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Specialized spatial cognition is associated with reduced cognitive senescence in a food-caching bird

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Senescence, the gradual reduction and loss of function as organisms age, is a widespread process that is especially pronounced in cognitive abilities. Senescence appears to have a genetic basis and can be affected by evolutionary processes. If cognitive senescence is shaped by natural selection, it may be linked with selection on cognitive abilities needed for survival and reproduction, such that species where fitness is directly related to cognitive abilities should evolve delayed cognitive senescence likely resulting in higher lifetime fitness. We used wild food-caching mountain chickadees, which rely on specialized spatial cognition to recover thousands of food caches annually, to test for cognitive senescence in spatial learning and memory and reversal spatial learning and memory abilities. We detected no signs of age-related senescence in spatial cognitive performance on either task in birds ranging from 1 to 6 years old; older birds actually performed better on spatial learning and memory tasks. Our results therefore suggest that cognitive senescence may be either delayed (potentially appearing after 6 years) or negligible in species with strong selection on cognitive abilities and that food-caching species may present a useful model to investigate mechanisms associated with cognitive senescence.

1. Introduction

Senescence is a process of gradual reduction and loss of function as organisms age, and it has been well documented both in animals and plants [1–4]. Although senescence was previously considered unobservable in wild populations because of high mortality rates prior to the potential age limit, there is now a plethora of evidence that senescence is widespread and detectable in the wild [4]. Because the timing and magnitude of senescence differs across species and the mechanisms of senescence seem to have a genetic basis [2,3,5–8], variation in senescence is likely a product of evolutionary processes and may be shaped by natural selection [7,9,10]. Important insights into the evolution of senescence can therefore be gained by comparing species with different life-history traits.

While senescence may concern numerous functions, most studies of organisms in their natural conditions have focused on reproductive output (e.g. [7,8]), mainly because it is logistically easier to study and also because the theory on trade-offs with regards to senescence is focused on reproductive output. Other functions important in both evolutionary biology and human health, such as cognitive function, have been mostly studied in the biomedical field using either humans or rodent models in the laboratory [11]. The cognitive function appears especially vulnerable to ageing processes, including both normal ageing and age-related cognitive disorders [11]. Furthermore, cognitive abilities are important for

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numerous critical functions across the animal kingdom and there are significant differences in cognitive abilities both across and within species [12–15]. Research on cognitive senescence, however, is limited to a few mammalian species in laboratory conditions [11]. Indeed, studies with captive animals likely detect higher levels of cognitive senescence, as impoverished captive environments likely have detrimental effects on cognitive abilities and associated neural structures [5,6], even though it is also possible that senescence is more frequently detected in captive or domesticated populations because they can be maintained alive despite potentially large effects of senescence. Therefore, investigating cognitive senescence in wild populations of individuals that differ in their reliance on cognitive abilities for survival would add to our understanding of the evolution of cognitive senescence.

We hypothesize that the timing and magnitude of cognitive senescence can be shaped by natural selection and that species with either specialized cognitive abilities or with high selection pressures on cognitive abilities should exhibit delayed and/or reduced cognitive senescence. Food-caching species that rely on remembering the locations of individual food caches for survival present a particularly good system for the study of cognitive senescence. These species not only use spatial cognition (learning and memory) to make and recover tens of thousands of individual caches, but appear to have evolved specialized spatial cognition associated with faster memory acquisition and more accurate and longer lasting spatial memory compared to non-caching species [12,13,15]. These specialized spatial cognitive abilities are associated with a relatively enlarged hippocampus, a brain region involved in spatial cognitive function, containing more and larger neurons [12,13,15]. Cognitive specialization in food-caching species appears to be shaped by natural selection, as evidenced by comparative studies of multiple populations inhabiting environments with different selection pressures on spatial cognition [15] and by documented associations between individual variation in spatial learning and memory ability and overwinter survival [16]. The notion that there is the selection for heightened spatial cognitive abilities in food-caching species leads us to our primary hypothesis, that age-related decline in spatial cognition should be delayed and/or minimized in food-caching species. While comparing multiple species with different reliance on cognition would be the best approach, it was not possible here; instead we focused on investigating the relationship between age and cognition in a single food-caching species. We predicted that age should have either no effect on spatial cognition, or that signs of cognitive decline would appear only in the oldest individuals.

Here we studied age-related spatial cognitive senescence in wild, food-caching mountain chickadees, *Poecile gambeli*. Mountain chickadees are small bodied (*ca* 11 g), highly resident passerines with a relatively short lifespan—annual survival rate *ca* 50% [17]. The oldest individual we have detected in our study system was 9 years old, however, most birds do not live past three years and more than 50% of birds do not survive their first year [17,18]. We have banded chickadees annually since 2014 (with some banding efforts starting in 2005), which allowed us to age birds from 1 to 6 years old at the time of this study. By comparing spatial cognitive performance between individuals of known ages, we were able to test for cognitive senescence in this specialized food-caching bird. We used a spatial learning and a memory task that is associated with food caching, cache retrieval and survival [15,16], and a reversal spatial learning task that is reflective of spatial cognitive flexibility, allowing animals to track changing spatial information [19,20]. We expect chickadees to reach peak cognitive performance during their first year of life as only juveniles with the best spatial cognitive abilities survive their first winter [16] and as spatial cognitive abilities of surviving juveniles do not change between their first and second year of life [16]. We showed previously that the strongest selection on spatial cognition occurs specifically during the first winter of life, as only individuals with better cognitive abilities survive their first winter and reproduce [16].

2. Methods

We used our long-term study system in northern Sierra Nevada north of Truckee, California, USA in Sagehen Experimental Forest (Sagehen Creek Field Station, University of California Berkeley) [16,19–21]. Our study area covers high (2400 m) and low (1900 m) elevation sites that differ in winter climate severity, with high elevations characterized by longer and more severe winter conditions (i.e. lower temperatures and higher and longer lasting snow cover). We have previously documented that chickadees at high elevation have better spatial learning and memory abilities as well as a larger hippocampus with a larger number of hippocampal neurons [19–22].

Since 2014, we have been trapping chickadees at both elevations and banding them with unique combinations of colour leg bands and passive integrated transponder (PIT)-tags. Birds were captured using mist nets near established feeders from late August to April and at nest-boxes (*ca* 350 boxes throughout both sites) from June to late July during the breeding season. In 2013, we began banding all nestling mountain chickadees in our nest-boxes with United States Geological Survey (USGS)-issued metal leg bands, which allows us to determine a precise age for these individuals upon recapture. We also periodically banded chickadees with USGS bands beginning in 2005. At the time of initial capture, all birds were categorized as juveniles (within their first year of life) or adults by a combination of factors including moult stage, plumage pattern and rectrix shape [23]. Birds identified as adults during banding could potentially be older than 1-year old, but considering our extensive annual banding and monitoring efforts and that chickadees are highly sedentary and do not move following post-natal dispersal, this is unlikely and new birds detected every year are likely to be either juveniles or 1-year old [18]. Birds for all age categories used in this study have been detected and banded either 1, 2, 3, 4, 5 or 6 years prior to the year of testing. We have previously shown that chickadees experience high mortality during their first winter [18] and that such mortality is associated with poor spatial learning and memory abilities [16]. As an age class, juvenile birds in their first year of life are not comparable in cognitive abilities to those that have survived their first winter as the selection on spatial cognitive abilities appears strong specifically during the first winter of life (e.g. [16,20]). At the same time, birds' cognitive performance did not change between their first and second winter of life [16], which suggests that chickadees reach their full cognitive abilities during their first winter. Because the goal of this study was to assess cognitive senescence, only adults of at least 1 year of age (birds that survived their first winter, reproduced and were tested during their second winter) were included.

The goal of this study was to test for potential evidence of cognitive senescence in a food-caching species with specialized spatial cognitive abilities. Although we tested our birds at both high and low elevations, elevation comparisons were mainly used to control for potential differences in cognitive performance in each age group while testing for the main effect of age regardless of elevation. Elevation differences, if present, were expected to be rather minor compared to the overall effect of the species—specialized spatial cognition.

(a) Spatial cognitive testing

We used our well-established methods to test spatial learning and memory and reversal spatial learning and memory abilities in wild PIT-tagged mountain chickadees [16,19–21]. All spatial cognitive testing was done using four spatial arrays (two at each elevation separated by *ca* 1.5 km within each elevation), each consisting of eight RFID-based feeders filled with black oil sunflower seeds, mounted equidistantly on a square aluminium frame (122 × 122 cm), and suspended *ca* 4 m above the ground. Each feeder contained an antenna embedded in the feeder perch attached to an RFID Arduino board [24], which controlled the motorized feeder door and could operate in three different modes: 'open', 'all' and 'target'. In 'open' mode, the feeder doors were permanently open allowing birds to see the food inside the feeders. In 'all' mode, the feeder doors were closed, preventing birds from seeing food inside the feeders, but would open when any PIT-tagged bird landed on the perch. The 'all' mode was used to habituate birds to the moving feeder doors. In 'target' mode, specific PIT-tag IDs were programmed (assigned) into each feeder's RFID board and the feeder door only opened when birds assigned to that feeder landed on the perch. 'Target' mode allowed access to food for birds assigned to that feeder, but prevented food access to those not assigned to that feeder. The time, date and ID of all PIT-tagged birds landing on the perch were recorded in all three modes.

We conducted two spatial cognitive tasks using 'target' mode; in both, each bird was assigned only to a single feeder out of eight possible feeders in the spatial array. All birds were assigned to feeders pseudorandomly, avoiding assigning birds to the feeder they used the most during the pre-testing period [16]. This allowed us to test spatial learning and memory ability by measuring the number of location errors—non-rewarding feeders visited prior to visiting the rewarding (assigned) feeder—over multiple trials. As a bird learns, we expect it to make fewer and fewer errors (e.g. visiting fewer unrewarding feeders) each trial. A trial began when a bird visited any feeder at the array and ended with a visit to the assigned, rewarding feeder [19,21]. As a measure of spatial cognitive performance, we used the mean number of location errors per trial over the first 3, 5, 10 and 20 trials as well as over the entire task following our previous work [16,19–21].

(i) Spatial learning and memory task

Feeders remained in 'open' mode for at least 10 days before being switched to 'all' mode on 27 December 2019 at high elevation and on 30 December 2019 at low elevation. Feeders at both elevations were switched to 'target' mode on 20 January 2020. Spatial cognitive learning and memory testing took place from 20 to 22 January 2020 at high elevation and 20 to 24 January 2020 at low elevation.

(ii) Reversal spatial learning and memory task

We also conducted a reversal spatial learning and memory task in which birds were re-assigned to a new rewarding feeder within the same feeder array. Individuals that had previously been assigned to the same feeder were each re-assigned to different feeders for reversal testing to minimize opportunities for social learning. During this task, birds were expected to learn that the previously rewarding feeder was no longer rewarding and to learn and remember the location of a new rewarding feeder [19,20]. Reversal spatial learning and memory testing took place from 24 to 29 January 2020 at low elevation. At high elevation, following the spatial learning and memory task, all feeders were returned to 'open' mode due to a malfunction on 24 January 2020 to re-start the testing. On 29 January 2020, both arrays at high elevation were again switched to 'all' mode and on 3 February 2020 to 'target' mode (again testing spatial learning and memory; however, we only use the data from the first task in this analysis), which lasted until 7 February 2020. The restart procedure was carried out to reset the spatial learning and memory test following the full pre-task procedure, proceeding from 'open' mode, to 'all' mode, to the second spatial learning and memory task (with different rewarding feeders), which directly preceded the reversal spatial learning and memory testing from 7 to 13 February 2020. This restart should provide comparable data as these birds had to learn the same standard reversal spatial task. Our feeder design also does not require learning any manipulations—the bird only needs to learn and remember the location of the rewarding feeder. Hence previous experience with the experimental set-up does not change performance [16].

(b) Statistical analyses

Data were analysed by either multiple regression analyses with the mean number of errors per trial over the first 20 trials or over the entire task as the dependent variable, age as a continuous independent variable and elevation as a categorical independent variable. Because individuals differ in the total number of trials they complete, we controlled for these differences by using the total number of trials as a covariate when using the number of location errors over the entire task [19]. We first used age as a continuous variable because we expect cognition to senesce gradually, rather than nonlinearly, and also because we expected that our 1-year-old group (birds that survived their first winter, reproduced and were tested during their second winter) have fully developed spatial cognition. We ran polynomial regression by adding age^2 to test for potential nonlinear associations. We also ran a repeated-measures general linear model with a different number of trials as a repeated factor (first 3, 5, 10 and 20 trials completed), and age and elevation as categorical variables, which should allow us to detect significant differences between any age groups in our study. Analyses were performed using R version 4.0.2 [25] and the 'car' package [26], while the repeated-measures analysis was performed in Statistica v. 13 [27]. Figures were generated in R using 'ggplot2' [28].

We did not include sex in our analyses because (i) both males and females rely equally on spatial cognition to retrieve their caches so we would not expect any sex differences, (ii) many of the birds in our study were of unknown sex and (iii) our previous extensive comparison of spatial cognitive performance showed no significant differences between males and females [29].

3. Results

(a) Spatial learning and memory task

There was a significant association between performance and age during the first 20 trials of the task, as well as a significant effect of elevation, with older birds and high elevation birds showing better performance (multiple regression – age: ß = −0.09, $F_{1,140} = 14.85$, $p = 0.0002$; elevation: $F_{1,140} = 4.21$, $p = 0.04$; figure 1). The interaction between age and elevation was not statistically significant ($F_{1,139} = 0.55$, $p = 0.47$) and was excluded. When using age^2 in a polynomial regression, it was not significant (age^2 – $F_{1,139} = 1.55$, $p = 0.21$, age: ß = −0.67, $F_{1,139} = 4.90$, $p = 0.028$; elevation – $F_{1,139} = 4.66$, $p = 0.03$). We found the same significant pattern of older birds performing better using the mean number of errors across the first 3, 5, 10 and 20 trials (repeated-measures GLM with the number of trials as a repeated factor and age as a categorical variable – age: $F_{5,136} = 3.47$, $p = 0.005$; elevation:

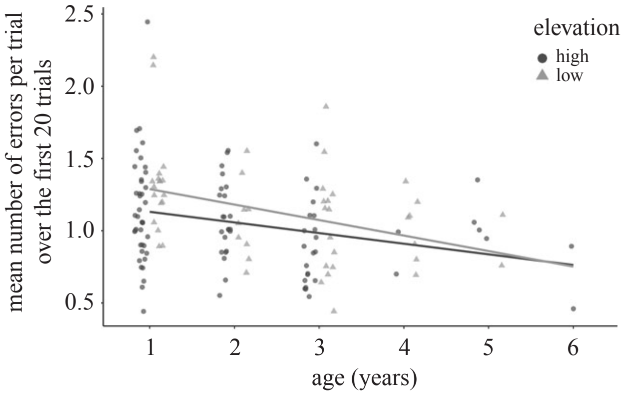

Figure 1. Mean number of location errors per trial over the first 20 trials of the spatial learning and memory task. Fewer errors indicate better cognitive performance.

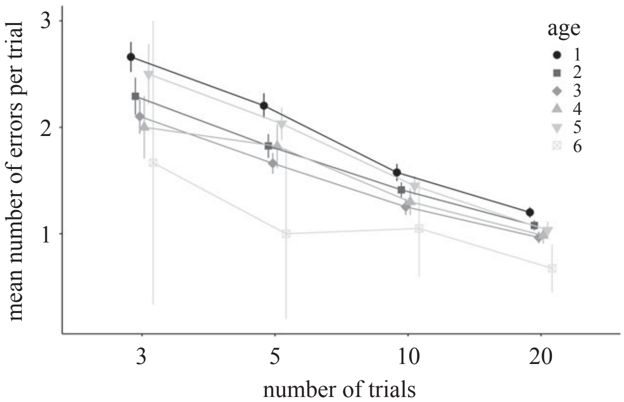

Figure 2. Mean number of location errors per trial over the first 3, 5, 10 and 20 trials of the spatial learning and memory task. Vertical bars indicate standard error. Fewer errors indicate better cognitive performance.

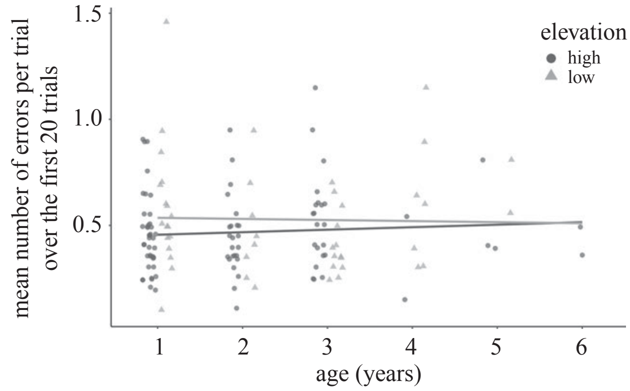

Figure 3. Mean number of location errors per trial during the first 20 trials of the reversal spatial learning and memory task. Fewer errors indicate better cognitive performance.

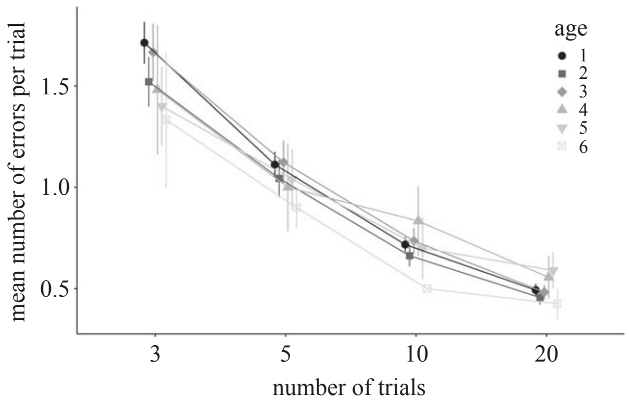

Figure 4. Mean number of location errors per trial during the first 3, 5, 10 and 20 trials of the reversal spatial learning and memory task. Vertical bars indicate standard error. Fewer errors indicate better cognitive performance.

$F_{1,136} = 2.91$, $p = 0.09$; number of trials: $F_{3,408} = 54.75$, $p < 0.001$; age by number of trials interaction: $F_{15,408} = 1.02$, $p = 0.43$; figure 2).

A similar, but not statistically significant, pattern with older birds tending to perform better was present with the mean number of location errors over the entire task (multiple regression, age as a continuous variable – age: ß = −0.02, $F_{1,139} = 3.01$, $p = 0.08$; elevation: $F_{1,139} = 20.72$, $p < 0.001$; total number of trials completed: $F_{1,139} = 123.1$, $p < 0.001$). The age by elevation interaction was not statistically significant ($F_{1,138} = 1.37$, $p = 0.24$) and was excluded. There were no significant differences between any of the age classes (age as a categorical variable – $F_{5,135} = 2.05$, $p = 0.75$; elevation – $F_{1,135} = 17.81$, $p < 0.001$; total number of trials – $F_{1,135} = 125.1$, $p < 0.001$).

(b) Reversal spatial learning and memory task

There was no statistically significant association between age and performance over the first 20 trials of the reversal spatial learning and memory task (multiple regression, age as a continuous variable – age: $F_{1,136} = 0.14$, $p = 0.71$; elevation: $F_{1,136} = 2.19$, $p = 0.14$; figure 3; elevation by age interaction was not statistically significant—$F_{1,135} = 0.26$, $p = 0.61$, and was excluded) or over the entire reversal spatial learning and memory task (multiple regression – age: $F_{1,135} = 0.13$, $p = 0.71$; elevation: $F_{1,135} = 2.63$, $p = 0.12$; total number of trials: $F_{1,135} = 44.74$, $p < 0.001$; elevation by age interaction was not statistically significant—$F_{1,134} = 0.95$, $p = 0.33$, and was excluded).

Polynomial regression with age^2 produced the same non-significant results with the mean number of errors per trial over the first 20 trials (age^2 – $F_{1,135} = 0.39$, $p = 0.53$; age – $F_{1,135} = 0.25$, $p = 0.61$; elevation – $F_{1,135} = 2.28$, $p = 0.13$). There were also no significant differences between any age groups in the mean number of errors per trial over the entire task (age as a categorical variable – $F_{5,131} = 0.34$, $p = 0.89$; elevation – $F_{1,131} = 2.55$, $p = 0.11$; total number of trials – $F_{1,131} = 41.52$, $p < 0.001$).

There were also no significant differences among age classes in performance during the first 3, 5, 10 and 20 trials of the reversal spatial learning and memory task (repeated-measures GLM number of trials as a repeated factor and age as categorical variable – age: $F_{5,132} = 0.29$, $p = 0.91$; elevation: $F_{1,132} = 0.01$, $p = 0.97$; the number of trials: $F_{3,396} = 66.94$, $p < 0.001$; age by number of trials interaction: $F_{15,396} = 0.61$, $p = 0.69$; figure 4).

4. Discussion

We detected no evidence of cognitive senescence for either spatial learning and memory or reversal spatial learning and memory abilities in food-caching mountain chickadees across 6 years of life. Older birds actually tended to perform better on the spatial learning and memory task, likely due to

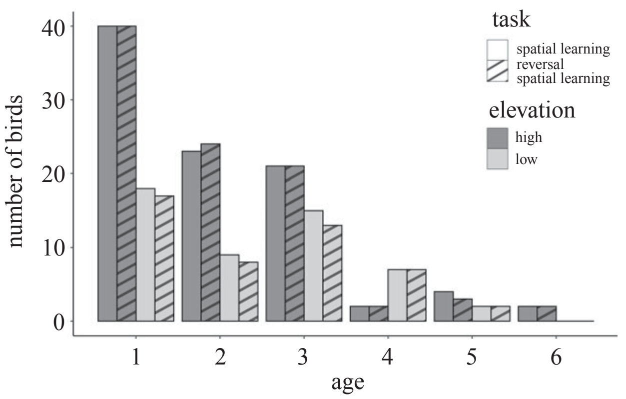

Figure 5. Number of birds of known age (in years) tested on each of the two cognitive tasks, spatial learning and memory (solid columns) and reversal spatial learning and memory (striped columns) at high and low elevation.

continuous selection [16] resulting in only the individuals with the best cognitive abilities surviving through multiple years. Our study had more younger birds and fewer older birds (figure 5), which can be expected in a small passerine bird with a relatively short lifespan. Such differences in age distribution should not impair our ability to detect age-related cognitive declines as they are expected due to ageing regardless of why the individual had survived longer. Better performance in older individuals, on the other hand, could be observed either because older individuals improved, or because better individuals survived longer. We think the latter is more likely in our case.

In our study, older birds had more exposure to the testing arrays from our previous years of research. We argue that such differences in experience are unlikely to directly affect cognitive performance because (i) our feeder design does not require any specific handling or manipulation to access food — all a bird has to do is to land on the open perch; (ii) all birds had extensive experience using these feeders during the pre-testing habituation period, with individuals visiting the feeders thousands of times during habituation in any given year; (iii) all feeders were fully opened before and after each year's testing period, so birds had much more exposure to feeders freely providing food compared to the relatively short testing period and (iv) most importantly, we previously showed that individual performance on both spatial tasks used in this study did not change in birds tested during consecutive years [16], which suggests no direct effect of experience with the testing apparatus on cognitive performance.

Similar to other species in the Paridae family [30], mountain chickadees are relatively short-lived birds with high adult overwinter mortality (*ca* 50% 16). Most birds in this system do not live past 3 years (figure 5), so we might expect birds to exhibit signs of senescence after 3 years of age based on average life expectancy. As food-caching birds, chickadees have highly specialized spatial cognition due to strong selection pressures on spatial cognitive abilities associated with memory-based cache retrieval and reliance on cached food for overwinter survival [12,13,15]. We have previously shown that individual variation in spatial learning and memory abilities in this population is under selection—juveniles with better spatial learning and memory abilities are more likely to survive their first winter while juveniles with worse abilities are more likely to die [16]. Food-caching chickadees depend heavily on their spatial cognitive abilities to survive through harsh winter conditions when access to food caches is critical. Any cognitive senescence negatively affecting spatial cognition would result in a higher probability of overwinter mortality, therefore, it can be expected that selection should favour delaying and reducing such age effects. Although we do not have data on senescence in other traits, surviving the winter means that these birds would be able to reproduce the following spring, and the more winters the bird can survive, the more lifetime reproductive output it will have. So, any mechanisms associated with delayed cognitive senescence can be expected to be favoured by natural selection as they are likely associated with higher overall fitness. Our finding, that older chickadees do not have worse spatial cognitive abilities compared to younger chickadees across 6 years of life, supports our hypotheses and suggest that chickadees may have some neural mechanisms greatly reducing age-related cognitive declines, even though it is possible that such decline occurs after the 6 years of life considering that the maximum lifespan can by up to 10 years [30]. Comparing cognitive senescence among food-caching and non-caching species may provide further insights into whether food-caching species indeed have delayed cognitive senescence.

We did not detect significant differences in cognitive senescence between elevations even though high elevation birds appear to have better spatial cognitive abilities associated with differences in hippocampus morphology [22]. While it may be expected that elevation differences in spatial cognitive abilities could also be associated with differences in cognitive senescence (perhaps only detectable after 6 years of age), it is also possible that population-level differences are much smaller in magnitude compared to species-level differences. In our case, chickadees at both elevations cache food and rely on cached food for survival, albeit with some differences between elevations (high elevation birds cache more food and have better spatial cognitive abilities). The overall evolution of food caching and associated spatial cognitive specialization in food-caching species was likely the main driver shaping cognitive senescence, which we predicted should be delayed.

Our study suggests that food-caching birds may serve as a novel model to investigate the genetic and molecular mechanisms involved in delayed cognitive senescence. A mechanistic understanding of the reduction in cognitive senescence in these species will lend valuable insights in the evolution of cognitive senescence as well as in the mechanisms regulating cognitive senescence.

Data accessibility. The data supporting this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.bg79cnp9t [31].

Authors' contributions. V.V.P. conceived the study. V.K.H., A.M.P., L.M.B., C.L.B. and V.V.P. collected data; V.K.H. processed all RFID data and generated the final dataset; V.K.H. and V.V.P. ran statistical analyses and co-wrote the first draft; E.S.B. provided all RFID technology support; all authors co-wrote the final manuscript.

Competing interests. We declare we have no competing interests.

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