Cory's Bittern, *Ixobrychus "neoxenus" exilis*: Morph, Mutant, or Mixed Bag?

PAUL SMITH

Fauna Paraguay, Encarnación, Departamento Itapúa, Paraguay and Para La Tierra, Reserva Natural Laguna Blanca, Municipalidad de Santa Barbara, Departamento San Pedro, Paraguay; email: faunaparaguay@gmail.com

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Cory's Bittern (*Ixobrychus "neoxenus" exilis*) is an enigmatic form, usually referred to as a rare dark colour phase or morph of Least Bittern (*Ixobrychus exilis* [Gmelin, 1789]). A review of the literature indicates that birds identified as Cory's Bittern show considerable plumage variation and commonly exhibit multiple plumage anomalies. Temporal and spatial clumping of records shows that they are of irregular occurrence; thus, they do not meet the criteria for recognition as a colour morph. Cory's Bittern should thus be viewed as a colloquial name that refers to any one of a number of abnormally dark-plumaged, genetically undefined and phenotypically heterogeneous Least Bitterns.

Key Words: Cory's Bittern; *Ixobrychus neoxenus*; *Ardetta neoxena*; Least Bittern; *Ixobrychus exilis*; leucism; melanism; Ontario; Florida

Introduction

Since its description as Ardetta neoxena (Cory 1886a, b), Cory's Bittern has captured the attention of ornithologists on account of its extreme rarity, striking plumage and disjunct distribution. Despite the confident assertion that the form is "without doubt perfectly distinct from any other known species" (Cory 1886a), doubts over its specific identity were soon expressed. After examining a number of specimens and publishing a series of papers (Scott 1889, 1891), Scott (1892a) stated, "I feel impelled to record the strong impression that I entertain, that it will ultimately be found to be a color phase of Botaurus exilis." Sharpe (1894) expressed the controversial opinion that "Ardetta neoxena of Cory seems to be founded on very old individuals of A. exilis, in which the rufous tips to the quills and the light stripes on the back have disappeared with age or wear," although on examination of a specimen, he later afforded it full species status (Sharpe 1898). Bangs (1915), on the other hand, referred to Cory's Bittern as a "case of nothing more or less than erythrism."

Bent (1926) concurred with the impression that Cory's Bittern is conspecific with Least Bittern (*Ixobrychus exilis*), but warned, "It should not be called a color phase of a dichromatic species, as it occurs too rarely and irregularly." Hellmayr and Conover (1948) indicated that "*neoxenus*" was synonymous with *exilis* and followed Bent in describing it as a "melano-erythristic mutation."

In a thorough review of the state of Cory's Bittern knowledge, Pittaway and Burke (1996) speculated that "Cory's Least Bitterns seen today probably result from a rare recessive allele in the population of typical birds" and that "The lack of intermediate morphs between typical and Cory's Least Bittern suggests a single gene

having two alleles for colour: dominant (typical) and recessive (Cory's)." The authors lamented the lack of available genetic material and highlighted the speculative nature of this hypothesis. This theory has subsequently been adopted in the modern literature (Hancock and Kushlan 1984; Gibbs *et al.* 1992; Sibley 2000), perhaps stemming in part from a widespread but incorrect understanding of the term "morph."

Polymorphism is correctly defined as "the coexistence in one interbreeding population of two or more distinct and genetically determined forms, the least abundant of which is present in numbers too great to be due solely to recurrent mutation" (Ford 1945). Polymorphism can occur in two forms: transient (where an advantageous gene spreads through the population) and balanced (where it is maintained at a fixed level by a balance of selective agencies). The definition "excludes continuous variation... and the appearance of heterozygous mutants subject to elimination by selection" (Ford 1955). As this definition excludes both plumage abnormalities (as suggested by Bent 1926) and the segregation of rare recessives (suggested by Pittaway and Burke 1996), the status of Cory's Bittern requires clarification.

This paper is a critical review of the published data that aims to re-examine the status of "neoxenus," with the hope that a pilot genetic study will one day be conducted to confirm or dismiss the hypotheses proposed.

Spatial Distribution

Cory's Bittern is known from very few documented records, most of which are from eastern North America before 1900 (Palmer 1976; Pittaway and Burke 1996; Sibley 2011) (Figure 1). Despite the range of the Least Bittern in the Americas — stretching from southern Canada to northern Argentina (Hancock and Kushlan

1984) — the 38 documented North American records are of the migratory subspecies *exilis* and are concentrated around the Great Lakes and Florida, with 22 records from Ontario; 7 from Florida; 2 each from Michigan, Ohio, and Illinois; and 1 each from Massachusetts, New York, and Wisconsin (Brewster 1902; Kumlien *et al.* 1948; Palmer 1976; Pittaway and Burke 1996; Sibley 2011). Additional undocumented sight records are listed by Pittaway and Burke (1996) and Sibley (2011) but, with the exception of a pair of recent reports by the same observer (D. Arbour, of Red Slough, Oklahoma – 15 August 2001 and 14 May 2012), they do not expand the known distribution.

All three South American records are of the resident subspecies *erythromelas* and are confined to a comparatively small area of southern Brazil (São Paulo State and Mato Grosso do Sul [Teixeira and Alvarenga 1985; Sibley 2011]) and adjacent Paraguay (Asunción [Clay *et al.* in press]). Though only one of the individuals was collected (Teixeira and Alvarenga 1985), the other two were documented by video (Sibley 2011) and photograph (Clay *et al.* in press) respectively. The South American subspecies are non-migratory, but undertake local movements in response to water conditions (Martínez-Vilalta and Motis 1992).

Temporal Distribution

All Ontario specimens of Cory's Bittern were taken in the breeding season between May and September (Cross 1892; Brown and Brewster 1893; Fleming 1902; Pittaway and Burke 1996; Sibley 2011), and 21 of the 22 specimens from Ontario were taken in a 10-year period between 1890 and 1900, with a single additional specimen taken in 1913. Pittaway and Burke (1996) list undocumented sight records from Ontario in "about 1921," 1923, 1927, 1928, 1932, 1939, 1941, 1950, "in the 1950s," 1973, and 1981. Cory's Bittern has thus not been documented in the "stronghold" of its range since 1913 and not reported there since 1981. Images of the specimens held in the Royal Ontario Museum can be consulted online at www.jeaniron.ca /2011/corys.htm.

Six of the first seven specimens of Cory's Bittern were taken in Florida, although the description of the type specimen taken in Florida in 1885 lacks a precise date (Cory 1886a): five specimens were taken between 9 July 1889 and 15 August 1891 (Scott 1889; Cory 1891; Chapman 1896). Although Scott (1892b) describes it as occurring "regularly though probably in small numbers at Lake Flirt and Lake Okeechobee," the next report from Florida was not until Bent and Copeland (1927) saw a bird on 7 April 1925. There are no further Florida reports until an undocumented sight record by J. Brunner in April 2003 (Sibley 2011). There have been no documented records of Cory's Bittern in Florida, the second core area of the range, for almost a century. All records correspond approximately to the breeding season.

The first Ohio specimen of Cory's Bittern was collected on 25 May 1907 in a "large colony of Least Bitterns" (Ruthven 1907), and the second, possibly a migrant bird, was photographed after flying into a building at Youngstown on 3 October 1949 (Pittaway and Burke 1996). In Illinois, Carpenter (1948) took a specimen on 1 June 1909 and another was collected by Eifrig (1915) on 23 May 1914. Cherrie (1896) reported the only specimen from Wisconsin, a male in full plumage on 22 May 1893, while Watkins (1895) reported a "fine male" from Michigan on 8 August 1894, which was followed by another Michigan male taken on 14 May 1904 (Taverner 1905). Brewster (1902) documents the only Massachusetts record, collected in a "yard" on 18 May 1901. Allen (1913) includes a photograph of a female taken at the Ithaca marshes, New York on 17 May 1913, although Bull (1985) was later unable to trace this specimen. Two modern sight records from Oklahoma — 15 August 2001 and 14 May 2012 — were also during the breeding season, but far removed from the traditionally understood "core range."

South American records account for almost half of the seven worldwide records since the 1950s (and all of the documented records), but none of the records prior to that date (Teixeira and Alvarenga 1985; Sibley 2011; Clay *et al.* in press). All South American records have been taken in the austral autumn during April and May. Consequently, all dated reports of Cory's Bittern are between April and October, with no reports from anywhere in the entire range between November and March. Wintering grounds, migration routes, and whether these differ from those of "normal" birds are all unknown.

Variation

Cory (1886a) described his *Ardetta neoxena* as "Top of the head, back, and tail dark greenish black, showing a green gloss when held in the light. Sides of the head and throat rufous chestnut, the feathers on the back of the neck showing greenish black tips. Breast and underparts nearly uniform rufous chestnut, shading into dull black on the sides; wing-coverts dark rufous chestnut; under wing-coverts paler chestnut. All the remiges entirely slaty plumbeous. Under tail-coverts uniform dull black." In addition he noted the presence of two white flank feathers, which he attributed to "albinism." Subsequent published descriptions of specimens ascribed to *neoxena*, however, show considerable divergence from this type description; some examples are summarized below.

Chapman (1896) noted great variation in the plumage of Cory's Bittern: "only three of my ten specimens of *neoxena* are alike." In comparing it to typical *exilis*, he added, "there is no regularity in the substitution of colors; hence these birds differ not alone in color, but also in pattern of coloration." Significantly, he added, "Nor do the known cases of dichromatism among Herons give us any ground for asserting that

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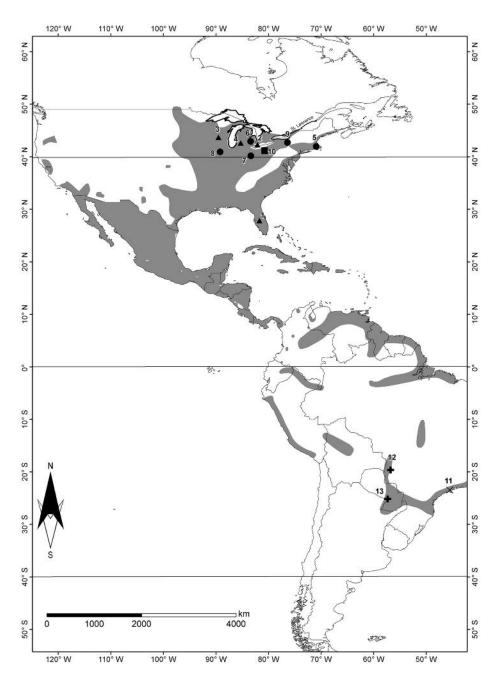


FIGURE 1. Distribution of the Least Bittern, *Ixobrychus exilis* (grey shading; BirdLife International and NatureServe 2013), and reports of Cory's Bittern (*I. "neoxenus" exilis*) in North and South America documented in 1880–1900 (triangles), 1900–1920 (circles), 1940–1960 (squares) 1960–1970 (cross), and 2010–2013 (plus signs). 1. Lake Okeechobee area, Florida, USA (Cory 1886a; Scott 1892a); 2. Toronto area, Ontario, Canada (Brown and Brewster 1893); 3. Lake Koshkonong, Wisconsin, USA (Cherrie 1896); 4. Jackson County, Michigan, USA (Watkins 1895); 5. Scituate, Plymouth County, Massachusetts, USA (Brewster 1902); 6. St Clair Flats, Michigan, USA (Taverner 1905); 7. Toledo, Ohio, USA (Ruthven 1907); 8. Rob Roy Marsh, Aurora, Illinois (Carpenter 1948) and Fox River, 40 miles northwest of Chicago, Illinois, USA (Eifrig 1915); 9. Ithaca Marshes, New York, USA (Allen 1913); 10. Youngstown, Ohio, USA (Pittaway and Burke 1996); 11. São Paulo, Brazil (Teixeira and Alvarenga 1985); 12. Pantanal, Mato Grosso do Sul, Brazil (Sibley 2011); 13. Asunción, Paraguay (Clay et al. in press).

neoxena is a dichromatic phase of exilis." However, while admitting that he could not "explain this unusual degree of variation," he opted instead to ignore it and consider Cory's Bittern a distinct but presumably highly variable species. Although seven of his ten specimens showed "melanistic or albinistic markings or both combined," Chapman (1896) did not consider the possibility that the form represented a heterogeneous range of phenotypic variations caused by diverse plumage abnormalities.

A male specimen from Florida (no. 44 806) is described as "completely melanistic" (Chapman 1896), while Carpenter (1948) reported a Cory's Bittern from Illinois that was "extremely albinistic yet decidedly melanistic," in which the pale areas of the plumage were entirely white, several irregular black patches were present, and there were only scattered chestnut feathers on the underparts. Allen's (1913) specimen from New York, however, showed no "albinistic tendencies." A sight record reported by Alex Lucas on 2 August 1939 along the Otonabee River at Rice Lake, Peterborough County, Ontario, was described as "chocolate-colored all over" (Pittaway and Burke 1996).

The second known specimen of Cory's Bittern reported by Scott (1891) from Florida (no. 3237) was described as "deep greenish-black" on the "entire upper surface," with this colour "also the general tone of the belly, sides, and flanks, though a few whitish and some chestnut feathers are mixed" and "bright chestnut" only on the "lower surface of the neck and throat." Furthermore, the greater, median, and mid lesser coverts are "dark like the back at the bases but shade into deep chestnut terminally."

A male specimen (no. 11 449, collection of W. E. D. Scott), also reported by Scott (1892a), is also dark greenish-black "both above and beneath," differing yet again in that the "feathers of the lower neck alone having traces (edgings) of dark chestnut, their centres being of the greenish black tone prevailing throughout the bird." In the same paper (no. 11 451) is said to be "very like Mr. Cory's original bird save that there are traces on the sides of the back of lines, much obscured, but of a general brownish tint, thus approaching Botaurus exilis." Cherrie's (1896) Wisconsin specimen, a male in full breeding plumage, "agrees minutely above (with the type specimen)" but below "the throat and neck are just a trifle paler chestnut, and there is just a little more white on the abdomen." Brewster's (1902) Massachusetts specimen had the "flanks, abdomen and under-tail coverts, slaty brown tinged with reddish."

In addition to other black markings on the head, the second specimen from Michigan reported by Taverner (1905) had a "triangular patch of black" below and behind the eye that reached from the bill before fading out on the ear coverts. Fleming's (1902) adult male (no. 14, collection of the Provincial Museum of Toronto) has chestnut sides of the head and the breast and ab-

domen black "slightly tinged with chestnut" but possesses "a clearly-marked black line running from the gape almost to the back of the head, on both sides,... [that] nearly divides the chestnut on the sides of the head."

Among the three modern South American records, similar variation is present. Teixeira and Alvarenga's (1985) bird did not show any greenish gloss on the black areas of the plumage and had entirely black secondaries. The specimen from Paraguay does show the greenish gloss on the black areas of the plumage, but possesses the typical yellowish bill colouration of "normal" exilis, not the "mostly blackish brown" associated with Cory's Bittern (Pittaway and Burke 1996), and has a black medial line down the centre of the foreneck (Clay et al. in press).

Fleming (1902) reports a young male (no. 15, collection of the Provincial Museum of Toronto) with "peculiar" feet so that "the green of the tarsus and toes is curiously mottled and blotched with reddish brown," leading to the speculation that "it may prove that the feet and legs of the nestlings are not colored as in the adult." However, the colour of the legs is not mentioned in the description of the type and in the subsequent literature is variably described as "blackish to brown" (Eifrig 1915), "dark(er) olive-green" (Sibley 2011), and brownish without yellow tinges (Teixeira and Alvarenga 1985), while the photograph in Clay *et al.* (in press) shows legs that resemble those of typically plumaged birds.

The morphometrics of Cory's Bittern have received scant attention. Chapman (1896) provided limited data for a small number of specimens that he examined, but elected not to discuss the results in his text. Presumably he was unable to detect any obvious diagnostic characteristics in his data.

Assortative Mating

In an attempt to explain the high rate of partial leucism in specimens of Cory's Bittern, Pittaway and Burke (1996) offered assortative mating resulting in inbreeding as a potential, if "unlikely" explanation. Thus, it may be inferred that the other highly variable plumage characteristics exhibited by the birds are to be treated as normal "morph" plumage. With no more likely explanation consistent with a morph hypothesis offered to explain the strong link with leucism, it seems relevant to address the evidence for assortative mating.

The tendency for Cory's Bittern to pair with other Cory's Bitterns was first reported by Scott (1891) recounting a letter received by him from Mr. J. F. Menge of Fort Meyers, Florida, regarding a nest discovered on 8 June 1890. Although the letter mentions four young birds in the nest, Mr. Menge did not provide a description of them and alludes to the parent birds, again without description. Never having seen these birds, Scott relies solely on this secondhand account. Fleming (1901) refers to a female on a nest, but again there is no description of her and no mention of her

mate. The assumption clearly made by the author is that Cory's Bittern is a valid species and, hence, the mate must be of the same species, an assumption supported by Ames (1901) who, describing the same bird and eggs, refers to it as Ardetta neoxena. Bent and Copeland (1927) recount another secondhand report from Mr. Oscar E. Baynard, who found a nest in Florida in 1927 and stated that "the young are always as black as Clapper Rails and that both adults are always dark-colored, evidence supporting the view that Cory's Least Bittern is a distinct species." The certainty expressed is at odds with the conclusions that may be reasonably drawn from an undocumented report of a single nest. Perhaps the only actual evidence of association in these birds is of a male and a female collected at Ashbridge's Bay, Toronto on 12 July 1900, although there is nothing to suggest that these birds were breeding or had even formed a pair beyond the collection date. In addition, a single pair of mated Cory's Bitterns would not be considered proof of assortative mating.

Although there is no real evidence that Cory's × Cory's pairs are the norm, there are also no published reports of mixed pairs as occurs commonly in other polymorphic herons (Hancock and Kushlan 1984). In fact the data available are too limited and unreliable to draw any conclusions at all.

Assortative mating as a consequence of mate choice based on morph appearance is extremely rare in birds and has been documented in the wild in very few avian taxa. In some polymorphic geese, for example, most birds select a mate with colour or pattern similar to that of the family in which they were raised (Cooke 1978; Abraham *et al.* 1983). However, even in these instances a considerable percentage of the pairs are mixed (15–18% in the Snow Goose, *Anser caerule-scens*), rendering secondhand statements that Cory's Bittern always mates with like highly suspect. Kalmus and Maynard-Smith (1966) and Seiger (1967) go so far as to state that sexual imprinting leading to absolute assortative mating in a species with two morphs would be a speciating mechanism.

Early authors convinced of the species status of *neoxena* and the collectors who supplied them with these valuable birds may be forgiven for assuming or even promoting the idea of like with like pairs. Clearly, early collectors were aware of the financial benefits that species status brought, and Pittaway and Burke (1996) mention at least one well-known Ontario collector, George Pearce, who destroyed specimens of normal *exilis* to promote the idea of species status and even dyed normal birds to sell to collectors. Perhaps not coincidentally, the same collector is the author of a supposed sight record of breeding birds at Lake Erie in 1923 (Pittaway and Burke 1996).

Pittaway and Burke (1996) do not assume assortative mating (although the references they cite do) and refer to assortative mating of any kind as "unlikely."

However, adopting the more likely scenario leaves us without an explanation as to why, if it is indeed a morph, Cory's Bittern shows such high levels of leucism and such random plumage variation overall.

Discussion

Although many specimens attributed to Cory's Bittern have shown only superficial similarity to the description of the type (Carpenter 1948), the extraordinary degree of plumage variation exhibited by specimens of Cory's Bittern seems to have been largely overlooked by modern authors.

Cory's Bittern specimens referred to as "partially albinistic" are more properly described as "partially leucistic" (van Grouw 2006). The enzyme tyrosinase, necessary for the chemical processes that produce melanins in vertebrates, is present in leucistic individuals but absent in albinistic ones; hence, partial albinism cannot exist (van Grouw 2006). Partial leucism is not an indicator of genetic health, as it results from an inherited disturbance disorder of pigment transfer during which deposition of melanin in the feather cells fails to occur (van Grouw 2006). According to Kettlewell (1973), "Melanic, melanistic and melanochroic forms refer to heterogeneous and genetically quite indeterminate groups." Furthermore multiple types of plumage aberrations in a single individual are often indicative of a genetic defect influencing several pigmentation systems (Buckley 1982; Davis and Blumin 2012). The irregular and varied plumage types seen in Cory's Bittern are thus explicable in the context of plumage aberrations resulting from genetic defects and are not consistent with the "distinct and genetically determined forms" required for recognition of polymorphism (Ford 1945, 1955). The variation observed is so great, in fact, that it is not even possible to attribute it to a single plumage aberration. Specimens ascribed to neoxenus seem to exhibit a random assortment of eumelanistic, leucistic, and phaeomelanistic aberrations, and potentially others, each of which may be influenced by any number of genes and pathways.

The localized spatial and temporal distributions of the birds led Pittaway and Burke (1996) to suggest that these represent places "where random processes allowed the Cory's morph to become temporarily established, because of chance colonization by a few individuals with the trait." However this begs the question: where did these colonizing individuals come from? The alternative and mutually exclusive explanation offered by the same authors is that Cory's is "an older form that is now at a selective disadvantage and has been replaced by the typical morph" (Pittaway and Burke 1996). However, this ignores the fact that the records clump temporally as well as spatially. In the context of a morph hypothesis, the first statement approximates transient polymorphism, but selective advantage is not consistent with an association with plumage abnormalities, nor is the latter scenario consistent with the summary statement "if our ideas about the genetics are correct, it is likely that Cory's Least Bitterns will turn up from time to time" (Pittaway and Burke 1996).

Aware of the potential for confusion between mutation and true polymorphism, Ford (1945) states that "any given gene subject to adverse selection must always be infrequent in the population; because being constantly eliminated, it is dependent for its existence upon mutation." Therefore, contrary to Pittaway and Burke's (1996) speculation, balanced polymorphism does not allow for temporary establishment of morphs but, in fact, demands permanence "in marked contrast to the distribution of rare genes maintained, ultimately, by mutation pressure" (Ford 1945).

Ford (1945) notes, "A balanced polymorphism in which the variation involved is environmental is generally the product of rather exceptional conditions." There is no indication that there is anything exceptional about the environmental conditions in any of the three main foci of records (Ontario, Florida, southeast South America) when compared with the rest of the range (Scott 1892b), nor do these areas have anything obviously in common that would favour the joint expression of this morph in such widely dispersed geographic locations. It should also be noted that the spatial patterns of occurrence observed in Cory's Bittern do not conform to distributional patterns exhibited by any other polymorphic Ardeid (Bent 1926).

A possible explanation for the observed spatial distribution that appears never to have been proposed is that the concentrations of specimens may be, at least in part, an artifact of observer effort. Ashbridge's Marsh, Toronto (now defunct), where most specimens were collected (Fleming 1906), was frequently used for shooting "so that the bird, though of retiring habits, could scarcely have chosen a more frequented piece of marsh" (Hubert Brown 1894 quoted in Pittaway and Burke 1996, page 38). With all the specimens in this area collected between 1890 and 1900, plus an additional one in 1913, and a similar pattern of temporal clumping seen in Florida, it seems pertinent to repeat the question first posed by Carpenter (1948): how did the morph evade detection prior to these dates? And given the high value of such specimens, why did their collection stop so abruptly? Thus, while the spatial distribution may conceivably be explained as an artifact of observer effort, it seems that temporal distribution cannot.

A recessive allele theory may be partly consistent with the available data on the rarity of Cory's Bittern, but it fails to explain temporal patterns, plumage variation, and the association with partial leucism. Although a single rare recessive allele might be expected to produce a single rare phenotype, rare but heterogeneous mutations would result in a variety of different but rare phenotypes that would be temporally and perhaps spa-

tially clumped. Observed patterns are thus consistent with recurrent mutations.

More important, regardless of whether mutation or recessive alleles is accepted as an explanation, in neither case are the resultant plumages correctly termed morphs. Consequently the basic premise of Pittaway and Burke's (1996) rare recessive allele theory, even if correct, falls outside the definition of polymorphism (Ford 1955), which excludes "segregation of rare recessives."

Conclusion

Cory's Bittern does not comply with Ford's (1945) definition of polymorphism: it has not been genetically determined, it shows extraordinary phenotypic variation, and it is not present in numbers too great to be due solely to recurrent mutation.

The rarity of these aberrations, coupled with a tendency for observers to label any *Ixobrychus exilis* that exhibits abnormally dark plumage characteristics with the name Cory's Bittern, is responsible for the enormous difficulties faced by those who try to define the plumage characteristics of the "morph." The most familiar phenotype, described by Sibley (2011), and understood today to be the typical Cory's Bittern, unduly generalizes the range of variation exhibited by birds ascribed to Cory's in the literature. The assumption of a single plumage type representing Cory's Bittern is an unfortunate byproduct of a general (if unconscious) acceptance by modern ornithologists that Cory's Bittern is a valid colour morph and, hence, must subscribe to a general form.

Pittaway and Burke (1996) state, "The almost complete disappearance of the Cory's Least Bittern... (are) important losses of genetic diversity and habitat to the Least Bittern." However, if, as seems likely, diverse and potentially unrelated factors, some of which may even be deleterious, are responsible for the variation, then no such loss of important genetic diversity is taking place. The appearance and disappearance of a localized population over a short period of time may be attributed to the lower fitness of such abnormally plumaged individuals (Buckley 1982; Slagsvold *et al.* 1988; Ellegren *et al.* 1997; Rutz *et al.* 2004). Their loss is to be expected.

Consequently, I propose that, following a line of thought that began with Bent (1926) and Carpenter (1948), Cory's Bittern should be viewed as a colloquial name referring to any one of a number of abnormally dark-plumaged and phenotypically heterogeneous Least Bitterns and not as a valid colour morph.

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Literature Cited

- **Abraham, K. F., C. D. Ankney,** and **H. Boyd.** 1983. Assortative mating by brant. Auk 100: 201–203.
- Allen, A. A. 1913. Cory's Least Bittern at Ithaca, New York. Auk 30: 559–561.
- Ames, J. H. 1901. Nesting of Cory's Bittern (*Ardetta neoxena*) and other notes. Auk 18: 106–107.
- Bangs, O. 1915. Notes on dichromatic herons and hawks. Auk 32: 481–484.
- Bent, A. C. 1926. Life histories of North American marsh birds: orders Odontoglossae, Herodiones and Paludicolae. Bulletin of US National Museum 135: 1–490.
- Bent, A. C., and M. Copeland. 1927. Notes on Florida birds. Auk 44: 371–386.
- Brewster, W. 1902. On the occurrence of Cory's least bittern (Ardetta neoxena) in eastern Massachusetts. Proceedings of the New England Zoological Club 3: 79–80.
- Brown, H. H., and W. Brewster. 1893. Capture of another Ardetta neoxena at Toronto, Ontario. Auk 10: 363–364.
- Buckley, P. A. 1982. Avian genetics. Pages 21–110 in Diseases of Cage and Aviary Birds. Edited by M. Petrak. Second edition. Lea and Febiger, Philadelpia, Pennsylvania, USA.
- Bull, J. 1985. Birds of New York State, Including the 1976 supplement. Comstock Publishing, Ithaca, New York, New York, USA.
- Carpenter, C. K. 1948. An early Illinois record of "Cory's Least Bittern." Auk 65: 80–85.
- Chapman, F. M. 1896. The standing of Ardetta neoxena. Auk 13: 11–19.
- Cherrie, G. K. 1896. Ardetta neoxena from Wisconsin. Auk
- Clay, R. P., P. Smith, and A. Lird. In press. First record of Cory's Bittern and the status of Least Bittern *Ixobrychus* exilis in Paraguay. Journal of Heron Biology and Conservation
- Cooke, F. 1978. Early learning and its effect on population structure. Studies of a wild population of snow geese. Zeitschrift für Tierpsychologie 46: 344–358.
- Cory, C. B. 1886a. Description of a new North American species of *Ardetta*. Auk 3: 262.
- Cory, C. B. 1886b. More news on *Ardea neoxena*. Auk 3: 408.
 Cory, C. B. 1891. Capture of a fourth specimen of *Ardetta neoxena*. Auk 8: 309.
- Cross, W. 1892. A new species for Ontario. Proceedings of the Ornithology Subsection of the Canadian Institute 1890– 1891: 41.
- Davis, J. N., and L. Blumin. 2012. Multiple color abnormalities in a wintering Mew Gull. Western Birds 43: 193–195.
- Eifrig, C. W. G. 1915. Cory's Least Bittern in Illinois. Auk 32: 98–99.
- Ellegren, H., G. Lindgren, C. R. Primmer, and A. P. Møller. 1997. Fitness loss and germline mutations in barn swallows breeding in Chernobyl. Nature 389: 593–596.
- Fleming, J. H. 1901. Nesting of Cory's Least Bittern at Toronto, Ontario. Auk 18: 106.
- Fleming, J. H. 1902. Cory's Bittern. Auk 19: 77-78.
- Fleming, J. H. 1906. Birds of Toronto, Ontario. Part 1 Water-birds. Auk 23: 437–453.
- **Ford, E. B.** 1945. Polymorphism. Biological Reviews 20: 73–88.

- **Ford, E. B.** 1955. Polymorphism and taxonomy. Heredity 9: 255–264
- Gibbs, J. P., F. A. Reid, and S. M. Melvin. 1992. Least Bittern in The Birds of North America, No. 17. Edited by A. Poole, P. Stettenheim, and F. Gill. The Academy of Natural Sciences, Philadelphia, Pennsylvania and The American Ornithologists' Union, Washington, DC, USA.
- Hancock, J., and J. Kushlan. 1984. The Herons Handbook. Christopher Helm, London, UK.
- Hellmayr, C. E., and B. Conover. 1948. Catalogue of birds of the Americas Part 1, Number 2. Spheniscidae, Gaviidae, Colymbidae, Diomedeidae, Procellariidae, Hydrobatidae, Pelecanoididae, Phaethontidae, Pelecanidae, Sulidae, Phalacrocoracidae, Anhingidae, Fregatidae, Ardeidae, Cochleariidae, Ciconiidae, Threskiornithidae, Phoenicopteridae, Anhimidae, Anatidae. Field Museum of Natural History, Chicago, Illinois, USA. Zoology Series 13: 1–434.
- Kalmus, H., and S. Maynard-Smith. 1966. Some evolutionary consequences of pegmatypic mating systems. The American Naturalist 100: 619–636
- Kettlewell, B. 1973. The Evolution of Melanism, the Study of a Recurring Necessity with Special Reference to Industrial Melanism in the Lepidoptera. Clarendon, Oxford, UK.
- Kumlien, L., N. Hollister, and A. W. Schorger. 1948. The birds of Wisconsin. The Passenger Pigeon 10: 107–113.
- Martínez-Vilalta, A., and A. Motis. 1992. Family Ardeidae (Herons). Pages 376–429 in Handbook of the Birds of the World, Volume 1: Ostrich to Ducks. Edited by J. del Hoyo, A. Elliott, and J. Sargatal. Lynx Edicions, Barcelona, Spain.
- Palmer, R. S. (editor). 1976. Handbook of North American Birds, Volume 1: Loons through Flamingos. Yale University Press, New Haven, Connecticut, USA, and London, UK
- **Pittaway, R.,** and **P. Burke.** 1996. Recognizable forms: Cory's Least Bittern. Ontario Birds 14: 26–42.
- Ruthven, A. G. 1907. Another specimen of Cory's Bittern. Auk 24: 338.
- Rutz, C., A. Zinke, T. Bartels, and P. Wohlsein. 2004. Congenital neuropathy and dilution of feather melanin in nestlings of urban-breeding northern goshawks (*Accipiter gentilis*). Journal of Zoo and Wildlife Medicine 35: 97– 103.
- Scott, W. E. D. 1889. A second specimen of Cory's Bittern (*Botaurus neoxenus*). Auk 6: 317–318.
- Scott, W. E. D. 1891. Note on the nests and habits of Cory's Bittern (*Botaurus neoxenus*). Auk 8: 309–310.
- Scott, W. E. D. 1892a. A description of the adult male of Botaurus neoxenus (Cory) with additional notes on the species. Auk 9: 141–142.
- Scott, W. E. D. 1892b. Notes on the birds of the Caloosahatchie region of Florida. Auk 9: 209–218.
- Seiger, M. B. 1967. A computer simulation study of the influence of imprinting on population structure. American Naturalist 101: 47–57.
- Sharpe, R. B 1894. [The geographical distribution of the Little Bitterns (*Ardetta*)]. Bulletin of the British Ornithologists Club XXI, xxxi. Reprinted in The Ibis, July 1894: 425–426.
- Sharpe, R. B. 1898. Catalogue of the Platalaeae, Herodiones, Steganopodes, Pygopodes, Alcae and Impennes in the collection of the British Museum. British Museum of Natural History, London, U.K.
- Sibley, D. 2000. The North American Bird Guide. Pica Press, Sussex, UK.

- Sibley, D. 2011. The mysterious dark Least Bittern. Accessed 2 April 2013. www.sibleyguides.com/2011/07/the-mys terious-dark-least-bittern/.
- Slagsvold, T., G. Rofstad, and J. Sandvik. 1988. Partial albinism and natural selection in the hooded crow *Corvus corone cornix*. Journal of Zoology 214: 157–166.
- **Taverner, P. A.** 1905. Description of second Michigan specimen of Cory's Least Bittern. Auk 22: 77–78.
- **Teixeira, D. M.,** and **H. M. F. Alvarenga.** 1985. The first recorded Cory's Bittern (*Ixobrychus "neoxenus"*) from South America. Auk 102: 413–414.
- **van Grouw, H.** 2006. Not every white bird is an albino: sense and nonsense about colour aberrations in birds. Dutch Birding 28: 79–89.
- Watkins, L. W. 1895. Cory's Least Bittern in Michigan. Auk 12: 77.

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