

More on the Origin of the Red-legged Thrush (*Turdus plumbeus*) of Dominica, West Indies

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Source: The Auk, 126(2) : 449-454

Published By: American Ornithological Society

URL: <https://doi.org/10.1525/auk.2009.02409>

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The Auk 126(2):449–454, 2009
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Printed in USA.

More on the Origin of the Red-legged Thrush (*Turdus plumbeus*) of Dominica, West Indies.—An analysis of 842 base pairs of two mitochondrial genes led Ricklefs and Bermingham (2008) to hypothesize that the Red-legged Thrush (*Turdus plumbeus*) was a recent arrival on the Lesser Antillean island of Dominica, perhaps introduced from Puerto Rico by humans. Olson drafted a commentary explaining why he found Ricklefs and Bermingham's (2008) hypothesis unlikely. Ricklefs prepared a reply, presenting information that Olson had criticized the original publication for lacking. This information had been present in the manuscript but was deleted during the editorial process. Here, Olson and Ricklefs together present an amplification of the data bearing on this case, followed by brief independent summaries of points on which they still disagree.

TAXONOMIC HISTORY AND MORPHOLOGY

Our knowledge of what is now known as *Turdus plumbeus* goes back nearly 300 years to when Mark Catesby (1731) first illustrated and described the "Red leg'd Thrush" that he saw in the Bahamas in 1725. By the time the species was discovered on Dominica, closely related but well-marked geographical representatives were treated as full species, whereas the practice of recognizing "sub-species" and designating them by trinomials was just beginning to take hold. Thus, the Red-legged Thrush (formerly segregated with *T. ravidus* of Grand Cayman in the genus *Mimocichla*) was known under no fewer than four specific names (Hellmayr 1934): *T. plumbeus* of the Bahamas, *T. rubripes* of western Cuba, *T. schistaceus* of eastern Cuba, and *T. ardosiaceus* (sometimes emended to *T. ardesiacus*) of Hispaniola and Puerto Rico. Although the Puerto Rican population was once segregated as *T. p. portoricensis*, this was considered by Hellmayr (1934:446) to be "an exceedingly poor race" and it is no longer considered valid.

When specimens of the species from Dominica were first examined by Sclater (1889:326), their relationships seemed so obvious to him that its nomenclatural designation was almost provisional:

As might have been expected, the Dominican *Mimocichla* belongs to the Porto Rican form. It is, in fact, so nearly similar that I do not see sufficient grounds for making it specifically distinct. The only difference apparent is the much greater whiteness of the belly in the Dominican specimens, whence those who adopt trinomials would, no doubt, call it *Mimocichla ardesiaca albiventris*.

Sclater had not looked very closely at those specimens. Two years later, when Allen (1891) redescribed the bird of Dominica as *M. verrillorum*, he correctly noted that it differed from the Puerto Rican form in ventral coloration and had more extensive white tipping on the tail feathers, a shorter bill, a much shorter and more rounded wing, and slightly longer tarsi.

Re-examination of specimens bears out the differences noted by Allen (1891) in ventral coloration and tail markings and most of the size differences between the two populations (Fig. 1). Length measurements of wing, tarsus, and bill from nares distinguish the two populations unambiguously (Table 1). In an analysis of variance of each measurement using Proc GLM in SAS, version 9.1 (SAS Institute, Cary, North Carolina), with island and sex as main effects, none of the interaction terms was significant ($P > 0.30$). With the interactions deleted, differences between islands were significant for wing ($F = 31.5$, $df = 1$ and 25 , $P < 0.0001$) and bill ($F = 47.6$, $df = 1$ and 25 , $P < 0.0001$), but not for tarsus ($F = 0.3$, $df = 1$ and 25 , $P = 0.59$). A discriminant analysis (Proc DISCRIM in SAS) based on the three measurements separated the two populations (Wilks's $\lambda = 0.243$, $F = 25.0$, $df = 3$ and 24 , $P < 0.0001$). Posterior classification was correct for all the Dominican specimens and all but one of the Puerto Rican specimens, and the generalized squared distance between the populations was 12.6 squared multiples of the within-populations standard deviation. Thus, by long-accepted morphological criteria, *T. p. albiventris* of Dominica would be regarded as a well-marked subspecies.

DISJUNCT DISTRIBUTIONS IN THE LESSER ANTILLES

Ricklefs and Bermingham (2008) suggested that the widely disjunct occurrence of Red-legged Thrushes on Dominica had to be the result of either (1) stepping-stone colonization from Puerto Rico, followed by extinction on the intervening islands; or (2) long-distance dispersal, plausibly by direct introduction by aboriginal humans or Europeans. Many Lesser Antillean birds other than the Red-legged Thrush have disjunct distributions. Adelaide's Warbler (*Dendroica adelaidae*), for example, occurs on Puerto Rico and St. Lucia, with an intervening population on Barbuda (but not Antigua, which was joined with Barbuda during glacial periods [Pregill et al. 1988]). The Forest Thrush (*Cichlherminia lherminieri*) currently ranges from St. Lucia to Montserrat but is missing from Martinique (Raffaele et al. 1998). The Rufous-throated Solitaire (*Myadestes genibarbis*) is found in Hispaniola, Jamaica, and the southern Lesser Antilles but is absent from islands between Hispaniola and Dominica (Miller et al.

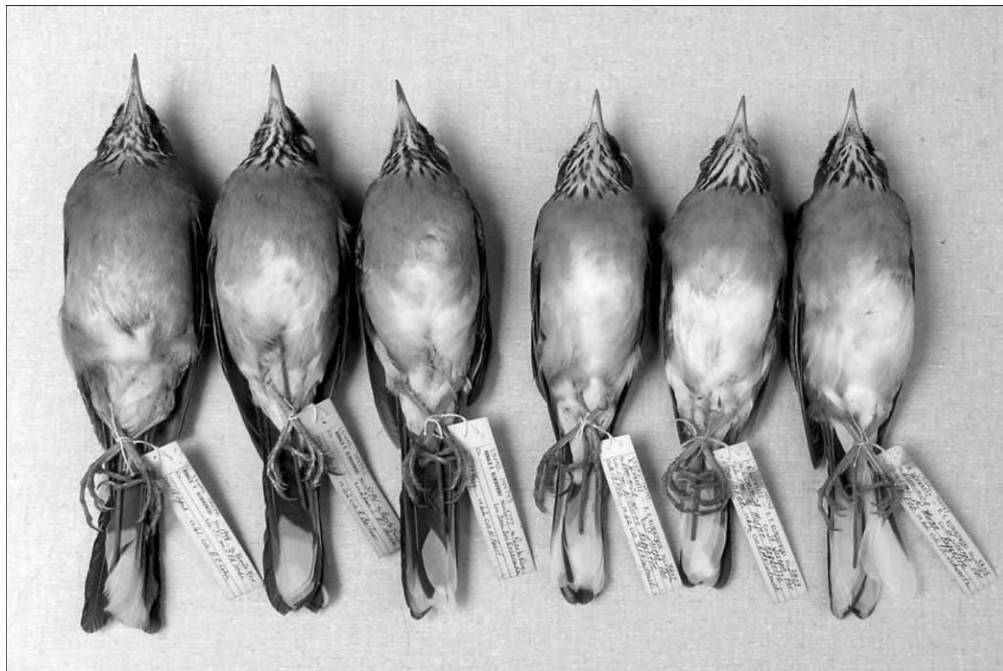


FIG. 1. Specimens of Red-legged Thrush from Puerto Rico (left) and Dominica (right) showing the relatively shorter bills, lighter underparts, more extensive buff coloration of underparts, and greater extent of white on the rectrices of Dominican individuals. Photograph of specimens from the Louisiana State Museum of Natural Science, courtesy of S. Claramunt.

2007). The Broad-winged Hawk (*Buteo platypterus*) occurs in Puerto Rico and from Dominica south in the Lesser Antilles but is absent on all the intervening islands except Antigua, where there is an endemic subspecies. The only native, resident orioles in the Lesser Antilles are *Icterus oberi* on Montserrat, *I. bonana* on Martinique, and *I. laudabilis* on St. Lucia, which can hardly be the result of either random colonization or human introduction. There must have been numerous extinctions among *Icterus* to produce such a pattern. Olson (1984) speculated that the natural distribution of the extinct subspecies of Puerto Rican Bullfinch (*Loxigilla portoricensis grandis*) would have included more islands than its historical occurrence only on St. Kitts, and this was confirmed by the discovery of a rostrum in a prehistoric deposit on Barbuda (Pregill et al. 1994, Steadman et al. 1997).

Avian distribution in the Lesser Antilles cannot be explained without widespread and repeated extinctions. The causes of these extinctions may prove difficult or impossible to determine but would include changes induced by Pleistocene climatic

fluctuations and by activities of humans, either aboriginal or European (Pregill and Olson 1981). The absence of Adelaide's Warbler from Antigua, for example, could well stem from almost complete clearing of the island for agriculture during the European colonial period (Pregill et al. 1988), but other factors would have to account for its extinction on most of the other islands between Puerto Rico and St. Lucia. Such factors could have been at work in causing the extinction of the Red-legged Thrush on the islands between Puerto Rico and Dominica.

THE FOSSIL RECORD

Ricklefs and Bermingham (2008:301) suggested that the absence of Red-legged Thrushes in "well-known fossil localities, both cultural and non-cultural, from Barbuda, Antigua, and St. Kitts (Pregill et al. 1988, Steadman et al. 1997, Reis and Steadman 1999)" indicates that the species was not present on those islands during the Holocene. The reference to Steadman et al. (1997) should have

TABLE 1. Measurements (mm; range and mean \pm SD) of Red-legged Thrushes from Puerto Rico (*Turdus plumbeus ardosiaacea*; 11 males and 7 females) and Dominica (*T. p. albiventris*; 8 males and 2 females).

	Variable	<i>T. p. ardosiaacea</i>	<i>T. p. albiventris</i>
Male	Wing	121.2–136.7, 129.1 \pm 4.2	113.1–123.2, 118.9 \pm 3.6
	Bill	16.1–18.0, 17.2 \pm 0.6	14.6–16.3, 15.7 \pm 0.5
	Tarsus	37.6–41.1, 38.7 \pm 1.0	36.3–39.3, 38.4 \pm 1.3
Female	Wing	116.2–128.9, 121.7 \pm 7.6	112.8–117.3, 115.0 \pm 3.2
	Bill	16.5–18.0, 17.3 \pm 0.5	15.3–15.6, 15.4 \pm 0.2
	Tarsus	36.1–37.9, 37.2 \pm 0.8	35.9–38.4, 37.1 \pm 1.8

been to Pregill et al. (1994), who summarized results from excavations of fossil localities including St. Eustatius, St. Kitts, Barbuda, Antigua, and Montserrat. Although bones of Scaly-breasted Thrasher (*Margarops fuscus*), Pearly-eyed Thrasher (*M. fuscatus*), and Brown Trembler (*Cinclocerthia ruficauda*) have been found in cultural sites and may have been eaten, bones of Red-legged Thrush have not been found on any of those islands.

The deposits on Antigua, although not archeological in nature, span the period of 4,300 to 2,500 years before present (Pregill et al. 1988), overlapping the period of human occupation. All the other Lesser Antillean bird remains would have been of similar age or more recent. Although absence of evidence is not evidence of absence, the little available data suggest that if there were natural extinctions of Red-legged Thrush on the islands between Puerto Rico and Dominica, these may have involved processes that took place more than 2,000 or 3,000 years ago.

DISPERSAL ABILITY OF RED-LEGGED THRUSHES

The most distant outliers of the Red-legged Thrush (Fig. 2) suggest that the species is fully capable of island-hopping from Puerto Rico to Dominica, where the greatest distance between islands is the ~140 km from Virgin Gorda to Anguilla. An endemic subspecies, *T. p. coryi*, is restricted to the island of Cayman Brac, which

is 145 km south of the Jardines de la Reina cays of southern Cuba, where an enigmatic specimen of Red-legged Thrush was collected in 1930 on Cayo Caballones (Buden and Olson 1989). This specimen resembles the birds from Cayman Brac, and both appear similar to intergrades between *T. p. rubripes* and *T. p. schistaceus*, although the zone of intergradation between these forms is now considerably to the east of Cayo Caballones or Cayman Brac (Buden and Olson 1989).

Of even greater interest, from the standpoint of dispersal, was the occurrence of Red-legged Thrushes on the Swan Islands of Honduras, 463 km south of the Isle of Pines, Cuba. There, C. H. Townsend collected 10 specimens in 1886 that were described as a new subspecies, *Mimocichla rubripes eremita* (Ridgway 1905). No trace of the species could be found in the Swan Islands in 1908, despite intensive searching (Lowe 1909, 1911), and it has not been seen since. Lowe (1909, 1911) questioned the validity of the subspecies, and the name *eremita* is now considered a synonym of *T. p. rubripes*, a treatment that was confirmed by examination of the specimens. The Swan Island population seems to have arisen from a chance colonization by several individuals from western Cuba that gave rise to a small population that may have become extinct through natural causes. In any case, the facts argue for the ability of the species to cross long distances over water to colonize remote islands.

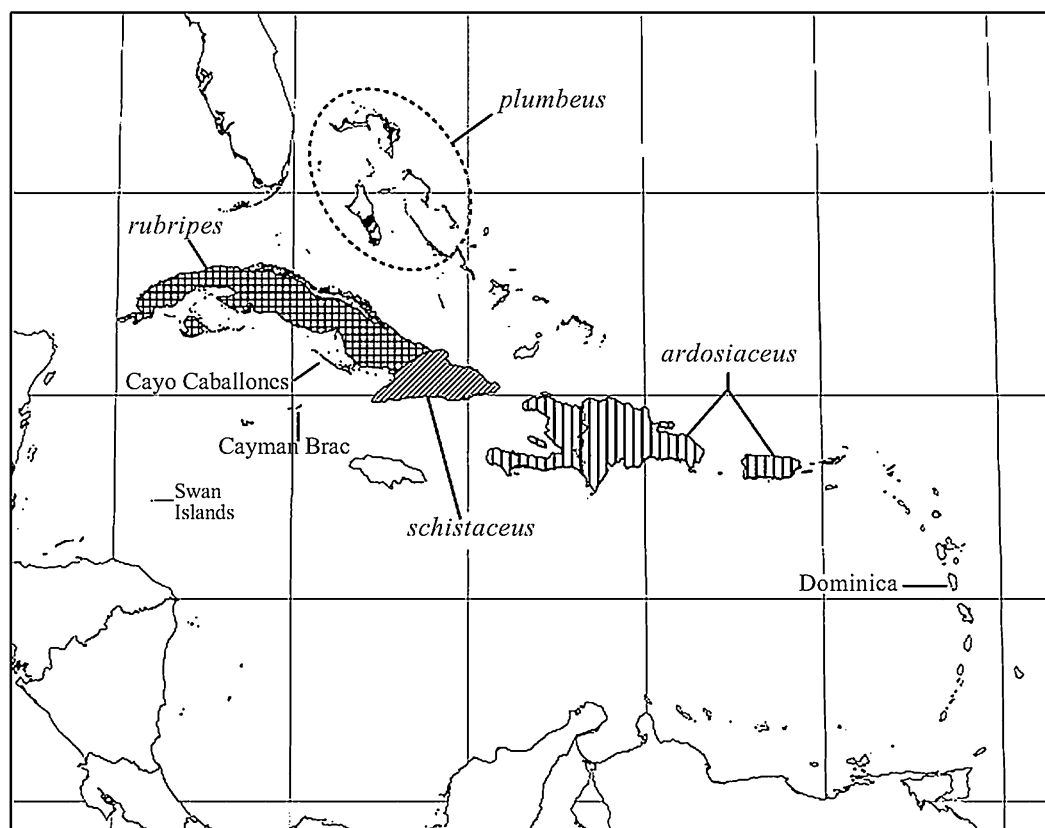


FIG. 2. Map showing the distribution of subspecies of Red-legged Thrush in the West Indies. The outlying populations of Cayman Brac and Dominica are regarded as valid subspecies (*T. p. coryi* and *T. p. albiventris*, respectively). The extinct population of the Swan Islands was identical with *T. p. rubripes*, and the specimen from Cayo Caballones, Cuba, is of uncertain identity.

OLSON'S CASE

The Lesser Antilles were first settled from South America by pre-ceramic people about 3,000–4,000 years ago. Between 1,500 and 2,000 years ago, the economy and settlement patterns changed and populations of ceramic-using horticultural people expanded; this is when trade between islands of the Greater and Lesser Antilles presumably first occurred (Wilson 2006), which greatly restricts the period during which the Red-legged Thrush could have been introduced to Dominica before differentiating into a well-marked subspecies. That time-frame makes the scenario unlikely.

It also strains credulity that a canoe load of people carrying cages with sufficient numbers of both sexes of thrush to establish a population would set out from Puerto Rico and travel >500 km, bypassing island after island, to release the birds on Dominica. Ricklefs and Bermingham (2008) suggest that thrush-sized passerines were eaten by Indians and also that Red-legged Thrushes were valued for their song. Although, before the arrival of Europeans, humans in the West Indies reared and transported numerous species of birds and mammals for food (Olson and Maíz López 2008), there is no evidence that any of these were released into the wild and survived. That Dominican Indians were aesthetically deprived of bird song is not likely, given that the island is one of the four in the Lesser Antilles that is home to the Rufous-throated Solitaire, a renowned songster.

Although morphological changes in vertebrates over short periods of time have been documented as visible examples of evolution (see references cited by Ricklefs below), these differences tend to manifest themselves as partially overlapping statistical clouds. For my part, I do not think that differences in size, proportions, coloration, and plumage pattern, such as seen between the Puerto Rican and Dominican thrushes, could have taken place in the two or three millennia during which humans might have moved birds from one island to the other.

The evidence that Ricklefs and Bermingham (2008) advanced for their hypothesis involves a “nano-smidgen” of a genome. Data from mtDNA data alone have been regarded as inadequate for understanding evolutionary history or for determining the validity, or lack thereof, of avian subspecies (Omland et al. 2006, K. Omland unpubl. data). For such a hypothesis to be viable, there should be additional molecular evidence.

Clearly, Red-legged Thrushes are capable of long-distance, overwater dispersal. Its occurrence on Dominica fits a pattern of island-hopping dispersal and multiple subsequent extinctions seen in many other species of birds in the Lesser Antilles. Its morphological differentiation is too great to be likely to have evolved in the 2,000 years or less when trade flourished between Puerto Rico and the Lesser Antilles, and the scenario of humans transporting thrushes directly from Puerto Rico as far as Dominica is implausible. Therefore, the occurrence of Red-legged Thrushes on Dominica, and on no other island between there and Puerto Rico, is almost certainly a result of natural processes.

RICKLEFS AND BERMINGHAM'S CASE

In his initial response to our study, Olson suggested that our interpretation of recent colonization by, or introduction of, Red-legged Thrushes to Dominica is incorrect because (1) “disjunct patterns

of distribution of birds in the Lesser Antilles are the rule rather than the exception” and (2) the species’ “morphological differentiation is too great to be likely to have evolved in the 2,000 years or less when trade flourished between Puerto Rico and the Lesser Antilles...”

We agree with Olson that disjunct distributions of such species as Adelaide's Warbler, Forest Thrush, Rufous-throated Solitaire, and *Icterus* spp. have resulted from the extinction of populations on intervening islands. Mitochondrial sequence divergence indicates, however, that these populations have been separated by long periods of independent evolution (Lovette et al. 1998, 1999; Miller et al. 2007; E. Bermingham and R. Ricklefs unpubl. data). Extinction is more likely on smaller islands, and this has produced a significant interaction between taxon age and island size in species–area relationships (Ricklefs and Bermingham 2004). Nevertheless, with the exception of the Red-legged Thrush, we have found no case of disjunction in any species lacking significant genetic separation between island populations.

Olson also infers, from its presence in such remote locations as the Cayman Islands and the Swan Islands, that the Red-legged Thrush is an adept island-hopper. Clearly, the species dispersed widely throughout the Greater Antilles in the past, as did Adelaide's Warbler and *Icterus* spp. in the Lesser Antilles. However, our phylogeographic survey suggests that present-day populations on Puerto Rico, Hispaniola, Cuba, the Cayman Islands, and the northern Bahama Islands do not presently exchange individuals, in spite of large population sizes and relatively short distances between islands. A striking conclusion from our phylogeographic work in the Lesser Antilles is that colonization appears to be episodic and to occur in relatively brief phases of widespread dispersal. This inference comes from the observation of both undifferentiated island populations distributed widely throughout the West Indies and deeper polytomies in the phylogenetic relationships of island populations of presently differentiated species (Ricklefs and Bermingham 2001).

Olson's second point was that populations could not become differentiated morphologically in the time since the earliest possible human transport of Red-legged Thrushes between Puerto Rico and Dominica. Although the measurements in Table 1 suggest considerable morphological (including plumage) differentiation of the Puerto Rican and Dominican populations, these differences are within the range of evolutionary changes in populations over brief periods observed in introduced species (Johnston and Selander 1964, 1971; Badyaev et al. 2000; Clegg et al. 2002; Price et al. 2008), after the introduction of competing species (Grant and Grant 2006), or in response to anthropogenic changes in the environment (Schmidt and Jensen 2003, Hendry et al. 2006).

Although we cannot reconstruct the history of a species with certainty, we believe that human introduction of the Red-legged Thrush to Dominica is plausible and certainly cannot be discounted. Olson may be right in concluding that Red-legged Thrushes occupied all the intervening islands between Dominica and Puerto Rico and that these populations disappeared before human occupation of the islands, but no other species in the West Indies shows such a pattern of distribution. We cannot know for certain whether pre-Columbian natives or early European colonists transported Red-legged Thrushes between Puerto Rico and Dominica, but trade was extensive and humans have distributed

other species widely throughout the West Indies, not to mention elsewhere in the world.

From our perspective, the important point is not the details of the distribution of the Red-legged Thrush, but rather the principle that gaps in distributions can be interpreted as extinction events. Within the Lesser Antilles, such gaps occur only within old, highly differentiated populations. Long-distance dispersal, or extinction of island populations in a recently spread species such as the Red-legged Thrush, would constitute a counter-example that might be explained as an artifact of human activity.

Acknowledgments.—S. Claramunt supplied measurements and photographs of Red-legged Thrushes in the Louisiana State Museum of Natural Science (LSU). S.L.O. thanks J. R. Jehl, K. E. Omland, and D. W. Steadman for information and comments on his original manuscript.—STORRS L. OLSON, *Division of Birds, Department of Vertebrate Zoology, National Museum of Natural History, P.O. Box 37012, Smithsonian Institution, Washington, D.C. 20013, USA (e-mail: olsons@si.edu)*; and ROBERT E. RICKLEFS, *Department of Biology, University of Missouri-St. Louis, 8001 Natural Bridge Road, St. Louis, Missouri 63121, USA (e-mail: ricklefs@umsl.edu)*.

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Received 10 December 2008, accepted 19 January 2009