

Geographic variation, hybridization, and taxonomy of New World *Butorides* herons

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ABSTRACT

The New World *Butorides* herons comprise three distinct forms whose taxonomy has been debated: the rufous-necked Green Heron (*B. virescens*) of North America, Central America, and the West Indies; the gray-necked Striated Heron (*B. striatus*) of South America and the Old World; and the dark Lava Heron (*B. sundevalli*) of the Galápagos Islands. An extensive analysis by Payne (1974) concluded that they interbreed freely where their ranges meet and should be considered conspecific. However, Monroe and Browning (1992) alleged that Payne's voucher specimens used as a hybrid index for *B. virescens* and *B. striatus* included juveniles and did not represent a continuous series; they concluded that *B. virescens* and *B. striatus* rarely interbreed and were specifically distinct. My reexamination of Payne's voucher specimens revealed that all had attained adult neck coloration and represent a continuous series. My reanalysis of Payne's data demonstrates increased variability and intermediacy in the contact zone between *B. virescens* and *B. striatus*, implying extensive hybridization there. However, the presence of apparently pure *B. virescens* and *B. striatus* phenotypes within the contact zone suggests that assortative mating does occur, supporting the treatment of the two forms as distinct species. Similarly, the persistence of pure *B. sundevalli* in a potential hybrid zone with *B. striatus* in the Galápagos Islands supports its treatment as a distinct species. Further information is provided on molts and plumages of *Butorides* herons.

INTRODUCTION

Studies of geographic variation in birds are crucial for testing hypotheses of phylogenetic relationships and speciation processes among closely related species (Zink and Remsen 1986). Where zones of phenotypic intermediacy occur between sister taxa, it is important to distinguish between primary intergradation (clinal variation) and secondary intergradation (hybridization). Hybridization, a genetic phenomenon that is widespread in birds (Grant and Grant 1992), is generally defined as interbreeding between populations in secondary contact (Sibley and Short 1964) and can be phenetically inferred by an increase in variability and intermediacy in concert (Schueler and Rising 1976).

The New World herons of the genus *Butorides* include three distinct forms: the rufous-necked Green Heron (*B. virescens*) of North America, Central America, and the West Indies; the gray-necked Striated Heron (*B. striatus*) of South America and the Old World; and the dark Lava Heron (*B. sundevalli*) of the Galápagos Islands.

The three forms were generally considered distinct species (e.g., Bock 1956, Peters 1931, Hellmayr and Conover 1948, Palmer 1962, Wetmore 1965, Slud 1967), although sometimes considered conspecific (Hartert 1920) or possibly conspecific (Eisenmann 1951, Parkes 1955), until Payne (1974) examined 837 New World *Butorides* specimens and found evidence of extensive hybridization between Green and Striated Herons where their ranges meet in southern Central America, the southern Caribbean islands, and coastal northern South America, and between Striated and Lava Herons in the Galápagos Islands. Payne (1974, 1979) and Payne and Risley (1976) concluded that the three forms represented a single, polymorphic species comprising six recognizable subspecies. This conclusion was partially accepted by the American Ornithologists' Union (1976, 1983), which lumped *B. virescens* and *B. striatus* into a single species, the Green-backed Heron *B. striatus*, but regarded *B. sun-*

devalli as specifically distinct.

In a critical reanalysis of specimens from the Panamanian contact zone between *B. virescens* and *B. striatus*, Monroe and Browning (1992) concluded that interbreeding between the two forms was limited and recommended that they be recognized as distinct species. This conclusion was accepted by the American Ornithologists' Union (1993, 1998), which resplit *Butorides* into three separate species.

Given the existence of individuals appearing intermediate between these forms in the areas where their ranges meet and the debated taxonomic significance of such individuals, the following review is offered to synthesize current knowledge and to stimulate further study of the geographic variation, hybridization, taxonomy, and identification of New World *Butorides* herons.

MOLTS PLUMAGES, AND SOFT PARTS

A sound analysis of geographic variation and taxonomy in birds is premised upon comparisons of individuals of like age, which in turn requires a thorough understanding of molts and plumages. Although *Butorides* herons are widespread and relatively common, the sequence of their molts and plumages remains surprisingly poorly known. The following descriptions are based upon *B. virescens*, the sequence of molts and plumages of which has been tentatively described (Oberholser 1912, 1974, Bent 1926, Palmer 1962, Davis and Kushlan 1994) and is presumably similar in poorly known *B. striatus* (Cramp and Simmons 1977, Marchant and Higgins 1990) and *B. sundevalli*.

Juvenal and immature plumages—The distinctive juvenal plumage of young birds of this genus is acquired before flight is attained. Juveniles are immediately diagnosable by heavy streaking on the brownish neck (usually absent in the center of the whitish throat) and upper breast, a brownish cast to the upperparts, and whitish underparts. Juveniles also possess distinctive wing feathers in which the coverts are more rounded, with broad, buffy margins and a buffy triangular spot at the tip of each covert that rapidly fades to white and wears away, and the remiges (primaries and secondaries) are broadly tipped with white. The tibial (thigh) feathers are often, but not always, marked with darker horizontal bars. In juveniles, the bill is paler than in adults.

The juvenal appearance is generally retained during the first fall and early winter until all body feathers are gradually replaced during the first prebasic molt, which begins a few weeks after attaining flight and lasts for several months until the first-basic plumage is obtained. During this period, an "immature" appearance is gradually acquired as the cap becomes more solid black, the chin and throat become a clearer white, and the sides of the neck lose their streaking, becoming more rufescent. However, the wing feathers do not molt; thus, the distinctive juvenile appearance of triangular white spots at the tip of each covert and white-tipped remiges is retained.

Subadult plumage—The first prealternate molt, beginning in late winter and ending in spring, is poorly known but apparently partial, probably limited to new head and neck feathers, scapulars and some wing coverts, and plumes on the back. The first alternate plumage, acquired by spring, is essentially a "subadult" plumage resembling that of the adult except that the back plumes are shorter, the wings retain some worn juvenal coverts, all juvenal flight feathers (each tipped with white), the chin, throat, and underparts are whiter, and the dusky stripes of the lower foreneck and upper breast are broader. It is important to note that the sides of the neck have essentially acquired adult coloration by this time but may be slightly brighter.

Adult plumage—Definitive basic adult plumage is obtained during the second prebasic molt, which begins in late spring or early summer, when the bird is about one year old, and is completed in the fall. The second prebasic molt, which begins earlier than subsequent prebasic molts, is usually complete, although molting of some juvenal secondaries and primaries may be further delayed. Adults subsequently undergo a partial but more extensive



Figure 1. Voucher specimens from the National Museum of Natural History used by Payne (1974) to score neck coloration of *Butorides* on a hybrid index scale (from left to right) of 1-9 (see Table 1 for further details). Photograph by Floyd E. Hayes.

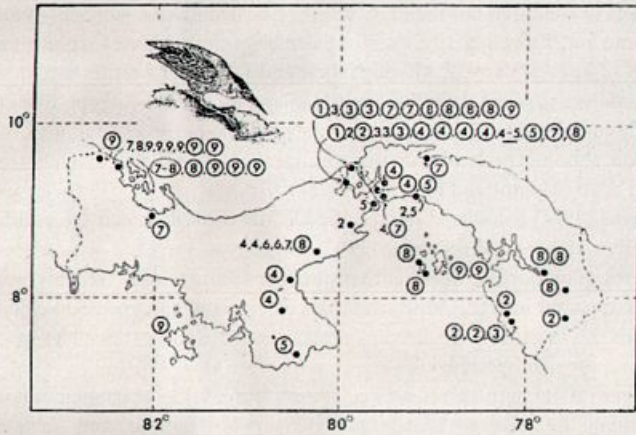


Figure 3. "Figure II" of Payne (1974) illustrating variation in neck color, represented by numbers (see Fig. 1), of *Butorides* specimens in Panama. Circled numbers represent winter birds (both residents and northern migrants) collected during October to April; uncircled numbers represent probable breeding residents collected from May to September. Reprinted by permission of Robert B. Payne and the British Ornithologists' Club.



Figure 5. This juvenile/immature nominate Striated Heron (*B. s. striatus*) from Argentina shows markings similar to those of similar-aged Green Heron, but it is a paler bird, with more washed-out gray-brown tones to the neck streaking, lacking the chestnut or rufescent tones of the Green Heron in Figure 4. Photograph by T. J. Ulrich/VIREO.

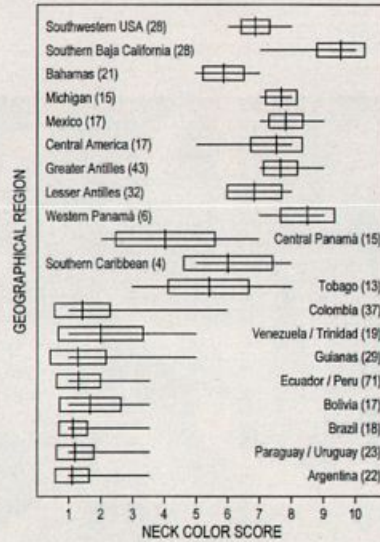


Figure 2. Geographic variation in neck coloration of New World *Butorides* herons (excluding the Galápagos Islands), based on a reanalysis of data in Payne (1974). Vertical line = mean score; box = ± 1 S. D.; horizontal line = range. Sample sizes are given for each geographical region. An outlier of "3" for the Lesser Antilles is not illustrated. Note the anomalous situation with *bahamensis* Green Herons, whose scores place them closer to birds of the southern Caribbean rather than the southeastern United States or northern Caribbean islands.



Figure 4. A typical nominate juvenile Green Heron (*B. v. virescens*) from eastern North America, photographed in July on Big John's Pond, at Jamaica Bay N.W.R., Queens, New York, New York. This bird shows streaking on the brownish neck and upper breast, a brownish cast to the upperparts, with whitish underparts. Wing coverts are more rounded than those of the adults and bear broad, buffy margins and a buffy triangular spot at the tip of each covert. In juveniles of all *Butorides* herons, the bill is paler than in adults. Photograph by A. Morris/Birds as Art.



Figure 6. Four immature specimens of Striated Heron (on the left; all from Brazil) and five immature specimens of Green Heron (on the right; from Central America and North America on the right). Note the grayer tones of neck coloration in Striated Heron and more rufescent tones in Green Heron. Photograph by Floyd E. Hayes.



Figure 7. A typical adult Green Heron photographed at Shark Valley, Everglades National Park, Florida. Photograph by A. Morris/Birds as Art.

prealternate molt from late winter to early spring and a complete prebasic molt from late summer to fall. In definitive alternate plumage, the back plumes of both sexes are longer than during definitive basic plumage.

Adults are readily distinguished from juveniles and immatures by their darker bill, solid rufous sides to the neck, greenish-gray upperparts lacking brown tones, longer back plumes, more pointed scapulars and wing coverts, narrower buffy margins to the wing coverts (which lack white spots), narrower white tips of flight feathers restricted to the inner primaries and secondaries, and darker brown-gray underparts.

The sexes are indistinguishable by plumage, but females average smaller than males. When breeding, the bill and loreal area become glossier black, and the iris and legs become more orange, especially in the male.

GEOGRAPHIC VARIATION

Butorides virescens—The Green Heron is represented by four currently recognized subspecies (Payne 1974, 1979, Hancock and Kushlan 1984, Davis and Kushlan 1994), though as many as 18 were once recognized (Oberholser 1912). Nominative *B. v. virescens*, a rufous-necked form, occurs from central and eastern North America southward to Panama and in the southern Caribbean islands east to Tobago. Body size averages larger in northern populations than in southern populations. Voous (1986) and Steadman et al. (1997) argued that a general Caribbean race should be recognized as *B. v. maculatus*, which averages smaller and slightly paler-necked than eastern North American *B. v. virescens*, but considerable overlap occurs with Central American populations of *B. v. virescens* (Payne 1974). A larger and paler-necked form, *B. v. anthonyi*, occurs in western North America. A distinctive purplish-necked form, *B. v. frazari*, inhabits southern Baja California (south of about 27° 20' N latitude). The smallest and palest form, *B. v. bahamensis*, occurs in the Bahama Islands. The North American populations of *B. v. virescens* and *B. v. anthonyi* migrate southward as far as Ecuador (Ridgely and Greenfield 2001), Colombia (Hilty and Brown 1986), Venezuela (Meyer de Schauensee and Phelps 1978), Trinidad (French 1973), Guyana (Snyder 1966), and Suriname (Haverschmidt 1968), where they occur primarily during winter and only rarely during summer (Hilty and Brown 1986). The other forms are relatively sedentary.

Butorides striatus—South America is inhabited by the nominate race of the Striated Heron *B. s. striatus* (other races occur in the Old World), which is typically gray-necked, although a small proportion of browner-necked individuals occurs throughout its range. The South American populations tend to be variable, with no distinct geographical trends in plumage or morphometric variation (Payne 1974). Although *B. s. striatus* is not known to undergo long-distance migratory movements, individuals are apparently resident in the

Galápagos Islands (Harris 1973) and have strayed to Cocos Island (Slud 1967), Bonaire (Voous 1986), Tobago (Payne 1974), and as far north as Costa Rica in Central America (Stiles and Skutch 1989) and St. Vincent in the Lesser Antilles (Bond 1964, Payne 1974).

Contact zone between Green and Striated Herons—In his comprehensive analysis of geographic variation within *B. virescens* and *B. striatus*, Payne (1974) compared neck coloration of all specimens that had “completed most or all of their postjuvenile molt” with a voucher series of nine specimens in the National Museum of Natural History (USNM; Washington, D. C.) representing a “smoothly graded series of nine colors from grey through brown and maroon” (Fig. 1, Table 1). In a critical reanalysis of Payne’s voucher specimens, Monroe and Browning (1992) incorrectly stated that “two of the voucher specimens (5 and 6) ... are whitish below as in the typical juvenal plumage.” In fact, specimen 5 is an adult lacking evidence of juvenal plumage. However, specimens 6, 7, and 8 each retain some juvenal wing feathers (white spots at the tips of the greater primary coverts and, in specimen 8, broad white tips to some remiges). Furthermore, specimen 6 possesses traces of barring on the tibial feathers (a condition not found in “all white-bellied juvenal *virescens*,” *contra* Monroe and Browning 1992) and a paler belly, both features representing traces of juvenal plumage. Although these three subadult voucher specimens have not yet acquired definitive adult plumage, each (including specimen 6) clearly completed most of its post-juvenile molt and possesses adult neck coloration, although neck coloration of specimen 6 may be slightly brighter than when adult (Monroe and Browning 1992).

Payne (1974) considered the specific identity of birds scored 4-6 as arbitrary, but Monroe and Browning (1992) alleged that “there is a definite break [in neck coloration] between voucher specimens 5 and 6.” However, this break is not apparent in Fig. 1, in which facial coloration of specimen 5 resembles specimen 6 more than specimen 4, whereas neck coloration resembles specimen 4 more than specimen 6.

Payne (1974) summarized neck coloration scores for 19 geographic regions (excluding the Galápagos Islands) in his “Figure I,” “Figure II,” and “Table 2.” Monroe and Browning (1992) were puzzled by the discrepancy between Payne’s (1974) “Figure I,” in which the 72 Panamanian specimens included 14 scored as 5 and none scored as 4, and “Figure II,” which included 11 scored as 4, five scored as 5, and one scored as 4-5. However, Payne stated in the legend of “Figure I” that “‘5’ in Fig. I = ‘4’ or ‘5,’” but his rationale for lumping scores 4 and 5 as “5” remains puzzling. A reanalysis of Payne’s data on geographical variation is presented in Fig. 2. In my reanalysis, I have included only specimens collected from May to September, most of which were probably breeding residents, from Mexico, Central America, Panama, Bahamas, Greater Antilles,



Figure 8. An adult Green Heron of the race *anthonyi* from western North America, photographed at Lake Cunningham Park, San Jose, California, in January 2001. Photograph by Peter LaTourrette.

Lesser Antilles, southern Caribbean, Venezuela, and Trinidad samples. Only wintering *B. virescens* are deleted from the Colombia sample. Specimens collected during October to April in these regions were excluded because they included Nearctic migrants in addition to residents. Southern Baja California specimens indicated by an "X" in Payne's (1974) "Figure 1" were described as having "a colour darker purple (less brown, more greyish) than colour 9"; for the purposes of analysis, I have scored these specimens as 10. I have limited southern Caribbean specimens to Aruba, Los Roques, and Margarita, and have treated Tobago specimens separately. Although all but one specimen from Tobago were collected during October to April, only one appears similar in size and neck color to nominate *B. virescens*, but it was collected during the North American breeding season; because these specimens appear to represent residents, all are herein included. Specimens from Espada, Venezuela, and Guajira, Colombia, were included within the southern Caribbean sample by Payne (1974), but these coastal localities are situated on the continent and are herein included within the respective country's sample. For South American countries excluding Colombia and Venezuela (with which the few Trinidad specimens were lumped), I scored the few specimens lumped as 3-4 in "Table II" of Payne (1974) as 3.5, which slightly reduces variability.

Payne also provided a detailed map of scores in Panama (see Fig. 3), where typical *B. virescens* occurred in western Panama in contrast with highly variable, intermediate populations in central Panama. Based on the increased variability and prevalence of intermediate specimens with neck coloration ranging from 4-6 in central Panama, southern Caribbean islands (Aruba, Los Roques, Margarita and Tobago), and coastal northern South America (Colombia and Venezuela), Payne concluded that secondary intergradation (hybridization) occurred between *B. v. virescens* and *B. s. striatus*.

Voous (1986) pointed out that the populations of *Butorides* in the Netherlands Antilles (Aruba, Bonaire, and Curaçao) were less variable than Payne's limited sample suggested. Of 123 records comprising 16 specimen, eight photographic, and 95 sight records (enigmatically these numbers do not add up), all but eight were rufous-necked *B. virescens*, including some migrants from North America (at least three of 16 specimens). Only one was an adult *B. striatus*, seen in Bonaire. Individuals of intermediate appearance, which comprised only 6% of the sample, included two from Aruba and five from Bonaire. However, the intermediate individuals likely comprised more than 6% of the resident population, as 19% of the specimens, along with an unestimated number of photographic and sight records, were represented by Nearctic migrants of *B. virescens*.

Monroe and Browning (1992) stated that *B. striatus* is the resident form on Trinidad, whereas *B. virescens* is resident on nearby Tobago. However, the situation on these islands is complex. According to Belcher and Smooker (1934), *B. striatus* was common on both islands but was known to nest only in Trinidad; they did not find *B. virescens* on Tobago but reported it to be rare in



Figure 9. A typical adult Striated Heron photographed at Manaus, Brazil. Photograph by Andrew Whittaker/VIREO.

Trinidad, where it nested in mangroves with eggs reported "to be more rounded on the average" than those of *B. striatus*. Junge and Mees (1958) stated that *B. striatus* was the most common species in Tobago but collected only a specimen of *B. virescens*. Specimens from Tobago were taken approximately a century ago, when the population appeared to be intermediate between *B. virescens* and *B. striatus* and included specimens of both species (scores ranging from 3-8; Fig. 2). However, the resident population today is comprised predominantly of rufous-necked *B. virescens* scoring higher on the index. *B. striatus* occurs in small numbers, possibly as a seasonal visitor, but the presence of intermediate individuals implies that hybridization occurs (Hayes unpubl. data). These observations suggest a recent historical shift toward typical *B. virescens* in Tobago. Payne's sample of *B. striatus* from Trinidad included only four specimens, with scores ranging from 1 to 3. However, the current Trinidad population appears much more variable than Payne's limited sample suggested, with a small proportion of intermediate individuals and *B. virescens* occurring only rarely, apparently as a winter migrant (Hayes, unpubl. data).

Monroe and Browning (1992) argued that specimens scored 1-5 represented *B. striatus*, whereas those scored 6-9 represented *B. virescens*. Although specimens scored 1-4 occur naturally throughout the South American range of *B. striatus* and specimens scored 6-9 occur naturally within the North American range of *B. virescens*, specimens scored as 5 in southern Central America, the southern Caribbean, and coastal northern South America appear to be truly intermediate. Outside the zone of overlap between the two species, specimens scored as 5 occur only in the pale-necked Bahamian population (29% of Payne's sample; n=21), which represents an exception to clinal variation and obviously does not represent *B. striatus*.

Monroe and Browning (1992) argued that neck coloration of the resident population of *B. striatus* in Panama was no more variable (scores ranging from 2-5) than the populations of *B. striatus* throughout South America (scores ranging from 1-4) and was merely shifted up by one level in the index. However, even when specimens obtained from October to April (which include North American migrants at the upper end of the scale and two possible residents scored at the lower end of the scale) are excluded, variability in central Panama still exceeds that of any other population (Fig. 2). Monroe and Browning also pointed out that no mixed breeding pairs had ever been reported, but failed to note that relatively few ornithologists reside within the region where intermediates occur and that visiting and resident ornithologists invariably studied other species of birds. They further speculated that the two Panamanian and one Colombian specimens scored as 6 were more likely vagrants from the Lesser Antilles than extreme variants of *B. virescens*, but given the extreme distance and east-west direction of movement from the Lesser Antilles, such long-distance vagrancy from populations thought to be relatively sedentary seems highly unlikely.

Table 1: Voucher specimens (see Fig. 1) from the National Museum of Natural History used by Payne (1974) to score neck coloration of *Butorides* on a hybrid index scale.

Score	Neck color	Catalogue number	Locality
1	gray	263848	Venezuela: Culata
2	gray, tinge brown	423096	Panama: Charco del Toro
3	gray, wash brown	444948	Panama: Río Indio
4	brownish gray	400113	Panama: Pesé, Herrera
5	grayish brown	448634	Panama: La Jagua
6	grayish red-brown	368472	Colombia: Guajira
7	reddish brown	206343	Panama: Río Indio
8	purplish brown	316840	Cocos Island
9	dark purplish brown	468699	Panama: Almirante



Figures 10 and 11. Two adult Striated Herons illustrating variability of neck coloration scores ranging from 1 (bird on left; taken at Pointe-a-Pierre, Trinidad, 7 October 2000) to 4 (bird on right; taken at Pointe-a-Pierre, Trinidad, 11 August 2001). The bird on the right could be mistaken for a Green Heron because of its somewhat rufous neck coloration, but the distinctly grayer hindneck is characteristic of many brown-necked Striated Herons. The possibility of hybrid origin cannot be ruled out in this case. Photographs by Floyd E. Hayes.



Figure 12. A typical adult Lava Heron (*B. sundevalli*) from the Galápagos Islands, Ecuador. Photograph by S. Bahrt/VIREO.

Based on their reanalysis of Panamanian specimens, Monroe and Browning (1992) concluded: "there is no substantial evidence that there is interbreeding, and certainly if it occurs at all, it must be at a low level." However, biologists have long recognized that hybridization can be inferred by an increase in variability and intermediacy in concert (Schueler and Rising 1976). The data in Fig. 2 clearly illustrate the increased variability and high proportion of intermediate individuals within the zone of contact between *B. virescens* and *B. striatus*, even when specimens of presumed Nearctic migrants (plus residents) are removed from the sample. Such a pattern strongly implies extensive secondary intergradation between the two forms in a relatively narrow hybrid zone between 8° and 10° N latitude.

Extensive hybridization between taxa often has been interpreted as evidence for lack of reproductive isolation, requiring that the taxa be considered conspecific according to the traditional biological species concept (BSC; Mayr 1970). However, the degree of hybridization must be considered, inasmuch as more than 10% of bird species retain the ability to interbreed and produce viable offspring with other closely related species, including non-sisters (Grant and Grant 1992). Johnson et al. (1999) proposed a new comprehensive biologic species concept (CBSC) applicable to birds: "An avian species is a system of populations representing an essentially monophyletic, genetically cohesive, and genealogically concordant lineage of individuals that share a common fertilisation system through time and space, represent an independent evolutionary trajectory, and demonstrate *essential but not necessarily complete reproductive isolation* from other such systems" (emphasis added). Assuming phenotype is correlated with genotype, the presence of "pure" phenotypes within a hybrid zone, even when hybridization is extensive, provides evidence of assortative mating; in this case, the two taxa demonstrate *essential* reproductive isolation and should be considered specifically distinct. In contrast, when all individuals within a hybrid zone are intermediate, free interbreeding is inferred and the two taxa should be regarded as conspecific.

In New World *Butorides*, the seemingly continuous variation in neck color from purplish-brown in the north to gray in the south strongly implies polygenic control of the deposition of gray eumelanin and rufous pheomelanin pigments in the distal barbules of neck feathers (Schodde et al. 1980). Each currently recognized subspecies appears to differ in the combination of alleles coding for neck coloration, with intermediate combinations occurring where the ranges of *B. virescens* and *B. striatus* meet. The presence of apparently pure *B. virescens* and *B. striatus* phenotypes within the contact zone suggests that although the two forms frequently hybridize, assortative mating does occur. However, the sample sizes of museum specimens are small, and it remains uncertain whether both forms actually breed within the hybrid zone.

In Tobago, a large body of recently collected data clearly indicates the presence of mostly "pure" phenotypes in an apparent hybrid zone (neck scores range from 1 to 8; Hayes unpubl. data), providing further evidence that assortative mating occurs. Thus, the two forms appear to maintain essential reproductive isolation and should be regarded as specifically distinct. However, further colorimetric, morphological, behavioral, and genetic studies are needed to shed light on the extent of gene flow and the stability of the hybrid zone.

Based on current taxonomy, *B. s. striatus* is thought to be more closely related to Old World taxa as well as to *B. sundevalli* than to *B. virescens*. Thus, the two forms are not considered sister taxa, although they retain the ability to hybridize. Amadon (1953) speculated that North American *B. virescens* was derived from Asia, whereas South American *B. striatus* was derived from Africa. Although this hypothesis may explain the current zone of secondary contact between the two taxa, it is unsupported by fossil or genetic evidence.

Butorides sundevalli—The Lava Heron is endemic to the Galápagos Islands, where its dark gray coloration enables it to blend in with a backdrop of exposed lava. Harris (1973) pointed out that *B. striatus* was also resident on the islands and that some specimens were intermediate between the two forms. Payne (1974) examined 50 specimens from the Galápagos Islands, which varied from blackish to pale gray as in *B. striatus*. The majority of the

specimens possessed blackish (26%) or dark-gray, nearly blackish underparts (34%), with a slightly paler throat (white-edged feathering, slight streaking or simply grayer). Twelve (24%) specimens with dark gray underparts had a lighter gray belly, blackish to dark gray sides of the neck and cheeks, and a throat streaked with whitish edges. Four (8%) specimens with gray underparts darker than *B. striatus* were also gray on the sides of the neck and cheeks, and streaked white and gray-brown on the upper breast with whitish feathers forming a midline. Finally, four (8%) pale specimens with light gray underparts resembled *B. striatus* from the mainland but were streaked white and gray-brown on the neck with no more than a trace of rufous on the upper breast.

Because the paler Galápagos birds differed from those of the mainland, Payne (1974) regarded them as local residents rather than vagrants and considered the high proportion of intermediate birds as evidence for free interbreeding between derived populations of *B. sundevalli* and more recent colonists of *B. striatus* from the mainland. Hancock and Kushlan (1984), however, regarded the variable forms of *B. sundevalli* as a situation of color polymorphism within the taxon rather than intergradation between *B. sundevalli* and *B. striatus*. Given the persistence of apparently pure phenotypes of *B. sundevalli* within a potential hybrid zone, the two forms do not appear to be interbreeding freely; thus, they may be considered specifically distinct. However, further studies of colorimetry, morphology, behavior, and genetics are needed to resolve the taxonomic status of *B. sundevalli* adequately.

LIMITS OF IDENTIFICATION

Identification of *B. virescens* and *B. striatus* is problematic in southern Central America, on southern Caribbean islands, and in coastal northern South America. Wetmore (1965) claimed that adult *B. striatus* possessed a lighter, more grayish-green back than *B. virescens*, but specimens' back coloration overlaps greatly between the two species. Thus, neck coloration remains the sole criterion for identification during all ages. Juvenile and immature specimens are often separable by the more rufous brown tones of *B. virescens* and grayer brown tones of *B. striatus* (Figs. 4, 5, 6). However, caution is warranted, especially in the field, because some juvenile and immature specimens from North American and South American populations are so similar that they cannot be safely distinguished. Because inexperienced observers often misidentify brown-necked immature *B. striatus* as *B. virescens*, accurate ageing of individual birds is crucial to correct identification to species.

Neck coloration in subadult and adult *B. virescens* typically ranges from reddish-brown to purplish-brown with no hint of gray (Fig. 7); Green Herons of the race *anthonyi* from the western United States are typically paler than eastern birds of the nominate form (Fig. 8). Because each neck feather of *B. virescens* is gray basally, a displaced tuft of feathers may reveal some gray tones, so caution is warranted in assessing neck colors. Neck coloration in adult *B. striatus* typically ranges from gray to brownish gray, with narrow rufous streaking anteriorly (Fig. 9). In browner-necked adults, which also may be mistaken by inexperienced observers for *B. virescens*, the brown is usually (though not always) more intense toward the front of the neck, where it merges with the rufous streaking, whereas the sides of the neck become grayer posteriorly (Figs. 10, 11). Hindneck coloration of adults often provides the best clue for identification: in *B. virescens*, it is always rufous without any hint of gray, whereas in *B. striatus* it is usually gray, but may be brownish gray. Truly intermediate individuals obviously cannot be identified.

In the Galápagos, most individuals of *B. sundevalli* are readily distinguished from *B. striatus* by their consistently darker plumage at all ages (Fig. 12). Only the palest individuals with a contrasting black cap and streaking on the foreneck can be considered to represent *B. striatus*, although if these birds actually represent a light morph of *B. sundevalli*, as suggested by Hancock and Kushlan (1984), *B. striatus* may not even occur in the Galápagos.

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