COMPARATIVE COGNITION

Spatial cognitive ability is associated with longevity in food-caching chickadees

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Cognitive abilities are hypothesized to affect survival and life span in nonhuman animals. However, most tests of this hypothesis have relied on interspecific comparisons of indirect measures of cognitive ability, such as brain size. We present direct evidence that individual variation in cognitive abilities is associated with differences in life span in a wild food caching bird. We measured the spatial cognitive abilities and tracked the life span of 227 mountain chickadees (*Poecile gambeli*) in their natural environment and found that individuals with better spatial learning and memory abilities involved in food caching lived longer. These results confirm that enhanced cognitive abilities can be associated with longer life in wild animals and that selection on cognitive abilities can lead to increased life span.

A long-standing assumption in biology is that enhanced cognitive abilities will result in the evolution of longer life spans as "smarter" individuals can better respond to unpredictable environmental conditions, increasing their potential for survival (e.g., cognitive buffer hypothesis) (*1*, *2*). In support of this hypothesis, some multispecies comparisons have reported positive associations between brain size and life span (*3*–*5*), but the conclusions drawn from cross-species comparisons of brain size are limited by confounds such as differences in energetic costs and time to maturity (*6*). Evidence from within-species comparisons is more mixed, with at least one comparison reporting a negative relationship between brain size and life span (*7*, *8*). Thus, while larger brain sizes are generally expected to be associated with enhanced cognitive abilities, comparisons of brain size may lead to spurious conclusions (*9*). A better opportunity to test the hypothesis that cognitive ability is associated with longevity is to relate variation in cognition to life span either within or across species (*9*–*11*). In particular, performing such a comparison using individual variation in cognitive abilities for an ecologically relevant task, within a population, can offer insight into the evolutionary processes that might lead to larger-scale evolutionary differences across species. Previous tests of this hypothesis have mostly focused on a single season [e.g., (*12*)] whereas studies investigating the association between cognition and survival over multiple years are rare (*11*). We present a direct test of this hypothesis by investigating the life spans of 227 individual wild, food-caching mountain chickadees (*Poecile gambeli*) with known fitness-related spatial cognitive abilities (*12*).

Spatial cognition in mountain chickadees

Mountain chickadees are nonmigratory, scatter-hoarding songbirds that inhabit montane environments and depend on food caches to survive the winter. Chickadees cache tens of thousands of food items across their home range during the autumn and then recover these caches during the winter using, at least in part, spatial cognitive abilities (*13*). Thus, the spatial learning and memory abilities required to recover caches are critical for overwinter survival. Our previous work with wild food-caching mountain chickadees, using the same field methods as in this study, showed that spatial learning and memory abilities are highly heritable (*14*, *15*), are under directional natural selection (*12*, *16*), and do not show senescence within the natural life span (*17*). During their first winter of life, chickadees with better spatial learning and memory abilities are more likely to survive the winter (*12*), and there are no differences in cognitive performance in the same individuals between their first and second year of life (*12*). Additionally, chickadees in harsher winter environments with higher demands on spatial cognition perform better on a spatial learning and memory task and have larger hippocampi with more hippocampal neurons, compared to chickadees from milder winter environments (*18*, *19*). By contrast, reversal learning ability, often used as a measure of cognitive flexibility (e.g., *20*, *21*, *22*, reviewed in *23*), is not associated with juvenile overwinter survival (*12*). Spatial learning and memory is well known to be involved in food caching (*13*, *24*, *25*), but reversal learning, although not fully independent of spatial cognition, is typically associated with inhibition and executive control function (e.g., *21*, *22*, reviewed in *23*) and is not involved in food caching.

Smart feeder arrays to test spatial cognitive abilities

We have developed and implemented a field-based radio frequency identification (RFID) feeder system to test both spatial learning and memory ability and reversal learning ability in wild chickadees banded with unique passive integrated transponder (PIT) tags (*26*–*28*). Over the last six years we have tested hundreds of chickadees annually and have continuously tracked surviving individuals for the past nine years (*17*), allowing us to directly test whether individual variation in spatial cognitive abilities is associated with differences in life span. We tested spatial learning and memory ability using standard methodology in which animals are expected to learn one of several available locations to obtain a food reward (e.g., *29*). We have previously confirmed that chickadees do indeed use spatial learning and memory, and not memory for local cues, to solve this task (*26*). To test reversal learning ability, we used a standard method of switching rewarding contingencies by changing the rewarding feeder once all birds learned the initial associations during the spatial learning task (*21*, *22*, *29*, reviewed in *23*). Both of these general tasks are commonly used across taxa and research groups (*29*).

We tested both cognitive abilities using our "smart" RFID-based feeders, which are arranged in eight-feeder spatial arrays and include motorized doors that open to provide a food reward when a PIT-tagged individual lands on the feeder perch (Fig. 1). For both tasks, we assessed performance by assigning each bird to one rewarding feeder and measuring the number of nonrewarding feeders visited (i.e., location errors) prior to visiting the assigned rewarding feeder in each trial across multiple trials (*12*, *26*, *27*). A trial begins when a bird visits any feeder in the array and ends with a visit to its single rewarding feeder; chickadees collect only one seed from the feeder and fly away from the array to either eat or cache the seed. Each trial lasts around 39s on average as the birds inspect the array feeders until they find the rewarding feeder (*30*). Every bird obtains a food reward during each trial regardless of cognitive performance so there is no negative reinforcement associated with poor cognitive performance. Prior to testing, all birds had access to the RFID feeders for at least one month when the feeder doors were open. Then, for at least 1 week before testing, all feeder doors were programmed to open to any PIT-tagged bird so that all birds became familiar with the testing apparatus. Birds were not required to manipulate anything to get food; they only needed to land on the perch. We assessed spatial learning and memory performance first, then immediately reassigned all birds to a new rewarding feeder to assess their reversal learning performance when birds needed to

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inhibit their memory of the previously rewarding feeder to learn the reversal association (*21–23*, *27*). Each cognitive task lasted four days. Most birds (>90%) near our feeders are banded with PIT-tags and most individuals participate in cognitive testing.

We used two performance metrics for each task that reflect different aspects of an individual's learning ability: (i) The mean number of location errors per trial made across the first 20 trials provides information on an individual's ability to learn their rewarding feeder (e.g., spatial memory acquisition), and (ii) the mean number of location errors per trial over the entire four-day testing period (controlling for the total number of trials completed) provides a measure of an individual's ability to remember their feeder location over four days (*12*). As a bird learns, it is expected to make fewer and fewer errors in each consecutive trial, and the mean number of errors over either the first 20 trials or over the four-day task captures this process—smaller mean number of errors per trial reflects better learning performance. Using these metrics, we have previously shown that individual variation in spatial learning and memory abilities is genetically heritable (*14*, *15*) and is associated with differences in survival during the first winter of life (*12*) and in reproductive investment (*16*). Both males and females rely equally on spatial abilities to recover their individual food caches and we previously showed that there are no sex differences in spatial learning and memory abilities [analysis included 109 males and 92 females (*31*)]. Previous work also showed no sex differences in spatial cognition and in the morphology of the hippocampus, a brain region involved in spatial learning, in food-caching chickadees (*18*, *19*, *32–35*).

All birds used in this study completed a minimum of 20 trials on each task and all birds successfully learned both tasks during the first 20 trials by performing at better than chance level. All birds that participated in the reversal learning task had previously successfully learned (e.g., better than chance performance) the initial spatial learning task in the previous four days. Participation in cognitive tasks was not associated with differences in cognitive performance: birds that did worse during the tasks participated in as many trials on average as birds that did better. Specifically, performance on the first 20 trials of the spatial learning and memory task did not correlate with total trials completed during the entire task (linear model: n = 227, $\beta \pm$ SE = −0.005 ± 0.095, χ^2_1 = 0.003, P = 0.960; fig. S1). This finding suggests that individuals with different cognitive abilities received the same amount of food on average during our cognitive testing. Performance on the spatial learning and memory task did not correlate with performance on the reversal learning task (linear model: n = 207, $\beta \pm$ SE = 0.04 ± 0.13, χ^2_1 = 0.11, P = 0.744; fig. S2), confirming that these tasks measure different cognitive abilities. Hence, the reversal task provides a meaningful comparison considering that it is not involved in cache retrieval and is not associated with performance on the spatial learning and memory task. A further control such as a color association task would also be useful, but unfortunately because of logistical constraints we do not have data on color-association tasks.

Fig. 1. Spatial testing array with RFID-equipped smart feeders. (**A**) Photograph of an eight-feeder spatial array, looking up from the ground. (**B**) Eight-feeder spatial array viewed from the side. (**C**) A mountain chickadee with a purple PIT tag leg band on the RFID perch watching the feeder door open.

We measured individual life spans through detections at RFID feeders during the fall and winter and at RFID-equipped nest boxes during the summer, through resightings of color bands during the summer (we identify all breeding birds every year using about 100 active nests), and through recaptures during regular annual autumn banding lasting from late August through December to January (*36*). Mountain chickadees are highly sedentary following a short postnatal dispersal prior to their first winter (*37*); therefore, we considered individuals not detected for a 12-month period or longer to be dead (*36*). We constructed two statistical models for each task to measure the relationship between life span and cognitive ability from the first year each individual completed cognitive testing. We modeled the relationship between life span and performance on the first 20 trials of each cognitive task by using life span as the response variable and cognitive performance (mean number of location errors per trial) as a fixed effect. For performance over the entire four-day task, we used performance score as the response variable and included life span and the total number of trials completed as fixed effects to control for variation in the number of trials completed among individuals (following *12*, *27*, *38*).

Our banding efforts began before we started measuring cognitive performance, so many individuals were tested at different ages. To determine whether our results were robust to differences in age at testing, we ran two additional versions of each statistical model, taking advantage of the fact that cognitive testing occurs only once per year, but many individuals completed cognitive testing in multiple years. The first additional test employed a bird's average testing score instead of its score from the first year it tested, and the second additional test involved running each model 100 times, but in each run a single cognitive performance score was randomly chosen for each bird from its list of scores from different years.

Spatial cognitive ability is associated with life span

Individual spatial learning and memory performance, but not reversal learning performance, was significantly associated with life span in mountain chickadees. Both the mean number of location errors per trial across the first 20 trials (negative binomial GLM: n = 227, $\beta \pm$ SE = −0.41 ± 0.13, χ^2_1 = 9.81, P = 0.002) and spatial learning and memory performance over the entire four-day spatial testing period, with the total number of trials as a covariate (gamma distributed GLM: n = 227, $\beta \pm$ SE = −0.12 ± 0.03, χ^2_1 = 13.82, P < 0.001), were associated with life span. Mountain chickadees lived on average 2.1 years (median = 2, max = 8) and those that showed better performance over the first 20 trials as well as over the entire spatial learning and memory task had longer life spans on average (Fig. 2). Indeed, our model predicts that individuals with the best spatial cognitive abilities will live 3.1 years on average, and those with the worst spatial cognition will live 1.2 years. Critically, all individuals performed better than expected by chance (< 3.5 errors) on both cognitive tasks, showing that all individuals learned the tasks.

Individuals first completed the spatial learning and memory task at an average of 1.8 years of age (median = 1 year) and participated in the task an average of 1.8 times in their lifetime (46% of birds tested in 2 or more years, range 1 to 6 years, fig. S3). The statistically significant relationship between performance on the spatial learning and memory task and life span remained when modeling individual performance averaged over all years the bird tested (first 20 trials: n = 227, β ± SE = −0.55 ± 0.15, χ^2_1 = 13.70, P < 0.001, entire testing period: n = 227, β ± SE = −0.08 ± 0.03, χ^2_1 = 7.08, P = 0.008) and when individual scores were randomly selected in 100 additional model runs (all P < 0.05 for first 20 trials and trials over the entire testing period; fig. S4). Considering that we have previously shown that individuals with poorer spatial cognitive performance were less likely to survive their first winter of life (*12*), we tested whether the results remained significant when juvenile individuals who died in their first winter were excluded. Among birds who survived their first winter, spatial learning and memory ability remained a statistically significant predictor of life span (first 20 trials: n = 178, β ± SE = −0.36 ± 0.15, χ^2_1 = 5.95, P = 0.015; entire cognitive task with number of trials as a covariate: n = 178, β ± SE = −0.12 ± 0.05, χ^2_1 = 7.34, P = 0.007), suggesting that our results were not driven by performance of first-year birds who died during their first winter.

By contrast, individual variation in performance on the reversal learning task was not significantly associated with life span (first 20 trials: n = 207, β ± SE = 0.23 ± 0.25, χ^2_1 = 0.83, P = 0.362; entire cognitive task with number of trials as a covariate: n = 207, β ± SE = 0.10 ± 0.06, χ^2_1 = 2.67, P = 0.103). Individuals completed the reversal task on average 1.6 times in their lifetime (39% of birds tested in 2 or more seasons, range 1 to 6, fig. S5), and the observed lack of a relationship between reversal performance and life span remained when modeling individual performance averaged over all seasons the bird tested (first 20 trials: n = 207, β ± SE = −0.08 ± 0.31, χ^2_1 = 0.07, P = 0.788, entire testing period: n = 207, β ± SE = −0.01 ± 0.06, χ^2_1 = 0.01, P = 0.913) and when individual scores were randomly selected in 100 additional model runs (all P > 0.05; fig. S6).

Discussion

Our findings provide support for the hypothesis that enhanced cognitive abilities can be associated with increased life span in a nonhuman species in the wild, furthering our understanding of how natural selection can shape spatial cognition. In food-caching mountain chickadees, natural selection is strongest on first-year birds, such that only juveniles with enhanced spatial learning and memory abilities survive their first winter (*12*). The results presented here further show that individuals with better spatial cognitive abilities are more likely to live longer, presumably because better spatial cognition allows them to cope with harsh and unpredictable environments by successfully retrieving cached food. Our model predicts that the individuals with the best spatial cognitive abilities will live on average two years longer than those with the worst spatial cognition. Mountain chickadees breed once per year, with an average clutch size of seven eggs (*39*); thus the individuals with the best spatial abilities may produce more than twice the number of offspring (e.g., 14 more offspring) than those with poorer cognition. In addition, we previously reported that females invest more in reproduction when paired with "smarter" males (*16*). Considering that spatial cognition has a genetic basis in this species (*14*, *15*), the longest-lived individuals may produce the most lifetime offspring who are likely to have the best spatial cognitive abilities.

While spatial cognitive abilities are important for recovery of food caches, which are critical for over-winter survival, chickadees also experience mortality due to other causes, most likely predation, especially during breeding. Spatial learning and memory abilities may not affect mortality due to these other causes, which likely contribute to additional variation in life span unexplained by cognitive abilities.

Though our results show an effect of spatial cognition on survival, they do not match the predictions of the cognitive buffer hypothesis, which proposes that cognitive flexibility should lead to increased survival when environmental conditions are unpredictable (*1*, *2*). Here we observed no effect of reversal learning ability on life span using performance on a single reversal task, often used as a measure of cognitive flexibility (*20*, *21*, *23*, *38*). Reversal learning ability is not known to be involved in food caching and we previously showed that individual variation in reversal learning abilities was not associated with differences in survival during the first winter of life (*12*). Instead, enhanced spatial learning and memory abilities may allow individuals to engineer a more predictable environment through food caching and the ability to retrieve caches, increasing survival, which over time results in a longer life span.

An important aspect of our experiment was that our experimental design did not favor individuals who performed better on the cognitive task as every bird received a food reward

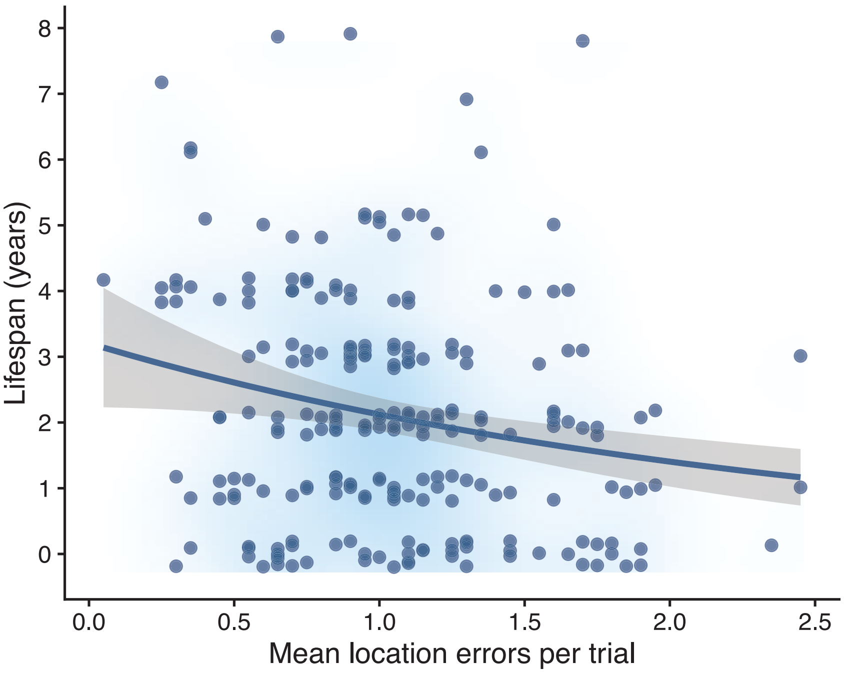

Fig. 2. Life span is associated with spatial learning and memory ability in mountain chickadees. Points represent individual birds and are jittered slightly on the *y*-axis. Trendline shows the model prediction and bootstrapped 95% confidence intervals for the model using mean location errors per trial over the first 20 trials. Background color shows density of points. Lower mean location errors per trial indicate better performance on the spatial learning and memory task.

at the end of each trial, regardless of its performance. We observed no relationship between performance on the spatial learning and memory task and number of trials completed during the four-day testing period. Thus, food received at our feeders was not a likely determinant of survival. Instead, survival differences appear to have occurred independently of our experimental paradigm.

Overall, our results suggest that specialized cognitive abilities, such as spatial learning and memory in food-caching species, can be associated with life span if such specialization increases survival over time. Although it may come as no surprise that spatial learning and memory ability promotes longevity in a species that relies on remembering the locations of cached food, our results are a clear demonstration of a link between cognition and fitness in a wild animal population. By contrast, reversal learning ability, which is not involved in food caching, was not associated with longevity. Our results highlight the value of long-term studies to identify associations between cognitive traits and life span, therefore improving our understanding of how cognition and life span can coevolve.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplemental Results
Figs. S1 to S6
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MDAR Reproducibility Checklist

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