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Research Article

Inter- and intra-individual variation in the feather coloration of American crows

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Avian feathers are remarkably diverse in both form and function. Coloration is among the most studied feature of feathers, but we know relatively little about melanin-based black coloration. Despite many crows (*Corvus* sp.) and other corvids having black feathers that appear uniform to human perception, their feather coloration could play an important role in social communication. We therefore tested whether the coloration of American crow *Corvus brachyrhynchos* feathers varied by age class and sex, two socially relevant variables. Using a visual modeling approach that accounts for the visual system of American crows, we measured the coloration of American crow feathers from museum specimens. We found that feather coloration varied by age class but not sex. Older individuals had feathers with different hue and more ultraviolet than younger crows. Discriminant function analyses correctly categorized individuals into age classes based on feather coloration with high classification success. The coloration of American crow feathers did not vary based on the time since the last molt and replacement, but did vary with the time since the specimen was collected. The visual modeling approach suggests that crows can discriminate among different feather regions. One region with particularly distinctive coloration properties was a facial mask, which could potentially function to minimize eye glare. Our results suggest that feather coloration in American crows (and potentially other seemingly monomorphic corvids) could reflect underlying qualities of those individuals that are important for social communication.

Keywords: corvids, *Corvus brachyrhynchos*, facial mask, melanin, plumage, visual communication

Introduction

Avian plumage provides a remarkably wide variety of adaptive functions (Stettenheim 1976, Terrill and Shultz 2023). From the advent of the dinosaur–avian lineage, feathers likely played a variety of roles beyond flight, including thermoregulation, antipredator defenses, and social communication (Cowen and Lipps 1982, Prum and Brush 2003,

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Dimond et al. 2011, Terrill and Shultz 2023). Feather morphology is similarly diverse, composed of hierarchical modular levels ranging from their molecular composition to their coloration and patterns (Terrill and Shultz 2023). One of the most studied features of feathers is their coloration (Hill and McGraw 2006, Stoddard and Prum 2011).

Feather coloration can be produced by pigmentation, including the deposition of carotenoids, melanins, and other pigments (Bradbury and Vehrencamp 1998, McGraw et al. 2005, Prum 2006). Black, gray, and brown colors are usually produced by melanins which, unlike carotenoids, are endogenously synthesized rather than derived from animals' diet (though can be influenced by it; Britton and Davidowitz 2023). Melanin-based coloration is less studied compared with carotenoid-based coloration (McGraw 2006, Lee et al. 2016). Despite this, melanin-based coloration of feathers has been demonstrated to have many functions, including protection against environmental pollutants (Chatelain et al. 2014), resistance to feather degradation (Bonser 1995), thermoregulation (Margalida et al. 2008), and signaling (McGraw et al. 2005).

The black color of crow *Corvus* sp. feathers and other corvids with black feathers is likely to be melanin-based (McGraw 2006, Lee et al. 2009a, 2009b, Lee et al. 2016). While not all black feathers are produced completely by melanin, black feathers likely contain melanin because no other black pigments are known in birds (McGraw 2006). Furthermore, melanin distribution has been described for the black plumage of large-billed crows *C. macrorhynchos* (Lee et al. 2009a, 2009b). In addition, Poelstra et al. (2013, 2015) have demonstrated how interspecific differences between all black carrion crows *C. corone* and hooded crows *C. cornix* with their grey torso may be influenced by expression differences in the melanogenesis pathway in conjunction with genes controlling positional information.

We still know relatively little about the potential signaling function of melanin-based black plumage coloration in corvids. This may be the case because humans perceive many corvid feathers to be monochromatic at first glance, although we do detect a colorful sheen or iridescence from feathers in some species such as the large-billed crow (Lee et al. 2012, 2016, Maniwa et al. 2025). The black feather coloration does, however, differ among species. While the sympatric large-billed crow and carrion crow in Japan appear to have similar coloration, a colorimetric analysis revealed differences in the coloration of their neck feathers: the neck feathers of large-billed crows have peak wavelengths that are higher than those of carrion crows (Maniwa et al. 2025). Given such inter-specific variation in black feathers, intraspecific variation in color used in social signaling is also a reasonable expectation. Indeed, the coloration of crow feathers in at least some species varies by sex (Lee et al. 2009a, Nam et al. 2016). In large-billed crows, males have feathers with a greater concentration of melanin than females, suggesting that male and female feathers appear differently (Lee et al. 2009a). Feather coloration could also reflect age (Grunst et al. 2014, Nam et al. 2016). In another corvid, the Eurasian magpie *Pica pica*, older individuals have feathers with structural colors that are brighter and more saturated than younger magpies (Nam et al. 2016). These differences may, however, be more or less distinctive to observing corvid conspecifics. We are unaware of any studies that have examined crow feather coloration using visual modeling that accounts for the crow visual system (Troscianko and Stevens 2015).

The American crow *C. brachyrhynchos* is relatively well studied both ecologically and socially (Caffrey et al. 2025). It is a socially complex, long-lived bird, and multiple modes of communication are likely to be important. Despite this, no previous studies have assessed variation in their feather coloration. We therefore examined coloration in American crow feathers to better understand patterns of variation within melanin-based, black plumage. In particular, we hypothesized that feather coloration of American crows would vary by age class and sex. American crows exhibit a cooperative breeding system in which age class and sex are important to roles within groups (Townsend et al. 2009, Caffrey et al. 2025), suggesting that signals conveying this information to conspecifics could be valuable. We had no specific predictions regarding the form or directionality of the feather coloration differences among the age classes or between the sexes, but we expected that individuals of different age classes and different sexes would exhibit distinctive feather coloration or color patterns. We measured reflectance properties (hue VIS, hue UV, saturation, luminance, and glossiness) of American crow feathers from museum specimens and analyzed them using species-specific modeling of animal perception (Troscianko and Stevens 2015). We estimated their age class based on each specimen's date of collection (death), known molt timing for crows (Caffrey et al. 2025), and plumage features such as tail shape.

Material and methods

Museum specimens

We collected and analyzed photographs of museum specimens of American crows in October and November 2023 at the Texas A&M University Biodiversity Research and Teaching Collections. We photographed 28 specimens (16 males, 9 females, and 3 unknown sex) that were primarily from Texas (25-Texas, 2-Oklahoma, and 1-Washington State). The sex of the specimens was determined when the specimens were originally prepared.

Photography collection

We photographed the specimens using standard methods that allowed us to measure feather coloration in both UV and human-visible spectra from the photographs (Stevens et al. 2007, Troscianko and Stevens 2015). We used a full spectrum camera (Sony a7 II Mirrorless camera converted to full spectrum by Kolari Vision) with an M42-M42 lens adjustable focusing helicoid (25–55 mm) and a Nikon El-Nikkor 80 mm (1:5.6) lens. To photograph in the human-visible spectrum, we attached a UV/IR blocking filter (Baader UV/

IR-Cut filter; 400–680 nm); to photograph in the UV spectrum, we attached a UV pass filter (Baader U-filter; 320–380 nm). The camera settings were the same across photographs (RAW format, 400 ISO, f/11 aperture, and exposure set to aperture priority).

We photographed each specimen individually inside a lightbox with an Iwasaki eye-color MT70D G12 6500K lightbulb (positioned 2 m above the specimen) as the only light source. We used a steel brush to remove the UV filter on the lightbulb. We placed the specimen atop black ethylene-vinyl acetate (EVA) foam to minimize UV background reflectance (Dell'Aglio et al. 2018). A 5 and 20% gray standard (Spectralon Labsphere) were positioned beside each specimen at the same height as the specimen. Using a wired remote to trigger the shutter, we photographed each specimen in three orientations (dorsal, ventral, and left lateral). In each orientation, we photographed the specimen in first the human visible spectrum and then the UV spectrum; we repeated this sequence three times (repositioning the bird before each human visible spectrum photograph so that each set of photographs was independent) such that we had 18 photographs total per specimen (3 orientations × 3 times × 2 spectra).

Visual modeling

We used the micaToolbox plugin (ver. 2.2.2) for Image J (ver. 1.53a; Rasband 1997, Stevens et al. 2007, Troscianko and Stevens 2015) to process the photographs. The photographs were linearized, standardized, and converted to multispectral images. The photographs were standardized using the 5 and 20% gray standard within each image. These multispectral images were converted to images that were representative of the visual sensitivity of peafowl *Pavo cristatus*, which represents birds with a violet-sensitive visual system and is recommended for modeling color vision in corvids (Håstad et al. 2005, Schaefer et al. 2006). The specific visual sensitivities of American crows are unknown, but they fall within the violet-sensitive category of avian visual systems (Ödeen and Håstad 2003, 2010). We used the spectral sensitivity of a camera system that was included within micaToolbox (Sony A7 Nikkor El 800 300–700). This process produced short wave (SW), medium wave (MW), long wave (LW), ultraviolet (UV), and double cone (D; double cone; 'luminance' or reflectance across all wavelengths) mapped images. We created regions of interest (ROIs; Fig. 1) within these images that defined specific feather patches and then measured the cone-catch values for the SW, MW, LW, UV, and D receptors of each ROI. The ROIs distinguished on the dorsal orientation included the tail, wings, body, neck, head, and forehead. The ROIs on the ventral orientation included the tail, body, neck, throat, and chin. The ROIs on the lateral orientation included the wing, top of the eye, side of the eye, and under the eye. In sum, we delineated 17 ROIs from the dorsal, ventral, and lateral orientations. All the ROIs should be visible to observing American crows during normal movements – while perched or on the ground, during calling and display, and even in flight; only the ventral tail might be hard to see except when American crows land or fly overhead. We converted these

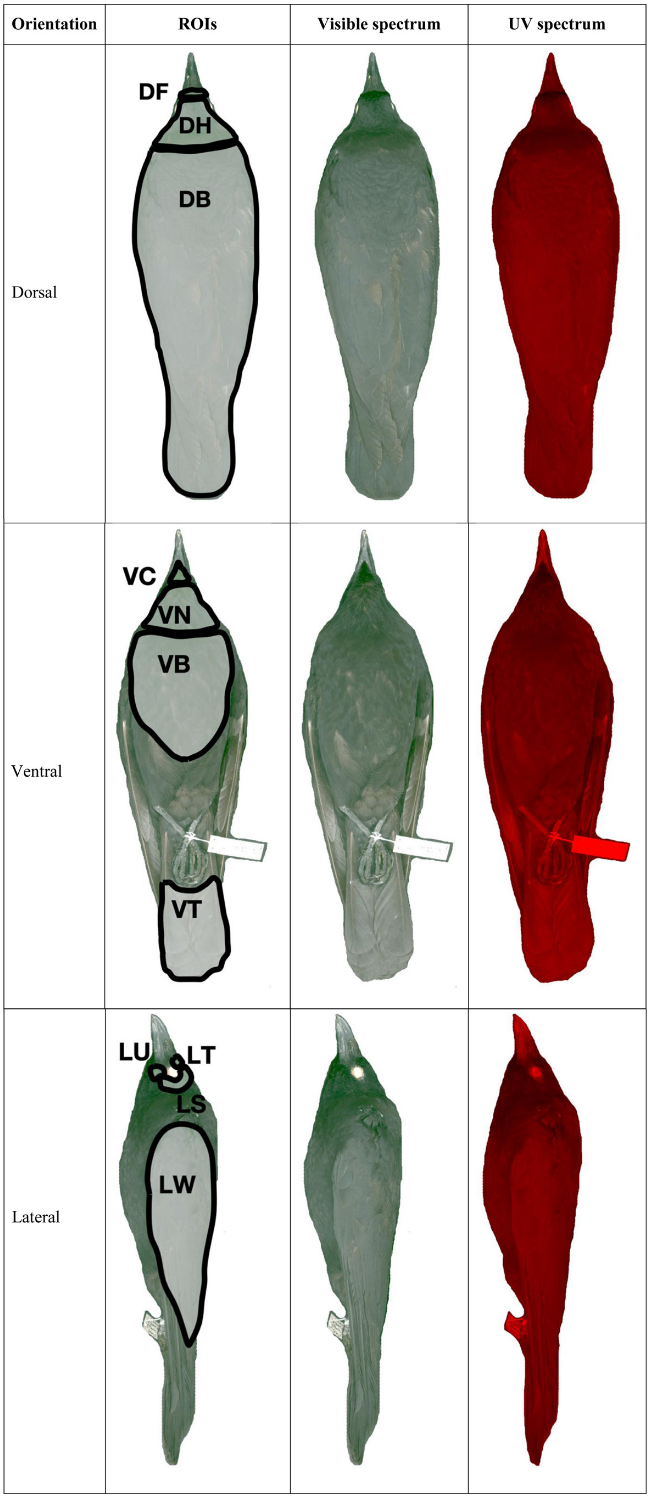

Figure 1. The final regions of interest (ROIs) on the dorsal, ventral, and lateral orientation. A representative American crow specimen (TCWC 11236) in the visible and UV spectrum using the avian vision phenotype.

cone-catch values into tetracolorspace values (Vorobyev and Osorio 1998, Stoddard and Prum 2008) of hue theta ('hue VIS'), hue phi ('hue UV'), and achieved chroma ('saturation') using the package 'pavo' (ver. 2.2.0; Maia et al. 2013, 2019) in the R programing environment (www.r-project.org). Finally, we calculated glossiness, a quality of mirror-like or specular reflectance characteristic of a smooth polished surface (Toomey et al. 2010); larger values indicate feathers that are glossier. For each ROI, we averaged the three sets of measurements that we obtained from each bird in each orientation.

We delineated ROIs based on our own assessments of major body regions, but it is possible that these regions were not also distinctive to American crows. As such, we performed a follow-up analysis to determine whether the colors of ROIs were distinct based on the visual system of American crows and should be considered separately. We used the chromatic receptor noise limited (RNL) model (Vorobyev and Osorio 1998) and the achromatic RNL model (Siddiqi et al. 2004) to estimate the discriminability of adjacent ROIs. In the chromatic model, we set the Weber fraction (an estimate of animal's ability to make discriminations) to 0.05 for their most numerous cone receptor type, and values for other cone types were a function of their frequency relative to the most numerous cone type. This parameterization, and the 0.05 fraction value for the most numerous receptor type, was preset in micaToolbox and is commonly used in avian studies (Vorobyev and Osorio 1998). In the achromatic mode, we set the Weber fraction to 0.34, which is the value for another avian passerine species, *Sturnus vulgaris* (Olsson et al. 2018). These models output values (ΔS) between ROIs that estimated whether American crows could likely discriminate ROIs from each other. A ΔS of three or greater generally indicates that animals can discriminate ROIs under natural viewing conditions in daylight (Siddiqi et al. 2004, Langmore et al. 2011). Based on this visual modeling, we determined that American crows would perceive some of these ROIs as being indistinguishable from adjacent ROIs based on achromatic and chromatic information (ΔS of less than three). In these instances, we combined multiple ROIs into a single ROI (Table 1–2). This resulted in 11 ROIs (Fig. 1; Supporting information) that were used in the subsequent analyses.

Age class and time since last molt

Age class and time since last molt were assessed by one experimenter (A. B. Clark unpubl.) with experience in handling American crows of all ages across all times of year, including many banded birds of known age. She made these assessments prior to the analyses and without knowing the color-variable data associated with each specimen. She assigned American crows into age classes using the known period of annual molt (based on Caffrey et al. 2025), tail feather shape, and tip wear. Tail feathers change shape with age: those of nestlings are relatively narrow and lance-shaped at the tips (Johnston 1961, Pyle 1997, Caffrey et al. 2025; A. B. Clark unpubl.) and the feathers that replace them are wider and increasingly squared off over the next two molts (Pyle 1997; A. B. Clark unpubl.). Beyond that time, it is not possible to estimate age. In general, the tail feather tips of most American crows wear visibly over the year, but especially those of immature birds. Further evidence of immatures in their second summer is the bronzy, 'sun-faded' color of their wings and tails (now > 12 months old; Supporting information). American crows during molt are unmistakable by tail or wing feathers of different lengths (replacement progresses from inner to outer feathers; Caffrey et al. 2025) as well as the scruffy appearance of head and body feathers. The clean-tipped, more central retrices in those few mixed-feather cases could be used for the age assessment.

Table 1. The original regions of interest (ROIs) and final ROIs used in the analyses. Some of the original ROIs were combined because their colors were not discriminable based on the American crow visual system. For example, the dorsal body, tail, and wings ROIs were not distinguishable based on the American crow visual system and were therefore merged into a single ROI (dorsal body, tail, and wings; 'DB'). The feather groups visible within the ROIs are described in the Supporting information.

Orientation	Original ROIs	Final ROIs	Final ROI abbreviations
Dorsal	Tail	Dorsal body, tail, and wings	DB
	Right wing		
	Left wing		
	Body		
	Neck	Dorsal head and neck	DH
	Head		
	Forehead	Dorsal forehead	DF
Ventral	Tail	Ventral tail	VT
	Body	Ventral body	VB
	Neck	Ventral throat and neck	VN
	Throat		
	Chin	Ventral chin	VC
Lateral	Wing	Lateral wing	LW
	Top of eye	Lateral top of eye	LT
	Side of eye (higher)	Lateral side of eye	LS
	Side of eye (lower)		
	Under eye	Lateral under eye	LU

Table 2. Mean ΔS values for regions of interest (ROI) comparisons using achromatic and chromatic information. Asterisks indicate adjacent ROIs within a given orientation that were discriminable (ΔS greater than 3).

Orientation	ROI comparison	Achromatic ΔS	Chromatic ΔS
Dorsal	Tail versus Right wing	1.46	0.58
	Tail versus Left wing	1.55	0.48
	Right wing versus Body	1.72	0.61
	Left wing versus Body	1.77	0.50
	Body versus Neck	3.72*	1.31
	Neck versus Head	1.96	0.44
	Head versus Forehead	7.73*	3.21*
Ventral	Body versus Neck	3.68*	1.34
	Neck versus Throat	2.45	0.49
	Throat versus Chin	3.52*	0.93
Lateral	Top of eye versus Side of eye (higher)	4.36*	1.38
	Side of eye (higher) versus Side of eye (lower)	1.97	0.51
	Side of eye (lower) versus Under eye	6.72*	2.01

Each specimen was placed into one of four age class categories. Category one was juveniles through their first birthday in early April (hatching based on northeast and especially Oklahoma populations; Supporting information) to their molt in summer, category two was immature but independent birds ('yearlings' before their second birthday), category three was young, but reproductively mature birds (2 year olds), and category four was reproductively mature birds of three or more years that could have been breeders, based on ages at first breeding in a 33-year study of a banded northeastern American crow population (McGowan 2001, Clark et al. 2006, Townsend et al. 2009). Category three birds in the northeast population and an Oklahoma population are unlikely to be breeders (McGowan 2001, Clark et al. 2006, Robinson 2009, Caffrey and Peterson 2015), presumably because of local competition for mates and territories among the many retained non-breeders in this long-lived species.

We scored time since last molt by assessing the American crows' plumage wear (e.g. blunted, worn tips on tails) compared with the expected molting period. American crows molt and grow new feathers once annually in late summer (Caffrey et al. 2025). We used the condition of the feathers and date collected to calculate the number of months since the probable last molt date. We assumed a molt period of late July–mid-September, based on both reported patterns (Caffrey et al. 2025) and that observed over > 30 years in the banded population in the northeast (K. McGowan and A. B. Clark unpubl.). By the annual molt when feathers are near 12 months old or more, the tips, especially those of retrices, are visibly worn; sometimes flight feathers are actually broken. Only a few American crow specimens showed the mixed flight feather lengths, worn tail feathers, and scruffy head and body feathers typical of being mid-molt. We estimated when the American crows last molted (0 = molted in the same month as their death to 12 = molted 12 months prior to their death). The exception was yearling birds (category one) who had grown feathers at 3–5 weeks as nestlings (feathering out estimated as 1 May); these birds only molt body feathers (non-flight feathers) as juveniles in their first August. Thus, by the time of the next annual molt period, their flight feathers were about 14–16 months old.

Statistical analysis

We performed mixed linear models (SAS; ver. 9.4) to examine whether the color variables (hue VIS, hue UV, saturation, luminance, and glossiness) varied by age class, sex, the interaction between age class and sex, ROI, and locality (Texas, Oklahoma, or Washington). We also included time since last molt and storage duration because feathers can change color over time (Tökölyi et al. 2008, Delhey et al. 2010). Storage duration was calculated as the date the specimens were photographed minus the date they were salvaged. We included storage duration in the models because specimens can fade and change color in storage (McNett and Marchetti 2005, Armenta et al. 2008, Doucet and Hill 2009). We also performed all pairwise comparisons of the ROIs to compare differences between ROIs. We used options for the variance component estimation and approximation of the degrees of freedom within the mixed models that are recommended for unbalanced data (i.e. method = REML; ddfm = kenward-roger; Spilke et al. 2005).

We also performed discriminant function analyses (DFA) using feather coloration (hue VIS, hue UV, saturation, luminance, and glossiness) of each ROI to predict age class. Finally, to confirm that our age class categories were accurate, we tested whether age class category and wing length were positively correlated, because previous work has found that older American crows have longer wings (Emlen 1936). We examined the relationship between crow age and wing length (straight-line distance between the angle of the wrist joint and the tip of the longest primary feather) to test whether morphological variation was related to the estimated age class (Johnston 1961).

Results

Coloration varied significantly across ROIs (hue VIS: $F_{10,202} = 7.36$, $p < 0.0001$); hue UV: $F_{10,202} = 5.60$, $p < 0.0001$; saturation: $F_{10,200} = 2.78$, $p = 0.0031$; luminance: $F_{10,202} = 43.90$, $p < 0.0001$; glossiness: $F_{10,202} = 5.17$, $p < 0.0001$; Fig. 2). Pairwise comparisons of the ROIs are displayed in the Supporting information. The hue VIS ($F_{1,14.6} = 10.56$, $p = 0.0056$) and hue UV ($F_{1,14.8} = 11.66$, $p = 0.0039$)

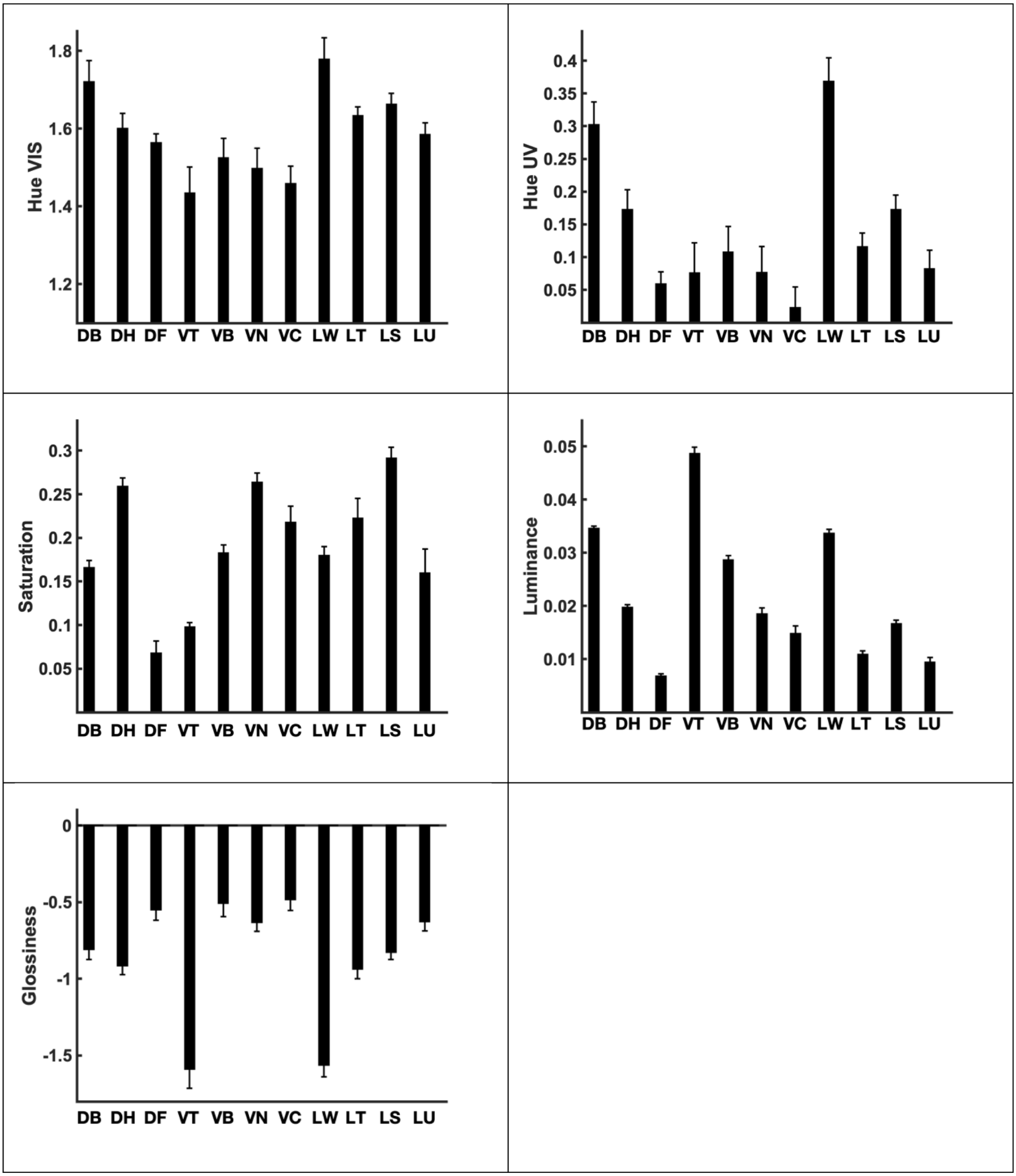

Figure 2. Color variables of the feather regions of interest (ROIs). Means (± SE) are displayed.

were significantly higher in crows that were older (Table 3, Fig. 3). There were no significant overall sex differences nor sex by age class interactions in any color variables ($p > 0.55$). Coloration was not significantly influenced by the time since last molt ($p > 0.35$) or locality ($p > 0.30$). Specimens with longer storage durations had significantly lower hue VIS ($F_{1,14.7}=6.52$, $p=0.022$; Fig. 4). A discriminant function analysis using feather coloration correctly classified individuals to the correct age class at levels above chance based on the DB ($F_{15,55.613} = 0.99$, $p=0.033$), VT ($F_{15,55.613}=2.95$, $p=0.0017$), and LW ($F_{15,55.613} = 1.97$, $p=0.035$) ROIs (Table 4).

Table 3. The effect of American crow age class, sex, region of interest (ROI), time since last molt, and storage duration on feather coloration. F values are displayed (with the numerator and denominator degrees of freedom in subscripts) and p-values in parentheses. Significant variables are indicated with an asterisk.

	Hue VIS	Hue UV	Saturation	Luminance	Glossiness
Crow age class	$10.56_{1,14.6}$ (0.0056)*	$11.66_{1,14.8}$ (0.0039)*	$0.19_{1,11.9}$ (0.67)	$3.03_{1,15}$ (0.10)	$0.24_{1,13.1}$ (0.63)
Sex	$0.17_{1,14.7}$ (0.69)	$0.04_{1,14.9}$ (0.85)	$0.37_{1,12.3}$ (0.56)	$0.01_{1,15.2}$ (0.92)	$0.27_{1,13.6}$ (0.61)
Crow age class × Sex	$0.36_{1,14.8}$ (0.56)	$0.13_{1,14.9}$ (0.72)	$0.13_{1,12.4}$ (0.73)	$0.00_{1,15.2}$ (0.95)	$0.22_{1,13.7}$ (0.65)
ROI	$7.36_{10,202}$ (< 0.0001)*	$5.60_{10,202}$ (< 0.0001)*	$2.78_{10,200}$ (0.0031)*	$43.90_{10,202}$ (< 0.0001)*	$5.17_{10,202}$ (< 0.0001)*
Crow age class × ROI	$5.22_{10,202}$ (< 0.0001)*	$4.60_{10,202}$ (< 0.0001)*	$0.81_{10,200}$ (0.62)	$0.85_{10,203}$ (0.58)	$1.05_{10,202}$ (0.41)
Time since last molt	$0.45_{1,14.6}$ (0.52)	$0.78_{1,14.8}$ (0.39)	$0.19_{1,12.1}$ (0.67)	$0.87_{1,15}$ (0.37)	$0.89_{1,13.3}$ (0.36)
Storage duration	$6.52_{1,14.7}$ (0.022)*	$2.47_{1,14.9}$ (0.14)	$0.11_{1,12.4}$ (0.75)	$4.13_{1,15.2}$ (0.060)	$0.00_{1,13.7}$ (0.96)
Locality	$0.94_{2,14.6}$ (0.41)	$0.96_{2,14.8}$ (0.41)	$0.97_{2,12}$ (0.41)	$0.13_{2,15}$ (0.88)	$1.21_{2,13.1}$ (0.33)

There was a statistically significant strong positive correlation between wing length and crow age class ($F_{1,19} = 10.99$, $p = 0.0036$; Fig. 5). The sex of the crow ($F_{1,19} = 3.51$, $p = 0.077$), interaction between the sex of the crow and age class ($F_{1,19} = 3.68$, $p = 0.070$), and locality ($F_{2,19} = 1.15$, $p = 0.34$) were unrelated to wing length.

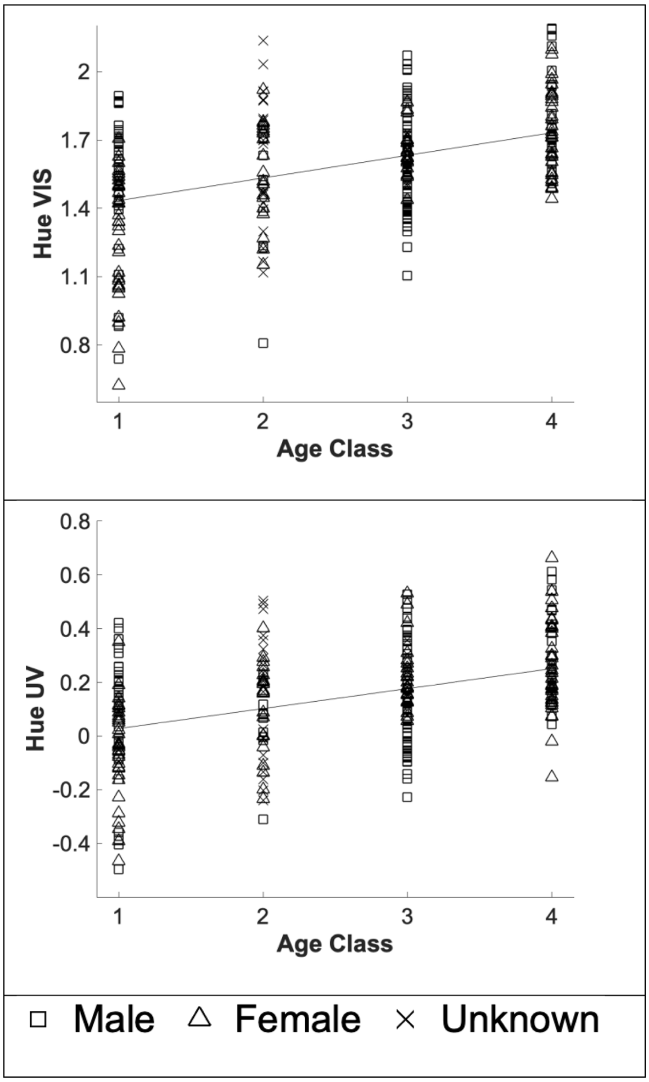

Figure 3. Feather coloration (hue VIS and hue UV) is positively related to American crow age class.

Discussion

The feather coloration of American crows varied by age class but not sex. In many species, plumage coloration changes as birds become older (Siefferman et al. 2005, Bitton and Dawson 2008, Boves et al. 2014, Nam et al. 2016). Consistent with these previous studies, we found that the hue of American crow feathers differs based on age class. Older American crows had feathers with a different hue (higher hue VIS) and more ultraviolet (higher hue UV) than younger American crows. Individuals were classified into age classes at levels above chance based on the feather coloration of the dorsal body, tail and wings (DB ROI), ventral tail (VT ROI), and lateral wing (LW ROI). We also found that American crow age class and wing length were positively correlated, confirming that our age class categorizations accurately represented age class, because older American crows typically have longer wings than younger American crows (Emlen 1936).

American crows could potentially assess the coloration of feathers to classify conspecifics into age categories, but experimental manipulation of feather coloration would be necessary to determine whether they actually do so. Evaluating

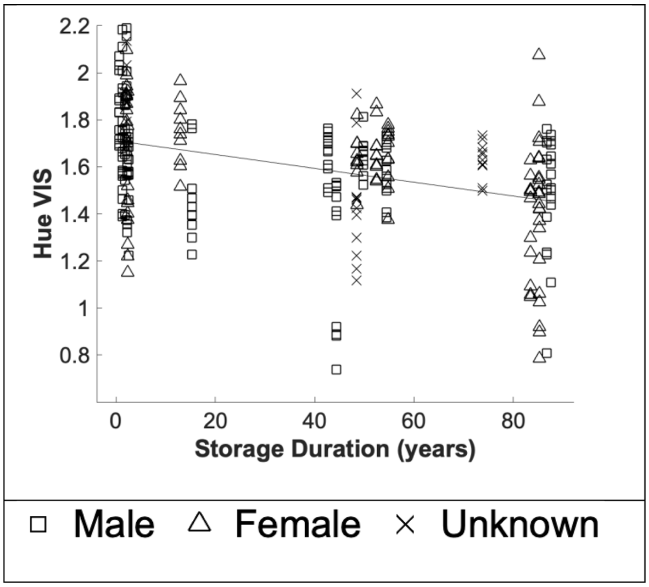

Figure 4. Hue VIS is negatively related to storage duration.

Table 4. The percentage of classifications performed correctly by age class using a discriminant function analysis with the feather coloration (hue VIS, hue UV, saturation, luminance, and glossiness) of specific regions of interest (ROIs). Wilks' lambda is also displayed, with the F value, numerator, and denominator degrees of freedom as subscripts, and p-value in parentheses. Chance level is 25% (four age class categories). Significant variables are indicated with an asterisk.

ROI	Classification success (%)	Classification success with cross-validation (%)	Wilks' lambda
DB	62.4	34.8	$0.99_{15,55.613}$ (0.033)*
DH	52.9	30.2	$1.17_{15,52.852}$ (0.32)
DF	57.7	17.5	$1.47_{15,52.852}$ (0.15)
VT	70.2	51.0	$2.95_{15,55.613}$ (0.0017)*
VB	62.5	43.4	$1.48_{15,55.613}$ (0.14)
VN	51.0	21.0	$1.07_{15,52.852}$ (0.4)
VC	44.3	21.1	$0.84_{15,52.852}$ (0.63)
LW	68.8	41.9	$1.97_{15,55.613}$ (0.035)*
LT	51.6	20.8	$0.75_{15,50.091}$ (0.72)
LS	51.3	20.5	$0.63_{15,52.852}$ (0.84)
LU	58.6	26.5	$0.68_{15,50.091}$ (0.79)

the age of conspecifics is useful to many avian species during mate choice (Côté and Hunte 1993, Richardson and Burke 1999), agonistic encounters (Magaña et al. 2011), or other contexts. For cooperatively breeding, territorial American crows, social contexts are many, including intra-group relations between parents and past offspring. Many young crows remain with parents through their second summer, but males, in particular, may stay with natal groups as they mature, when they sometimes contend with their fathers for breeding (Townsend et al. 2009). Non-breeders take part in between-family, territorial disputes, during which plumage might advantageously signal the greater strength of a family with older males. Conversely, signals of youth could reduce aggression toward younger birds on and off territory, as seen in other species (Senar 1999, Conover et al. 2000, Morimoto et al. 2006, Mitrus 2007, Nam et al. 2016). American crow social relations across their long lives can be complex, with unrelated birds sometimes joining established families, and neighboring families visiting or temporarily coalescing (Clark et al. 2006), as well as unfamiliar birds meeting annually in large, winter flocks (Caffrey et al. 2025). Easy age assessment could figure in a wide range of social contexts. Because we did not know the exact age of the specimens, we were unable to examine whether feather coloration varied among the oldest age class (category 4) of American crows. Category 4 birds could only be said to be at least three years old. In a banded population in New York, American crows are documented to reach 19 years old in the wild (K. J. McGowan and A. B. Clark unpubl.) and older males in this population have lost fights with younger mature males – their sons or males from neighboring territories (Robinson 2009, Caffrey et al. 2025). It is possible that feather coloration plays a role in identifying males beyond their prime, leading to such aggression.

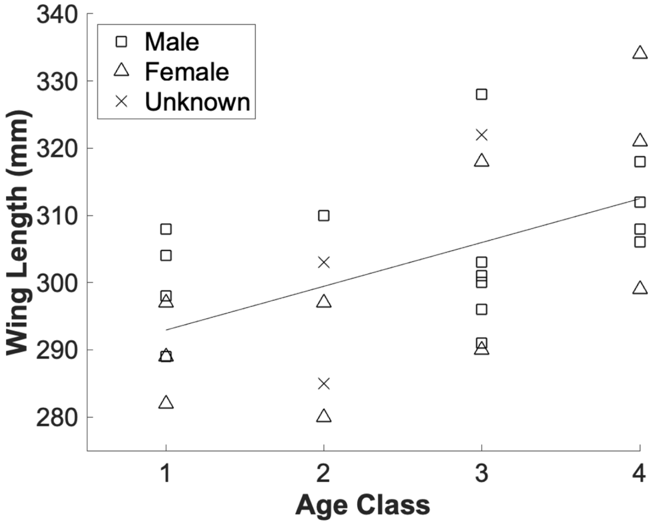

Figure 5. Wing length and American crow age class are positively related.

In some avian species, the coloration of feathers also differs between the sexes (Price and Birch 1996, Holt et al. 2016). However, we did not find any differences in coloration (hue, saturation, luminance, or glossiness) between the sexes in American crows, suggesting that they may not be using coloration to discriminate between the sexes. They may instead rely on morphological and acoustic differences to differentiate between males and females. Within a regional population, adult female American crows have smaller heads and shorter tarsus lengths than males (Johnston 1961, Caffrey 1992, Ludwig et al. 2009). Female American crows also have higher frequency calls across contexts than males (Yorzinski et al. 2006, Mates et al. 2015).

One caveat is that we did not measure feather iridescence (due to limitations in using museum specimens; but see Hogan and Stoddard 2018). Iridescent feathers are those that appear differently depending on the angle at which they are viewed (Bradbury and Vehrencamp 1998). Several other *Corvus* species show weak iridescence in their secondaries through single-layer melanosomes (Lee et al. 2016). Fish crows *C. ossifragus*, which are sympatric with American crows in the eastern USA, are also reported to be iridescent and qualitatively exhibit more iridescence than American crows (McGowan 2020). Unlike the American crow, the fish crow is a pair breeder living in large flocks outside of the breeding season (McGowan 2020). While sympatric, the fish crow is not closely related to American crows. American crows' nearest relative is the carrion crow, while fish crows appear most closely related to the Tamaulipas crow *C. imparatus* and Sinaloa crow *C. sinaloae* (Jønsson et al. 2016, Garcia-Porta et al. 2022). The carrion crow has been described as less glossy than the rook *C. frugileus* (Madge 2020), the latter being one of the species having weak iridescence (Lee et al. 2016). In contrast, Tamaulipas and Sinaloa crows are qualitatively described as glossy purple and deep blue, suggestive of iridescence (Rodríguez-Flores et al. 2020a, 2020b). A future study examining possible sex differences in iridescence in both American and fish crows would be very informative, as would a broader phylogenetic study of feather coloration and sex differences in *Corvus* in relation to habitat or breeding systems.

Another limitation concerns our sample size. Future studies that quantify coloration in a larger number of individuals could reveal more subtle patterns that we may have been unable to detect with our limited samples. In addition, our specimens were primarily from one state (Texas); a broader geographic sampling could uncover additional insights into variation in feather coloration in American crows more generally. Furthermore, because our specimens were not tracked from birth, we were unable to determine their exact ages. As such, we estimated their ages based on feather patterns and classified them into four age categories. The fourth age category was the broadest and included birds that were estimated to be three or more years old. Because wild American crows have been documented to live past 14.5 years (Clapp et al. 1983) and even up to 19 years (K. McGowan and A. B. Clark, four banded birds, unpubl.), this fourth age category could potentially include birds with large age differences. Future studies that examine corvid feather coloration using individuals of known ages would be informative, especially in the case of birds that are older than three years. Finally, this study used photographic methods to quantify the coloration of American crows, following protocols to accurately quantify coloration (e.g. using a full spectrum camera with known spectral sensitivity, high-quality reflectance standards, and repeated sampling of each specimen; Troscianko and Stevens 2015). Additional studies could use spectrometric methods to further examine American crow coloration, gathering point measurements and generating reflectance spectra.

Even though the coloration of American crow feathers appears relatively uniform to the human eye, our visual modeling approach suggests that American crows can discriminate among different feather regions. For example, the feather coloration of the dorsal body, tail, and wings is discriminable from the feather coloration of the dorsal head and neck. Differences in coloration among these feather regions could signal other qualities of the American crows that were not investigated in this study, such as their condition (Delhey et al. 2010), health (Saks and Hõrak 2003), or dominance status (Santos et al. 2011). Within-body color differences among feathered areas could also serve to accentuate the position of feathers and body parts in visual signaling, which is notable across *Corvus* in such behaviors as wing-tail flicking, postural displays, and other behaviors (Goodwin 1976, Coombs 1978, Caffrey et al. 2025; A. B. Clark unpubl.). We also found that the glossiness of the American crow feathers was relatively low. The low glossiness was likely influenced, in part, by the photographic set-up (intensity and position of the light source relative to the specimens). Because perceived glossiness is low at lower light intensities and greater distances between the light source and glossy object (Zhu et al. 2022), additional studies that vary these parameters could further examine the conditions under which feather regions appear glossy.

One feather region with particularly distinctive coloration properties was the dorsal forehead. These feathers had low hue VIS, hue UV, saturation, and luminance. Because these feathers are near the eyes, they could potentially function to minimize eye glare. In other species, dark markings around the eyes may reduce eye glare (Ficken and Wilmot 1968, Burtt 1984, 1986, Brooke 2010, Yosef et al. 2012), just as human athletes apply eye black beneath their eyes for this purpose (DeBroff and Pahk 2003). In these other species, the coloration of the dark markings around the eyes typically contrasts with the coloration of the surrounding area, such as the black eye stripe of male shrikes that is surrounded by light-colored feathers (Yosef et al. 2012). In contrast, the black feather coloration around the eyes of American crows does not contrast as sharply with the surrounding black feathers of the rest of their face. Regardless, future studies could examine whether these American crow feathers serve an anti-glare function, perhaps specifically during ground foraging in open areas when the head is angled downward. Alternatively (or in tandem), the dark feathers near American crow eyes may function in other contexts, such as signaling condition, identity, or other qualities. Anecdotally, many other corvid species also have these dark facial feathers, suggesting that this is a conserved trait and warranting additional studies into possible adaptive value.

Feather coloration is not static and can change across a year as a result of bacterial activity, ectoparasites, abrasion, solar irradiation, and other factors (Örnborg et al. 2002, Figuerola and Senar 2005, Tubaro et al. 2005, Tökölyi et al. 2008, Shawkey et al. 2009, Delhey et al. 2010, Valdez and Benitez-Vieyra 2023). However, we did not find that American crow feather coloration varied based on the number of months since the last molt. Studies have also found that museum specimens can change color while in storage, with the directionality and magnitude of change varying based on the species and feather region (McNett and Marchetti 2005, Armenta et al. 2008, Doucet and Hill 2009). Indeed, we found that American crow specimens that had longer storage durations had lower hue VIS.

In cooperative breeders, including American crows and many other corvids (Iwaniuk and Arnold 2004), plumage coloration could play an important role in communication. Because nonbreeding individuals help breeding individuals raise their young (Brown 1978), it could be especially valuable for nonbreeding individuals to advertise their breeding status to minimize aggression from breeders (Beauchamp 2003, Bruintjes and Taborsky 2008). Individuals could also benefit by signaling their quality as a potential mate to maximize their chances of becoming a breeder rather than a helper. For example, in cooperatively breeding azure-winged magpies *Cyanopica cyanus*, males with more brilliant and saturated blue plumage during the non-breeding season were more likely to become breeders (Solís et al. 2008). Investigations into how cooperatively breeding species use plumage coloration to communicate could enhance our understanding of this relatively uncommon breeding system (Cockburn 2006).

Overall, we found that the coloration of American crow feathers is not uniform within individuals, and varies based on age class but not sex. Relatively few studies have examined variation within or between individuals in corvid feather coloration. Given the wide range of complex social organizations and long life histories in this taxon (Rowley 1973a, 1973b, Goodwin 1976, Jønsson et al. 2012), variation in feather coloration would be a rich topic to address from a comparative perspective. It would be interesting to uncover how individual and species differences in feather coloration might vary with such factors as habitat, communication, social structure, and phylogeny.

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Author contributions

Jessica L. Yorzinski: Conceptualization (equal); Formal analysis (lead); Funding acquisition (lead); Methodology (lead); Writing – original draft (lead); Writing – review and editing (equal). **Anne B. Clark**: Conceptualization (equal); Methodology (supporting); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.stqjq2chg (Yorzinski and Clark 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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