FEATURED PHOTO

FIRST EVIDENCE FOR ECCENTRIC PREALTERNATE MOLT IN THE INDIGO BUNTING: POSSIBLE IMPLICATIONS FOR ADAPTIVE MOLT STRATEGIES

JARED WOLFE, School of Renewable Natural Resources, Louisiana State University Agricultural Center and Louisiana State University, Baton Rouge, Louisiana 70803; jwolfe5@tigers.lsu.edu

PETER PYLE, Institute for Bird Populations, P. O. Box 1346, Point Reyes Station, California 94956; ppyle@birdpop.org

In the family Cardinalidae, the prealternate molt varies in extent from none in the Northern Cardinal (*Cardinalis cardinalis*) to including all secondary coverts, three tertials (secondaries 7–9), and four central rectrices in the Indigo Bunting (*Passerina cyanea*; Pyle 1997a, b). But replacement of primaries during the prealternate molt has not been documented within the family. In fact, in North American landbirds as a whole, replacement of primaries during definitive prealternate molt is rare, so far documented only in the Yellow Warbler (*Dendroica petechia*), Nelson's Sparrow (*Ammodramus nelsoni*), Bobolink (*Dolichonyx oryzivorus*), and Lesser Goldfinch (*Spinus psaltria*; Pyle 1997a, Willoughby 2007, Pyle and Kayhart 2010). Pyle and Kayhart (2010) postulated that prealternate molt originally evolved from the need to replace bleached and dysfunctional feathers, and that colorful alternate plumage is a result of subsequent sexual selection. Here, we present evidence from a wild living Indigo Bunting for an eccentric definitive prealternate molt in which outer but not inner primaries are replaced (Pyle 1997b, 1998).

On 18 April 2011, we captured a single alternate-plumaged male Indigo Bunting in the Peveto Woods Bird Sanctuary in Cameron Parish, Louisiana. The upper image on this issue's outside back cover shows the right wing of this bird; the pattern of replacement in the left wing was identical. Primaries 6–9, secondaries 6–9, rectrices 1–2, all secondary (lesser, median, greater, carpal, and alula) coverts, and the lesser (but not greater) alula were replaced, presumably during the previous definitive prealternate molt. We aged it as older than its second calendar year on the basis of the definitive primary coverts being broad with blue edges and black centers (Pyle 1997b). All flight feathers were similarly edged blue and centered dark. Our record represents the first evidence of primary replacement during the prealternate molt in the Cardinalidae (Pyle 1997a).

Alternatively, this Indigo Bunting may have interrupted its previous prebasic molt and subsequently reinitiated it at the same time as the prealternate molt. The contrast of inner and outer primaries may simply reflect suspension of molt, as proposed by Howell (2010) for the Lesser Goldfinch, in contrast to Willoughby (2007), who assumed primaries were replaced during the prealternate molt. Thus the second phase of the prebasic molt of some Lesser Goldfinches (in the spring, prior to breeding) could be coinciding with the prealternate molt, giving the false appearance of an extensive prealternate molt (Howell 2010). In this Indigo Bunting, however, we do not believe such a suspension occurred because primary coverts are typically replaced with the corresponding primaries during the definitive prebasic molt. If the prebasic molt had been suspended the 5th and 6th primary coverts should also contrast (in the upper photo on the outside back cover, note that the first primary covert is almost entirely obscured by the outer greater covert). Conversely, during eccentric molts zero to three outer primary coverts are typically replaced (Pyle 1997a), and the lack of contrast among the 4th, 5th, and 6th primary coverts supports our assertion that primary replacement was part of an eccentric definitive prealternate molt. The central rectrices and tertials were also replaced in the prealternate molt—if they were of the basic plumage they would have been molted first and so more worn than the other feathers, normally grown later in molt. The extensiveness of this prealternate molt further suggests that the replacement of the outer primaries was a continuation of this molt (Pyle 1997a). Additionally, interruption of the prebasic molt has never been documented in the Indigo Bunting. We believe that the most parsimonious explanation for the replacement of primaries in this Indigo Bunting is an incomplete prealternate molt rather than an interrupted prebasic molt.

The molt strategies of the Indigo Bunting are unique among North American birds. Its formative and basic plumages often don't occur in the United States because the preformative, prebasic, and prealternate molts typically take place away from and south of the breeding range. The Indigo Bunting's preformative and prealternate molts are more extensive than those of most other North American passerines, with many individuals replacing all secondary coverts during both molts and some individuals replacing outer primaries during the prealternate molt (as demonstrated by the example we present here). Among North American passerines, eccentric prealternate molts have been noted only in Nelson's Sparrow and, as discussed above, possibly in the Lesser Goldfinch (Pyle 1997b). Similar replacement of outer primaries has also been found in adults, after their second year, of certain shorebirds, such as the Little Stint (*Calidris minuta*), Bristle-thighed Curlew (*Numenius tahitiensis*), and Lesser Sand Plover (*Charadrius mongolus*) (Pearson 1984, Marks 1993, Balachandran and Hussain 1998). Like the passerines mentioned above, these shorebirds can undergo extensive and eccentric preformative molts and definitive prealternate primary molts (see Pyle 2008). The similarities in molt strategy and extent between these shorebirds, the passerines mentioned above, and the Indigo Bunting, are presumably due to similar selective pressures—based on increased exposure to sun due to habitat preferences and seasonal migration—driving convergent evolution (Pyle 2008).

In addition to their distinct patterns of molt, the male Indigo Bunting's age-related patterns of plumage coloration are also unique. For example, in definitive basic plumage, male Indigo Buntings after their second year are typically predominantly brown, many showing brown-edged tertials and wing coverts (Pyle 1997b), as in the lower image on the outside back cover of an after-second-calendar-year male captured on 8 March 2010 in Oaxaca, Mexico. Note the predominantly brown inner and predominantly blue outer greater coverts forming a color gradient; the shift implies a change in the hormonal cues responsible for the deposition of brown melanin and the structure responsible for blue coloration during the prebasic molt. Conversely, second-calendar-year males in their formative plumage have, on average, more extensive blue in the replaced tertials and wing coverts than their older counterparts (Pyle 1997a, Migration Research Foundation 2011), as shown in the upper image on the inside back cover, of a second-year Indigo Bunting captured on 18 April 2011 at Peveto Woods, the same day as the after-second-year male with prealternate molt of primaries discussed previously. Note that this individual was undergoing the first prealternate molt (e.g., replaced outer median coverts in photo) and, in contrast to after-second-year males, had identifiable retained juvenile primary coverts (brown and worn), inner primaries, and outer secondaries in an eccentric preformative replacement pattern (outer primaries 5–9 and inner secondaries 6–9 are of the formative plumage). Although this individual has more blue coverts than does the older male in the lower image, it shows a similar trend toward bluer-edged feathers from proximal to distal in the greater coverts.

To confirm that formative-plumaged male Indigo Buntings show, on average, more blue than definitive-plumaged males we reviewed specimens at the Louisiana State University Museum of Natural Science (Wolfe), University of California, Berkeley, Museum of Vertebrate Zoology (Pyle), and California Academy of Sciences (Pyle). Fifteen males collected in Honduras, Mexico, and Panama between 16 October and 7 March, in formative (n = 5) and basic (n = 10) plumage, support the assertion that formative-plumaged males, on average, are bluer than their counterparts in definitive basic plumage (Figure 1). Thus, in winter, many young male Indigo Buntings are brighter in coloration than adult males, a pattern unique, to our knowledge, among North America's migratory landbirds.

Variation during winter in the male Indigo Bunting's plumage color appears to be due in part to differences in the timing of the preformative and prebasic molts with respect to variation in the hormones responsible for the synthesis of the feather structure responsible for blue coloration. For example, the definitive prebasic molt of wing coverts could occur earlier, prior to a hormonal shift necessary for the generation of blue. If a later preformative molt of greater coverts occurs after this shift, bluer plumage may develop. Bluer plumage reflecting later molt may signal a second-year individual's low quality and poor condition on the wintering grounds. Such males are less cryptic than their more mature counterparts and may suffer higher levels of predation (Froehlich et al. 2005). However, this shift toward blue can also be seen among the greater coverts within individuals of both age groups; inner coverts are typically replaced earlier than outer coverts (Pyle 1997a, b), and in some individuals these inner coverts are edged brown, with distal and later-replaced coverts becoming bluer gradually. For example, the after-second-year individual shown on the lower inside back cover was also captured at Peveto Woods on 18 April, and it had replaced four bright blue inner greater coverts (alternate) and retained three brown central (basic) and two predominantly blue (basic) outer greater coverts.

Surprisingly little is known about where and when Indigo Buntings undergo the preformative and prebasic molts (Pyle 1997b, Pyle et al. 2009). Our examination of specimens revealed that in some birds the preformative molt takes place on the winter grounds in November and December, whereas others largely complete the definitive prebasic molt at molt-migration stopover locations in August and September, before arrival on the winter grounds (see Pyle et al. 2009). This implies a hormonal shift leading to bluer feather edging in both age groups from September to November. At McGill Bird Observatory in Montreal, Canada, however, hatching-year male Indigo Bunting have been captured in or after preformative molt, and after-hatching-year males have been captured in or after prebasic molt during fall (McGill Bird Observatory 2011, M. Gahbauer pers. comm.). Males undergoing preformative molt were captured later (late September to early October) than those undergoing prebasic molt (early to mid-September), further supporting our inference that later preformative molt may result in bluer plumage. Individual variation in the timing of both molt and hormone levels could explain individual variation in the amount of blue in the coverts, especially in definitive basic plumage. The location and timing of molts of the Indigo Bunting and other molt-migrants appear to be very plastic, depending on breeding success and climatic conditions (Pyle et al. 2009), and such flexibility could also help explain the extensive color variation in male Indigo Buntings of both age groups.

The definitive alternate plumage of the male Indigo Bunting is much more brilliantly blue than the brown and duller blue definitive basic plumage (Pyle 1997a, Migration Research Foundation 2011), whereas the first alternate plumage is variably brown and blue. The variability of the brown in these alternate plumages is due to the relationship between two factors: (1) the variation in the amount of blue and brown arising during the preformative and definitive prebasic molts, as described above, and (2) the subsequent extent of prealternate molts. Thus some after-second-year male buntings with less complete definitive prealternate molt retain brown-edged wing coverts, as shown in the lower image on the inside back cover. Because the Indigo Bunting's basic and formative plumages occur largely on the winter grounds they are not well treated by North American field guides. Ornithologists, bird watchers, and banders encountering

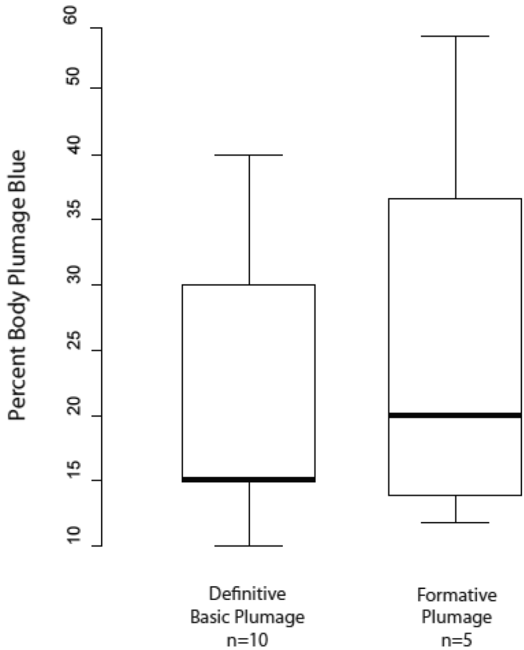

Figure 1. Visual estimation of percent body plumage that is blue in museum specimens of the Indigo Bunting in definitive basic and formative plumages collected between 22 October and 25 February in the winter range (Mexico, Panama, and Honduras); none of the individuals was undergoing a prealternate molt.

Indigo Buntings may intuitively, and mistakenly, associate the amount of blue in a male Indigo Bunting's plumage with age. Rather, we recommend that age determination be based primarily on the color and condition of the primary coverts: black, blue, and relatively fresh in older adults and brown and worn in second-year birds. In spring, this criterion may be critical because outer primaries can be replaced on the winter grounds in both age groups, during the preformative molt in second-year birds and during the prealternate molt in after-second-year birds, as we have demonstrated.

The occurrence of prealternate molt is correlated positively with migration (Svensson and Hedenstrom 1999, Pyle 2008, Howell 2010), supporting the hypothesis that prealternate molt evolved in response to increased feather wear and was subsequently repurposed by sexual selection (Pyle and Kayhart 2010). The breeding success of birds migrating to the neotropics is affected by the quality of habitat encountered the winter on grounds, that is, conditions migrants experience in tropical latitudes affect subsequent summer breeding (Nott et al. 2002, Norris et al. 2004). Similarly, survivorship over the winter may limit migrants' population growth (Saracco et al. 2008). Honest signals reflecting the quality of an individual's winter territory may be critical for the establishment of social hierarchies and in sexual selection for breeding. Therefore, while in North America establishing territories for breeding, migrant birds that undergo prealternate molt in the winter range wear an honest signal representative of the parasites, stress, and food resources they experienced in the tropics. Despite strong theory for the prevalence of prealternate molt among migrants, the relationship between evolutionary history and contemporary environmental influences on the presence and extent of prealternate molt has not been studied. Female Indigo Buntings undergo molts that are similar in extent to those of males (Pyle 1997a; specimen examination), yet their color changes little, further supporting the hypothesis that extensive prealternate molts of both sexes evolved in response to feather wear and that males' blue evolved after the prealternate molt was in place.

Here we have provided the first evidence of an eccentric prealternate molt in the family Cardinalidae. Our observation supports previous assertions that extensive prealternate molt should be expected among long-distance migrants that occupy open habitats and experience levels of solar exposure higher than those of their resident counterparts (Pyle 2008). We recommend that ornithologists, banders, and bird watchers be aware of and investigate the possibility of eccentric definitive prealternate molts in other species with such patterns of life history.

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