



LIKELY HUMAN INTRODUCTION OF THE RED-LEGGED THRUSH (*TURDUS PLUMBEUS*) TO DOMINICA, WEST INDIES

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ABSTRACT.—Recent avian colonists to the West Indies have expanded their ranges through the archipelago in stepping-stone fashion, occupying virtually all of the available islands with suitable habitat. Consequently, gaps in the distributions of colonists can be interpreted as extinction events. One exception to this pattern is the weakly differentiated population of the Red-legged Thrush (*Turdus plumbeus*) on Dominica, removed by 600 km and many suitable islands from the nearest conspecific population. Mitochondrial DNA sequences show that the Dominican population is practically indistinguishable genetically from that of Puerto Rico. Large genetic distances among other adjacent island populations emphasize the recent derivation of the Dominican population from Puerto Rico, likely the result of human introduction. Received 20 March 2006, accepted 25 May 2007.

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Probable Introducción de *Turdus plumbeus* por Humanos a Dominica, Antillas Occidentales

RESUMEN.—Las aves que han colonizado recientemente las Antillas Occidentales se han expandido a través del archipiélago “saltando” de isla en isla, ocupando prácticamente todas las islas disponibles con hábitat adecuado. Consecuentemente, los vacíos en la distribución de las especies colonizadoras pueden ser interpretados como eventos de extinción. Una excepción a este patrón es la población de *Turdus plumbeus* escasamente diferenciada que se encuentra en Dominica, la cual está separada por 600 km y por varias islas con hábitat adecuado de la población coespecífica más cercana. Las secuencias de ADN mitocondrial muestran que la población de Dominica es prácticamente indistinguible genéticamente de la población de Puerto Rico. Distancias genéticas grandes entre otras poblaciones en islas adyacentes enfatizan la derivación reciente de la población de Dominica desde Puerto Rico, probablemente como resultado de introducción por parte de humanos.

RECENT NATURAL EXPANSIONS of such species as the Bare-eyed Robin (*Turdus nudigenis*) and Shiny Cowbird (*Molothrus bonariensis*) throughout the West Indies (Bond 1956), as well as molecular phylogeographic analyses of other widespread species, indicate that colonization by birds occurs primarily in rapid, stepping-stone fashion. Accordingly, gaps in species distributions can be attributed to the disappearance of individual island populations, providing a unique window on the process of extinction (Ricklefs and Bermingham 2001). A striking exception to the pattern of island-by-island colonization among birds of the West Indies is the disjunct, but weakly differentiated, population of the Red-legged Thrush (*T. plumbeus*) on the island of Dominica in the Lesser Antilles (Bond 1956, Raffaele et al. 1998). The nearest other

population of *T. plumbeus* occurs on Puerto Rico in the Greater Antilles, ~600 km to the northwest, beyond several sizable islands in the northern Lesser Antilles (e.g., Guadeloupe, Montserrat, St. Kitts–Nevis) that include habitat suitable for the species. The population on Dominica could have originated either from stepping-stone colonization followed by extinction of intervening island populations or from long-distance dispersal, whether natural or assisted by humans. If humans played a role, the Red-legged Thrush population on Dominica would have had insufficient time to diverge genetically from its source. Mitochondrial-DNA sequence analysis indicates recent derivation of this population from Puerto Rico, which suggests that native Caribbean islanders or early European settlers may have introduced these attractive songbirds.

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STUDY SYSTEM AND METHODS

The Red-legged Thrush is a medium-sized (~75 g) forest-dwelling songbird that occurs throughout the Greater Antilles (Cuba, Hispaniola, Cayman Brac, Puerto Rico), except Jamaica, and on some of the northern Bahama Islands, in addition to the single, disjunct population on Dominica (Fig. 1). P. L. Sclater originally described the Dominican population in 1889 as *Mimocichla ardesiaca albiventris*, but the early nomenclature is confusing. Ridgway (1907) applied the name *Mimocichla ardosiacea albiventris*, which he distinguished from *M. a. ardosiacea* of Hispaniola, *M. a. portoricensis* of Puerto Rico, and *M. rubripes* of the Bahamas, Cuba, and the Cayman Islands. Bond (1956) placed all the populations in *M. plumbea* (see Johnston 1969) but retained the subspecies *albiventris* for the Dominican population. *Mimocichla* is now generally placed within *Turdus*, and *T. plumbeus* is sometimes considered two separate species, the Western Red-legged Thrush (*T. plumbeus*; Bahamas, Cuba, Cayman Brac) and Eastern Red-legged Thrush (*T. ardosiaceus*; from Hispaniola to

the east) (Sibley and Monroe 1990, American Ornithologists' Union 1998).

Using blood and tissue samples obtained nondestructively, we sequenced 842 base pairs (bp) of the mitochondrial ATPase 6 and ATPase 8 genes from 44 individuals representing the Greater Antilles (Cuba: $n = 2$; Cayman Brac: $n = 2$; Hispaniola: $n = 9$; Puerto Rico: $n = 22$; New Providence, Bahamas ($n = 2$); and Dominica ($n = 7$). Dominican birds were captured on 2 August 1991 at Pointe Ronde, on the northwest coast. Puerto Rican birds were captured at the Guanica and Maricao forests in the western part of the island and at El Yunque in the northeast, on various visits between 1993 and 2002. Blood samples were preserved in either Queen's lysis buffer or PureGene lysis buffer. DNA was extracted from each sample following the protocols of Seutin et al. (1991, 1993) or the PureGene manual. Polymerase chain reaction (PCR) amplification and sequencing followed protocols described by Lovette et al. (1998). GenBank sequence numbers are AY115254–AY115257 and DQ100575–DQ100612. A haplotype network was produced by hand.

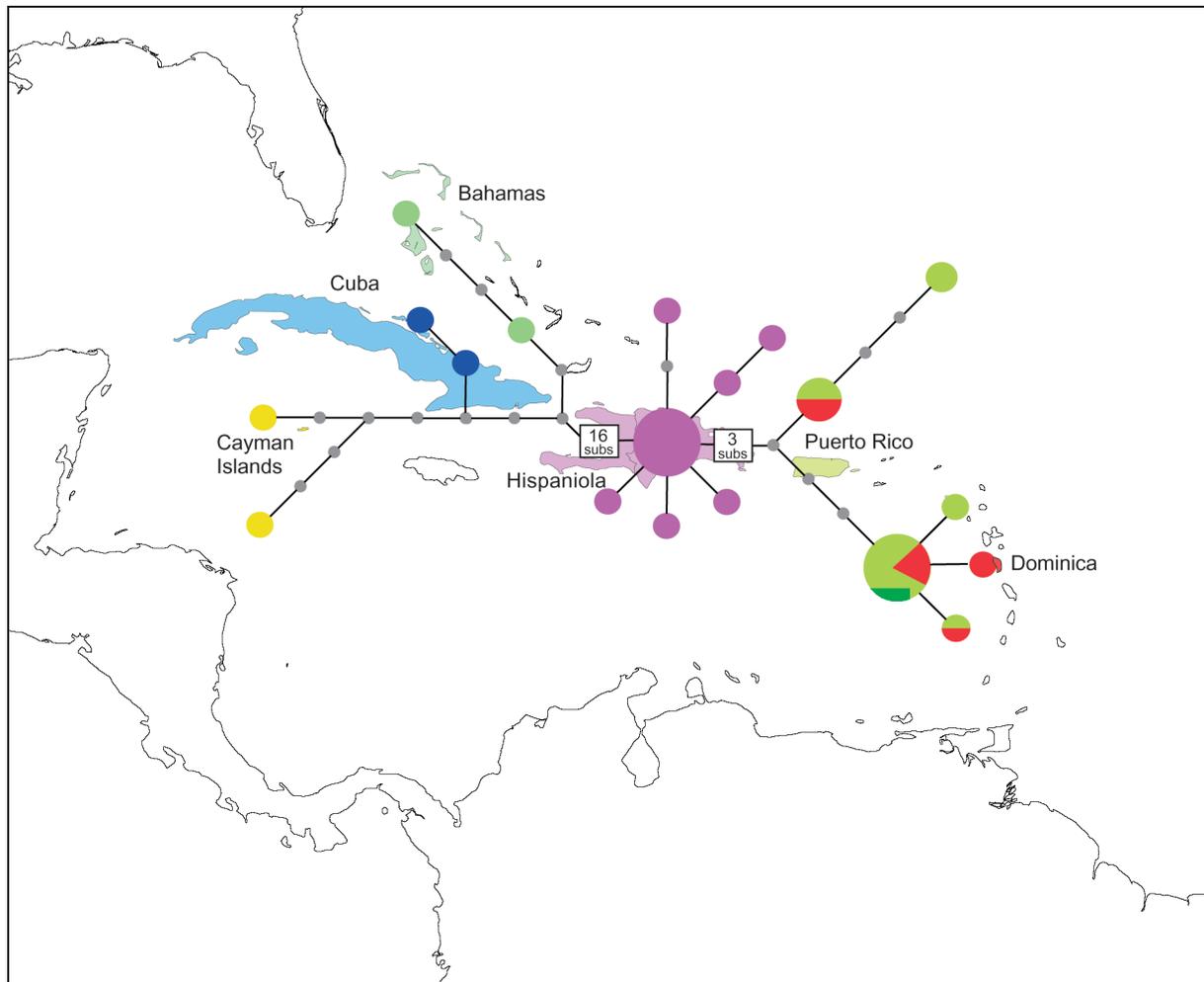


FIG. 1. Distribution of the Red-legged Thrush in the West Indies, overlaid with a haplotype network based on the mitochondrial ATPase 6 and 8 genes. Each line segment in the network represents a single nucleotide substitution. Solid gray symbols represent inferred but unsampled haplotypes. In Puerto Rico, haplotypes showed no geographical structure.

RESULTS AND DISCUSSION

The seven Dominican birds represent four haplotypes that are either identical to or, in one case, a single nucleotide substitution different from, those of the Puerto Rican birds (Fig. 1 and Table 1). Thus, the arrival of the Red-legged Thrush on Dominica is recent—plausibly within the 6,000 years of human occupation of the West Indies (Wilson 1997).

Although the populations of Red-legged Thrush on Dominica and Puerto Rico are practically undifferentiated genetically, change in mitochondrial DNA (mtDNA) is slow enough that absence of change can represent an extensive period of time. Assuming an average nucleotide-substitution rate for avian mtDNA of about 10^{-8} per nucleotide per year (Avice 1994, Lovette 2004), the average time before a genetic change occurs between populations in 842 bp of the cytochrome-*b* gene would be ~120,000 years, considerably beyond the period of human presence in the West Indies. Ho et al. (2005) have argued that the short-term substitution rate for avian mtDNA is $\sim 4 \times$ this level, owing to deleterious amino-acid substitutions (nonsynonymous mutations) lacking sufficient time to be eliminated by selection, which would bring the expected period before such a genetic change occurred down to ~30,000 years. Thus, prehuman, natural long-distance colonization cannot be ruled out.

Another issue is the unique mtDNA haplotype (E; Table 1) on Dominica, which is one mutation step from the common haplotype (C) on Puerto Rico. This mutation (G→C) occurred in the first position of codon 203 of the ATPase 6 gene, resulting in a glutamic acid→glycine substitution. It may represent an unsampled haplotype from Puerto Rico, or it may have arisen locally after the population of Red-legged Thrush became established. In the latter case, the seven Dominican individuals represent independent mitochondrial lineages extending back in time some fraction of the period since colonization. At the higher rate of mutation suggested by Ho et al. (2005), the probability of at least one mutation among seven lineages is 0.35 for an average lineage age of 200 years, and 0.67 for 500 years. Accordingly, a mutation within a reasonable period for human introduction of the species is a distinct possibility.

Weighing against natural long-distance dispersal are (1) the genetic isolation of populations of Red-legged Thrush on adjacent islands in the Greater Antilles (Cuba-Cayman Brac-Hispaniola-

Puerto Rico; Fig. 1) and the absence of the species from Jamaica, which indicates the lack of recent gene flow over short distances; (2) the dearth of records of conspicuous and easily identified vagrant Red-legged Thrushes outside their breeding range (Bond 1956, and supplements); and (3) inference from the mtDNA haplotype network in Fig. 1 that the founder population on Dominica included at least three females, assuming that each haplotype shared with Puerto Rico was derived from there. The species is not known to flock.

Weighing against stepping-stone dispersal followed by extinction of intervening populations is the absence of Holocene fossils of the Red-legged Thrush from the northern Lesser Antilles, including 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). These deposits nonetheless contain bones of thrashers (*Margarops* spp. and *Cin-clocerthia* spp.) and the thrush *Cichlherminia lhermineri*, which are extant species similar in size and habitat to *T. plumbeus* and likely were eaten by Saladoid (500 B.C. to 400 A.D.) peoples of the northern Lesser Antilles. Fossils of other species of *Turdus* are known from Jamaica (Pregill et al. 1991), and *T. plumbeus* is known from Bahamian fossil localities on New Providence (Olson and Hilgartner 1982), where there is an extant population, and from Little Exuma (Olson and Hilgartner 1982) and Middle Caicos (D. W. Steadman pers. comm.), where the species no longer exists. Some of these fossils were recovered from cultural sites, which raises the possibility that they were transported to those sites from other islands, or that native West Indians hunted local populations to extinction. The Red-legged Thrush is sufficiently widespread and common throughout its present range that recent natural extinction is unlikely (Ricklefs and Cox 1972).

Pre-Columbian cultural artifacts in the West Indies indicate extensive trade between islands (Watters 1997). Fossil remains of animals such as Hispaniolan rodents (*Isolobodon* spp.) and Puerto Rican flightless rails (*Nesotrochis* spp.) in cultural deposits outside their native distributions document human transportation of endemic animals among islands (Olson 1982). These remains indicate that Amerindians apparently practiced some form of animal husbandry as well (Olson and Pregill 1982, Reitz and Wing 1999). A large South American rodent, the Agouti (*Dasyprocta leporina*), was distributed among most of the islands before the arrival of Europeans, evidently transported by Amerindians as a source of food (Wing 1989). The Red-legged Thrush is an attractive bird with a melodious song, well suited to being kept in captivity and transported between islands; it may also have been eaten (Reis and Steadman 1999). Modern Carib Indians of northern South America, who gave rise to the Saladoid colonization of the West Indies beginning ~2,500 years ago (Rouse 1992), keep many species of birds, often hand-rearing the young to tame them (G. Bourne pers. comm.). Columbus mentioned “wild birds tamed in their houses” seen in villages on Cuba during his first voyage (Morison 1963:84).

The example of the Red-legged Thrush emphasizes that human transportation of animals has not necessarily been limited to food resources. Certainly, modern Western cultures have actively transported familiar garden birds to the far corners of the earth (e.g., Long 1981, Duncan 1997). Pre-Columbian Americans introduced species far from their native ranges in association with the

TABLE 1. Haplotypes of individual Red-legged Thrushes sampled from Puerto Rico and Dominica, following the network in Figure 1 from top to bottom.

Haplotype	Individuals from Puerto Rico (<i>n</i>)	Individuals from Dominica (<i>n</i>)
A	3	
B	2	2
C	14	3
D	2	
E		1
F	1	1

Note: Haplotype E is one step from haplotype C and may represent a Puerto Rican haplotype that was not sampled or a new haplotype on Dominica.

feather trade (Haemig 1978, 1979). Thus, although it is well established that humans caused the extinction of many island populations of birds and mammals, cases of disjunct or other unusual distributions lacking genetic differentiation between populations may also include intentional or inadvertent introductions by non-European or colonial European humans. If the natural spread of populations through island groups occurs in a stepping-stone fashion—as observed for most birds in the West Indies (Ricklefs and Cox 1972, Ricklefs and Bermingham 2001) and, for example, *Drosophila* in Hawaii (DeSalle 1995)—then gaps in distributions provide evidence for the extirpation of intervening populations. Combined with ecological and molecular phylogenetic analyses, distributional gaps provide a tool for studying the causes of extinction. However, a case like that of the Red-legged Thrush, which provides evidence of human introductions that may predate the period of scientific discovery, should make us cautious when interpreting present-day distributions of many animals and plants (e.g., Vences et al. 2004, Kasapidis et al. 2005).

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