

# Variation and hybridization in Green Heron (*Butorides virescens*) and Striated Heron (*B. striata*) in central Panama, with comments on species limits

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## Abstract

The rufous-necked Green Heron (*Butorides virescens*) of North America and the Caribbean hybridizes with the gray-necked Striated Heron (*B. striata*) of South America in central Panama and on islands of the southern Caribbean. Based on a color photograph of nine voucher specimens used as a hybrid index, we obtained neck color scores (ranging from gray to purplish brown) of 42 live individuals photographed in central Panama during 10–16 July 2011. Neck color scores ranged from 1–8 ( $\bar{x}=3.7$ ,  $SD=2.2$ ). Presumed *B. striata* with scores of 1–3 comprised 52% of the population, presumed *B. virescens* with scores of 7–8 comprised 14% of the population, and presumed hybrids

with a score of 5 comprised 14% of the population. The proportion of intermediate scores of 4–6 was slightly but not significantly lower than a sample of 44 museum specimens collected from 1908–1966 (33% versus 43%). The increased variability and intermediacy of neck color within the contact zone strongly implies that hybridization still occurs between the two species in central Panama. Because random mating tends to reduce variability around an intermediate phenotype, the current full range of phenotypes among herons presumably breeding in central Panama suggests a tendency toward assortative mating despite frequent hybridization. The two taxa appear to have achieved essential reproductive isolation,

thus supporting their current treatment as distinct species.

## Introduction

Two species of *Butorides* herons are currently recognized: the rufous-necked Green Heron (*B. virescens*) of North America and the West Indies, and the gray-necked Striated Heron (*B. striata*) of South America (including dark *B. s. sundevalli* of the Galapagos Islands) and the Old World (A.O.U. 1998, Banks et al. 2003). They were usually treated as distinct species until Payne (1974) provided evidence of extensive hybridization where their ranges meet in central Panama, several southern Caribbean islands, and coastal northern South America. Based on

Score: 1



Score: 2



Score: 3



Payne's (1974) conclusions, the American Ornithologists' Union (1976, 1983) merged Green Heron and Striated Heron into a single species, Green-backed Heron (*B. striata*).

Specimens from the Panamanian contact zone were subsequently re-analyzed by Monroe and Browning (1992), who concluded that Payne's (1974) voucher specimens used as a hybrid index included juveniles and did not represent a continuous series. Monroe and Browning's (1992) conclusions that *B. virescens* and *B. striata* seldom hybridized and should be regarded as distinct species were accepted by the American Ornithologists' Union (1993, 1998), which re-split *B. striata* into Green Heron (*B. virescens*) and Striated Heron (*B. striata*).

Hayes (2002) re-examined Payne's (1974) voucher specimens and published a photograph demonstrating that all had attained adult neck coloration and appeared to represent a continuous series. A re-analysis of Payne's (1974) data demonstrated increased variability and intermediacy in the contact zone between *B. virescens* and *B. striata*, implying hybridization (see, e.g., Schueler and Rising 1976). Hayes (2002) noted that phenotypically "pure" *B. virescens* and *B. striata* coexisted within the contact zone, suggesting that assortative mating occurred, but noted that the sample size of museum specimens was small and it remained uncertain whether both parental phenotypes actually bred within the hybrid zone.

At the eastern end of the hybrid zone, Hayes (2006) analyzed historic and current variability of the two taxa in Trinidad and Tobago by comparing museum speci-

mens and live individuals in the field with a color photograph of Payne's (1974) voucher specimens used as a hybrid index. In Trinidad, the population is dominated by *B. striata*; in nearby Tobago, the population is dominated by *B. virescens*, but with an increase in variability and intermediacy suggestive of hybridization. Hayes (2006) demonstrated a significantly lower proportion of intermediate phenotypes in the current Tobago population compared with museum specimens, suggesting a shift within the past century toward relatively "pure" phenotypes. Hayes (2006) concluded that the two taxa tended to mate assortatively and therefore appeared to have achieved essential reproductive isolation, supporting their current treatment as distinct species.

In this study we review the historical status of *Butorides* herons in Panama and document current variation among *Butorides* herons in the hybrid zone of central Panama. We compare our data with specimens collected >45 years ago to infer the extent of hybridization, gene flow, and assortative mating between the two taxa and to assess whether a recent shift in the direction of gene flow has occurred in the region, based on scoring neck coloration and inferring gene flow from phenotype.

**Historical status in Panama**

Early ornithologists were confused by the status of *Butorides* herons in Panama. Thayer and Bangs (1906) identified a specimen collected in central Panama in 1904 as *B. striata*. Oberholser (1916)

Neck color variation (counter-clockwise from bottom left of page 00, scores 1 through 8) of potentially breeding adult *Butorides* herons along a 6-km section of the Chagres River in central Panama on 14 and 15 July 2011. Photographs by Floyd Hayes.



described rufous-necked specimens from southern Central America and northern South America, including ten specimens from Panama, as a new subspecies of *B. virescens*, which he named *B. v. hypernotius*. Oberholser (1916) also described 22 rufous-necked specimens from the Pearl Islands in the Bay of Panama as a new endemic subspecies of *B. virescens*, which he named *B. v. margaritophilus*. Stone (1918) reported two specimens of *B. striata* and one specimen of *B. v. hypernotius* collected in central Panama in 1911 and 1912. Hallinan (1924) collected five specimens of *B. virescens* and observed

two active nests with eggs and chicks at Balboa, central Panama, on 13 May 1916.

Griscom (1929) collected a specimen identified as *B. s. striata* at El Real, Darién, in eastern Panama, which he claimed to be the first report from Central America, but overlooked earlier reports from Panama by Thayer and Bangs (1906) and Stone (1918). Griscom (1929) believed Hallinan's (1924) specimens of *B. virescens* represented a new subspecies of *B. striata*, which he described and named as *B. s. patens*. Griscom (1935) later summarized the status of all *Butorides* taxa in Panama. Hellmayr and Conover (1948) synonymized *B. v. hypernotius* with *B. v. maculatus* of the West Indies, attributed *B. striata* specimens collected by Thayer and Bangs (1906) and Hallinan (1924) to *B. s. patens*, and regarded Griscom's (1929) specimen of *B. s. striata* as the only record from Panama, but overlooked Stone's (1918) report.

Van Tyne (1950) obtained eight specimens and "many satisfactory sight records" of *B. striata* on Barro Colorado Island in central Panama, reported a nest of *B. striata* with eggs on 28 July 1925 and half-grown fledglings on 11 August 1925, stated that *B. virescens* was not a breeding resident, and questioned the validity of *B. s. patens*. Eisenmann (1952) reported both resident and migratory forms of *B. virescens* and resident *B. striata* at Barro

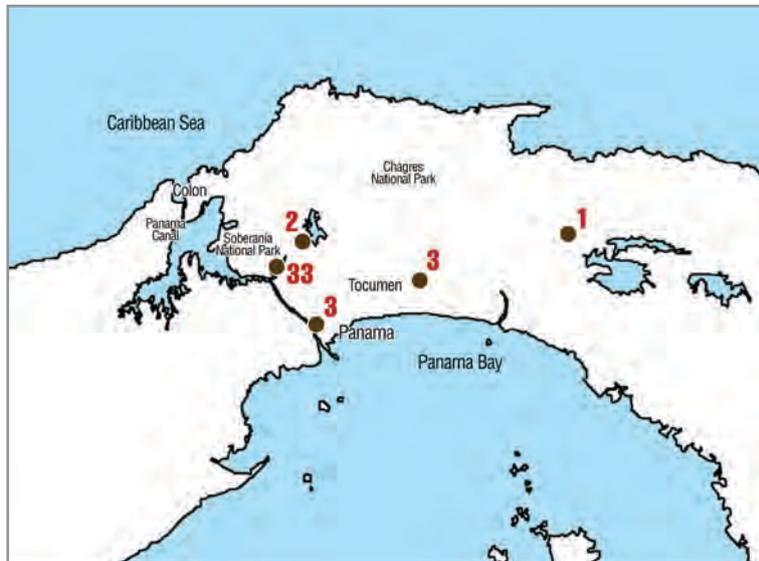


Figure 1. Sampling localities of *Butorides* herons in Panama during 10–16 July 2011. Numbers represent the number of samples at each locality.

Colorado Island and reported second-hand accounts of "supposedly" *B. virescens* nests with eggs on 24 March (T. Gilliard) and 28 April 1935 (Skutch).

Wetmore (1965) summarized data from many new specimen and sight records of four taxa in Panama: (1) migrant *B. v. virescens* from North America, a common winter visitor from October to April; (2) resident *B. v. maculatus*, common west of the Canal Zone but ranging eastward to near Colombia; (3) resident *B. v. margaritophilus*, endemic to the Pearl Islands; and (4) resident *B. s. striata*, ranging from central Panama eastward and more common toward the east. Wetmore (1965) found a nest of *B. virescens* with eggs in west-central Panama on 25 February 1956 and attributed earlier reports of nesting *B. virescens* on Barro Colorado Island to *B. s. striata*. Wetmore (1965) synonymized *B. s. patens* with *B. s. striata* and suggested the possibility of "occasional mixed mating among" *B. virescens* and *B. striata* "when they range

together," but dismissed *B. s. patens* as individual variation within *B. s. striata*.

Using a series of voucher specimens for scoring neck coloration on a scale of 1–9 (from gray-necked *B. striata* to rufous-necked *B. virescens*), Payne (1974) reported considerable variation in neck color scores among 44 specimens from central Panama, collected from 1908–1966 (dates from online specimen catalogs), with a mean score of 4.8 (SD=2.1, range=1–9; Table 1). A subset of 15 specimens collected from May–September, which probably eliminated migratory *B. v. virescens*, averaged slightly lower scores ( $x=4.1$ , SD=1.6, range=2–7; Table 1). Payne's (1974) data revealed a cline of predominantly rufous-necked birds in western Panama to predominantly gray-necked birds in eastern Panama, with a higher proportion of intermediate phenotypes (scores of 4–6) in central Panama than in western Panama. Payne (1974) pointed out that *B. v. margaritophilus* from the Pearl Islands was similar to populations from other Caribbean islands and later subsumed *B. v. maculatus* and *B. v. margaritophilus* into *B. v. virescens* (Payne 1979).

Little has been published on the status of *Butorides* herons in Panama during the past few decades. Recent field guides (Ridgely 1976, Angehr and Dean 2010) tend to echo the conclusions of Wetmore (1965) and Payne (1974). Willis and Eisenmann (1979) noted that *B. virescens* had become rare and *B. striata* was nearly extirpated at Barro Colorado Island in central Panama, due to competition for food with an introduced species of peacock bass (*Cichla pleiozona*).

Time period	NECK COLOR SCORES								
	1	2	3	4	5	6	7	8	9
1908–1966 (May–Sep only)	0	3	3	3	3 <sub>a</sub>	2	1	0	0
1908–1966 (year-round)	2	4	6	11	6	2	6	6	1
2011 (July)	7	10	5	3	6	5	5	1	0

a: includes one specimen scored as "4–5" by Payne (1974)

Table 1. Frequency of neck color scores of *Butorides* herons in central Panama based on museum specimens collected during 1908–1966 (Payne 1974) and photographs of live birds in 2011 (this study).

## Methods

During 10–16 July 2011, we searched for *Butorides* herons in wetlands in central Panama between 78° 45' and 80° 00' W longitude. Searches were conducted by foot, car, and motorboat. A GPS unit was used to obtain coordinates of different sampling locations. For each *Butorides* found, we attempted to obtain digital photographs clearly illustrating its neck coloration. We tried to avoid sampling the same bird twice and scrutinized photographs of similar appearing birds to ensure that each sample was a unique individual (e.g., differences in lore coloration, distribution of coloring on neck, pale edges of wing coverts, etc.). We compared each photographed individual with a photograph of a series of nine voucher specimens used by Payne (1974) as a hybrid index in which neck coloration was scored on a scale of 1–9, ranging from gray to dark purplish-brown (see Figure 1 of Hayes 2002). Because juveniles and immatures have streaked necks (always browner than adults of *S. striata*), only adults and subadults that had fully acquired adult neck coloration (Hayes 2002) were scored. When an individual appeared intermediate in neck coloration between two voucher specimens, we chose the specimen it most closely resembled. Our neck color scores were based on a group consensus by the authors.

According to Payne (1974), specimens scored 1–4 (gray to brownish gray) occur throughout the South American range of *B. striata*, and specimens scored 6–9 (grayish red-brown to purplish brown) occur throughout the North American range of *B. virescens*. Potential hybrids, especially those that have backcrossed with a parental phenotype, may be difficult to distinguish from presumably “pure” phenotypes (Hayes 2006). Individuals scored as 5 occur only in the hybrid zones and in isolated *B. v. bahamensis* of the Bahamas (Payne 1974); thus, individuals with a neck coloration score of 5 in Panama presumably represent hybrids, whereas those with lower or higher neck coloration scores may be either relatively “pure” or hybrid genotypes.

We compared our data on current neck color variation in central Panama with historical data published by Payne (1974) for 44 specimens collected from central Panama (excluding offshore islands) between 79–81° W longitude, during the period of 1908–1966 (dates from online specimen catalogs). Because neck color scores were ordinarily ranked and did not meet the assumptions of parametric statistical tests, nonparametric

Mann-Whitney *U* tests (*z* statistic) and two-sample chi-square tests ( $\chi^2$  statistic) were used to compare the distribution of neck coloration scores between current and historical time periods (Zar 1998).

## Results

We obtained neck color scores from 42 individuals in central Panama, all on the east side of the Panama Canal between 78° 54.42' and 79° 41.54' W longitude (Fig. 1). All neck color scores were obtained during 10–16 July 2011, and most of our samples (79%) were obtained from a boat along a 6-km section of the Chagres River east of Gamboa (Figure 1). Our data revealed considerable variability in neck color scores, ranging from 1–8 ( $\bar{x}=3.7$ ,  $SD=2.2$ ; Frontispiece and Table 1). Mean neck color scores were lower, although not significantly, than those of museum specimens collected during May–September ( $\bar{x}=4.1$ ;  $z=0.72$ ,  $P=0.47$ ). Mean neck color scores were significantly lower than museum specimens collected year-round ( $\bar{x}=4.8$ ;  $z=2.29$ ,  $P=0.02$ ), presumably reflecting a lower proportion (or absence) of migratory *B. v. virescens* from North America in our sample. Presumed *B. virescens* with scores of 7–8 comprised 14% of the population, presumed *B. striata* with scores of 1–3 comprised 52% of the population, and presumed hybrids with a score of 5 comprised 14% of the population. No birds were observed with a score of 9, which is relatively rare in *B. virescens* (Payne 1974).

When neck scores were collapsed into three categories (1–3, 4–6, and 7–9), a lower proportion of intermediate phenotypes (4–6) occurred among our sample of live individuals than for specimens collected during May–September (33% versus 53%), but the differences were not significant ( $\chi^2_2=2.01$ ,  $P=0.37$ ; Table 1). The proportions of phenotypes between our sample of live individuals and specimens collected year-round differed significantly ( $\chi^2_2=6.23$ ,  $P=0.04$ ), but the proportion of intermediate phenotypes in our sample was only slightly lower (33% versus 43%) and contributed only 9% of the overall chi-square value. The significant differences between our sample of live individuals and specimens collected year-round is attributable to proportionately more gray-necked phenotypes (scores of 1–3; 52% versus 27%) and fewer rufous-necked phenotypes (scores of 7–9; 14% versus 30%) in our sample, presumably reflecting a lower proportion (or absence) of migratory *B. v. virescens* from North America in our July sample.

No two individuals were seen within 10

m of each other; thus, none were suspected of being mated pairs. One apparently nesting individual flew with a stick in its bill, but we could not determine its identity. Most individuals were adults. We obtained photographs of three juveniles (excluded from our sample) along the Chagres River near Gamboa on 14 and 15 July. Two had mostly attained adult neck coloration, which was bright rufous, clearly identifying them as *B. virescens*. The third also had a rufous neck but with heavier streaking and was almost certainly *B. virescens*.

## Discussion

Although some criticize the use of hybrid indices as too crude and subjective, independent studies yield nearly identical results (Corbin and Barrowclough 1977). Independent scoring of neck coloration of museum specimens of *Butorides* herons from Panama using voucher specimens (Monroe and Browning 1992), and from Trinidad and Tobago using a color photograph of Payne's (1974) voucher specimens (Hayes 2006), yielded results very similar to those of Payne (1974). Independent scoring of neck coloration of live *Butorides* herons in the field in the United States Virgin Islands (Hayes and Hayes 2006) and in Trinidad and Tobago (Hayes 2006) using a color photograph of Payne's (1974) voucher specimens also yielded results nearly identical to those of Payne (1974).

In this study we chose to score neck coloration based on photographs of live birds, which we considered more objective than scoring neck coloration based on observations in the field. Our initial assessments of neck color scores were nearly always within  $\pm 1$  score of our final consensus. However, variation in lighting and exposure potentially affects the scoring of neck coloration in photographs of live birds. In a few individuals represented in multiple photographs, the neck color score varied by  $\pm 1$  score, in which case our chosen score was based on the average of the photographs. We conclude that using Payne's (1974) voucher specimens to score neck color in *Butorides* herons is accurate within  $\pm 1$  score.

Our data indicate that all phenotypes ranging from 1–8 are present during the month of July, at a time when migratory *B. v. virescens* from North America is unlikely to be present, and when local populations of *Butorides* nest with published egg dates ranging from 25 February (Wetmore 1965) to 28 July (Van Tyne 1950). As discussed above, the identity of *Butorides* herons nest-

ing in central Panama has been disputed. Van Tyne (1950) carefully identified *B. striata* nesting on Barro Colorado Island and questioned the credibility of earlier reports of nesting *B. virescens*; thus, it remains uncertain whether *B. virescens* actually breeds in central Panama. Our observations of both immature and adult *B. virescens* during the breeding season strongly suggest that they nest in the area, although some or all may be non-breeding migratory individuals from elsewhere.

The increased variability and intermediacy of *Butorides* herons in central Panama, in contrast with populations dominated by *B. virescens* in western Panama and populations dominated by *B. striata* in eastern Panama, strongly implies that hybridization still occurs between the two taxa in central Panama. Because random mating within a hybrid zone tends to reduce variability around an intermediate phenotype, the current presence of the full range of phenotypes among herons presumably breeding in central Panama suggests that most *B. virescens* and *B. striata* mate assortatively despite frequent hybridization. We concur with Hayes (2002, 2006) that the two taxa appear to have achieved essential reproductive isolation (Johnson et al. 1999), thus supporting their current treatment as distinct species.

On the southeastern Caribbean island of Tobago, Hayes (2006) demonstrated a historical decline in the proportion of intermediate phenotypes (neck color scores of 4–6), which accounted for 72% of 18 specimens collected from 1892–1913 but only 34% of 50 live individuals during 2000–2002, suggesting a recent increase in assortative mating despite occasional hybridization. Our data from central Panama suggest a similar historical decline in the current proportion of intermediate phenotypes (33% with neck color scores of 4–6) compared with specimens collected year-round 65–103 years earlier (43%) and using a smaller subset of specimens collected during May–September (53%). The lack of statistical significance could be explained by the more recent dates of specimens collected from central Panama (compared with Tobago), dilution of the year-round sample by migrant *B. virescens* with high neck color scores, and the small number of specimens in the May–September sample. Although it is premature to conclude that any historical shift in gene frequencies has occurred in central Panama, such a pattern should be looked for in future decades.

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