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Authors: Winters, Caitlin P., and Jawor, Jodie M.

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RESEARCH ARTICLE

Melanin ornament brightness and aggression at the nest in female Northern Cardinals (*Cardinalis cardinalis*)

Caitlin P. Winters[1] and Jodie M. Jawor[1,a]*

[1] University of Southern Mississippi, Department of Biological Sciences, Hattiesburg, Mississippi, USA
[a] Current address: Department of Biology, New Mexico State University, Cruces, New Mexico, USA
* Corresponding author: jjawor@nmsu.edu

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ABSTRACT

Research is increasingly addressing the evolution and use of sexually selected traits in females. One strong area of interest is the display of intrasexual aggression and how female ornaments are used in intrasexual competition. One particular type of ornament focused on for its use in intrasexual aggression in both sexes is the melanin pigmented ornaments. Over the course of 2 breeding seasons in a southeastern Mississippi population of cardinals, we assessed brightness of the melanin face mask plumage ornament in female Northern Cardinals (*Cardinalis cardinalis*) and compared it to behavioral responses during intraspecific simulated nest intrusions (SNIs). All females responded to the SNI, but face mask brightness did not co-vary with the level of aggression shown. Our findings do not support earlier work suggesting that the face mask in female Northern Cardinals is an indicator of aggression at the nest. Potentially, differences in behavior and environmental variables between populations of cardinals could be factors in this difference and deserve further assessment. Future research should investigate other populations of cardinals to fully assess the communicative malleability of this ornament type and different selective pressures on female ornamentation and behavior.

Keywords: female ornamentation, intrasexual aggression, northern cardinals, melanin ornamentation

Brillo de los ornamentos con melanina y agresión en el nido en las hembras de *Cardinalis cardinalis*

RESUMEN

Un mayor número de investigaciones se está enfocando en la evolución y el uso de caracteres seleccionados sexualmente en las hembras. Un área de fuerte interés es el despliegue de agresiones intra-sexuales y cómo los ornamentos de las hembras son usados en la competencia intra-sexual. Un tipo particular de ornamento bajo estudio debido a su uso en la agresión intra-sexual, en ambos sexos, son los ornamentos pigmentados con melanina. En este trabajo, evaluamos durante dos estaciones reproductivas en una población de *Cardinalis cardinalis* del sudeste de Mississippi, el brillo del ornamento con melanina del plumaje de la máscara facial en las hembras de *C. cardinalis* y comparamos esto con las respuestas comportamentales durante simulaciones de intrusiones intra-específicas al nido. Todas las hembras respondieron a las simulaciones de intrusiones intra-específicas al nido, pero el brillo de las máscaras faciales no covarió con el nivel de agresión evidenciado. Nuestros resultados no apoyan trabajos anteriores que sugieren que la máscara facial en las hembras de *C. cardinalis* es un indicador de agresión en el nido. Las diferencias potenciales en comportamiento y en las variables ambientales entre las poblaciones de *C. cardinalis* podrían causar estas diferencias y merecen evaluaciones adicionales. Futuras investigaciones deberían investigar otras poblaciones de *C. cardinalis* para evaluar integralmente la maleabilidad comunicativa de este tipo de ornamento y de diferentes presiones de selección en la ornamentación y en el comportamiento de las hembras.

Palabras clave: agresión intra-sexual, *Cardinalis cardinalis*, ornamentación de la hembra, ornamentación con melanina

INTRODUCTION

Sexually selected traits have been widely examined in males for a variety of species (Andersson 1994). Initially, less attention was given to sexually selected traits in females, although this has changed with time (Amundsen 2000, Amundsen and Pärn 2006, LeBas 2006, Kraaijeveld et al. 2007, Clutton-Brock 2009). As in males, females have a wide variety of sexually selected traits, for example colorful plumage ornaments and behaviors like song or aggressive displays used in communication and interactions with conspecifics. In many species, female ornaments are not as elaborate as male ornaments. This lack of elaborate ornaments may protect against nest depredation, be linked to females redirecting resources into reproduction, or help females avoid male harassment (Amundsen and Pärn 2006,

Dale et al. 2015, Hosken et al. 2016). Female ornaments, however, even when less elaborate, still convey information to conspecifics.

An increasing number of studies have been conducted to understand how ornaments convey information on aspects of condition, behavior, and individual quality in females (Amundsen 2000, Amundsen and Pärn 2006, Clutton-Brock 2009, Nordeide et al. 2013, Hosken et al. 2016). For example, plumage ornament expression has been found to positively co-vary with age (Bitton et al. 2008, Hegyi et al. 2008, Wiebe and Vitousek 2015) and various condition measures, including immune response (Piersma et al. 2001, Hanssen et al. 2006, Gladbach et al. 2010, Grindstaff et al. 2012, Laczi et al. 2013, Lumpkin et al. 2014). In addition, female dominance status (Murphy et al. 2009a, 2009b, Crowhurst et al. 2012) and reproductive behavior and success (Bókony and Liker 2005, Remeš et al. 2011, Midamegbe et al. 2013, Remeš and Matysioková 2013) co-vary positively with ornamentation. In a number of species, males have been shown to prefer more ornamented females as mates (Pilastro et al. 2003, Griggio et al. 2005, 2009, Torres and Velando 2005, Bitton et al. 2008, Chan et al. 2009, Rowe and Weatherhead 2011, but see Wolf et al. 2004). A widely studied behavior associated with ornamentation (in both sexes) is intrasexual aggression and how ornaments convey information on competitive ability.

Among bird species, females display intrasexual aggression for a wide variety of reasons, and becoming dominant over conspecifics can yield significant benefits. Females may be aggressive over mating opportunities and mate guarding (Jonart et al. 2007, Pärn et al. 2008, Papadopoulos et al. 2009), territorial ownership (Koloff and Mennill 2011, Muck and Goymann 2011, Lloyd-Jones and Briskie 2016), and access to breeding resources (Jawor et al. 2006, Cain and Ketterson 2012, Grønstøl et al. 2014, Moreno 2015). For example, Tree Swallow (*Tachycineta bicolor*) studies have shown that females are aggressive over access to limited nesting resources (nest cavities) and that more aggressive females are better at acquiring this limited resource (Rosvall 2008, 2011a, 2008b). In Red Junglefowl (*Gallus gallus spadiceus*), older females and females with greater social experience were more likely to be dominant in flocks, and those individuals showing greater levels of aggressive behavior were more likely to become dominant (Kim and Zuk 2000). Studies investigating aggression and ornamentation have shown that more ornamented females are often more behaviorally aggressive and become dominant (Murphy et al. 2009a, 2009b, Baldauf et al. 2011, Midamegbe et al. 2011, Beck 2013). Crowhurst et al. (2012) showed that Diamond Firetail (*Stagonopleura guttata*) females with more white spots on their sides were dominant at food resources, and Moreno (2015) showed that more ornamented European Pied Flycatcher (*Ficedula hypoleuca*) females are more successful at defending nest cavities. Together, findings such as these demonstrate that individuals showing greater aggressive behavior gain benefits and that ornaments can function in aggressive interactions and communication in females.

Melanin ornaments (e.g., black or gray colors) have been strongly associated with conveying information concerning aggressive behavior (reviewed in Jawor and Breitwisch 2003, Senar 2006), although they can also convey information on condition (Piault et al. 2012, Guindre-Parker and Love 2014, Wiebe and Vitousek 2015). In both sexes, larger and darker, melanin ornaments (specifically eumelanic or black-colored ornaments) are associated with higher social dominance, often achieved by a demonstration of greater aggressive behavior (reviewed in Jawor and Breitwisch 2003, Senar 2006). Here, we investigated how a melanin-pigmented plumage ornament, the face mask, co-varies with intrasexual aggression in female Northern Cardinals (*Cardinalis cardinalis*). Female cardinals display both intrasexual and intersexual aggression over territories and nesting resources (Jawor et al. 2004, DeVries et al. 2015). In female cardinals, previous work found that face mask expression co-varied with aggressive behavior at the nest (Jawor et al. 2004). Females with a larger and darker face mask tended to be more behaviorally aggressive when faced with a simulated nest intruder (SNI). The assessment system used in Jawor et al. (2004), however, did not separate ornament brightness (how much light is reflected from the ornament) from mask area, but instead blended the 2 into a single scoring system. The amount of light reflected by melanin ornaments influences perceived ornament color and may be linked to the amount of melanin deposited in feathers, as has been shown for carotenoids (McGraw 2006, Montgomerie 2006), and greater pigment deposition in an ornament is often assumed to indicate a higher quality ornament. Additionally, the cells that produce melanin pigments are also responsive to testosterone, the same steroid hormone that can positively influence aggressive behavior, providing a potential physiological link between a communicative ornament and a behavior (Jawor and Breitwisch 2003, McGraw 2006, Bókony et al. 2008). Here, we reevaluated nest defense aggression in the female Northern Cardinal and investigated face mask brightness, specifically by using color reflectance spectrometry, and compared this to behavior shown during SNIs to determine if ornament brightness alone can provide information on aggressive behavior, improving our understanding of how this ornament is used in communication in cardinals.

METHODS

Study Site and General Information

This study was conducted during 2 breeding seasons in 2010 and 2013 at the Lake Thoreau Environmental

Education and Research Center (31°25′30″N, 89°25′30″W), owned and maintained by the University of Southern Mississippi (USM), Hattiesburg, Mississippi, USA. This area is a 131 ac longleaf pine (*Pinus palustris*) forest with understory growth of various herbaceous species. Adult females, all at least 1 year of age but exact ages were unknown, included in the study were captured passively during the nonbreeding and early breeding seasons at food-baited mist nets and walk-in traps. All captured birds were banded with a U.S. Fish and Wildlife Service (USFWS) numbered band and a series of 3 plastic color bands in unique combinations to allow later identification. Individuals had melanin ornamentation measured (see below) and were released at their point of capture. During the early breeding season, territory boundaries and pairs were identified by observation of color-banded individuals. With the initiation of breeding (late March), we searched for nests daily and, once ownership of the nest was confirmed by color band identification and females had been incubating a completed clutch for 3 days, performed an SNI. We performed SNIs after clutches were completed and incubation had begun to avoid nest abandonment, which can occur if females are agitated at the nest prior to and during egg laying or on the first day of incubation (J.M.J. personal observation). Birds were captured and banded under USFWS Bird Banding Permit (#23479); Mississippi Department of Wildlife, Fisheries, and Parks Scientific Collecting Permit (#0319131); and USM's Institutional Animal Care and Use Committee approval (#08081401).

Simulated Nest Intrusions (SNIs)

Intrasexual aggressive behavior was assessed using an SNI based on methods described in Jawor et al. (2004) and modified slightly based on DeVries et al. (2015). On the day of SNI assessment, between 0600 and 1000 hr, a female Northern Cardinal decoy (mounted in a perching posture) was placed 1 m from the nest of a focal female after the focal female had left for a break in incubation. Nests were observed for female incubation behavior prior to SNIs, and females were allowed to leave the nest on their own initiative before setting up the decoy.

The SNI trial began once the female located the decoy and lasted either 5 min or until the female had struck the decoy. Focal females were given a single behavioral score of 1 to 5 representing a composite of behavior typically seen during aggressive interactions and corresponding to the highest level of aggression shown. A score of 1 was assigned if the focal female returned to the nest but stayed more than 15 m from the nest and showed no aggressive behavior, a score of 2 if the focal female came within 5–15 m of the decoy and displayed no aggressive behavior, a score of 3 if the focal female came within 5 m of the decoy but displayed no aggressive behavior, a score of 4 if the focal female came within 5 m of the decoy and displayed aggressive behavior (e.g., depressed crest, lowered body, song production, wing opening and shivering, flying over the model without striking it, and rapid chipping), and a score of 5 if the focal female struck the decoy. For analyses, females received a single score corresponding to the highest level of aggressive behavior observed during the trial. All females returned to their nests to resume incubation; therefore, the lowest possible score a female could receive was 1.

Ornament Measurement and Analysis

When females were captured for banding, the melanin face mask of females was measured for brightness (e.g., amount of reflected light) using an Ocean Optics USB4000 color reflectance spectrometer with a UV-VIS (215–2000 nm) deuterium tungsten halogen light source (Ocean Optics DH-2000) and a reflection/backscattering measurement probe (T200-RT, 250–800 nm) outfitted with an aluminum shield that held the probe 1 cm from the surface of the feathers at a 45° angle and shielded the probe from outside light (following J. Endler personal communication). The spectrometer was calibrated before measurements using a white Ocean Optics diffuse reflectance standard (WS-1) and a black photographic reference (Kodak). Brightness was averaged across all wavelengths from 300 to 700 nm using SpectraSuite (Montgomerie 2006). Spectra for eumelanic ornaments are flat in shape, but they can differ in the measure of reflected light (brightness); more light reflected is a lighter color, more grayish than black, and less light reflected is a darker color, closer to full black. Face mask brightness was determined after SNIs had occurred.

Additionally, while birds were in hand, a mask score was determined following methods described in Jawor et al. (2004); mask scores ranged from 1 to 5, with a higher number indicating both a larger and darker mask. A score of 1 represents a very light grey mask that extended from the bill 1–3 mm. Increasing mask scores correspond to a progressively larger and darker mask, with a score of 2 extending just to the eyes and 3–4 mm below the bill but light grey in color; a score of 3 extending to behind the eyes and 5 mm below the bill and medium grey in color; a score of 4 extending to behind the eyes and 5 mm or more below the bill and a dark grey in color; and a score of 5 extending behind the eyes and 5 mm below the bill and black in color. Mask score was compared to mask brightness and to behavior shown during SNIs. Mask scores and plumage brightness were all determined by one researcher (C.P.W.).

Statistical Analyses

Statistical analyses were conducted using IBM SPSS Statistics 20. Data were not normally distributed, and thus

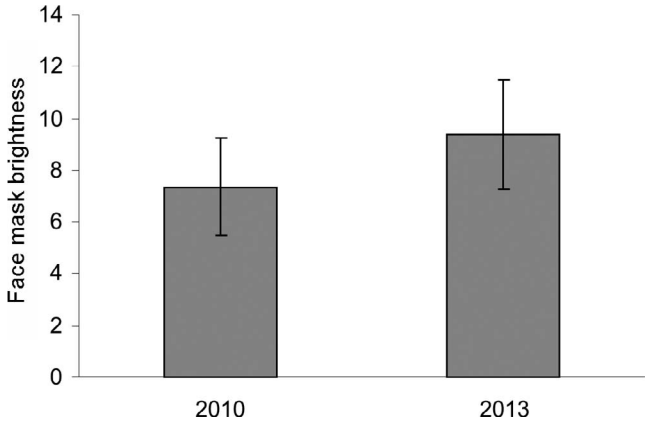

FIGURE 1. Average face mask brightness in female Northern Cardinals in 2010 ($n = 13$) and 2013 ($n = 10$). Higher numbers equate to greater intensity, which means more light reflected and an overall brighter color (in the case of melanin a lighter color).

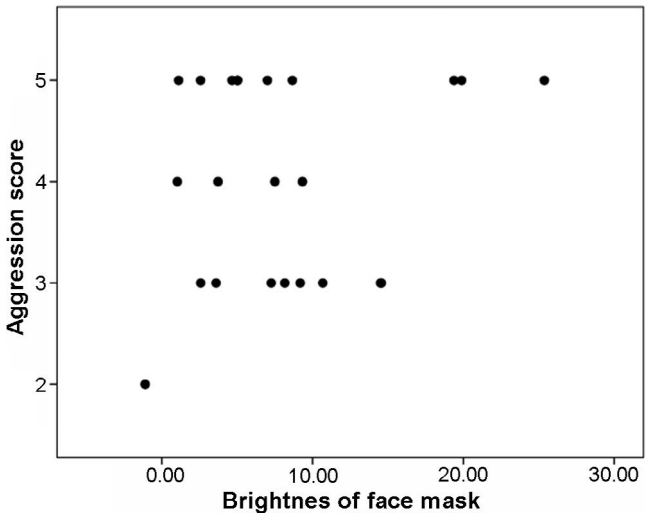

FIGURE 2. Aggression score and face mask brightness in female Northern Cardinals. Lower aggression scores correspond to a less aggressive response; lower brightness values correspond to darker face mask coloration.

nonparametric tests were used as necessary. Although this study was conducted over 2 years, females appear in the data set only once (one female assessed in 2010 and 2013 had data from 1 year excluded; which year was excluded was determined randomly), and the ornaments a female possessed in the year she was behaviorally assessed were used in analyses of behavior collected from that same year. No female was assessed for ornaments in one year and then assessed for behavior in a different year (e.g., assessed for behavior in 2010 and ornaments assessed in 2013).

We used independent sample *t*-tests to investigate differences in ornament brightness or behavior between the years of the study; no significant differences were discovered between years (see results). Because both ornament expressions (brightness and mask score) and aggression displayed were not normally distributed, Spearman rank correlations were used to compare face mask brightness to aggression score, face mask score to aggression score, and face mask brightness to face mask score.

RESULTS

We assessed 23 females for intrasexual aggression during SNIs and for face mask expression ($n = 13$ in 2010; $n = 10$ in 2013). All females had some level of melanin face mask expression; face masks were quite variable among females. There were no differences in face mask brightness between the 2 years of this study (independent samples *t*-test: $t = 0.72$, df = 21, $P = 0.48$; Figure 1).

Aggressive responses during SNIs tended to be category 3 or higher (e.g., females coming within 5 m of the decoy, some either displaying aggressive postures to the decoy or striking it). There was no difference between years in the highest level of aggression shown by females during SNIs (independent samples *t*-test: $t < 0.0001$, df = 21, $P = 1.00$). When comparing the aggression score achieved by a female with face mask brightness, no significant association was found between ornament brightness and aggressive behavior shown (Spearman rank correlation: $r_s = 0.078$, $P = 0.72$, $n = 23$; Figure 2).

Mask brightness, assessed via color reflectance spectrometer, did not co-vary with mask score, a measure determined by visual assessment of color and area simultaneously (Spearman rank correlation: $r_s = -0.214$, $P = 0.40$, $n = 23$). Mask score did not co-vary with the level of aggression shown by females during SNIs ($r_s = -0.133$, $P = 0.66$, $n = 23$).

DISCUSSION

Our results show that the brightness of the melanin-pigmented face mask plumage ornament in Northern Cardinal females in a southeastern Mississippi population did not seem to co-vary with behavior shown during a simulated nest intrusion. Additionally, we compared aggression to the previously developed mask scoring system for female cardinals (Jawor et al. 2004) and found neither co-variation between mask scores and aggressive behavior in this population nor co-variation between mask score and mask brightness. Initially, we attempted to interpret earlier findings where both a larger and darker face mask (assessed in a simultaneous score) was found to indicate aggressive behavior at the nest to determine whether any one component of the ornament was influential. We focused on brightness of the

ornament because this trait could indicate pigment deposition, and typically ornaments with greater pigment deposition are considered higher quality ornaments displayed by high quality individuals. Our findings did not support earlier reports from Jawor et al. (2004) of a northern population of Northern Cardinal (Ohio), where females with a larger and darker face mask (measures combined into a single score) showed higher levels of aggression toward simulated nest intruders. Using the same scoring system in the current study, we saw no indication that the mask score co-varied with aggressive behavior. Several factors, behavioral and ecological, could have influenced the outcomes observed here and led to the differences with previous research.

In the Ohio population of Northern Cardinal (roughly 1,198 km from current study population), initially investigated for aggressive behavior at the nest (Jawor et al. 2004), intraspecific brood parasitism was identified through genetic analyses (Linville 1997). Additionally, opportunistic behavioral observations occurred in the Ohio population of females approaching nests that were not theirs only to be attacked and chased by the actual nest-owning female (J.M.J. personal observation). There is little evidence that the intraspecific brood parasitism identified in the Ohio population is occurring in the Mississippi population studied here (C.P.W. and J.M.J. personal observation). For a different study in Mississippi, both authors completed nest watches while focal females were laying eggs, and eggs were marked for laying order immediately after they were laid (Winters 2011). In all of these observations, we had no female at a nest that was not her own, and we had no eggs removed or added after they were marked. This apparent lack of intraspecific brood parasitism in this southern population would need to be confirmed with appropriate genetic analyses, but it suggests a population difference in this particular behavior. Potentially, the lack of brood parasitism has led to no selective pressure for an ornament that advertises how aggressive a female will be concerning the defense of her nest and its contents. Alternatively, the face mask of female cardinals could still be a signal of aggressive intent and behavior, but in this southern population it may not be used in a nest defense context. Female cardinals participate with their mate in territory defense, aggressively attacking both male and female territory intruders (DeVries 2013). This ornament is possibly used exclusively in territorial aggression and not in maternally related aggression in the Mississippi population under study here. Future assessment of territorial aggression and ornamentation in females would allow this distinction to be made.

Environmental differences exist between the populations of cardinals assessed here and in Jawor et al. (2004) that could also impact the ornament/behavior association. Individuals in the Mississippi population defend territories that appear larger than in the Ohio population assessed in Jawor et al. (2004), and nesting habitat appears to be more abundant in Mississippi compared to Ohio, where land clearing has occurred to a greater extent (J.M.J. personal observation.). This finding suggests that different local environmental and selective pressures may be affecting these populations. Knell (2009) showed that when population density is increased by reduced habitat availability, aggressive interactions are more likely, and individuals showing more aggressive behavior can benefit from being able to acquire and hold onto limited resources. Potentially, where female cardinals have less suitable habitat for nesting (e.g., Ohio population) and population density is concentrated in smaller areas of high habitat quality, more aggression is displayed to acquire and defend the limited nesting resources available, leading to the display of an ornament communicating aggressive ability in defending nesting resources and nests. Coupled with potential nest parasitism, this may be a stronger combination of selective factors to facilitate the linking of an ornament to aggressive nest defense behavior in the Ohio population. Studies designed to test behavior and ornamentation in disparate cardinal populations simultaneously could further determine this possibility.

The potential geographic variation suggested here is not unusual because in a number of species with broad geographic ranges, such as the Northern Cardinal (Halkin and Linville 1999), variation in ornament expression and information content has been found between populations (Roulin et al. 2009, Holand et al. 2011, Dey et al. 2012, Simpson et al. 2015, Argüelles-Ticó et al. 2016). For example, in the Common Yellowthroat (*Geothlypis trichas*), ornaments that are the focus of mate choice and that co-vary with condition and behavior in males vary between populations (Thusius et al. 2001, Dunn et al. 2010, Freeman-Gallent et al. 2010, Whittingham et al. 2015). In some populations of the Common Yellowthroat, the yellow bib on the throat of males is the focus of choice, whereas in others it is the black face mask; similar measures of quality co-vary with these different ornaments between populations. In widespread populations of the Barn Swallow (*Hirundo rustica rustica* in Europe, *H. r. erythrogaster* in North America, and *H. r. gutturalis* in Japan), variation exists in what ornaments seem to be the focus of mate choice and sexual selection in both sexes (Safran and McGraw 2004, Aparicio et al. 2012, Hasegawa and Arai 2013). Clearly, population variation can exist in ornament expression, and local selective factors will impact how and whether ornaments convey information and are used in communication; therefore,

variation in findings between this current study and Jawor et al. (2004) may represent normal ornament variation possible in a wide-spread species like the Northern Cardinal.

Two potential impacts on aggressive behavior not assessed here are body size and condition. Larger and/or individuals in better physical condition may be more likely to initiate more aggressive responses to intruders, either real or simulated, and may have a better chance at winning these interactions. In the Northern Cardinal past work has found that carotenoid-based plumage ornaments can indicate body size and condition (Jawor et al. 2004, Jawor and Breitwisch 2004); however, this has not been the case for melanin-based ornaments. Furthermore, neither size nor condition has been found to covary with hormone production (Jawor 2007, DeVries et al. 2011), territory and nest defense (DeVries et al. 2012, 2015), or parental care behavior (Jawor et al. 2004, Jawor and Breitwisch 2004, DeVries and Jawor 2013) in the Northern Cardinal. Previous findings concerning condition, size, and behavior are from both the current study population in Mississippi and the Ohio population previously studied and suggest that body size and condition may not play a strong factor in aggressive behavior in this species. Future studies with Northern Cardinals should investigate more aspects of behavior, ornamentation, body size, and physiological condition between populations, thus elucidating the possibility that populations of this wide-spread species are locally adapted and varied in ornament expression and what those adaptations communicate.

In conclusion, we found that Northern Cardinal females in a southeastern Mississippi population did not show covariation between aspects of melanin coloration and aggression. Reduced nesting habitat availability and the occurrence of brood parasitism in northern populations of this species may have selected for an ornament conveying information on competitive ability and/or nest defense motivation vs. southern populations where nesting habitat is more abundant and nest parasitism may be lower, or even nonexistent. Findings here suggest that melanin ornaments and aggressive behavior could be more malleable in terms of how and why they are expressed, and future work is needed to incorporate multiple levels of physiology and behavior to understand how selection has shaped this ornament–behavior association in the Northern Cardinal and other species with melanin ornamentation.

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Author contributions: C.P.W. and J.M.J conceived the idea, design, method development, and experiment; C.P.W. and J.M.J performed the experiments (collected data); C.P.W. wrote the paper with edits from J.M.J.; J.M.J. contributed materials, resources, and funding.

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