Potential Mechanisms Driving Population Variation in Spatial Memory and the Hippocampus in Food-caching Chickadees

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Synopsis Harsh environments and severe winters have been hypothesized to favor improvement of the cognitive abilities necessary for successful foraging. Geographic variation in winter climate, then, is likely associated with differences in selection pressures on cognitive ability, which could lead to evolutionary changes in cognition and its neural mechanisms, assuming that variation in these traits is heritable. Here, we focus on two species of food-caching chickadees (genus Poecile), which rely on stored food for survival over winter and require the use of spatial memory to recover their stores. These species also exhibit extensive climate-related population level variation in spatial memory and the hippocampus, including volume, the total number and size of neurons, and adults’ rates of neurogenesis. Such variation could be driven by several mechanisms within the context of natural selection, including independent, population-specific selection (local adaptation), environment experience-based plasticity, developmental differences, and/or epigenetic differences. Extensive data on cognition, brain morphology, and behavior in multiple populations of these two species of chickadees along longitudinal, latitudinal, and elevational gradients in winter climate are most consistent with the hypothesis that natural selection drives the evolution of local adaptations associated with spatial memory differences among populations. Conversely, there is little support for the hypotheses that environment-induced plasticity or developmental differences are the main causes of population differences across climatic gradients. Available data on epigenetic modifications of memory ability are also inconsistent with the observed patterns of population variation, with birds living in more stressful and harsher environments having better spatial memory associated with a larger hippocampus and a larger number of hippocampal neurons. Overall, the existing data are most consistent with the hypothesis that highly predictable differences in winter climate drive the evolution and maintenance of differences among populations both in cognition and in the brain via local adaptations, at least in food-caching parids.

Introduction

Animals inhabiting temperate environments experience regular and highly predictable seasonal variation in climate and availability of food. Food caching is a behavioral adaptation that allows non-migratory animals to survive temporal periods when food is scarce and/or unpredictable (e.g., Vander Wall 1990; Pravosudov and Roth 2013) by relying on food stored previously during periods of relative abundance (Vander Wall 1990). Reliance on stored food for over-winter survival can be predicted to vary within species depending on the harshness of winter conditions, which varies predictably along climatic gradients (e.g., Pravosudov and Roth 2013); in harsher environments with colder and longer winters, cached food might be more critical. Food
caching and cache retrieval are dependent on cognitive mechanisms, therefore both cognition, or the neuronal process involved in acquisition, retention, and use of information (Dukas 2004), in general, and spatial memory ability in particular (e.g., Krebs et al. 1989; Sherry et al. 1989; Pravosudov and Roth 2013), can be expected to be associated with degree of reliance on food caches.

Birds of the family Paridae are scatter-hoarding species, which cache individual food items in separate locations, and use spatial memory to relocate caches (Krebs et al. 1989; Sherry et al. 1989; Vander Wall 1990; Pravosudov and Roth 2013). Mountain chickadees *Poecile gambeli* and black-capped chickadees *P. atricapillus* occupy geographic ranges along strong gradients of climatic severity, which are associated with elevation (mountain chickadees) as well as latitude and longitude (black-capped chickadees), across North America. Along these climatic gradients, both species have been hypothesized to vary significantly in their reliance on cached food, and have been shown to exhibit significant differences in neuroanatomical features associated with variation in spatial learning and memory ability (reviewed by Pravosudov and Roth 2013). In both species, individuals living in harsher climates (i.e., higher latitudes, higher elevations) have a larger hippocampus, more and larger hippocampal neurons, higher rates of adult hippocampal neurogenesis, and better spatial memory than do conspecifics inhabiting milder climates (Pravosudov and Clayton 2002; Roth and Pravosudov 2009; Roth et al. 2011; Chancellor et al. 2011; Freas et al. 2012, 2013b). Whereas interspecific variation in spatial memory and the hippocampus has always been considered a product of natural selection (e.g., Krebs et al. 1989; Sherry et al. 1989), the mechanisms generating equally large intraspecific variation in populations along climatic gradients remain debatable (Pravosudov and Roth 2013; Pravosudov et al. 2015). Multiple mechanisms may underlie variation in spatial memory and hippocampal morphology, but their relative contributions may be quite different. Here, we focus more specifically on the roles of:

(1) Natural selection/local adaptation to climate—predictably variable climatic conditions may result in differential selective pressures, resulting in the evolution of populations with variable caching propensity, hippocampus morphology, and spatial memory ability. “Memory ability” here is defined not only as the ability to remember the locations of numerous food caches, but also a specific measure of accuracy and/or duration of the retention of memory. Assuming that variation in spatial memory ability and hippocampal morphology is heritable, differential winter mortality would be expected to result in local adaptations and lead to climate-related differences among populations.

(2) Behavioral plasticity—variable climatic conditions may result in adaptive plasticity in caching propensity, spatial memory, and hippocampal morphology in response to changing environmental conditions and differences in food-caching experiences. For example, more memory use associated with higher food caching intensity might affect both memory and the hippocampus (Clayton and Krebs 1994; Maguire et al. 2000).

(3) Developmental differences—variable climatic conditions may result in differential stress in early life, resulting in hippocampal morphology and behavior suited to environmental stressors in a given natal environment, varying across climatic ranges. Developmental stress is well known to affect development of the brain, resulting in differences in cognitive ability, and spatial memory in particular, later in life (e.g., Nowicki et al. 2002; Pravosudov 2009; Buchanan et al. 2013).

(4) Epigenetic effects—variable climatic conditions may result in differential epigenetic modification underlying differences in memory ability and the hippocampus (and any potential developmental or plastic effects mediated by epigenetic mechanisms). These may or may not be inherited transgenerationally.

In this review, we discuss the possible relative contributions and role of each of these mechanisms in generating and maintaining the observed population-level variation in spatial memory and hippocampus morphology in food caching mountain and black-capped chickadees along climatic gradients. We argue that despite some degree of plasticity in at least some hippocampal properties, such as hippocampal volume, the overall pattern of variation observed across chickadee populations is most consistent with the hypothesis that variation in severity of winter climate drives differential selection on spatial memory and hippocampal morphology, and this results in population-level differences, i.e., local adaptation. While all of the mechanisms discussed below likely contribute to population variation jointly, the existing evidence suggests that
natural selection driving local adaptation has resulted in genetic changes underlying major differences in memory and the brain. All support for the natural selection hypothesis is, however, still indirect, and future studies should focus on both testing for heritability of variation in memory and hippocampus morphology, and on measuring fitness consequences of such variation.

Local adaptation

The main \textit{a priori} hypothesis at the center of all studies of climate-related variation in spatial memory and hippocampal morphology in food-caching chickadees implicates natural selection as the direct evolutionary mechanism responsible for such variation (Pravosudov and Clayton 2002; Roth and Pravosudov 2009; Roth et al. 2011, 2012a; Freas et al. 2012, 2013a, 2013b; Pravosudov and Roth 2013). This hypothesis is based on several key assumptions:

(1) Food caching and cache recovery, which are based at least in part on spatial memory and the hippocampus, are critical for overwinter survival.

(2) Relatively more severe winter climate characterized by colder and longer winters and associated with limited and unpredictable food supplies is associated with higher reliance on cached food.

(3) Greater reliance on food caches in more severe winter climate increases the strength of selection on food caching propensity and on the mechanisms of successful recovery of caches, including hippocampus-based spatial memory.

(4) Differential selection on food caching propensity and on spatial memory and the hippocampus associated with highly predictable population differences in the severity of winter produces significant variation in these traits via differential mortality (e.g., Pravosudov and Roth 2013).

The hypothesis based on natural selection predicts that birds in populations experiencing colder and longer winters should (1) cache more food, (2) have better spatial memory (accuracy, retention, and/or recall), and (3) have a larger hippocampus, with more and larger hippocampal neurons and higher rates of hippocampal neurogenesis in adults compared with birds from milder climates.

Spatial memory ability and hippocampal morphology should be available to selection provided that these traits are variable, that variation in these traits is heritable, and that birds with better spatial memory have a higher probability of surviving over winter in harsher climates. While it is unquestionable that there is large individual variation both in spatial memory and in hippocampal morphology (Pravosudov and Clayton 2002; Roth and Pravosudov 2009; Roth et al. 2011, 2012a; Freas et al. 2012), it is not yet known whether such variation in food-caching chickadees is heritable, or has survival consequences dependent on severity of winter climate, despite that this assumption is key in all comparative interspecific studies (e.g., Sherry 2006). As such, direct evidence for natural selection generating local, climate-associated variation in spatial memory and hippocampal morphology (i.e., local adaptation) is lacking. There is substantial indirect evidence, however, pointing toward local adaptation as the main factor explaining overall population-level variation in cognition and in the brain across populations of chickadees along climatic gradients.

Common garden experiments reveal experience-independent population-level variation in memory and the brain

In black-capped chickadees, birds from different climates collected at the nests with their eyes still closed and hand-reared and maintained in the same laboratory conditions showed significant population differences in spatial memory ability (accuracy, but not longevity) and in the total number of hippocampal neurons and adults’ rates of hippocampal neurogenesis (Roth et al. 2012a, 2012b). These results are consistent with the local adaptation hypothesis and argue against at least one alternative hypothesis that differences among populations of black-capped chickadees could be based mainly on post-development plasticity due to potential differences in environment and experience (Roth et al. 2012a). Moreover, there were significant differences among populations in hippocampal gene expression in these “common garden” birds despite that they were reared and maintained in identical environmental conditions (Pravosudov et al. 2013). Many of the differentially expressed genes have been previously implicated in hippocampal function.

Similarly, in mountain chickadees living along an elevation gradient of winter climate severity, juvenile birds from different elevations captured prior to their first winter and housed under standard laboratory conditions exhibited significant differences in caching propensity, spatial memory, and hippocampal morphology (Freas et al. 2012, 2013b).

It is important to note that these common garden experiments cannot rule out potential contributions
of early developmental (in the case both of black-capped chickadees and mountain chickadees) or early post-fledging (in the case of mountain chickadees) trigger effects, such that some events in potentially narrow developmental windows could lead to measurable variation later in life (e.g., Clayton and Krebs 1994). However, there is no evidence, thus far, supporting these hypotheses as the main explanations for population-level variation, as populations in harsher environments show better spatial memory, an enlarged hippocampus with more neurons and increased hippocampal rates of neurogenesis (see discussion below). This trend runs opposite to that predicted under the hypothesis that developmental differences drive population variation in chickadees’ spatial memory and hippocampal morphology, except in the unlikely situation when rearing in milder environments across both species presents more stressful developmental conditions.

**Differences in rates of exploration of novel environments**

In mountain chickadees, birds from high elevations with harsher environments explore novel environments more slowly than do birds from low elevations (Kozlovsky et al. 2014). Exploration rates for novel environments are often used to describe individual differences in personality traits and, at least in some parids, they are known to be heritable (Drent et al. 2003; Dochtermann et al. 2014). Exploration rates for novel environments and ability to learn may also be components of a suite of correlated behavioral traits (e.g., Kozlovsky et al. 2014), and elevation-related differences in both of these traits may be produced by natural selection acting on other behavioral phenotypes, such as spatial memory ability.

**Differences in social dominance**

In mountain chickadees, elevation-related differences in climate were associated with differences in social-dominance rank in pairwise social interactions (Kozlovsky et al. 2014). Mountain chickadees from high elevations (associated with more accurate spatial memory) were socially subordinate to chickadees from lower elevations. While it is possible that differences in spatial memory and hippocampal morphology are linked with the ability to obtain a high social rank as a behavioral personality trait, such differences likely reduce potential movement between elevations irrespective of how or why they exist. If chickadees from high elevations were to disperse to lower elevations, they would likely suffer higher mortality due to their socially subordinate status (Kozlovsky et al. 2014). At the same time, chickadees from low elevations would likely suffer higher winter mortality if they were to disperse to higher elevations due to their lower propensity for caching food and less accurate spatial memory associated with smaller hippocampal volume and significantly smaller number of hippocampal neurons (Kozlovsky et al. 2014). Such reduced movement between climatic zones might be expected to favor the evolution of local adaptations via natural selection.

**Variation in female mate preference**

Assortative mating is an important mechanism usually associated with the evolution of local adaptations and divergence of populations (e.g., Kondrashov and Shpak 1998). Females’ preference for a particular phenotype should increase the fitness of this phenotype over any other phenotypes present in a population. Mountain chickadee females from high elevation populations, when presented with multiple independent choices between males from high-elevation versus low-elevation populations under laboratory conditions (Branch et al. 2015), showed a significant preference for males from high elevation. Females from low elevation, however, had no significant preference. Considering that both the propensity for caching food and good spatial memory appear to be especially valuable at high elevations where winters are more severe, female preference for local males, which are likely adapted to their local environments, should be adaptive specifically at higher elevations and increase females’ fitness through the production of locally adapted offspring. At low elevations, such differences in memory and hippocampal morphology may be less essential, which might explain no preference for low elevation females (Branch et al. 2015). Notably, females do not need to directly assess males’ cognitive abilities in order to choose mates that are best adapted to local climate—they need only to discriminate between local and non-local males. There are significant differences in the structure of song between male mountain chickadees from high versus low elevations (Branch and Pravosudov 2015), and differences in dialect are well-known to be used by females to discriminate between local and non-local males (Baker et al. 1987; Rowell and Servedio 2012).

**Heritability of spatial memory and hippocampal morphology**

Although there are no data on heritability of spatial memory ability and the morphology of the
hippocampus in chickadees, or in birds in general, evidence based on mammals suggests a rather high degree of heritability both for memory and hippocampal volume (e.g., McGee 1979; Linn and Petersen 1985; Lyons et al. 2001; Sullivan et al. 2001; Wright et al. 2002; van Erp et al. 2004; Fears et al. 2009; Knowles et al. 2013; Hopkins et al. 2014). Because birds are subject to the same selective processes and share basic neural architecture and processing with mammals, it is likely that heritability of memory and hippocampal morphology is also high in birds. Moreover, estimates of heritability in mammals are likely conservative, as they are generally derived from measures of hippocampal volume, which is rather plastic (e.g., Roth et al. 2010). If the volume of the hippocampus shows high heritability, hippocampal neuron number, which shows little plasticity in chickadees (LaDage et al. 2009; Roth et al. 2012a; Freas et al. 2013b), may be expected to be even more heritable. As there is little yet known about the heritability of neural and behavioral traits in birds, and a paucity of data pertaining to the heritability of traits in non-human animals in general, future studies are needed to confirm this expectation.

Climate-dependent variation in breeding and social dominance inhibit movement along a climatic gradient in resident birds

Variation in climate among adjacent populations might lead to reduction in movement between populations, thereby facilitating local adaptations via differences in timing of breeding and in associated population-level differences in social dominance. This potential mechanism might stem from several critical and well-established components that have not been linked previously:

1. Most species of birds adjust timing of breeding to the current environmental conditions. Longer and colder winters result in later breeding and, subsequently, in later fledging and later dispersal of juveniles.
2. Timing of breeding and fledging have a strong effect on the success of group recruitment in winter and on social rank within the group, such that later fledged individuals are likely to become socially subordinate to earlier fledged individuals.
3. Survival during winter is dependent on social rank, with the most subordinate members of the group suffering the highest mortality.

In combination, these patterns might reduce movement from harsher to milder climates, but would have no effect on any movements from more benign to harsher climatic conditions. At the same time, harsher climatic conditions should favor superior spatial memory and a larger hippocampus containing more neurons as specific adaptations to such conditions. Individuals dispersing from milder climates toward a harsher climate would lack these adaptations, and likely suffer higher mortality compared with local individuals.

Harsher climates are associated with later breeding

Whereas there is significant variation in the timing of breeding within and across many avian species, it is well recognized that climatic conditions, and ambient temperature in particular, play a major role in such variation (e.g., McCleery and Perrins 1998; Dunn and Winkler 1999; Both et al. 2004; Charmantier et al. 2008; Visser et al. 2009; Vedder et al. 2013). Colder spring weather is almost always associated with delayed breeding even within the same general climatic zone (e.g., Vedder et al. 2013). Moreover, ambient temperature directly and causally affects the timing of reproduction (e.g., Visser et al. 2009). Within species, the start of breeding correlates with fledging date and individuals
breeding earlier fledge their young earlier (Nilsson and Smith 1988; Nilsson 1989).

Winter climate varies predictably on a large continental scale along a longitudinal gradient, with colder and longer winters in more northern environments. Accordingly, spring conditions also arrive later in more northern environments, and breeding commences at later dates. Locations at higher elevation are characterized by colder and longer winters compared with those at lower elevation. Such elevation-related changes in climate can occur over short distances, depending on the steepness of the mountain’s slope, and might result in significant interspecific and intraspecific differences in the timing of breeding for birds in close geographic proximity. For example, just a difference of 600 m in elevation is associated with approximately 2 weeks difference in the commencement of breeding in mountain chickadees nesting only ca. 20 km apart at our research site in the Sierra Nevada in northern California (Kozlovsky et al. 2015).

Timing of breeding is associated with social dominance rank of juveniles after dispersal
At least one of the determinants of social dominance rank in most avian species, including parids, is timing of fledging (Arcese and Smith 1985; Nilsson and Smith 1988; Holberton et al. 1990; Sandell and Smith 1991; Koivula et al. 1993; Velando 2000; Snell-Rood and Cristol 2005). In parids, when social groups that will overwinter together begin to form in late summer, unrelated and previously unacquainted juveniles join resident adults (Ekman 1989; Hogstad 1989). Juveniles that arrive and join the groups first have been reported to integrate into social groups more successfully and to be socially dominant over juveniles that join the groups later (Nilsson and Smith 1988). This association is likely directly linked with the time of breeding as earlier fledged juveniles more likely initiate dispersal and settle in social groups earlier than do juveniles that fledged later (Nilsson and Smith 1988; Nilsson 1989), and earlier fledging is directly associated with higher success in recruitment into a social group and higher social rank (Nilsson and Smith 1988). In food-caching willow tits (P. montanus), there is a strong association between fledging date and social rank, as well as overall survival over winter (Nilsson and Smith 1988).

Lower social dominance rank is associated with lower fitness
It is widely assumed that social rank has consequences for fitness and that low social status is associated with lower probability of survival (e.g., Piper 1997). Parids arguably experience highest mortality during the winter, with average mortality rates for adults over winter being close to 50%; that for juveniles is likely even higher (e.g., Hogstad 1989). Social dominance is directly associated with the probability of surviving over winter such that the lowest-ranking individuals suffering the highest winter mortality (Desrochers et al. 1988; Hogstad 1989; Ratcliffe et al. 2007).

Most evidence linking status of social dominance with survival is based on correlational data (Ratcliffe et al. 2007); therefore, it is possible that low-ranking individuals are simply in inferior condition compared with the higher-ranking individuals. If that were the case, subordinate individuals’ higher risk of mortality might be a result of their inferior condition rather than their low social rank. Experimental evidence, however, fails to support this explanation. For example, it is well documented that subordinate individuals are forced into suboptimal foraging areas as well as areas where risk of predation is higher (Ekman 1989; Hogstad 1989). Experimental manipulation of dominance by removing dominant individuals from social groups yields significant changes in subordinate individuals’ condition and anti-predatory behavior (Ekman and Lilliendahl 1993; Koivula et al. 1994; Witter and Swaddle 1995), suggesting a causal relationship between social dominance and the probability of survival over winter.

Adult individuals in resident avian taxa such as parids usually do not exhibit significant movements after their first breeding (e.g., Ekman 1989; Hogstad 1989; Harrap and Quinn 1995) and so juveniles dispersing during late summer from the location where they hatched and to where they overwinter in social groups likely represent the main potential source of gene flow. As a result, any conditions that would decrease juveniles’ survival in wintering social groups would likely reduce movements and settlement into the habitats characterized by such conditions.

Connecting climate, timing of breeding, social dominance, and survival
Drawing from the three points discussed above, the following patterns emerge: (1) birds from colder and harsher climates breed later than do birds from milder climates, even within close geographical proximity; (2) if dispersing juveniles from a colder climate move and join wintering social groups in milder environments (e.g., moving down the mountain, or moving south), they will likely face higher mortality due to low social status as a result of later
fledging relative to resident juveniles. Differences in timing of reproduction due to climatic differences should significantly reduce movements from populations in the harsher climates to populations in the milder climates. This reduced movement could arise via climate-based variation in timing of breeding alone, without any additional trade-offs or lack of specific adaptations to the more benign winter environment. However, a combination of reduced movements from more benign climatic conditions, and potentially strong selection on traits allowing successful survival over winter in harsher environments, could result in reciprocal isolation along the climatic gradient. Young that fledge in milder climates would likely have higher mortality rates during winter if they move to harsher climates because they lack adaptations facilitating survival in harsher environments (e.g., enhanced spatial memory). Taken together, these conditions suggest that individuals may experience the best fitness outcome by remaining within the range of their natal climatic conditions. While this cannot per se rule out the influence of plasticity, developmental differences, and epigenetic mechanisms in driving population-level phenotypic differences, limited movement along climatic gradients in combination with potentially strong climate-related differences in selection pressures can lead to the evolution of local adaptations. At the same time, there are numerous environmental differences among populations experiencing similar climates (e.g., chickadees in Kansas and Washington state are similar in their cognition and the brain, yet their habitats are quite different) such that if population-level differences were driven primarily by an alternative mechanism, we would predict that populations at different locations within a cline would also vary.

Finally, it is important to note that although this new hypothesis was generated in reference to the extensively studied parids, the mechanisms described here likely operate in many species with dominance-structured social systems and dispersal across climatic gradients. Species may exhibit local adaptations with socially/developmentally limited movement if they meet the following conditions: (1) distribution along a pronounced gradient of winter climate, (2) post-natal dispersal occurring prior to the first winter, (3) status as a winter resident, and (4) social dominance associated with living in social groups.

Environment- and experience-based plasticity

Phenotypic plasticity is the ability of individuals to change their phenotypes depending on the demands of the environment, and is predicted to be the most adaptive in new or variable environments (West-Eberhard 1989; Dudley and Schmitt 1996; Agrawal 2001). Individuals must be able to adjust their behavior in order to mitigate effects of a changing environment. However, when conditions are consistent or predictably variable, plasticity may be less important and even selected against (Agrawal 2001). Seasonality of climate in temperate zones is highly predictable and winter predictably presents challenging conditions for foraging due to higher metabolic demands associated with a significant shortage of food. Given such predictability of harsh periods during the yearly cycle, evolving permanent adaptations to such periods might be expected. Although plasticity is usually predicted when environmental changes are unpredictable (e.g., Agrawal 2001), populations having varying degrees of reliance on cached food for survival over winter may still vary in spatial memory and hippocampal morphology as a result of plastic responses associated with variable severity of climate. However, available data on plasticity of spatial memory and the hippocampus do not seem to support the idea that plasticity is the main mechanism behind population-level variation in spatial memory and hippocampal morphology across populations of chickadees.

Experience-based plasticity in hippocampus development

There is some evidence that the amount of memory-based experiences can affect hippocampal volume (Clayton and Krebs 1994; Clayton 1996, 2001; Maguire et al. 2000; Woollett and Maguire 2011), and so it is possible that differences among populations in hippocampal morphology are mainly due to differential caching activity across populations, as populations in harsher environment cache significantly more food. Some experience in caching is necessary to trigger normal hippocampal development in juvenile food-caching birds (Clayton and Krebs 1994; Jolliffe 1997; Clayton 1998). Clayton and Krebs (1994) compared hippocampal volume and number of neurons in marsh tits, Parus palustris, allowed to store and retrieve caches post-fledging with birds that were prevented from caching. Cache-deprived birds developed significantly smaller hippocampi with fewer neurons than those allowed to experience caching. Likewise, these deprived birds had hippocampal size similar to that of control chicks that were 3 weeks younger (also with no experience in caching). Normal hippocampal development in parids, therefore, appears to be triggered by experience in storing and retrieving caches at least
three times (e.g., caching three food items) within the first 3 weeks after fledging (Clayton and Krebs 1994; Clayton 1996, 2001).

The most critical detail here is that the amount of food-caching experience required to trigger normal hippocampal development is very small, and any additional food-caching experience does not seem to produce any additional effects on hippocampal morphology. There appears to be a rather small threshold for experience-dependent hippocampal growth to occur, such that birds allowed regular opportunities to cache show no additional increases in hippocampal size relative to individuals limited to the minimal threshold (Clayton and Krebs 1994; Clayton 1996).

LaDage et al. (2009) investigated the role of caching-related memory experiences in 3- to 4-month-old wild-caught mountain chickadees and found no significant differences in hippocampus size or neuron number between individuals allowed to cache and those experimentally deprived of food-caching opportunities for several months. Hippocampal neurogenesis rates, however, were significantly reduced in the cache-deprived group, suggesting that deprivation of caching experiences was effective (LaDage et al. 2010). That hippocampal volume and the total number of neurons did not change in response to differences in food-caching-related memory experiences suggests that such experiences do not continue to affect hippocampal morphology beyond a very low threshold (e.g., just a few caches) (Clayton 2001) necessary to trigger normal hippocampal development (LaDage et al. 2009).

The fact that such a low “trigger” threshold is needed for normal development of the hippocampus (Clayton and Krebs 1994; Clayton 1996, 2001) limits the potential effect of differences in caching intensity on variation in spatial memory and hippocampus morphology among chickadee populations. In all of these populations, all birds likely cache well above the developmental threshold. At the same time, there is no evidence that caching 100,000 food items would affect hippocampal morphology differently than caching 50,000 items. In fact, the only available evidence directly contradicts this (Clayton and Krebs 1994; Clayton 1996, 2001).

In humans, it has been argued that acquiring memories can alter hippocampal size in adults (Maguire et al. 2000; Woollett and Maguire 2011), as the posterior hippocampi in brains of adult taxi-drivers were significantly larger than those of control subjects not driving taxis. In addition, within the taxi-driver group, there was a positive relationship between the amount of time an individual spent as a driver and the sizes of their posterior hippocampi (Maguire et al. 2000). Extensive use of spatial memory as a taxi-driver, therefore, has been argued to affect some hippocampal properties reflected by changes in hippocampus volume. The mechanisms underlying these changes in volume remain unknown, but it is likely that changes either in dendritic branching (which is known to occur rapidly) (e.g. Chen et al. 2010), neuron soma size (e.g., Freas et al. 2013a), or the number of glial cells (Roth et al. 2013) may have contributed to such changes. Intriguingly, in drivers that failed to pass the test after studying, there was no correlation between the time spent studying and hippocampal volume (Woollett and Maguire 2011), suggesting that there may be some genetic component to volumetric plasticity. Most importantly, however, there is no evidence that volumetric changes are associated with changes in total number of neurons, yet there are pronounced differences among populations in the number of hippocampal neurons in food-caching chickadees (Pravosudov and Roth 2013). Hippocampal volume in birds is well known to change based on environmental conditions (e.g., Smulders et al. 2000; LaDage et al. 2009; Tarr et al. 2009; Roth et al. 2012a; Freas et al. 2013b), yet such changes do not involve the number of neurons (LaDage et al. 2009; Roth et al. 2012a; Freas et al. 2013b). In fact, the total number of hippocampal neurons was statistically similar between wild birds and birds either hand-reared or collected as juveniles and maintained in a uniform laboratory environment for months, despite obviously large differences in experiences among these groups of birds (LaDage et al. 2009; Roth et al. 2012a; Freas et al. 2013b).

Seasonal plasticity
Seasonal variation in cognition and the brain following variation in cognitive demands may provide support for the hypothesis that variation among populations is driven by plasticity-based mechanisms. For example, seasonal fluctuations in birds’ song production and in related regions of the brain (Nottebohm 1981; Smith et al. 1997) suggest that seasonal variation may also occur in brain regions devoted to spatial memory because both storage and retrieval of caches have a clear seasonal pattern (Brodin 2005; Pravosudov 2006; Pravosudov et al. 2015). To date, however, the evidence for seasonal variation in hippocampal morphology and spatial memory and its association with seasonal variation in food caching and retrieval remains equivocal. Seasonal changes in day-length are associated with caching propensity, but experimental manipulation
of photoperiod affects only caching rates and not hippocampal volume (Krebs et al. 1995; MacDougall-Shackleton et al. 2003; Hoshooley et al. 2005). Several studies have reported seasonal differences in hippocampal neuron incorporation rates in black-capped chickadees (Barnea and Nottebohm 1994), as well as increased hippocampal volume and neuron number during the autumn compared with other seasons (Smulders et al. 1995, 2000). Some studies reported a 30% seasonal increase in hippocampal volume in black-capped chickadees during the peak of food caching (Smulders et al. 1995); however, similar studies revealed no significant seasonal differences in hippocampal volume or total number of neurons (Barnea and Nottebohm 1994; Hoshooley and Sherry 2004; Hoshooley et al. 2007). Hoshooley and Sherry (2007) reported seasonal differences in hippocampal morphology in black-capped chickadees, but these results ran opposite to the differences shown by Smulders et al. (1995, 2000). Hoshooley and Sherry (2007) found smaller hippocampal volume and fewer neurons in the autumn than in the spring. Adult hippocampal neurogenesis rates have been reported to either not vary seasonally or vary out of sync with food caching patterns (Hoshooley and Sherry 2004, 2007). Likewise, hippocampal neurogenesis rates do not respond to experimental manipulation of caching rates (Krebs et al. 1995; Hoshooley et al. 2005; MacDougall-Shackleton et al. 2003). There appears to be little consistent evidence of seasonal variation in food caching being related to any hippocampal property, even though hippocampal volume, at least, is well known to be plastic.

If spatial memory and hippocampal morphology directly respond to variation in cognitive demands related to food-caching, it might be expected that these traits would also vary among years, as there is large year-to-year variation in caching rates (Haftorn 1956). While there are no data directly linking yearly variation in caching rates with differences in memory or in the hippocampus, the data for climate-related variation among populations of chickadees have been collected over multiple locations and over multiple years, and the differences were highly consistent with average severity of winter climates (Pravosudov and Clayton 2002; Roth et al. 2010, 2012a; Freas et al. 2012, 2013a, 2013b). Such consistency indirectly argues against plasticity-based variation as the main driver of variation among populations and supports the selection hypothesis.

Social complexity hypothesis

The social complexity hypothesis posits that individuals living in more complex social situations (e.g., larger or mixed-species flocks) may have evolved superior cognitive abilities (e.g., complex communication: Freeberg 2006; problem solving: Byrne and Bates 2007; transitive inference: MacLean et al. 2008) as an adaptive response to complex sociality. If chickadees living in harsher environments also have more complex social structure, variation in spatial memory may result from differences in social structure across populations. There is, however, little evidence to support the presence of consistently more complex social groups in harsher environments. Few species tolerate higher latitudes and more extreme environments (Pianka 1966; Moldenke 1975; Qian and Ricklefs 2007); therefore, species richness is likely lower at higher latitudes and at higher elevations where climates are relatively harsh. While the number of conspecifics in a group may also vary across climatic gradients, this remains unknown in black-capped and mountain chickadees, the primary species showing strong climate-related variation in spatial memory and hippocampal morphology.

Either the structure or the complexity of the habitat may influence the need for enhanced cognitive abilities, but the pattern of variation seen across North America in black-capped chickadees also contrasts with these predictions. For example, in locations like Kansas and Washington, where the climate is milder and floral composition is more complex (Moldenke 1975; Qian and Ricklefs 2007), birds have smaller hippocampi and worse memory than those living in Alaska and Minnesota, where the climate is harsher and there is less vegetative diversity. Mountain chickadees, similarly, inhabit montane pine forests, and while species of pine vary with elevation, high and low elevations appear to have similar species composition.

Overall, the available evidence suggests that post-developmental, experience-based plasticity cannot fully explain population-level variation in chickadees’ spatial memory and hippocampal morphology. There are differences both in spatial memory and in hippocampal morphology in naïve juvenile black-capped and mountain chickadees prior to their first winter when potential differences in retrieval of food-caches might be present. Likewise, large differences in spatial memory, caching propensity, and hippocampal morphology persist even under laboratory conditions (Roth et al. 2010, 2012a; Freas et al. 2012, 2013a, 2013b), despite that captivity itself results in
decreased hippocampal volume (LaDage et al. 2009; Roth et al. 2012a; Freas et al. 2013b). Even when black-capped chickadees from the harshest (Alaska) and mildest (Kansas) populations were hand-reared in the laboratory from day 10, birds from Alaska cached more food items, had better spatial memory, performed better in problem-solving tasks, and had significantly more neurons and higher rates of neurogenesis in the hippocampus than did birds from Kansas (Roth et al. 2012a). Taken together, the evidence does not support the idea that differences among populations along climatic gradients are due in large part to post-development plasticity. Likewise, we know of no evidence linking population differences in spatial memory and hippocampal morphology with differences in habitat, social structure, or social complexity.

**Developmental plasticity**

Experiences that animals have during development are well known to affect cognition and the brain. Most studies of developmental effects on cognition and the brain focus on how stress affects these phenotypes, and a large body of literature is devoted to how stress affects spatial memory, learning, the hippocampus, and the high vocal center of birds (reviewed by Pravosudov 2009; Schoech et al. 2011). In these studies, animals are experimentally stressed via manipulation of glucocorticoids, nutritional restriction, or other stressors such as restraint or parasites (see Schoech et al. 2011). Effects on spatial memory, spatial learning, and the hippocampus are generally negative, and in animals that rely heavily on spatial memory (e.g., food-caching animals) these effects can be detrimental to survival (Dukas 1999; Pravosudov 2009). For example, in western scrub-jays (*Aphelocoma californica*) nutritional restriction in early post-hatching chicks led to significantly higher levels of corticosterone (CORT) in nestlings and had a marginal effect on adrenocortical responses in yearlings (Pravosudov and Kitaysky 2006). Yearling western scrub-jays that were exposed to nutritional stress during early post-hatching development had smaller hippocampi with fewer neurons than did controls, and also performed worse both in recovering caches and in a spatial associative learning task (Pravosudov et al. 2005). A similar study on rats showed that malnutrition during early development impaired spatial learning in the Morris water maze (Bedi 1992).

In food-caching mountain and black-capped chickadees, harsher environments are likely to induce more stress than milder environments because of longer winters with lower temperatures, more snowfall, and more snow cover, all of which increase energetic demands while limiting availability of food (Pravosudov and Roth 2013). If developmental stress drives variation in spatial memory and hippocampal morphology across populations of chickadees, and nutritional stress is greater in harsher environments compared with milder environments, then chickadees from harsh environments should have worse spatial memories, smaller hippocampal volume, and fewer hippocampal neurons. This is, however, contrary to the trend observed across chickadee populations varying both along latitudinal and elevational gradients. Chickadees from harsher environments perform better on experimental spatial-learning tasks, and have larger hippocampi with more neurons than do individuals inhabiting milder environments (Roth and Pravosudov 2009; Roth et al. 2011, 2012a; Freas et al. 2012, 2013b).

A few studies have suggested that some aspects of learning may be enhanced, rather than reduced, in birds that have experienced developmental stress (e.g., Calandreau et al. 2011; Goerlich et al. 2012; Crino et al. 2014). In captive-bred zebra finches (*Taeniopygia guttata*), direct manipulation of CORT resulted in faster acquisition of a novel foraging task, but differences occurred only during the first stage of the task when birds were habituating to the test apparatus (Crino et al. 2014). These results, then, can be explained by differences in neophobia across treatment groups, rather than as resulting from differential stress per se (Spencer and Verhulst 2007). Whether stress affects learning in zebra finches remains unknown. The differences in response to novelty found in zebra finches are not found in mountain chickadees from different climatic environments (Kozlovsky et al. 2014, 2015), and neophobia is not likely a major component of spatial learning or of differences in the hippocampus.

When Japanese quail (*Coturnix japonica*) were exposed to various unpredictable stressors over 1 week, stress increased the latency to learn the location of a reward within a spatial maze, but had no effect on the number of errors made in learning the location of the reward (Calandreau et al. 2011). The stressed quails, however, appeared to learn a spatial reversal-learning task more quickly (Calandreau et al. 2011). In domestic chickens (*Gallus gallus*), a combination of stresses from handling, restraint, social environment, unfavorable temperatures, and deprivation of food or water resulted in a positive effect on an associative learning task (Goerlich et al. 2012). In both studies, birds were tested immediately following exposure to stress; therefore, any persistent effects on
learning remain unknown. In chickadees, any potential stress resulting from differences in their environment would likely be predictable and chronic throughout development, but differences in the hippocampus and in spatial learning between birds from different populations are correlated with climatic severity despite any posited alternative variation in development across these environments. For population-level variation in spatial memory to be mediated by stress, then, similar stressors outside of climatic severity would have to persist systematically across populations. The alternative that populations from milder environments experience more stress during development, which would be consistent with differences in memory and in the hippocampus, does not appear plausible as this would require that predictably milder environments are more stressful.

Additionally, some known stress-mediated differences in associative learning are sex specific, with females solely driving the difference in associative learning (Goerlich et al. 2012). These data are also inconsistent with the hypothesis that variation in chickadees’ spatial memory might exist as a result of developmental differences, as there are no differences between the sexes in the hippocampus or in spatial memory (Petersen and Sherry 1996; Pravosudov and Clayton 2002; Roth et al. 2011).

Based on the large body of evidence supporting a negative effect of developmental stress on cognition and the brain (especially as it pertains to spatial memory and the hippocampus), and the lack of congruence between chickadees and systems supporting a positive role of developmental stress, it is unlikely that developmental stress plays a significant role in driving the observed variation in spatial memory or the hippocampus in chickadees from different climatic environments. Furthermore, mountain chickadees from different elevations do not differ across a host of developmental parameters (e.g., fluctuating asymmetry, mass, tarsus-length, and feather-length) at 16 days post-hatching (Kozlovsky et al. 2015), which might predictably vary alongside developmental stress.

**Epigenetic modification of memory**

In coining the term epigenetics, Waddington referred broadly to the study of processes underlying changes in phenotype but acting “above” the level of the genome itself (Waddington 1957). In current usage, this term can refer to a range of sources of phenotypic variation, from the cellular-level processes driving differential gene expression across individuals in response to different environmental stimuli (e.g., any of several types of epigenetic control mechanisms; sensu Nanney 1958), to the transgenerational inheritance of traits acquired by individuals within their lifetime (i.e., epigenetic inheritance, sensu Jablonka and Raz 2009). Epigenetics provides a molecular mechanism for all plastic and developmental processes affecting phenotypic variation in cognition and in the brain.

**Epigenetic control mechanisms**

Epigenetic control mechanisms regulate compaction and transcription of DNA, and play a well-established role in memory formation, maintenance, and recall through task-, region-, gene-, time-, or signaling-cascade-specific changes in the regulation of gene expression, primarily via DNA methylation and post-translational modification of histones (Sweatt 2009). Manipulation of histone modifications and DNA methylation in the central nervous system result in altered formation of memory (reviewed by Day and Sweatt 2011). Most existing research investigating the epigenetic basis of memory formation and maintenance centers around hippocampus-dependent tasks, as both histone modification and DNA methylation are associated with hippocampal formation of memory, and histone modifications change in response both to stress and exercise (Miller and Sweatt 2007; Collins et al. 2009; Reul et al. 2009). As such, stress-mediated variation in patterns of DNA methylation and histone modification may modulate epigenetic control of spatial memory within our system, in which chickadees across different populations are likely to experience differential levels of chronic stress.

Stress hormones modulate brain function via alteration of the structure of neurons. The hippocampus is highly vulnerable to stress (McEwen 1999), due to its high density of glucocorticoid receptors, direct afferent input from stress-activated regions of the brain (reviewed by Segal et al. 2010), and epigenetic modulation of the release of endogenous neuromodulators, including corticotropin-releasing hormone (CRH) (Chen et al. 2004, 2006, 2010; reviewed by McClelland et al. 2011). Within a variety of experimental paradigms, stress in early life has demonstrable adverse effects on spatial learning either enduring throughout life or emerging in later life. Specifically, chronic stress in early life (e.g., chronic deprivation of food as a chick) results in change both to structure and function of hippocampal neurons (Brunson et al. 2005). Chronic stress in early life results in upregulation of CRH expression in the hippocampus (Ivy et al. 2010), and leads to...
Almost invariably associated with impaired learning longed stress during development should experience stress, individuals experiencing more acute or prolonged stress during development should experience impairment of the formation of spatial memory is not yet well understood, but several studies implicate the epigenetic regulation of stress-related genes, and hippocampal CRH gene expression in particular (McGill et al. 2006; Sweatt 2009; Bale et al. 2010).

Likewise, histone modification is a known regulator of the formation of hippocampal memory, primarily via post-transcriptional methylation, acetylation, phosphorylation, and ubiquitination. Histone acetylation, in particular, regulates both spatial learning, and contextual and cued fear learning via CAM response element-binding protein pathway (CBP) and the histone deacetylase pathway in the hippocampus (Alarcon et al. 2004; Korzus et al. 2004; Wood et al. 2006; Vecsey et al. 2007). Mice deficient in histone phosphorylation and acetylation in the hippocampus show impaired fear conditioning and spatial learning (Chwang et al. 2007). In rats, CBP is modulated during the establishment of a spatial memory, likely resulting in an epigenetic tag for hippocampus-dependent consolidation of memory (Boursiges et al. 2010). Restraint-stressed rats showed differential levels of histone-H3 methylation varying with duration of stress, indicating a complex and regionally specific pattern of chromatin remodeling within the hippocampus as a result of different types and durations of experimental stress (Hunter et al. 2009). Conversely, environmental enrichment results in increased histone acetylation in the hippocampus, and improved spatial memory (Williams et al. 2001; Fischer et al. 2007).

Formation and maintenance of memory is clearly regulated via epigenetic mechanisms; however, variation in expression along these pathways is unlikely to significantly explain the known variation in memory and in hippocampal morphology associated with climatic variation in black-capped and mountain chickadees. Under the hypothesis that variation results from epigenetic modification of memory formation resulting from variation in environmental stress, individuals experiencing more acute or prolonged stress during development should experience deficits in memory. Indeed, environmental stress is almost invariably associated with impaired learning and memory (Wilson et al. 2007; Chen et al. 2010; but see Crino et al. 2014) under any of the known epigenetic mechanisms. However, chickadees living under harsher conditions with stronger seasonal fluctuation have more accurate spatial memory as well as larger hippocampi with more hippocampal neurons.

Notably, the impairment of hippocampus-dependent behavior, which may occur as a result of stress, is often reversible (e.g., Szyf et al. 2005), and thus may represent adaptive plasticity rather than neuronal damage (McEwen 2010). In chickadees, the predictable fluctuation of environmental conditions may select against plasticity in hippocampal morphology, as unnecessary plasticity may be costly to maintain. Theoretically, epigenetic effects of environmental stress could explain population-level variation in chickadees’ spatial memory and hippocampal morphology if populations living under milder climatic conditions were subject to more intense or chronic stress than were their counterparts from harsher environments. However, this scenario is unlikely, as low availability of food and associated climate-driven stresses are the only likely stressors varying systematically across the entire latitudinal and elevational gradient of these populations. In other words, it is unlikely that across all of these sample populations, individuals from the milder climates are experiencing the same unaccounted stress (e.g., high risk of predation).

Likewise, under the hypothesis that variation results from epigenetic modification of memory formation resulting from variation in environmental stress, the environment that individuals experience during early development must predict the harsher conditions of future seasons (i.e., subsequent winters), when memory becomes essential for survival. For example, clutch size in great tits is plastic in populations in which it is associated with peak availability of invertebrates in the summer months (Visser et al. 2009). In other populations, however, in which spring conditions do not reliably indicate availability of food in the successive summer months, clutch size does not appear to be plastic. Based on this scenario, chickadees experiencing harsher winter conditions might be predicted to increase physiological allocation of resources toward improved memory and thereby to better cope with upcoming winter conditions (given that in our populations a harsher winter always predicts a harsher spring).

**Epigenetic inheritance**

Whether variation in spatial memory and hippocampal morphology may result from epigenetic inheritance of these phenotypes remains in question. While
instances of epigenetic transmission of a behavioral phenotype via maternal effects are known (e.g., Szyf et al. 2005; Goerlich et al. 2012; Benoit et al. 2015), instances of true epigenetic inheritance, i.e., multigenerational inheritance of environmental information via the germ line by offspring not conceived at the time of environmental experience, appear rather uncommon, particularly in vertebrates (reviewed by Jablonka and Raz 2009). Only one study, to date, has convincingly demonstrated multigenerational epigenetic inheritance of a learned association (Dias and Ressler 2014). F0 mice were taught via associative conditioning to fear a particular odor cue, and their subsequent F1 and F2 offspring showed fear in response to those same cues. Notably, in this study, the F0 generation was required to learn the relevant association, but the F1 and F2 then demonstrated an inherited fear association. This is an important distinction, in that this study does not demonstrate inherited variation in the ability to learn, but in the learned association itself. In order for epigenetic variation to explain differences in chickadees’ spatial memory and hippocampal morphology, the ability to learn per se must be subject to heritable epigenetic modification. While it remains theoretically possible, we are not aware of any system in which the ability to learn particular, ecologically relevant association varies on the basis of epigenetic modification stemming from variation in the environment.

In addition, the response demonstrated by Dias and Ressler (2014) is mediated by hypomethylation of the Olfr151 gene, leading to enhancement along the Olfr151 neuroanatomical pathway. As chemoreceptors, olfactory receptor cells are uniquely stimulus-specific among sensory receptors and therefore, an analogous scenario is unlikely to exist for pathways regulated by any other sensory system. In fact, Dias and Ressler (2014) conditioned control mice to fear an auditory cue, which was not transmitted beyond the F0 generation. The visual system, which is the primary sensory mediator of cache retrieval, is responsive to stimuli (light of varying wavelengths) which are found in some combination across nearly any environment; therefore there is unlikely to be a pathway that would allow for regulation in response to a particular type of visual stimulus. Even if the regulatory pathway were replicable in other sensory systems, there is not a consistent and readily associable cue differentiating locations of caches (or other stimuli related to spatial memory) across populations of chickadees under variable climatic stress.

In general, the relevance of epigenetic effects for the evolution of most organisms remains speculative (Richards et al. 2010). Based on available data on epigenetic effects on learning and memory, epigenetic mechanisms do not appear likely to explain population-level variation in memory and in the hippocampus in chickadees living under different climatic conditions.

**Conclusions**

In this review, we have considered several major mechanisms that might produce the variation in spatial memory and in the hippocampus observed in multiple populations of two species of chickadees. While there may be other sources of such variation unrelated to local adaptations and not considered in our review, most existing evidence, however indirect, aligns with the hypothesis that the overall pattern in population variation in the ability to store and retrieve stored food, as well as in spatial memory ability and its neural mechanisms, is mainly due to natural selection associated with differential selection pressures in variable climatic conditions across both latitudinal and elevational gradients. While other factors can, and likely do, contribute to at least some phenotypic variation within this or any similar system, the major predictions associated with some of the major drivers of population-variation in chickadees’ spatial memory run contrary to the observed patterns of variation across populations. Further research should focus on validating predictions of this hypothesis not only within food-caching species, but also in other systems in which natural selection may result in local adaptation and population-level variation in cognitive phenotypes and associated neural morphology, e.g., systems in which selective pressure varies widely across a climatic range and individuals rely heavily on a particular behavioral adaptation for survival.

However convincing, the evidence for natural selection acting on spatial memory and the hippocampus remains indirect, and future research should include attempts to accumulate direct evidence for local adaptation. In particular, it would be important to demonstrate fitness consequences associated with variation in spatial memory and hippocampus morphology. Likewise, future research should focus on identifying the basis of variation in spatial memory and hippocampal phenotype via genetic pathways, and identifying alleles driving such variation. Alternatively, considering recent evidence that parallel evolution can involve different genetic pathways (Soria-Carrasco et al. 2014), more focus should be placed specifically on quantifying trait heritability and investigating variation among individuals of
known pedigrees. Such evidence, if obtained, would demonstrate directly that natural selection is involved in generating and maintaining variation in spatial memory and the hippocampus among populations of food-caching chickadees.

Acknowledgments
The authors thank two reviewers and the Editor, Dr Harold Heatwole, for constructive criticisms that significantly improved our manuscript.

Funding
V.V.P., R.C., C.L.B., and D.Y.K. were supported by the National Science Foundation grant [IOS-1351295 to V.V.P.].

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