocampal neurogenesis rates (Roth et al., 2012; Freas et al., 2012), these results might also be explained by both improvements in memory flexibility allowing learning new information and forgetting associated with retrieval of more food caches.

A lack of any significant associations between adult hippocampal neurogenesis rates and food-caching activity in all previous seasonal comparisons (review in Pravosudov & Roth 2013; Pravosudov et al., 2015) is inconsistent with the previous hypotheses. If hippocampal neurogenesis is involved specifically in memory improvements associated with more food caching, it is expected that within a year, higher food caching activity should be associated with higher neurogenesis rates (e.g. Barnea & Nottebohm, 1994). None of the available data match these predictions (Hoosholey & Sherry, 2004; Hoshooley et al., 2007; Hoosholey & Sherry, 2007). Even the first landmark study (Barnea & Nottebohm, 1994), which is always used as an example of association between adult hippocampal neurogenesis and food caching, actually showed highest neuron incorporation rates by end of November-December in birds injected with a new neuron marker in October (Pravosudov et al., 2015). The peak of food caching, on the other hand, is usually in September-early October (e.g. Pravosudov, 2006), so these new neurons were not likely there during the peak of food caching.

The observed seasonal patterns, however, fit much better if we assume that higher neurogenesis rates are associated with cache retrieval-based forgetting. Chickadees start retrieving caches in late fall and likely continue through spring (e.g. Pravosudov, 2006). At the same time, the actual cache retrieval pattern may depend on weather, availability of other food, etc. – and so variation in highest neurogenesis rates between November and spring may be explained by variation in cache retrieval activity.

In the lab, chickadees that were allowed to cache and retrieve food on a daily basis had higher hippocampal neurogenesis rates than birds experimentally prevented from caching (LaDage et al., 2010). Again, this finding is consistent with neurogenesis-based forgetting as chickadees were both caching and retrieving caches. Interestingly, in non-caching, parasitic cowbirds (*Molothrus ater*), which use spatial memory for host nests throughout the breeding season, the highest neurogenesis was reported in late summer after breeding (Guigueno et al. 2016), which is also consistent with the idea of neurogenesis-based forgetting of no longer relevant information.

Migratory behavior

It has been hypothesized that migratory behavior is associated with more spatial memory use and at least some comparisons indeed showed that compared to non-migratory subspecies, migratory subspecies performed better in a spatial memory task (Cristol et al., 2003; Pravosudov et al., 2006). Migratory birds were hypothesized to have higher reliance on spatial memory similar to food-caching birds since they may need to remember details of permanent stopover locations as well as details of both breeding and wintering areas. Migratory species/subspecies have larger hippocampus than non-migratory species, but at least in one comparison of migratory and non-migratory white-crowned sparrows (*Zonotrichia leucophrys*), adult migratory birds had higher hippocampal neurogenesis rates than adult non-migratory sparrows, but similar to that in juveniles from both subspecies (LaDage et al., 2011). Non-migratory adults, on the other hand, had lower hippocampal neurogenesis rates than the juveniles from both subspecies. Reduction in hippocampal neurogenesis rates with age is a well-known phenomenon and it has also been associated with more cognitive flexibility and less memory retention in younger individuals and the opposite relationship in older animals (Akers et al. 2014). Migratory adults, however, did not have reduced neurogenesis rates compared to juveniles, at least at the time of sampling during fall after they arrived at the wintering grounds. Higher neurogenesis at that time might be associated with discarding past memories formed during migration allowing for higher memory flexibility at wintering grounds. Since no comparative data are available on either memory retention or memory flexibility in migratory and non-migratory species/subspecies, it is too early to make any conclusions about potential trade-offs among memory retention, memory capacity/load, memory flexibility and adult neurogenesis. But we can make predictions based on hypothesized associations that migratory species (1) should have higher memory capacity and larger memory load and (2) should be less cognitively flexible compared to non-migratory species. Higher neurogenesis rates in migratory birds may be associated with the need to reduce memory load and to reduce proactive interference. In this case, similar to that in food-caching species, neurogenesis might function to reduce the negative effects of proactive interference associated with stronger memories.

Memory capacity, proactive interference and neurogenesis

So far, available data suggest that better memory retention is associated with reduced cognitive flexibility, and higher cognitive flexibility is associated with worse memory retention. At the same time, adult neurogenesis-mediated forgetting appears to be one of the mechanisms involved in maintaining cognitive flexibility – higher neurogenesis rates decrease memory retention but increase cognitive flexibility, while lower neurogenesis rates seem to increase memory retention but decrease cognitive flexibility (Akers et al. 2014; Frankland et al. 2013; Epp, Mera, Kohler,Jesselyn & Frankland, 2016).

Existing evidence connecting adult neurogenesis with memory retention and flexibility comes from a few model species, primarily lab rodents. A big question is whether this relationship is maintained across species with different life histories or even across populations experiencing different environments and hence differential selection pressures. In other words, can we expect that species/populations with higher hippocampal neurogenesis rates have worse memory retention and higher memory flexibility than species/populations with lower neurogenesis rates? While there are little data available on this question, they actually seem to show the opposite. For example, food-caching species seem to have higher hippocampal neurogenesis rates (Hoshooley & Sherry, 2007) than non-caching species, but they have better spatial memory (Biegler, McGregor, Krebs, & Healy, 2001; Pravosudov & Roth 2013) and also show more proactive interference/less cognitive flexibility (Hampton et al. 1998; Lewis & Kamil 2006; Croston et al. 2017). In food-caching chickadees, birds in harsher winter environments have better spatial memory (Pravosudov & Clayton 2002; Roth et al. 2012), including longer memory retention (Freas et al. 2012), but they also have higher hippocampal neurogenesis rates compared to birds from milder environments (Chancellor et al., 2011; Roth et al. 2012; Freas et al. 2012). At the same time, chickadees in harsher environments seem to show less cognitive flexibility compared to chickadees from milder environments (Croston et al. 2017).

Indeed, in food-caching species, it appears that better spatial memory is associated with higher hippocampal neurogenesis rates, but with lower memory flexibility due to higher levels of proactive interference. We propose memory capacity and load as the missing, but crucial component in interspecies comparisons (Fig. 1). Higher memory capacity has been suggested to increase proactive interference (Steinwascher & Meiser, 2016), and it is likely that higher memory load should also increase proactive interference.

Species with high demands on memory, such as food-caching species, are likely to have higher memory capacity than non-caching species, as they need to store an enormous number of memories for food cache locations. Chickadee populations in harsher environments also cache more food compared to chickadees from milder winter environments (Roth et al., 2012; Freas et al., 2012), which is likely associated with larger memory load. Higher memory capacity and the need to remember more caches (e.g. more memory load) are likely mediated by a larger hippocampus and a larger total number of hippocampal neurons (Pravosudov & Roth, 2013). However, food-caching species and populations in harsher environments also have higher neurogenesis rates (Hoshooley & Sherry, 2007; Roth et al., 2012; Freas et al., 2012), which is thought to reduce memory retention and increase memory flexibility. We hypothesize that increased hippocampal neurogenesis is a mechanism to reduce negative effects of proactive interference associated with larger memory capacity and load without affecting the retention of relevant memories by mediating forgetting of no longer relevant memories. If cognitive flexibility is advantageous and older memories associated with larger memory load should increase proactive interference and reduce cognitive flexibility, it can be expected that selection should favor some mechanisms that would allow reducing proactive interference while still maintaining long-lasting memories. Rapid neurogenesis-assisted forgetting specifically of no longer relevant memories, such as memories of retrieved caches, may serve as such a mechanism.

Species with specialized memory, such as food-caching species, deal with constantly changing information making some memories irrelevant while other memories remain relevant. Considering that selection for memory retention of relevant memories in food-caching species is likely high (e.g. Biegler et al., 2001; Pravosudov & Roth, 2013), irrelevant memories associated with recovered food caches should be rapidly discarded, which should reduce memory load and hence reduce proactive interference. Therefore, higher neurogenesis rates in species or populations that cache more food may serve a critical function of constantly clearing memories of recovered caches. At the same time, higher neurogenesis rates might not fully compensate for higher memory retention and higher memory capacity and load, which might explain why food-caching species/populations with better memory may still have lower memory flexibility and higher levels of proactive interference compared to species/populations with less memory use associated with less caching.

Finally, all scatter-hoarding species, such as chickadees and jays, space their food caches so that they are not close together. Such a strategy which was previously argued to reduced cache pilferage (Waite & Reeve, 1993), should also reduce proactive interference, as different caches would be associated with a different set of cues (Croston et al., 2017; Lewis et al., 2013).

The extent of memory flexibility and proactive interference might be a trade-off among memory retention, memory capacity and load, and adult neurogenesis rates. Given the same memory capacity/load, memory retention and adult neurogenesis might determine the extent of memory flexibility, but the need for larger memory capacity associated with larger memory load should change the association between memory retention and memory flexibility. To test these ideas, we need more comparative analyses of different species/different populations with different degrees of specialization of memory in combination with experiments manipulating memory load.

Memory specialization and better memory retention versus memory generalization and higher cognitive flexibility– which is better?

The predictability of the environment and ecology of different species should be the main factors predicting whether cognitive flexibility should be advantageous. When the environment is predictably variable, meaning that a change in the environment is to be expected, animals should benefit the most from being cognitively flexible (Lefebvre et al., 2004; Pravosudov & Roth, 2013). Conversely, completely unpredictable environments that do not provide reliable cues should select against learning altogether (Dunlap & Stephens, 2009). Results from cross-generational studies with the fruit fly showed that certain regimens of environmental changes will favor the evolution of learning while others will select against it (Dunlap & Stephens, 2009). At the other extreme, when the environment is very predictable, natural selection should favor the evolution of innate behaviors rather than learning.

In between these two extremes, the degree of environmental unpredictability likely determines whether cognitive flexibility would be advantageous. The key here is whether memory retention and cognitive flexibility indeed represent a trade-off. If there is no cost of flexibility it should always be favored, but species and populations do differ in degree of cognitive flexibility (Lefebvre et al. 2004; Croston et al. 2017; Bond, Kamil & Balda, 2007), suggesting some costs must exist. If there is a trade-off between memory retention and memory flexibility, different conditions would favor either longer retention or higher flexibility. If the environment changes rapidly and rather unpredictably, the value of previously learned information should be low and the ability to rapidly learn new associations should be favored. If the environment changes more predictably and previously-learned associations retain their value over long periods of time, memory retention should be favored over memory flexibility. For example, in food-caching species, food caches may be used for months after they were originally stored, therefore, memory retention is essential for successful cache retrieval. At the same time, food-caching species seem to exhibit more proactive interference than non-caching species (Hampton et al. 1998) and so appear less cognitively flexible. In contrast, it may be predicted that nomadic species that constantly move should have the highest degree of cognitive flexibility as the value of being able to learn and then discard new information as they move should be higher than retaining past memories which are no longer relevant.

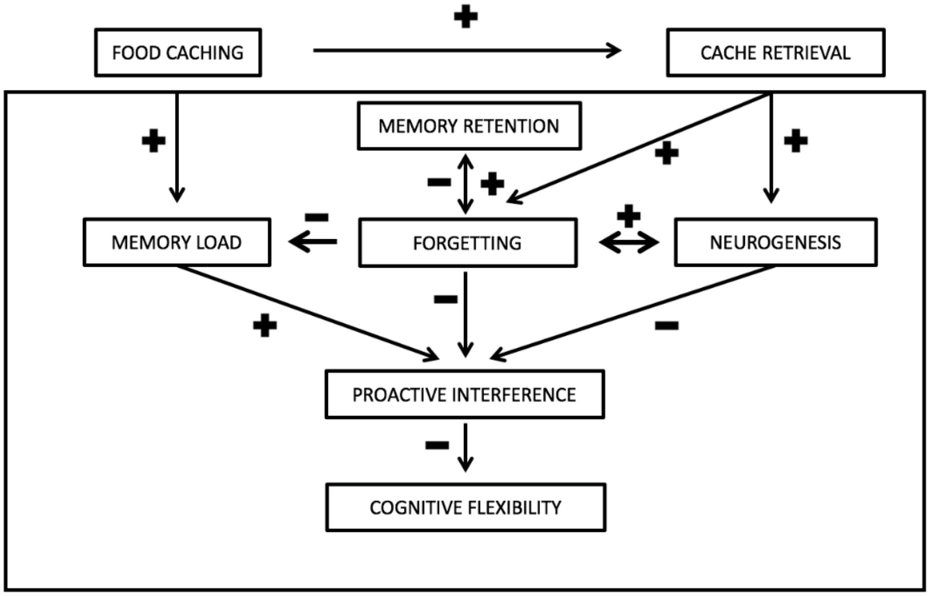

Figure 1. Hypothesized relationships among memory components thought to influence proactive interference and cognitive flexibility. Memory load is expected to increase

proactive interference and reduce cognitive flexibility while forgetting should reduce memory load and to increase flexibility. Higher memory retention may reduce forgetting, while retrieval of memories resulting in no longer relevant information should increase forgetting via increased hippocampal neurogenesis rates. Above the frame is the example of food caching where more food caching increases memory load and provides more opportunities for cache retrieval. More cache retrieval, in turn, should increase forgetting of retrieved caches and so should reduce memory load and reduce interference while also being associated with increased adult hippocampal neurogenesis rates.

Future directions

Unfortunately, most existing studies on the relationship among memory retention, memory interference, memory capacity/load, forgetting and neurogenesis are based on just a few model species, such as humans and lab rodents. Historically, psychologists studying animal learning have focused on general principles of learning, which is well suited to study in a few model species. While inter- and intra-specific variation in spatial memory (mainly acquisition and retention) has received considerable attention (e.g. Sherry 2006; Pravosudov & Roth 2013), there is lack of comparative studies investigating such variation in memory flexibility and only a handful of studies attempted comparative analyses of memory flexibility in different species/populations that differ in their life history traits and in their memory needs and use (e.g. Gonzalez et al., 1967; Hampton et al., 1998; Bond et al., 2007; Croston et al., 2017). Most cognitive traits including memory appear to have genetic basis (e.g. Croston et al. 2015), which suggests that they may be affected by natural selection resulting in both inter- and intra-specific variation.

Comparing multiple species has many challenges considering numerous species differences that may affect cognitive performance (e.g. Pravosudov & Roth 2013) and so it is critical to consider these differences when designing comparative studies. Within-species, population comparisons seem to provide a good alternative which allows comparing cognition in the same species, which is likely to respond similarly to experimental procedures (Pravosudov & Roth 2013). At the same time, comparing populations that may be under different selection pressures should allow better understanding of suggested trade-offs between memory and memory flexibility. Experimental manipulations now possible with wild animals in their natural environment should also allow direct tests for such trade-offs. Small resident birds in particular provide a convenient model to test many of the questions discussed here and link individual variation in cognitive traits to variation in fitness (Croston et al. 2017; Cauchoix 2017). Finally, some traits such as forgetting, might be difficult to measure, but, on the other hand, memory retention can be measured and memory load can also be manipulated experimentally both in the lab and in the field. So, a combination of memory retention, performance in reversal tasks and manipulation of memory load should allow testing the hypotheses discussed here.

In the end, however, only comparative analyses in combination with careful experimentation can provide the answers to the following questions:

(1) Do memory retention and memory flexibility indeed represent a trade-off? A few existing studies seem to support the idea of such trade-off as a few species compared and studies of lab rodents suggest that animals that retain memories longer do worse in a reversal learning task (less flexible) and animals that do better at reversal learning are worse at memory retention (Akers et al., 2014). Moreover, experimental studies manipulating hippocampal neurogenesis rates also suggest that improving memory

retention by reducing neurogenesis rates leads to less memory flexibility and improving flexibility by increasing neurogenesis rates leads to reduced memory retention (Akers et al., 2014; Epp et al. 2016). More studies comparing species/populations that differ in either memory retention or memory flexibility are needed to address the generality of this hypothesis and, most importantly, whether potential inter and intra-specific differences in the association between memory retention and memory flexibility have been shaped by natural selection. It is also important to use reversal tasks that do not rely on binary and re-usable choices (e.g. Cauchoix et al. 2017) as such tasks mainly test animals' ability to learn the rules that the rewarding choices always alternate. To test for potential trade-offs between memory retention and flexibility, reversal or serial reversal tasks should involve learning non-repeatable associations during each reversal, which will allow testing both memory retention and memory flexibility as a function of increasing memory load.

(2) Does memory load directly affect memory retention, proactive interference and memory flexibility? It is difficult to test for potential differences in memory capacity, but it is possible to experimentally manipulate memory load. Even when we see the suggested relationship between memory retention and memory flexibility, it might potentially be a product of differences in memory experiences and, more specifically, memory load. If individuals have higher memory load (e.g. food-caching species/populations with higher food caching rates), such load might directly affect memory flexibility. By experimentally increasing memory load, it should be possible to test (a) whether larger memory load increases proactive interference and (b) whether such effect is the same or different among different species with potentially different memory demands (e.g. food-caching vs non-caching species). Combining experimentation with memory load and comparative approach using species/populations with different demands on memory should allow for better

understanding of the relationship between these memory components and relative contributions of experience and natural selection.

(3) Does variation in developmental conditions affect the relationship between memory retention, proactive interference and memory flexibility? There are studies showing that developmental stress negatively affects hippocampal neurogenesis rates throughout life (Lemaire, Koehl, Le Moal, & Abrous, 2000). As adult neurogenesis seems to be involved in forgetting/memory retention/proactive interference relationship, it is thus possible that developmental stress might also affect all memory components.

(4) Finally, new research focused on neurogenesis in ecologically-relevant comparisons addressing inter- and intra-specific variation should consider neurogenesis role in forgetting and in reducing proactive interference associated with memory flexibility within the memory retention-memory flexibility paradigm. Measuring neurogenesis rates in all suggested above studies would bring better understanding of how neurogenesis may be involved in mediating memory and memory flexibility trade-offs.

Acknowledgements

VVP was supported by the NSF IOS1351295 and CLB was supported by the NSF DDIG 1600845.

References

Akers, K. G., Martinez-Canabal, A., Restivo, L., Yiu, A. P., de Cristofaro, A., Hsiang, H.-L., Wheeler, A. L., Guskjolen, A., Niibori, Y., Shoji, H., Ohira, K., Richards, B. A., Miyakawa, T., Josselyn, S. A., & Frankland, P. W. (2014). Hippocampal neurogenesis regulates forgetting during adulthood and infancy. *Science, 344*, 598-602.

Altman, J., & Das, G. (1967). Postnatal neurogenesis in the guinea-pig. *Nature, 214,* 1098–1101.

Altman, J., & Das, G. D. (1965). Post-natal origin of microneurons in the rat brain. *Nature, 207,* 953–956.

Anderson, M. C., & Neely, J. H. (1996). Interference and inhibition in memory retrieval. In E. L. Bjork & R. A. Bjork (Eds.), Memory. Handbook of perception and cognition (pp. 237–332). San Diego, CA: Academic Press.

Audet, J.-N., & Lefebvre, L. (2017). What's flexible in behavioral flexibility? *Behavioral Ecology*, *28*, 943-947.

Badre, D., & Wagner, A. D. (2006). Computational and neurobiological mechanisms underlying cognitive flexibility. *Proceedings of the National Academy of Sciences of the United States of America, 103,* 7186–7191.

Barker, J. M., Wojtowicz, J. M., & Boonstra, R. (2005). Where's my dinner? Adult neurogenesis in free-living food-storing rodents. *Genes Brain and Behavior*, *4*, 89-98.

Barnea, A., & Pravosudov, V. V. (2011). Birds as a model to study adult neurogenesis: bridging evolutionary, comparative and neuroethological approaches. *European Journal of Neuroscience*, *34,* 884-907.

Barnea, A., & Nottebohm, F. (1994). Seasonal recruitment of hippocampal neurons in adult free-ranging black-capped chickadees. *Proceedings of the National Academy of Sciences of the United States of America*, *91*, 271-221.

Bebus, S. E., Small, T. W., Jones, B. C., Elderbrock, E. K., & Schoech, S. J. (2016). Associative learning is inversely related to reversal learning and varies with nestling corticosterone exposure. *Animal Behaviour*, *111*, 251–260.

Becker, S. (2005). A computational principle for hippocampal learning and neurogenesis. *Hippocampus*, *15*, 722–738.

Becker, S., MacQueen, G., & Wojtowicz, J. M. (2009). Computational modeling and empirical studies of hippocampal neurogenesis-dependent memory: Effects of interference, stress and depression. *Brain Research*, *1299*, 45–54.

Biegler, R., McGregor, A., Krebs, J. R., & Healy, S. D. (2001). A larger hippocampus is associated with longer-lasting memory. *Proceedings of the National Academy of Sciences of the United States of America*, *98*, 6941-6944.

Bjork, R. A. (1970). Positive Forgetting: The noninterference of items intentionally forgotten. *Journal of Verbal Learning and Verbal Behavior*, *9*, 255–268.

Bjork, R. A. (1989). Retrieval inhibition as an adaptive mechanism in human memory. In H. L. Roediger III & F. I. M. Craik (Eds.), Varieties of memory and consciousness: Essays in honour of Endel Tulving (pp. 309–330). Hillsdale: NJ: Erlbaum.

Bond, A. B., Kamil, A. C., & Balda, R. P. (2007). Serial reversal learning and the evolution of behavioral flexibility in three species of North American Corvids (*Gymnorhinus cyanocephalus*, *Nucifraga columbiana*, *Aphelocoma californica*). *Journal of Comparative Psychology*, *121*, 372-379.

Burghardt, N. S., Park, E. H., Hen, R., & Fenton, A. A. 2012. Adult-born hippocampal neurons promote cognitive flexibility in mice. *Hippocampus*, *22*, 1795-1808.

Cauchoix, M., Hermer, E., Chaine, A. S., Morand-Ferron, J. 2017. Cognition in the field: comparison of reversal learning performance in captive and wild passerines. *Scientific Reports*, 7, 12945.

Chambers, R. A., Potenza, M. N., Hoffman, R. E., & Miranker, W. (2004). Simulated apoptosis/neurogenesis regulates learning and memory capabilities of adaptive neural networks. *Neuropsychopharmacology*, *29*, 747–758.

Chancellor, L. V., Roth II, T. C., LaDage, L. D., & Pravosudov, V. V. (2011). The effect of environmental harshness on neurogenesis: a large scale comparison. *Developmental Neurobiology*, *71*, 246-252.

Cheng, K., & Wignall, A. E. (2006). Honeybees (*Apis mellifera*) holding on to memories: response competition causes retroactive interference effects. *Animal Cognition*, *9*, 141–150.

Crick, C., & Miranker, W. (2006). Apoptosis, neurogenesis, and information content in Hebbian networks. *Biological Cybernetics*, *94*, 9–19.

Cristol, D.A., Reynolds, E.B., LeClerc, J.E., Donner, A.H., Farabaugh, C.S. & Ziegenfus, C.W.S. (2003). Migratory dark-eyed juncos, *Junco hyemalis*, have better spatial memory and denser hippocampal neurons than nonmigratory conspecifics. *Animal Behaviour, 66,* 317-328.

Croston, R., Branch, C. L., Kozlovsky, D. Y., Dukas, R., Pravosudov, V. V. (2015). Heritability and the evolution of cognitive traits. *Behavioral Ecology*, *26*, 1447-1459.

Croston, R., Branch, C. L., Pitera, A. M., Kozlovsky, D. Y., Bridge, E. S., Parchman, T. L., & Pravosudov, V. V. (2017). Predictably harsh environment is associated with reduced cognitive flexibility in wild food-caching mountain chickadees. *Animal Behaviour, 123*, 139–149.

Dukas, R. (1999). Costs of memory: ideas and predictions. *Journal of Theoretical Biology, 197*, 41–50.

Dukas, R. (2004). Evolutionary Biology of Animal Cognition. *Annual Review of Ecology, Evolution, and Systematics, 35*, 347–374.

Dunlap, A. S., & Stephens, D. W. (2009). Components of change in the evolution of learning and unlearned preference. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 3201–3208.

Epp, J. R., Mera, R. S., Kohler, S., Jesselyn, S. A., & Frankland, P. W. (2016). Neurogenesis-mediated forgetting minimizes proactive interference. *Nature Communications*, *7*, 10838.

Feng, R., Rampon, C., Tang, Y.-P., Shrom, D., Jin, J., Kyin, M., Sopher, B., Martin,G. M., Kim, S.-H., Langdon, R. B., Sisodia, S. S., & Tsien, J. Z. (2001). Deficient neurogenesis in forebrain-specific Presenlin-1 knockout mice is associated with reduced clearance of hippocampal memory traces. *Neuron*, *32,* 911-926.

Festini, S. B., & Reuter-Lorenz, P. A. (2014). Cognitive control of familiarity: directed forgetting reduces interference in working memory. *Cognitive Affective & Behavioral Neuroscience*, *14*, 78-89.

Frankland, P. W., Köhler, S., & Josselyn, S. A. (2013). Hippocampal neurogenesis and forgetting. *Trends in Neurosciences*, *36*, 497–503.

Freas, C., LaDage, L. D., Roth II, T. C., & Pravosudov, V. V. (2012). Elevation related differences in memory and the hippocampus in food-caching mountain chickadees. *Animal Behaviour*, *84*, 121-127.

Garthe, A., Behr, J., & Kempermann, G. (2009). Adult-generated hippocampal neurons allow the flexible use of spatially precise learning strategies. PLoS ONE 4: e5464.

Gonzalez, R. C., Behrend, E. R., & Bitterman, M. E. (1967). Reversal learning and forgetting in bird and fish. *Science*, *158*, 519–521.

Gould, E., Beylin, A., Tanapat, P., Reeves, A. & Shors, T.J. (1999) Learning enhances adult neurogenesis in the hippocampal formation. *Nature Neuroscience*, *2*, 260-265.

Guigueno, M. F., MacDougall-Shackleton, S. A., & Sherry, D. F. (2016). Sex and seasonal differences in hippocampal volume and neurogenesis in brood-parasitic brown-headed cowbirds (*Molothrus ater*). *Developmental Neurobiology*, *76*, 1275-1290.

Guskjolen, A., Epp, J. R., & Frankland, P. W. (2017). Hippocampal neurogenesis and forgetting. In: The Hippocampus from Cells to Systems, Structure, Connectivity, and Functional Contributions to Memory and Flexible Cognition. D. E. Hannula & M. C. Duff, (Eds), Springer International Publishing.

Hampton, R. R., Shettleworth, S. J., & Westwood, R. P. (1998). Proactive interference, recency, and associative strength: comparisons of black-capped chickadees and dark-eyed juncos. *Animal Learning and Behavior, 26*, 475-485.

Hardt, O., Nader, K., & Nadel, L. (2013). Decay happens: The role of active forgetting in memory. *Trends in Cognitive Sciences*, *17*, 111–120.

Hoshooley, J. S., & Sherry, D. F. (2007). Greater hippocampal neuronal recruitment in food-storing than in non-food-storing species. *Developmental Neurobiology*, *67*, 406-414.

Hoshooley, J. S., & Sherry, D. F. (2004). Neuron production, neuron number, and structure size are seasonally stable in the hippocampus of the food-storing black-capped chickadee (*Poecile atricapillus*). *Behavioral Neuroscience*, *118*, 345-355.

Hoshooley, J. S., Phillmore, L. S., Sherry, D. F., & MacDougall-Shackleton, S. A. (2007). Annual cycle of the black-capped chickadee: seasonality of food-storing and the hippocampus. *Brain Behavior and Evolution*, *69*, 161-168.

Hoshooley, J. S., Phillmore, L. S., & MacDougall-Shackleton, S. A. (2005). An examination of avian hippocampal neurogenesis in relationship to photoperiod. *Neuroreport*, *16*, 987-991.

Jacoby, L. L., Hay, J. F., & Debner, J. A. (2001) Proactive interference, accessibility bias, and process dissociations: valid subjective reports of memory. *Journal of Experimental Psychology*, *27*, 686-700.

Johnson, K. M., Boonstra, R., & Wojtowiccz, J. M. (2010). Hippocampal neurogenesis in food-storing red squirrels: the impact of age and spatial behavior. *Genes, Brain and Behavior*, *9*, 583-591.

Kempermann, G. (2008). The neurogenic reserve hypothesis: what is adult hippocampal neurogenesis good for? *Trends in Neurosciences*, *4*, 163-169.

Kitamura, T., Saitoh, Y., Takashima, N., Murayama, A., Niibori, Y., Ageta, H., Sekiguchi, M., Sugiyama, H., & Inokuchi, K. (2009). Adult neurogenesis modulates the hippocampus-dependent period of associative fear memory. *Cell*, *139*, 814-827.

Kramer, P. J., & Golding, J. M. (1997). Adaptive forgetting in animals. *Psychonomic Bulletin & Review*, *4*, 480-491.

Kuhl, B. A., & Wagner, A. D. (2009). Forgetting and retrieval. In: Handbook of Neuroscience for the Behavioral Sciences, G. G. Berntson & J. T. Cacioppo, (Eds.), John Wiley & Sons.

LaDage, L., Roth II, T. C., & Pravosudov, V. V. (2011). Hippocampal neurogenesis is associated with migratory behavior in adult but not juvenile white-crowned sparrows (*Zonotrichia leucophrys ssp*.). *Proceedings of the Royal Society B: Biological Sciences*, *278*, 138-143.

LaDage, L. D., Roth II, T. C., Fox, R. A., & Pravosudov, V. V. (2010). Ecologically-relevant spatial memory use modulates hippocampal neurogenesis. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 1071-1079.

Lefebvre, L., Reader, S. M., & Sol, D. (2004). Brains, innovations and evolution in birds and primates. *Brain, Behavior and Evolution*, *63*, 233–246.

Lemaire, V., Koehl, M., Le Moal, M., & Abrous, D. N. (2000). Prenatal stress produces learning deficits associated with an inhibition of neurogenesis in the hippocampus. *Proceedings of the National Academy of Sciences of the United States of America*, *97*, 11032-11037.

Lewis, J. L., Kamil, A. C., & Webbink, K. E. (2013) Changing room cues reduces the effects on proactive interference in Clark's nutcrackers, *Nucifraga columbiana*. *Journal of Experimental Psychology, 39*, 187-192.

Lewis, J. L., & Kamil, A. C. (2006). Interference effects in the memory for serially presented locations in Clark's nutcrackers, *Nucifraga columbiana*. *Journal of Experimental Psychology: Animal Behavior Processes*, *32*, 407–418.

Martinez-Canabal, A. (2015). Rewiring, forgetting and learning. Commentary: a critical period for experience-dependent remodeling of adult-born neuron connectivity. *Frontiers in Neuroscience*. *9*, 298.

Mery, F., & Kawecki, T. J. (2003). A fitness cost of learning ability in *Drosophila melanogaster*. *Proceedings of the Royal Society B: Biological Sciences*, *270*, 2465–69.

Olson, A. K., Eadie, B., Ernst, C., & Christie, B. R. (2006). Environmental enrichment and voluntary exercise massively increase neurogenesis in the adult hippocampus via dissociable pathways. *Hippocampus*, *16*, 250–260.

Patel, S. N., Clayton, N. S., & Krebs, J. R. (1997). Spatial learning induces neurogenesis in the avian brain. *Behavioural Brain Research*, *89*, 115–128.

Plaçais, P. Y., & Preat, T. (2013). To favor survival under food shortage, the brain disables costly memory. *Science*, *339*, 440–442.

Postman, L., Stark, K., & Fraser, J. (1968). Temporal changes in interference. *Journal of Verbal Learning and Verbal Behavior*, *7*, 672–694.

Pravosudov, V. V., & Roth II, T. C. (2013). Cognitive ecology of food hoarding: the evolution of spatial memory and the hippocampus. *Annual Reviews of Ecology, Evolution and Systematics*, *44*, 18.1-18.21.

Rodriguez, W. a., Borbely, L. S., & Garcia, R. S. (1993). Attenuation by contextual cues of retroactive interference of a conditional discrimination in rats. *Animal Learning & Behavior*, *21*, 101–105.

Pravosudov, V. V., Roth II, T. C., LaDage, L. D., & Freas, C. A. (2015). Environmental influences on spatial memory and the hippocampus in food-caching chickadees. *Comparative Cognition and Behavior Reviews*, *10*, 25-43.

Pravosudov, V. V. & Roth II, T. C. (2013). Cognitive ecology of food hoarding: the evolution of spatial memory and the hippocampus. *Annual Reviews of Ecology, Evolution and Systematics*, *44*,173-193.

Pravosudov, V. V. (2006). On seasonality of food caching behavior in parids: do we know the whole story? *Animal Behavior*, *71*, 1455-1460.

Pravosudov, V. V. & Clayton, N. S. (2002). A test of the adaptive specialization hypothesis: population differences in caching, memory and the hippocampus in black-capped chickadees (*Poecile atricapilla*). *Behavioral Neuroscience, 116*, 515-522.

Roth II, T.C., LaDage, L. D., Freas, C., & Pravosudov, V. V. (2012). Variation in memory and the hippocampus across populations from different climates: a common garden approach. *Proceedings of the Royal Society B: Biological Sciences*, *279,* 402-410.

Sherry, D. F. 2006. Neuroecology. *Annual Reviews in Psychology*, **57**, 167-169.

Snell-Rood, E. C. (2013). An overview of the evolutionary causes and consequences of behavioural plasticity. *Animal Behaviour*, *85*, 1004–1011.

Steinwascher, M. A., & Meiser, T. (2016). How a high working memory capacity can increase proactive interference. *Consciousness and Cognition*, *44*, 130-145.

Storm, B. C., & Bjork, R. A. (2016). Do learners predict a shift from recency to primacy with delay? *Memory & Cognition*, *44*, 1204–1214.

Strang, C. G., & Sherry, D. F. (2014). Serial reversal learning in bumblebees (*Bombus impatiens*). *Animal Cognition*, *17*, 723–734.

Swan, A. A., Clutton, J. E., Chary, P. K., Cook, S. G., Liu, G. G., & Drew, M. R. (2014). Characterization of the role of adult neurogenesis in touch-screen discrimination learning. *Hippocampus*, *24*, 1581-1591.

van Praag, H., Christie, B. R., Sejnowski, T. J., & Gage, F. H. (1999). Running enhances neurogenesis, learning, and long-term potentiation in mice. *Proceedings of the National Academy of Sciences of the United States of America*, *96*, 13427–13431.

Waite, T. A., & Reeve, J. D. (1993). Food storage in gray jays: source type and cache dispersion. *Ethology*, *93*, 326-336.

Watkins, M. J., & Watkins, O. C. (1976). Cue-overload theory and the method of interpolated attributes. *Bulletin of the Psychonomic Society*, *7*, 289–291.

Weisz, V. I., & Argibay, P. F. (2012). Neurogenesis interferes with the retrieval of remote memories: Forgetting in neurocomputational terms. *Cognition*, *125*, 13–25.

Wixted, J. T. (2004). The psychology and neuroscience of forgetting. *Annual Review of Psychology*, *55*, 235–269.

Yau, S. Y., Li, A., & So, K. F. (2015). Involvement of adult hippocampal neurogenesis in learning and forgetting. *Neural Plasticity*, *2015*, 1–13.