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*Photo: Ruth E. Bennett*

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# New sightings of melanistic Green Herons (*Butorides virescens*) in the Caribbean suggest overlooked polymorphism

Jacob R. Drucker[1], Ruth E. Bennett[2,3], Lila K. Fried[4], Mona L. Kazour[5], and Darin J. McNeil, Jr.[2,6]

**Abstract** Intraspecific variation in animal coloration arises from the expression of heritable genes under different selection pressures and stochastic processes. Documenting patterns of intraspecific color variation is an important first step to understanding the mechanisms that determine species appearance. Within the heron genus *Butorides*, plumage coloration varies across space, among distinct taxonomic groups, and within polymorphic populations. The melanistic Lava Heron (*B. striata sundevalli*) of the Galápagos has been the subject of considerable taxonomic confusion and debate, while an erythristic morph of Green Heron (*B. virescens*) has been largely overlooked in recent literature. Here we report a new sighting of three melanistic individuals of Green Heron from Útila, Bay Islands, Honduras, in February 2017. In light of our discovery, we conducted a review of aberrantly plumaged Green Herons and present evidence for the existence of two previously unrecognized color morphs, both primarily found in coastal mangroves of the western Caribbean region. We are the first to formally describe a melanistic morph of Green Heron and discuss the widespread and highly variable erythristic morph within the context of a color-polymorphic Green Heron. We show that the two morphs overlap spatially, and we recommend future work to determine the genetic and selective drivers of this color variation.

**Keywords** Ardeidae, erythrism, Honduras, melanism, polymorphism, Útila

**Resumen** Nuevas observaciones de individuos melánicos de *Butorides virescens* en el Caribe sugiere un polimorfismo ignorado—La variación intraespecífica en la coloración animal proviene de la expresión de genes heredables bajo diferentes presiones de selección y procesos estocásticos. La documentación de los patrones de variación intraespecífica del color es un primer paso importante para comprender los mecanismos que determinan la apariencia de las especies. Dentro de las garzas, la coloración del plumaje en el género *Butorides* varía a lo largo del espacio, entre distintos grupos taxonómicos y dentro de poblaciones polimórficas. El melánico *B. striata sundevalli* de las Galápagos ha sido objeto de considerable confusión taxonómica y debate; mientras que el morfo rojizo de *B. virescens* ha sido ampliamente ignorado en la literatura reciente. Aquí presentamos una nueva observación de tres individuos melánicos de *B. virescens* en Útila, islas de la bahía, Honduras, en febrero de 2017. A la luz de nuestro descubrimiento, realizamos una revisión de individuos de esta especie con plumaje aberrante y presentamos evidencia de la existencia de dos morfos de color no descritos previamente y encontrados primariamente en los manglares costeros de la región del Caribe occidental. Somos los primeros en describir formalmente un morfo melánico de *B. virescens* y discutir la extensión y alta variabilidad del morfo rojizo dentro del contexto del color polimórfico de la especie. Mostramos que ambos morfos se superponen espacialmente y recomendamos un trabajo futuro para determinar los factores genéticos y selectivos de esta variación de color.

**Palabras clave** Ardeidae, eritrismo, Honduras, melanismo, polimorfismo, Útila

**Résumé** De nouvelles observations de Hérons verts (*Butorides virescens*) mélaniques dans la Caraïbe suggèrent l'existence d'un polymorphisme mal connu—La variation intraspécifique de la coloration animale provient de l'expression de gènes héréditaires sous différentes pressions de sélection et processus stochastiques. La documentation des modèles de variation de la coloration intraspécifique est une première étape importante pour comprendre les mécanismes qui déterminent l'apparence d'une espèce. Au sein des hérons du genre *Butorides*, la coloration du plumage varie en fonction du lieu, parmi des groupes taxonomiques distincts, et au sein de populations polymorphes. Le héron strié mélanique (*B. striata sundevalli*) des Galápagos (*Lava Heron* en anglais) a fait l'objet de confusions et de débats taxonomiques considérables, tandis qu'une forme érythristique du Héron vert (*B. virescens*) a été largement négligée dans la littérature récente. Nous signalons ici une nouvelle observation de trois individus mélaniques de Héron vert, à Útila, Islas de la Bahía, Honduras, en février 2017. À la lumière de notre découverte, nous avons procédé à un examen des Hérons verts dont le plumage était aberrant, et nous présentons des preuves de l'exis-

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tence de deux formes de coloration précédemment non reconnues, toutes deux principalement présentes dans les mangroves côtières de l'ouest de la région Caraïbe. Nous sommes les premiers à décrire officiellement une forme mélanique du Héron vert et à discuter de la forme érythristique répandue et très variable dans le contexte de la coloration polymorphe de cette espèce. Nous montrons que les deux formes se chevauchent spatialement et nous recommandons que des recherches soient réalisées pour déterminer les facteurs génétiques et sélectifs de cette variation de coloration.

**Mots clés** Ardeidae, érythrisme, Honduras, mélanisme, polymorphisme, Útila

Intraspecific variation in coloration occurs commonly throughout the natural world. Geographic color variation is pervasive across taxa and may result from local adaptation to environmental conditions or stochastic processes such as genetic drift (Zink and Remsen 1986). In addition to geographic variation in color expression, a species may exhibit color polymorphism whereby a population exhibits two or more co-occurring and heritable color types that occur at frequencies greater than those expected by recurrent mutations (Huxley 1955, Roulin 2004). Color polymorphism is genetically distinct from geography-based clinal variation in color expression, and the frequency of morph occurrence is typically driven by selection and to a lesser extent by genetic drift (Gray and McKinnon 2007). The frequency and number of morphs may vary over a species' range, and color polymorphisms are not typically associated with other traits that determine taxonomic identity such as differences in vocalizations, morphology, and life history. Finally, variation in coloration may be caused by spontaneous, often recurrent mutations, as in the cases of rare melanistic or leucistic individuals that occur within an otherwise monomorphic population (van Grouw 2017). The distinction between aberrant coloration like leucism and color polymorphism is the subject of debate, and no clear guideline exists as to the frequency at which a color type needs to be present in a population in order to qualify as a formal morph (Ford 1945, van Grouw 2017).

The heron genus *Butorides* provides a complex example of color variation within a taxonomic group; plumage within this genus varies both clinally across geographies and polymorphically within populations (Payne 1974, Hayes 2002). While both members of *Butorides* were once considered conspecific under the common name "Green-backed Heron" (*B. striatus*; AOU 1993), the genus is presently comprised of two species readily discerned visually by neck plumage: the rufous-necked Green Heron (*B. virescens*) of North America and the Caribbean, and the gray-necked Striated Heron (*B. striata*) of South America, eastern Panama, and the Old World (AOU 1998).

Green Heron encompasses 5 recognized subspecies, while Striated Heron contains 21 subspecies, of which just 2 occur in the Western Hemisphere (Clements *et al.* 2016). In Green Heron, subspecies are separated primarily on the basis of morphological measurements, with *B. v. anthonyi* of western North America being the largest and *B. v. bahamensis* of the Bahamas being the smallest. The plumages of these subspecies vary, with *B. v. frazari* of southern Baja, Mexico, having darker, heavily purple tones in its neck while *B. v. anthonyi* and *B. v. bahamensis* have paler rufous tones. The widespread nominate *B. v. virescens* averages intermediate among the other subspecies, although it exhibits much variation in plumage tones. *B. v. maculatus* of Central America and the Caribbean looks similar to *B. v. virescens*, but is larger. (Oberholser 1912a, Payne 1974, Monroe and Browning 1992, Hayes 2002).

In the Americas, Green Heron and Striated Heron exhibit species-specific neck color with an intermediate zone in central Panama, the southern Caribbean, and Tobago (Hayes 2002), and well-documented variation in northern South America, eastern Panama, and the southern Caribbean where the two species hybridize (Payne 1974, Hayes 2006, Hayes *et al.* 2013). Neck color was used by Linnaeus (1758a, 1758b) to differentiate Green Heron and Striated Heron in his original descriptions of these species. Later, Payne (1974) introduced a plumage scoring system to rank neck color of individuals across this spectrum, which has been useful in describing *Butorides* throughout the Americas (Hayes 2006, Hayes *et al.* 2013). On the Payne scale, lowest-scoring individuals (1) have fully pale gray necks, while the highest-scoring individuals (9) have dark purplish-maroon necks. Exceptionally high-scoring birds (8–9) are known to make up a large percentage of the population in northwestern and southeastern Panama (Wetmore 1965, Payne 1974). High-scoring birds are also known from the Caribbean, where they have caused taxonomic confusion in the past. A high-scoring individual from the Swan Islands, Honduras, was initially described as its own species, *B. saturatus* (Ridgway 1888), based on its dark plumage, but is now considered a synonym of *B. virescens* (Fisher and Wetmore 1931) that ranks highly on the Payne scale. High-scoring birds are also known from Puerto Rico; Tamaulipas and Quintana Roo, Mexico; and Florida (Payne 1974).

In addition to the specific variation in neck color, two geographically restricted morphs are known to occur in *Butorides*. The first is a uniformly reddish-brown (i.e., erythristic) morph described in Green Heron throughout coastal areas of Middle America and the Caribbean. Specimens showing strong reddish pigment in the neck, breast, back, and belly feathers and lacking the typical white throat stripe, white malar lines, and pale wing and covert edging of Green Heron have been collected from Madeira Hummock, Florida; the main island of Cuba; the Isle of Pines, Cuba; and the Pearl Islands, Panama (Bangs 1915). A series of Cuban specimens with this plumage pattern was originally classified as a separate species, *B. brunescens*, with no finding of color introgression with the typical Green Heron (Lembeye 1850, Oberholser 1912b). However, the discovery of a breeding population of aberrantly plumaged Green Herons on the Pearl Islands of Panama, of which 10 collected specimens expressed a gradient of dark red plumage similar to the erythristic Cuban morph and "every stage of intermediate coloring" (Thayer and Bangs 1905:142), caused debate and taxonomic confusion. Oberholser (1912b) claimed the Pearl Island specimens retained a gular

stripe down the ventral side of the neck and wing edgings, and were therefore not *B. brunescens*, though the text description of Thayer and Bangs (1905) clearly describes some individuals that completely lack throat and neck markings. Ultimately, Bangs (1915) classified all of these aberrantly dark and red plumage types as an erythristic morph of Green Heron in agreement with the current taxonomy (AOU 1998). Later work by Payne (1974) described Pearl Island birds as high-scoring Green Heron on his *Butorides* neck color index. However, this plumage type has not been discussed in detail in the past century.

Somewhat better known, but still poorly understood, is a melanistic population of Striated Heron from the Galápagos Islands currently classified as the Lava Heron (*B. striata sundevalli*). Typical adults from this population have uniformly dark-gray plumage, reduced or absent malar and throat stripes, and reduced or absent wing covert edging. Their bills also average longer and thicker than other Striated Herons, and they forage with less movement (Kushlan 2009). On seven of the Galápagos Islands, Lava Herons coexist with other Striated Herons that appear identical to those on the mainland, and plumage intergrades are common (Payne 1974, Harris 1982). The taxonomic position of Lava Heron has been the subject of considerable debate. It has periodically been considered a full species, though the South American Classification Committee rejected a proposal to elevate it to full species status in 2002 and maintains its classification as a melanistic morph of Striated Heron (Hartert 1920, Harris 1973, 1982, Kushlan 1983, Hancock and Kushlan 1984, AOU 1993, 1998, Gill and Donsker 2017).

Records of other aberrantly plumaged Green Herons exist from the Caribbean region, with plumages undescribed by the Payne (1974) scale. Two exceptionally dark individuals with primarily black, iridescent plumage, and lacking yellow lores, malar stripes, and gular stripes were reported from Cuba (McLachlan 2011). These individuals represent the first documented case of melanism in this species. In February 2017, we encountered three melanistic individuals from Útila, Honduras, bearing a strong resemblance to those documented by McLachlan (2011) 1,113 km away.

In light of our finding, we sought to determine if evidence existed of an undocumented melanistic morph of Green Heron in the Caribbean region. We compiled records of atypical Green Heron plumage in the Caribbean region from published literature, the eBird database (Sullivan *et al.* 2009), and specimens from the Museum of Comparative Zoology and National Museum of Natural History. We performed an exhaustive search of all eBird checklists with images of Green Heron from all countries in Middle America and all U.S. states with a Gulf of Mexico coastline up to October 2017. Here we describe our field observations of the melanistic individuals from Útila, Honduras, and include them in a review of Green Heron plumage variation in Middle America and the Caribbean region.

## Observations

On 4 February 2017, we observed three melanistic Green Herons along Rock Harbor Canal in Útila, Bay Islands, Honduras (16°06'N, 86°56'W). The canal is surrounded by mangrove forest dominated by *Rhizophora mangle* and *Conocarpus erectus* and is integrated within a matrix of four other forest types: *Laguncularia* mangrove forest, a transition zone, back-beach forest, and freshwater swamp forest (Fickert and Grüninger 2010). All three melanistic birds were solitary and observed perched or skulking low on the stilt roots of a *Rhizophora mangle*. We also observed at least five typically plumaged (Payne 1974) Green Herons throughout the canal, though never in direct proximity to the melanistic individuals.

**Fig. 1.** First melanistic Green Heron encountered in Útila, Bay Islands, Honduras, on 4 February 2017. Photograph by Darin J. McNeil, Jr.

We photographed two of the melanistic individuals and observed several minutes of playback-prompted vocal behavior of one bird, though recordings were not successfully made. We detected no differences between the calls of the melanistic and normal-plumaged Green Herons. The first melanistic individual observed (Fig. 1) completely lacked the typical buffy-white gular stripe, malar stripes, and yellow lores of Green Heron, and instead exhibited a uniformly dark gray throat, breast, and belly with hints of rufous and purple. The cap showed the species' typical blue-black coloration, but the cap color extended to the throat instead of to the top of the bill. The bill was uniformly dark and the lores showed the same blue-black color as the cap. The upper back and scapulars were characterized by medium-length dark plumes with a greenish iridescence. The wings were dark with greenish iridescence and completely lacked the pale margins that Green Heron typically shows on the upperwing coverts.

**Fig. 2.** Second melanistic Green Heron encountered in Útila, Bay Islands, Honduras, on 4 February 2017. Photograph by Ruth E. Bennett.

**Table 1.** Descriptions of the six types of Green Heron plumage found in the Caribbean and Middle America with documentation and locations of all aberrantly plumaged individuals. UNK = unknown

| ID | Plumage Type[a] | Description | Documented By | Documentation | Date (m/yyyy) | Location | Geographic Coordinates |
|---|---|---|---|---|---|---|---|
| 1 | a | typical adult | NA | NA | NA | NA | NA |
| 2 | b | melanistic | Drucker *et al.* | Fig. 1, this study | 2/2017 | Útila, Bay Islands, Honduras | 16°06'N, 86°55'W |
| 3 | b | melanistic | Drucker *et al.* | Fig. 2, this study | 2/2017 | Útila, Bay Islands, Honduras | 16°06'N, 86°55'W |
| 4 | b | melanistic | Drucker *et al.* | text description, this study | 2/2017 | Útila, Bay Islands, Honduras | 16°06'N, 86°55'W |
| 5 | b | melanistic | D. Bell | S17478571[b] | 1/2014 | Camino San Felipe, Yucatan, Mexico | 21°33'N, 88°11'W |
| 6 | b | melanistic | A. McLachlan | McLachlan 2011 | 2/2011 | Cayo Santa María, Cuba | 22°39'N, 79°03'W |
| 7 | b | melanistic | A. McLachlan | McLachlan 2011 | 2/2011 | Cayo Santa María, Cuba | 22°39'N, 79°03'W |
| 8 | NA | intermediate | K. Alpízar-Trejos | Alpízar-Trejos 2012 | 12/2011 | Isla del Coco, Costa Rica | 05°32'N, 87°03'W |
| 9 | c | erythristic | R. Martinez | S32072621[b] | 10/2016 | Ambergris Caye, Belize | 17°53'N, 88°01'W |
| 10 | c | erythristic | O. Komar | S38006866[b] | 7/2017 | Útila, Bay Islands, Honduras | 16°06'N, 86°54'W |
| 11 | c | erythristic | J. Vandermeulen | S34579208[b] | 2/2017 | Cayo Las Brujas, Cuba | 22°37'N, 79°10'W |
| 12 | c | erythristic | T. Moulton | S34342637[b] | 2/2017 | Cayo Coco, Cuba | 22°30'N, 78°24'W |
| 13 | c | erythristic | C. Lange | S26696142[b] | 1/2016 | Caye Caulker, Belize | 17°44'N, 88°02'W |
| 14 | c | erythristic | P. Bedrossian | S37789711[b] | 1/2017 | Roatán, Bay Islands, Honduras | 16°16'N, 86°35'W |
| 15 | c | erythristic | L. Jones | S31943553[b] | 10/2016 | Toledo, Belize | 16°13'N, 88°56'W |
| 16 | c | erythristic | R. Martinez | S29764187[b] | 5/2016 | Stann Creek, Belize | 16°35'N, 88°24'W |
| 17 | c | erythristic | L. Owens | S14223460[b] | 5/2013 | Blackbird Caye, Belize | 17°18'N, 87°48'W |
| 18 | c | erythristic | D. Faulder | S18366517[b] | 2/2012 | Ambergris Caye, Belize | 17°54'N, 87°58'W |
| 19 | c | erythristic | J. Lembeye | Lembeye 1850 | 1800s | Cuba | UNK |
| 20 | c | erythristic | W. Brown | Thayer and Bangs 1905 | 2/1904 | Isla del Rey, Panama | 8°24'N, 78°55'W |
| 21 | c | erythristic | W. Brewster | MCZ 72982[c], Bangs 1915 | 3/1902 | Madeira Hummock, Florida | 27°17'N, 82°47'W |
| 22 | c | erythristic | W. Palmer and J. Riley | NMNH 172719[d], Oberholser 1912a | 7/1900 | Nueva Gerona, Isle of Pines, Cuba | 21°41'N, 82°50'W |
| 23 | d | typical juvenile | NA | NA | NA | NA | NA |
| 24 | e | dark juvenile | R. Rumm | S40053158[b] | 10/2017 | Guanaja, Bay Islands, Honduras | 16°27'N, 85°52'W |
| 25 | e | dark juvenile | O. Komar | S38041019[b] | 7/2017 | Útila, Bay Islands, Honduras | 16°06'N, 86°55'W |
| 26 | e | dark juvenile | J. Peters | Peters 1913 | 2/1913 | Camp Mengel, Quintana Roo, Mexico | 18°13'N, 88°37'W |
| 27 | f | red juvenile | A. and J. Raddatz | S27930610[b] | 1/2016 | Laguna Larga, Ciego de Ávila, Cuba | 22°32'N, 78°22'W |
| 28 | f | red juvenile | S. Barnard | S34098072[b] | 1/2017 | Roatán, Bay Islands, Honduras | 16°16'N, 86°36'W |

[a]Plumage types match plates in Fig. 4.
[b]Checklist number in eBird database (Sullivan *et al.* 2009)
[c]Harvard Museum of Contemporary Zoology
[d]Smithsonian Institution National Museum of Natural History

The tail was slate gray, and the legs and feet were gray with some yellow on the toes.

The second individual was substantially darker than the first, with a steely blue-black head, throat, breast, and belly (Fig. 2). As with the first individual, it lacked the buffy-white gular and malar stripes, yellow lores, and yellow on the lower mandible. A dark purple streak extended down the center of the throat. The upper back and scapulars were characterized by long, black plumes with blue iridescence that contrasted with the bird's body plumage. The wings were black with a bluish cast and showed no pale edging on the upperwing coverts. The legs and feet were primarily yellow in contrast with the first individual. The third dark individual we observed strongly resembled the second (Fig. 2), but was almost certainly a different individual at ~1 km distance from the second bird.

None of these dark birds showed streaking on the underparts,

**Table 1.** cont.

| ID | Age | Malar Stripes | Gular Stripe | Belly Color | Upperwing Covert Color | Upperwing Covert Edging | Edging Color | Leg Color | Mandible Color | Lore Color | Auricular Color | Throat Color |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | AHY | present | present | gray | green | broad | white | yellow | yellow | yellow | rufous | rufous |
| 2 | AHY | absent | absent | black | green | absent | NA | gray | black | black | black | black |
| 3 | AHY | absent | absent | black | green | absent | NA | yellow | black | black | black | black |
| 4 | AHY | absent | absent | black | green | absent | NA | yellow | black | black | black | black |
| 5 | AHY | UNK | UNK | black | green | UNK | NA | gray | black | UNK | black | black |
| 6 | AHY | absent | absent | black | green | absent | NA | gray | black | black | black | black |
| 7 | AHY | absent | absent | black | green | absent | NA | gray | black | black | black | black |
| 8 | AHY | absent | absent | gray | green | broad | red | gray | yellow | black | black | gray |
| 9 | AHY | reduced | absent | gray | green | UNK | NA | gray | black | black | black | rufous |
| 10 | AHY | absent | absent | gray | green | reduced | white | yellow | black | black | rufous | rufous |
| 11 | UNK | reduced | reduced | UNK | green | broad | white | yellow | black | black | rufous | rufous with light streaking |
| 12 | AHY | absent | absent | red | red | absent | NA | gray | black | black | rufous | rufous |
| 13 | AHY | reduced | absent | gray | green | absent | NA | yellow | black | black | rufous | rufous |
| 14 | AHY | absent | absent | UNK | green | absent | NA | UNK | black | black | rufous | rufous |
| 15 | AHY | absent | UNK | gray | green | absent | NA | yellow | yellow | gray | rufous | rufous |
| 16 | AHY | absent | absent | gray | green | reduced | red | yellow | black | black | black | rufous |
| 17 | AHY | absent | absent | gray | green | broad | white | yellow | black | black | black | rufous |
| 18 | AHY | absent | absent | gray | green | broad | red | orange | black | black | gray | rufous |
| 19 | AHY | absent | absent | red | green | reduced | red | dark | dark | dark | rufous | rufous |
| 20 | UNK | absent | absent | gray-red | green | reduced | red | dark | dark | UNK | UNK | rufous |
| 21 | ASY | absent | absent | red | red | reduced | red | UNK | UNK | UNK | rufous | rufous |
| 22 | AHY | absent | absent | gray | green | reduced | red | UNK | black | black | rufous | rufous |
| 23 | HY | present | present | white to cream | green | broad | white | yellow | yellow | yellow | rufous | white with rufous streaking |
| 24 | HY | absent | absent | gray | green | absent | NA | yellow | black | gray | gray | gray with rufous and white streaking |
| 25 | HY | absent | UNK | gray | green | absent | NA | yellow | black | black | rufous | brown-black with white streaking |
| 26 | UNK | absent | UNK | UNK | UNK | reduced | red | UNK | UNK | UNK | rufous | dusky, edged with white |
| 27 | SY | reduced | absent | gray | green and red | absent | NA | yellow | black | black | rufous | rufous with gray and white streaking |
| 28 | SY | absent | absent | red | red | absent | NA | yellow | black | brown | rufous | rufous |

molt limits, rounded upperwing coverts, or tear-shaped spots on the wing coverts, indicating that they had obtained their formative plumage (Hayes 2002). The difference in back plume length among individuals suggests that they were in varying stages of auxiliary molt (Pyle and Howell 2004).

## Review of Aberrantly Plumaged Green Herons

In addition to the birds described above, we found photographs of 15 Green Herons exhibiting aberrant pigment expression within the eBird database from Cuba, Mexico, Belize, and the Honduran Bay Islands. We combined these records with descriptions of two melanistic Green Herons by McLachlan (2011), a record of a single intermediately plumaged Green Heron from Costa Rica (Alpízar-Trejos 2012), historic descriptions of two erythristic Green Herons (Lembeye 1850, Thayer and Bangs 1905) and one dark juvenile (Peters 1913), and two representative skins of "*B. brunescens*" in Table 1 to describe 26 aberrantly plumaged Green Herons in Middle America and the Caribbean. The geographic locations of all birds described in Table 1 are plotted in Fig. 3. These individuals differed from the Green Heron plumages described by Payne (1974) with regards to bill color, lore color, face and throat markings, and presence and coloration of upperwing covert edging. All featured individuals lacked or had substantially reduced malar and gular stripes. Moreover, all featured individuals showed black, gray, or brown lores as opposed to the yellow lores of Green Heron outside of the high breeding period, though six birds showed some yellowish or greenish coloration in the orbital skin. Twenty-two individuals

had an entirely dark bill, instead of the extensive yellow in the mandible displayed by Green Heron outside of the high breeding period. Variability existed in the coloration of upperwing coverts in this group, with most birds lacking or having reduced covert margin edging compared to the typical Green Heron. Thirteen individuals showed uniformly-colored primary and secondary coverts without pale margins. Eleven birds showed rufous or white edging on these coverts, though the extent of the edging was reduced in most of these individuals. Margins were not discernible in two individuals.

Coloration in the neck and face was variable in the aberrantly plumaged birds, forming two distinct plumage types: melanistic individuals with excessive dark pigment expressed, and erythristic individuals with excessive reddish pigment expressed (Fig. 4). Each of these two plumage types exhibited a range of color variation. The following descriptions refer to adult Green Herons, aged by the shape of their median and lesser coverts (Davis and Kushlan 1994). Melanistic birds (individuals 2–7; Table 1, Figs. 1, 2, and 4b) were characterized by extremely dark, blackish plumage, as represented by our description above of the birds we observed on Útila and by McLachlan (2011) in Cuba. These melanistic individuals ranged from strikingly dark, steely-blue birds (individuals 3, 4, and 6; Fig. 4b), to those with a browner, sootier appearance (individuals 2, 5, and 7).

Erythristic birds (individuals 9–22; Table 1, Fig. 4c) showed neck colors similar to typical Green Herons. However, unlike typical Green Herons, erythristic birds lacked gular and malar stripes or had greatly reduced ones. Additionally, the black crown feathers of typical Green Heron often extended below the eye or intruded around it for erythristic birds. Bills and lores of erythristic birds were predominantly black. Plumage details around their face and throat were variable. Their bellies also showed a range of color expression. Most were darker gray than the typical Green Heron, occasionally blending with the rufous neck coloration. Some extreme individuals (12, 19–21; Table 1) showed entirely rufous bellies, with rufous also expressed in their upperwing coverts.

While these two groupings are convenient for characterizing plumage traits, they are not absolute, and one bird from Isla del Coco, Costa Rica (individual 8; Table 1), showed strong rufous tones in its overall sooty color, indicative of both melanism and erythrism. Descriptions of some Green Herons from the Pearl Islands, Panama (Thayer and Bangs 1905), are similarly intermediate.

We found five records of immature birds that differed substantially from typical Green Herons in their first plumage cycle, lacking many typical juvenile features such as the characteristic teardrop shaped spots on the upperwing coverts. Though variable in plumage coloration, all juveniles showed uniformly-colored coverts and margins, reduction in neck streaking, a black mandible, and black or brown lores. Juveniles also fell into two plumage types based on having either reddish or greenish upperwing coverts and mantle color. Two immature individuals, which we call "red juveniles" (individuals 27 and 28; Table 1), exhibited predominantly reddish-brown coloration (Fig. 4f) with either reddish or red and green upperwing coverts and rufous on the neck, belly, and mantle. Streaking on the neck was greatly reduced from that of the typical immature Green Heron. The reddish color in their upperparts was drabber than the underparts with more brown tones. Both of these birds had fully black bills and black or brown lores, which is clearly distinct from the yellow bill and lores of typical juvenile Green Heron (Fig. 4d).

Three immature birds, which we call "dark juveniles" (individuals 24–26; Table 1), showed green upperwing coverts and man-

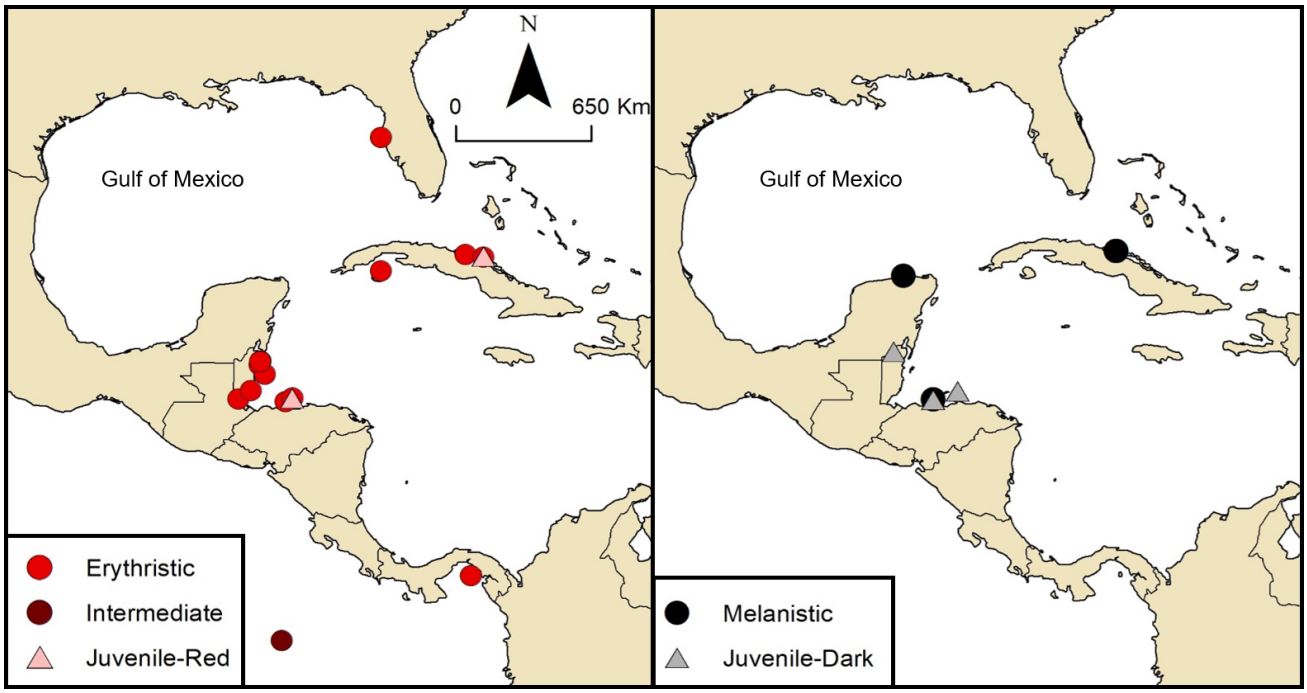


**Fig. 3.** Map of localities where we found records of erythristic (red points) and melanistic (black points) Green Herons. Locations compiled from Table 1.

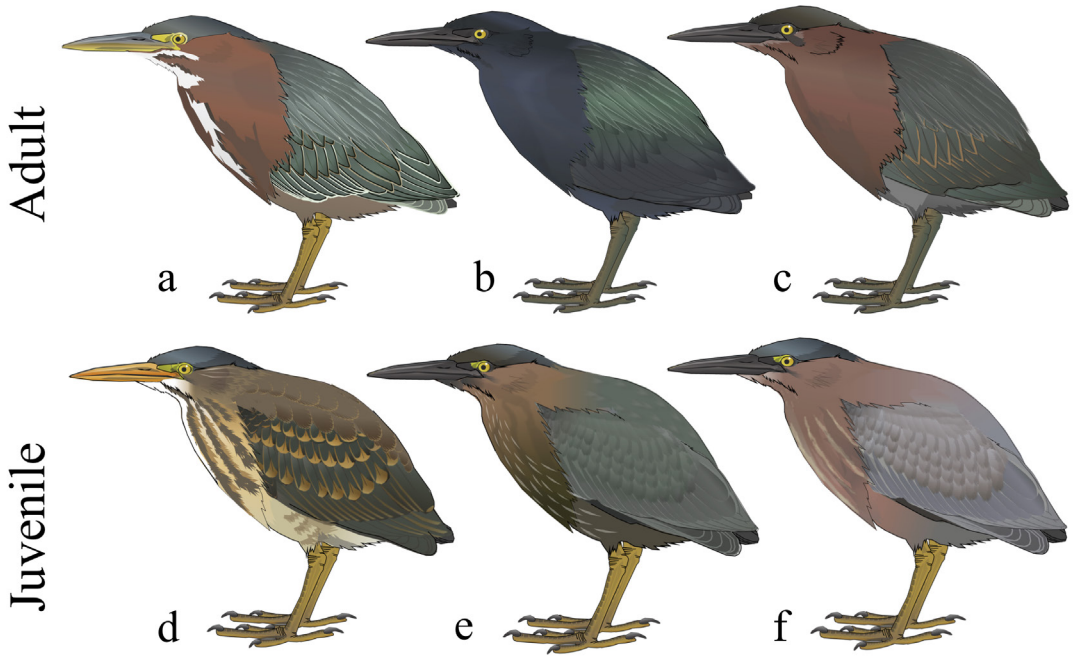


**Fig. 4.** Plumage variation in Green Heron in the polymorphic Caribbean population: a) typical adult, b) melanistic adult, c) erythristic adult, d) typical juvenile, e) dark juvenile, and f) red juvenile. Art by Darin J. McNeil, Jr.

tles with reddish coloration restricted to the sides of the neck, some upperwing covert margins, and some scapulars (Fig. 4e). These individuals were unique in the darkness of the neck, belly, and vent plumage. Unlike the reddish plumage of individuals 27 and 28 (Table 1, Fig. 4f), these individuals exhibited dark gray and black feathers around the brown and white streaks. They displayed diffuse streaking on the throat and sides of neck, which is greatly reduced from the neck streaking of typical immature Green Herons and had a mix of black, brown, and off-white coloration. Their mantle and base color to their upperwing coverts were gray to green. Their faces resembled many adult erythristic birds, with the black crown extending below the eye to the gape. As with the red juveniles, they had predominantly black bills and lores, though individual 25 showed some yellowish green around its orbital skin.

## Discussion

Our finding of 21 adult and 5 immature Green Herons with aberrant coloration suggests the presence of two widespread morphs of Green Heron throughout the western Caribbean in addition to typical birds: a melanistic morph in which birds show an excess of black pigment and an erythristic morph in which birds show an excess of red pigment. While we found one potential intermediate in our sample, all other individuals were readily classifiable into one of these two categories, which justifies treatment of two separate morphs. This is remarkable because no contemporary references describe or depict polymorphisms of this common and widespread species.

We believe the melanistic morph (Fig. 4b) is almost certainly rare within its limited range, as it is known from only six records on Útila, Honduras; Cuba; and the Yucatan (Fig. 3), while many records of typical Green Herons (Fig. 4a) are available. The blackish coloration on the neck, breast, and belly, and the absence of a gular stripe, malar stripes, and pale edging on the wing coverts set them apart from previously described plumages of Green Heron and render them unscorable on Payne's (1974) plumage scale (F. Hayes pers. comm.). Although Green Heron is well represented in ornithological inventories from the Caribbean, no inventory has reported plumage colorations comparable to the melanistic individuals we report here (Salvin 1890, Bond 1936, Monroe 1968, Udvardy 1976).

Erythristic Green Herons were more common than the melanistic morph. These birds resemble Oberholser's (1912b) description of the previously recognized *B. brunescens* of Cuba (Lebeye 1850), exhibiting "uniform chestnut neck and sides of head, [and] dark, inconspicuous wing edgings . . . nor any indication of a median light or white stripe on throat or jugulum" (Oberholser 1912b:54). However, the range of variation in traits such as belly and covert color exceeded that described for *B. brunescens.* Furthermore, *B. brunescens* was thought to be endemic to Cuba and the Isle of Pines, but we found these erythristic birds to be widespread, occurring in both mainland and insular populations (Fig. 3). The strongest variation and most intensely colored individuals (e.g., individual 12; Table 1) appear on small satellite islands or in archipelagos. Oberholser (1912b:54) furthermore describes a "dark, dull, almost uniform . . . brownish coloration of juvenal *Butorides brunescens*." This depiction matches the red juvenile birds in our sample (Fig. 4f), which we suspect may molt into erythristic adult plumage.

The three dark juveniles we report with green coverts and upperparts (individuals 24–26; Table 1, Fig. 4e) show previously undescribed plumages. A single record of an aberrantly plumaged Green Heron from Quintana Roo, Mexico, displayed remarkable similarity to this plumage type, with a dusky neck and throat, reddish sides of the neck, and a dark gray breast (Peters 1913). Aside from the possible record in Mexico, this juvenile plum-

age has only been documented in the Bay Islands of Honduras, where melanistic adults have been recorded. Given the presence of aberrantly dark wing coverts, neck, breast, and belly, it is possible that these birds will molt into the melanistic plumage types described in this paper. However, all three of these juveniles show face patterns that resemble the erythristic phenotype. We therefore cannot conclusively state what the adult plumages of these juveniles will be, though they will undoubtedly fall somewhere along the spectrum of described adult variation.

While differences in neck and covert color between individuals were dramatic enough to provide a basis for the categorizations used here, we found extensive variation in other traits (Table 1). Although bills and lores were predominantly dark, several individuals showed some yellow in either the lower mandibles or the lores. While leg color was predominantly yellow in most birds, seven had mostly gray legs, four of which were melanistic. Of the 11 birds that had edging on the upperwing coverts, only 3 had whitish edging, while 8 had reddish edging. This level of variation is strongly reminiscent of the variation described in Green Herons on the Pearl Islands of Panama (Thayer and Bangs 1905), but has never been described at the spatial extent treated here.

The range of variation in plumage types that we describe here is typical of high plumage variability in *Butorides* in general (Payne 1974, Hayes 2002). Within the melanistic Lava Heron of the Galápagos, high plumage variation also occurs, and individuals exhibit a complex spectrum of melanistic plumages (Harris 1982, Kushlan 2009). In adults, the most dramatic of these are entirely sooty-gray birds, with black bills and lores, silvery black plumes, and bright orange eyes and legs. However, features such as gular and malar stripes; yellow lores, eyes, and legs; and broad, pale edging on the upperwing coverts vary in color and intensity throughout the population. Juvenile Lava Herons are also variable, exhibiting a range of white to reddish-buff streaking on the neck and upperwing coverts. Like the immatures we describe from the Caribbean, young Lava Herons show a general dichotomy between individuals with green upperwing coverts and reddish-brown upperwing coverts. Interestingly, juvenile Lava Herons retain the whitish tear-drop shaped markings on the tips of the wing coverts typical of all *Butorides*, unlike the juveniles we describe in the Caribbean.

We were unable to obtain morphological data for the birds in our sample, but measurements from historical accounts (Oberholser 1912b, Bangs 1915) placed aberrantly plumaged birds in the range of the resident *B. v. maculatus* of Central America and the Caribbean.

All of our observations and the majority of records we report occurred in or near mangrove habitat on small islands or along a coastline. Early observations of erythristic individuals from the Isle of Pines, Cuba, also noted an association between this morph and mangrove habitat (Todd 1917:185). The melanistic Lava Heron of the Galápagos also occurs along island coastlines, suggesting that dark, low-contrast plumaged birds in the genus *Butorides* may experience a selective advantage in coastal or mangrove environments. A recent meta-analysis found support for the hypothesis that bird polymorphisms evolve as a response to differences in detectability in varying light conditions (Galeotti *et al.* 2003), as may occur between mangrove and more open habitat. A general relationship has also been described between excessive melanin production across taxa and occupancy of high-salt environments like salt-marshes (Grenier and Greenberg 2006). Melanism is furthermore believed to have evolved in some bird species as a response to the increased presence of feather-degrading bacteria in salt-water ecosystems (Peele *et al.* 2009). The stronger molecular structure in the reddish pigment caused by erythrism would also be more advantageous in these settings than in feathers of typical birds with less dark pigment. Despite the parallels with these studies that show a selective advantage of a melanistic morph, further research will be needed to confirm why these polymorphisms occur in Green Heron within the geographic region we describe.

Melanistic polymorphisms have been found to be linked to point-mutations in a single gene, *MC1R*, in multiple species of birds (Mundy 2005). However, a recent study points out that our understanding of the genetic basis of plumage coloration is still very limited, especially given that color expression is a function of both heritable genes and environmental and physiological factors that influence gene expression (Roulin and Ducrest 2013). Given the range of variability in the expression of black, red, and brown coloration in the many aberrantly plumaged Green Herons in the Caribbean, it is unlikely that a single genetic mutation is responsible for the full range of plumages we describe. Additionally, considering the disjunct polymorphic population of Lava Heron in the Galápagos (Payne 1974, Hayes 2002), it seems likely that dark, low-contrast plumage has evolved multiple times within the genus.

To begin the process of elucidating the mechanisms driving variation in Green Heron polymorphs, more data must be gathered from the Caribbean region to further document the morphological and geographical span of these plumage types. We therefore encourage field guide authors to include these plumages in their work in order to heighten awareness of these morphs, which appear to be fairly common. Furthermore, we stress the importance of collecting genetic, behavioral, and demographic data from these aberrantly plumaged birds to determine the selective mechanism that maintains this polymorphism. Finally, we hope that field observers will continue to add photographs to online databases of bird images that serve as increasingly powerful tools for professional and amateur biologists.

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