

Genetic Ancestry and Indigenous Heritage in a Native American Descendant Community in Bermuda

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ABSTRACT Discovered in the early 16th century by European colonists, Bermuda is an isolated set of islands located in the mid-Atlantic. Shortly after its discovery, Bermuda became the first English colony to forcibly import its labor by trafficking in enslaved Africans, white ethnic minorities, and indigenous Americans. Oral traditions circulating today among contemporary tribes from the northeastern United States recount these same events, while, in Bermuda, St. David's Islanders consider their histories to be linked to a complex Native American, European, and African past. To investigate the influence of historical events on biological ancestry and

native cultural identity, we analyzed genetic variation in 111 members of Bermuda's self-proclaimed St. David's Island Native Community. Our results reveal that the majority of mitochondrial DNA (mtDNA) and Y-chromosome haplotypes are of African and West Eurasian origin. However, unlike other English-speaking New World colonies, most African mtDNA haplotypes appear to derive from central and southeast Africa, reflecting the extent of maritime activities in the region. In light of genealogical and oral historical data from the St. David's community, the low frequency of Native American mtDNA and NRY lineages may reflect the influence of

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genetic drift, the demographic impact of European colonization, and historical admixture with persons of non-native backgrounds, which began with the settlement of the islands. By comparing the genetic data with genea-

logical and historical information, we are able to reconstruct the complex history of this Bermudian community, which is unique among New World populations. *Am J Phys Anthropol* 000:000–000, 2011. © 2011 Wiley-Liss, Inc.

Situated nearly 650 miles east of Cape Hatteras, North Carolina, Bermuda is truly a lone outpost in the middle of the Atlantic Ocean (Fig. 1). Neither North American nor Caribbean, this former British colony has escaped the attention of most anthropologists and colonial historians, due, perhaps, to its small size (only 22 square miles), remote location, or lack of prehistoric human presence. Nevertheless, in the age when people, information, and trade moved “only as fast as the wind and waves allowed,” (Jarvis 2002:587), Bermuda lay at the crossroads of the new Atlantic world. Indeed, historians note that one out of every ten sailing vessels traveling between the Caribbean and Europe passed within 50 miles of the islands (Jarvis, 2002, 2010).

Bermuda was instrumental to the role of English colonization and expansion in the Atlantic, including the trans-Atlantic slave trade. Founded within five years of the British Crown’s colonization of Jamestown in Virginia, it was settled before most of Anglo America was even conceived (Jarvis, 2010). In fact, Bermuda was completely uninhabited until the Virginia-bound Sea Venture crashed upon its shores in 1609. During the nine months required to repair the vessel, the English discovered that the island, long thought by the Spanish and Portuguese to be haunted (they referred to it as “the Isle of Devils”), was a fertile paradise with great colonial potential. Its unintended discovery led the Virginia Company to dispatch hundreds of English settlers to populate the island over the next several years (Woodward, 2009).

In 1615, control of Bermuda was given over to the British Crown and a new charter was granted to the Somers Island Company, a joint stock venture that maintained the colony for the next 69 years. By 1625, most of the island was under cultivation. The presence of an official militia to guard the coast, a ring of forts, nine mostly Puritan parishes, an elected assembly to pass laws, private land ownership, and an exportable commodity (tobacco) all attest to an active and highly functional New World Atlantic stronghold early in England’s colonial endeavors (Rothwell, 1989; Jarvis, 2002, 2010).

The islands’ first settlers were of widely varied backgrounds. There were prosperous English planters, as well as master craftsmen. There were indentured laborers from the British Isles consisting primarily of boys and young men, sent as apprentices or servants to the highest bidders, as well as young women destined to be wives of the single men there (Lefroy, 1981). And, there were the least desirable recruits—those plucked fresh from London’s slums and jails—who, at times, worked but mostly just taxed the patience of early governors (Smith, 1976; Bernhard, 1999).

Persons of color came to Bermuda even before the colony took shape. In 1603, “[o]ne Ventrullia, a Negroe” crew member aboard a Spanish sailing vessel, went ashore in Bermuda (Wilkinson, 1958: 23), and, according to Captain John Smith, two “indians from Virginia” were on board the Sea Venture when it crashed in 1609 (Smith, [1624] 1966). With the arrival of “one Indian and a Negroe (the first thes Ilands had ever had)” on the Edwin in August 1616, Bermuda became the first Eng-

lish colony to “import” its non-white labor, a full three years before Africans “arrived” in Virginia (Lefroy, 1981). These early arrivals were likely a West Indian Carib and an African brought to the Caribbean by the Dutch, the first to import West African labor to the area, or the British, who took over the slave trade in this region of the Atlantic (Craven, 1937; Curtin, 1969; Smedley, 1999).

By 1617, the number of Africans in the colony must have been on the rise, as Bermudian Robert Rich makes reference to the island’s “good store of [blacks]” (Ives, 1984: 25). Indeed, numerous historical sources indicate that, during the first half of the 17th century, the black workforce continued to trickle into Bermuda on English vessels island hopping in the Caribbean in search of specialized labor, and as part of cargo looted from Spanish, Dutch, and French vessels by English privateers (Colonial Records of Bermuda, 1616–1713, Vol. I: 107–113; Bernhard, 1999) (Fig. 2). There is also evidence to suggest that blacks may have come on English vessels directly from Africa to Bermuda (Sainsbury, 1860), although shipping logs are vague on this point.

Over the next several decades, “Indians” began arriving in Bermuda *en masse*, as either captives from British raids on nearby Spanish, Portuguese, and Dutch colonies, or as prisoners captured in wars with Native American tribes in New England. For example, in 1644–1645, a privateer named Captain Jackson, arrived in Bermuda from Jamaica with a group of blacks and Indians that he had taken from the Spanish (Lefroy, 1981). Around the same time, Massachusetts governor John Winthrop wrote about Pequot Indian captives who were sent to Bermuda to be sold as slaves, many of whom were bought by colonists on Bermuda’s St. David’s Island (Winthrop, 1908). There was clearly concern over the increase in the non-white population as evidenced by the enactment of “[A]n Act to restrayne the insolencies of [Bermudian] Negroes,” the first English law to specifically address non-white labor (Colonial Records of Bermuda, 1616–1713, Vol. 1: n.p.).

Ultimately, Bermuda proved to be an agricultural failure, as limited land, shallow soil, and frequent droughts made tobacco cultivation unprofitable. The stagnation in food production led to a much lower demand for labor, prompting the passage of a number of laws intended to curb the growth of the non-white population, including limitations on slave imports and taxation on slave owners (Lefroy, 1981). In spite of these measures, the increasing non-white population during the late 17th and early 18th centuries proved so troubling to British land owners that laws passed in 1705, and, again, in 1730 gave free “Negroes, Indians and Mulattoes [all persons of mixed white and non-white ancestry]” the choice of leaving the island or face risk of (re)enslavement. In 1761, following an unsuccessful slave conspiracy, and continually until Emancipation in 1834, the Bermuda legislature passed laws designed to contain growth of the non-white population (Journals of the House of Assembly, Bermuda, 1759–1779, Vol. II).

ST. DAVID'S ISLAND

St. David's Island was one of the first of the six principal islands in the Bermuda chain to be settled. It is roughly one square mile in size, encompassing an area of approximately 650 acres. While easily accessible by ship, the island was geographically isolated from the rest of Bermuda until finally connected to the mainland by a bridge in 1934. Nestled between the colony's 17th century harbors (Town Harbor to the north and Castle Harbour to the south), St. David's was at once geographically remote from the mainland and at the center of all things Bermudian.

Several historians also contend that St. David's was ground zero for the arrival of hundreds of indigenous North Americans who were enslaved in colonial New England, and then brought to Bermuda as labor (Smith, 1976; Packwood, 1975; Bernhard, 1999). During the early part of the 17th century, European colonists from New England were becoming embroiled in bloody conflicts with their indigenous neighbors. Ultimately, colonial victories resulted in not only the control of indigenous lands, but also the capture and enslavement of numerous native individuals. Archival sources indicate that many of those captured and enslaved were brought to St. David's Island, following major conflicts with the Pequot Nation (1634–1638) and the Wampanoag Confederacy (1675–1676) (Colonial Records of Bermuda, 1616–1713, Vol. II; Winthrop, 1908; Lauber, 1913; Van Wyck, 1937; Boissevain, 1981;

Ellis and Morris, [1906] 2001; Van Rensselaer, [1909] 2007). By the mid-17th century, Scottish and Irish prisoners from the English Civil War joined black and Indian slaves on St. David's (Smith, 1976: 25). Ostracized by the other white inhabitants, these individuals were relegated to an inferior position shared with their black and Indian compatriots, with whom they freely intermingled (Smith, 1976; Rothwell, 1986).

The extent of this interaction led to a high degree of admixture on St. David's, as numerous historical records reference white females and women of color giving birth to children of mixed ancestry (Colonial Records of Bermuda, 1616–1713; Sainsbury, 1860; Ogilvy, 1883; Strode, 1932; Lefroy, 1981). Historians explain this phenomenon in two different ways. According to one scholar, the often volatile mix of Indian tribes on St. David's prompted local slavers to import Carib females in the hopes of alleviating tensions between these groups. However, these men allegedly preferred Bermuda's enslaved African females, resulting in children with indigenous fathers and African mothers (Rothwell, 1989). By contrast, another historian contends that most of the "natives" in Bermuda during the mid 17th century were females, making it unlikely that these women would have found native partners (Bernard, 1999). Thus, under this scenario, the admixed population would consist of persons with Amerindian female and African or European male parentage. In either case, the resulting increase in the admixed population was apparently alarming to Bermuda authorities of

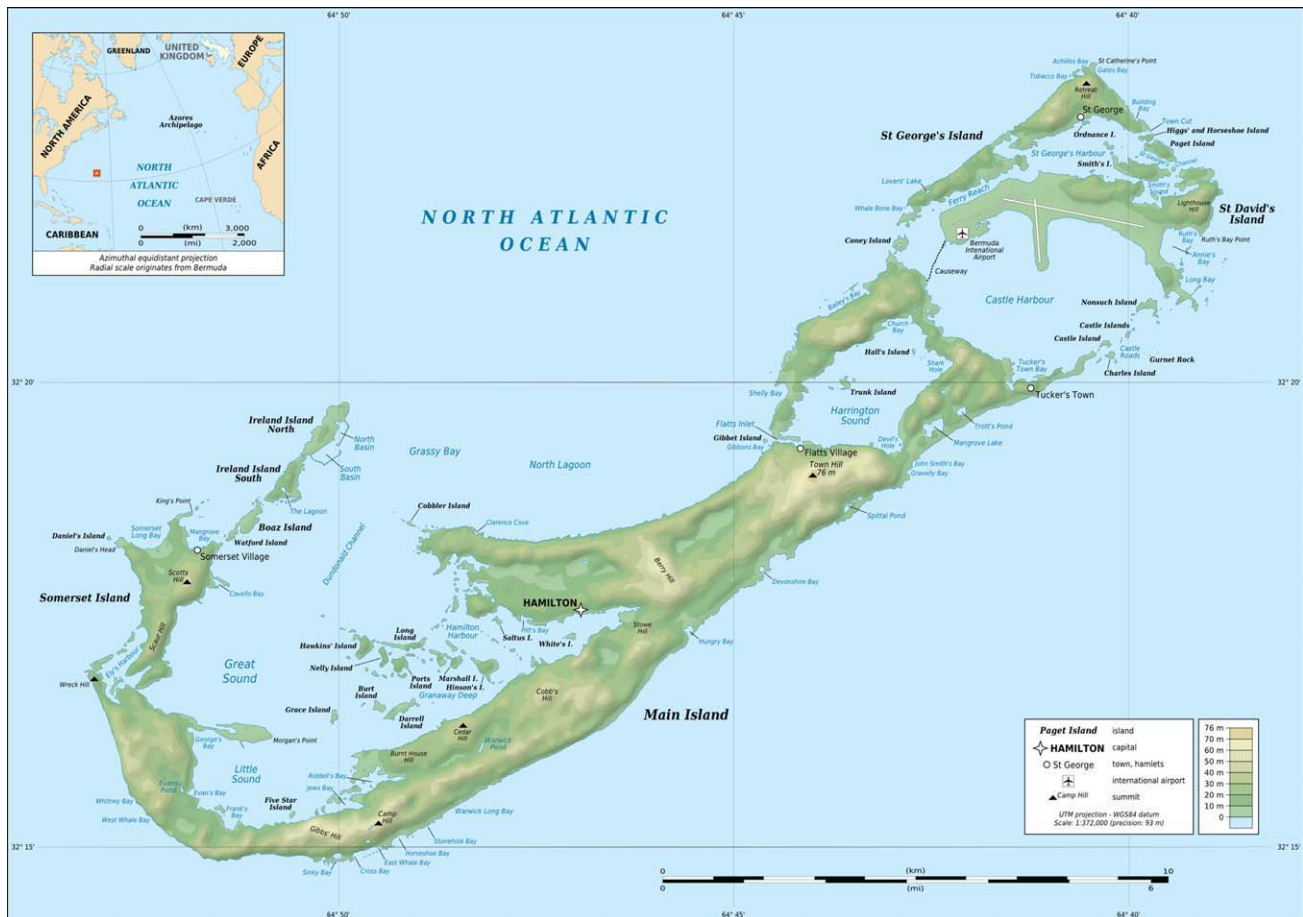


Fig. 1. A topographic map of Bermuda. Used courtesy of Eric Gaba, Wikimedia Commons, 2011.

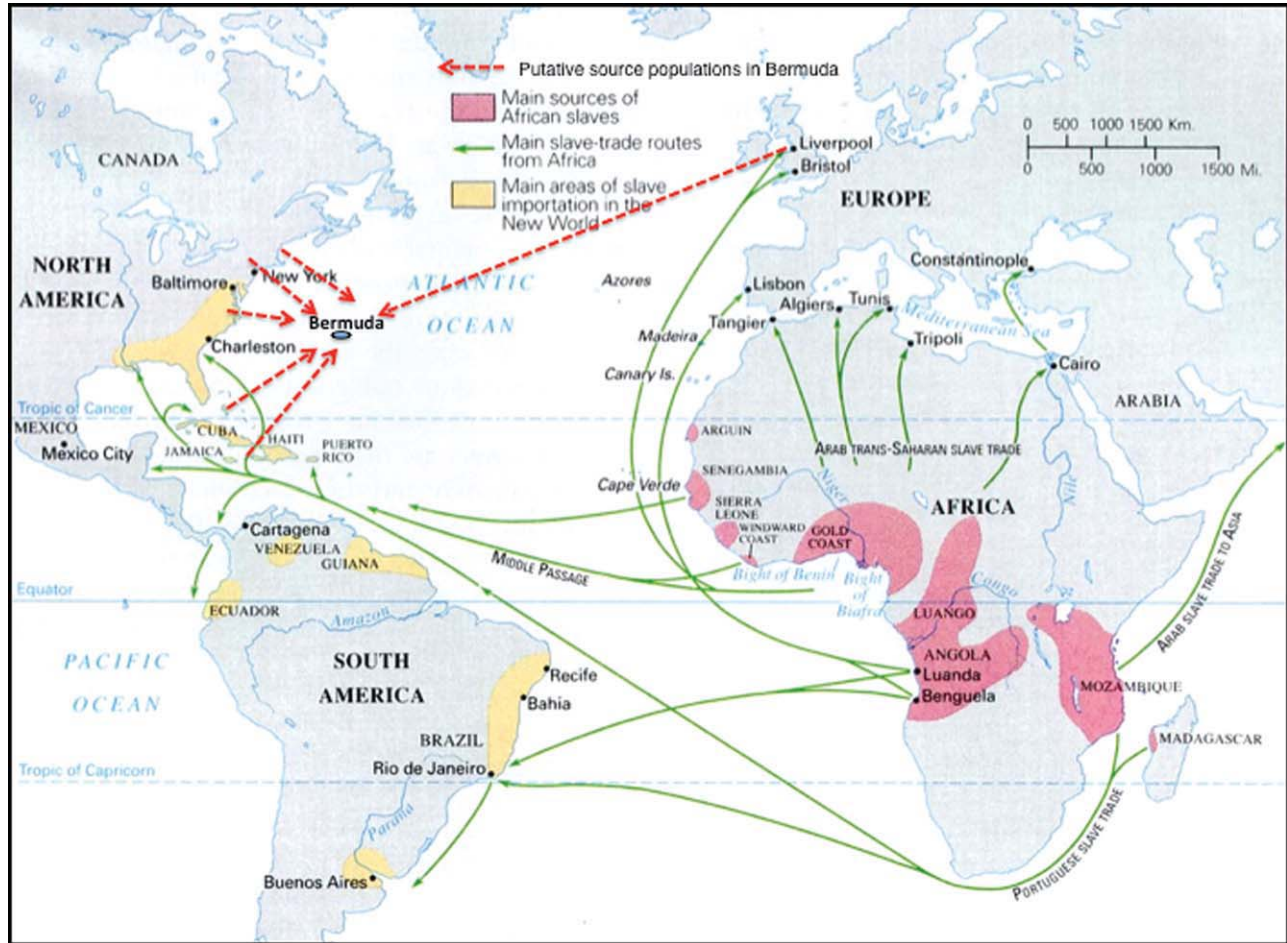


Fig. 2. Map of the Atlantic region showing connections between Bermuda and other regions through the trans-Atlantic slave trade.

the time as, in 1663, the General Assembly enacted new laws designed to control miscegenation (Lefroy, 1981).

By the 18th century, Portuguese immigrants began arriving in Bermuda, having come from the impoverished colonial outposts of Portugal's maritime empire, Madeira and the Azores, to work as shipbuilders and seafarers. These immigrants quickly established themselves as skilled workers, and are credited with the successful revitalization of Bermuda's agricultural industry. Bermuda's liberal immigration policies during this time allowed for a temporary open-door system between Bermuda and the Portuguese colonies. By the turn of the 20th century, many became naturalized Bermudians, bringing relatives to the island, purchasing homes and land, and hiring immigrant workers of their own from their homelands. Large construction projects and tourism provided more opportunities for these workers well into the 20th century (Jones, 2004).

More recently, St. David's Island became known for its large US military presence. This included the US Army's Fort Bell/Kindley Field, the Kindley Air Force Base, and the USNAS Bermuda (Jones, 2004). From World War II until it was finally closed in 1995, the base was a temporary home to tens of thousands of young servicemen who passed through this peaceful and picturesque land.

Persistence of Native American identity in Bermuda

While St. David's was originally settled in much the same way as other parts of Bermuda, its unique population history and geographic separation from the rest of Bermuda make it distinctive today in both the cultural and physical characteristics of its inhabitants (many Bermudians claim they can recognize a St. David's Islander by appearance and accent alone; see Rothwell, 1989; Simon, 2007). The persistent belief held by many of its residents that they descend directly from indigenous Americans stems largely from a long-standing tradition linked to a complex set of oral narratives, documentary references, and genealogical records (Bragdon, 1998). Existing biological data seem to corroborate this notion, as a 1960 World Health Organization dental study of St. David's Island school-aged children noted the existence of shovel-shaped incisors amongst them. The prevalence of the "Indian tooth," common among Native American populations (Devoto et al., 1971; Kharat et al., 1990), caused a stir among St. David's Islanders, as it was considered the first scientific validation of what had been island legend for generations (Peters, 2002).

This legacy is an important feature of the distinctive identity of present-day residents of the Island (Bragdon, 1998). It is also what prompted the extension of our genetic study of New England's Seaconke Wampanoag Tribe (see Zhadanov et al., 2010) to include the Bermudians of St. David's Island. Subsequent investigation into the origins of these groups, including work with archival materials, oral histories, material culture, and genealogical data, suggested that these geographically distinct peoples might be historically and biologically linked.

To investigate the influence of the historical past on the ancestry, diversity, and identity of St. David's Islanders, we analyzed genetic variation among members of this community. Based upon the oral history of St. David's Islanders, and also historical details obtained from archival sources, we expected to find a modest frequency of Native American genetic lineages among St. David's Islanders. Given the centuries of admixture resulting from enslavement and colonization, we also expected to find that West African and West European lineages comprised a significant component of the genetic make-up of this Bermudian population. Finally, in light of the historical record, which revealed that (a) Bermuda had no indigenous population at the time of colonization, (b) Bermuda served as a dumping ground for enslaved indigenous North Americans and Africans during the 17th and 18th centuries, and (c) Western Europeans have, from early in the settlement of the Island until well into the 20th century, populated the islands in great numbers, we anticipated that the genetic profile of St. David's Islanders would be unique relative to other English-speaking islands in the Caribbean. Our analysis has provided insights into St. David's Island history extending back to its initial settlement in the early 17th century, and helped us delineate the genetic contributions of people from several continental regions to Bermudian populations, whose paths crossed during the period of colonization and transatlantic slavery.

METHODS

Participants

In June 2009, we undertook a genetic and genealogical study of attendees of the St. David's Islander Reconnection Festival, a bi-annual celebration of Native American heritage held in Bermuda. Buccal samples and family history information were obtained from 133 participants following informed consent. After excluding 16 individuals who shared common ancestry with other participants through either maternal or paternal descent, and another six persons who were not part of the St. David's community, we worked with a total of 111 participants. These individuals represent approximately 6% of the population of St. David's Island. Sample and data collection was undertaken with approval from the University of Pennsylvania IRB and the Bermuda Hospitals Board.

Historical and genealogical data

To better understand St. David's Island history prior to beginning the genetic analysis, we reviewed primary source materials about Bermuda. These documents included Early Bermuda Records 1619–1826 (Hallett, 1991); 19th Century Church Registers of Bermuda (Hallett, 1995); 19th Century Church Registers of Bermuda

(Hallett, 2005); Bermuda under the Sommer Islands Company, 1612–1684: Civil Records, Vol. I–III (Hallett, 2005; various slave registries housed at the Bermuda Archives; and 17th century correspondence between early Bermuda settlers and the Royal Society in London (Hall and Hall, 1965). We also collected genealogical information from all study participants, and conducted detailed interviews with 28 participants who were native to St. David's Island concerning their family history and cultural traditions. This information provided a crucial genealogical and historical context within which to interpret the genetic data.

Mitochondrial DNA diversity

To elucidate the maternal genetic ancestry of the St. David's Islanders, we examined mtDNA variation in 111 male and female participants through direct sequencing of the control region, and analysis of single nucleotide polymorphisms (SNPs). The SNP analysis involved screening the samples for markers that identify the basal structure of the mtDNA phylogeny (3594, 7256, 8701, 9540, 10873, 12705, 13650, 14783) (Zhadanov et al., 2010). These markers were analyzed using TaqMan[®] assays (Applied Biosystems), and read on an ABI 7900HT Fast Real-Time PCR system. Once assigned to a basal lineage, the samples were screened for additional markers that define specific haplogroups and their sub-branches using PCR-RFLP analysis (Gokcumen et al., 2008; Rubenstein et al., 2008; Zhadanov et al., 2010).

In addition, for each sample we sequenced 1121 base pairs (bp) of the mtDNA control region using previously published methods (Behar et al., 2007; Gokcumen et al., 2008; Rubenstein et al., 2008; Zhadanov et al., 2010). All sequences were read on an ABI 3130xl Gene Analyzer, and aligned and edited with the SEQUENCHER 4.8 software tool (Gene Codes Corporation). All mutations were ascertained relative to the revised Cambridge Reference Sequence (rCRS; Anderson et al., 1981; Andrews et al., 1999). The coding region SNPs and control region sequences defined the maternal haplogroup and haplotypes, respectively, for each individual.

Y-chromosome diversity

We investigated the paternal genetic ancestry of the St. David's Islanders by screening 53 male samples for phylogenetically informative biallelic markers in the non-recombining region of the Y-chromosome (NRY) that define paternal haplogroups and their major sub-branches (Zhadanov et al., 2010). This high-resolution SNP analysis was undertaken in a hierarchical fashion according to published information (Y Chromosome Consortium, 2002; Karafet et al., 2008). The markers analyzed include LLY22g, MEH2, M2, M3, M19, M20, M33, M35, M112, M130, M146, M150, M172, M173, M174, M182, M194, M199, M223, M253, M267, M269, M285, M343, M346, M410, P7, P12, P15, P25, P37.2, P215, P297, and PN2. All markers were screened using custom TaqMan assays, and scored on an ABI 7900HT Fast Real-Time PCR System.

Paternal haplotypes were further defined by analyzing 17 Y-chromosome short tandem repeats (STRs) that are part of the AmpF[®]STR[®] Y-filer PCR Amplification Kit (Applied Biosystems). A separate multiplex reaction was also used to characterize six additional fragment length polymorphisms (M17, M60, M91, M139, M175, and M186)

and two additional Y-STRs (DYS388 and DYS426). Polymerase chain reaction (PCR) products were run with GeneScan[™] 500 LIZ[®] Size Standards on an ABI 3130xl Gene Analyzer. The combination of SNPs and STR alleles defined paternal lineages for each male individual.

Statistical and phylogenetic analysis

To assess the population affinities of St. David's Islanders, we compared their mtDNA haplogroup frequencies to those from a number of different populations. These included populations from three presumed source areas—the British Isles, West Africa, and the eastern United States (Richards et al., 1996, 1998; Bolnick and Smith, 2003; Salas et al., 2004)—as well as others from Portugal, the Azores and Madeira (Pereira et al., 2000; Brehm et al., 2003). In addition, we compared the Bermudian mtDNA data to those from four former British and non-British colonies in the Caribbean, African American populations from the eastern United States, the Seaconke Wampanoag Tribe of Massachusetts, and Brazilian populations (Alves-Silva et al., 2000; Gonzalez et al., 2003; Benn-Torres et al., 2007; Hünemeier et al., 2007; Mendizabal et al., 2008; Stefflova et al., 2009; Zhadanov et al., 2010). Similarly, we compared the Bermudian NRY haplogroup frequencies to those of European, African, and Native American populations (Capelli et al., 2003; Gonçalves et al., 2005; Bolnick et al., 2006; Stefflova et al., 2009; Balaesque et al., 2010), three other admixed populations in the United States and the Caribbean (Mendizabal et al., 2008; Stefflova et al., 2009; Zhadanov et al., 2010), and Portugal, the Azores, and Madeira (Gonçalves et al., 2005).

For both the mtDNA and NRY data sets, the haplogroup frequencies were used as allele frequencies to estimate F_{ST} genetic distances between populations using Arlequin v.3.11 software (Excoffier et al., 2005). These inter-population F_{ST} genetic distances were represented in two dimensions through multi-dimensional scaling (MDS) (Kruskal and Wish, 1978) using SPSS 17.0 (SPSS 2009).

In addition, we analyzed the phylogenetic relationships among Y-STR haplotypes using NETWORK 4.6.0.0 (Bandelt et al., 1995, 1999). The Y-chromosome lineages used to generate the networks consisted of 16 Y-SNPs and 17 Y-STRs. DYS385 was excluded from the network analysis because it represents a duplicated STR locus. For this reason, the actual order of alleles cannot be determined without further genotyping (Gusmao et al., 2006). The Y-STR loci were weighted based on the inverse of their variances. A reduced median–median joining approach was utilized with the MP post-processing function (Polzin and Daneschmand, 2003).

RESULTS

mtDNA diversity

Among the 111 individuals, we identified 29 mtDNA haplogroups that encompassed 67 distinct haplotypes, based on coding region SNPs and control region sequences (Table 1; Supporting Information Tables 1 and 2).

Native American haplogroups. A single individual exhibited a mtDNA of Native American ancestry. This haplotype belonged to A2i (Achilli et al., 2008; van Oven and Kayser, 2009), a branch of the pan-American haplogroup A2 (Schurr, 2004). The hypervariable region 1 (HVS1) haplotype for this Bermudian A2i mtDNA (no. 1;

TABLE 1. mtDNA haplogroup distribution in Bermudians

Geographic origin	Haplogroup	N	%		
Americas	A2i	1	<1%		
Africa	L0a1a	1	68%		
	L0a1b	12			
	L0a2a	1			
	L1b	10			
	L1c	6			
	L2a	12			
	L2b	2			
	L2c	2			
	L3b	3			
	L3d	3			
	L3e	15			
	L3f	3			
	L3k	3			
	L4b	3			
	Europe	H		6	31%
		H6		4	
J1c		13			
J2a		1			
K1a		1			
K1c		1			
T2b		1			
T2d		1			
U2		1			
U5a		1			
U7		1			
V7a		1			
W		1			
South Asian		R6	1	<1%	
East Asian	C	1	<1%		

“N” represents the total number of individuals in the study from each haplogroup, and “%” indicates the relative proportion of the mtDNAs originating in a specific geographic region.

Supporting Information Table 2) has been reported at high frequencies in several Ojibwa/Chippewa groups from North Dakota, Minnesota and Wisconsin (Malhi et al., 2001; Shook and Smith, 2008), described in two Micmac, one Sisseton/Wahpeton Sioux, and one Quapaw (Malhi et al., 2001), and identified in three archaeological populations located in Illinois and southwestern Ontario (Shook and Smith, 2008; Stone and Stoneking, 1998). Closely related haplotypes were also found in Kickapoo and Ojibwa/Chippewa populations. In fact, the HVS1+HVS2 sequence for this haplotype was an exact match with ones seen in a Micmac and a Wisconsin Chippewa (Malhi et al., 2001). However, A2i has not yet been identified among Caribbean or southeastern US populations (Martinez-Cruzado et al., 2001; Bolnick and Smith, 2003; Benn-Torres et al., 2007; Mendizabal et al., 2008). Therefore, this haplogroup appears to be restricted to Algonquian and Siouan speakers, and appears at greater frequencies and higher diversity in Algonquian populations.

According to his family records, this participant traces his maternal heritage to a woman who emigrated from Virginia to Bermuda in the mid-1840s, a decade before emancipation in Bermuda, but almost half a century after the slave trade was officially outlawed there. According to the family's oral traditions, this woman was an escaped African slave. However, the participant also stated that he thought that he had an indigenous ancestor, although uncertain as to which side of his family tree this individual appeared.

Another mtDNA haplotype was recognized as belonging to haplogroup C, a lineage that is common among

TABLE 2. mtDNA haplogroup frequencies in Bermudians and comparative populations

Hg	Bermudians	African Americans ^a	West Africans	Seaconke Wampanoag	Native Americans ^b	British ^c	Dominicans	Grenadians	Trinidadians	Cubans
A	0.01	0.01			0.58		0.08		0.02	0.23
B					0.17					0.02
C	0.01				0.24		0.04			0.05
D							0.16		0.02	0.03
H	0.09	0.05		0.11		0.51		0.02	0.06	0.09
I				0.03						
J	0.13	0.01				0.22				0.04
K	0.02	0.02				0.04				0.01
R6	0.01									
T	0.02	0.01				0.08				0.02
U	0.03	0.01	0.12			0.06		0.04		0.06
V	0.01					0.02				0.01
W	0.01	0.01								
L0	0.13	0.06		0.03			0.12	0.08	0.02	0.02
L1	0.14	0.17	0.20	0.07			0.44	0.18	0.24	0.09
L2	0.14	0.24	0.24	0.18			0.12	0.33	0.30	0.13
L3	0.24	0.39	0.43	0.54			0.04	0.25	0.30	0.20
L4	0.03	0.02								0.01

The “undetermined” haplogroups from several papers were not included in these totals.^a African-Americans from Philadelphia (Steffova et al., 2009)

^b Native Americans from the eastern United States (Bolnick and Smith, 2003)

^c Individuals from England and Wales (Richards et al., 1996)

Native American populations (Schurr, 2004). However, its control region sequence lacked the substitution at 16325 and the deletions at 290 and 291 that define C1, the haplogroup that is found throughout the Americas (Tamm et al., 2007; Achilli et al., 2008; Fagundes et al., 2008). Genealogical information also confirmed this participant to have European maternal ancestry. Haplogroup C is rare in Europe (e.g., Richards et al., 1996, 1998). Thus, while the original source of this haplotype in this participant’s maternal lineage is not clear, it belongs to an East Eurasian branch of this haplogroup, and therefore, is not indigenous in origin.

African haplogroups. The majority of mtDNA lineages observed in Bermudians (68%) originated in Africa. Two of the African haplogroups of highest frequency (L0a and L3e) are commonly found among populations from Central-West and Southeast Africa, an area that stretches from Cameroon and Gabon down to Angola and east across the continent to Mozambique. These haplogroups are also less common (<5%) among African Americans (Salas et al., 2005), and Afro-Caribbean populations (Benn-Torres et al., 2007). Haplogroups L3e and L0a also appear in Brazil (Alves-Silva et al., 2000; Bandelt et al., 2001; Hünemeier et al., 2007), the only former Portuguese colony in the Americas.

Two other high frequency haplogroups (L1b and L2a) in our data set are commonly found among West African groups, African-American groups, and people of African ancestry throughout the Caribbean and in Brazil (Alves-Silva et al., 2000; Martinez-Cruzado et al., 2001; Salas et al., 2004; Benn-Torres et al., 2007; Hünemeier et al., 2007; Mendizabal et al., 2008). These are likely to have been introduced to the Americas through the trans-Atlantic slave trade.

West Eurasian haplogroups. West Eurasian haplogroups comprised 31% of the Bermudian mtDNA haplotypes. Among these haplogroups, J1c was the most common. Haplogroup J is observed in various parts of Western Europe including Scotland, Wales, Ireland, and

England, where it comprises more than 15% of the mtDNAs there (Richards et al., 1996, 1998), and also in Portugal, where it represents 3–6% of the mtDNAs (Pereira et al., 2000). Haplogroup H, the most common lineage in Central and Western Europe (Richards et al., 1996, 1998; Pereira et al., 2000; Achilli et al., 2004; Loogvali et al., 2004), was the second most common amongst these lineages (9%). The remaining 11 West Eurasian haplogroups appeared in single individuals. This finding suggested there was high genetic heterogeneity of the original source population(s) of these lineages, as well as possible contributions from post-settlement migrations to Bermuda from Europe (or the United States).

Our comparison of Bermudian mtDNA data to those of putative source and Caribbean populations (Table 2) yielded two important insights into the population history of Bermuda. First, the mtDNA haplogroup distribution in St. David’s Islanders was distinctive from that of all of the other populations. In addition, the haplogroup distribution consisted almost exclusively of lineages from only two major source populations (68% African and 31% European), with less than 1% being Native American in origin.

The haplogroup data were also used to estimate F_{ST} genetic distances among Bermudians and other populations. This analysis revealed that St. David’s Islanders were significantly different ($P < 0.05$) from the other 16 populations, while some populations, including West Africans, African-Americans, and populations from Trinidad and Grenada, were not significantly different from one another (Supporting Information Table 3). The plotting of the F_{ST} values through MDS showed that St. David’s Islanders were situated between West African, Caribbean, and Brazilian populations, being closest to Cubans and northeastern Brazilian groups. The high frequency of African haplogroups, and low to moderate frequencies of Amerindian lineages, in this set of populations undoubtedly contributed to this pattern. Bermudians also showed modest affinities with European populations (Portuguese and British), but were quite distant from Native American populations (Fig. 3).

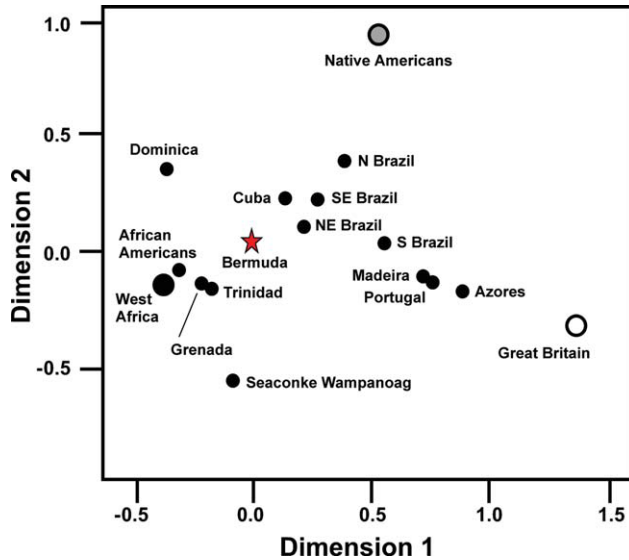


Fig. 3. An MDS plot based on mtDNA F_{ST} genetic distances among seventeen populations from Bermuda, the British Isles, West Africa, Portugal, Madeira, the Azores, the Americas, and the Caribbean. The MDS plot stress value was 0.18. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Y-chromosome diversity

Among 53 male participants, we observed 12 distinct NRY haplogroups that encompassed 47 distinct haplotypes, based on SNP and STR data (Table 3, Supporting Information Tables 4 and 5).

Native American haplogroups. A single participant belonged to the pan-American NRY haplogroup Q1a3a*. Haplogroup Q1a3a is strictly associated with the indigenous peoples of the Americas, and is defined by the presence of the M3 SNP (Karafet et al., 2001; Lell et al., 2002; Bortolini et al., 2003; Underhill et al., 1996). M3 itself is found “downstream” from the M242 and M346 markers, which define haplogroup Q1a3 in Central and East Asia (Seielstad et al., 2003; Sengupta et al., 2006; Karafet et al., 2008). Based on numerous studies, M3 occurred on the Q1a3 lineage roughly 10–15,000 years ago as human expansion into the Americas was underway (Underhill et al., 2006, 2001; Bortolini et al., 2003; Zegura et al., 2004; Bailliet et al., 2009).

The Y-STR haplotype for this Q1a3a* individual did not match any previously published Y-chromosome haplotype (no. 1, Supporting Information Table 5). A Mayan from Guatemala had the most similar haplotype, being identical at 16 out of 17 STRs typed in that individual (Willuweit and Roewer, 2007). In addition, two Native American Q1a3a Y-chromosomes from the southeastern United States were similar to the Bermudian haplotype. One was from a Seminole who had a single repeat difference when comparing 10 of the 19 Y-STR loci analyzed in our study (DYS19, DYS385a/b, DYS389I, DYS389II, DYS390, DYS391, DYS392, DYS393, DYS439), and the other came from a Cherokee who had two repeat differences at two loci (Bolnick et al., 2006). While genealogical information for this individual was limited, he recalled family oral history about a male ancestor who came to Bermuda from North America centuries ago. Thus, we cannot rule out the possibility that this haplo-

TABLE 3. Y-chromosome haplogroup frequencies in Bermudian men

Geography	Haplogroup	N	%
Americas	Q1a3a*	1	2
Africa	B	2	32
	E1a	1	
	E1b1a	15	
Europe	E1b1b1	2	66
	G2a	2	
	I1	3	
	I2a	2	
	I2b	1	
	J2b	1	
	R1a1	4	
	R1b1b2	20	

“N” represents the total number of individuals in the study from each haplogroup, and “%” indicates the relative proportion of the Y-chromosomes originating in a specific geographic region.

type has persisted from the early settlement of the island.

African haplogroups. Eighteen individuals, or about one-third of the Bermudian male participants, had three NRY haplogroups of African ancestry. The first (E1b1a) accounted for the vast majority of the African NRY samples (83%). Its prevalence initially suggested either the effects of genetic drift or a founder effect through the introduction of a small number of African men to Bermuda from a specific geographic area during the early settlement of the islands. However, E1b1a is also the most common haplogroup in West and Central African populations (Underhill et al., 2001; Semino et al., 2002; Cruciani et al., 2004). In addition, the extensive STR variation in the 15 haplotypes suggested that multiple individuals bearing E1b1a Y-chromosomes contributed to the genetic diversity seen in Bermuda today (Supporting Information Fig. 1 and Table 5).

West Eurasian haplogroups. West Eurasian haplogroups accounted for the majority of the male participants and the vast majority of their Y-chromosomes. One haplogroup, R1b1b2, which is very common in Europe and found at frequencies of more than 75% in England and Wales (Capelli et al., 2003; Balaesque et al., 2010) and between 50 and 60% in Portugal, Madeira and the Azores (Gonçalves et al., 2005), encompassed more than half of these individuals, and was represented by 17 different STR haplotypes (Supporting Information Fig. 1 and Table 5). This finding suggested that many Bermudians have a paternal genetic connection to the British Isles, from which the initial colonists came, and probably also Portugal, Madeira, and the Azores, from which skilled craftsmen and sailors arrived in the 18th and 19th centuries.

We compared the Bermudian males to those from a number of other populations (Table 4). The F_{ST} genetic distances based on the NRY haplogroup frequencies showed that Bermuda was significantly different ($P < 0.05$) from all three putative source populations, as well as from all but two comparative populations, these being the Cubans and the Seaconke Wampanoag (Supporting Information Table 3). When genetic distances were mapped on a MDS plot, Bermudians also showed stronger genetic affinities with Portuguese and British populations compared to African-American and African

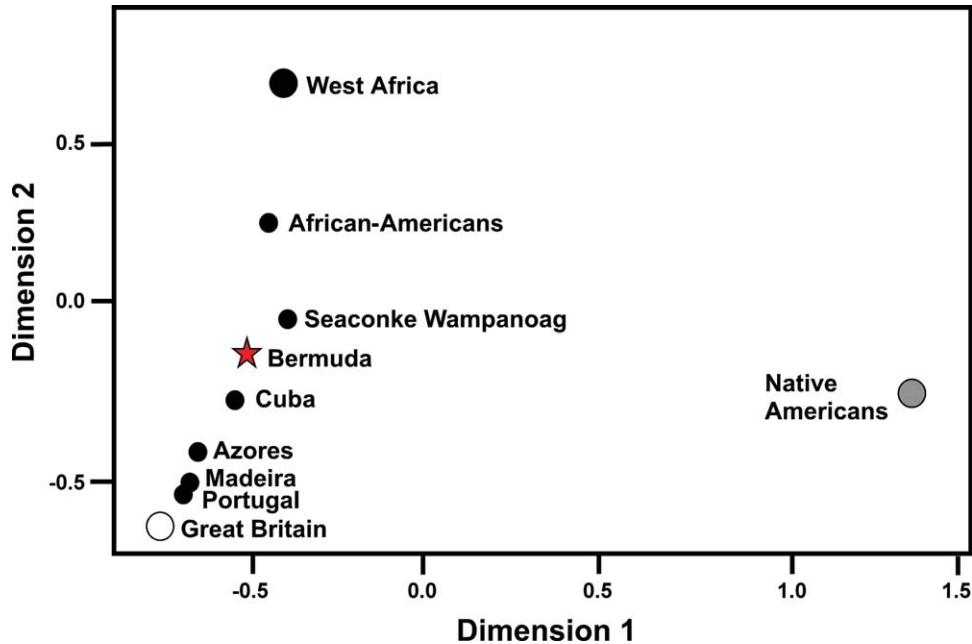


Fig. 4. An MDS plot based on NRY F_{ST} genetic distances among ten populations from Bermuda, the British Isles, West Africa, Portugal, Madeira, the Azores, the Americas, and the Caribbean. The MDS plot stress value was 0.12. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

TABLE 4. *Y-chromosome haplogroup frequencies of Bermudians and comparative populations*

Hg	Bermudians	Native Americans ^a	West Africans	British ^b	African Americans ^c	Seaconke Wampanoag	Cubans
C		0.18					
Q	0.02	0.82			0.02	0.12	
E1b1b	0.04		0.06	0.02	0.03	0.06	0.06
G	0.04			0.01	0.01	0.06	
I	0.11			0.19	0.09		0.09
J	0.02			0.02	0.02	0.06	0.05
K							0.02
R1a	0.07			0.05			0.02
R1b	0.38			0.71	0.19	0.23	0.55
A					<0.01		
B	0.04				0.02		
E1a	0.02		0.15		0.02	0.06	0.02
E1b1a	0.27		0.70		0.54	0.23	0.17
E2			0.09		0.06		
O					<0.01		0.02
S						0.18	

^a Based on data from Native American tribes in the northeast and southeast United States (Bolnick et al., 2006); non-native haplogroup frequencies were not included because the resolution of these haplogroups was not equivalent to that used in this study.

^b Individuals from England, Scotland and Wales (Capelli et al., 2003; Balaesque et al., 2010).

^c African-Americans from Philadelphia (Stefflova et al., 2009)

groups, while being quite distant from Native American tribes (Fig. 4).

DISCUSSION

In the Americas, the peopling of the New World continues to be a significant research question within the field of anthropology. Investigations into the settlement of the Americas have attempted to delineate the larger dimensions of human population movements through the use of mtDNA and Y-chromosome analyses (e.g., Forster, 2004; Schurr, 2004; Tamm et al., 2007). More specifically, they have attempted to answer questions about the timing of the human entry into the Americas, the number of times human groups migrated to the New World, the

source areas from which ancestral Native American populations originated, and the routes that they took to reach the Americas. While investigators have asked similar questions concerning the African diaspora (e.g., Salas et al., 2004), few with an interest in population movements in the Americas have asked such questions concerning the indigenous American diaspora. As a result, the genetic consequences of enslaving and relocating indigenous peoples around the New World are not well understood (e.g., Carvalho et al., 2008).

This analysis was conceived as an extension of our work with the Seaconke Wampanoag Tribe of Massachusetts (see Zhadanov et al., 2010). Based on interviews with Seaconke tribal members and St. David’s Islanders, and on genealogical and archival information, we were

interested in learning what mtDNA and NRY analyses might reveal about the indigenous American heritage of these Bermudians. While our data reveal a small indigenous genetic contribution to Bermudian participants (1% mtDNA and 2% NRY haplotypes), our findings offer a number of new insights into the complex biological ancestry that emerged from the early settlement and colonization of Bermuda. This study is the first to examine human genetic variation in Bermuda, as well as the first to use genes and genealogy to better understand Bermuda's early and complex role in Britain's New World expansion, including its place in the trans-Atlantic slave trade, neither of which have been well understood from this perspective.

Genetic ancestry of modern St. David's Islanders

Judging from the genetic data, St. David's Islanders appear to be an admixed population of predominantly European and African ancestry. In addition, by analyzing the specific haplogroups present in this population, we are able to infer the likely geographic sources of these lineages. For instance, the high frequency of mtDNA haplogroups L0a and L3e is surprising, as both occur at low frequency among African Americans and in other Anglo-Caribbean populations (Salas et al., 2004; Benn-Torres et al., 2007). Likewise, these two haplogroups are minority lineages among most West Africans (Salas et al., 2004). However, haplogroups L0a and L3e occur at a higher frequency in central and southern Africa, namely in the former Portuguese colonies of Gabon, Angola, and Mozambique (Salas et al., 2004), and are common in the Portuguese colony of Brazil (Alves-Silva et al., 2000).

Thus, based upon the historical record, we surmise that the English may have purchased or, more likely, stolen African slaves from the Portuguese during the ongoing trans-Atlantic slave trade and preferentially introduced them to Bermuda but not their other colonies. Conversely, the small size of Bermuda may have contributed to the expanded frequencies of the L0a and L3e lineages through genetic drift over the past several centuries. This pattern may not be observed in the larger colonies, particularly in light of the official cessation of slave importation to Bermuda in the early to mid-18th century.

Similarly, the high frequency of European mtDNA haplogroup J1c could be attributed to the 17th century arrival in St. David's of a few early settlers from England, Scotland, or Wales, where haplogroup J is relatively common (approximately 15%; Richards et al., 1996, 1998). Individuals bearing this lineage may also have come to Bermuda as skilled workers from the Azores or Madeira during the 18th century, where this haplogroup occurs in low frequency (8% and 3%, respectively) (Brehm et al., 2003; Santos et al., 2003). The heterogeneity of the rest of the European mtDNA lineages, including the 16 other haplogroups represented by four or fewer individuals, further suggests that the European women who continued to arrive in Bermuda were of varied ethnic backgrounds.

The Y-chromosome diversity, characterized by a high frequency (51%) of haplogroup R1b1b2, initially suggested a founder effect, in which many Bermudians had a paternal ancestor that was one of the original settlers that arrived from Great Britain. However, STR genotype data reveal considerable haplotypic diversity within this

haplogroup, and therefore the presence of multiple founding individuals from Britain or Western Europe. In addition, the high number of distinct European NRY haplogroups also suggests that a diverse group of male settlers arrived from various parts of Great Britain, or other regions of Western Europe, such as Portugal, the Azores or Madeira, over the past several centuries. This pattern would also be consistent with an introduction of new male Y-haplogroups through relationships with soldiers during the decades-long United States military presence on Bermuda.

The high frequency of haplogroup E1b1a (28%) shows a similar pattern for African male lineages, which were likely introduced during the trans-Atlantic slave trade. Like its European analogues, this African haplogroup is highly diverse at the haplotype level when Y-STR data are considered. This observation suggests that a diverse set of African men, or possibly African-American military servicemen, were the paternal ancestors to approximately one-third of those sampled.

St. David's Islanders compared to other populations in the Caribbean

The pattern of genetic diversity in the St. David's Islanders is unlike any other population in the Caribbean and the Americas. In contrast to the continental areas of North, Central, and South America, or the nearby Caribbean islands, Bermuda was uninhabited when Europeans first arrived in the early 17th century, as Bermuda had no indigenous population. Although Native Americans were forcibly introduced to the island, it appears there was no clash of cultures between incoming Europeans, American natives, and African blacks (Bernhard, 1999), a pattern that defined the early colonial era throughout the rest of the Americas. The surviving 17th century record reveals a portrait of an emerging multiracial society where, although slavery was widespread, slave families, like white families, made up the normal order of society. "Whites and blacks, mulattos and Indians, masters, slaves and servants shared the same economic pursuits, obeyed the same laws, worshipped in the same churches and lived together in the same houses" (Bernhard, 1999: 99).

The frequencies of mtDNA lineages on St. David's Island are generally consistent with these accounts. These data reveal clear contributions from populations originating in two primary source areas, namely, Africa and Europe, as was reported in oral historical and archival data. More than two-thirds of the mtDNAs (68%) are of African origin, and approximately one-third of them (31%) are of European origin. By contrast, Native American lineages constitute less than 1% of Bermudian mtDNAs, somewhat less was expected based on oral histories and archival data. This pattern is different from that of any Caribbean islands where there is either more than 80% African mtDNAs, as in the case of many British colonies like Grenada and Trinidad (Benn-Torres et al., 2007), or more than 80% combined African and Amerindian mtDNA lineages, as observed in the former Spanish colonies of Cuba and Puerto Rico (Martinez-Cruzado et al., 2001, 2005; Mendizabal et al., 2008) and the former Portuguese colony of Brazil (Alves-Silva et al., 2000). Thus, Bermuda has more European mtDNA lineages than most other former European colonies in the Americas, with the possible exception of the United States and Canada.

The NRY haplogroup data likewise reveal clear contributions from the same two major source areas. However, the trend is reversed, with European lineages accounting for 66% of St. David's Islander Y-chromosomes and African lineages accounting for 32% of them. Native American haplogroups comprised only 2% of Bermudian Y-chromosomes, less than anticipated based on oral history and archival data. This distribution is most similar to that of Cuba, which includes 78% European male lineages and 20% African male lineages (Mendizabal et al., 2008). The similarity between the NRY haplogroup distributions of these two former European colonies is reflected in the non-significant F_{ST} genetic distance between them. Thus, this pattern may be the result of similar patterns of admixture between peoples of European and African descent in the early settlement of the islands, and colonial policies toward indigenous populations during that time.

Persistence of Native American lineages among St. David's Islanders

Genetic analysis of St. David's Islanders, a majority of whom claims ancestry from indigenous populations that traditionally inhabited what is now New England, reveals a complex mixture of maternal and paternal lineages of Native American, European, and African origin. This pattern has been observed in other populations, particularly in several Native American tribes of North America (e.g., Santos et al., 1996; Huoponen et al., 1997; Malhi et al., 2003; Bolnick et al., 2006; Zhadanov et al., 2010). As such, this result is not entirely unexpected in light of British colonial policy concerning the enslavement of peoples in and around the New World. In fact, given this colonial history, it is remarkable that any indigenous lineages survive in this Bermudian population today.

Nevertheless, we detected a single mtDNA haplotype to be of Native American ancestry, one that belongs to haplogroup A2i. After taking into account the genealogical context of this participant's maternal heritage, we conclude that this haplotype was not associated with the early forced migration of Native Americans to Bermuda. While uncertain whether the post-emancipation migration of this indigenous lineage speaks to a broader recognition of a Native American cultural familiarity early in the 19th century, detection of this haplotype reveals a connection between indigenous Americans and St. David's Island, which may have contributed to the Native American heritage ideology that is present on the island today.

The presence of the NRY haplogroup Q1a3a* can be understood in the same way. This indigenous haplogroup is found among indigenous populations from the Arctic Circle to Patagonia. Given the genealogical context of this sample, we cannot rule out the possibility that this indigenous lineage persists from the early founding of Bermuda. However, we note that European colonizers were not only masters at invading indigenous lands and enslaving its citizens all over the New World, including North America, South America, and the Caribbean, but also successful privateers, looting one another's "cargo" as circumstances provided. Thus, given the paucity of genealogical details provided, we cannot identify with certainty the place from which this indigenous Y-chromosome lineage originated.

What we can conclude, however, is that the presence of this indigenous haplotype in Bermuda evinces the movement of aboriginal individuals to this location, most likely from North America based on the Y-STR haplotype. The circumstances of this movement are not presently well understood. However, the presence of a Q1a3a* haplotype in Bermuda speaks to the indigenous heritage ideology that is present on the island today.

In light of genealogical and oral historical data collected from the St. David's community, we can speculate that the low frequency of indigenous lineages is a result of genetic drift eliminating low frequency types in a relatively small island like Bermuda (e.g., Helgason et al., 2003, 2009; Santos et al., 2003; Montiel et al., 2005), while at the same time increasing the frequency of other lineages (mtDNA haplogroups L0a and J1c). The loss of indigenous lineages also likely reflects the demographic impact of European colonization and historical intermarriage with persons of non-indigenous backgrounds, resulting in the replacement of Native American mtDNAs and NRY lineages with European or African ones (see Karttunen, 2005). Indeed, many St. David's Island participants characterize themselves ethnically as "Native American," yet characterize the ethnicities of their maternal and paternal ancestors as being "mixed," "colored," "Bermudian," and "Black," leading us to consider the possibility that the self-proclaimed "Native St. David's Islander" designation may be a feature of a more modern-day ethnogenetic identity (see Ben-Yehuda, 1995; Haley and Wilcoxon, 1997, 2005; Kohl, 1998). It may further reflect a self-reflexive appreciation for the intricacies of a complex historical past.

This recognition also helps to explain the fact that at least some of the genealogical and oral historical data provided by participants is inconsistent with our reckoning of genetic ancestry. While often, and understandably, the reporting of deep ancestry can be murky, the repeated accounts that direct lineal descendants were "Native American," "Pequot," "Wampanoag," "Mohawk," and "Indian" are not entirely supported by the analysis of mtDNA and Y-chromosome variation. Reports of such relations could also reflect the extent of long forgotten contacts and interactions with people of European and African descent. As we have observed with the Seaconke Wampanoag, "the high frequency of nonnative haplotypes in this population, along with the paucity of Native American haplotypes, reveals the substantial changes in the genetic composition . . . in post-contact American history" (Zhadanov et al., 2010: 8).

We are also mindful that, by relying too heavily on genetic methods to measure "indigeneity," we may miss the significant impact of cultural practices on the maintenance of this identity (see Ben-Yehuda, 1995; Kohl, 1998). St. David's Islanders have never understood their identity as being entirely biologically based. A cursory examination of participant genealogies reveals a deep awareness that their histories are complex and, in places, uncertain.

At the same time, a large number of individual community members have expressed great interest in knowing as much as possible about their genetic genealogy. In this regard, the genetic markers used in this study survey only a small fraction of the total human genome for variants that are useful for reconstructing human phylogeography. The remainder of the genome that was not examined here also provides information about individual and population histories (e.g., Schroeder et al., 2007,

2009; Mendizabal et al., 2008). Thus, to better understand the biological ancestry of postcolonial Native American derived populations in the US and Caribbean, it will be necessary to analyze biparentally inherited autosomal markers, which may preserve, in some form, the genetic contributions of all native ancestors from previous generations.

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