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VARIATION AND HYBRIDIZATION IN THE GREEN HERON (*BUTORIDES VIRESCENS*) AND STRIATED HERON (*B. STRIATA*) IN TRINIDAD AND TOBAGO, 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 Panama and southern Caribbean islands. I analyzed historic and current variability of the two taxa in Trinidad and Tobago by comparing museum specimens and live individuals in the field with a color photograph of nine voucher specimens used as a hybrid index. In Trinidad, the population is dominated by *B. striata*, whereas *B. virescens* and intermediate individuals are rare. In Tobago, *B. virescens* is the predominant form, with small numbers of *B. striata* and intermediate individuals. The increased variability and intermediacy of individuals in Tobago strongly implies hybridization, and the higher proportion of intermediate individuals among museum specimens suggests a shift within the past century toward relatively "pure" phenotypes. Neck color was unrelated to clinal variation, seasonality, or habitat. The distribution of phenotypes differs markedly between populations of *Butorides* in Trinidad and Tobago, which are separated by only 36 km, suggesting that competitive exclusion may preclude *B. virescens* from colonizing Trinidad and *B. striata* from colonizing Tobago. Because the two taxa may often have opportunities to interbreed on Tobago but tend to mate assortatively, they appear to have achieved essential reproductive isolation, thus supporting their current treatment as distinct species.

Key words: Butorides striata, *Butorides virescens*, Green Heron, hybridization, species limits, Striated Heron, Tobago, Trinidad, variation

Resumen: VARIACIÓN E HIBRIDIZACIÓN DE LA GARCITA VERDE (*BUTORIDES VIRESCENS*) Y LA GARCITA ESTRIADA (*B. STRIATA*) EN TRINIDAD Y TOBAGO, CON COMENTARIOS ACERCA DE LOS LÍMITES DE LA ESPECIE. La Garcita Verde (*Butorides virescens*) con cuello rufo de Norteamérica y el Caribe se hibridiza con la Garcita Estriada (*B. striata*) con cuello griz de Suramérica, en Panamá y las islas caribeñas del sur. Se analizó la variabilidad histórica y actual de ambos taxas a través de la comparación de especímenes de museo y animales vivos con una fotografía a color de nueve de nueve ejemplares utilizados como patrones del híbrido. En Trinidad la población está dominada por *B. striata*, mientras que *B. virescens* e individuos intermedios son raros. En Tobago, *B. virescens* es la forma predominante, con pequeños números de *B. striata* e individuos intermedios. La variabilidad incrementada incrementada y los caracteres intermedios en los individuos de Tobago sugieren fuertemente hibridización y la mayor proporción de individuos intermedios entre los especímenes de museo sugiere un cambio en el siglo pasado hacia los fenotipos "puros". El color del cuello no estuvo relacionado a variaciones clinales, estacionales o de hábitat. La distribución de los fenotipos difiere marcadamente entre las poblaciones de *Butorides* en Trinidad y Tobago, que estan separadas tan solo por 36 km, lo que sugiere que la exclusión competitiva evita la colonización de Trinidad por *B. virescens* y la de Tobago por *B. striata*. Como ambos taxas tienen frecuentes oportunidades de entrecruzarse en Tobago, pero tienen un apareamiento asociativo, parece ser que han alcanzado un aislamiento reproductivo esencial que apoya su tratamiento actual como especies diferentes.

Palabras clave: Butorides striata, *Butorides virescens*, Garcita Estriada, Garcita Verde, hybridización, límites de especies, Tobago, Trinidad, variación

Résumé : VARIABILITE ET HYBRIDATION ENTRE LE HERON VERT (*BUTORIDES VIRESCENS*) ET LE HERON STRIE (*B. STRIATA*) A TRINITE ET TOBAGO: COMMENTAIRES SUR LES FRONTIERES D'ESPECES. Le Héron vert (*Butorides virescens*) à cou roux d'Amérique du Nord et de la Caraïbe, se croise avec le Héron strié, à cou gris d'Amérique du Sud, du Panama et des îles du sud des Antilles (*B. striata*). J'ai étudié la variabilité historique et actuelle et deux taxons à Trinité et Tobago en comparant des spécimens de Muséum et des individus vivants en liberté avec des clichés en couleur de neuf spécimens utilisés comme index hybride. A Trinité, la population est dominée par *B. striata*, alors que *B. virescens* et les individus intermédiaires sont rares. A Tobago, *B. virescens* est la forme prédominante, avec un nombre faible de *B. striata* et d'individus intermédiaires. La plus variabilité et situation intermédiaire croissante à Tobago implique fortement la présence d'hybridation et la plus grande proportion d'individus intermédiaires dans les spécimens de Muséums suggère une dérive pendant le siècle passé vers des phénotypes relativement « pures ». La couleur du cou n'est pas liée à une variation clinale, ou de saisonnalité ou d'habitat. La distribution des phénotypes diffère nettement entre les populations à *Butorides* de Trinidad et de Tobago, séparées de seulement 36 km, suggérant qu'une exclusion compétitive empêche *B. virescens* de coloniser Trinidad et *B. striata* de coloniser Tobago.

Bien que les deux taxons on des possibilités de se croiser à Tobago, ils tendent à s'associer préférentiellement de manière homogène. Ils semblent donc avoir atteint un isolement reproductif suffisant, allant donc dans le sens de leur traitement actuel en tant qu'espèce séparé.

Mots-clés : Butorides striata, *Butorides virescens*, Héron strié, Héron vert, hybridation, limites d'espèces, Tobago, Trinité, variabilité

HYBRIDIZATION, THE INTERBREEDING between morphologically distinct populations in secondary contact (Short 1969), is a genetic phenomenon widespread in birds, even between non-sister taxa (Grant and Grant 1992), and can be inferred phenotypically by an increase in variability and intermediacy in the contact zone (Schueler and Rising 1976). Where zones of phenotypic intermediacy occur between parapatrically distributed taxa, documenting the gradient of change in geographic variation and the distribution of phenotypes (or, preferably, genotypes) within the contact zone is important to distinguish between primary intergradation (clinal variation) and secondary intergradation (hybridization), to infer the extent of gene flow and the development of isolating mechanisms, and to interpret the taxonomic significance of hybridization (e.g., Remington 1968, Short 1969, Woodruff 1973, Schueler and Rising 1976, Moore 1977, Barton and Hewitt 1985a, b, Harrison 1990).

The heron genus *Butorides* has been the subject of a disputed taxonomic history that remains unresolved. Two species are currently recognized: (1) the rufous-necked Green Heron (*B. virescens*) of North America, Central America, and the West Indies; and (2) the gray-necked Striated Heron (*B. striata*) of South America (including dark *B. s. sundevalli* of the Galápagos Islands), Eurasia, Africa, and Australia (American Ornithologists' Union 1998, Banks *et al.* 2003). David and Gosselin (2002) recently pointed out that *Butorides* is feminine, requiring that *B. striatus* be changed to *B. striata* (Banks *et al.* 2004). The two forms were generally treated as distinct species (e.g., Peters 1931, Hellmayr and Conover 1948, Bock 1956, Palmer 1962, Wetmore 1965), but sometimes considered conspecific (Hartert 1920) or possibly conspecific (Eisenmann 1952, Parkes 1955), until Payne (1974) provided evidence of extensive hybridization between *B. virescens* and *B. striata* where their ranges meet in southern Central America, several southern Caribbean islands, and coastal northern South America. Based on the conclusions of Payne (1974, 1979) and Payne and Risley (1976), the American Ornithologists' Union (1976, 1983) lumped the two forms into the Green-backed Heron (*B. striata*).

In a subsequent reanalysis of specimens from the Panamanian contact zone between *B. virescens* and *B. striata*, Monroe and Browning (1992) concluded that Payne's (1974) voucher specimens used as a hybrid index included juveniles and did not represent a continuous series. They concluded that *B. virescens* and *B. striata* seldom hybridized and should be regarded as distinct species. The American Ornithologists' Union (1993, 1998) accepted their conclusions. Hayes (2002), however, demonstrated that Payne's (1974) voucher specimens had all attained adult neck coloration and represented a continuous series; furthermore, a reanalysis of Payne's (1974) data demonstrated increased variability and intermediacy in the contact zone between *B. virescens* and *B. striata*, implying extensive hybridization. Because phenotypically "pure" *B. virescens* and *B. striata* phenotypes coexisted within the contact zone, Hayes (2002) tentatively concluded that assortative mating occurred, supporting their treatment as distinct species, 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, the ranges of *B. v. virescens* (resident throughout eastern North America, Central America, and the Caribbean) and *B. s. striata* (resident throughout South America) meet in Trinidad and Tobago, where populations are dominated by *B. striata* in Trinidad but by *B. virescens* on Tobago (ffrench 1973, 1991). On the latter island, individuals of both species and intermediates have been collected (Payne 1974). In this paper I document historic and current variability of the two taxa in Trinidad and Tobago, and attempt to assess several potential environmental correlates for variability (clinal variation, seasonality, or habitat), infer the degree of gene flow and development of reproductive isolation between the two taxa, and interpret the taxonomic significance of hybridization.

STUDY AREA AND METHODS

STUDY AREA

Trinidad and Tobago are large continental islands

located on the continental shelf of South America just north of the Orinoco River Delta (Fig. 1). Situated only 19 km from the continental mainland, Trinidad is larger (4520 km^2) and higher in elevation (up to 925 m), and possesses a greater diversity of wetlands (Kenny and Bacon 1981). Freshwater wetlands include rivers, swamps, marshes, rice fields, reservoirs, fish ponds, drainage canals, and sewage ponds; saltwater wetlands include mangrove swamps, salt marshes, river mouths, and mudflats. Tobago is located farther from the continent (118 km) but only 36 km from Trinidad; being smaller in size (306 km^2) and lower in elevation (up to 576 m), Tobago's wetlands average smaller and rice fields are lacking.

METHODS

I photographed a series of nine voucher specimens used by Payne (1974) as a hybrid index in which neck coloration was scored from 1-9, ranging from gray to dark purplish brown (see Fig. 1 of Hayes 2002). 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* (Payne 1974, Hayes 2002). Potential hybrids, especially those that have backcrossed with a parental phenotype, may be difficult to distinguish from presumably "pure" phenotypes. Individuals scored as 5 occur only in the hybrid zone and in isolated *B. v. bahamensis* of the Bahamas; thus, individuals with a neck coloration score of 5 in Trinidad and Tobago presumably represent hybrids, but those with lower or higher neck coloration scores (especially 4 or 6) may also be hybrids (Payne 1974, Hayes 2002).

Direct comparisons with a color photograph of hybrid index specimens were used to score neck coloration of museum specimens or photographs of museum specimens collected in Trinidad and Tobago from 1897 to 1913 (see Acknowledgments), and for live individuals observed throughout the country from October 2000 to August 2002. When an individual appeared intermediate in neck coloration between two voucher specimens, which often occurred, I chose the specimen it most closely resembled. 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. Because the apparent shade of neck coloration tended to vary by ±1 score depending on the angle of lighting, the only individuals scored were non-flying individuals carefully observed from the side in good lighting conditions with binoculars (7×) or a telescope (25×).

Because many localities were sampled repeatedly (up to 28 times) to obtain large sample sizes, and because none of the birds were banded or marked, many individuals were probably sampled repeatedly. To minimize the probability of including repeated samples in the following analyses, I chose the highest number of individuals scored within a day for each locality separated by a distance of >1 km from the nearest locality, and excluded data sampled on other days. In addition to the two islands (Trinidad and Tobago), localities were lumped into four arbitrarily defined regions to test for clinal variation: (1) western Trinidad, (2) central and eastern Trinidad, (3) western Tobago, and (4) central and eastern Tobago (Fig. 1).

To evaluate potential environmental correlates of variability in neck color, I recorded the following variables for each heron examined: (1) water salinity as either fresh or salt (including brackish); (2) presence or absence of a patch of mangroves (*Rhizophora mangle*, *Avicennia germinans*, *Laguncularia racemosa*, or *Conocarpus erecta*) > 0.25 ha in area within 50 m of the individual; and (3) season, with March-May as spring, June-August as summer, September-November as autumn, and December-February as winter.

STATISTICAL ANALYSES

Because neck coloration scores were ordinally ranked and did not meet the assumptions of parametric statistical tests, nonparametric Mann-Whitney *U* tests (*U* or *z* statistic), Kruskal-Wallis tests (*H* statistic), and two-sample chi-square tests with Yates correction (χ^2 statistic) were used when appropriate to compare the distribution of neck coloration scores between geographic regions, time periods, and habitat classes, respectively (Zar 1998). All probabilities are two-tailed with $\alpha = 0.05$.

RESULTS

HISTORICAL STATUS IN TRINIDAD

Anecdotal accounts of early ornithologists and a limited number of specimens indicate that Trinidad historically has been inhabited primarily by *B. striata* (Belcher and Smooker 1934, Junge and Mees 1958, Herklots 1961, ffrench 1973). Belcher and Smooker (1934:579) reported that *B. virescens* was a rare breeding resident whose eggs were described

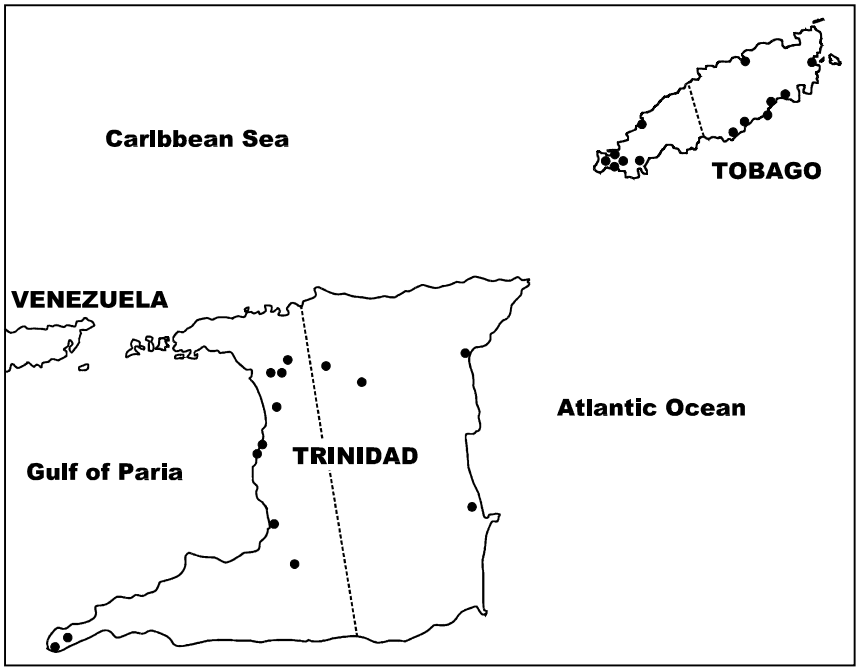

Fig. 1. Sampling localities of *Butorides* herons in Trinidad and Tobago during 2000-2002. Dashed lines on each island represent the division of regions: (a) western Trinidad, (b) central and eastern Trinidad, (c) western Tobago, and (d) central and eastern Tobago.

as "more rounded on the average" than those of *B. striata*. Herklots (1961) reported sight records of *B. virescens*, but provided no further details. ffrench (1973) regarded the purported breeding of *B. virescens* in Trinidad as uncertain and suggested that sight records pertained to migrants. Payne (1974) reported neck coloration scores of four specimens from Trinidad ranging from 1-3 ($\bar{x}$ = 1.5, SD = 1.0). The six specimens I examined from Trinidad, collected from 1902 to 1951 (BMNH, USNM, YPM), ranged from 1-3 ($\bar{x}$ = 1.5, SD = 0.8) and did not differ significantly from Payne's (1974) sample (U = 15.5, P = 0.43).

CURRENT STATUS IN TRINIDAD

Of 40 individuals examined in the field, neck coloration scores varied from 1-6, with 57.5% scored as 1 and 95% with a score of 1-3 ($\bar{x}$ = 1.7, SD = 1.1; Table 1). Although no specimens of *B. virescens* were collected, three sightings were accepted recently by the Trinidad and Tobago Rare Bird Committee, including two subadults with adult neck coloration at Trincity on 31 January 1998, a presumed adult at Pointe-a-Pierre on 21 March 1998, and an adult at San Rafael on 10 January 1999 (White and Hayes 2002). However, neck coloration was not scored on any of these individuals.

Intermediate individuals were rare in Trinidad. Birds with a neck coloration score of 4, representing brown-necked *B. striata* or hybrid *B. virescens* × *striata*, were recorded at Caroni on 2 June 2001 and at Pointe-a-Pierre on 7 October 2000 (see Hayes 2002 for a photograph of the latter). A presumed hybrid individual with a score of 5 was seen at Caroni on 28 June 2001 and on 19 April, 30 May, and 2 June 2002. Adults with neck coloration scores of 6, representing either *B. virescens* or hybrids, were noted at Cacandee on 21 April 2001 and at Fullarton on 26 May 2002.

HISTORICAL STATUS IN TOBAGO

In the late 19th and early 20th centuries, Tobago was inhabited by both taxa of *Butorides* with a high proportion of intermediate individuals. Belcher and Smooker (1934) regarded *B. striata* as common and *B. virescens* as rare. Perhaps influenced by Belcher and Smooker (1934), Junge and Mees (1958) reported that *B. striata* was more common but the only specimen collected was *B. virescens*. In contrast to earlier reports, Herklots (1961) and ffrench

Table 1. Frequency of neck color scores of *Butorides* herons in different time periods, islands, regions, seasons, water salinities, and habitats. Specimen data from Trinidad are insufficient for analysis. Data for region, season, salinity, and habitat are based on live individuals observed from 2000-2002.

	Neck Color Scores							
Variable	1	2	3	4	5	6	7	8
Island								
Trinidad (2000-2002)	23	10	5	1	0	1	0	0
Tobago (Payne 1974)	0	0	2	0	4	6	0	1
Tobago (1892-1913)	0	0	2	0	5	8	0	3
Tobago (2000-2002)	1	4	3	2	3	12	20	5
Region								
western Trinidad	16	9	4	1	0	1	0	0
central/eastern Trinidad	7	1	1	0	0	0	0	0
western Tobago	1	4	3	0	3	8	14	3
central/eastern Tobago	0	0	0	2	0	4	6	2
Season: Trinidad								
summer	11	7	4	0	1	0	0	0
autumn	9	1	1	1	0	0	0	0
winter	3	2	0	0	0	0	0	0
Season: Tobago								
summer	0	1	0	0	1	2	6	3
autumn	1	3	3	2	2	6	10	2
winter	0	0	0	0	0	4	4	0
Water salinity: Trinidad								
freshwater	15	5	3	1	0	0	0	0
saltwater	8	5	2	0	1	0	0	0
Water salinity: Tobago								
freshwater	1	4	3	1	1	9	12	5
saltwater	0	0	0	1	2	3	7	0
Habitat: Trinidad								
mangroves	5	4	2	0	1	0	0	0
non-mangroves	18	6	3	1	0	0	0	0
Habitat: Tobago								
mangroves	0	0	0	0	1	1	4	0
non-mangroves	1	4	3	2	2	11	16	5

(1973) reported *B. virescens* as a common resident. Herklots (1961) attributed several sight records of *B. striata* in Tobago to R. ffrench, who later regarded sight records of *B. striata* in southwest Tobago as uncertain (ffrench 1973) and eventually omitted the species from Tobago's avifauna (ffrench 1996). Payne (1974) reported neck coloration scores of 13 specimens from Tobago ranging from 3-8 ($\bar{x}$ = 5.38, SD = 1.33; Table 1), indicating that both taxa as well as intermediates were present. Neck coloration scores from 18 specimens I examined from Tobago, collected from 1892-1913, also ranged from 3-8 ($\bar{x}$ = 5.72, SD = 1.41; Table 1 and Appendix) and did not differ significantly from Payne's (1974) sample (U = 131.5, P = 0.55). The proportion of specimens with a neck coloration score of 5 (presumed hybrids) varied from 31% (Payne 1974) to 28% (this study).

CURRENT STATUS IN TOBAGO

Of 50 individuals examined in the field, neck coloration scores ranged from 1-8 ($\bar{x}$ = 5.86, SD = 1.84; Table 1). Mean neck coloration scores did not differ significantly from the museum specimens I

examined (z = 1.21, P = 0.23). However, when neck scores were lumped into three categories (1-3, 4-6, and 7-8), proportionately more intermediate phenotypes (scores of 4-6) occurred among specimens (72%) than live individuals (34%; Table 1) and the distribution of neck scores differed significantly between live individuals and specimens (χ^2 = 8.17, df = 3, P = 0.02). Presumed *B. virescens* with scores of 7-8 comprised 50% of the population and presumed *B. striata* with scores of 1-3 comprised 16% of the population (Table 1). Presumed hybrids with a score of 5 comprised only 6% of the population (Table 1), significantly less than the specimens I examined (28%; χ^2 = 4.13, df = 1, P = 0.04). No birds were observed with a neck score of 9, which is very rare in *B. virescens* (1.4% of 147 specimens from the Greater and Lesser Antilles; Payne 1974). Mean neck coloration scores were significantly higher in Tobago than in Trinidad (z = 7.43, P < 0.001).

The only specimens of adult *B. striata* taken in Tobago were two males with neck coloration scores of 3 collected at Sandy Point on 25 April 1903 (AMNH 469318, 469318). An adult *B. striata* at Buccoo from 17 January to 9 February 1998 was the first sighting accepted by the Trinidad and Tobago Rare Bird Committee (White and Hayes 2002). Between 24 May and 7 August 2001, I identified a minimum of six (up to four seen in a day) adult *B. striata* with neck coloration scores of 1-3 in southwestern Tobago. The following year, I found three different adult *B. striata* with scores of 1-3 in southwestern Tobago on 11 June 2002. A *B. striata* with a neck score of 1-3 (seen too briefly to score) was seen at Englishman's Bay, north-central Tobago, on 8 October 2001.

ENVIRONMENTAL CORRELATES

Significant variation in neck coloration occurred among the four regions (H = 56.5, P = 0.006; Table 1). However, nonparametric multiple comparison tests revealed no significant differences between the two Trinidad regions or between the two Tobago regions (P > 0.05). Each region in Trinidad differed from both regions in Tobago and each region in Tobago differed from both regions in Trinidad (P < 0.05). Neck coloration did not differ significantly among seasons in either Trinidad (H = 1.86, P = 0.39) or Tobago (H = 4.3, P = 0.12), between freshwater and saltwater habitats in Trinidad (U = 214.5, P = 0.50) or Tobago (U = 271, P = 0.68), or between mangrove and non-mangrove habitats in Trinidad (U = 208, P = 0.19) or Tobago (U = 152.5, P = 0.53; Table 1).

DISCUSSION

Although some criticize the use of a hybrid index as crude and subjective, Corbin and Barrowclough (1977) demonstrated that independent studies yielded nearly identical results. With regard to Payne's (1974) hybrid index specimens, I found a color photograph of the specimens to be highly useful and reasonably accurate for scoring neck coloration of museum specimens and in the field. Payne (1974) and I examined specimens independently, yet obtained similar results. When colleagues accompanied me in the field and shared excellent views of an individual, their independent assessment of neck coloration was always within ±1 score of my own.

The resident population of *Butorides* in Trinidad is dominated by gray-necked *B. striata* (scores of 1-2) with a minority of brown-necked individuals (scores of 3-4) within the normal range of variation throughout South America. The range of dates for *B. virescens* (10 January to 26 May) suggests that it is a rare visitor to Trinidad, either as a Nearctic migrant or a visitor from Tobago. There is no credible evidence that *B. virescens* has ever bred in Trinidad.

In Tobago, the current population consists predominantly of *B. virescens*, with a small number of *B. striata* and intermediate individuals. The higher proportion of intermediate individuals among museum specimens, probably contributing to the uncertainty of earlier accounts by ornithologists, suggests a phenotypic shift within the past century toward relatively pure phenotypes. Some individuals of *B. virescens* may represent migrants from farther north, but if so, the proportion is likely small, given the rarity of *B. virescens* in Trinidad. Whether *B. striata* actually breeds in Tobago or is a rare but regular non-breeding visitor from Trinidad remains uncertain (breeding of *Butorides* herons in Tobago is poorly documented). My observations of multiple individuals during the wet season coincided with the peak breeding season for wading birds in Trinidad, including *Butorides* herons, as well as the peak season for vagrancy of non-breeding waterbirds from mainland South America (ffrench 1991). The increased variability and intermediacy of the Tobago population, in contrast with its neighboring islands in the Lesser Antilles and Trinidad (Payne 1974, Hayes 2002), strongly implies hybridization, indicating that at least some *B. striata* breed in Tobago.

There is no evidence that neck color variability in Trinidad and Tobago is related to clinal variation

within an island, seasonality, or habitat. The seemingly continuous variation in neck color from gray to purplish-brown strongly implies polygenic control of the deposition of gray eumelanin and rufous phaeomelanin pigments in the distal barbules of neck feathers (Schodde *et al.* 1980). Brown-necked individuals of *B. striata* with elevated levels of rufous phaeomelanin pigments in the neck also tend to have more extensive rufous on the underparts and wing covert margins than gray-necked individuals (Hayes pers. obs.). Whether neck color variability in *B. virescens* and *B. striata* is adaptive or represents genetic drift in isolated populations remains unknown, but the darker coloration of *B. s. sundevalli* in the Galápagos Islands is thought to enhance foraging success in a backdrop of bare, blackish lava (Snow 1975).

The distribution of phenotypes differs markedly between populations of *Butorides* in Trinidad and Tobago, which are separated by only 36 km. An accomplished disperser, *B. virescens* is widely distributed on islands throughout the Caribbean, including Tobago, but only rarely visits Trinidad, suggesting that competitive exclusion by resident *B. striata* precludes it from successfully colonizing the island. Small numbers of *B. striata* frequently wander to Tobago from Trinidad or mainland South America, and vagrancy within the Caribbean has been documented on St. Vincent in the Lesser Antilles (AMNH 325358, with a neck score of 3, taken on 18 July 1924; Bond 1964, Payne 1974) and St. John in the Greater Antilles (neck score of 2, present from 25-29 May 2003; F. E. Hayes unpubl. photos). My observations in 2001 and 2002 suggest that small numbers of *B. striata* visit Tobago frequently enough to form a small breeding population, yet the island's population of *Butorides* remains dominated by relatively "pure" *B. virescens* phenotypes, suggesting that competitive exclusion precludes the successful establishment of *B. striata*. The historical shift toward relatively "pure" phenotypes of both taxa in Tobago suggests the occurrence of assortative mating despite occasional hybridization. Because the two taxa may have frequent opportunities to interbreed freely on Tobago but interbreed only occasionally, they appear to have achieved *essential* reproductive isolation (Johnson *et al.* 1999), thus supporting their current treatment as distinct species.

Given that these two taxa, which differ morphologically only in neck (and perhaps belly) coloration, appear to behave as distinct species, the number of species in *Butorides*, which includes up to 26 subspecies currently subsumed within *B. striata* and four within *B. virescens* (Hanckock and Kushlan 1984, Hayes 2002), may be greater than currently recognized. Finally, these conclusions are based on the inherent limitations of scoring live individuals in the field based on specimen scores, and inferring gene flow from phenotype. Behavioral studies of mated pairs and genetic analyses are needed to adequately resolve the species limits of *Butorides* herons.

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Appendix. Neck coloration scores of adult *Butorides* specimens from Tobago examined in this study. AMNH = American Museum of Natural History, New York, NY; BMNH = Natural History Museum, London, UK; FMNH = Field Museum of Natural History, Chicago, IL; NRM = Naturhistoriska Riksmuseet, Stockholm, Sweden.

Specimen	Date (M-D-Y)	Sex	Neck Color Score
AMNH 156503	unknown	male	5
AMNH 156504	04-24-1903	female	5
AMNH 469318	04-25-1903	male	3
AMNH 469319	04-25-1903	female	5
AMNH 469320	04-25-1903	male	3
AMNH 469321	04-24-1903	male	6
AMNH 469322	04-24-1903	female	5
AMNH 469223	04-24-1903	unknown	5
AMNH 469324	03-04-1897	male	6
AMNH 469325	04-27-1903	unknown	6
BMNH 1914.7.6.2	05-21-1913	unknown	6
BMNH 1914.12.1.536	12-29-1907	unknown	6
BMNH 1969.43.28	04-24-1903	unknown	6
FMNH 33642	04-20-1892	male	8
FMNH 33659	04-20-1892	male	8
FMNH 33662	04-15-1892	male	8
FMNH 33676	04-20-1892	female	6
NRM 568904	04-24-1903	male	6