VARIATION AND HYBRIDIZATION IN THE GREEN HERON (BUTORIDES VIRESCENS) AND STRIATED HERON (B. STRIATA) IN TRINIDAD AND TOBAGO, WITH COMMENTS ON SPECIES LIMITS

FLOYD E. HAYES

Department of Life Sciences, University of the West Indies, St. Augustine, Trinidad and Tobago.
Current address: Department of Biology, Pacific Union College, Angwin, CA 94508, USA. floyd_hayes@yahoo.com

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 populations 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 rojo de Norteamérica y el caribe se hibridiza con la garcita estriada (B. striata) con cuello gris 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 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 la hibridización y la mayor proporción de individuos intermedios entre los especímenes de museo sugiere un cambio en el siglo pasado hacia los fenótipos “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 están 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 entrecruzar 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, hibridización, límites de especies, Tobago, Trinidad, variación

Résumé : Variabilité et Hybridation Entre le Heron Vert (Butorides virescens) et le Heron Strie (B. striata) à Trinité et Tobago. Commentaires sur les frontières d’espèces. 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. À 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 phénomènes relativement « purs ». La couleur du cou n’est pas liée à une variation clinaire, ou de saisonnalité ou d’habitat. La distribution des phénomènes 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.
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 intermediary in the contact zone (Schueler and Rising 1976). Where zones of phenotypic intermediary 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 1993, 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 intermediary 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 km²) 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 km²) 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 (7x) or a telescope (25x).

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 (χ² 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 α = 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.
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.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Neck Color Scores</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Island</td>
<td></td>
</tr>
<tr>
<td>Trinidad (2000-2002)</td>
<td>23</td>
</tr>
<tr>
<td>Tobago (Payne 1974)</td>
<td>0</td>
</tr>
<tr>
<td>Tobago (1892-1913)</td>
<td>0</td>
</tr>
<tr>
<td>Tobago (2000-2002)</td>
<td>1</td>
</tr>
<tr>
<td>Region</td>
<td></td>
</tr>
<tr>
<td>western Trinidad</td>
<td>16</td>
</tr>
<tr>
<td>central/eastern Trinidad</td>
<td>7</td>
</tr>
<tr>
<td>western Tobago</td>
<td>1</td>
</tr>
<tr>
<td>central/eastern Tobago</td>
<td>0</td>
</tr>
<tr>
<td>Season: Trinidad</td>
<td></td>
</tr>
<tr>
<td>summer</td>
<td>11</td>
</tr>
<tr>
<td>autumn</td>
<td>9</td>
</tr>
<tr>
<td>winter</td>
<td>3</td>
</tr>
<tr>
<td>Season: Tobago</td>
<td></td>
</tr>
<tr>
<td>summer</td>
<td>0</td>
</tr>
<tr>
<td>autumn</td>
<td>1</td>
</tr>
<tr>
<td>winter</td>
<td>0</td>
</tr>
<tr>
<td>Water salinity: Trinidad</td>
<td></td>
</tr>
<tr>
<td>freshwater</td>
<td>15</td>
</tr>
<tr>
<td>saltwater</td>
<td>8</td>
</tr>
<tr>
<td>Water salinity: Tobago</td>
<td></td>
</tr>
<tr>
<td>freshwater</td>
<td>1</td>
</tr>
<tr>
<td>saltwater</td>
<td>0</td>
</tr>
<tr>
<td>Habitat: Trinidad</td>
<td></td>
</tr>
<tr>
<td>mangroves</td>
<td>5</td>
</tr>
<tr>
<td>non-mangroves</td>
<td>18</td>
</tr>
<tr>
<td>Habitat: Tobago</td>
<td></td>
</tr>
<tr>
<td>mangroves</td>
<td>0</td>
</tr>
<tr>
<td>non-mangroves</td>
<td>1</td>
</tr>
</tbody>
</table>

(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 ($\chi = 1.21, P = 0.23$). 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 ($\chi^2 = 8.17$, df = 3, $P = 0.02$). Presumed $B. virens$ with scores of 7-8 comprised 50% of the population (Table 1). Presumed hybrids with a score of 5 comprised only 6% of the population (Table 1). Presumed hybrids with a score of 5 comprised only 6% of the population (Table 1). Presumed hybrids with a score of 5 comprised only 6% of the population (Table 1). Presumed hybrids with a score of 5 comprised only 6% of the population (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 $B. virens$ (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 $B. virens$ has ever bred in Trinidad.

In Tobago, the current population consists predominantly of $B. virens$, 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 $B. virens$ may represent migrants from farther north, but if so, the proportion is likely small, given the rarity of $B. virens$ 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 (Ifrench 1991). The increased variability and intermedicy 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 (Hancock 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.

ACKNOWLEDGMENTS

I thank P. A. Buckley, D. B. McNair, R. B. Payne, J. V. Remsen, Jr., and an anonymous reviewer for reviewing earlier drafts. Field work in Trinidad and Tobago was funded indirectly by Caribbean Union College, the Tobago House of Assembly, and the University of the West Indies. For their companionship and patience in the field I thank B. Hayes, M. Hayes, M. Kenefick, K. Lallsingh, N. Lallsingh, and numerous others who accompanied me less frequently. Examination of museum specimens in the U. S. National Museum of Natural History (USNM) and the American Museum of Natural History (AMNH) was financed by a Study and Travel Grant from the University of the West Indies, St. Augustine. For their assistance with museum specimens, I thank C. Angle (USNM), M. Foster (USNM), J. Weicker (AMNH), P. Rasmussen (USNM), and P. Sweet (AMNH). I also thank J. Bates and D. Willard for loaning specimens from the Field Museum of Natural History (FMNH), M. Adams for providing photographs of specimens in the (British) Natural History Museum (BMNH), G. Frisk for providing photographs of a specimen in the (Swedish) Naturhistoriska Riksmuseet (NRM), and K. Zyskowski for providing photographs of specimens in the Yale-Peabody Museum (YPM). I also thank J. Eitniear, A. Kratter, R. Payne, and K. Vooos for providing pertinent literature.

LITERATURE CITED


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.

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