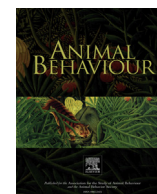




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## Special Issue: Cognitive Ecology

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

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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 intraspecific 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 favour either end of the continuum between memory retention and memory flexibility depending on life history and environment. More stable environments may favour memory retention over flexibility whereas rapidly changing environments may favour 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 favoured when higher capacity is beneficial such as in food-caching species. More research is necessary to understand whether inter- and intraspecific 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.

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Animals are able to modify their behaviour 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 behavioural responses to fit new contingencies and this is usually referred to as cognitive flexibility. Behavioural 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 learnt associations are changed or reversed (Anderson & Neely, 1996; Strang & Sherry, 2014). For example, in a colour association reversal learning task, an animal may be presented with two different colour 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 behaviour and only responds to the new contingency. Similarly, in a 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

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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 colours or two spatial locations). An alternative version involves nonrepeatable choices at each reversal (e.g. a different colour or spatial location at each reversal).

Behavioural ecologists have greatly expanded the use of the term 'behavioural flexibility' to include any behaviours that allow animals to adjust to changing environments, including behavioural innovations and problem solving. Such diversification of the term has produced confusion as different behaviours used to describe behavioural 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 behaviours 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 show both inter- and intraspecies 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 intraspecific 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 (1) species differ in memory flexibility and (2) there appears to be a trade-off between cognitive flexibility and memory retention.

Interspecific variation in cognitive flexibility suggests that there should be a cost to being cognitively flexible. Some of these costs may be energy-related, such as the energy needed to maintain a long-term memory (Plačais & 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 noncaching 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 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; Jacoby, Hay, & Debner, 2007; 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, memory performance in Clark's nutcrackers improved in a spatial reversal learning task when the birds were given new spatial cues during the reversal phase compared to their performance in a reversal task with the same spatial cues as during the initial learning (Lewis, Kamil, & Webbink, 2013). Similarly, laboratory rats showed significant interference after learning a second task, but such interference was significantly reduced when the context (e.g. 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 learnt information is affected, or forgotten, by learning new, similar information. For example, honey bees, *Apis mellifera*, that were trained to turn right on a green landmark 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 learnt 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 a serial reversal task is used with just two possible choices (e.g. [Cauchoix, Hermer, Chainé, & 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 a task does not allow testing for memory retention or 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 previously during each reversal stage. Such an 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 'list' or two 'lists' of rewarded locations performed worse during recall of the second list than during recall of 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, Small, 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 behaviour in a rapidly changing environment.

Based on human studies, it appears that retroactive interference is stronger when the interval between learning new information and recalling old information is short. When the interval between learning new information and recalling the older information is longer, retroactive interference decreases. Conversely, proactive interference increases as the time between learning new information and recalling it increases – older information is recalled more accurately than 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, whereas 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 behavioural and cognitive flexibility and therefore, remembering and forgetting are intimately related (e.g. [Kramer & 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 \(1965, 1967\)](#). 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, Eadie, 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, Beylin, Tanapat, Reeves, & Shors, 1999](#); [Kempermann, 2008](#); [van Praag et al., 1999](#)). 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, Mera, Kohler, Jesselyn, & Frankland, 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 differ from older neurons; new cells 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 resulted in worse performance in a reversal learning task (Epp et al., 2016). These findings support the idea that increased neurogenesis reduces proactive interference and enhances learning of new information, but at a cost of reduction in memory retention (e.g. forgetting), whereas reduced neurogenesis enhances memory retention but it also impedes learning new information because of proactive interference.

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, Boonstra, & Wojtowicz, 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; Becker, MacQueen, & Wojtowicz, 2009; Burghardt, Park, Hen, & Fenton, 2012; Epp et al., 2016; Feng et al., 2001; Frankland et al., 2013; Garthe, Behr, & Kempermann, 2009; Guskjolen, Epp, & Frankland, 2017; Hardt, Nader, & Nadel, 2013; Kitamura et al., 2009; Martinez-Canabal, 2015; Swan et al., 2014; Weisz & Argibay, 2012; Yau, Li, & So, 2015).

## RE-EVALUATING NEUROGENESIS IN ECOLOGICALLY RELEVANT PARADIGMS

Most of research on forgetting and neurogenesis have been conducted with model systems such as laboratory rodents and have 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 intraspecific variation in this relationship and how such variation might be associated with different selection pressures despite great interest in inter- and intraspecific variation in adult neurogenesis rates (Barnea & Pravosudov, 2011).

### Food-caching Animals

Recent advances in our understanding of the involvement of adult neurogenesis in forgetting requires reconsideration of most current ecologically based hypotheses about the role of adult neurogenesis. Previously, adult hippocampal neurogenesis was 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 (Barker, Wojtowicz, & Boonstra, 2005; Barnea & Nottebohm, 1994; Hoshoooley & Sherry, 2007; Johnson et al., 2010; LaDage, Roth, Fox, & Pravosudov, 2010, 2011; Roth, LaDage, Freas, &

Pravosudov, 2012). While species/population comparisons did find that animals with higher demands for food caches indeed have higher hippocampal neurogenesis rates (Freas et al., 2012; Roth et al., 2012), these results might also be explained both by improvements in memory flexibility allowing learning new information and by 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, Roth, LaDage, & Freas, 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 (Hoshoooley, Phillmore, Sherry, & MacDougall-Shackleton, 2007; Hoshoooley & Sherry, 2004, 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 the highest neuron incorporation rates in 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, usually occurs in September–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 autumn 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 the highest neurogenesis rates between November and spring may be explained by variation in cache retrieval activity.

In the laboratory, 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 noncaching, 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, MacDougall-Shackleton, & Sherry, 2016), which is also consistent with the idea of neurogenesis-based forgetting of information that was no longer relevant.

### Migratory Behaviour

It has been hypothesized that migratory behaviour is associated with more spatial memory use, and at least some comparisons indeed showed that, compared to nonmigratory subspecies, migratory subspecies performed better in a spatial memory task (Cristol et al., 2003; Pravosudov, Kitaysky, & Omanska, 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 hippocampi than nonmigratory species, but at least in one comparison of migratory and nonmigratory white-crowned sparrows, *Zonotrichia leucophrys*, hippocampal neurogenesis rates in adult migratory birds were higher than those in adult nonmigratory birds but similar to those in juveniles from both subspecies (LaDage et al., 2011). Nonmigratory adults, on the other hand, had lower hippocampal neurogenesis rates than juveniles of



both subspecies. Reduction in hippocampal neurogenesis rates with age is a well-known phenomenon (Akers et al., 2014). Migratory adults, however, did not have reduced neurogenesis rates compared to juveniles, at least at the time of sampling during autumn 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 the wintering grounds. Since no comparative data are available on either memory retention or memory flexibility in migratory and nonmigratory 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 nonmigratory 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; Epp et al., 2016; Frankland et al., 2013).

Existing evidence connecting adult neurogenesis with memory retention and flexibility comes from a few model species, primarily laboratory 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 few data available on this question, they actually seem to show the opposite. For example, food-caching species seem to have higher hippocampal neurogenesis rates (Hoshoooley & Sherry, 2007) than noncaching species, but they have better spatial memory (Biegler, McGregor, Krebs, & Healy, 2001; Pravosudov & Roth, 2013) and also show more proactive interference/less cognitive flexibility (Croston et al., 2017; Hampton et al., 1998; Lewis & Kamil, 2006). 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, Roth, LaDage, & Pravosudov, 2011; Freas et al., 2012; Roth 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

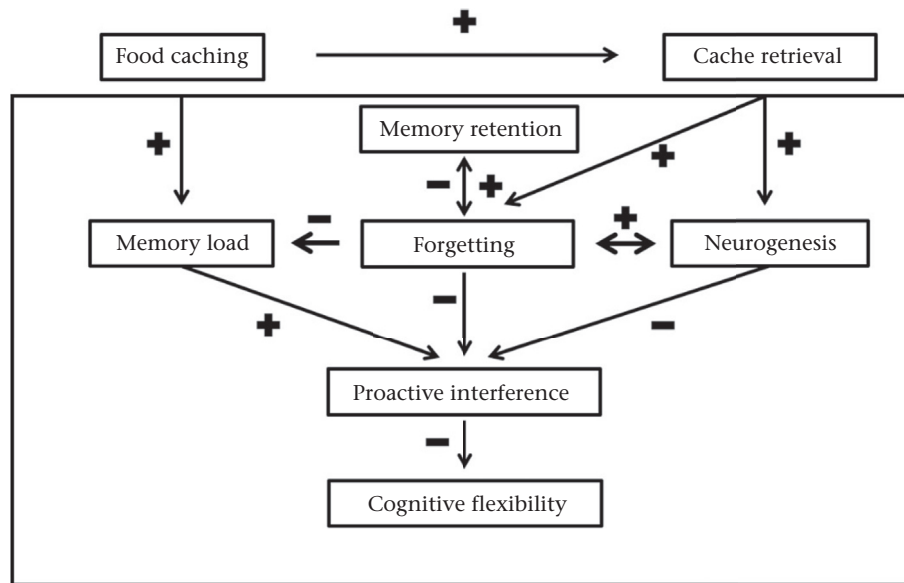
memory capacity has been suggested to increase proactive interference (Steinwascher & Meiser, 2016), and it is likely that higher memory load should also increase proactive interference.

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 (Freas et al., 2012; Roth 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 (Freas et al., 2012; Hoshoooley & Sherry, 2007; Roth 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 memories that are no longer relevant. If cognitive flexibility is advantageous and older memories associated with larger memory load increase proactive interference and reduce cognitive flexibility, it can be expected that selection should favour some mechanisms that would allow reducing proactive interference while still maintaining long-lasting memories. Rapid neurogenesis-assisted forgetting of irrelevant 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, as some memories become 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 reduce 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 between memory retention, 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/populations with different degrees of specialization of memory in combination with experiments manipulating memory load.



**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.

## MEMORY SPECIALIZATION AND RETENTION VERSUS MEMORY GENERALIZATION AND COGNITIVE FLEXIBILITY – WHICH IS BETTER?

The predictability of the environment and the 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 favour 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 favour the evolution of innate behaviours 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, then it should always be favoured, but species and populations do differ in their degree of cognitive flexibility (Bond, Kamil, & Balda, 2007; Croston et al., 2017; Lefebvre et al., 2004), suggesting some costs must exist. If there is a trade-off between memory retention and memory flexibility, then different conditions would favour either longer retention or higher flexibility. If the environment changes rapidly and rather unpredictably, the value of previously learnt information should be low and the ability to rapidly learn new associations should be favoured. If the environment changes more predictably and previously learnt associations retain their value over long periods, memory retention should be favoured over memory flexibility. For example, in food-caching species, food caches may be used for months after they were originally stored and, therefore, memory retention is essential for successful cache retrieval. At the same time, food-caching species

seem to exhibit more proactive interference than noncaching 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 that are no longer relevant.

## 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 laboratory 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 intraspecific variation in spatial memory (mainly acquisition and retention) has received considerable attention (e.g. Pravosudov & Roth, 2013; Sherry, 2006), there is lack of comparative studies investigating such variation in memory flexibility and only a handful of studies have 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. Bond et al., 2007; Croston et al., 2017; Gonzalez et al., 1967; Hampton et al., 1998). Most cognitive traits, including memory, appear to have a genetic basis (e.g. Croston, Branch, Kozlovsky, Dukas, & Pravosudov, 2015), which suggests that they may be affected by natural selection resulting in both inter- and intraspecific 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 that allows comparing cognition of the same species in different populations, which are 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 a 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 (Cauchoix et al., 2017; Croston et al., 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 laboratory 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 of the species compared and studies of laboratory rodents suggest that animals that retain memories longer do worse in a reversal learning task (are 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 intraspecific 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 reusable 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 nonrepeatable 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 an effect is the same or differs among species with potentially different memory demands (e.g. food-caching versus noncaching species). Combining experimentation with memory load and a comparative approach using species/populations with different demands on memory should allow for a better understanding of the relationship between these memory components and the relative contributions of experience and natural selection.

(3) Does variation in developmental condition 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 intraspecific variation should consider the role of neurogenesis in forgetting and in reducing proactive interference associated with memory flexibility within the memory retention–memory flexibility paradigm. Measuring neurogenesis rates in all of the studies suggested above would bring a better understanding of how neurogenesis may be involved in mediating memory and memory flexibility trade-offs.

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