



Feather coloration decreases over time in captive Swamp Sparrows

Danae Diaz Wong¹ · Sönke Johnsen¹ · Stephen Nowicki¹

Received: 30 December 2025 / Revised: 24 August 2026 / Accepted: 13 September 2026
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Abstract

Plumage coloration functions as an important visual signal in many avian species, yet the effects of captivity on pheomelanin-based ornaments continue to be poorly understood. In this study, we examined the variation in redness of the cap patch in wild-caught Swamp Sparrows (*Melospiza georgiana*) held in captivity for a year. Reflectance spectra were measured first at capture in spring 2021 (May) and then in August 2022 (after one full and one partial molt). Our results revealed a significant decline in cap patch redness. However, individual rankings did not significantly shift. These findings suggest that captivity may alter ornamentation while still preserving relative differences among individuals, which is an important consideration for studies aiming to release wild birds that have been held in captivity.

Keywords Captivity · Cognition · Color · Visual signaling

Zusammenfassung

Die Gefiederfärbung von in Gefangenschaft gehaltenen Sumpfsammern nimmt mit der Zeit ab.

Die Gefiederfärbung dient bei vielen Vogelarten als wichtiges visuelles Signal, doch die Auswirkungen der Gefangenschaft auf pheomelanin-basierte Ornamente sind nach wie vor kaum erforscht. In dieser Studie untersuchten wir die Variation der Rötung des Scheitelflecks bei wild gefangenen Sumpfsammern (*Melospiza georgiana*), die ein Jahr lang in Gefangenschaft gehalten wurden. Die Reflexionsspektren wurden zunächst beim Fang im Frühjahr 2021 (Mai) und anschließend im August 2022 (nach einer vollständigen und einer teilweisen Mauser) gemessen. Unsere Ergebnisse zeigten einen signifikanten Rückgang der Rötung des Scheitelflecks. Die Rangordnung der einzelnen Vögel verschob sich jedoch nicht signifikant. Diese Ergebnisse deuten darauf hin, dass die Gefangenschaft zwar die Ornamentierung verändern kann, die relativen Unterschiede zwischen den Individuen jedoch erhalten bleiben. Dies ist ein wichtiger Aspekt für Studien, die auf die Auswilderung von in Gefangenschaft gehaltenen Wildvögeln abzielen.

Introduction

Plumage coloration is an important social and sexual signal in birds, reflecting both individual condition and environmental context. Both carotenoid- and melanin-based colorations are suggested to reflect the underlying condition (Weaver et al. 2017), although the mechanisms that link physiology to signal expression differ between pigment types. Carotenoid-based coloration in birds depends on dietary access to carotenoids and their metabolic conversion

to forms involved in pigmentation. Melanin, by contrast, is synthesized endogenously and variation in melanin-based coloration is frequently associated with oxidative stress, hormone profiles, and overall metabolic capacity (Jawor and Breitwisch 2003; McGraw 2008). Melanin-based coloration can be found in two forms: eumelanin and pheomelanin. Pheomelanin-based coloration is particularly interesting because pheomelanin synthesis (as opposed to eumelanin) is linked to processes that mitigate oxidative damage, such that variation in pheomelanin-based ornamentation may reflect an individual's ability to manage intracellular damage (Galván and Solano 2016).

Because plumage coloration can be sensitive to environmental conditions, understanding how captivity influences its expression is important for assessing signal plasticity. Holding wild-born birds in captivity through one or more

Communicated by I. Maggini.

✉ Danae Diaz Wong
dmd76@duke.edu

¹ Duke University, Durham, NC, USA

molt cycles provides a controlled way to examine these changes (Doucet et al. 2012). Captivity reduces predation risk, stabilizes food availability, and often improves survival relative to free-living conspecifics (e.g., Fischer and Romero 2019). Such changes could, in theory, enhance color expression by alleviating environmental stressors and improving nutritional status. Indeed, captive conditions have been shown to increase reproductive output, extend lifespan, and improve body condition in some bird species (Calisi and Bentley 2009). On the other hand, the reduced selective pressure of captivity might therefore lessen physiological constraints that maintain variation in coloration, potentially leading to a decrease in signal intensity or a decrease in overall signal variation across individuals.

Swamp Sparrows (*Melospiza georgiana*) exhibit a rust-colored pheomelanin-based cap patch that varies in size and redness, and that has been suggested to function in social signaling (Olsen et al. 2008). This species thus provides an opportunity to explore how captivity alters the expression of a socially relevant ornamental trait. By tracking cap coloration in wild-caught individuals housed in captivity, we assess how captive conditions may influence ornamental traits corresponding to changes from their natural environment and condition.

We measured the spectral reflectance of male Swamp Sparrows' cap patches when initially captured and approximately 1 year later. Individuals were originally captured in the spring of 2021. Between measurements, individuals underwent a complete molt in the fall of 2021 and then a partial molt, including head cap feathers, in late winter/early spring of 2022. Measuring variation of cap patch coloration allowed us to assess whether captivity maintains, enhances, or reduces expression of a prominent pheomelanin-based ornament, providing insight into how environmental context shapes signal expression.

Methods

Male swamp sparrows ($n = 20$) were captured by mist net in Crawford County, PA, USA in May 2021. Color measurements were taken from all individuals on the day they were captured. Males were distinguished from females by the presence of an enlarged cloacal protuberance that is characteristic of males during breeding season. Males were then transferred to Duke University (Durham, NC, USA) for cognitive testing associated with a different project. Captive birds were caged individually ($46 \times 22 \times 26$ cm) in an approved animal housing room. Individuals were kept on a seasonally varying light–dark cycle (following the photoperiod of the location where they were captured) and at an average 24 °C. All housing and care followed established protocols for this species (e.g., Podos et al. 1999). Although

males were housed individually, they were kept in the same room and could both hear and see the other males. Birds were provided with food ad libitum (Kaytee Supreme Canary and Finch Food, Chilton, WI), as well as a cuttlefish bone (as a calcium source) and water, and supplemented with approximately five mealworms three times a week. Individuals were released at their capture location after the study was complete.

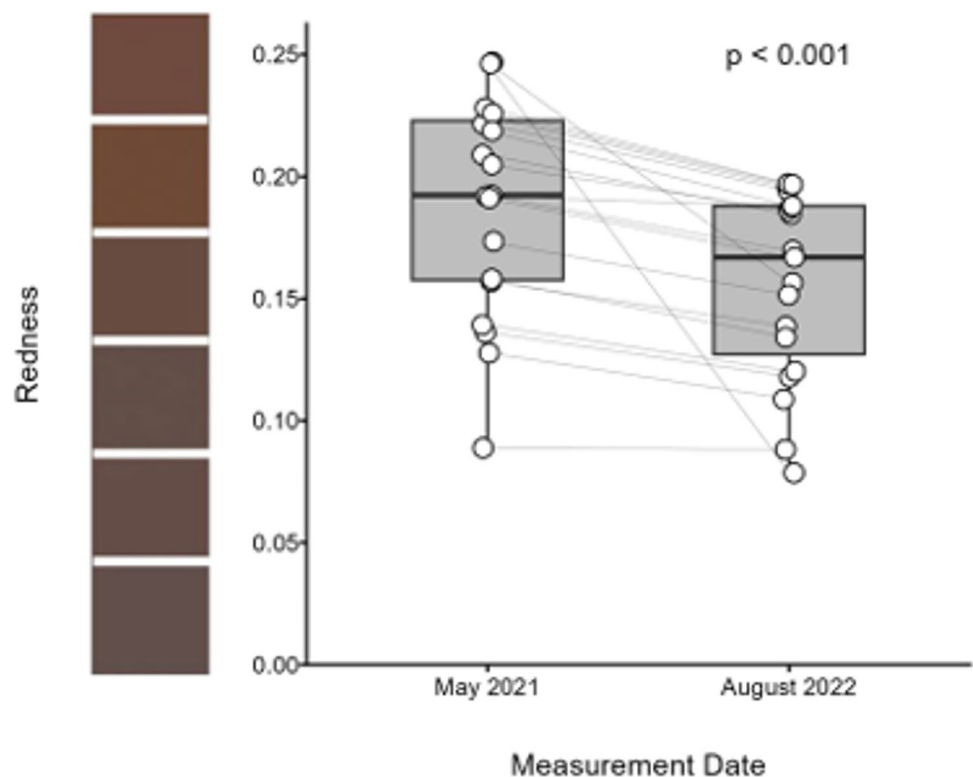
When initially captured in May 2021 and again in August 2022, we made spectral reflectance measurements from a standardized location on each individual's head cap patch (the pheomelanin patch closest to the center of the top of the head) using an integrating sphere with an 8 mm diameter window with a Spectralon insert positioned to narrow the opening to 3 mm (ISP-REF; Ocean Insight Inc.; Dunedin, FL) and a spectrometer (USB-2000; Ocean Insight). Measurements were calibrated with a > 98% diffuse reflectance standard (WS-1; Ocean Insight) and taken over a wavelength range of 400–800 nm. Redness was calculated by averaging redness values over five samples per bird to account for any variation that might have occurred in positioning of the integrating sphere. We used these average spectra to calculate a “redness” score by averaging nominal red (average reflectance over 600–700 nm) and green (average reflectance over 500–600 nm) channels and then calculating $(\text{red} - \text{green}) / (\text{red} + \text{green})$ (Tedore and Johnsen 2016).

We used a Wilcoxon signed-rank test (Conover 1980) to assess whether redness of the cohort significantly differed between the time they were captured and after a year in captivity. We used a Wilcoxon signed-rank test to assess whether cohort redness changed significantly between capture and after 1 year in captivity as well as a Kendall's rank correlation test to determine if individual rankings of redness varied across years, independently of mean color change in the cohort (Conover 1980). All analyses were done using R v4.3.1 (R Core Team 2025).

Results

Of the 20 males captured in May 2021, 19 survived until the following August. These 19 males showed a significant decrease in cap redness over the year of captivity (Wilcoxon signed-rank test, $W = 190$, $p < 0.001$, $r = 0.88$) (Fig. 1). Furthermore, although there were some shifts in rankings, reflectance values upon initial capture and after 1 year in captivity were strongly and positively correlated with each other, indicating that individuals tended to maintain their relative coloration ranking across years (Kendall's $\tau = 0.63$, $T = 139$, $p < 0.001$).

Fig. 1 Redness score differed significantly between years, with individuals becoming less red on average in Year 2 (2022) compared to Year 1 (2021). Color swatches to the left of the y-axis represent how sparrow caps with varying redness values would appear to a human viewer when viewed under a standard D65 illuminant. Box plots show the median (center line), interquartile range (boxes), and 1.5* interquartile range whiskers. Overlaid points represent unique individuals per year, jittered for visibility, and outliers are plotted beyond the whiskers



Discussion

The redness of the sparrows' cap patches decreased on average across individuals over the course of 1 year in captivity (Fig. 1). One might expect that reduced social pressures (such as the absence of mating activity and territory defense) and physiological stressors could allow individuals to allocate more resources toward coloration, but there are countervailing possibilities for why coloration decreased instead. One potential explanation is that the lessened ecological and social stressors of captivity altered the pressures that normally maintain signal intensity. In wild populations, pheomelanin-based traits can function as condition-dependent indicators of oxidative balance, with only individuals capable of managing oxidative stress able to invest heavily in plumage coloration. For example, oxidative stress is thought to constrain the allocation of resources toward pheomelanin synthesis, feather maintenance, and other costly processes (Galván and Solano 2009). If so, high-quality individuals could afford to express larger or more saturated ("redder") ornamental patches, whereas lower-quality individuals cannot. By reducing exposure to ecological challenges such as fluctuating food resources, parasites, or predation risk, captivity may have diminished variation in resistance to oxidative damage across individuals. This reduced stress could, in turn, diminish the advantages of differential signaling, thereby leading to both reduced mean coloration in general, which we

observed through stabilized ranks across years. On the other hand, it is worth noting that these wild-caught individuals are likely to experience human-induced stress upon and following capture. Human-induced stress is introduced through the handling during capture itself, relocation to a novel enclosure, and human presence during husbandry, for example. Although ecological stressors may be reduced in captivity, this novel stressor could independently influence coloration.

Another possibility is that captive diets, while nutritionally sufficient in terms of macronutrients and minerals, may lack specific precursors or cofactors required for optimal pheomelanin synthesis. Pheomelanin production relies on the availability of certain amino acids (e.g., cysteine, tyrosine) and enzymatic activity within the melanogenesis pathway (Hill and McGraw 2006). Even subtle reductions in amino acid availability or metabolic function could alter pigment synthesis and/or deposition. Similarly, artificial diets may not replicate the natural variation in food sources that birds encounter in the wild, potentially constraining pigment production despite otherwise improved caloric intake.

Finally, it is possible that the reduced social and ecological complexity of captive environments changes the functional value of signal maintenance. In the wild, plumage coloration may play a central role in mate attraction or competitive interactions, contexts where the consequences of dull coloration are high. In captivity, where reproductive

opportunities are absent and aggressive encounters are minimized, investment in ornamentation may no longer be beneficial. Instead, individuals may allocate resources toward self-maintenance rather than ornamental traits. Such a shift would be consistent with theoretical predictions that the honesty and elaboration of signals are maintained only under conditions where they provide fitness benefits (Cotton et al. 2004). Throughout their time in captivity, males were housed individually but in the same room. Therefore, although we are unable to eliminate the possibility of such social pressures, as Swamp Sparrow males are antagonistic with or without female presence, it was at the very least significantly reduced.

Our findings illustrate that the expression of a color ornament may be reduced under captive conditions, even when food and other resources are abundant. This pattern underscores the importance of ecological and social contexts in shaping signal expression, and suggests that the links between condition, stress physiology, and ornamentation may be more nuanced than predicted by simple condition-dependence models. Future work should explicitly test the nutritional and physiological mechanisms underlying pheomelanin expression in captivity, as well as assess whether similar declines are observed across other melanin-based or carotenoid-based traits. Additionally, future studies may clarify the proximate basis of our results by comparing captive birds with cohorts of wild birds from particularly productive versus poor years.

Acknowledgements We thank Susan Peters and Jill Soha for their guidance and expertise with the experimental setup, and Katherine Henson, Clara Howell, and Emily Zhou for assistance with bird husbandry and constructive feedback throughout the project. We also thank the Pymatuning Laboratory of Ecology for housing and the use of its facilities while collecting birds, and the Pennsylvania Game Commission for access to field sites.

Data availability The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval All experiments conducted during this study comply with current US law. 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 672712 and Pennsylvania state collecting permit 51755.

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