

The relationship between a feather ornament and cognitive abilities in swamp sparrows

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Abstract

Cognitive traits can influence fitness, yet they are rarely observable to potential mates. Plumage signals may provide indirect cues, particularly pheomelanin-based coloration as its synthesis draws on resources also required for central nervous system (CNS) development. We asked whether the area and redness of a feathered pheomelanin-based head cap patch ornament predicted cognitive abilities in male swamp sparrows (*Melospiza georgiana*). The redness of the cap patch was calculated from spectral reflectance measurements, and area was calculated using ImageJ. Males were then tested on a battery of cognitive tasks. We found that cap patch redness and area were highly correlated. Additionally, we found that birds with larger and redder caps performed worse on an inhibitory control task, and birds with redder caps performed better on a color reversal task. Furthermore, we found birds with larger cap patches to perform better on the novel foraging and spatial learning tasks. Performance on a color association task correlated positively with performance on a color reversal task, but no other cross-task correlations were detected. These results suggest that pheomelanin-based coloration may be associated with specific cognitive abilities. Our findings highlight the potential for feather pigmentation to serve as a reliable indicator of certain cognitive traits while emphasizing domain specific variation in performance across cognitive tasks.

Introduction

Reliable animal communication signals play an important role in social interactions, including mate choice, where individuals may benefit by assessing the quality of potential partners. For a signal to be reliable (i.e., “honest”), however, it must not only correlate with the trait it advertises but also be costly to produce, with higher-quality individuals more able to afford to produce the signal (reviewed in Maynard-Smith and Harper 2003; Searcy and Nowicki 2005). One trait of interest in this context is cognitive ability, a factor increasingly recognized as important in mate selection due to its potential to confer advantages such as better provisioning or behavioral flexibility (e.g. Branch et al. 2019; Cauchard et al. 2013). Several studies have shown that the cognitive abilities of the individual being chosen (e.g. Chen et al. 2019), and sometimes those of the chooser (Álvarez-Quintero et al. 2021), can influence mate choice (Boogert et al. 2011). Individuals in a natural setting rarely can directly observe another individual’s cognitive abilities, however. Thus, animals may rely instead on correlated traits that reliably signal cognitive ability (reviewed in Peters et al. 2014). Here we ask if an ornamental feather coloration trait serves as a reliable indicator of cognitive abilities in a wild bird, the swamp sparrow (*Melospiza georgiana*).

Researchers have suggested secondary sexual traits such as vocalizations (Dubois et al. 2018; Peters et al. 2014), courtship displays (Keagy et al. 2012), or coloration (Rincón-Rubio et al. 2023) may serve as reliable indicators of cognitive performance. Few studies have tested these relationships under ecologically relevant conditions, however. Among potential signals of cognitive abilities, feather pigmentation is a well-studied ornament known to correlate with condition-dependent attributes such as oxidative stress, nutritional status, and immune function (Bortolotti et al. 2006; McGraw et al. 2005). Although melanin-based plumage traits have been extensively studied in relation to physiological

condition and behavioral syndromes (e.g. Ducrest et al. 2008; Roulin 2004), whether melanin-based ornamentation reflects cognitive abilities has received little empirical attention.

Among the pigments involved in avian feather coloration, pheomelanin represents an especially promising but underexplored candidate for signaling cognitive abilities. Most previous studies linking ornamentation to cognition have focused on carotenoid-based traits (e.g., Boogert et al. 2011; Simons et al. 2012). Pheomelanin differs distinctly in its biosynthetic pathways and regulatory mechanisms (McGraw 2006; Ducrest et al. 2008) and may therefore convey different information about individual phenotypes (Roulin 2004). Carotenoids in most vertebrates must be acquired through diet and are commonly studied in the context of mate choice (Dale et al. 2015; Hill 1991). In contrast, melanin pigments—including eumelanin and pheomelanin—are synthesized endogenously (McGraw 2006). Pheomelanin produces the yellow to reddish-brown coloration found in certain feathers, skin, and hair (Ito and Wakamatsu 2003) and requires cysteine, an amino acid that also plays a crucial role in synthesizing glutathione (GSH), a key intracellular antioxidant (Galván & Alonso-Alvarez 2008; Ito & Wakamatsu 2008; Lu 2013). Therefore, individuals with more intense pheomelanin-based coloration may already have sufficient cysteine to meet their physiological needs (Leclaire et al. 2019). Cysteine also is essential for nervous system development, suggesting an additional trade-off: under resource limitation, cysteine may be preferentially allocated toward cognitive development rather than pigment deposition (Stearns 1986; Galván and Alonso-Alvarez 2009). Despite these plausible links, pheomelanin has been understudied in the context of the role it may play in signaling cognitive abilities, with only one study having investigated the relationship between pheomelanin levels and brain volume (Galván and Møller 2011). Our study helps fill this gap by asking whether pheomelanin-based coloration could serve as a reliable indicator of cognitive abilities in a wild bird population.

Here, we ask whether a pheomelanin-based trait predicts performance on several cognitive tasks. Swamp sparrows have a pheomelanin-based ornament: a variable red-brown head cap patch that has been suggested to influence mate choice (Olsen et al. 2008, Greenberg and Olsen 2010). Swamp sparrows have been shown previously to successfully perform cognitive tasks in captivity (Dubois et al. 2018). Using wild-caught males held in captivity, we quantified cognitive abilities using tasks targeting associative learning, reversal learning, spatial memory, and behavioral flexibility. Cognitive performance in birds has been shown to be domain-specific rather than general (Searcy and Nowicki 2019, Shettleworth 2012), so it is possible that only some—but not all—tasks will be correlated with coloration. Here, we use “domain-specific” to indicate that performance on cognitive assessments is primarily task-specific rather than reflecting a single, generalized cognitive ability. The cap patch of swamp sparrows varies in both area and redness. For this reason, we measured both the area and redness of individuals’ head cap patches using digital image analysis and spectrometry, respectively. It is possible that cap patch area and redness may serve as independent metrics of coloration given that some studies have shown that ornament color and area may signal different types of information (Freeman-Gallant et al. 2010, Klomp et al. 2016). Furthermore, environmental variables may affect patch area and redness differently. For example, diet may affect pheomelanin-based coloration more than patch area (Roulin

2004; Isaksson et al., 2011). We predicted that more colorful individuals (i.e. with larger and/or redder cap patches) would perform better on at least some cognitive tasks.

Materials and Methods

Bird collection and housing

Male swamp sparrows were captured by mist net in Crawford County, PA, USA (State Gameland #213) in May 2021 (n = 20) and May 2022 (n = 8). Color measurements were taken from all captured individuals. A subset of males in 2021 (n = 14) were determined from preliminary measurements to encompass the range of color variation observed in the field and were transferred to Duke University (Durham, NC, USA) for cognitive testing. All eight birds captured in 2022 were transferred to Duke for testing. Captive birds were caged singly (46 x 22 x 26 cm), kept on a seasonally varying light:dark cycle, and provided with food and water *ad libitum*.

Cap patch measurements

Spectral reflectance measurements (400–800 nm) were taken from a 3 mm diameter circular area on a standardized location on each individual's head cap patch using an integrating sphere (ISP-REF; Ocean Insight Inc.; Dunedin, FL) coupled to a spectrometer (USB-2000; Ocean Insight). For the 2021 cohort, measurements were collected during initial capture, whereas for the 2022 cohort, they were collected after participants arrived at Duke several days after capture. Reflectance was calibrated with an approximately 100% diffuse reflectance standard (WS-1; Ocean Insight). We used these reflectance spectra to calculate a “redness” index by averaging the reflectance over nominal red (600–700 nm) and green (500–600 nm) spectral regions and then calculating $(\text{red} - \text{green})/(\text{red} + \text{green})$ (Tedore and Johnsen 2016).

The red feathers on swamp sparrow head caps are often interspersed with black feathers; that is, caps differ both in how red the red feathers are and the extent to which red feathers cover the entire cap area (Fig. 1). We measured the area of the red pigmented region using ImageJ (Rasband 1997–2018) (Fig. 2). Photographs were taken from a relatively constant position (approximately 12 in) with a ruler in the frame to serve as a reference during area measurements. Photos were taken under fluorescent bulbs (Ecolux with Starcoat SP 35/41, correlated color temperature 3,500–4,100 K, General Electric) with ballast (Hi-Lume 3D/Eco-10, Lutron Electronics) operating at 50–60 W. In ImageJ, the image was split into red, green, and blue channels. Using the red channel, which maximized the achromatic contrast between the red feathers and the surrounding black feathers, the red colored area was traced. In cases where areas of black feathers were surrounded entirely by red feathers, the area of outer envelope of the red region was measured. After this, the black areas were measured individually and their areas subtracted from the overall area. Both measurements (redness of the red feathers on the cap patch and total red-feathered area of the head cap) were calculated from an average of five samples per bird to

account for any variation that might have occurred in positioning of the integrating sphere and photos, respectively.

Cognitive tests

Cognitive abilities were tested between May and September in 2021 and 2022, using tasks adapted from previous studies of cognition in swamp sparrows (Dubois et al. 2018) and song sparrows (*Melospiza melodia*), a closely related congener (Boogert et al. 2011, Anderson et al. 2017, Soha et al. 2019). Individuals were given a neophobia test and five cognitive tests: novel foraging, color association, color reversal, spatial learning, and inhibitory control, always in that order (described more completely below, and in Anderson et al. 2017). Upon meeting task-completion criteria, birds progressed to the next task. We used the number of trials to reach the completion criteria in each task as an inverse measure of performance (i.e., a measure of how quickly they learned the task). Tests were run every weekday afternoon between 12:30–5:00 PM, after subjects had been deprived of food for approximately four hours prior to ensure they were motivated to participate. Every individual was tested for a maximum of six trials a day, with 20 minutes between each trial. Each trial ran for up to two minutes. Every test was run in the individual's home cage, with blinders on each side of the cage to ensure that birds could not see other individuals while they were undergoing trials. A trial began as soon as the cage was closed after the testing apparatus was placed within it. The trials ended when the bird either completed the task correctly, or after a maximum of two minutes, whichever came first. Criteria to pass each task were designed using established methods in previous studies of swamp and song sparrows (Boogert et al. 2011, Anderson et al. 2017, Dubois et al. 2018, Soha et al. 2019). An observer outside of the testing room scored each trial, watching via live-stream video. One male died after completing the spatial learning task and thus did not contribute to the sample size for the final task in the testing sequence (inhibitory control). When interpreting performance on all cognitive tasks below, given scores reflect number of attempts to reach criteria. Individuals with higher scores took longer to reach the criteria and therefore are considered worse performers. Conversely, individuals with lower scores were able to solve the tasks in fewer trials and therefore are considered better performers.

Neophobia

Before beginning the cognitive tests, neophobia was measured as a non-cognitive covariate to isolate the potential confounding effects of fear on behavioral performance. Subjects were presented with a foraging grid (13.5 x 9 x 2.5 cm plastic blocks having six wells 1.3 cm in diameter and 0.8 cm deep) in their home cage for the first time. One mealworm was placed randomly in four of the six wells, all of which were uncovered. Neophobia was measured as the time (in seconds) each bird took to remove the first mealworm from the foraging grid. This measure was used as a fixed effect in analyzing the relationship between patch characteristics and cognition (see below).

Task 1- Novel foraging

In the novel foraging task, individuals learned to remove a plastic lid covering the wells of the foraging grid to obtain the reward of a mealworm found in the well (Fig. 3A). This task represents a novel foraging technique for swamp sparrows, as they do not exhibit similar foraging behavior in the wild. Novel foraging was shaped in the first four stages, and stage five was used as the task. In stage 1, the wells were completely uncovered, and the disks were placed next to the well. In stage 2, the disks were placed to slightly cover the well openings. In stage 3, the disks were placed to half cover the well openings. In stage 4, the disks were tipped into the wells, covering most of them. To advance through stages 1–4, a bird must have completed four out of five consecutive attempts correctly.

After shaping the behavior (stages 1–4), performance on the novel foraging test itself was based on stage 5. In stage 5, the disks completely covered the wells, and birds had to lift the lids open with their beaks to obtain the food reward. Birds had to complete five out of six trials consecutively to pass the task. The test score was the number of trials it took to pass.

Task 2- Color association

Following successful completion of the novel foraging task, birds were tested on a color association task. In this task, two foraging grids were used (12 total wells), and the birds were tested for their ability to learn to associate one of two colors (blue or yellow) with the food reward. Four wells were covered with their assigned color, four were covered with the unassigned color, and four were left empty (Fig. 3B). The positions of the baited and un-baited wells were assigned randomly in each trial. The rewarded color was balanced across subjects. The two prepared grids were placed directly adjacent to each other in the cage, in the same position in each cage. To complete the task, each bird had to either (1) remove at least two of the disks of the rewarded color and none of the unrewarded color, or (2) remove all four of the rewarded color lids before removing any of the unrewarded color. Individuals had to successfully complete the task four out of five consecutive times to pass. The test score was the number of trials it took to achieve the four out of five criterion.

Task 3- Color reversal

After learning the color association task, birds were next tested with a color reversal task. In this task, the procedures were the same as those described for the color association task, except the rewarded and unrewarded colors were switched (Fig. 3C). Thus, the bird had to unlearn their previously learned association and learn the new one. The passing criterion was the same as the color association task described above.

Task 4- Spatial learning

On completion of the color reversal task, birds were tested in a spatial learning task requiring them to learn the location of a food reward. For this task, small (6.4 x 6.4 cm) blocks (the same material as the foraging grids) with one well in each block were used. Each of the blocks were placed in one of the four corners of the individual's cage. The wells were covered using a subject's most recently learned disk color (i.e., of the rewarded color of the color reversal task) (Fig. 3D). A preliminary spatial preference test was done by baiting all four blocks for seven consecutive trials to ensure that a preferred or ignored side was not chosen as the assigned baited side. In the subsequent spatial learning trials, we randomly chose one corner (neither preferred nor ignored). Once assigned a well, only the assigned corner was rewarded for the spatial task itself. The task was considered complete if the bird removed the lid on the baited block first in six of seven consecutive trials. The test score was the number of trials it took to complete the task. Subjects that were unable to complete the task within 60 trials were considered to have failed and assigned a score of 60.

Task 5- Inhibitory control

Birds next were given an inhibitory control task (Fig. 3E) in which they were first trained to find a mealworm inside a black opaque cylinder (4 cm diameter, 5 cm length), which they could extract by reaching with their beak into one or the other open end of the cylinder. Training with the opaque cylinder served to shape the behavior. Once an individual successfully removed the mealworm four out of five consecutive times from the opaque cylinder, a clear cylinder of identical dimensions was substituted for the opaque one. Inhibitory control was measured by how many trials it took for an individual to learn to access the mealworm from one end or the other of the cylinder even though they could see the reward through it. A bird was considered to have passed the inhibitory control test once it removed the mealworm from the clear cylinder without pecking at the side for six out of seven consecutive trials. The test score was the number of trials it took to pass.

Statistical analysis

All analyses were conducted in R v4.4.3 (R Core Team, 2018). We used a correlation matrix to assess whether performance on one cognitive test correlated with another and expected that only color association and color reversal would correlate given prior work on this species (DuBois et al. 2018) and its congener, the song sparrow (Anderson et al. 2017). We also used linear regression to assess the relationship between the two ornament metrics: area and redness. To achieve normality, color association was log-transformed, and novel foraging was reciprocally transformed. All other data were normally distributed and did not require transformations. Normality was confirmed using Shapiro-Wilk normality tests and QQ-Plots.

We used a Bayesian multi-response multilevel model under the R package "brms" (Bürkner 2017) to test if cognitive performance explained variation in cap patch coloration. Cap patch area and redness were set as the response variables and scores for the six cognitive tests (novel foraging, spatial learning, color association, color reversal, spatial learning, and inhibitory control) as the explanatory variables. Year was

included as a group effect because 13 birds were tested in 2021 and eight were tested in 2022. Neophobia was also included as a fixed effect. The model was run for 10,000 iterations under a Gaussian distribution with priors set under normal and gamma distributions for fixed effects and standard deviations, respectively (Lemoine 2019). Bayesian confidence statements tend to be conservative: for example, claims based on 95% posterior intervals have Type S error (where a significant effect is found, but the directionality is incorrect) rates between 0 and 2.5%.

Results

Relationships among cognitive measures

There was a positive correlation between performance on the color association and color reversal tasks (Pearson's correlation, $n = 21$, $r^2 = 0.740$, $p < 0.001$). No other significant correlation existed between performance on the various cognitive tasks.

Relationship Between Cognitive Measures and Patch Coloration

We found the two metrics of the cap patch, redness and area, to be highly correlated (linear regression model, $F = 20.07$, $r^2 = 0.5136$, $p < 0.001$, Fig. 4). When assessing performance on cognitive tasks, higher scores on the cognitive tasks suggest individuals took longer to solve the task, and therefore higher scores suggest negative associations. We found that both cap patch area and cap patch redness were negatively associated with inhibitory control and positively associated with spatial learning and novel foraging (although only marginally for redness) (Fig. 5). Additionally, redness was individually positively associated with color reversal (Fig. 5A).

(A)

(B)

Figure 5 Posterior distributions for models testing if crown patch (A) redness and (B) area are associated with cognitive test scores. The solid pink curve shows the posterior density; the solid pink vertical line marks the posterior median. The pink shaded region indicates the 95% highest density interval (HDI). The dashed vertical line at zero represents the null hypothesis value. Significant relationships are those that have no credible intervals overlapping with zero. It is important to note that higher scores on cognitive tasks suggest individuals take longer to solve the task, and therefore higher scores suggest negative associations. Parameter values (x-axis) differ in A versus B given variation in scale of measurements: for area (mm^2) versus redness.

Discussion

We found mixed evidence that the cap patch of swamp sparrows correlates with their performance on a variety of cognitive tasks. Specifically, we found that both the redness and area of the cap patch are negatively associated with inhibitory control (Fig. 5), such that individuals with redder or larger patches performed worse on this task. In contrast, cap patch redness was positively associated with performance on the color reversal task (Fig. 5a). Cap patch area also showed a positive relationship with novel foraging and spatial learning (Fig. 5b), with larger-patched individuals tending to perform better. Pheomelanin-based traits are condition-dependent and share a biosynthetic pathway with glutathione through their mutual reliance on cysteine, linking pigmentation to oxidative state and potentially to neural development (Galván & Alonso-Alvarez 2008; 2009). Under resource limitation, individuals are likely to preferentially allocate resources to critical functions such as neural development and antioxidant defense over secondary sexual characteristics (such as pheomelanin coloration). Yet the strength and direction of any such relationship remain unclear, as pheomelanin-based traits have received little empirical attention as signals of cognitive performance (Galván & Møller 2011). Our findings provide some insight on this point. Overall, we found that cap patch characteristics were associated with performance on some cognitive tasks but not others, and not always in the same direction. Together, these results indicate that the redness and area of the cap patch may be associated with either higher or lower performance, depending on the task presented.

Our two metrics, redness and patch area, were highly correlated. Both patch area and redness may be influenced by shared hormonal mechanisms. For example, testosterone has been shown to regulate the expression of both melanin-based coloration and ornament size in birds (Jawor & McGlothlin 2008, Peters et al. 2004), so if testosterone levels vary, this could simultaneously enhance both size and color intensity of an ornament. Additionally, given that investment in ornamental traits often reflects overall body condition, which influences both feather development and pigment availability (Hill & Montgomerie 1994, Griggio et al. 2009), only individuals in better condition may develop both redder and larger cap patches. Although we measured each patch five times and used the average as the color to mediate potential variation due to placement when measuring, it is important to note that some swamp sparrow patches have black feathers integrated with red and we cannot eliminate the possibility that these black feathers may have influenced redness score. Furthermore, environmental variables (e.g., diet, food availability, weather, parasite load, etc.) likely affect patch size and redness differently (Roulin 2004, Isaksson et al. 2011). Our findings suggest that even if area and redness are regulated by distinct pathways, their observed correlation may arise from shared physiological influences or condition-dependent allocation, highlighting the interplay between ornamental trait expression and individual quality.

Performance on the color association and color reversal tasks was highly correlated, but there were no other significant correlations among other tasks. This replicates the findings of DuBois et al. (2018) and is consistent with a modular view of cognition, in which selection acts on specific cognitive abilities in response to a species' ecology and life history (Shettleworth 2010, Krebs et al. 1989). This pattern is less consistent with the idea of a generalized cognitive ability, where performance on one task predicts broader cognitive capacity (Burkart et al. 2017, Seed et al. 2009, Emery & Clayton 2004). The strong

correlation between color association and color reversal, alongside the absence of correlations among the other tasks designed to assess distinct cognitive abilities, suggests that the distinction between general and domain-specific cognition may not be strictly dichotomous. Instead, our findings may reflect a pattern of partial domain-generality, in which some, but not all, cognitive domains share an underlying mechanism or selective pressure, while others remain functionally independent (Shaw et al. 2015, Cauchoix et al. 2018). It is important to emphasize that while these tasks were designed to assess particular cognitive abilities, they are not definitive measures of those abilities. Overall, a key takeaway from the relationships observed across cognitive tasks is the importance of using multiple tasks when evaluating animal cognition.

The lack of correlation on performance across tasks may reflect the distinct behavioral demands each task places on individuals. Like many birds, swamp sparrows occupy structurally complex environments with a dynamic resource base requiring continual adjustment to changing conditions (Greenberg 1989). We found that cap patch redness and area were positively correlated with novel foraging and spatial learning, which may facilitate efficient resource acquisition under changing ecological conditions, potentially conferring fitness advantages in habitats characterized by spatial and temporal variability. Empirical work on exploration–exploitation trade-offs suggests that individuals capable of flexible, novelty-driven foraging are better able to locate and exploit new or unpredictable resources, particularly in heterogeneous environments (Hills et al. 2015). Learning something new often requires suppressing old habits or dominant responses, so inhibitory control has been found to often support novel learning (Munakata et al. 2011, Diamond 2013). However, not only did we find no relationship between the tasks designed to test these two traits, but we also found that one was positively associated (novel foraging) with patch redness, and one was negatively associated (inhibitory control). Existing literature demonstrates that behavioral tendencies such as impulsivity and exploratory behavior are negatively linked with inhibitory control (Maclean et al. 2014). We found that redder individuals perform worse on the inhibitory control task but better on novel foraging. Performance on novel foraging tasks is often linked with risk-taking behavior or boldness; thus, it is not surprising that we found that redness, which was positively related to novel foraging, was negatively related to inhibitory control. Lastly, we found that color reversal was also positively associated with redness. Given that the task designed to test color reversal required un-learning of the original color association task, and that novel foraging has positive associations with redness, this may provide further support for partial domain-generality and may elucidate some of our results.

Our findings are correlational and do not demonstrate causal relationships between ornamentation and cognition. The observed associations may instead reflect shared underlying factors such as resource availability, past experiences and biases, or shared behavioral syndromes (i.e. “personality traits”), for example. Although our battery of tasks was based on previous studies with this species and the closely related song sparrow (Anderson et al. 2017, Dubois et al. 2017, Soha et al. 2019), it may not fully capture the cognitive traits most relevant to fitness in swamp sparrows. More specifically, tasks designed to assess complex behavioral phenomena such as novel foraging, spatial learning, and inhibitory control as we do here are unlikely to be underpinned by one single cognitive ability. In order to make claims about

cognition, future studies should ideally be able to specify what abilities underpin these more complex behaviors and assess them directly (Rowe and Healy 2013). Additionally, the captive setting—particularly the absence of natural social and territorial behaviors—may have influenced motivation and performance. While cap patch redness has been linked to reproductive success (Olsen et al. 2008), this does not imply a direct relationship with any cognitive ability. An alternative possibility is that cap patch redness may be indicative instead of other traits, such as aggressive ability, that may directly influence reproductive success. Overall, these results highlight the complexity of links between ornamental traits and performance on cognitive tasks and suggest that more integrative approaches will be necessary to better understand these relationships.

Conclusions

In conclusion, we found that performance across a battery of five cognitive tests did not correlate with each other except for the color association and color reversal tasks. Thus, our findings suggest that cognition is not necessarily entirely domain specific. We also found the two color metrics we measured, cap patch area and redness to be highly correlated, meaning that individuals with bigger patches also had redder patches on average. Finally, we found that there were positive associations with cap patch area and performance on the novel foraging and spatial learning tasks, which suggests that cap patch may serve as a signal of these specific cognitive traits. However, we also found negative associations between redness and inhibitory control as well as between patch area and color reversal.

Declarations

Conflict of Interest Statement:

The authors declare no conflicts of interest.

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Ethical Note:

All procedures were approved under Duke University Animal Care and Use protocols A260-19-12 and A182-22-10, and University of Pittsburgh Animal Care and Use protocol IS00019264, as well as US federal collecting permit SCCL 672712 and Pennsylvania state collecting permit 51755. All guidelines for the treatment of animals in behavioral research of the Animal Behavior Society and the Association for

the Study of Animal Behavior were followed. We carefully observed all trials and birds exhibited no signs of stress during testing. In between trials, we housed and cared for individuals using standard operating procedures approved by the Duke University Division of Laboratory Animal Resources and designed to maximize health and minimize potential stress of captivity. After behavioral testing was complete, individuals were released at the site of capture during a subsequent field season, after peak breeding season to avoid undue aggression when released, but about six weeks before the onset of fall migration to give individuals time to re-acclimate to the wild before migrating.

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Figures



Figure 1

Image of four different adult male swamp sparrows illustrating variation in cap patch area and/or redness.

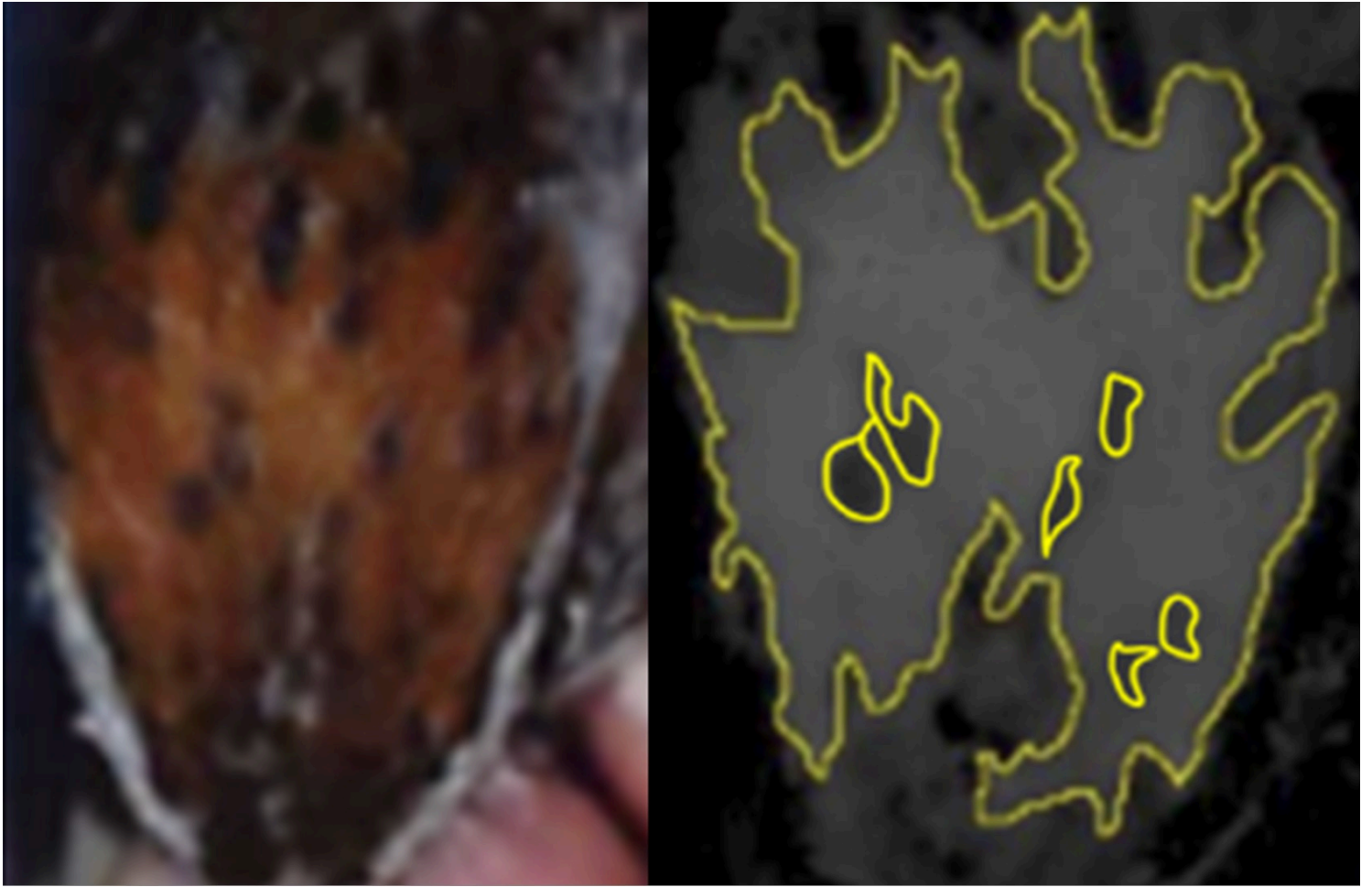


Figure 2

Example image used for quantifying cap patch area. (Left) Photograph of head cap patch. (Right) the red channel of the photo on the left, with the area of the head cap patch traced in yellow

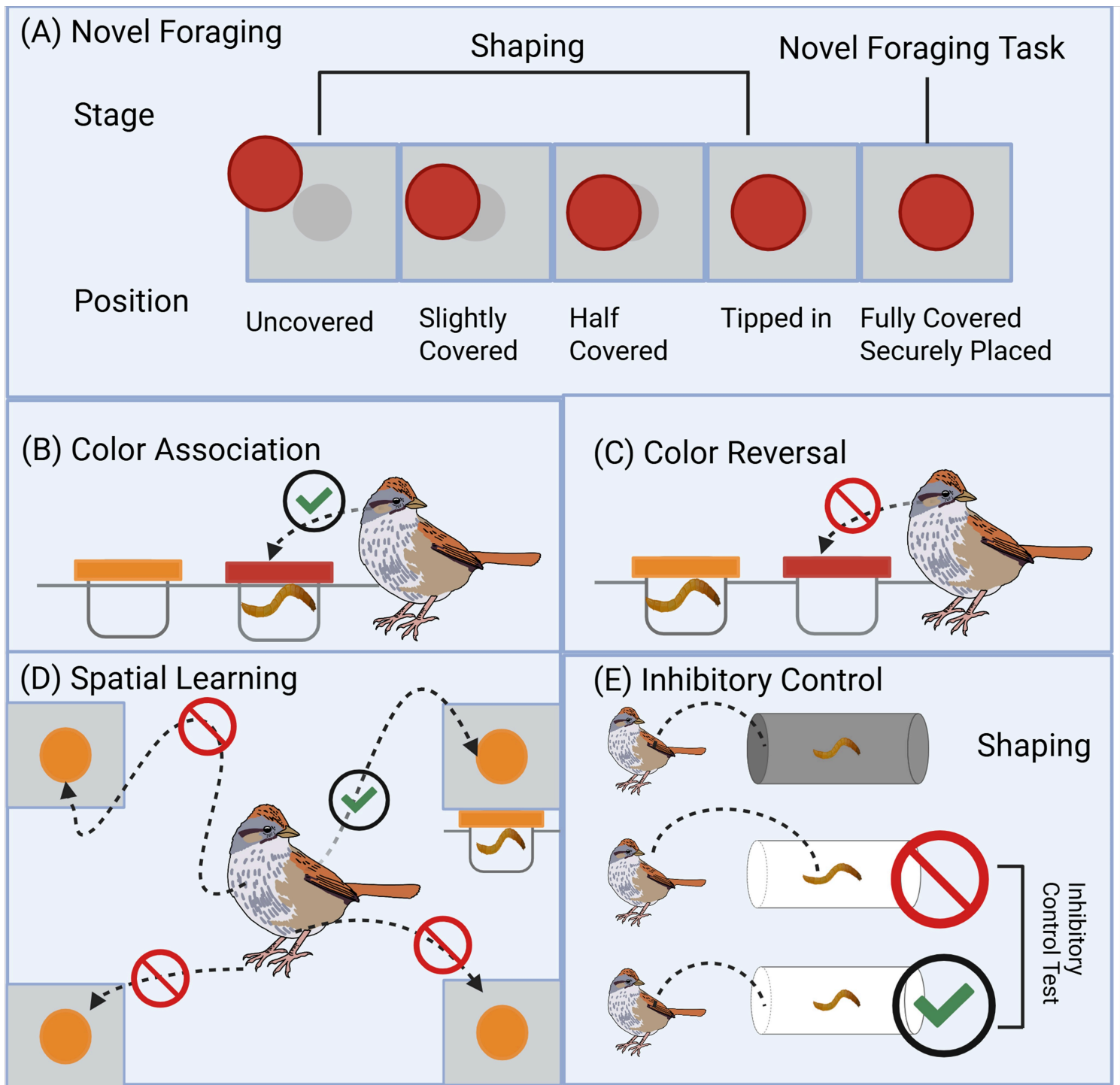


Figure 3

Graphic representation of each of the five tests. (A) Novel Foraging – individuals learned to flip a chip covering a well to access a food reward (mealworm) underneath (B) color association – individuals learned that only a specific colored chip was associated with a food reward and (C) color reversal where the originally unrewarded color became rewarded (D) spatial learning – individuals had to learn of the four corners of their enclosure, what corner was baited with a food reward regardless of what route they took as long as they visited the baited well first and (e) inhibitory control – individuals learned that they had to go around a clear cylinder to receive food reward, even though food reward was visible.

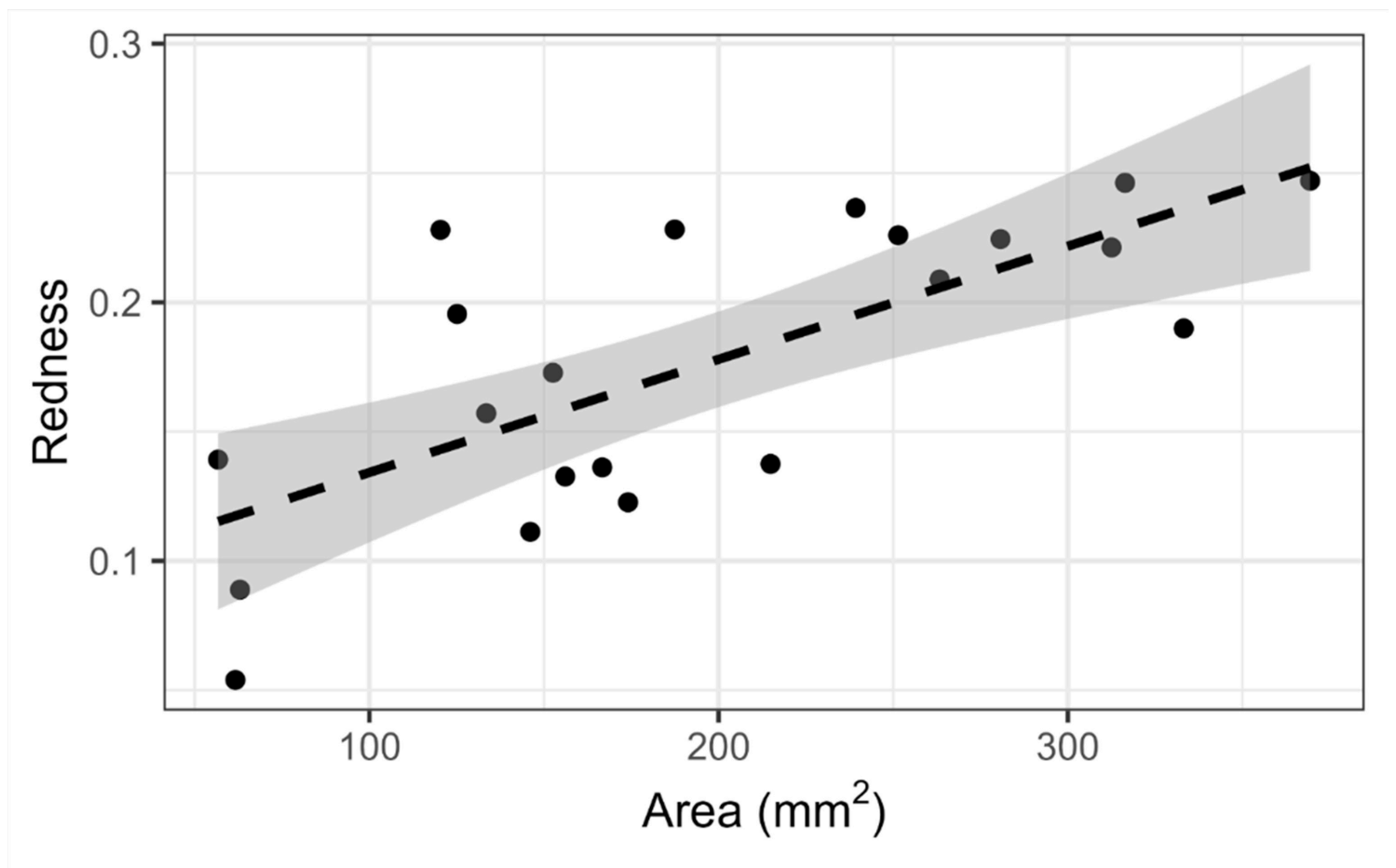


Figure 4

Relationship between cap patch area and redness score. The line represents the fit of a significant linear regression model.

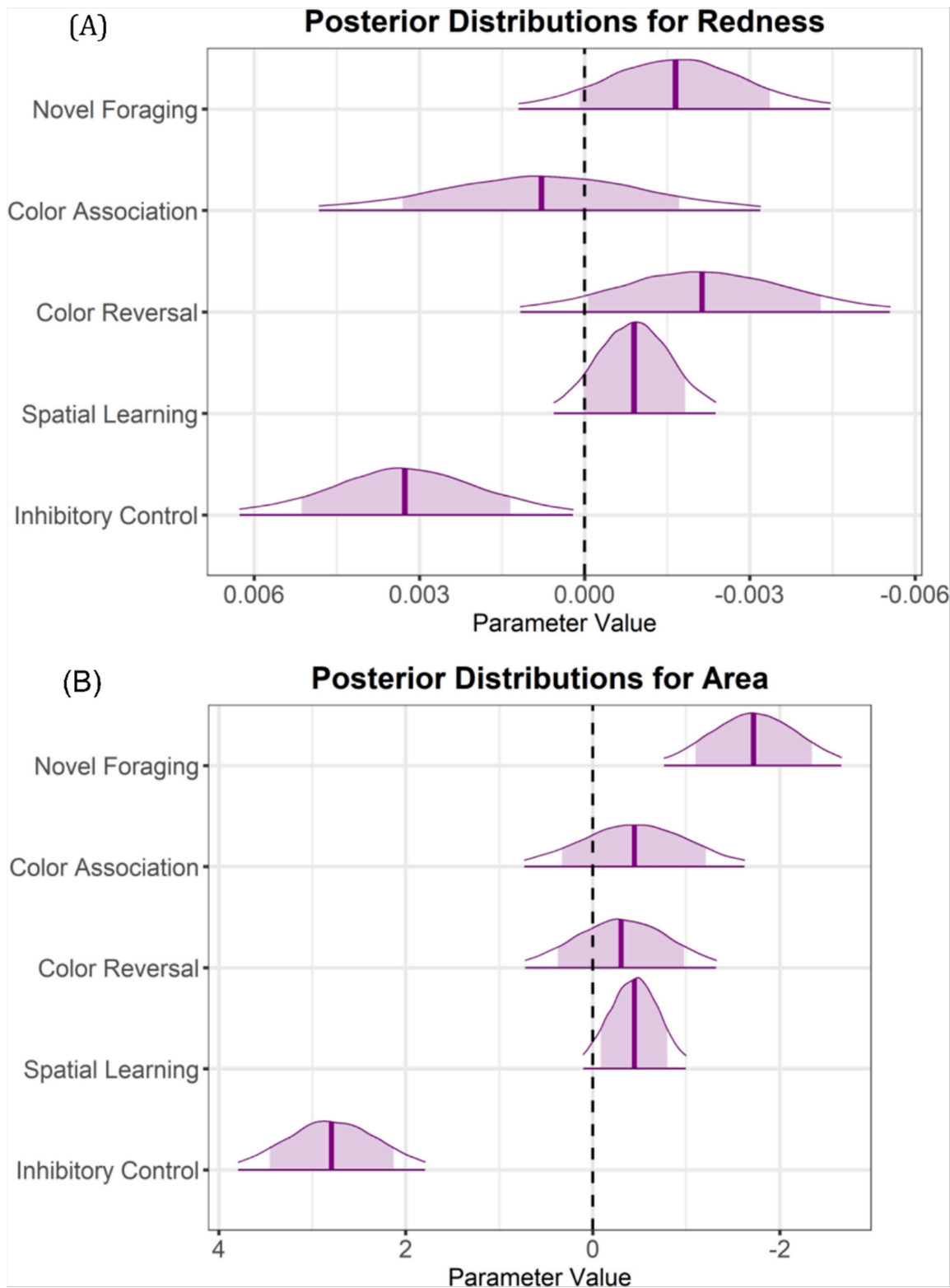


Figure 5

Posterior distributions for models testing if crown patch (A) redness and (B) area are associated with cognitive test scores. The solid pink curve shows the posterior density; the solid pink vertical line marks the posterior median. The pink shaded region indicates the 95% highest density interval (HDI). The dashed vertical line at zero represents the null hypothesis value. Significant relationships are those that have no credible intervals overlapping with zero. It is important to note that higher scores on cognitive

tasks suggest individuals take longer to solve the task, and therefore higher scores suggest negative associations. Parameter values (x-axis) differ in A versus B given variation in scale of measurements: for area (mm^2) versus redness.