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THE GENUS *ICTERUS* IN THE WEST INDIES

Orlando H. Garrido[1], **James W. Wiley**[2,4] , **& Arturo Kirkconnell**[3]

[1]Calle 60 & 1706 entre 17 y 19, Marianao 13 (Playa), La Habana, Cuba.

[2]Maryland Cooperative Fish & Wildlife Research Unit, University of Maryland Eastern Shore, 1120 Trigg Hall, Princess Anne, Maryland 21853, USA. *E-mail*: jwwiley@mail.umes.edu

[3]Museo Nacional de Historia Natural, Calle Obispo No. 61, Plaza las Armas, Ciudad La Habana, Cuba.

Resumen. – El género *Icterus* en las Antillas. – Examinamos especímenes de las especies endémicas del genero *Icterus* en las Antillas, así como de los *I. prosthemelas* y *I. prosthemelas praecox*, junto con la información disponible sobre su historia natural, suplida con nuestras observaciones de campo en las islas. Determinamos que la morfología, historia natural, vocalización, y las diferencias moleculares, así como el patrón de distribución entre las islas, definen claramente las formas de *Icterus* de las Antillas como miembros de una superspecie, con alloespecies distintas en las diversas islas. Por lo tanto, proponemos que éstas alloespecies de las Antillas constituyen especies endémicas de las islas respectivas, y así proponemos el arreglo siguiente: *I. northropi* (Andros y Abaco), *I. melanopsis* (Cuba, Isla de Pinos y algunos cayos de la zona norte), *I. dominicensis* (La Española, incluyendo Île de la Gonâve, Île de la Tortue, Île-à-Vache, y Isla Saona), *I. portoricensis* (Puerto Rico), *I. oberi* (Montserrat), *I. bonana* (Martinique), y *I. laudabilis* (St. Lucia).

Abstract. – We examined specimens of endemic *Icterus* species in the West Indies, as well as *I. prosthemelas* and *I. prosthemelas praecox*, along with available information on their natural history, supplemented with our field observations in the islands. We determined that morphological, natural history, vocalization, and molecular differences, as well as the pattern of distribution among islands, clearly define the West Indian *Icterus* forms as members of a superspecies, with distinct allospecies in the different islands. Therefore, we propose that these West Indian allospecies constitute endemic species from their respective islands, and propose the following arrangement: *Icterus northropi* (Andros and Abaco), *I. melanopsis* (Cuba, Isla de Pinos, and some northern keys), *I. dominicensis* (Hispaniola, including Île de la Gonâve, Île de la Tortue, Île-à-Vache, and Isla Saona), *I. portoricensis* (Puerto Rico), *I. oberi* (Montserrat), *I. bonana* (Martinique), and *I. laudabilis* (St. Lucia). *Accepted 25 May 2005.*

Key words: Greater Antillean Oriole, *Icterus dominicensis*, *Icterus melanopsis*, *Icterus northropi*, *Icterus portoricensis*, taxonomy, West Indies.

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[4]*Corresponding author.*

INTRODUCTION

The family Icteridae is represented in the West Indies by nine genera: *Dolichonyx*, *Agelaius*, *Nesopsar*, *Sturnella*, *Xanthocephalus*, *Dives*, *Quiscalus*, *Molothrus*, and *Icterus*. Of these, the best represented is *Icterus*, with 12 species and subspecies. Only three of these forms are not resident breeders*:* *I. spurius*, transient in Cuba, Jamaica, and some of the Bahama Islands, and vagrant in Hispaniola; *I. cucullatus*, casual or vagrant in Cuba; and *I. galbula*, transient and winter resident in the Greater Antilles, and vagrant in some Lesser Antilles. West Indian *Icterus* species and subspecies are resident as follows: *I. dominicensis northropi* Allen in The Bahamas; *I. d. melanopsis* (Wagler) in Cuba, Isla de Pinos (now Isla de la Juventud), and some northern keys; *I. d. dominicensis* Linnaeus in Hispaniola; *I. d. portoricensis* Bryant in Puerto Rico; *I. laudabilis* Sclater in St. Lucia; *I. oberi* Lawrence in Montserrat*;* *I. bonana* (Linnaeus) in Martinique; *I. icterus* (Linnaeus), introduced and established in Puerto Rico, Mona, St. Thomas, Jamaica, St. John, Antigua, Dominica, Grenada, and Trinidad; and *I. leucopteryx* (Wagler) in Jamaica, Grand Cayman, and San Andrés. Currently, only *I. bonana, I. oberi*, and *I. laudabilis* are considered endemic species (A. O. U. 1998, Raffaele *et al.* 1998). With the exception of *I. leucopteryx* and *I. icterus*, there is general agreement that all resident West Indian *Icterus* are within the *I. dominicensis* superspecies complex (Lovette *et al.* 1999). The taxonomic status of the various Antillean island populations, however, has been long disputed (Blake 1968, Sibley & Monroe 1990).

In support of his hypothesis that the Lesser Antillean species evolved from Greater Antillean ancestors, Bond (1956) considered the Lesser Antillean *I. oberi*, *I. bonana*, and *I. laudabilis* as derived "representatives of *I. dominicensis*." Blake (1968) also considered the Lesser Antillean orioles as derived from *I. dominicensis*, with which he thought they may be conspecific. In his biogeographic analysis of West Indian birds, Lack (1976) suggested ancestral *I. dominicensis* from Central America colonized the Greater Antilles, then spread into the Lesser Antilles, subsequently evolving into the three present-day species. Most recently, Lovette *et al.* (1999) examined the Lesser Antillean oriole species, using mitochondrial DNA sequences to determine relationships among these populations, and concluded that *I. oberi*, *I. bonana*, and *I. laudabilis* are evolutionarily significant units that meet species criteria under the phylogenetic species concept. Because of the consistently large mitochondrial divergences among Lesser Antillean *Icterus* populations, Lovette *et al.* (1999) concluded that the Lesser Antillean oriole populations are as genetically distinct as many avian species.

Until recently, *I. dominicensis* consisted of populations from southern Veracruz, northern Oaxaca, Tabasco, Chiapas, and the Yucatan Peninsula south on the Caribbean slope of Central America to extreme western Panama, and The Bahamas and West Indies (A. O. U. 1998). Using a molecular analysis of phylogeny, Omland *et al.* (1999) reached the conclusion that the forms of *Icterus prosthemelas* (Black-cowled Oriole) and the *dominicensis* group (Greater Antillean Oriole; including *dominicensis, melanopsis, portoricensis*, and *northropi*) were distinct species, which was subsequently accepted by the A. O. U. (2000: 853). Omland *et al.* (1999) had the impression that some of the subspecies included in the *dominicensis* group also could be distinct species, rather than subspecies, but they did not have suitable information on natural history, vocal behavior, and plumage differences to elaborate on those relationships. Therefore, the four West Indian taxa were retained as conspecific (A. O. U. 2000).

The recognition of *I. prosthemelas* is not new. Although originally described as a species by Strickland (1850) under the genus

Xanthornus, Hellmayr (1937) considered it conspecific with the Bahaman population *northropi* Allen, 1890, as *I. prosthemelas northropi*, and separate from the subspecies *dominicensis, melanopsis*, and *portoricensis*. Conversely, Bond (1938) considered *northropi* distinct from *prosthemelas* and derived from Cuban *melanopsis*. Phillips & Dickerman (1965) described the species *praecox* from Panamá and Costa Rica, recognizing *I. prostemelas* as a distinct species. Blake (1968), however, retained the two Central American populations as subspecies, *I. d. prosthemelas* and *I. d. praecox*, considering them conspecific with the *dominicensis* group (*northropi, dominicensis, melanopsis,* and *portoricensis).*

Our purpose here is to establish species limits among the resident populations of Greater Antillean *I. dominicensis*, with additional comments on Lesser Antillean *Icterus* species. We also make some comparisons with *I. leucopteryx*. To do so, we draw upon morphometric, plumage, ecological, and behavioral data collected for these populations.

METHODS

A total of 683 specimens was examined from Cuban and North American museums, including Museo Nacional de Historia Natural de Cuba, Instituto de Ecología y Sistemática (Cuba), American Museum of Natural History, Louisiana State Museum of Natural Science, Museum of Comparative Zoology (Harvard), U. S. National Museum of Natural History, Academy of Natural Sciences of Philadelphia, Carnegie Museum, and Field Museum of Natural History. Conventional measurements of wing chord (flattened against the ruler), tail, tarsus, and exposed culmen were taken to the nearest 0.1 mm with calipers and ruler, following Baldwin *et al.* (1931). Only adult specimens (n = 526) were used in comparing morphometrics within and among species.

We present summary descriptive statistics (mean, SD, and range) for the specimens. Unpaired t-tests were used to test for equality of means among populations. We used Bonferroni's correction in conducting multiple tests of means. Further, we used ANOVA analyses to determine if differences exist among island populations. Body measurements were plotted to assess the pattern of spatial segregation among populations. The hypothesis of separation derived from the plots of body measurements was tested using discriminate function analysis (DFA) (Kleinbaum & Kupper 1978). SPSS for Windows (SPSS 1999) was used to run DFA and cluster analyses. We used the single linkage method and squared Euclidean measure to conduct cluster analyses. Standard deviation is used as the measure of variation about the mean. Level of significance was set at 0.05.

Most data on behavior and ecology of *I. dominicensis* were gathered incidental to other studies in Cuba, Isla de Pinos, Hispaniola, Bahamas (Abaco), and Puerto Rico. Some intensive studies were made from blinds placed near nests, from which we obtained data on food delivered to chicks. Most recordings of vocalizations were obtained from Reynard's (Reynard 1969, 1981; Reynard & Garrido 1988, Reynard & Sutton 2000) publications, or recordings deposited in his private collection. Recordings of *northropi* vocalizations were provided by Bruce Hallett. Additional recordings were obtained by Wiley in Cuba, Isla de Pinos, and Puerto Rico. Raven (Ver. 1.0) sound analysis software was used to analyze vocalizations.

RESULTS AND DISCUSSION

Plumage. We compared the Bahamas *northropi* (n = 28) with populations of *I. prosthemelas*, examining a total of 182 *prosthemelas* specimens from Mexico south to Costa Rica, and additional specimens (n = 43) of *I. p. praecox*.

TABLE 1. Mean, SD, sample size (in brackets), and range for wing, tail, culmen, tarsus, and weights, in 526 adult specimens of the *Icterus dominicensis* group, *I. p. prosthemelas*, *I. p. praecox*, *I. bonana*, *I. oberi*, and *I. laudabilis*.

Populations & localities	Measurements (mm)				
	Wing	Tail	Culmen	Tarsus	Weight (g)
MALES					
I. d. northropi (Bahamas)	98.4 ± 2.4 (15) 93.5–102.0	91.6 ± 3.0 (16) 87.0–98.0	20.5 ± 1.1 (15) 18.9–23.4	25.3 ± 1.0 (16) 23.6–27.5	
I. d. melanopsis (Cuba)	94.3 ± 4.0 (70) 82.0–102.0	87.1 ± 3.8 (69) 77.0–95.0	18.7 ± 1.2 (66) 16.3–22.0	24.0 ± 2.1 (56) 21.0–32.0	38.7 ± 1.9 (34) 35.0–42.0
I d. melanopsis (Isla de Pinos)	95.0 ± 3.5 (20) 87.0–100.0	88.0 ± 4.6 (19) 81.0–94.0	19.1 ± 1.1 (18) 17.5–22.5	24.1 ± 1.1 (18) 21.8–26.3	38.0 ± 0.8 (5) 37.1–39.2
I. d. dominicensis (Hispaniola)	96.0 ± 3.9 (64) 85.0–103.0	84.3 ± 4.1 (65) 73.5–93.0	20.2 ± 1.3 (62) 17.2–25.0	22.5 ± 1.2 (64) 19.0–25.0	36.5 ± 1.1 (10) 35.0–38.3
I. d. portoricensis (Puerto Rico)	96.9 ± 3.4 (37) 89.0–103.5	85.8 ± 3.3 (37) 78.0–94.0	21.8 ± 1.2 (36) 19.4–23.8	23.2 ± 1.2 (35) 20.1–26.4	41.0 ± 1.6 (27) 37.2–44.9
I. p. prosthemela	89.3 ± 3.2 (75) 82.0–96.0	90.8 ± 5.2 (80) 70.0–103.0	17.8 ± 1.0 (80) 15.9–20.9	22.6 ± 1.1 (76) 19.1–24.7	26.8 ± 2.7 (6) 23.0–30.0
I. p. praecox	89.2 ± 2.6 (17) 82.0–93.0	87.9 ± 3.8 (15) 82.0–93.5	18.6 ± 1.2 (18) 17.1–20.9	23.3 ± 1.3 (18) 20.1–26.0	
I. bonana (Martinique)	89.0 ± 6.1 (3) 82.0–93.0	84.7 ± 7.1 (3) 77.0–91.0	20.0 ± 0.1 (3) 19.9–20.0	23.8 ± 1.0 (3) 23.0–24.9	
I. oberi (Monserrat)	91.5 ± 2.0 (11) 87.1–94.0	96.1 ± 2.5 (9) 92.4–99.8	22.1 ± 1.0 (10) 20.5–24.2	25.8 ± 0.6 (11) 24.9–26.4	38.0 ± 1.0 (7) 36.0–39.0
I. laudabilis (St. Lucia)	106.2 ± 4.7 (10) 98.0–112.0	96.6 ± 4.2 (10) 88.0–105.0	23.7 ± 1.4 (10) 21.5–26.0	25.0 ± 0.8 (9) 23.7–26.6	39.8 ± 1.0 (2) 39.1–40.5
FEMALES					
I. d. northropi (Bahamas)	92.5 ± 2.0 (11) 90.5–95.5	86.2 ± 4.1 (12) 77.5–91.0	19.9 ± 0.9 (12) 18.3–21.2	24.5 ± 1.0 (12) 23.1–26.3	
I. d. melanopsis (Cuba)	91.3 ± 2.8 (35) 86.0–97.0	84.1 ± 3.4 (34) 76.0–91.0	18.8 ± 1.3 (34) 16.2–22.5	23.3 ± 1.1 (29) 20.9–26.0	35.4 ± 2.0 (25) 30.0–38.5

TABLE 1. Continued.

Populations & localities	Measurements (mm)				
	Wing	Tail	Culmen	Tarsus	Weight (g)
I. de. melanopsis (Isla de Pinos)	92.7 ± 2.7	85.4 ± 3.5	18.5 ± 1.0	23.5 ± 1.8	35.5 ± 1.1
	(7)	(7)	(7)	(7)	(7)
	88.0–96.0	81.0–90.0	17.4–20.0	20.7–25.5	34.0–37.0
I. d. dominicensis (Hispaniola)	92.1 ± 2.7	82.6 ± 3.2	19.9 ± 1.8	22.8 ± 1.2	35.0 ± 1.4
	(40)	(40)	(40)	(40)	(9)
	86.0–102.0	72.0–88.0	17.1–24.7	20.7–25.0	33.0–40.0
I. d. portoricensis (Puerto Rico)	92.1 ± 2.7	83.2 ± 2.9	21.7 ± 1.5	22.9 ± 1.4	36.6 ± 1.2
	(28)	(28)	(25)	(26)	(22)
	86.5–99.0	80.0–91.0	19.3–24.9	20.1–25.0	34.0–38.9
I. p. prosthemelas	84.1 ± 2.6	87.3 ± 4.4	17.1 ± 1.5	22.9 ± 1.3	
	(38)	(39)	(39)	(36)	
	79.0–89.0	78.0–98.0	11.8–19.9	21.0–27.2	
I. p. praecox	83.7 ± 1.8	84.8 ± 3.5	18.4 ± 1.3	23.2 ± 1.2	
	(18)	(18)	(14)	(16)	
	80.0–86.5	78.0–91.0	16.2–20.5	21.0–25.0	
I. bonana (Martinique)	84.5 ± 6.4	91.0	19.5 ± 0.6	23.4 ± 1.8	
	(2)	(1)	(2)	(2)	
	80.0–89.0	—	19.0–19.9	22.1–24.7	
I. oberi (Monserrat)	81.7 ± 3.7	94.0 ± 4.0	20.6 ± 1.0	24.3 ± 1.0	33.7 ± 1.4
	(7)	(7)	(7)	(7)	(6)
	75.1–85.3	84.2–95.0	19.5–25.3	22.0–27.2	31.5–35.8
I. laudabilis (St. Lucia)	103.6 ± 5.3	90.8 ± 4.4	22.7 ± 1.1	25.4 ± 0.7	34.9 ± 0.8
	(8)	(7)	(8)	(7)	(3)
	94.0–111.0	86.0–98.5	21.3–24.2	24.2–26.5	34.0–35.5

We found comparison of immature individuals was a critical analysis, because this age class showed even more differences in plumage than did adults.

Although its measurements are closer to those of the Greater Antillean group (Table 1, Fig. 1), *northropi* more closely resembles the Central America *I. prosthemelas* in plumage color and pattern (Jaramillo & Burke 1999). Plumage differences between *northropi* and *prosthemelas* include: young and immature *prosthemelas* have the entire upperparts greenish and have a black forehead, face, and white throat bib, whereas *northropi* lacks the black on the throat (although some individuals may have black on the chin) and the upperparts are olive-gray, with more yellowish on the head. In adult *northropi*, the rump is dull yellow with a tinge of greenish, not vivid yellow with a shade of orange as in *prosthemelas*. On the other hand, *prosthemelas* and *praecox* are quite similar in the adult plumage, but the juveniles of *praecox* have much more extensive black on throat, extending to the lower breast. The back is black rather than olive-green. In addition, *praecox* has a greenish-yellow lower abdomen and undertail feathers, whereas the yellow underparts of *northropi* are less pure, with a tinge of greenish. Also, in *northropi* the underparts, lesser wing coverts, lower back,

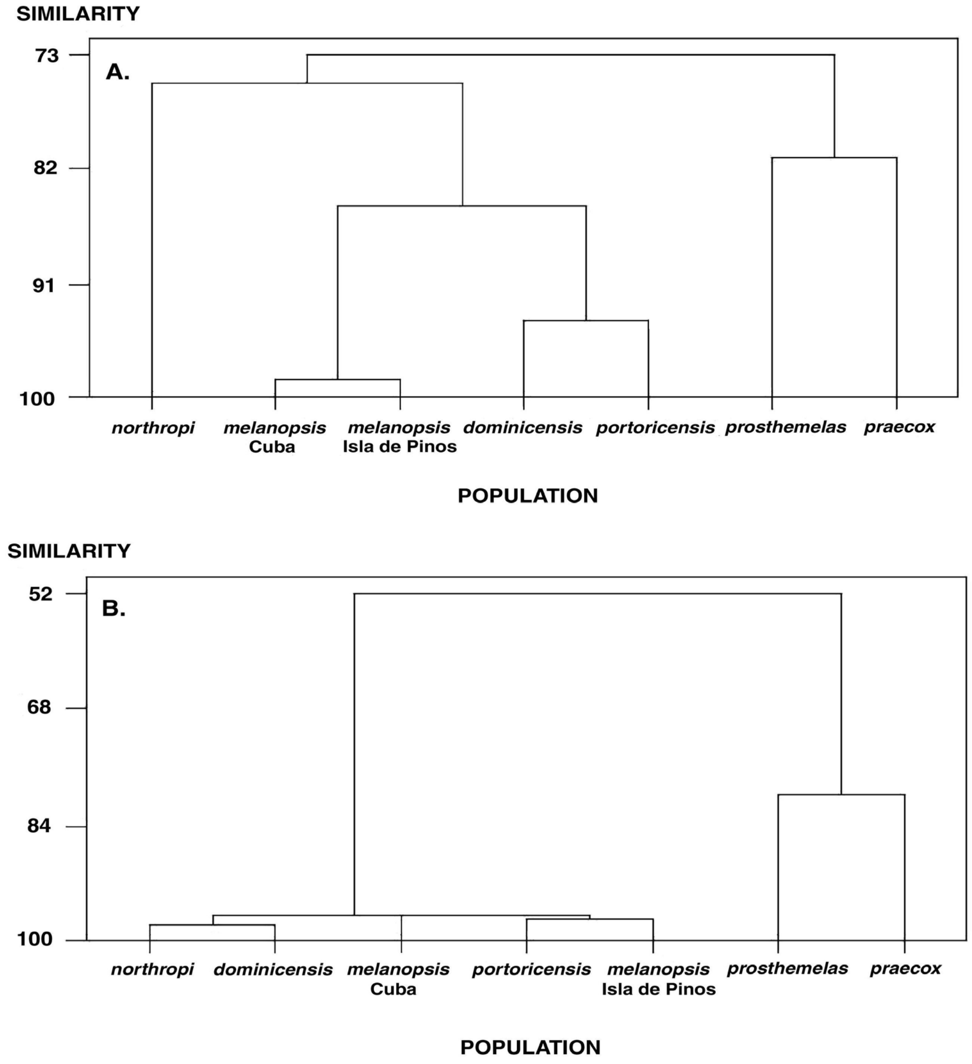

FIG. 1. Cluster analysis of relationships among populations of *Icterus* in The Bahamas and Greater Antilles and *I. p. prosthemelas* and *I. p. praecox* of mainland Mexico and Central America, based on morphometric measurements (wing, tail, culmen, tarsus). The single linkage method and squared Euclidean measure were used to conduct the cluster analyses. A = males; B = females.

rump, and tail coverts are greenish-yellow, being most vivid on the abdomen and rump. The median coverts are pale sulfur yellow and the greater coverts are brown with a thin white fringe. The lower coverts are black. Older *northropi* immatures have a black throat patch which extends on the auriculars, chin, and throat. Eventually, black feathers appear on the head, breast, and back. The wings and tail are brownish. Juvenile *northropi* are olive above with a yellowish rump and upper tail coverts. The throat is yellowish, whereas the breast is dull olive and the flanks, belly, and vent are dull yellow. The dusky wings have yellow tips to the median and greater coverts, creating two yellowish wing bars (Jaramillo & Burke 1999). Also, the black zone of the anterior underparts of Bahamian birds is more restricted and without a tinge of cinnamon, as present in *prosthemelas* and *praecox*.

Bahamian birds differ in pattern and coloration from the three Greater Antillean taxa (*melanopsis, dominicensis*, and *portoricensis*). As with *I. prosthemelas*, no sexual dimorphism in coloration occurs in the Greater Antillean group. The upperparts are more or less the same in all populations. Among adults, *melanopsis* exhibits the most extensive area of black on the underparts, where the yellow pattern is more restricted and almost reaches the undertail coverts and thigh. Some individuals may have a yellow lower belly. Some *portoricensis* specimens show the same extensive black on the underparts. *Icterus d. dominicensis* and *I. d. northropi* show the least extended black pattern on the underparts, with the black barely reaching the upper belly, as in *prosthemelas*, and yellow on rest of the belly. In *I. d. dominicensis*, the black pattern reaches the upper or mid-belly; the yellow is more extended and occurs as blotches or patches within the black, and may reach the lower belly and onto the flanks. In *I. d. portoricensis* the extension of yellow to the mid-back or lower upperparts and rump is about the same as in *melanopsis, dominicensis*, and *northropi*, but in *portoricensis* the yellow pattern is more confined in the lower belly. The amount of yellow on the shoulder is similar in all Greater Antillean populations.

As in *I. d. northropi*, *I. p. prosthemelas*, and *I. p. praecox*, the differences in the plumage patterns between immature and juvenile Greater Antillean *I. dominicensis* are much more obvious than in adults, although the extension of the black color of the throat varies with age. Younger juveniles lack black on the throat, whereas older individuals begin to show a few black feathers or display a partially developed black patch on the throat.

In juvenal plumage, the upperparts of *melanopsis* are more olive green, except the yellow mid-back and rump, than others in the *I. dominicensis* group. *Icterus d. northropi* is less olive and more brownish, with a more greenish, less yellowish, rump. Both *portoricensis* and *dominicensis* are brownish-gray above, not olive, with *portoricensis* being even tawnier, and with an olive-yellow rump; the head is darker than the back. *Icterus d. portoricensis* has a tawny-yellow head and tawny rump, although some individuals may have a yellowish-olive rump, that is lighter than that of *dominicensis*. In contrast, the rump of *I. d. dominicensis* is olive, rather than tawny. Thus, juvenile *I. d. portoricencis* can be distinguished by its darker upperparts.

Juvenile *I. d. northropi* has the most yellow coloration among the populations, whereas the underparts of *melanopsis* are more olive overall, except the throat, where a black suffusion begins. *Icterus d. dominicensis* is less olive, more yellowish on the abdomen and anal coverts, but has decidedly darker tawny-brown on the breast compared to other Greater Antillean subspecies, with the throat showing only a suffusion of black. *Icterus d. portoricensis* is more uniformly tawny-brown on the underparts, deep tawnish on the breast, and much less so around the anal coverts. Some *portoricensis* individuals are more olive colored on lower belly; the throat is almost completely devoid of black, being even lighter (yellowish-brown) than the breast.

The undertail coverts may be black in all of the populations. In *I. d. northropi* these feathers are yellow-tipped as in *I. prosthemelas*, whereas *portoricensis* and *dominicensis* may have yellowish-tawny or even greenish feathers. *Icterus d. melanopsis* may have some yellow-tipped coverts. An important character that distinguishes *prosthemelas* from the Bahamian and Greater Antillean taxa is that the tail

TABLE 2. Sexual size dimorphism among populations of *Icterus dominicensis*, *I. p. prosthemelas*, and *I. p. praecox*. Comparisons made with unpaired t-test. Parametric test used if populations showed normal distribution; if not, Welch's approximate t is shown, which assumes Gaussian populations with different SDs.

Populations	Measurement	Mean ± SD (N)		t	df	*P*[1]
		Males	Females			
I. d. northropi	Wing	98.4 ± 2.4 (1500)	92.5 ± 2.0 (11)	6.72	23	< 0.0001***
(Bahamas)	Tail	91.6 ± 3.0 (16)	86.2 ± 4.1 (12)	3.89	19	0.001**
	Culmen	20.5 ± 1.1 (15)	19.9 ± 0.9 (12)	1.82	24	0.082 ns
	Tarsus	25.3 ± 1.0 (16)	24.5 ± 1.0 (12)	2.25	24	0.034*
I. d. melanopis	Wing	94.3 ± 4.0 (70)	91.3 ± 2.8 (35)	4.43	92	< 0.0001***
(Cubas)	Tail	87.1 ± 3.8 (69)	84.1 ± 3.4 (34)	4.07	72	< 0.0001***
	Culmen	18.7 ± 1.2 (66)	18.8 ± 1.3 (34)	-0.47	64	0.636 ns
	Tarsus	24.0 ± 2.1 (56)	23.3 ± 1.1 (29)	2.05	82	0.044*
	Weight	38.7 ± 1.9 (34)	35.4 ± 2.0 (25)	6.33	249	< 0.0001***
I. d. melanopis	Wing	95.0 ± 3.5 (20)	92.7 ± 2.7 (7)	1.76	13	0.103 ns
(Isla de Pinos)	Tail	88.0 ± 4.6 (19)	85.4 ± 3.5 (7)	1.57	13	0.140 ns
	Culmen	19.1 ± 1.1 (18)	18.5 ± 1.0 (7)	1.46	12	0.170 ns
	Tarsus	24.1 ± 1.1 (18)	23.5 ± 1.8 (7)	0.86	7	0.421 ns
	Weight	38.0 ± 0.8 (5)	35.5 ± 1.1 (7)	8.58	10	< 0.0001***
I. d. dominicensis	Wing	96.0 ± 3.9 (64)	92.1 ± 2.7 (40)	6.06	100	< 0.0001***
(Hispaniola)	Tail	84.3 ± 4.1 (65)	82.6 ± 3.2 (40)	2.31	96	0.023*
	Culmen	20.2 ± 1.3 (62)	19.9 ± 1.8 (40)	0.93	67	0.356 ns
	Tarsus	22.5 ± 1.2 (64)	22.8 ± 1.2 (40)	-1.30	83	0.196 ns
	Weight	36.5 ± 1.1 (10)	35.0 ± 1.4 (9)	2.94	17	0.0092**
I. d. portoricensis	Wing	96.9 ± 3.4 (37)	92.1 ± 2.7 (28)	6.35	62	< 0.0001***
(Puerto Rico)	Tail	85.8 ± 3.3 (37)	83.2 ± 2.9 (28)	3.49	61	0.001**
	Culmen	21.8 ± 1.2 (36)	21.7 ± 1.5 (25)	0.30	44	0.30 ns
	Tarsus	23.2 ± 1.2 (35)	22.9 ± 1.4 (26)	0.78	49	0.439 ns
	Weight	41.0 ± 1.6 (27)	36.6 ± 1.2 (22)	8.20	47	< 0.0001***
I. p. prosthemelas	Wing	89.3 ± 3.2 (75)	84.1 ± 2.6 (38)	9.31	90	< 0.0001***
	Tail	90.8 ± 5.2 (80)	87.3 ± 4.4 (39)	3.75	87	< 0.0001***
	Culmen	17.8 ± 1.0 (80)	17.1 ± 1.5 (39)	2.69	55	0.009*
	Tarsus	22.6 ± 1.1 (76)	22.9 ± 1.3 (36)	-1.12	60	0.269 ns
I. p. praecox	Wing	89.2 ± 2.6 (17)	83.7 ± 1.8 (18)	7.23	28	< 0.0001***
	Tail	87.9 ± 3.8 (15)	84.8 ± 3.5 (18)	2.46	28	0.020*
	Culmen	18.6 ± 1.2 (18)	18.4 ± 1.3 (14)	0.49	27	0.628 ns
	Tarsus	23.3 ± 1.3 (18)	23.2 ± 1.2 (16)	0.07	31	0.943 ns

[1] * = < 0.05, ** = < 0.001, and *** = < 0.0001.

feathers of none of the *prosthemelas* specimens show lighter or greenish tips, and the feathers are partly bicolor. In the West Indian subspecies, they are more uniformly colored grayish, brownish, greenish, or tawny. Also, the young juveniles and fledglings of the West Indian taxa are devoid of the black patch on the throat, which is clearly present in even fledglings of *prosthemelas*.

We also compared the Lesser Antillean taxa *I. laudabilis*, *I. oberi*, and *I. bonana* with West Indian *I. dominicensis*. *Icterus laudabilis* has the underparts, shoulder, and rump orange instead of yellow. Immature *laudabilis* are much darker than even Puerto Rican birds, sometimes having chestnut-brown on the breast. *Icterus oberi* has the same color and pattern as *laudabilis*, but the underparts are yellowish-tawny rather than orange, with the rump more yellowish-tawny. Immature *I. bonana* are chestnut throughout the underparts, with an even deeper hue of chestnut on the breast. The upper section of the rump is tawny, but deep chestnut in the lower part, whereas the head is dark brown, almost mahogany.

Adults of *I. oberi* are quite similar to *I. laudabilis*, but the light colors are less orange, and more tawny-yellowish. Immature *oberi* look more like *melanopsis* or *dominicensis*, being entirely yellowish-green from throat to the anal coverts. The ventral tail feathers are grayish-green, with no yellow or greenish tips, as in *prosthemelas*. The upperparts are greenish-yellow, with a hue of olive, more yellowish on the head, and more olive on the back with a greenish-olive rump. The upperside of the tail feathers is greenish-tawny, brighter toward the edges. In all these aspects, the juvenile *oberi* seems closer to the *dominicensis* group than to *prosthemelas*, although this interpretation is tentative considering that similarities may not necessarily indicate a closer relationship. Omland & Lanyon (2000) used mitochondiral DNA sequences to examine plumage characters in *Icterus*, finding high frequencies of evolutionary convergence and reversal of plumage characters. Allen & Omland (2003) subsequently used another phylogenetic marker (nuclear intron data) to examine oriole plumage patterns, again concluding that plumage evolution in the New World orioles has been highly homoplastic.

Morphometrics. For morphometric analyses, we compared only males with males and females with females because of sexual size dimorphism among the populations (Table 2). Sexual size dimorphism was particularly evident in wing measurements among the island and mainland populations examined (Table 2). All populations, except Isla de Pinos birds, were dimorphic in at least two of the measured characters.

In general, *northropi* is considerably larger than *prosthemelas*, with wings of males averaging 98.4 ± 2.4 mm, compared with 89.3 ± 3.2 mm (t = 12.46, $P < 0.001$) in *I. p. prosthemelas* and 89.2 ± 2.6 mm (t = 10.26, $P < 0.001$) in *I. p. praecox*; wings of females averaging 92.5 ± 2.0 mm in *northropi*, compared with 84.1 ± 2.6 mm (t = 11.51, $P < 0.001$) in *prosthemelas* and 83.7 ± 1.8 mm (t = 11.97, $P < 0.001$) in *praecox* (Tables 1 & 3). Between males of *northropi*, *prosthemelas*, and *praecox*, differences were found also in culmen and tarsus length (Tables 1 & 3). Female *northropi* and *prosthemelas*, differed in measurements of culmen and tarsal length (Tables 1 & 3).

Among the Bahamas and Greater Antillean populations, substantial size differences were found among all island populations, except between birds from Isla de Pinos and Cuba (Tables 1 & 3). For that reason, the Cuban and Isla de Pinos populations were combined in subsequent analyses. Females showed substantially less difference in size measurements among populations than did males (Table 3).

Analyses of measured body parts using

TABLE 3. Morphometric comparisons among populations of *Icterus dominicensis* in the Bahamas and Greater Antilles, as well as comparisons with *I. p. prosthemelas* and *I. p. praecox*. T-test for equality of means used, 2-tailed, using Bonferroni's correction for multiple tests, with significance level set at 0.05. Sample sizes are presented in Table 1.

Species	t-values and levels of significance[1]							
compared with	Males				Females			
	Wing	Tail	Culmen	Tarsus	Wing	Tail	Culmen	Tarsus
Icterus d. northropi								
melanopsis (Cuba)	3.82	4.43	5.46*	2.42	1.35	1.73	2.69	3.09
melanopsis (Isla de Pinos)	3.19	2.66	3.63	3.22	-0.15	0.44	3.24	1.48
dominicensis	2.30	6.62**	0.83	8.85**	0.54	3.14	-0.12	1.45
portoricensis	1.53	5.99*	-3.50	6.22**	0.48	2.69	-3.94	3.45
prosthemelas	12.46**	0.80	-6.24**	9.51**	11.51***	-0.86	7.96**	4.37*
praecox	10.26***	2.93	4.88*	5.32*	11.97***	0.97	3.48	2.98
Icterus d. melanopis (Cuba)								
melanopsis (Isla de Pinos)	-0.72	-0.91	-1.43	-0.23	-1.21	-0.89	0.66	-0.41
dominicensis	-2.50	4.12	-6.82**	5.06*	-1.17	1.93	-3.08	1.87
portoricensis	-3.40	1.73	-12.45***	2.12	-1.13	1.17	-8.06**	1.11
prosthemelas	8.28**	-5.00	4.59*	4.57*	11.53***	-3.53	5.27*	1.42
praecox	6.38**	-0.77	0.21	1.88	12.05***	-0.67	1.01	0.23
Icterus d. melanopis (Isla de Pinos)								
dominicensis	-1.02	3.39	-3.12	5.32*	0.57	2.04	-2.11	1.42
portoricensis	-2.01	2.08	-7.84**	2.78	0.52	1.74	-5.39*	0.95
prosthemelas	6.54**	-2.31	4.55*	5.16*	7.69**	-1.31	3.14	-10.47***
praecox	5.70*	0.06	1.35	2.22	8.04**	0.37	0.14	0.41
Icterus d. dominicensis								
portoricensis	-1.21	-1.94	-5.74*	-2.91	-0.06	-0.72	-4.15	-0.49
prosthemelas	11.02***	-8.36**	11.63***	-0.77	13.29***	-5.40*	7.63**	-0.39
praecox	8.49**	-3.28	4.92*	-2.37	13.80***	-2.24	3.47	-1.27

TABLE 3. Continued.

Species	t-values and levels of significance[1]							
compared with	Males				Females			
	Wing	Tail	Culmen	Tarsus	Wing	Tail	Culmen	Tarsus
Icterus d. portoricensis								
prosthemelas	11.41***	-6.24**	17.24***	2.44	12.14***	-4.69*	11.95***	0.13
praecox	9.12**	-1.87	9.27**	-0.16	12.63***	-1.65	7.30**	-0.73
Icterus p. prosthemelas								
praecox	0.09	2.50	-2.65	-1.98	0.71	2.37	-3.15	-0.93

[1] * = $P < 0.05$, ** = $P < 0.01$, and *** = $P < 0.001$.

ANOVA revealed significant differences among *I. dominicensis* populations: males, Wing: $F_{3, 202} = 7.487$, Tail: $F_{3, 202} = 18.174$, Culmen: $F_{3, 193} = 53.330$, Tarsus: $F_{3, 202} = 21.797$, all $P < 0.0001$; females, Wing: $F_{3, 117} = 0.538$, $P = 0.657$ ns; Tail: $F_{3, 117} = 4.409$, $P = 0.006$; Culmen: $F_{3, 114} = 21.107$, $P < 0.0001$; Tarsus: $F_{3, 110} = 6.320$, $P = 0.001$.

To further examine size differences among *I. dominicensis* populations, we used linear discriminant analysis to classify specimens into groups ("Island": Bahamas, Cuba, Hispaniola, and Puerto Rico), using lengths of cord, tail, culmen, and tarsus as predictors. For males, the analysis produced a true group classification proportion of 1.00 for Bahama specimens, 0.731 for Cuban specimens, 0.667 for Hispaniolan specimens, and 0.706 for Puerto Rico individuals, for an overall proportion correct of 0.7326 (127 of 175) (Wilks' lambda = 0.333; df = 12, $P < 0.0001$). For females, the analysis produced lower true group and overall classification proportions: 0.833 for Bahama specimens, 0.657 for Cuban specimens, 0.350 for Hispaniolan specimens, and 0.680 for Puerto Rico individuals, for an overall proportion correct of 0.571 (64 of 112) (Wilks' lambda = 0.515; df = 12, $P < 0.0001$).

A cluster analysis of populations of Bahamian and Greater Antillean *I. dominicensis* and mainland *I. prosthemelas* and *I. p. praecox* supported a stronger phenetic similarity among island forms than between those populations and *I. prosthemelas* and *I. p. praecox* (Fig. 1). Analyses of male and female birds from the Bahamas and Greater Antilles varied somewhat, with females showing tighter similarity, whereas males showed a broader range of relationship. In both sexes, however, Bahama individuals clustered with other Greater Antillean populations, distant from *I. prosthemelas* and *I. p. praecox*.

Natural history. As is typical for most endemic West Indian birds, natural history information for *Icterus* is scarce. Nevertheless, being vicariant forms, it is obvious that the different island populations show some close similarities in habitat and nidification.

Icterus dominicensis occurs mainly at low elevations, but Hispaniolan and Puerto Rican birds are common also at higher elevations, up to 1100 m in the Dominican Republic and to 1000 m in Puerto Rico, where appropriate habitat is available. They prefer palm habitats in most islands, but also occur in pine forest (Bahamas), broadleaf forest, including shade plantations, farmland, parks, and even in dry lowland forest and desert scrub forests. In Hispaniola, the oriole is particularly fond of foraging in *Erythrina poeppigiana* (Leguminosae) trees planted in hedgerows.

Among Lesser Antillean species, *I. oberi* occurs mainly on mountain slopes at an altitude of 800 m and higher, but also in wooded zones at low elevation; *I. bonana* occurs throughout Martinique, including mixed forest, and humid forest to an altitude of 700 m or more, but prefers mangrove and dry forest habitats; and *I. laudabilis* occurs in coastal zones, including mangroves, dry zones, to high altitude, and humid forests (Bénito-Espinal 1990, Evans 1990, Bénito-Espinal & Hautcastel 2003).

Nests are quite similar among the island populations; i.e., a woven, shallow basket-shaped structure with a side entrance, suspended from the undersides of leaves of palms, including coconut, or mango trees. Bond (1936) noted that the nesting habits of *northropi* resemble those other populations in the *dominicensis* group. Most Bahamian and Greater Antillean *Icterus* lay clutches of three, occasionally four, eggs, which are oval in shape. The exception is *I. leucopteryx*, with 3–5 eggs per clutch (Raffaele *et al.* 1998). Among the subspecies of *I. dominicensis*, clutches we observed averaged 3.0 ± 0.2 (n = 20; r = 3–4) for Cuba and Isla de Pinos, 3.1 ± 0.3 (15; 3–4)

TABLE 4. Food items delivered to chicks at nests of *Icterus dominicensis* in Cuba, Dominican Republic, and Puerto Rico.

Food classes	Number of items (%)		
	Isla de Pinos, Cuba n = 57 (4 nests)	Dominican Republic n = 31 (2 nests)	Puerto Rico n = 109 (5 nests)
Animal			
Insects	43 (75)	27 (87)	95 (87)
Other invertebrates	2 (4)	—	3 (3)
Small *Anolis* lizard	—	—	1 (1)
Plant			
Fruit	12 (21)	4 (13)	10 (9)

for Hispaniola, and 3.0 ± 0.4 (17; 2–4) for Puerto Rico. One nest we examined in Abaco Island, Bahamas, contained three eggs. Eggs of Hispaniolan *Icterus* are white with a bluish tinge, spotted with reddish-brown, the marking heaviest toward the larger end, and measure 21.7 ± 0.7 x 16.1 ± 0.3 mm (n = 5). Cuban eggs are greenish-white, with spots and dots brownish with lilac-grayish and olives hues, especially around the larger end; 23.8 ± 0.6 x 16.8 ± 0.4 (n = 17; Cuba and Isla de Pinos). Eggs of *portoricensis* averaged 24.1 ± 0.6 x 17.5 ± 0.6 mm (n = 12), are white with a bluish hue, and are lightly marked with lavender-gray-brown speckles and spots, concentrated at the large end. Three eggs (from one nest) examined in Abaco Island were pale greenish-white, with medium to dark brown spots concentrated at the large end, but lightly distributed throughout the egg.

In contrast, Lesser Antillean orioles usually lay two-, sometimes three-egg clutches: *I. oberi* lays two whitish eggs marked with brown, 23.4 x 17.3 mm (n = 1) (Bénito-Espinal & Hautcastel 2003); *I. bonana* produces 2–3 eggs, generally 2, cream white with bluish tinge, marked with brown spots at the broad end, 24.7 x 15.0 mm (n = 4) (Bénito-Espinal & Hautcastel 2003); *I. laudabilis* lays 2–3 white eggs, speckled with chestnut or dark brown, especially on the large end, 25.0 x 17.5 mm (n = 3) (Danforth 1935, Keith 1997, Bénito-Espinal & Hautcastel 2003).

Breeding season of *I. domenicensis* usually begins in February and continues throughout the summer, but this is variable, and may occur, irregularly, through the year (Gundlach 1876, Bond 1936, Wetmore & Swales 1931, Stockton de Dod 1978, Valdés Miró 1984, Raffaele 1989, White 1998, Latta *et al.* in press; pers. observ.), with Cuban birds breeding from February through July, Hispaniolan birds primarily March through June, and Puerto Rican birds from February through July, although breeding occurs irregularly through the rest of the year in Puerto Rico.

Feeding ecology is uniform through the islands, with *I. dominicensis* feeding on fruits, flowers, nectar, and insects. Wetmore (1916) conducted the only detailed studies of *I. dominicensis* food habits, examining stomachs of 71 Puerto Rican birds from January to August. The stomachs contained 99.8% animal matter, mainly orthopertans, beetles, spiders, and earwigs. A few vertebrates (frogs, anole) were also found in the stomachs. This high proportion of animal material contrasts with our observations of food delivered to nests (see below) and may be related to a bias in the detectability of plant materials in stomach remains.

TABLE 5. Characteristics (mean ± sd, range in parentheses) of songs in four *Icterus dominicensis* populations.

Race	N	Duration (s)	Number of elements	Frequency (Hz)		Emphasized element
				Low	High	
North Andros, Bahamas	16	2.4 ± 0.48	9.4 ± 1.31	1591 ± 197.1	5467 ± 352.1	7
		(1.2–2.9)	(6–11)	(1225–1942)	(4541–5745)	
Cuba						
Long call	8	3.0 ± 0.16	11.3 ± 0.46	1651 ± 306.6	4172 ± 116.2	5
		(2.8–3.2)	(11-12)	(1378–2339)	(3998–4291)	
Short call	7	1.9 ± 0.22	5.9 ± 0.38	2165 ± 243.7	4934 ± 166.2	1
		(1.5–2.2)	(5–6)	(1813–2541)	(4712–5165)	
Isla de Pinos, Cuba	16	1.8 ± 0.29	8.1 ± 0.68	1638 ± 199.7	4324 ± 166.1	7
		(1.4–2.4)	7–9	1128–1846	(4052–4665)	
Puerto Rico	7	2.0 ± 0.19	5.3 ± 0.49	1189 ± 113.9	6640 ± 135.6	3
		(1.8–2.3)	(5–6)	(1019–1363)	(6434–6824)	

Our observations from blinds placed at *I. dominicensis* nests revealed food brought to chicks consisted mostly of small invertebrates (mostly insects), but also some fruits (Table 4). Cuban birds provided chicks with proportionately more fruit than animal matter compared with Puerto Rican and Dominican Republic birds (Table 4). Invertebrates are often gleaned from the underside of leaves, including palm fronds, but are also extracted from within flower blossoms or, using its bill in a gaping movement, by prying open curled leaves, bark, or bromeliads to expose prey. Outside of the breeding period, *I. dominicensis* rely more on fruit, flowers, and nectar as major food sources (pers. observ.). Flowers of wild and cultivated orange (*Citrus sinensis*, *C. aurantium*), agave (*Agave* spp.), and mountain immortelle *Erythrina poeppigiana* are particularly attractive to *I. dominicensis*, which sometimes flock in considerable numbers at these food resources.

Wetmore & Swales (1931) noted that several observers reported *I. dominicensis* as occurring in flocks (foraging?) of as many as 50 birds. Most foraging flocks consist of from 5 to 20 adult and immature birds, particularly during "winter" roaming for food resources, but the oriole is usually seen only in family groups.

Among the Lesser Antillean *Icterus*, Arendt (pers. com.) observed adult *oberi* delivering small arthropods (insects, spiders, among others) to nestlings. Evans (1990) notes the diet is almost exclusively insects. Adult *bonana* fed nestlings butterflies, caterpillars, small grasshoppers, among other insects, whereas *laudabilis* fed its nestlings fruit pulp (e.g., bananas, mangos), as well as small arthropods (e.g., insects, spiders) (Evans 1990, Bénito-Espinal & Hautcastel 2003). Danforth (1935) found insects (lepidoptera larvae, weevil, cerambycid beetle) and locust eggs in two *laudabilis* stomachs,

Vocalizations. Song is a good indicator of phylogenetic relationships among some species of icterids (Price & Lanyon 2002). The differences found among the vocalizations of *I. dominicensis* from the Bahamas, Cuba, Puerto Rico, and Hispaniola are much more obvious than are differences in their morphology

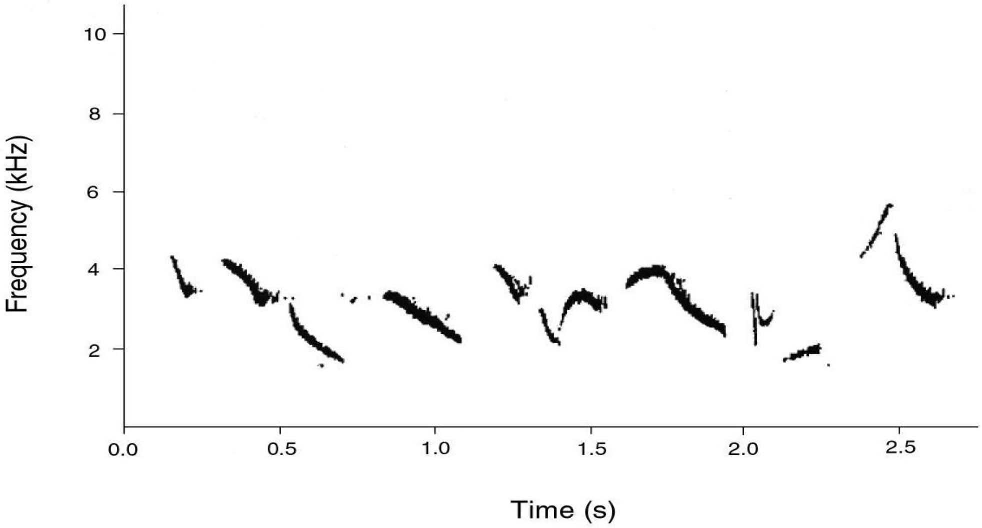

FIG. 2. Song sonograph of *Icterus dominicensis northropi*, Andros Island, The Bahamas (Bruce Hallet).

(Figs 2–6). We found little within-population variation in song among island subspecies (Table 5). Also, it is interesting to point out that the two subspecies that show more affinities in its morphology [*melanopsis* and *dominicensis*; Omland &. Lanyon (*in* Jaramillo & Burke 1999)], differ most in their vocalizations.

Maynard (1915) described the song of *I. d. northropi* as "*Poor Willy, poor Willy, poor.*" White (1998) noted the song of Bahamian birds as a rising whistle followed by two quick notes; the triad ("*Poor Willy*") is repeated, and then the song ends with the whistle. Bahamian orioles showed the greatest frequency range in song, with that vocalization averaging 2.4 ± 0.48 (r = 1.2–2.9) s in duration and consisting usually of nine (r = 6–11) emphatic whistled elements (Fig. 2, Table 5).

Cuban birds sing long (typically 3.0 ± 0.16 s and consisting of 11–12 whistled elements) and short (1.9 ± 0.22 s, 5–6 elements) songs (Figs 3 & 4, Table 5). The song of Isla de Pinos birds typically more closely resembles the short song of mainland Cuba birds, consisting of 7–9 elements and lasting 1.8 ± 0.29 s (Fig. 5, Table 5).

The song of Hispaniolan orioles is a short series of high-pitched whistles, which Stockton de Dod (1978) noted are very weak and barely audible. Hispaniolan birds sing infrequently, primarily around dawn.

Songs of Puerto Rican birds consist of high-pitched whistles, some seeming exclamatory and others querulous (Raffaele 1989). The song is typically short, lasting about 2.0 ± 0.19 s, and consisting of 5–6 elements, although songs are often strung together in sequence (Fig. 6, Table 5).

Throughout its range, the most commonly heard call of *I. dominicensis* is a sharp "*check*!," sometimes slurred, as Wetmore & Swales (1931) described for Hispaniolan birds as a harsh "*chur-r-r-r.*"

*Systematic arrangement***.** It appears to us that the systematic arrangements for West Indies *Icterus* populations proposed by 19th and early 20th century authors, which were based mainly on morphological characters, without evi-

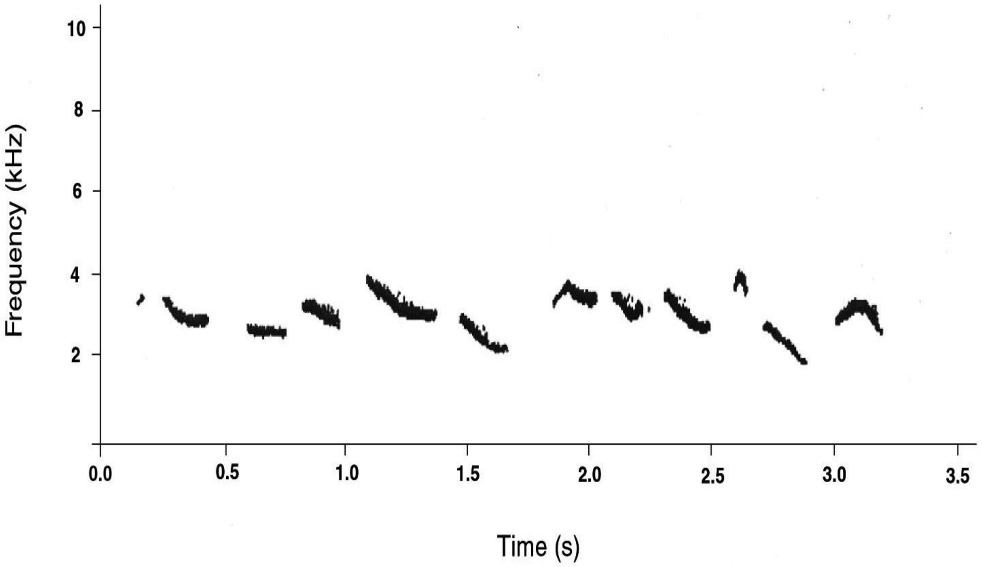

FIG. 3. Sonograph of long song of *Icterus dominicensis melanopsis*, Cuba (Reynard CB309-4).

dence of behavior, vocalizations, or genetics, are correct. Morphological, natural history, vocalization, and molecular differences, as well as the pattern of distribution among islands, clearly define the Bahamian and Greater Antillean *I. dominicensis* populations as members of a superspecies, with distinct allospecies in the different islands. This interpretation of the populations is in accord with the new concept of biological species proposed by Johnson *et al.* (1999): "A system of populations representing an essentially monophyletic, genetically cohesive, and genealogically concordant lineage of individuals that share a common fertilization system through time and space, represent an independent evolutionary trajectory, and demonstrate essential but not necessarily complete reproductive isolation from other such systems." Although the island populations of *Icterus* are allopatric and it is not possible to demonstrate reproductive isolation, the level of behavioral, ecological, and morphological difference among the populations are at least as great as those among other West Indian species groups; e.g., *Spindalis* (Garrido *et al.* 1997).

As suggested by Omland *et al.* (1999), we found differences among Bahamian and Greater Antillean *I. dominicensis* populations that included morphological (size and plumage) and behavioral (especially vocalization) distinctions. Additional morphological characters have been noted by others as distinctions among populations of *I. dominicensis*; e.g., Bahamian birds have bulkier bills than the other subspecies (Jaramillo & Burke 1999). Further, Jaramillo & Burke (1999) presented wing formulae of *I. p. praecox, I. p. prosthemelas*, and *I. dominicensis northropi*, *I. d. melanopsis*, *I. d. dominicensis*, and *I. d. portoricensis*, demonstrating differences among these subspecies (Table 6).

The recent study of Omland *et al.* (1999) comparing the mitochondrial DNA of the orioles suggests that more than one species is involved in what was formerly known as the *Icterus dominicensis* (Black-cowled Oriole), but now split into *Icterus prosthemelas* (Black-

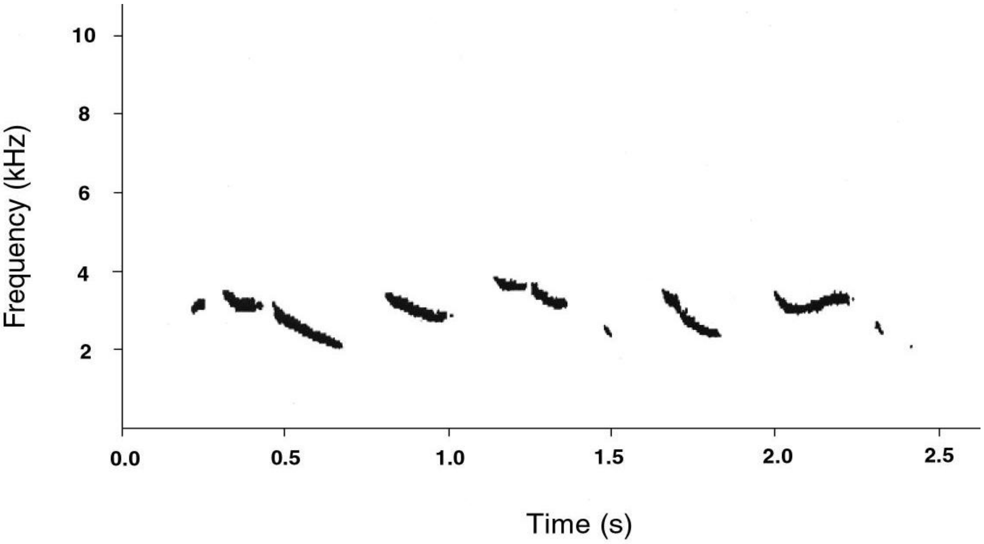

FIG. 4. Sonograph of short song of *Icterus dominicensis melanopsis*, Cuba (Reynard CB309-2).

cowled Oriole) and *I. dominicensis* (Greater Antillean Oriole), containing the several forms in the Bahamas and Greater Antilles. The phylogenetic reconstructions by Lovette *et al.* (1999) placed the mainland taxon *I.* [*d.*] *prosthemelas* basal to a cluster of Antillean lineages. The internode separating *I. prosthemelas* and the Antillean group was long and universally well supported. This agrees with our examination of these populations, based on morphological characters (Fig. 1). In their molecular phylogeny of *Icterus*, Omland *et al.* (1999) included the *I. dominicensis* (*prosthemelas* and *dominicensis*) group in the mtDNA clade containing *I. spurius* and *I. cucullatus*, supporting a phylogenetic lineage. In addition, Omland &. Lanyon (*in* Jaramillo & Burke 1999) noted that *portoricensis* may be more closely related to the Lesser Antillean orioles (St. Lucian, Montserrat, and Martinique) than to other members of the *dominicensis* complex. Omland &. Lanyon (*in* Jaramillo & Burke 1999) also found that *I. d. melanopsis* and *northopi* were more closely related than they were to other members of the *dominicensis* group.

Lovette *et al.* (1999) concluded that the three Lesser Antillean oriole species and the Puerto Rican population of *dominicensis* are more closely related to one another than they are to Central American *prosthemelas*. Their phylogenetic assemblage of the four eastern Caribbean populations supports the hypothesis that the Lesser Antillean populations were derived from Greater Antillean ancestors (Bond 1956, Lack 1976). Species that inhabit neighboring biogeographic regions are often close relatives (Wiley 1988), which we suggest for the complex of *I. Dominicensis.*

Therefore, we propose that these West Indian allospecies constitute endemic species from their respective islands. We propose the following systematic arrangement, including their common and technical names:

Icterus northropi Allen, 1890 (Bahamas Oriole)
Islands of Andros and Abaco (presently rare on the latter). Bond (1936) considered

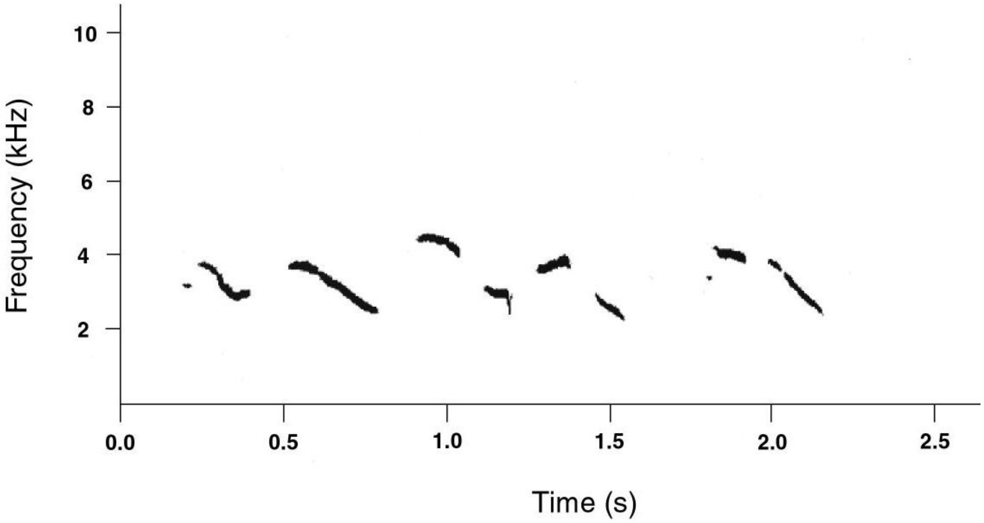

FIG. 5. Sonograph of song of *Icterus dominicensis melanopsis*, Isla de Pinos, Cuba.

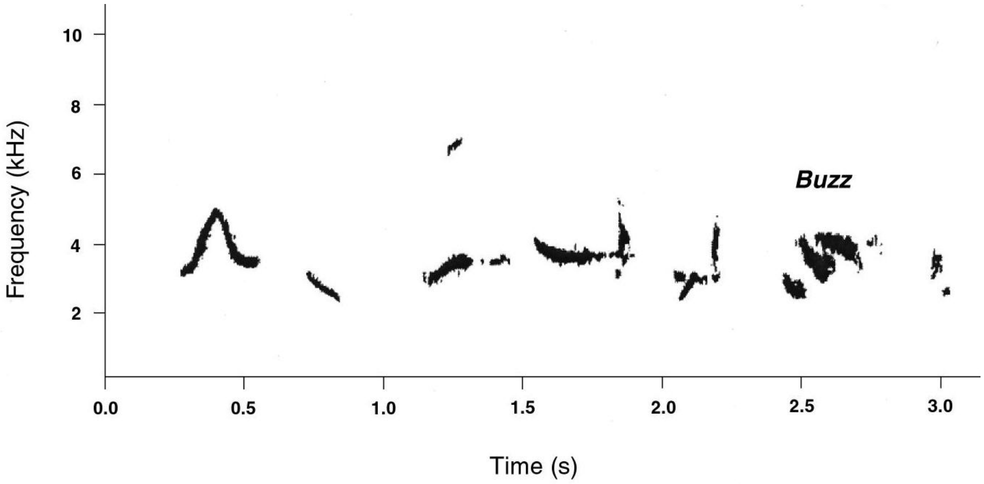

FIG. 6. Sonograph of song with terminal "*buzz*" of *Icterus dominicensis portoricensis*, Puerto Rico (Reynard 1).

I. northropi as restricted to the Bahaman Islands of Andros and Abaco, but later (1956) regarded *northropi* as conspecific with *dominicensis, melanopsis,* and *portoricensis*, as did Blake (1968). Based on field observations, Smith & Smith (1997, pers. com.) agreed with Ridgway's (1902) earlier arrangement where *northropi* is distinct from the *dominicensis* group.

Icterus melanopsis (Wagler), 1829 (Cuban Oriole)

Cuba, Isla de Pinos, and some northern keys (cayos Guillermo, Coco, Paredón

TABLE 6. Wing formulae for six races of *Icterus dominicensis and I. prosthemelas* demonstrating differences among the forms (after Jaramillo & Burke 1999).

Species	Wing formula
I. p. praecox	P9 < P8 < P7 > P6 > P5; P9 ≈ P2; P8–P5 emarginate
I. p. prosthemelas	P9 < P8 < P7 < P6 > P5; P9 ≈ P3; P8–P6 emarginate
I. d. northropi	P9 < P8 < P7 ≈ P6 > P5; P9 ≈ P4; P8–P6 emarginate
I. d. melanopsis	P9 < P8 < P7 > P6; P9 ≈ P4; P8–P5 emarginate
I. d. dominicensis	P9 < P8 >» P7 > P6; P9 ≈ P6; P8–P5 emarginate
I. d. portoricensis	P9 < P8 < P7 ≈ P6 > P5; P3 < P9 < P4; P8–P5 emarginate

Grande). A comparison of specimens from Cuba and Isla de Pinos showed no differences in measurements and coloration.

Icterus dominicensis (Linnaeus), 1766 (Hispaniolan Oriole)
Hispaniola, including Île de la Gonâve, Île de la Tortue, Île-à-Vache, and Isla Saona.

Icterus portoricensis Bryant, 1866 (Puerto Rican Oriole)
Puerto Rico.

Icterus oberi Lawrence, 1880 (Montserrat Oriole)
Montserrat.

Icterus bonana (Linnaeus), 1766 (Martinique Oriole)
Martinique.

Icterus laudabilis Sclater, 1871 (St. Lucia Oriole)
St. Lucia

Implications for conservation. All West Indian populations of *Icterus* have been affected by moderate to extensive habitat loss, mostly as a result of conversion from natural habitat to agricultural use by man, but also because of natural disasters (e.g., volcano eruption in Montserrat; Lovette *et al.* 1999). Associated with that habitat conversion is the recent arrival of the Shiny Cowbird (*Molothrus bonariensis*), for which *I. dominicensis* is a primary host (Friedmann 1963, Post & Wiley 1977, Cruz *et al.* 1989). Some populations have experienced high rates of brood parasitism; e.g., Puerto Rico, where 100% of *I. dominicensis* nests in some lowland areas (Wiley 1985) and 61% of nests in upland sites (Pérez-Rivera 1986) have been found parasitized by *M. bonariensis*. Whereas substantial management effort has been directed at the control of the cowbird in parts of lowland Puerto Rico, those activities have been directed to benefit the endangered Yellow-shouldered Blackbird (*Agelaius xanthomus*) (Wiley *et al.* 1991). Nevertheless, those management efforts undoubtedly had positive effects on *Icterus* populations in lowland Puerto Rico. Unfortunately, in upland Puerto Rico and in other islands where no conservation efforts have been undertaken yet, nest parasitism has had actual or suspected substantial effect on *Icterus* populations (Cruz & Wiley 1989; Baltz 1996, 1997; Wiley & Garrido, pers. observ.). The brood parasitism issue is a difficult problem to solve, especially given the limited conservation resources of most of the countries with *Icterus* populations. To date, management efforts have been expensive and labor intensive, and consist mainly of trapping and removing cowbirds. Although those efforts are locally effective (Wiley *et al.* 1991, U. S. Fish & Wildlife Service 1996), a biologically sound and sustainable management strategy is needed that also targets *Icterus*. Nevertheless, until such a strategy is developed, similar cowbird trapping programs at national and international levels are important to ensure against brood parasitism-related population declines from which orioles may not be able to recover.

The data presented here and by Lovette *et al.* (1999) support the evolutionarily distinct lineages of the several populations of *I. dominicensis* and Lesser Antillean *Icterus.* An awareness of those lineages has substantial conservation value. The elevation of the Greater Antillean and Bahamian *I. dominicensis* populations to single-island endemic status underscores the evolutionary significance of the forms, and should help to promote local and international awareness of the species' importance to island and regional biodiversity, with concomitant effort to undertake effective conservation programs.

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