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Variation in plumage reflectance but not song reflects spatial cognitive performance in black-capped chickadees (*Poecile atricapillus*)

Laura Robayo Noguera[1] · **Chloe A. L. Stevenson**[2] · **Tianconghui Wang**[2] · **Matteo K. Pasquale**[1] · **Carrie L. Branch**[1,2]

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Abstract

In seasonally variable environments, enhanced cognitive abilities may allow animals to adjust their behavior to changing conditions. Nonmigratory food-caching birds, like chickadees, rely on specialized spatial cognition to successfully cache and retrieve food items and survive the winter. Previous studies have linked spatial cognitive performance in chickadees to enhanced fitness, including survival and reproduction; however, it remains unknown whether females assess male cognitive ability via direct observation or secondary sexual traits. In this study, we investigated whether variation in common secondary sexual traits of songbirds, song and plumage, serve as indicators of cognitive ability in black-capped chickadees (*Poecile atricapillus)* when accounting for dominance rank. To explore this, we brought wild male black-capped chickadees into captivity, tested their performance in three spatial cognitive abilities (spatial learning, cognitive flexibility, and long-term retention), determined the relative social dominance ranks among all individuals, measured plumage reflectance in six body regions, and recorded their *fee-bee* songs to assess the relationship between these variables. Our findings show that birds with brighter white plumage and greater contrast between black and white plumage patches showed better spatial learning and memory performance. In contrast, we found no significant associations between cognitive performance and song variation. Our results suggest that females may use some secondary sexual traits as signals for cognitive performance, although, we suggest direct observation may also be important for mate choice involving cognitive ability in chickadees. This work provides insights into female mating decisions, highlighting the complex nature of sexual selection and female preferences.

Keywords Spatial cognition · Cognitive flexibility · Sexual selection · Secondary sexual traits

Introduction

Animals living in temperate regions face seasonal changes characterized by variations in climate and availability of resources. While many species migrate to different locations to overwinter, others use alternative strategies, including hibernation or food storage. Food-hoarding species store food in times of abundance to retrieve and consume later in times of scarcity, such as over the winter. Larder-hoarding species defend few large stores, while scatter-hoarding species store food in many locations scattered across their home ranges to reduce pilfering (Vander Wall 1990; Pravosudov & Roth 2013). Many food-caching birds are scatter hoarders and rely on specialized spatial learning and memory to recover thousands of food stores (Pravosudov and Roth 2013). Because birds need to recover food items cached weeks prior, they must rely on long-term memory retention for accurate recovery (Hitchcock and Sherry 1990). The

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✉ Laura Robayo Noguera
lrobayon@uwo.ca

✉ Carrie L. Branch
cbranch6@uwo.ca

Chloe A. L. Stevenson
csteve86@uwo.ca

Tianconghui Wang
cheriswang136@gmail.com

Matteo K. Pasquale
matteopasquale44@gmail.com

[1] Department of Psychology, University of Western Ontario, London, ON, Canada

[2] Department of Biology, University of Western Ontario, London, ON, Canada

development of such specialized cognitive abilities represents a high metabolic cost in vertebrates and may lead to tradeoffs in other physiological or behavioral traits (Mink et al. 1981; Isler and Van Schaik 2006).

Due to such high metabolic cost, selection for enhanced cognitive abilities and underlying brain tissue may be constrained (Isler and Van Schaik 2006). Indeed, research investigating possible relationships between cognitive performance and fitness-related traits is somewhat equivocal (Boogert et al. 2011a; Searcy and Nowicki 2019). For example, research in song sparrows (*Melospiza melodia)* and New Zealand robins (*Petroica longipes*) shows no relationship between larger song repertoire size and cognitive performance (Boogert et al. 2011b; MacKinlay and Shaw 2019; Sewall et al. 2013), while work in great tits (*Parus major*) shows a positive relationship between variation in plumage characteristics (used by females to identify possible mates) and better cognitive performance (Cauchard et al. 2017). Furthermore, studies in Satin bowerbirds (*Ptilonorhynchus violaceus*) show that males with better cognitive performance have higher mating success (Keagy et al. 2012), while male New Zealand robins show weak evidence for a positive relationship between spatial cognitive abilities and reproductive output (Shaw et al. 2019).

One critical factor to consider when assessing the relationship between cognition and fitness-related traits is the ecological relevance of the cognitive task itself; which often varies widely among studies investigating such links (Mettke-Hofmann 2014; Morand-Ferron et al. 2016; Henke-Von Der Malsburg et al. 2020). For scatter-hoarding species, superior spatial learning and memory abilities, including cognitive flexibility and long-term memory retention are thought to be highly adaptative, because they allow animals to relocate their food caches and modify their caching behavior based on changing conditions and previous experiences (Sherry 1984; Martin et al. 2022; Benedict et al. 2023). More recent work in wild mountain chickadees (*Poecile gambeli*) provides support for the long-hypothesized relationship between spatial cognitive abilities and fitness in food-caching birds. Research shows that selection acts on the spatial learning and memory abilities of chickadees, such that it has a genetic basis (Branch et al. 2022; Semenov et al. 2024) and is associated with higher fitness, including enhanced survival, longevity, and reproductive output (Branch et al. 2019; Sonnenberg et al. 2019; Welklin et al. 2024). More specifically, in a year of high resource abundance, females socially mated (as opposed to extra-pair mated) to males with better spatial cognition laid larger clutches. Since females are the only sex to lay eggs, clutch size is controlled by the female. This flexible response to variation in male phenotype suggests that females can identify males with better spatial cognition and adjust their reproductive investment accordingly (Branch et al. 2019). In the same study system, at the population level, researchers found that high-elevation birds outperformed low elevation birds on a spatial learning and memory task, while low elevation birds outperformed high elevation birds on a reversal learning task, suggesting a tradeoff between spatial learning and memory abilities and cognitive flexibility (Croston et al. 2017; Tello-Ramos et al. 2019). Although spatial cognitive performance plays a significant role in the survival of some food-caching birds, specifically in chickadees, and female chickadees invest more in reproduction when socially mated to a male with better spatial cognition, how females are able to identify males that exhibit enhanced cognitive abilities remains unknown.

Secondary sexual traits are those that differ between males and females of the same species and are used in male-male competition or by females when choosing a mate. These traits are shaped by sexual selection, and in many species, secondary sexual characteristics manifest as physical differences or dimorphism, including size, coloration, or the presence of ornaments (e.g., large antlers in male deer, tail feathers of peacocks), or behavioral traits like vocalizations or mating dances (e.g., vocalizations in male frogs, courtship displays in the birds of paradise; Shuker and Kvarnemo 2021). These sexually selected traits may signal genetic fitness, health, or resource-holding potential to prospective mates, as well as weapons in direct competition between males for access to females (Avise and Ayala 2009). Among temperate passerines, plumage and song are common secondary sexual traits used by females to identify and mate with high-quality males (Ptacek 2000). Black-capped chickadees (*Poecile atricapillus)* exhibit achromatic plumage with contrasting patches of gray, white, and black feathers. From the perspective of a human observer, males and females appear monochromatic, however, research has shown that males have brighter white plumage patches and greater contrast among adjacent regions of black and white patches compared to females (Mennill et al. 2003). In addition, like most bird species, black-capped chickadees are tetrachromats, meaning they can perceive ultraviolet (UV) light, and some of their plumage patches reflect in this range (Mennill et al. 2003; Doucet et al. 2005).

Regarding song, both female and male black-capped chickadees can produce the species-specific *fee-bee* song, however, males produce these songs significantly more often than females (Hahn et al. 2017; Montenegro et al. 2020). The song of male black-capped chickadees functions to defend territories from conspecific males and to attract females (Otter and Ratcliffe 1993). In black-capped chickadees, females prefer dominant males as both social and extra-pair mates (Hahn et al. 2017) and may use variation in plumage and song to assess rank (Otter et al. 1997; Mennill et al. 2003). For instance, dominant males have brighter white and darker black plumage regions, show a greater contrast in their plumage patches, and exhibit higher UV reflectance in black plumage regions compared to subordinate males (Mennill et al. 2003; Doucet et al. 2005). In addition, dominant males produce *fee-bee* songs with more consistent frequency ratios, sing earlier at dawn, for a longer duration, and at higher rates compared to subordinate males (Otter et al. 1997; Hahn et al. 2017).

Considering that spatial cognitive abilities are important for chickadees' fitness and have a genetic basis, female chickadees would be expected to prefer mating with males that have enhanced cognitive abilities. Furthermore, female chickadees use variation in song and plumage to assess mates; therefore, in this study, we investigated whether variation in male song or plumage may serve as indicators of cognitive abilities, including spatial learning and memory, cognitive flexibility, and long-term memory retention. To address this question, we brought wild male black-capped chickadees into captivity to assess the relationship between three spatial cognitive tasks (spatial learning, cognitive flexibility, and long-term retention) and variation in two secondary sexual traits (song and plumage). We also assessed dominance rank using pair-wise interactions among all males, as previous work has demonstrated the importance of social dominance in mate choice. We predict that males who perform better in the tasks will show brighter white and darker black plumage regions, show a greater contrast in their black and white plumage patches, and exhibit higher UV reflectance in their black plumage regions compared to males who perform worse on the cognitive tasks. In addition, we predict that males who perform better on the cognitive tasks will produce more consistent *fee-bee* songs (e.g., smaller coefficient of variation; Lohr 2008) across multiple acoustic song measures compared to those who perform worse. Finally, work in mountain chickadees shows no relationship between spatial cognitive abilities and social dominance rank (Heinen et al. 2021), therefore, we do not expect dominance rank to be related to cognitive performance in male black-capped chickadees.

Methods

Subjects and housing

For this study, we captured 16 male black-capped chickadees (*Poecile atricapillus*) in November 2023 at Western University, London, Ontario (43.008331, -81.282327) using temporary platform feeders, potter traps, and mist nets in combination with hanging feeders and vocal playbacks. Upon capture, we color-banded all individuals, measured mass (g) and wing length (mm), estimated age using plumage characteristics of the outermost tail feathers (hatch year versus after hatch year; Pyle 1997), and collected a small blood sample for PCR-based sex determination. Birds were placed in individual cages (46 × 46 × 46 cm) at the Advance Facility for Avian Research (AFAR) on Western University campus; each cage contained a cuttlebone, food dish, water dish, three perches, a caching block, and shallow bowl of sand (Figure S1). Temperature was set to 20 °C during captivity and animals had ad libitum access to water (supplemented every other day with Oasis Vita Drops for small birds) and food (shelled and unshelled black-oil sunflower seeds, mealworms, and ground Mazuri Exotic Animal Nutrition, St. Louis, MO), unless otherwise specified. Birds were held in captivity for four weeks prior to any behavioral or cognitive testing. For all behavioral tests, the day before every testing day, one hour prior to lights off, birds were temporarily placed in smaller holding cages (30.5 × 30.5 × 40.5 cm) connected to automated doors that allowed entrance into the larger behavioral testing room (2.8 × 2.8 m) via light manipulation (Figure S2; Pravosudov and Clayton 2002), and placed back in their housing cages after finishing cognitive testing.

From November 2023 to February 2024, birds were exposed to a winter light cycle (10 h of light:14 h of dark). During this time, birds were habituated to the housing and behavioral testing rooms and tested in three different cognitive tasks. We also determined their social dominance rank via pairwise interactions and measured plumage reflectance. In March 2024, we shifted the light cycle to a spring photoperiod (14 h of light:10 h of dark) until April 2024. Once birds were habituated to the new light cycle, *fee-bee* songs were recorded (see Fig. 1b for timeline). Once all data was collected, the birds were banded with aluminum Canadian Wildlife Service (CWS) bands and released back into the wild, where they were originally captured. During captivity one of the 16 individuals had to be euthanized due to an unexpected injury, so he was only included for cognitive testing. Another of the individuals did not solve the cognitive flexibility task and therefore could not participate in the long-term memory task, so only data for spatial learning, plumage, dominance, and song were included in the analyses. Finally, one male did not sing during song recordings, so this bird was not included in song analysis (see Table S1 for breakdown of sample sizes).

Cognitive testing

Two identical behavioral testing rooms were used for all cognitive testing, which included a spatial learning task, a reversal learning task (proxy for cognitive flexibility), and a long-term retention task (Strang and Sherry 2014; Morand-Ferron et al. 2022). All three tasks involved the same testing room setup; two simplified trees, each with 10 equally spaced reward sites (20 in total); each reward site consisted of a wooden perch, and a drilled hole or caching site with a

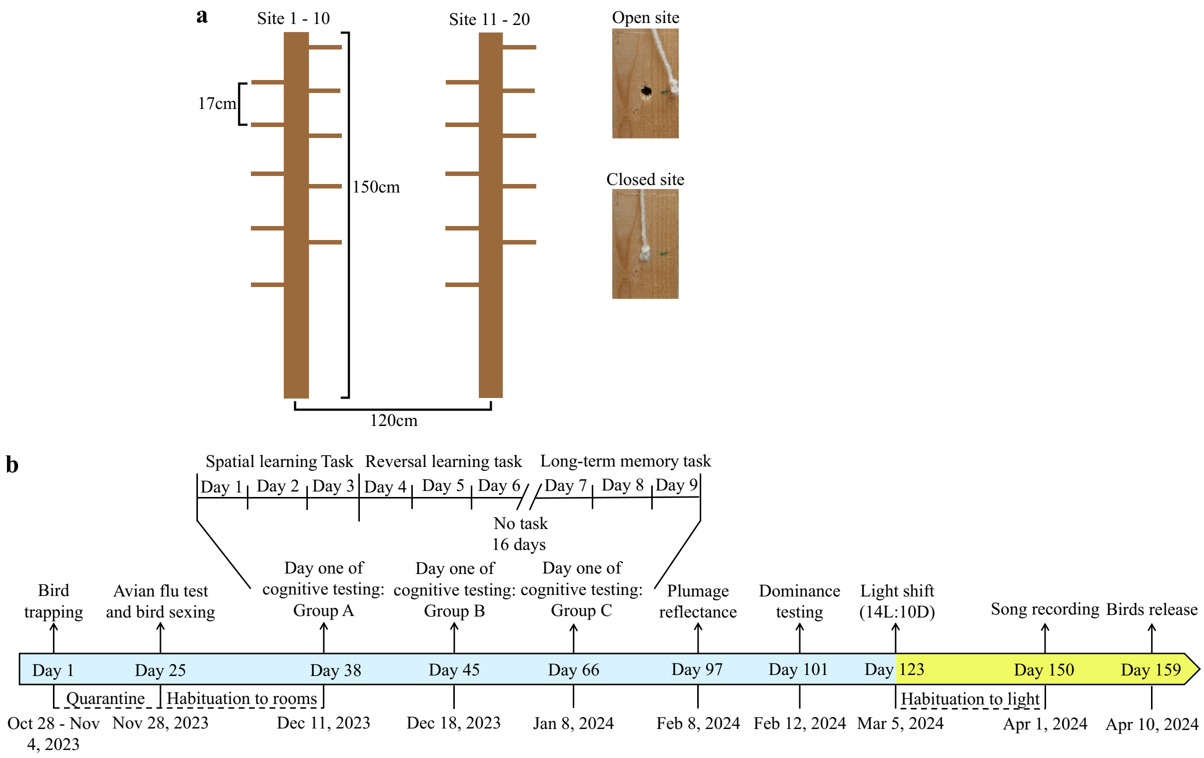

Fig. 1 **a** Left, shows a diagram of the two simplified trees used for cognitive testing. Measurements show height, distance between trees, and the distance between the perches (equal for all). Right, shows pictures of an open and closed caching site with a knotted string. **b** Detailed timeline of experiment. Above, a timeline of the cognitive testing. In the first three days the birds were tested on the spatial learning task (Days 1–3), in the next 3 days the birds were tested on the reversal learning task (Days 4–6), then they were not tested for 16 days, and in the last three days of cognitive testing the birds were tested on the long-term memory task (Days 7–9). Below, a summarized timeline from catch date to release date. After the birds were captured, they were habituated to the housing and behavioral rooms, tested in three different cognitive tasks, their social dominance rank was determined, and their plumage reflectance was measure; After that, the light cycle was shifted (14L:10D), the birds were habituated to the light, their *fee-bee* song were recorded, and then they were released back to the wild

knotted string placed above the hole (Fig. 1a). Birds were required to remove the knot from the hole with their bills to access a mealworm reward (Freas et al. 2012). Prior to testing, individuals were habituated to the testing room for two 30-min periods on two different days. During the first trial of the spatial learning task, all sites were open (no knot covering the caching site) and one was randomly baited with a mealworm visible to the bird. For all subsequent trials and cognitive tests, the reward sites were covered with the knot and the mealworm was not visible to the bird. All test trials were performed one hour after lights turned on for the birds. The day before testing, birds were moved into smaller holding cages one hour prior to lights off and deprived of food until their first test trial to increase motivation to complete the task. For every cognitive task, birds were individually tested by releasing them into the behavioral testing room. Birds were divided into 3 groups such that no more than 5 individuals were tested on the same day (Fig. 1b).

To test spatial learning and memory performance, each bird was randomly assigned to one of the 20 reward sites (e.g., site A) and was tested on 5 trials per day for three consecutive days (15 trials in total; Fig. 1b). Five birds were tested each day in sequential order such that all birds completed trial one before starting trial two, and so on. The order birds were tested in was switched every other day to minimize order effects on motivation or performance. To assess performance, we measured the number of non-rewarding sites visited, or errors (max 19), and latency (s) to find the reward site. A visit was defined as landing on the perch beside the site and removing the knot. A trial began when a bird flew into the behavioral testing room and ended when the bird visited the correct reward location. All birds had a maximum of 20 min to complete each trial. Once birds found the reward site, they were allowed to consume the piece of mealworm and remained in the testing room for three minutes before being moved back into their holding cages, again using light manipulation. This was done to maintain motivation to complete the task (i.e., birds can learn that solving the task means going back into their home cage so they will prolong solving, potentially leading to spurious results).

To test cognitive flexibility, we used a single reversal test. After completing three days (15 trials) (Fig. 1b) of the spatial learning and memory task, all birds were reassigned, semi-randomly, to a new reward site in the previously non-rewarding tree. Birds now only received a reward from this new site (e.g., site B). Again, each bird was tested on 5 trials per day for three consecutive days, the number of incorrect sites visited (errors) and latency (s) to find the new rewarding site were measured, and visits the birds made to their previously assigned site were noted (e.g., site A, max 1 per trial). Again, birds had a maximum of 20 min to complete each trial.

Sixteen days after the last day of the cognitive flexibility task (Fig. 1b), birds' long-term memory was tested, using the reversal site as the reward location (e.g., site B). Again, birds were tested on 5 trials each day for three consecutive days. The number of errors and the latency to find the rewarding site was measured and all the birds had a maximum of 20 min to complete each trial.

Social Dominance rank

To determine the relative social dominance ranks among all individuals, we conducted pairwise interactions over 15 days. Each of the 15 individuals were tested once a day and all pair combinations were tested (105 pairwise interactions in total). Birds were released into the behavioral testing room (same room used for cognitive testing) one at time and order was determined randomly using a coin flip. Once the first bird flew in, the door of bird two was immediately opened. We recorded all interactions between the two birds in the behavioral testing room, including direct interactions where one bird chased or supplanted the other and more passive interactions where one bird tended to avoid the other bird when it moved in their general direction. A minimum of three consecutive direct interactions or six indirect interactions were used to assign an individual as the winner for each pairing (Pravosudov et al. 2003; Kozlovsky et al. 2014). We then used these outcomes to assign each individual a rank from 1 to 15 depending on the number of wins and losses across all pairings, with 1 being the most dominant and 15 the least dominant of the group.

Plumage reflectance

Using an Ocean Insight Flame-T-UV–VIS Spectrometer and Balanced Deuterium Tungsten light source, we measured plumage reflectance in six body regions (patches) of each male individual (Fig. 2a): white cheek (behind the auriculares), white breast, black cap, black bib, black nape and gray mantle. We used the white diffuse reflectance standard provided by Ocean Insight to set the light standard prior to taking any measurements. For analyses we used reflectance readings from 300 to 700 nm, consistent with the avian visual spectral range (Doucet et al. 2005). We placed the probe (equipped with a solid black pen cap that maintained a 5 mm distance between the surface of the birds' plumage and the end of the probe) directly on the birds' feathers. Birds were held by one researcher (CALS) as the other (LRN) collected reflectance measures. We took three measures from each plumage region, moving the probe away and back from the patch between each reading. All birds were measured in

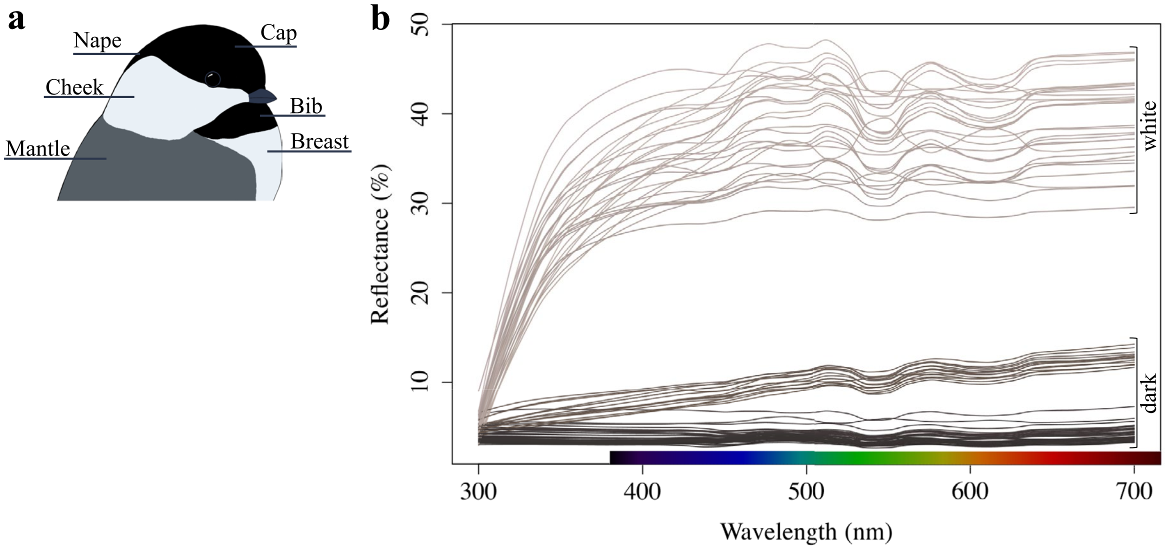

Fig. 2 **a** Illustration of a black-capped chickadee showing the six body regions measured for plumage reflectance. **b** Average reflectance curves for all patches measured for 15 males grouped by white and dark patches. Reflectance curves are color coded based on wavelength measures using the *col = spec2rgb()* function in Pavo

the same laboratory room setting on the same day and the overhead lights were turned off to reduce interference from additional light sources.

We used the package Pavo (Maia et al. 2019; v4.3.1, R Core Team 2023) to summarize the reflectance data and obtain color values for analysis. First, spectrographs were read into Pavo, and the three measurements taken from each patch of each individual were averaged and smoothed (smoothing span of 0.2; Fig. 2b). We then calculated the color values for each patch, including mean brightness (B2) and UV chroma (S1U). Mean brightness (B2) is the mean relative reflectance over the entire spectral range, and UV chroma (S1U) is the relative contribution of the UV spectral range (300–400 nm) to the total brightness (B1) (Maia et al. 2019). Additionally, we grouped the white patches (cheek and breast) and the dark melanin-based patches (cap, bib, nape and mantle) to obtain the mean brightness and mean UV chroma of the grouped patches (mean brightness of white patches, mean UV chroma of white patches, mean brightness of dark patches, and mean UV chroma of dark patches). Finally, we determined the contrast between adjacent white and dark plumage regions (black bib – white breast, black bib – white cheek, white cheek – black cap, white cheek – black nape, and white cheek – grey mantle) calculating the difference between the mean brightness values of each pair of regions (Mennill et al. 2003).

Song measures

Following cognitive testing and plumage measurements, we shifted the birds' photoperiod to be consistent with spring breeding conditions (14L:10D). Birds were exposed to the new photoperiod for four weeks (from March 5 to April 1, 2024; Fig. 1b) to encourage singing (Dawson et al. 2001). Following acclimation to the new photoperiod, each male was individually released into the behavioral testing room (same used for cognitive testing) at dawn for a maximum time of 20 min. Foam mattress toppers (1.5 × 2 m) were fixed to the walls of the room to reduce echoes and reverberation. Birds were free to move around the room and we recorded the *fee-bee* songs of each bird using a MixPre 3 II digital recorder with a 48 kHz sampling rate and 16-bit resolution, and an unidirectional Sennheiser ME-66 microphone to obtain between 10–30 songs per bird. Recordings were saved to a SD card and uploaded for storage after each recording session as .wav files. Song analysis was conducted using spectrograms configured in Raven Pro 1.6 (Cornell Lab of Ornithology) with a Hann window and DFT of 512. We used the selection function in Raven Pro 1.6 to extract the following song variables: delta frequency of *fee* note (change in frequency across the *fee* note), delta time of *fee* note (*fee* note duration), frequency 5% of *fee* note, frequency 95% of *fee* note, peak frequency of *fee* note, delta frequency of *bee* note (change in frequency across the *bee* note), delta time of *bee* note (*bee* note duration), frequency 5% of *bee* note, frequency 95% of *bee* note, and peak frequency of *bee* note. With the information from the selections, we also calculated total song length (seconds), percent *fee* note length (percentage of song length), percent *bee* note length (percentage of song length), glissando of the *fee* note (the frequency at the beginning of the *fee* note divided by frequency at the end of the *fee* note), and frequency ratio (the frequency at the end of the *fee* note divided by frequency at the beginning of the *bee* note). These song variables provide information about individual identity and have been associated with social dominance rank (Christie et al. 2004; Hahn et al. 2017; Ratcliffe and Otter 1996).

Statistical analysis

For all three cognitive tasks, we calculated the mean number of errors made by each bird and the mean time taken to find its reward site (latency), across the total fifteen trials. Additionally, for the reversal learning task, we summarized the number of visits made to the spatial learning location (e.g., location A, 'perseverative errors') across the 15 trials (max of 15 errors). We only counted the first visit to a location as an error, so the maximum number of errors a bird could make in a single trial was 19 out of 20 total rewarding sites. We used the *lm()* function in R Core Team v4.3.1, 2023 to assess the relationship between mean number of errors made by the birds across trials (i.e., the learning curves); and the *cor.test()* function to understand the relationship between errors and latency within the same task for the three tasks, the relationship between the errors of the three different tasks, and the relationship between the latency of the three different tasks. Finally, we used *lm()* to assess the effect of social dominance on the cognitive performance measures.

For the following analyses, each full model included mean number of errors and latency to complete the task as the predictor variables, and the plumage or song measure of interest as the response variable. For the plumage reflectance measures, we used a principal component analysis (PCA) including mean brightness and UV chroma of all 6 patches to reduce the number of variables and assess which patches might explain the variation in the dataset; then, we used *lm()* to assess the relationship between cognitive performance of the three cognitive tasks and the variables that loaded highest on the first four principal components (PCs) as described above. We also used *lm()* to calculate the relationship between cognitive performance of the three cognitive tasks and the grouped plumage variables, including mean brightness of white patches, mean UV chroma of white patches, mean brightness of melanin patches, and mean UV chroma of melanin patches. Finally, we calculated the relationship between cognitive performance on each of the three tasks and brightness contrast between white and dark adjacent patches using *lm()*. We used a Bonferroni correction to correct for multiple comparisons.

To assess song variation we conducted two PCAs, one using the mean values (results in Supplemental Materials) and the other using the coefficient of variation of 15 song variables, including delta frequency of *fee* note, delta time of *fee* note, frequency 5% of *fee* note, frequency 95% of *fee* note, peak frequency of *fee* note, delta frequency of *bee* note, delta time of *bee* note, frequency 5% of *bee* note, frequency 95% of *bee* note, peak frequency of *bee* note, song length, percent *fee* note length, percent *bee* note length, glissando ratio of *fee* note, and frequency ratio. Then, we assessed the relationship between song variation and cognitive performance in the three tasks using *lm()*. For both of the PCAs, we ran linear models with the first three PCs or directly with the variables that loaded highest on those PCs, depending on whether it was one or more selected variables on each PC. We also ran linear models with the glissando of the *fee* note and the frequency ratio, as these two variables have been shown to be relevant for female mate choice (Ratcliffe and Otter 1996). For all PCAs, the number of PCs included was selected so that the cumulative proportion of variation explained was at least 85%, and within each PC the highest loading variables were determined using eigenvectors from *rotation()* in *prcomp()* in R Core Team. We used the relative drop or break in the eigenvectors compared to the other variables to select variables for statistical analysis. We used a Bonferroni correction to correct for multiple comparisons.

Results

Cognitive performance

Across the 15 trials (across three days), birds showed significant improvement in their spatial learning and memory performance ($t_{233} = -4.37$, $p < 0.001$), reversal learning performance ($t_{218} = -8.34$, $p < 0.001$), and long-term memory performance ($t_{218} = -5.41$, $p < 0.001$) measured by a reduction in location errors (Fig. 3). Additionally, birds that completed the task faster made significantly fewer errors in both the spatial learning task ($r = 0.51$, $p = 0.044$) and the reversal learning task ($r = 0.61$, $p = 0.017$) (Figure S3), however, there was no significant relationship between latency to complete the task and number of errors for the long-term memory task ($p > 0.05$). Regarding the relationship between different cognitive tasks, birds that made fewer errors on the reversal learning task also made significantly fewer errors on the long-term memory task ($r = 0.56$, $p = 0.03$), however, there was no significant relationship between mean errors on the other tasks (spatial learning and reversal learning, or spatial learning and long-term memory) or the latency of any of the tasks (spatial learning and reversal learning, spatial learning and long-term memory, or reversal learning and long-term memory), $p > 0.05$.

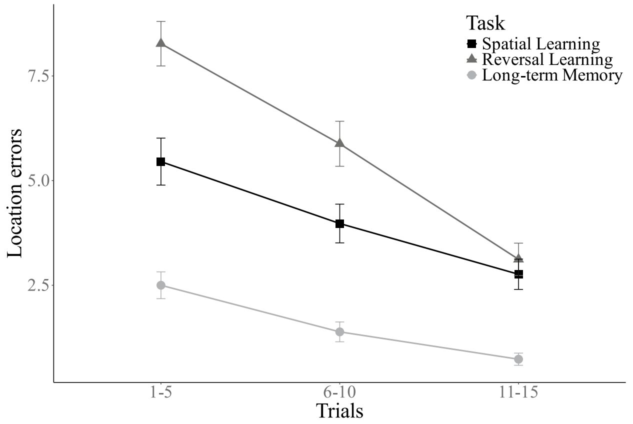

Fig. 3 Mean number of location errors across the first 5, 10 and 15 trials for all birds tested on the spatial learning, reversal learning, and long-term memory tasks. Spatial learning is represented by black squares, reversal learning is represented by dark gray triangles, and long-term memory is represented by light gray circles. Error bars represent standard errors of the mean

Social dominance and cognition

We used linear models to assess the relationship between social dominance and cognitive performance on each of the three tasks. We found that social dominance rank was not significantly related to spatial learning performance (Full model: $F_{2,12} = 0.26$, $p = 0.77$; Location errors: $t_{12} = 0.08$, $p = 0.94$; Latency: $t_{12} = -0.68$, $p = 0.51$), reversal learning performance (Full model: $F_{2,11} = 0.69$, $p = 0.52$; Location errors: $t_{11} = 1.11$, $p = 0.29$; Latency: $t_{11} = -0.99$, $p = 0.34$), or long-term memory performance (Full model: $F_{2,11} = 1.24$, $p = 0.33$; Location errors: $t_{11} = 1.43$, $p = 0.18$; Latency: $t_{11} = 0.09$, $p = 0.92$); therefore, we did not include dominance rank in any of the following analyses.

Association between plumage variation and cognitive performance

Principal component analysis of plumage variables

After conducting a PCA with the plumage variables described above, we found that 42% of the variance was explained by PC1, 26% of the variance was explained by PC2, 13% of the variance was explained by PC3, and 11% of the variance was explained by PC4, totaling 92% of the variation in the dataset explained by the first 4 PCs (Table S2). Mean brightness of the black bib loaded highest on PC1 (eigenvector coefficient: 0.98), mean brightness of the white cheek loaded highest on PC2 (eigenvector coefficient: 0.95), mean brightness of the white breast loaded highest on PC3 (eigenvector coefficient: – 0.79), and mean brightness of the black nape loaded highest on PC4 (eigenvector coefficient: 0.91) (Table S3). Since a single variable loaded highest on each PC compared to the other variables included in the PCA (Table S3), we performed the following analyses using these specific variables (mean brightness of the black bib, white cheek, white breast, and black nape).

Spatial learning performance and plumage reflectance

We used a Bonferroni correction to correct for multiple comparisons, therefore, statistical significance was set at $p \leq 0.006$. The full model, including number of errors and latency on the spatial learning task, revealed a significant relationship with the mean brightness of the white cheek (Full model: $F_{2,12} = 9.83$, $p = 0.0029$). Specifically, individuals with brighter white cheeks completed the task faster (Latency: $t_{12} = -4.05$, $p = 0.0016$; Fig. 4a), however, there was no significant relationship between mean number of errors and brightness of the white cheek (Errors: $t_{12} = 0.27$, $p = 0.79$). All other models for the plumage variables of interest (mean brightness of the black bib, white breast, and black nape) showed no significant relationship with the spatial learning performance (Table S4).

The full model with the brightness of the combined white patches (cheek and breast) did not reach statistical significance (Full model: $F_{2,12} = 7.68$, $p = 0.0071$). However, birds that completed the task faster had significantly brighter white plumage patches (Latency: $t_{12} = -3.64$, $p = 0.003$; Fig. 4b), but there was no significant relationship between mean number of errors and brightness of the white patches (Errors: $t_{12} = 0.39$, $p = 0.70$). There were no significant relationships among the UV chroma of the combined white patches, the brightness of the combined dark patches or the UV chroma of the combined dark patches with the spatial learning and memory performance (Table S4).

Spatial learning performance and plumage contrast

To correct for multiple comparisons, a significance level of $p \leq 0.005$ was used for all analyses. The full model, including number of errors and latency on the spatial learning task, with the contrast between the black bib and the white cheek, was statistically significant (Full model: $F_{2,12} = 9.07$, $p = 0.0039$); in particular, birds that completed the task faster had significantly higher contrast between these patches (Latency: $t_{12} = -4.04$, $p = 0.0017$; Fig. 5a), however, there was no significant relationship between mean number of errors and the contrast between these patches (Errors: $t_{12} = 0.66$, $p = 0.52$). The full model for spatial learning and contrast between the black cap and the white cheek was statistically significant (Full model: $F_{2,12} = 9.88$, $p = 0.0029$); in particular, birds that completed the task faster had significantly higher contrast between these patches (Latency: $t_{12} = -3.98$, $p = 0.0018$; Fig. 5b), however, there was no significant relationship between mean number of errors and the contrast between these patches (Errors: $t_{12} = 0.08$, $p = 0.93$).

The full model for spatial learning and contrast between the black nape and white cheek was statistically significant (Full model: $F_{2,12} = 9.39$, $p = 0.0035$); in particular, birds that completed the task faster had significantly higher contrast between these patches (Latency: $t_{12} = -3.88$, $p = 0.0022$; Fig. 5c), however, there was no significant relationship between mean number of errors and the contrast between these patches (Errors: $t_{12} = 0.08$, $p = 0.93$). The full model for spatial learning and contrast between the grey mantle and white cheek was statistically significant (Full model: $F_{2,12} = 10.5$, $p = 0.0023$); in particular, birds that completed the task faster had significantly higher contrast between

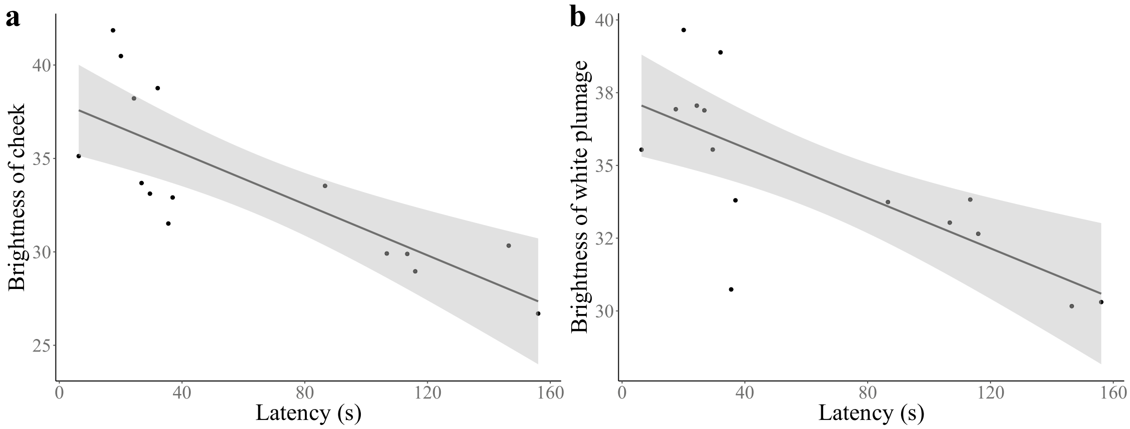

Fig. 4 Relationship between (**a**) the mean latency in the spatial learning task and the mean brightness of the cheek, and (**b**) the mean latency in the spatial learning task and the mean brightness of the combined white plumage patches. Black lines represent linear model predictions, and the shaded area around the line represents the standard error

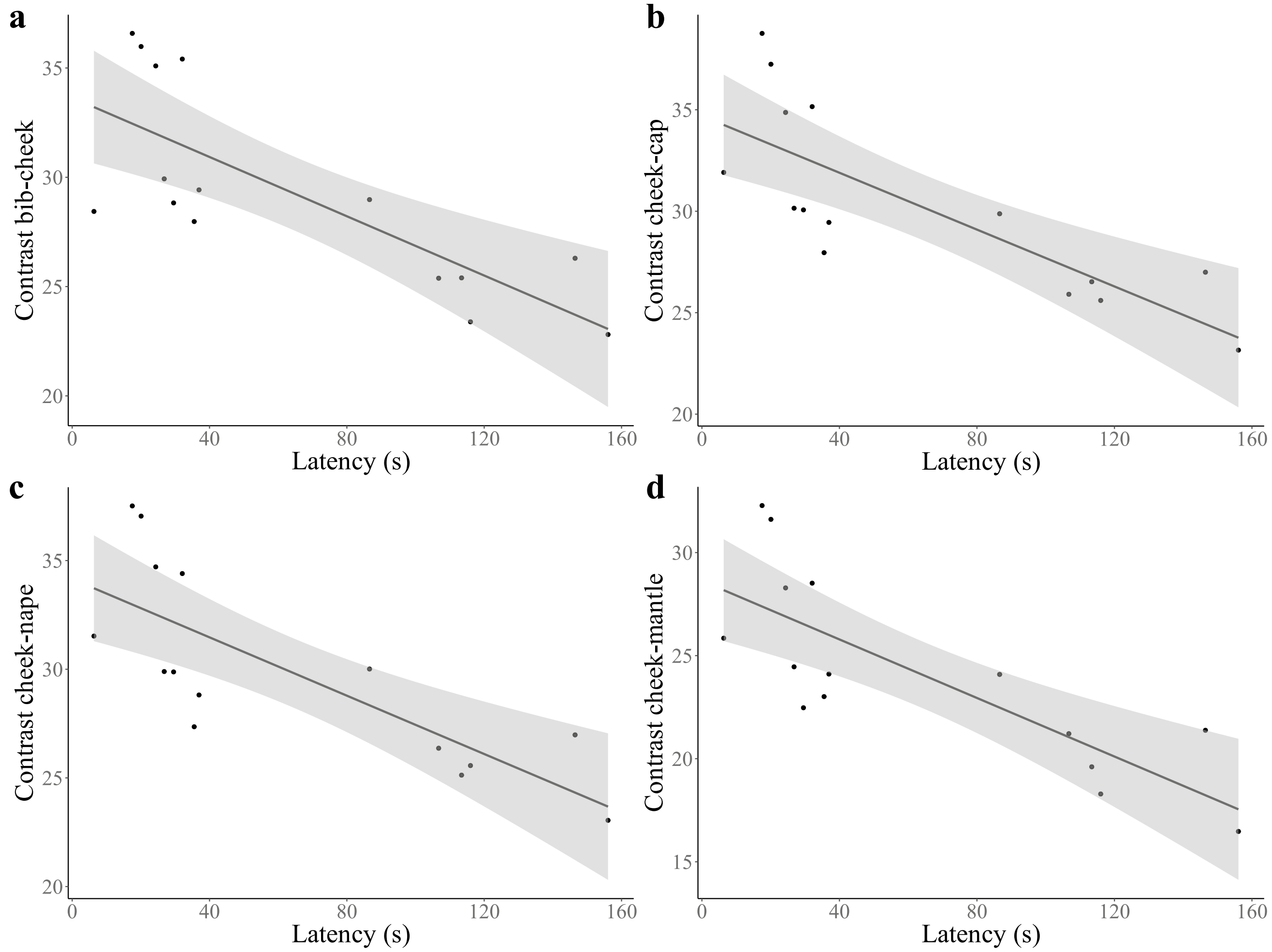

Fig. 5 Relationship between (**a**) the mean latency in the spatial learning task and the contrast between the bib and the cheek, (**b**) the mean latency in the spatial learning task and the contrast between the cheek and the cap, (**c**) the mean latency in the spatial learning task and the contrast between the cheek and the nape, and (**d**) the mean latency in the spatial learning task and the contrast between the cheek and the mantle. Black lines represent linear model predictions and the shaded area around the line represents the standard error

these patches (Latency: $t_{12} = -4.26$, $p = 0.0011$; Fig. 5d), however, there was no significant relationship between mean number of errors and the contrast between these patches (Errors: $t_{12} = 0.47$, $p = 0.65$). Finally, the full model for spatial learning and the contrast between the black bib and the white breast was not statistically significant (Table S4).

Reversal learning performance and plumage reflectance

To correct for multiple comparisons, a significance level of $p \leq 0.006$ was used for all analyses. The full model, including mean number of errors and latency to complete the reversal learning task, with the mean brightness of the white cheek, black bib, white breast, and black nape, all showed no statistically significant relationships; in addition, the number of visits to the old rewarding location (e.g., perseverative errors) was not correlated with the mean brightness of the white cheek, black bib, white breast, or black nape (Table S4). The same models with brightness and UV chroma of the combined dark patches and the combined white patches showed no statistically significant relationships with the reversal learning performance; additionally, the number of visits to the old rewarding location was not correlated with the brightness or UV chroma of the combined dark patches or the combined white patches (Table S4).

Reversal learning performance and plumage contrast

To correct for multiple comparisons, a significance level of $p \leq 0.005$ was used for all analyses. The full model, including mean number of errors and latency on the reversal learning task, with the contrast between the black bib and the white breast, the black bib and the white cheek, the white cheek and the black cap, the white cheek and the black nape, or the white cheek and the gray mantle, showed no statistically significant relationships for all models (Table S4). Additionally, the number of visits to the old rewarding location (e.g., perseverative errors) was not correlated with the contrast between the black bib and the white breast, black bib and the white cheek, the white cheek and the black cap, the white cheek and the black nape, or the white cheek and the gray mantle (Table S4).

Long-term memory performance and plumage reflectance

To correct for multiple comparisons, a significance level of $p \leq 0.006$ was used for all analyses. The full model, including mean number of errors and latency to complete the long-term memory task, with the mean brightness of the white cheek, black bib, white breast, and black nape, all showed no statistically significant relationships (Table S4). In addition, the full models with brightness and UV chroma of the combined dark patches and the combined white patches showed no statistically significant relationships with the long-term memory performance (Table S4).

Long-term memory performance and plumage contrast

To correct for multiple comparisons, a significance level of $p \leq 0.005$ was used for all analyses. The full models, including mean number of errors and latency to complete the long-term memory task, with the contrast between the black bib and the white breast, the black bib and the white cheek, the white cheek and the black cap, the white cheek and the black nape, and the white cheek and the gray mantle, all showed no statistically significant relationships (Table S4).

Association between song variation and cognitive performance

Principal component analysis of song variables

We conducted two separate principal component analyses of the 15 song variables described above, one for the mean values of each measure and one for the coefficients of variation of these measures, to assess consistency in song production (e.g., Lohr 2008). The results of the mean values PCA are reported in the Supplemental Materials (Tables S5 and S6). The PCA of the coefficients of variation of the song variables showed that 68% of the variance in the dataset was explained by PC1, 11% of the variance was explained by PC2, and 10% of the variance was explained by PC3, with a total of 89% explained by these first three principal components (Table S7). For PC1 the delta frequency of the *fee* note (eigenvector coefficient: 0.61) and the delta time of the *fee* note (eigenvector coefficient: 0.42) loaded the highest compared to the other variables, for PC2 the delta frequency of the *fee* note (eigenvector coefficient: – 0.52) and the delta time of the *bee* note (eigenvector coefficient: – 0.63) loaded the highest compared to the other variables, and for PC3 the delta frequency of the *fee* note (eigenvector coefficient: – 0.46) and the delta time of the *fee* note (eigenvector coefficient: 0.44) loaded the highest compared to the other variables (Table S8). As shown in Table S8, more than one variable loaded highest in the three PCs, therefore, we conducted the statistical analysis with the PCs.

Spatial learning performance and song variation

A significance level of $p \leq 0.005$ was used for all models to correct for multiple comparisons. The full models for spatial learning and memory, including mean number of errors and latency to complete the spatial learning task, with each of the first three PCs from the coefficient of variation PCA, showed no statistically significant relationships (Table S9). Additionally, when applying the same model with the glissando of the *fee* note and the frequency ratio, we found no significant relationships (Table S9).

Reversal learning performance and song variation

To correct for multiple comparisons, a significance level of $p \leq 0.005$ was used for all models. When applying the full models assessing the relationship between reversal learning, including number of errors and latency on the reversal learning task, with each of the first three PCs from the coefficient of variation PCA, there were no statistically significant relationships (Table S9); also, there were no statistically significant relationships between the number of visits to the old rewarding location (e.g., perseverative errors) and the song variables that loaded highest on the first three PCs from the coefficient of variation PCA (Table S9). Finally, when applying the same model with the glissando of the *fee* note and the frequency ratio, we found no significant relationships (Table S9).

Long-term memory performance and song variation

To correct for multiple comparisons, a significance level of $p \leq 0.005$ was used for all models. When applying the full models assessing the relationship between long-term memory performance, including mean number of errors and latency to complete the long-term memory task, with each of the first three PCs from the coefficient of variation PCA, there were no statistically significant relationships with PC1, PC2, or PC3 (Table S9). Additionally, when applying the same model with the glissando of the *fee* note and the frequency ratio, we found no significant relationships (Table S9).

Discussion

In this study, we aimed to assess the relationship between spatial cognitive abilities and two secondary sexual traits in male black-capped chickadees: variation in song structure and plumage reflectance, both used by females in mating decisions (Otter et al. 1997; Doucet et al. 2005). Previous research has demonstrated that spatial cognitive abilities enhance survival and reproductive success in a closely related chickadee species, primarily due to their reliance on specialized spatial cognition to recover food caches over winter (Branch et al. 2019; Pravosudov & Roth 2013; Sonnenberg et al. 2019; Welklin et al. 2024). Given that females have previously been shown to increase reproductive investment when mated to males with better spatial cognitive abilities (Branch et al. 2019), we hypothesized that secondary sexual traits associated with spatial cognitive performance might serve as indicators for female mating decisions.

Among the two secondary sexual traits we measured, song and plumage, variation in achromatic plumage reflectance revealed significant associations with cognitive performance in male black-capped chickadees. Specifically, we found significant relationships between spatial learning and memory performance and the brightness of white plumage, as well as the contrast between black and white patches. Males with brighter white plumage patches, particularly on their cheeks, completed the spatial learning and memory task faster, consistent with better spatial learning performance, as the number of errors and latency to complete the task were significantly correlated (Figure S3a). Additionally, when analyzing the contrast among black and white patches, birds that performed the spatial learning and memory task faster showed higher contrast between adjacent patches, particularly when one of the patches in the contrast comparison was the white cheek. While number of errors and latency to complete the task are highly correlated, only the latency to complete the task was significantly associated with variation in plumage patches. This finding suggests that efficiency in completing the task, as opposed to accuracy, may be more important for fitness, particularly when the cost of exploring multiple sites is low. For example, in our experiment, the caching sites were close together on the artificial trees and birds could easily move among 5 sites in less than 5 s.

Previous research has shown that dominant males exhibit darker black and brighter white plumage regions and, therefore, greater contrast between black and white plumage regions. In addition, males with brighter white plumage regions and higher UV chroma in their black plumage patches exhibited higher reproductive success (Doucet et al. 2005; Mennill et al. 2003). Our results suggest that some of these plumage traits related to mate quality and reproductive success correspond to performance on a spatial learning and memory task. Specifically, males that performed the spatial task faster exhibited brighter white plumage and higher contrast between adjacent black-white patches, suggesting that females' choice for these plumage traits may reflect choice for better spatial cognitive ability. Although some of these traits were previously associated with higher dominance rank, here we found no relationship between spatial cognitive performance and social dominance. This may be because the dominance rank of males in a flock changes over time depending on the age of each individual, while spatial cognitive abilities remain consistent over time in chickadees (Mennill et al. 2003; Sonnenberg et al. 2019; Welklin et al. 2024).

While previous research highlights the role of social dominance in female mate choice (Hahn et al. 2017), our study found no correlation between social dominance rank and spatial cognitive performance, consistent with work in wild chickadees (Heinen et al. 2021). However, we did observe significant relationships between cognition and plumage variation. This raises interesting questions about how and when females rely on secondary sexual traits to identify male cognitive performance, or quality more broadly, and when they might choose a mate of higher dominance versus one with better spatial cognitive abilities. Females share territories with males throughout the year and can observe their caching behavior, so it is possible that they integrate both direct observations and secondary sexual characteristics when assessing male cognitive abilities (Branch et al. 2019; 2023). Furthermore, females may prefer different males as social versus extra-pair mates, since social males provide direct benefits via parental care and access to territories, while extra-pair males provide indirect genetic benefits. Future research could directly investigate female mate preferences by observing their behavior as males complete cognitive tasks (e.g., Chen et al. 2019).

Although we found evidence that cognitive abilities are associated with plumage variation, we found no support for a relationship between cognitive performance and variation in song structure, albeit based on the specific song traits we measured. Chickadees are socially monogamous, forming social pair bonds during the fall that persist throughout the winter when they are in flocks of unrelated individuals. At this time, males sing significantly less compared to the spring and summer (Phillmore et al. 2006). It is possible that females prioritize variation in plumage, a short-range signal, assessable during the fall when birds are living in flocks and heavily rely on their specialized spatial abilities for cache recovery. Indeed, females from wild chickadee populations do not choose social mates solely based on cognitive abilities, as they are likely limited by available unpaired males in the fall (i.e., pairs stay together year after year resulting in limited unpaired birds to choose from; Branch et al. 2023). If this is the case, we might expect female choice for enhanced spatial cognitive abilities to manifest via extra-pair paternity during the breeding season.

Consistent with previous work in other songbirds, we found no association between spatial cognition and variation in song structure when the light cycle mimicked spring conditions (Dawson et al. 2001; Boogert et al. 2011a; Sewall et al. 2013). These results suggest that if females consider spatial cognitive abilities when choosing extra-pair mates, song structure is unlikely to serve as a reliable indicator. That said, differences in chickadee song performance, such as daily singing routines (e.g., Huang et al. 2022) or countersigning (e.g., Shackleton and Ratcliffe 1994) may be associated with spatial cognition and should be assessed in future work. In conclusion, our study highlights significant relationships between cognitive abilities and plumage variation in male black-capped chickadees, but not with variation in song structure. It is likely that females use multiple traits, including plumage characteristics, song features, and direct observation to inform their mate choice decisions, and that females' mate preferences may vary depending on the context, e.g., social versus extra-pair mates and age or experience of the female.

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Author contribution Conceptualization: LRN, CLB; Methodology: LRN, CLB; Data collection: LRN, CLB, CALS, TW, MKP; Formal analysis and investigation: LRN; Writing—original draft preparation: LRN; Writing—review and editing: LRN, CLB, CALS, TW, MKP; Funding acquisition: LRN, CLB; Supervision: CLB.

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Data availability Data will be made available upon acceptance.

Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval All procedures performed in the study were approved by the University of Western Ontario Animal Care and Use Committee, protocol number 2023-092. Scientific permits for collection and banding of birds were provided by Environment and Climate Change Canada, permit numbers SC-OR-2023-0009 and 10978.

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