

Taylor & Francis
Taylor & Francis Group

Studies on Neotropical Fauna and Environment

ISSN: 0165-0521 (Print) 1744-5140 (Online) Journal homepage: www.tandfonline.com/journals/nnfe20

Plumage ontogeny and color polymorphism in the forest-dwelling Crested Eagle inferred from citizen-science photographs

Matías A. Juhant

To cite this article: Matías A. Juhant (29 Sep 2026): Plumage ontogeny and color polymorphism in the forest-dwelling Crested Eagle inferred from citizen-science photographs, Studies on Neotropical Fauna and Environment, DOI: 10.1080/01650521.2026.2733824

To link to this article: https://doi.org/10.1080/01650521.2026.2733824

View supplementary material

Published online: 29 Sep 2026.

Submit your article to this journal

View related articles

View Crossmark data

Full Terms & Conditions of access and use can be found at
https://www.tandfonline.com/action/journalInformation?journalCode=nnfe20

STUDIES ON NEOTROPICAL FAUNA AND ENVIRONMENT
https://doi.org/10.1080/01650521.2026.2733824

Taylor & Francis
by informa

Check for updates

Plumage ontogeny and color polymorphism in the forest-dwelling Crested Eagle inferred from citizen-science photographs

Matías A. Juhant

Acopian Center for Conservation Learning, Hawk Mountain Sanctuary, Orwigsburg, PA, USA

ABSTRACT

The Crested Eagle (*Morphnus guianensis*) is a near threatened forest-dwelling raptor whose elusive habits and low population density have long constrained knowledge of its delayed plumage maturation and color polymorphism. The number and sequence of molt cycles leading to the definitive basic plumage, as well as the phenotypic patterns underlying discrete morph-types, remain poorly understood. I analyzed a dataset of 152 photographed individuals from citizen science repositories (eBird and WikiAves Brasil) to investigate plumage ontogeny and color polymorphism. Photographic evidence suggests that the Crested Eagle (1) acquires its definitive basic plumage after four annual molt cycles, passing through four distinguishable non-definitive basic plumages; (2) the first and second basic plumages are monomorphic, after which morphs begin to differentiate following the second annual molt; and (3) upon acquisition of definitive basic plumage, three discrete morph-types are present (brownish-barred, whitish-barred, and unbarred-black). By inferring the plumage sequences, phenotypic patterns within age classes, and the onset of morph differentiation, this study provides a framework that advances understanding of previously poorly known aspects of the biology of the Crested Eagle.

ARTICLE HISTORY
Received 28 May 2026
Accepted 11 September 2026

KEYWORDS
Apex predator; cryptic species; delayed plumage maturation; harpiinae; morph-types

Introduction

The Neotropics harbor one of the greatest diversities of raptor species globally, and this assemblage is characterized by wide variation in overall coloration and plumage patterns (Ferguson-Lees and Christie 2001). This phenotypic diversity reflects the presence of species from multiple evolutionary lineages inhabiting diverse biogeographical regions (Raposo Do Amaral et al. 2009; Fuchs et al. 2012; Johnson et al. 2016). Several endemic and near-endemic Neotropical species exhibit delayed plumage maturation, during which individuals undergo multiple annual molt cycles before acquiring their definitive basic plumage. This pattern is documented in New World vultures (Cathartidae, e.g. Andean Condor [*Vultur gryphus*], and King Vulture [*Sarcoramphus papa*]), medium- to-large-sized hawks and eagles (Accipitridae, e.g. *Geranoaetus* spp., *Buteogallus* spp., Crested Eagle [*Morphnus guianensis*], and Harpy Eagle [*Harpia harpyja*]), and caracaras (Falconidae, e.g. *Daptrius* spp.) (Ferguson-Lees and Christie 2001; Cabot and de Vries 2004; Seipke 2007; Clark and Schmitt 2017; Pallinger and Menq 2022). Some of these species also exhibit discrete color polymorphisms, with three distinct color forms (morph-types) occurring within a single breeding population in their definitive basic plumage, including White-tailed Hawk (*Geranoaetus albicaudatus*), Variable Hawk (*Geranoaetus polyosoma*), and Crested Eagle (Ferguson-Lees and Christie 2001; Clark and Schmitt 2017; Pallinger and Menq 2022; Juhant 2026a). However, critical gaps remain concerning the number and sequence of molt cycles leading to definitive basic plumage, as well as the phenotypic aspect of the discrete morph-types, which are still described using broad, non-standardized terms such as 'light,' 'dark,' or 'intermediate' morphs.

The Crested Eagle, often called 'the ghost' of Neotropical forests, is one of the least-known and most elusive raptors of the region, owing to its secretive habits and low population density. Along with the Harpy Eagle, the Crested Eagle is one of only two representatives of the subfamily Harpiinae in the Neotropics (Gregory et al. 2024). Its distribution overlaps with that of the Harpy Eagle, ranging from southern Mexico through Central America and into South America, reaching as far south as northeastern Argentina (Ferguson-Lees and Christie 2001; Gomes and Sanaiotti 2015; Schulenberg 2020; Smith 2020).

CONTACT Matías A. Juhant juhant@hawkmountain.org
Supplemental data for this article can be accessed online at https://doi.org/10.1080/01650521.2026.2733824.
© 2026 Informa UK Limited, trading as Taylor & Francis Group

Published online 29 Sep 2026

The Crested Eagle exhibits a patchy distribution and is considered rare to very rare, often regarded as even rarer than the Harpy Eagle (Ferguson-Lees and Christie 2001); for every ~100 Harpy Eagle nests mapped, only about 10 have been recorded for the Crested Eagle (Aguiar-Silva et al. 2013). This rarity is closely linked to the Crested Eagle's strict dependence on tall, pristine forests and to its requirement for large annual home ranges of 25–50 km^2 (Jullien and Thiollay 1996; Whitacre et al. 2012). As these habitats are increasingly fragmented, the Crested Eagle is classified as Near Threatened (BirdLife International 2017).

Large tropical forest raptors commonly exhibit delayed plumage maturation but rarely display discrete color polymorphism; the Crested Eagle is unique in being the only large Neotropical forest raptor known to combine both traits (Ferguson-Lees and Christie 2001). This unusual combination highlights the importance of understanding phenotypic aspects (i.e. overall coloration and pattern) across age classes and among discrete morph-types. Resolving age-related plumage sequences and distinguishing morph-types are therefore essential for accurately aging individuals and assigning morph-types through direct observation, providing a stronger foundation for demographic studies. Despite repeated references in field guides and general accounts to delayed plumage maturation and the presence of morph-types, the number and sequence of molt cycles leading to definitive basic plumage have never been documented in detail. Similarly, morph classification has remained coarse, typically being limited to simplified categories such as 'light' and 'dark,' with a third, poorly defined morph, occasionally referred to as the 'extreme' morph, characterized by entirely uniform black plumage (Ferguson-Lees and Christie 2001; Clark and Schmitt 2017; Pallinger and Menq 2022). Consequently, the ontogenetic stage at which morphs become reliably identifiable has never been empirically assessed. Moreover, the lack of standardized nomenclature for assessing plumage sequences and morph-types constrains clear and consistent communication.

Interpretation of plumage ontogeny and color polymorphism in the Crested Eagle requires a framework that integrates established principles of age-class terminology based on flight-feather molt patterns, delayed plumage maturation, and discrete morph-types. In Accipitriformes, flight feathers (primaries, secondaries, and rectrices) are replaced in a determinate sequence during successive molt cycles (Stresemann and Stresemann 1966; Edelstam 1984; Clark 2004; Juhant 2026a, 2026b), and the nomenclature used to describe plumage sequences is based on these successive molt cycles (Howell et al. 2003). Because new and old flight and body feathers can be distinguished by differences in wear, coloration, and shape (Seipke 2007; Juhant 2026a, 2026b), plumage sequence can be inferred from feather condition. Older feathers are generally lighter and more worn than newer ones, whereas the flight feathers of younger individuals, particularly those in basic I plumage, are shorter, narrower, and more pointed than those of older birds, producing a ragged trailing edge to the wing. Together, these traits allow plumage sequences to be reconstructed and compared among individuals, providing a basis for recognizing recurring phenotypic patterns associated with particular age classes (Seipke 2007; Juhant 2026b). Within this framework of delayed plumage maturation, variation among individuals of the same age class can then be evaluated to distinguish discrete color morphs and develop a consistent nomenclature based on stable phenotypic patterns. Because these inferences are derived primarily from photographic evidence rather than observations of individuals of known age, the resulting plumage sequence and timing of morph differentiation should be regarded as working hypotheses based on the available evidence. These hypotheses provide a framework for examining plumage ontogeny and color polymorphism in the present study.

To test and further develop this framework, I analyzed a dataset of photographs of Crested Eagles from citizen science repositories (eBird and WikiAves Brasil), with the following objectives: (1) to document the sequence of plumages from basic I (juvenile) to definitive basic plumage (adult) based on annual molt cycles; and (2) to assess the phenotypic expression of discrete morph-types and assign formal nomenclature to them. These results also provide important insights for conservation, as knowledge of age structure and morph-types can guide understanding of population dynamics and morph frequencies.

Materials and methods

Photographic database based on citizen science

I compiled a dataset of 152 photographs of Crested Eagles exclusively from eBird and WikiAves Brasil, encompassing records available up to September 2025. To prevent duplication, I cross-checked each record within and across platforms, as multiple links occasionally referred to the same individual. I excluded poor-quality photographs (i.e. those in which parts of the body were not visible or overall image quality was low). When individuals were photographed repeatedly over time (e.g. pairs with fledglings

in Darién, Panama; Barra do Bugres, Mato Grosso, Brazil; and Manacapuru, Amazonas, Brazil) or by multiple photographers during a single visit, I retained only the highest-quality images and the clearest views of each individual. Photographs of nestlings were included only when individuals had passed the natal down stage and displayed a fully developed contour of flight feathers. Detailed counts of included photographs, along with their categorization by age class and morph-type, are provided in Online Supplemental Tables S1–S9.

Referencing individuals from the online supplemental material in the results

The individuals I selected to support statements throughout the Results were chosen because their photographic records clearly exhibited the diagnostic traits of each proposed age class or morph-type. At first mention within each age class or morph-type, I cite individuals by their source table, label number, and repository source and number (e.g. Table S1, label #6 WA5548221) (ML Macaulay Library; WA WikiAves). For brevity, subsequent citations within each age class or morph-type refer to the label only (e.g. #6 WA5548221), with the corresponding table indicated at first mention in each section. As a result, readers can efficiently locate the corresponding records and associated links in the Online Supplemental Tables for each individual referenced in the Results.

Plumage sequences and age class assignment

The sequence of flight-feather replacement is highly conserved among Neotropical Accipitriformes; therefore, closely related species with documented molt patterns provide an appropriate comparative framework for inferring plumage sequences in species for which these patterns remain unknown, such as the Crested Eagle. Accordingly, I used the three species of *Geranoaetus* and the Bay-winged Hawk (*Parabuteo unicinctus unicinctus*) as comparative models because they are medium- to large-sized raptors that require four annual molt cycles before attaining definitive basic plumage and exhibit both continuous and discrete color variation (Seipke 2007; Juhant 2026a, 2026b; Juhant, unpubl. data). Comparative analyses focused on the sequence and extent of flight-feather replacement, as well as age-related changes in feather shape, wear, and coloration. This comparative framework was used to infer the expected transitions between successive plumage sequences (i.e. the age-class boundaries following each annual molt cycle) in the Crested Eagle.

To assess plumage sequence and infer age-class boundaries, I considered the serial or stepwise molt (*Staffelmauser*) of the primaries. Each annual molt cycle initiates a new wave of primary replacement at p1, resulting in the partial replacement of the primaries and the coexistence of multiple feather generations within an individual (Stresemann and Stresemann 1966; Edelstam 1984; Clark 2004). Accordingly, the presence and position of replaced and unreplaced primaries were used to identify distinct molt waves and characterize the progression of primary molt. This pattern has been documented in medium- to large-sized Neotropical raptors (Seipke 2007; Clark and Schmitt 2017; Juhant 2026a, 2026b), but detailed species-specific information remains limited, including for the Crested Eagle (Clark and Schmitt 2017). The temporal pattern of primary replacement described by Juhant (2026b) – with the first primary molt beginning at approximately nine months of age, lasting approximately eight months, and subsequent molt cycles recurring at approximately 12-month intervals from the onset of the primary molt – was used as a temporal reference for assigning age-classes boundaries.

In addition to the primary molt patterns, I also assessed the feather replacement patterns of the secondaries and rectrices as additional criteria for assigning individuals to age classes. For the secondaries, I assessed replacement to the three molt centers at s1, s5, and s12, considering the proximal progression from s1 and s5 and the distal progression from s12 (Miller 1941; Juhant 2026b). For the rectrices, I considered the replacement using the sequence generally described as beginning with r1, followed by r6, r4, and r3, with r5 and r2 typically replaced later as a reference for age-class assignment (Edelstam 2001; Juhant 2026b).

I assigned individuals to age classes following the nomenclature of Howell et al. (2003), designating juveniles as basic I, successive intermediate stages as subsequent basic plumages, and adults as definitive basic plumage, after which only the term basic followed by the final Roman numeral was used to simplify terminology and facilitate consistent reference to successive plumage stages.

Morph-types assignment

I assigned morph-types only after all individuals had been assigned to an age class, so that color variation was evaluated independently of ontogenetic stage. Within each age class, morph-types were assigned based on visual assessment of qualitative plumage traits, including overall coloration, barring patterns,

and dorsal–ventral contrast. No quantitative color measurements were used. I included only individuals in definitive basic plumage because raptors are not known to change morph-type after acquiring this plumage stage (e.g. Briggs et al. 2010). Individuals in non-definitive basic plumage stages were excluded because they represent transitional developmental stages and do not yet reflect the final expression of definitive basic plumage in overall coloration and pattern. Individuals in basic III and basic IV plumages were classified only into two broad categories, light-plumaged and dark-plumaged, rather than assigned to discrete morphs. I adopted this conservative approach because the sample size of dark-plumaged individuals in these age classes was low, limiting the identification of consistent diagnostic traits for reliable morph delimitation.

Results

I identified four successive non-definitive basic plumages and established age-class boundaries based on body and flight-feather phenotypic traits in relation to flight-feather molt patterns from 152 photographed Crested Eagle individuals obtained from citizen-science repositories. I primarily inferred plumage sequences from perched individuals, as most photographed Crested Eagles were recorded while perched. Although only a limited number of individuals were photographed in flight, those with visible flight feathers provided key reference points for interpreting age-class -specific phenotypes and validating the proposed plumage sequences. Figures 1 and 2 summarize the inferred plumage sequences and phenotypic aspects of each age class from different positions, whereas Figure 3 illustrates the phenotypic aspects of the three morph-types assigned after four annual molt cycles in basic V plumage.

Basic I (juvenile; ≤8 months; no annual molt cycle completed; N = 8)

Body and flight-feather phenotypic aspects.— This age class was exclusively monomorphic. The overall plumage was predominantly white (Table S1, label #6 WA5548221), although some individuals showed a light brownish wash on the ventral side (#2 ML467395241). On the ventral side, the underwings were white, while the primaries and secondaries were black with multiple fine white bands and a conspicuous white wing tip (#6 WA5639311). On the dorsal side, secondaries were either uniformly blackish, with rectrices showing less distinct dark bands (#1 ML154929361), or grayish with conspicuous black bands on both secondaries and rectrices (#6 ML611870354). In some individuals, the upperwings were white with multiple prominent black spots (#6 ML610246262). The alula, and the median and greater primary coverts were black (#6 ML610246262). The crest was entirely white (#6 WA5548221), and eye color was dark (#6 ML608436122).

Flight-feathers molt patterns.— Flight feathers showed a uniform, straight edge, as all feathers were from the same generation (#6 WA5639311).

Basic II (second year; 9–20 months; one annual molt cycle completed; N = 27)

Body and flight-feather phenotypic aspects.— This age class was exclusively monomorphic. The overall plumage was bicolored with the dorsal side being grayish marked by conspicuous dark feathers, although whitish spots could persist on the median and greater upperwing coverts, and the rectrices showed multiple fine, well-defined bands (Table S2, #18 WA3085160, #26 ML427487941). The dorsal feathers began molting simultaneously with the inner primaries (#5 ML 616,902,304, ML616902306). While the ventral side remained predominantly white, as it was in basic I plumage (#4 ML633659342, #10 ML471905141). The crest was entirely white, with a conspicuous black tip (#13 WA2893763) or a washed black tip (#18 WA3085160), and eye color was dark (#7 WA 3,011,540) or light (#5 ML 616902304).

Flight-feathers molt patterns.— Flight feathers showed two generations, with newly grown feathers on the ventral side contrasting clearly with those retained from basic I plumage; these new feathers also exhibited a clearer and more distinct banding pattern (#4 ML633659342, #10 ML471905141). These two individuals showed similar levels of primary-feather replacement but differed in the extent of secondary and rectrix molt; consequently, the trailing edge of the flight feathers appeared irregular.

Basic III (third year; 21–32 months; two annual molt cycles completed; N = 31)

Body and flight-feather phenotypic aspects.— This age class was dimorphic. Light-plumaged individuals were overall tricolored (Table S3, #1 ML371685351, #26 ML618625221). The dorsal side was overall black, with the upperwing coverts showing a conspicuous grayish or whitish feathers retained from previous age classes (#25 ML294309181, #26 ML608838877). The ventral side showed a gray head and chest contrasting with a white belly (#9 WA5689695), although some

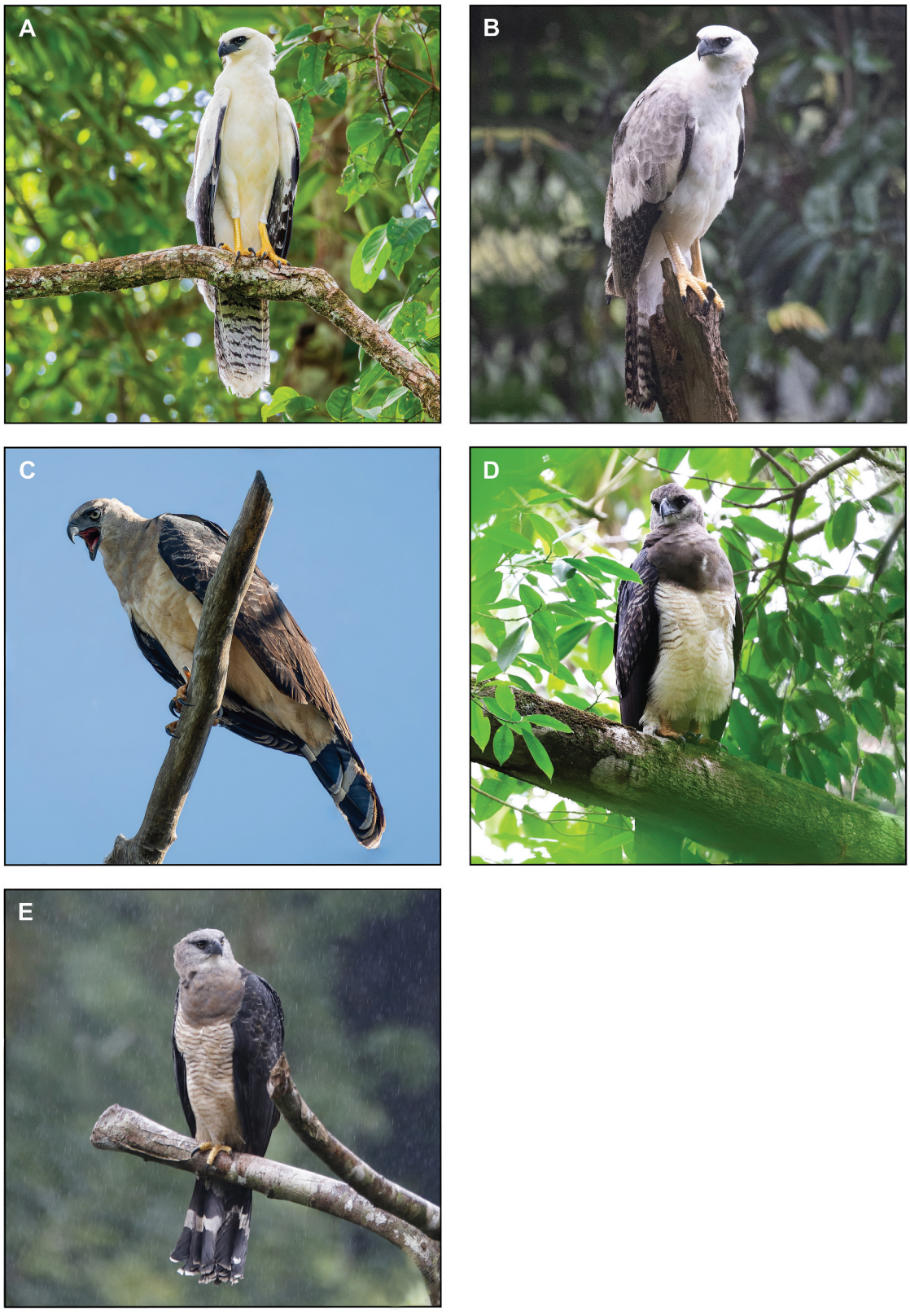


Figure 1. Plumage sequences and phenotypic aspect (overall coloration and pattern) of each age class of the Crested Eagle based on eBird photographs deposited in the Cornell Lab of Ornithology |Macaulay Library. (A) Basic I (juvenile; ≤8 months; no annual molt cycle completed; ML 608,436,122), photographed by Eric Kershner. (B) Basic II (second year; 9–20 months; one annual molt cycle completed; ML 616,902,296), photographed by John C. Mittermeier. (C) Basic III (third year; 21–32 months; two annual molt cycles completed; ML 580,818,621), photographed by Priscilla Diniz. (D) Basic IV (fourth year; 33–44 months; three annual molt cycles completed; ML 617,492,158), photographed by Alexander Alvarado Chacón. (E) Basic V (adult; ≥45 months onwards; four or more annual molt cycles completed; ML 626,217,817), photographed by Diego Monsalve Serna.



Figure 2. Plumage sequences and phenotypic aspect (overall coloration and pattern) of each age class of the Crested Eagle based on eBird photographs deposited in the Cornell Lab of Ornithology |Macaulay Library. (A) Basic I (juvenile; ≤8 months; no annual molt cycle completed; ML 608,271,696), photographed by Patricia Mejia. (B) Basic II (second year; 9–20 months; one annual molt cycle completed; ML 471,905,141), photographed by Nailson Júnior. (C) Basic III (third year; 21–32 months; two annual molt cycles completed; ML 371,689,521), photographed by José Santos Zúñiga Sánchez. (D) Basic IV (fourth year; 33–44 months; three annual molt cycles completed; ML 140,279,621), photographed by Rick Szabo. (E) Basic V (adult; ≥45 months onwards; four or more annual molt cycles completed; ML 640,004,231), photographed by Cameron Rutt.



Figure 3. Phenotypic aspect (overall coloration and pattern) of each morph-type of the Crested Eagle in Basic V plumage (adult; ≥45 months onwards; four or more annual molt cycles completed) based on eBird photographs deposited in the Cornell Lab of Ornithology |Macaulay Library. (A) brownish-barred morph-type (ML 626,217,817), photographed by Diego Monsalve Serna. (B) whitish-barred morph-type (ML 180,388,161), photographed by Victor Castanho. (C) unbarred black morph-type (ML 142,597,131), photographed by Daniel Aldana.

individuals started to exhibit fine, brownish bars, especially on the thighs and lower belly (#4 WA6678533, #7 WA1649416). The degree of banding in the flight feathers varied as some individuals showed few, well-defined bands on primaries, secondaries, and rectrices (#4 WA6678533, #11 WA4912388, #19 ML622341674), while others exhibited multiple, narrower bands (#1 ML371689521, #17 WA4624843, #18 ML240005521). The crest was uniformly dark (#22 WA5521320), and eye color was dark (#3 WA7024977) or light (#13 ML580818621).

Flight-feathers molt patterns.— Newly replaced and older flight feathers in the primaries and secondaries were less conspicuous than those in the rectrices; consequently, the trailing edge of the rectrices appeared irregular (# 1 ML371689521, #20 WA3934699). It appears that in this age class all flight feathers from basic I plumage were molted (# 1 ML371689521, #20 WA3934699).

Body and flight-feather phenotypic aspects.— Dark-plumaged individuals were overall blackish, with conspicuous remnants of whitish feathers, especially on the belly and upperwings (Table S4 #2 ML41420521, #3 WA3886876). The dorsal side was mostly black, and the upperwing coverts showed conspicuous grayish or whitish feathers retained from previous age classes (#33 WA886876). The ventral side showed a gray head and chest contrasting with a whitish belly marked with black lines or dots (#2 ML41420521, #4 WA4314408). The degree of banding in the flight feathers likely varied among individuals some exhibited multiple narrow bands (#5 WA4202977), whereas others may have shown more distinct, well-defined bands, although this was not well documented except for the rectrices (#2 ML41420521). The crest appeared possibly uniformly dark, although this trait was poorly documented, and eye color was dark (#3 WA3886876) or light (#5 WA4202977).

Flight-feathers molt patterns.— It appears that newly replaced and older flight feathers in the primaries and secondaries were less conspicuous, like in light-plumaged individuals (#5 WA4202977). In this individual, the inner new basic III primaries showed a similar phenotypic aspect to basic II primaries, while the remaining flight feathers belonged to basic II plumage.

Basic IV (fourth year; 33–44 months; three annual molt cycles completed; N = 16)

Body and flight-feather phenotypic aspects.— Light-plumaged individuals resembled those in basic V but showed less defined coloration and patterns (Table S5, #9 WA6378074). The dorsal side was predominantly black, with variation on the upperwings, which were mainly grayish (#10 WA5194592), although some individuals still exhibited a few whitish feathers (#4 WA1855820). On the ventral side, the head, throat, and chest exhibited well-defined colors, whereas the belly, thighs, and undertail coverts showed irregular brownish barring (#10 WA5194592). The barred secondaries were not uniformly aligned, as they consisted of retained feathers from previous age classes (#5 WA2452420, #6 WA560139). The crest was uniformly dark (#4 WA1855820), and eye color was dark (#1 ML617492158) or light (#9 WA6378074).

Flight-feathers molt patterns.— The phenotypic aspect of the primaries and secondaries in basic IV

plumage were completely different from those of the previous three age classes (#5 WA2452420, #6 WA560139). The contrast between new and old flight feathers was conspicuous in this age class, especially on the dorsal side, with older feathers appearing brownish and newer feathers showing more vivid coloration (#2 ML140279621).

Body and flight-feather phenotypic aspects.— Dark-plumaged individuals were overall blackish, and some resembled those in basic V but showed less well-defined coloration and patterns (Table S6, #3 WA5475769, #5 WA6287817). The dorsal side was predominantly black, with some variation on the upperwings, which were mainly black (#1 WA2085758), or back with whitish tip (#3 WA5475769). On the ventral side, the head, throat, chest, belly, thighs, and undertail coverts exhibited well-defined colors, although individual variation resulted in irregular coloration across these traits (#3 WA5475769, #5 WA6287817, #6 ML199588731). The crest was uniformly dark (#3 WA5475769), and eye color was dark (#3 WA5475769) or light (#5 WA6287817).

Flight-feathers molt patterns.— The contrast between new and old flight feathers was conspicuous in this age class, especially on the dorsal side, with older feathers appearing brownish and newer ones showing more vivid coloration (#1 WA1844663).

Basic V (adult; ≥45 months onwards; four or more annual molt cycles completed; N = 70)

Body and flight-feather phenotypic aspects.— This age class was polymorphic, comprising three discrete plumage morphs (Figure 3). The brownish-barred morph exhibited an overall light-colored plumage (Figure 3A). The dorsal side may be uniformly black (Table S7, #19 WA5602239), uniformly black with banded secondaries (#12 WA5030395), or show gray spotting on the upperwing coverts (#7 ML631003734). The ventral side was also highly variable, with individuals showing gray or whitish throats, light to intense gray bellies, and brownish-barred white bellies and undertail coverts that varied in intensity, width, and surface coverage (#30 WA6917459, #31 WA6861572, #32 WA3760692). The number of bands on the primaries and secondaries, as well as the width of the rectrix bands, was highly variable. Some individuals showed few bands on the primaries and secondaries and broad rectrix bands (#15 ML640004231), whereas others exhibited multiple bands and narrow rectrix bands (#24 WA6302847, #26 WA4309190). The width of the rectrix bands was particularly evident in perched individuals (#2 ML539363981, #8 ML626217817, #19 WA5549324). The crest could be either uniformly dark (#32 WA3760692) or black with a central white band (#17 WA253772), and eye color was dark (#10 WA5310028) or light (#20 WA6857453).

Flight-feathers molt patterns.— Flight feathers showed a uniform, straight edge, as all feathers corresponded to basic V plumage without retained feathers from previous generations; this pattern was also consistent across the following morph-types.

Body and flight-feather phenotypic aspects.— The white-barred morph exhibited an overall dark-colored plumage, but with conspicuous white barring on the underwings, belly, thighs, and undertail coverts (Figure 3B). The degree of barring on the body varied among individuals – some exhibited multiple narrow bands (Table S8, #19 WA3411489), whereas others showed fewer but broader bands (#10 WA2237190). The chest was uniformly black, and the throat ranged from grayish to whitish, with a distinct central gular line (#2 ML580121581) or entirely black (#10 WA2237190). The head and cheeks were light gray, with whitish tips on the cheeks (#1 ML636497444). The dorsal side was black (#19 WA3515948), with white spots on the marginal and lesser upperwing coverts (#1 ML636497444). While on the ventral side, the primaries and secondaries were black with multiple narrow white bands and a conspicuous black wing tip (#2 ML457333481), or fewer bands and a conspicuous black wing tip (#19 WA3506140). The rectrices showed two conspicuous grayish bands on both dorsal and ventral sides (#1 ML636497444, #2 ML457333481). The crest was uniformly black (#11 ML489115411), and eye color was dark (#11 ML489115411) or light (#2 ML609811141).

Body and flight-feather phenotypic aspects.— The unbarred-black morph exhibited a complete dark-colored plumage (Figure 3C). Although some individuals exhibited small whitish spots on the thighs (Table S9, #5 ML193961161). Rectrices showed two distinct gray bands on both dorsal and ventral sides when perched (#5 ML193961161), and three gray bands on the ventral side in flight (#8 ML173988991). The underwings were black, with white spots on the greater underwing coverts, while the primaries and secondaries were black with multiple broad white bands and a conspicuous black wing tip (#8 WA3465858). The crest was entirely black (#4 ML142597091) or displayed a subterminal white band (#5 ML193961161), eye color was dark (#1 ML632527418) or light (#4 ML203247091).

Discussion

Based on photographs of 152 individuals available on citizen science platforms, and using a framework established through comparisons with more well-studied raptors, the present analyses indicate that the Crested Eagle acquires its definitive basic plumage after four annual molt cycles, progressing through four distinguishable non-definitive basic plumages. The analyses further support the recognition of three morph-types based on discrete color traits: brownish-barred, whitish-barred, and unbarred-black. Despite the limitations inherent to this approach, the resulting framework provides a practical tool for assigning age classes and morph-types, facilitating future studies and improving data quality in assessments of population age and morph-type structure in this cryptic forest raptor.

Delayed plumage maturation and color polymorphism

The Crested Eagle is unique among Neotropical raptors in exhibiting delayed plumage maturation and color polymorphism. Yet, despite this uniqueness, early ontogenetic stages are characterized by conspicuous white plumage that is widely shared with other Neotropical forest-dwelling raptors, either transiently during development or persisting into the definitive basic plumage – regardless of body size or phylogenetic position – such as *Leptodon* spp., Harpy Eagle, *Spizaetus* spp., White-necked Hawk (*Buteogallus lacernulatus*), and *Pseudastur* spp. (Ferguson-Lees and Christie 2001; Clark and Schmitt 2017; Pallinger and Menq 2022). The repeated occurrence of conspicuous white plumage across unrelated taxa indicates that this trait has evolved independently in multiple lineages rather than representing a unique derived character of any single clade, likely reflecting shared selective pressures in Neotropical forest raptors. Although the ecological or evolutionary function of this coloration remains unresolved, its strong geographic clustering is notable. This pattern appears largely restricted to the Neotropics, with only limited parallels among African and Indo-Malayan forest raptors (Thiollay 1985), pointing to a biogeographically structured evolutionary syndrome rather than a universal raptor trait.

Extending this coloration framework to Neotropical forest raptors, discrete coloration patterns within a species, regardless of age, have been linked to morph-types, and under this framework some tropical raptors have been classified as polymorphic (e.g. Pallinger and Menq 2022). However, color polymorphism is typically defined as the occurrence of multiple genetically based color phenotypes within populations (e.g. White and Kemp 2016). Because plumage-based phenotypes often differ between basic I plumage and definitive basic plumage stages, age-specific expression of coloration and pattern must be explicitly accounted for when interpreting phenotypic trait. In this context, some species exhibit discrete morph-types in basic I plumage that converge into a single phenotype – monomorphic – after successive annual molt cycles upon acquiring definitive basic plumage, as exemplified by the Gray-headed Kite (*Leptodon cayanensis*), and such cases may not meet the strict definition of polymorphism *sensu* White and Kemp (2016). In contrast, other species show a monomorphic basic I plumage that transitions into multiple phenotypic morphs through successive annual molt cycles toward definitive basic plumage, thereby maintaining discrete morphs in the breeding population, as observed in the Crested Eagle in this study. Collectively, these patterns highlight the complexity of color polymorphism in Neotropical forest raptors and highlight the need for further research beginning with careful documentation of plumage ontogeny to improve interpretation of evolutionary and ecological patterns of coloration.

Age-related plumage in relation to the post-fledging period

Neotropical Harpiinae exhibit some of the longest post-fledging periods of parental care among raptors. In the Harpy Eagle, fledging remains within 1,500 m of the nest for up to 28–29 months and continue to be provisioned by their parents (Muñiz-López et al. 2012; Urios et al. 2017). In terms of age-related plumage, this extended period of parental dependency means that Harpy Eagles remain within the natal territory during basic I and II plumages and may even overlap with the onset of basic III. Although precise data on the post-fledging period of the Crested Eagle are lacking (but see Whitacre et al. 2012), available evidence suggests that it shares similar life-history traits. Because the Crested Eagle is so rare and elusive, accurate age-class assignment in non-definitive basic plumage is particularly valuable: encountering individuals in basic I and II plumages strongly suggests that a breeding pair – and potentially a nest – is nearby. By contrast, individuals in basic III or later stages are likely independent and dispersing. Careful assignment of age classes in non-definitive basic plumage thus provides a powerful indirect tool for inferring breeding proximity and early dispersal dynamics, with direct implications for the

ecological study and conservation of this elusive forest raptor.

Strengths and limitations of the methodological approach

Accurate interpretation of plumage ontogeny and color polymorphism depends on reliable assignment of age classes and morph-types. The methodological framework applied here provides a practical approach for studying this cryptic, low-density apex raptor, although some limitations should be acknowledged. In particular, the low sample size of dark-plumaged individuals in basic III and basic IV introduces uncertainty in interpreting variation within these age classes. Age-class assignments are based on biological inference rather than known-age individuals; however, these inferences are supported by the predictable stepwise flight-molt pattern, in which successive annual molt cycles generate distinct feather generations that allow reconstruction of plumage progression. Despite these constraints, this study provides the first systematic assessment of plumage ontogeny and color polymorphism in the Crested Eagle, establishing a consistent framework for age- and morph-type classification. Future research using marked, known-age individuals will be essential to validate and refine these assignments, and in the meantime this framework provides a foundation for further studies on plumage ontogeny and color polymorphism in the Crested Eagle and may be applicable to other low-density Neotropical apex raptors, such as the Harpy Eagle.

Pros and cons of citizen science photo repositories

The present study relies entirely on photographs obtained from citizen science platforms, highlighting their value as a complementary resource for ornithological research, particularly for cryptic forest and low-density species such as the Crested Eagle. Photographic records are especially valuable for qualitative assessments because they allow direct examination of plumage patterns across individuals, age classes, and morph-types across the entire distribution range. The continuous addition of new photographs also means that these repositories are dynamic and expanding, increasing the likelihood of documenting rare plumage stages or age classes that would otherwise be difficult to observe through fieldwork, particularly given the challenges of surveying the vast Neotropical rainforest. Despite these advantages, some limitations remain. Most records, particularly those from WikiAves, consist of a single photograph of an individual, often taken from only one angle, which can limit the evaluation of certain plumage characters. In addition, the use of photographs from online repositories may limit the presentation of representative individuals within figures, as some images cannot be reproduced directly and readers may need internet access to examine the full range of plumage variation through the provided links.

The behavior of the Crested Eagle further constrains the photographic documentation of molt patterns of the flight feathers because, unlike many other Neotropical forest raptors that frequently soar above the canopy, it is more often observed perched high within the forest interior (Whitacre et al. 2012), making photographs of individuals in flight relatively uncommon. Consequently, the usefulness of photographic records for documenting molt patterns depends strongly on the posture of the individual. Photographs of perched individuals with the wings spread can provide valuable information on the flight feathers, whereas photographs showing only folded wings offer limited opportunities for assessing molt. Despite these limitations, citizen science photo repositories represent a unique and continually expanding source of information on plumage variation in rare or elusive species and can substantially complement traditional field observations.

Conclusion

Given the extreme rarity and elusiveness of the Crested Eagle the breadth of available photographic data is remarkable. For the first time, these data allow a detailed characterization of plumage variation both within and among age classes, as well as across morph-types. None of the standard field guides for Neotropical raptor identification (e.g. Ferguson-Lees and Christie 2001; Clark and Schmitt 2017; Pallinger and Menq 2022) provide comparable resolution on plumage ontogeny or define the age at which morphs become reliably diagnosable. As a result, many phenotypic traits associated with delayed plumage maturation and color polymorphism in this species have remained largely anecdotal rather than empirically established. By synthesizing citizen science photographic records at an unprecedented scale, this study provides a robust framework for investigating plumage ontogeny and color polymorphism in the Crested Eagle and illustrates the value of opportunistic photographic data for advancing our understanding of the biology of this rare, low-density cryptic forest raptor.

Acknowledgments

I am grateful to the many contributors to eBird and WikiAves Brasil whose photographic records of the Crested Eagle across the Neotropics made it possible to investigate the plumage ontogeny and color polymorphism. I also wish to apologize to the observers whose records were not included in the database, while emphasizing my deep appreciation for their valuable contributions. Vanessa Claire Powell assisted in the logistics of obtaining the photographs used to prepare the three figures, and I thank the Cornell Lab of Ornithology | Macaulay Library for permission to use the photographs. This is Hawk Mountain Sanctuary contribution to conservation science number 434.

Author contributions

CRediT: **Matías A. Juhant:** Conceptualization, Data curation, Investigation, Methodology, Writing – original draft, Writing – review & editing.

Disclosure statement

I do not have any potential conflicts of interest to disclose.

ORCID

Matías A. Juhant http://orcid.org/0000-0002-9612-9778

References

Aguiar-Silva FH et al. 2013. Harpy Eagle nesting territories in Brazilian forests, during the past 15 years. Proceedings of the I Worldwide Raptor Conference; Bariloche: Universidad Nacional del Comahue, Río Negro, Argentina.

BirdLife International. 2017. Species factsheet: Crested Eagle *Morphnus guianensis*. https://datazone.birdlife.org/species/factsheet/crested-eagle-morphnus-guianensis

Briggs CW, Woodbridge B, Collopy MW. 2010. Temporal morph invariance of Swainson's Hawks. J Raptor Res. 44 (1):70–73. https://doi.org/10.3356/JRR-09-06.1

Cabot J, de Vries T. 2004. Age-and sex-differentiated plumages in the two colour morphs of the variable Buzzard *Buteo polyosoma* a case of delayed maturation with subadult males disguised in definitive adult female plumage. Bull Br Ornithol Club. 124(4):272–285.

Clark WS. 2004. Wave moult of the primaries in accipitrid raptors, and its use in ageing immatures. In: Chancellor RD, Meyburg BU, editors. Raptors wordwide. WWGBP and BirdLife; p 795–804.

Clark WS, Schmitt NJ. 2017. Raptors of Mexico and Central America. Princeton University Press.

Edelstam C. 1984. Patterns of moult in large birds of prey. Ann Zoologici Fennici. 21(3):271–276.

Edelstam C. 2001. Raptor moult patterns and age criteria. In: Ferguson-Lees J, Christie DA, editors. Raptors of the world. Houghton Mifflin Harcourt; p 50–53.

Ferguson-Lees J, Christie DA. 2001. Raptors of the world. Houghton Mifflin.

Fuchs J, Johnson JA, Mindell DP. 2012. Molecular systematics of the caracaras and allies (Falconidae: Polyborinae) inferred from mitochondrial and nuclear sequence data. Ibis. 154(3):520–532. https://doi.org/10.1111/j.1474-919X.2012.01222.x

Gomes FBR, Sanaiotti TM. 2015. A review of the distribution of the Crested Eagle, *Morphnus guianensis* (Daudin, 1800) (Accipitridae: Harpiinae), including range extensions. Rev Bras Ornitol. 23(1):36–63. https://doi.org/10.1007/BF03544289

Gregory SMS, Sangster G, Worthy TH, Scofield RP. 2024. Falling through the cracks: a family-group name for a clade of hawks and eagles (Accipitridae) including *Morphnus* Dumont, 1816, *Harpia* Vieillot, 1816, *Harpyopsis* Salvadori, 1875 and *Macheiramphus* Bonaparte, 1850. Avian Syst. 2:5–17.

Howell SNG, Corben C, Pyle P, Rogers DI. 2003. The first basic problem: a review of molt and plumage homologies. Condor. 105(4):635–653. https://doi.org/10.1093/condor/105.4.635

Johnson JA, Brown JW, Fuchs J, Mindell DP. 2016. Multilocus phylogenetic inference among New World vultures (Aves: Cathartidae). Mol Phylogenet Evol. 105:93–99. https://doi.org/10.1016/j.ympev.2016.08.025

Juhant MA. 2026a. Age, physical lesion, and behavior in a polyandrous social trio of variable hawks. J Raptor Res. 60(3):1–6. https://doi.org/10.3356/jrr2568

Juhant MA. 2026b. Framing the natural history of the bay-winged hawk (*Parabuteo unicinctus unicinctus*) for accurate taxonomic assessment. Ornithol Res. 34(1):14. https://doi.org/10.1007/s43388-026-00282-3

Jullien M, Thiollay JM. 1996. Effects of rain forest disturbance and fragmentation: comparative changes of the raptor community along natural and human-made gradients in French Guiana. J Biogeogr. 23(1):7–25. https://doi.org/10.1046/j.1365-2699.1996.00963.x

Miller AH. 1941. The significance of molt centers among the secondary remiges in the Falconiformes. Condor. 43 (2):113–115. https://doi.org/10.2307/1364415

Muñiz-López R, Limiñana R, Cortés GD, Urios V. 2012. Movements of Harpy Eagles *Harpia harpyja* during their first two years after hatching. Bird Study. 59(4):509–514. https://doi.org/10.1080/00063657.2012.722190

Pallinger F, Menq W. 2022. Aves de Rapina do Brasil. Editorial Privately Published.

Raposo Do Amaral FR et al. 2009. Patterns and processes of diversification in a widespread and ecologically diverse avian group, the buteonine hawks (Aves, Accipitridae). Mol Phylogenet Evol. 53(3):703–715. https://doi.org/10.1016/j.ympev.2009.07.020

Schulenberg TS. 2020. Harpy Eagle (*Harpia harpyja*), version 1.0. In: Schulenberg TS, editor. Birds of the world. Cornell Lab of Ornithology. https://doi.org/10.2173/bow.hareag1.01

Seipke SH. 2007. Aging Black-chested Buzzard-Eagles (*Geranoaetus melanoleucus*). In: Bildstein KL, Barber DR, Zimmerman A, editors. Neotropical raptors. Hawk Mountain Sanctuary; p 220–228.

Smith JW. 2020. Crested Eagle (*Morphnus guianensis*), version 1.0. In: Schulenberg TS, editor. Birds of the world. Cornell Lab of Ornithology. https://doi.org/10.2173/bow.creeag1.01

Stresemann E, Stresemann V. 1966. Die Mauser der Vögel. J Ornithol. 107(1):1–448. https://doi.org/10.1007/BF01670791

Thiollay JM. 1985. Species diversity and comparative ecology of rainforest Falconiformes on three continents. In: Newton I, Chancellor RD, editors. Conservation studies on raptors. Paston Press; p 167–179.

Urios V, Muñiz-López R, Vidal-Mateo J. 2017. Juvenile dispersal of Harpy Eagles (*Harpia harpyja*) in Ecuador. J Raptor Res. 51(4):439–445. https://doi.org/10.3356/JRR-16-54.1

Whitacre DF, López J, López G. 2012. Crested Eagle. In: Whitacre DF, editor. Neotropical birds of prey. Cornell University Press; p 164–184.

White TE, Kemp DJ. 2016. Colour polymorphism. Curr Biol. 26(13):R517–R518. https://doi.org/10.1016/j.cub.2016.03.017