CONSERVATION TAXONOMY OF THE GREATER ANTILLEAN ORIOLE (*ICTERUS DOMINICENSIS*): DIAGNOSABLE PLUMAGE VARIATION AMONG ALLOPATRIC POPULATIONS SUPPORTS SPECIES STATUS

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Abstract: Allopatric populations, such as those present on islands, pose special challenges to identifying taxonomic boundaries which can be practically addressed using diagnostic criteria. To assess the taxonomic and, hence, conservation status of the four island populations of the Greater Antillean Oriole (*Icterus dominicensis*), we examined 156 male specimens of *I. dominicensis* for six discrete and three continuous plumage characters. The four island populations proved to be 100% diagnosable. *Icterus d. northropi* differed from all other taxa by having the greatest extent of yellow on the venter (non-overlapping with other taxa). *Icterus d. portoricensis* was distinguished from all other taxa by the presence of a black upper rump (yellow in other taxa) and the least extent of yellow on the rump (non-overlapping with other taxa). *Icterus d. melanopsis* and *I. d. dominicensis* were fully discriminated from *I. d. northropi* and *I. d. portoricensis* by the aforementioned characters and from each other by upper-tail covert color (black and ≥ 50% yellow, respectively). Our findings support recent studies suggesting that the four island groups represent distinct allospecies consistent with interpretations of both the phylogenetic and evolutionary species concepts. With elevation to full species, conservation priorities need to be revisited, particularly for the critically endangered Bahamas taxon (*I. d. northropi*).

Key words: conservation taxonomy, Greater Antillean Oriole, *Icterus dominicensis*, plumage variation, species limits, West Indies islands

Resumen: Taxonomía para la Conservación de *Icterus dominicensis*: una Variación Diagnosticable en el Plumaje entre Poblaciones Alopátricas Apoya el Estado Específico. Poblaciones alopátricas, como las presentes en las islas, plantean desafíos especiales a la identificación de los límites taxonómicos que pueden abordarse en la práctica con criterios de diagnóstico. Para evaluar la taxonomía y, por tanto, el estado de conservación de las cuatro poblaciones isleñas de *Icterus dominicensis* se examinaron 156 ejemplares machos para seis caracteres discretos y tres caracteres continuos del plumaje. Las cuatro poblaciones insulares demostraron ser 100% diagnosticables. *Icterus d. northropi* difería de todos los restantes taxones por tener el mayor grado de amarillo en el vientre (que no se traslapan con otros grupos taxonómicos). *Icterus d. portoricensis* se distinguió de todos los otros grupos taxonómicos por la presencia de una rabadilla negra (de color amarillo en otros taxones) y el menor grado de amarillo en la parte posterior (que no se traslapan con otros grupos taxonómicos). *Icterus d. melanopsis* y *I. d. dominicensis* fueron totalmente discriminados de *I. d. northropi* y de *I. d. portoricensis* por los caracteres mencionados y entre ellos por el color de la parte superior de la rabadilla (negro y amarillo ≥ 50%, respectivamente). Los resultados respaldan estudios recientes que sugieren que los cuatro grupos de las islas representan distintas aloespecies, coherente con la interpretación de ambos conceptos de especie, el filogenético y el evolutivo. Con la elevación al nivel de especies, las prioridades de conservación necesitan ser revisadas, en particular para el taxón en peligro crítico de Bahamas (*I. d. northropi*).

Palabras clave: Icterus dominicensis, islas de las Indias Occidentales, límites de las especies, taxonomía para la conservación, variación de plumaje

Résumé : Taxonomie et Conservation de l'Oriole à Capuchon (*Icterus dominicensis*): le Diagnostic des Variations de Plumage dans les Populations Allopatriques Confirme le Statut d'Espèce. Les populations allopatriques, telles que les populations insulaires, offrent des défis particuliers quant à l'identification de limites taxonomiques grâce à des critères de diagnostic. Afin d'évaluer la taxonomie et le statut de conservation de quatre populations insulaires d'Oriole à capuchon (*Icterus dominicensis*), nous avons relevé sur 156 spécimens mâles de *I. dominicensis* 9 variables du plumage : six variables discrètes et trois continues. Les quatre populations insulaires s'avèrent être 100% diagnostiquées. *Icterus d. northropi* diffère de tous les autres taxons par une plus grande étendue de couleur jaune sur le ventre (sans chevauchement avec d'autres taxons). *Icterus d. portoricensis* se distinguait de tous les autres taxons par la présence de couleur noire sur le haut du croupion (jaune chez les autres taxons) et moins de jaune sur le croupion (sans chevauchement avec d'autres taxons). *Icterus d. melanopsis* et *I. d. dominicensis* étaient totalement séparés de *I. d. northropi* et *I. d. portoricensis* par les variables précitées et séparées l'un de l'autre par la couleur des couvertures sus-caudales (noir et ≥ 50% jaune, respectivement). Nos résultats étayent les études récentes qui suggèrent que les quatre groupes insulaires représentent des espèces allopatriques distinctes, en cohérence avec les interprétations phylogénétiques et évolutives. En élevant le statut des sous-espèces

à celui d'espèces, les priorités de conservation doivent être revues, en particulier pour le taxon Bahamas (*I. d. northropi*) en danger d'extinction.

Mots clés : Antilles, conservation de la taxonomie, *Icterus dominicensis*, Oriole à capuchon, variation de plumage, limites spécifiques

Prior to the emergence of molecular techniques, morphology, song, and plumage characters played the most important roles in designating avian taxa (Coyne 1994, Peterson 1998). Today, in spite of increased emphasis on molecular systematics and the phylogenetic species concept, morphology and plumage characters are still viewed as valuable for defining species limits (Helbig *et al.* 2002, Wiens 2004). Research has shown that sexually selected traits, such as bird plumage characters, are likely to evolve quickly (Omland and Lanyon 2000), making them useful for delineating young taxa.

The taxonomic status of the Greater Antillean Oriole (*Icterus dominicensis*) has long been disputed. Four island subspecies are currently recognized from the Bahamas (*I. d. northropi*), Cuba (*I. d. melanopsis*), Hispaniola (*I. d. dominicensis*), and Puerto Rico (*I. d. portoricensis*). In the past, these populations were either lumped with (Hellmayr 1935) or separated from (Phillips and Dickerman 1965) populations of the similarly plumaged Black-cowled Oriole (*I. prosthemelas*) of Central America (see Garrido *et al.* 2005 for history of taxonomy). Recent molecular and plumage analyses confirmed the substantial genetic distance between *I. dominicensis* and *I. prosthemelas*, which suggested that plumage similarities arose through convergent evolution (Omland *et al.* 1999, Omland and Lanyon 2000).

Using mitochondrial cytochrome *b* and ND2 markers, Omland *et al.* (1999) found a substantial genetic distance (> 5%) separating *I. d. portoricensis* from both *I. d. northropi* and *I. d. melanopsis*. However, *I. d. northropi* and *I. d. melanopsis* differed by only 0.7%, which was more typical of subspecies within the genus (but see Baker *et al.* 2003, Kondo *et al.* 2004, and Cortes-Rodríguez *et al.* 2008). Unfortunately, because only cytochrome *b* could be sequenced from *I. d. dominicensis*, the genetic relationships among the group remained unclear. Omland and Lanyon (2000) subsequently mapped plumage characters on their genetic tree, showing *I. d. dominicensis* close to *I. d. portoricensis* and distinct from the sister taxa *I. d. northropi* and *I. d. melanopsis*. These relationships were later confirmed by Sturge *et al.* (2009) in a reanalysis using both cytochrome *b* and ND2 markers for all four taxa. Omland and Lanyon (2000) indicated a

substantial number of plumage characters separating males of each of the four taxa. *Icterus d. northropi*, for example, was separated from *I. d. melanopsis*, *I. d. dominicensis*, and *I. d. portoricensis* by six, five, and seven characters, respectively. Although these plumage characters could be inferred as diagnosable, the authors did not indicate sample sizes or possible within-taxon variation in their plumage assessments. Additional differences in adult morphology, juvenal plumage, and vocalizations prompted Garrido *et al.* (2005) to elevate each of the island groups to full allospecies status. On the basis of mitochondrial DNA differences, Sturge *et al.* (2009) later echoed this call. Support for elevating these taxa to full species could be strengthened by demonstrating 100% reciprocal diagnosability of the four taxa, a species criterion frequently relied on by ornithologists (Helbig *et al.* 2002, de Queiroz 2005). The studies by Omland and Lanyon (2000) and by Garrido *et al.* (2005) did not establish reciprocal diagnosability.

Taxonomic decisions often have profound ramifications for conservation (e.g., McNeely 2002, Dubois 2003, Mace 2004), which may be especially important for insular populations (Hayes 2006, Phillimore and Owens 2006). Among the four oriole subspecies, the Bahamas population appears to be at high risk of extinction. Although it formerly occurred on Abaco, the population there apparently became extirpated in the 1990s (White 1998). Today, it persists only on Andros, where the population was liberally estimated to comprise 150-300 individuals (Baltz 1997). Elevation of each of the four subspecies to full species status would change their conservation priority, particularly for the Bahamas form (Hayes 2006). Although taxonomy should inform conservation, as we seek to do here, conservation priorities should never influence taxonomic decisions (Bowen and Karl 1999).

In this study, we evaluated the taxonomic status of the four West Indies populations of *I. dominicensis* for conservation purposes. We analyzed plumage variation to determine whether reciprocal diagnosability exists among the allopatric populations.

METHODS

We examined 156 male specimens of *I. dominicensis* from six museums to evaluate six

Table 1. Plumage colors and measurements from adult male study skins of Greater Antillean Orioles (*Icterus dominicensis*). For discrete color characters (B = black, Y = yellow, B / Y = equally black and yellow, W = white), proportion of specimens having each color is indicated. For mensural characters (yellow on venter and rump), low and high values are indicated. Diagnosably relevant characters are indicated in bold. Because of minor damage to some specimens, sample sizes varied slightly among the characters assessed.

Character	*I. d. northropi* (Bahamas) *n* = 9	*I. d. melanopsis* (Cuba) *n* = 47-49	*I. d. dominicensis* (Hispaniola) *n* = 51-52	*I. d. portoricensis* (Puerto Rico) *n* = 45-46
Upper rump color	B = 0% Y = 100%	B = 0% Y = 100%	B = 0% Y = 100%	**B = 100% Y = 0%**
Flank color	B = 0% Y = 100%	B = 100% Y = 0%	B = 29% Y = 71%	B = 100% Y = 0%
Belly color	B = 0% Y = 100%	B = 100% Y = 0%	B = 100% Y = 0%	B = 98% Y = 2%
Upper-tail coverts color	B = 38% Y = 50% B / Y = 12%	**B = 100% Y = 0%**	**B = 0% Y = 98% B / Y = 2%**	B = 100% Y = 0%
Under-tail coverts color	B = 0% Y = 100%	B = 100% Y = 0%	B = 32% Y = 64% B / Y = 4%	B = 93% Y = 2% B / Y = 5%
White tips to retrices	B = 0% W = 100%	B = 92% W = 8%	B = 78% W = 22%	B = 89% W = 11%
Yellow on venter (%)	**56.8-64.3**	6.7-37.3	17.8-48.8	19.6-44.3
Yellow on rump (mm)	39.4-51.2	29.4-51.6	32.2-55.2	**12.4-28.6**

plumage characters that reportedly vary among this group (Omland and Lanyon 2000). Five of these discrete characters were based on color of the feather tract being either black or yellow. These included the upper rump (dorsum, but distinct from the lower rump, which was yellow in all island forms; c.f. Omland and Lanyon 2000), flank (venter, at point of leg attachment), belly (venter, 1 cm anterior to leg attachments), upper-tail coverts (longest two terminal-most feathers), and under-tail coverts (longest two terminal-most feathers). For tail coverts, both black and yellow were often present and we recorded the color of highest proportion; however, in some cases, the terminal-most coverts were either missing or equally black and yellow, and recorded as such (i.e., we recorded three character states). For the sixth discrete character, tips of the outermost retrices were examined against a black background and identified as either black or white.

We also collected mensural data for three continuous characters using digital calipers (to nearest 0.1 mm). Using straight-line measurements not following the contour of the body, we recorded black on the venter (continuous area of black along midsagittal line from throat to belly, excluding black and yellow mottling at the transition between black anteriorly and yellow posteriorly), yellow on the venter (continuous area of yellow along midsagittal line from belly to undertail coverts, including mot-

tling), and yellow on the rump (continuous area of yellow along midsagittal line from rump to, and including, the upper-tail coverts). Because black and yellow on the venter covaried, we calculated and considered only the proportion of the venter that was yellow (i.e., yellow divided by the sum of black and yellow).

Because we were looking for diagnosable characters, we report only species-descriptive data. Some specimens exhibited minor damage, resulting in sample sizes varying slightly among the characters assessed.

RESULTS

When plumage color and mensural data were considered together, the four island populations proved to be 100% diagnosable (Table 1). *Icterus d. northropi* differed from all other taxa by having the greatest extent of yellow on the venter (non-overlapping with other taxa). *Icterus d. portoricensis* was distinguished from all other taxa by the presence of a black upper rump (yellow in other taxa) and the least extent of yellow on the rump (non-overlapping with other taxa). *Icterus d. melanopsis* and *I. d. dominicensis* were fully discriminated from *I. d. northropi* and *I. d. portoricensis* by the aforementioned characters and from each other by upper-tail covert color (black and ≥ 50% yellow, respectively).

Pairwise comparisons indicated that populations

Table 2. Plumage characters providing pairwise diagnosis among the four Greater Antillean Oriole (*Icterus dominicensis*) populations. Within each comparison (cell), asterisks indicate functionally related characters.

Populations	*I. d. melanopsis*	*I. d. dominicensis*	*I. d. portoricensis*
I. d. northropi	3 independent characters: Flank color Belly color* Under-tail coverts color Yellow on venter*	1 independent character: Belly color* Yellow on venter*	3 independent characters: Upper rump color* Flank color Yellow on venter Yellow on rump*
I. d. melanopsis		1 independent character: Upper-tail coverts color	1 independent character: Upper rump color* Yellow on rump*
I. d. dominicensis			2 independent characters: Upper rump color* Upper-tail coverts color Yellow on rump*

were diagnosable by up to three functionally independent characters (Table 2). We considered two sets of characters to be functionally related: belly color and extent of yellow on the venter, and upper rump color and extent of yellow on the rump. Populations from geographically distant islands were sometimes distinguished by fewer diagnostic characters than those from adjacent islands. Thus, *I. d. northropi* was more similar to *I. d. dominicensis* than adjacent *I. d. melanopsis*, and *I. d. portoricensis* was more similar to *I. d. melanopsis* than adjacent *I. d. dominicensis*.

Several characters were variable within a single population, including flank color in *I. d. dominicensis*, upper-tail coverts color in *I. d. northropi*, and undertail-coverts color in *I. d. dominicensis* and *I. d. portoricensis*. All *I. d. northropi* had white tips (sometimes faint) to the outer rectrices, as described by Omland and Lanyon (2000), but so did several or more individuals from each of the other populations.

DISCUSSION

Our findings of diagnosable plumage characters support the conclusion of Garrido *et al*. (2005) and Sturge *et al*. (2009) that the four island groups represent distinct allospecies, consistent with interpretations of both the phylogenetic and evolutionary species concepts (Cracraft 1983, Mayden 1997, de Queiroz 2005). In delineating full species for allopatric taxa, Helbig *et al*. (2002) recommended 100% reciprocal diagnosability based on one or more functionally independent characters and level

of divergence equivalent to closely related sympatric species. As we show here, the allopatric populations of *I. dominicensis* meet the conservative criteria of Helbig *et al*.

In our pairwise comparisons, populations were diagnosable from each other based on one to three plumage characters, but the number of diagnosable characters did not correspond to geographic proximity. *Icterus d. northropi*, for example, was readily diagnosed from both *I. d. melanopsis* (the nearest population) and *I. d. portoricensis* by three characters, but differed from *I. d. dominicensis* by only one character. However, molecular, morphological, vocalization, and additional plumage characters, including those of juveniles, provide strong support for *I. d. northropi* and *I. d. melanopsis* being sister taxa well separated from *I. d. dominicensis* and *I. d. portoricensis* (Omland *et al*. 1999, Omland and Lanyon 2000, Garrido *et al*. 2005, Sturge *et al*. 2009). *Icterus d. melanopsis* and *I. d. dominicensis* also differ the most in vocalizations (Jaramillo and Burke 1999, Garrido *et al*. 2005). Thus, plumage similarity between *I. d. northropi* and *I. d. dominicensis* likely arose through convergence (Omland and Lanyon 2000). *Icterus d. portoricensis* was also readily diagnosed from *I. d. northropi* and *I. d. dominicensis* (the nearest population) by three and two characters, respectively, but differed from *melanopsis* in only one character. However, *I. d. portoricensis* may be the most distinct among this group, as it appears more closely related to the Lesser Antilles oriole taxa, *I. oberi* and *I. laudabilis*,

in molecular and other plumage characters (Omland *et al*. 1999, Omland and Lanyon 2000). Although Omland and Lanyon (2000) treated white tips on the retrices as fixed, present only in *I. d. northropi*, we observed them on some specimens of all taxa.

Based on comparative data reported by Omland and Lanyon (2000), plumage differences among the allopatric *I. dominicensis* populations were comparable to those of sympatric oriole species. Of three sympatric species that readily nest alongside each other in Central America (Howell and Webb 1995), the Altamira Oriole (*I. gularis*) differed from the Spot-breasted Oriole (*I. pectoralis*) in four characters and from the Streak-backed Oriole (*I. pustulatus*) in six characters. Sympatric Baltimore (*I. galbula*) and Orchard (*I. spurius*) Orioles in eastern North America also differed in four characters. By comparison, *I. d. northropi* differed from *I. d. melanopsis*, *I. d. dominicensis*, and *I. d. portoricensis* in six, five, and seven characters, respectively. The latter three taxa were less well differentiated, with one to three characters separating them.

The substantial plumage differences between *I. d. northropi* and *I. d. melanopsis* have evolved in spite of the molecular similarity and relatively recent separation of these taxa (0.7% sequence divergence for cytochrome *b* plus ND2; Omland *et al*. 1999; Sturge *et al*. 2009). Both natural and sexual selection have been proposed as drivers for rapid plumage evolution, with sexual selection believed to operate more rapidly (e.g., Warren *et al*. 2005, Mila *et al.* 2007). Rapid plumage evolution in orioles can occur in the absence of sexual selection, either by genetic drift within small populations resulting in rapid fixation of alleles (Kondo *et al*. 2008) or by natural selection, though sexual selection is thought to be the most likely cause of rapid plumage evolution in orioles (Omland and Lanyon 2000, Baker *et al*. 2003, Kondo *et al*. 2004, 2008, Hofmann *et al*. 2008a, b). Although all *I. domincensis* taxa are sexually monochromatic, at least with respect to human vision (Garrido *et al*. 2005; c.f. Eaton 2005), sexual selection can still act on plumage characters of monochromatic species (Amundsen and Pärn 2006).

Because conservation priority setting depends heavily on systematics, our findings have added importance. Our interest in the taxonomy of this group arose from concerns about the conservation status of the Bahamas population (Hayes 2006). Population surveys have given a "liberal" estimate of 50-100 *I. d. northropi* on North Andros, and 100-200 on South Andros (Baltz 1997). If these estimates are accurate, the Bahama Oriole, as a full species, should qualify as critically endangered, based on the IUCN Red List criterion of an estimated population of < 250 mature individuals. Though the Bahama Oriole formerly occurred on Abaco, it disappeared in the early 1990s for unknown reasons (White 1998). It may be in decline on Andros as well, as only one oriole in juvenal plumage was observed in the 1997 survey by Baltz (1997). Threats to this population include: recent arrival of the Shiny Cowbird (*Molothrus bonariensis*; Baltz 1995), a brood parasite that heavily parasitizes *I. dominicensis* (Wiley 1985, 1988); lethal yellowing disease (Ogle and Harries 2005) in its primary breeding habitat, the introduced Coconut Palm (*Cocos nucifera*; Currie *et al*. 2005, M. R. Price *et al*. unpubl. data); introduced animals, plants, and exotic diseases; habitat change associated with global warming and rising sea levels; and continued human development accompanied by possible renewed logging of the Caribbean Pine (*Pinus caribaea*) forest (Smith and Vankat 1992). The other taxa face similar threats, and would also benefit from the conservation priority they would receive as a result of elevation to species status (Garrido *et al*. 2005). As the rarest bird species in the Bahamas (Hayes 2006), the Bahama Oriole could join the Bahama Parrot as an avian flagship species (Reynolds and Hayes 2009), stimulating much-needed conservation activities on Andros.

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Appendix 1. Male specimens (*n* = 156) examined from the following museums: Carnegie Museum of Natural History (CMNH); Field Museum of Natural History (FMNH); Louisiana State Museum of Zoology (LSUMZ); United States National Museum of Natural History (USNM).

Icterus dominicensis northropi.–Abaco, the Bahamas (2): CMNH 130996; FMNH 29818. Andros, the Bahamas (7): CMNH 30962, 30976; LSUMZ 146653, 146654, 146657, 146658; USNM 257099.

I. d. dominicensis.–Hispaniola (52): CMNH 91567, 91328; FMNH 1084, 1086, 1087, 1090, 1095, 1088, 1100, 1103, 1105, 1112, 1120, 1122, 1125, 29732, 29735, 29741, 29742, 29747, 29748, 29750, 29752, 29809, 29745, 29746, 29753; USNM 249421, 249544, 249545, 249546, 249547, 249548, 250448, 250449, 250453, 250573, 251580, 251581, 251583, 252842, 252890, 252891, 264790, 264792, 280459, 280460, 305585, 327892, 573657.

I. d. melanopsis.–Cuba (31): CMNH 138759; FMNH 29807, 72054, 111981, 375109, 375112, 375113, 375116, 375117, 375122; USNM 171277, 171448, 171449, 171451, 171452, 171453, 172642, 172647, 177467, 177834, 177866, 200391, 310429, 316264, 355986, 395830, 395831, 395836, 396651, 454581, 454583. Isla de la Juventud (Isla de Pinos) (15): CMNH 39460, 39531, 39548, 39549, 39550, 39774, 39779, 39871, 39903, 39940; USNM 172816, 172819, 324041, 324042, 324043. Unknown location (3): FMNH 29810, 308980; USNM 31989.

I. d. portoricensis.–Puerto Rico (46): CMNH 38843, 38844, 39078, 39097, 39118, 39157, 39227, 39252, 39326; FMNH 29686, 29687, 29692, 29695, 29696, 29697, 29700, 29701, 29708, 29712, 29714, 29715, 29716, 29717, 29724, 29727; USNM 17154, 168974, 169058, 169061, 171544, 231637, 231639, 231642, 231645, 231646, 231650, 231651, 231653, 238221, 238222, 238224, 238385, 238386, 355970, 355976, 355981.