A Novel Commensal Proxy for Tracing Indigenous Interaction in the Ceramic Age Lesser Antilles, Caribbean: Ancient Mitochondrial DNA of Agouti (Dasyprocta sp.)

by

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B.A. (Cum Laude), Mount Holyoke College, 2018

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in the
Department of Archaeology
Faculty of Environment

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Abstract

The agouti (Dasyprocta sp.) was one of the many commensal species humans translocated to the Caribbean from South America as early as ca. A.D. 500. Their widespread archaeological presence in the Lesser Antilles, including on Carriacou, Grenada, makes them valuable proxies for reconstructing pre-Columbian human interactions between the islands and continent. This study applies a genetic commensal model to agouti, a novel commensal proxy offering an ideal opportunity for commensal research. Mitochondrial DNA (mtDNA) was extracted from archaeological agouti bones from seven sites across the Lesser Antilles. Of 30 tested, 26 specimens (Sabazan (n = 5) and Grand Bay (n = 19) on Carriacou, Macabou (n = 1) on Martinique, and BK77 Grand Case (n = 1) on Saint Martin) were successfully amplified. Analysis shows that archaeological sequences belong to Dasyprocta leporina and relate to a single continental clade, likely from northern South America or Trinidad. This is the first study to provide genetic evidence for species identification of archaeological Caribbean agouti. Results provide new data informing continental and Caribbean agouti population structure and offer insight into the origin and dissemination of agouti in the Caribbean. Agouti appear to have rapidly established viable, reproducing populations on Carriacou around ca. A.D. 400/600, but the population status on other islands is unclear. This study contributes to the ongoing discussion regarding the relationships between humans and continental translocates in the Caribbean and emphasizes the potential of the commensal model for the global study of ancient translocations and island interactions. Analytic findings are significant for the archaeological, ecological, and genetic study of the Caribbean and South America, prompting the need for continued study of Caribbean commensals and additional sampling focusing on pre-Columbian agouti from coastal South America. Results highlight the potential of the commensal model for the global study of ancient translocations and island interactions. This study also brings to light new data for both pre-Columbian and modern agouti, informing upon the Caribbean agouti’s taxonomic classification and population structure in the Caribbean and South America. Finally, results have implications for Caribbean ecology, refining the timing of potential ecological repercussions brought on by translocates in the islands.
Keywords: Pre-Columbian; CytB; Commensal Model; Carriacou; Martinique; Saint-Martin
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<td><em>Anno domini</em></td>
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Chapter 1.

Introduction

Translocations have been recorded throughout most of human history; when humans moved, they brought alongside them – knowingly or unknowingly – commensals, organisms living in close association with humans. The genetic information of ancient translocated commensals is a valuable tool for reconstructing ancient human interactions; evolutionary relationships can inform upon the geographic origins and levels of interaction or isolation (Matisoo-Smith 1994, 2017; Storey et al. 2012a). As they entered the Caribbean, human groups brought with them a multitude of familiar plants and animals from the continent, which they used to facilitate their management of the islands starting after ca. A.D. 500 (Newsom and Wing 2004; Giovas et al. 2012). The majority of archaeological remains of continental commensals are located in the Lesser Antilles (Giovas 2019a), cementing the islands’ close relationship to the continent (Hofman et al. 2007). In particular, the remarkable faunal assemblage found on Carriacou (Giovas et al. 2012) offers a unique opportunity for research. However, in the Caribbean the use of the commensal model for genetic research has been limited. The abundance of skeletal remains of non-native fauna (LeFebvre 2007; Giovas et al. 2012; Giovas 2016), the presence of rare ritual paraphernalia (Kaye et al. 2004; Fitzpatrick et al. 2009,) and bone artifacts (Kaye et al. 2004: 85; Giovas 2013: 72; Giovas 2017; Giovas 2018) found on Carriacou suggest that the island shared privileged interactions with the continent and islands in the North. However, much like the rest of the Caribbean, in particular the southern Lesser Antilles (Fitzpatrick 2006), much remains unknown of the origins, chronology, and patterns of interaction sustained by pre-Columbian human groups. This project will reconstruct human pre-Columbian continental connections to Carriacou by extracting and analyzing ancient mitochondrial DNA (mtDNA) from the commensal agouti (Dasyprocta sp.), translocated to the Lesser Antilles in pre-Columbian times. Genetic analyses from this study provide the first ever sequences of ancient agouti specimens which is significant for archaeological, ecological, and genetic research. This study contributes to the ongoing discussion regarding the relationships between humans and continental translocates in the Caribbean and has implications for the global study of ancient translocations and island
interactions. This study provides new ancient genetic materials from hot and humid environments and adds to the potential for aDNA research in tropical regions, where materials are typically more degraded and more difficult to amplify. Below I discuss the relevant background and present the research design and objectives. I conclude by outlining my thesis structure.

1.1. Research Background

Since the initial settlement of the insular Caribbean ca. 4000 B.C. (Napolitano et al. 2019), the region has sustained complex human mobility, which flowed more or less continuously between the continent and islands (Hofman et al. 2007, 2014; Callaghan 2011; Fitzpatrick 2013). The colonization of the insular Caribbean can seemingly be divided into two clusters (Napolitano et al. 2019), consolidating the four periods commonly ascribed to Caribbean chronology (Rouse 1986, 1989). Trinidad, which was connected to the continent by a land bridge during the Early Holocene (Boomert 2000; Tankersley et al. 2018), stands apart from this chronology with the oldest recognized radiocarbon dates in the region (ca. 6500 B.C. and 5500 B.C.) (Napolitano et al. 2019). The first cluster, associated to the Archaic and Lithic Ages, dates from ca. 3850 B.C. to A.D. 550 (Napolitano et al. 2019), when Central American (Rouse 1992: 69; Wilson et al. 1998) and South American (Callaghan 2003; Pagán-Jiménez et al. 2015) groups first reached the Greater Antilles and Northern Lesser Antilles (Napolitano et al. 2019). The second cluster, associated to the Early-Ceramic and Late-Ceramic Ages, dates from ca. 550 B.C. to A.D. 1450, and is largely associated with the cultural group known as the Saladoid, which originated from Venezuela (Wilson 2007). Ceramic Age colonization initially occurred in the Lesser Antilles Puerto Rico and the Virgin Islands, and later extended into the Greater Antilles and the Bahama Archipelago in the North.

Caribbean inhabitants maintained continental connections throughout pre-Columbian times (Keegan 2004: 34; Hofman et al. 2011: 77). Objects and architecture of ceremonial or ritual significance in the Ceramic Age (Siegel 1989, 1996; Wilson et al. 1998; Wilson 2007; Keegan 2009) evidence strong links to the Orinoco basin in South America. This phenomenon is particularly visible in the Lesser Antilles, where the strategic geographic positioning between the Greater Antilles and the continent stimulated human interaction (Hoogland and Hofman 1999; Hofman et al. 2007). Despite the ubiquity of canoe manufacturing and travel (Shearn 2020), artifacts relating to seafaring are infrequent in
the archaeological record, and only a few boats and paddles have been recovered from a handful of islands (Fitzpatrick 2013; Shearn 2020). The paucity of canoe remains in the archaeological record does not reflect the constant intense interactions which occurred throughout pre-Columbian times.

The magnitude of interaction is most visible in Caribbean archaeological assemblages (Hofman and Hoogland 2011): lithic (Hofman 2010) and ceramics artifacts (Hofman et al. 2007), clays and tempers (Isendoorn et al. 2008; Fitzpatrick et al. 2008), lapidary objects of various stone types (Cody 1993; Garcia-Casco et al. 2013; Queffelec et al. 2018), animal tooth pendants (Laffoon et al. 2014), and gold-copper alloy (guanin) ornaments (Valcárcel Rojas and Martínón Torres 2013) were exchanged between the continent and the islands. Translocations of continental flora and fauna also accompany human interaction in the Caribbean throughout pre-Columbian times. Continental translocates such as maize (Zea mays) (Pearsall 2002; Mickleburgh and Pagán-Jiménez 2012; Pagán-Jiménez 2011, 2013, Pagán-Jiménez et al. 2015), dogs (Canis lupus familiaris) (Boomert 2000; Newsom and Wing 2004: 204; Wing 2012; Grouard et al. 2013), guinea pigs (Cavia porcellus) (Giovas et al. 2012; LeFebvre and deFrance 2014; Lord et al. 2020), and agouti (Dasyprocta sp.) (Newsom and Wing 2004: 205; Wing 2012; Giovas et. al 2012) support the extensive nature of regional interaction throughout Central and northern South America. The broad origins of archaeological materials and of many of these translocated taxa point to diverse human origins and extensive patterns of interaction, however analyses so far have only been able to indicate broad regional patterns (e.g., Laffoon et al. 2016).

The genetic information of ancient translocated commensals is a valuable tool for reconstructing ancient human interactions; in the Pacific, rats (Rattus exulans) (Matisoo-Smith 1994; Matisoo-Smith and Robins 2004), chickens (Gallus gallus) (Storey et al. 2012b), and pigs (Sus sp.) (Allen et al. 2001) have all been successfully utilized to trace human mobility. In the Caribbean however, genetic studies of archaeological samples have been limited, in part due to the challenging preservation conditions to which aDNA is subject to in tropical regions (Smith et al. 2003; Hofreiter et al. 2015). A few studies have been successful in extracting aDNA from human remains (Lalueza-Fox 2001, 2003; Mendisco et al. 2015; Schroeder et al. 2018). Recent analyses by Kimura et al. (2016), Lord et al. (2018, 2020), and Oswald et al. (2020), have established the potential for the application of genetic commensal models in the Caribbean, albeit on a very
limited number of taxa. So far, only aDNA from guinea pig (*C. porcellus*) (Kimura et al. 2016; Lord et al. 2018, 2020), and hutia (*Geocapromys ingrahami*) Oswald et al. (2020) have been analyzed to reconstruct pre-Columbian human interactions. This limited dataset provides limited perspectives on the interactions taking place, particularly in a region as complex as the Caribbean (e.g. Hofman and van Duijvenbode 2011): “reconstruction of exchange networks should not be limited to just one of the possible goods that may have circulated through it” (Cody 1993, citing Hirth 1984: 2).

Agouti (*Dasyprocta* sp.), one of several translocated continental fauna found on Carriacou, is a suitable proxy for analyzing the levels of interaction and the diversity of geographic origins tying the island to the continent. The agouti is a medium sized rodent, weighing 2 – 6 kg, in the family Dasyproctidae, native to the continental Neotropics and Trinidad. Agouti were introduced from the South American continent to the Lesser Antilles beginning in approximately ca. A.D. 500 (Newsom and Wing 2004: 107) and possesses a well-established archaeological distribution in the Lesser Antillean islands (Newsom and Wing 2004: 205; Giovas et al. 2019a), including on Carriacou (Giovas et al. 2012). Despite the agouti’s prevalence among Caribbean translocates, many questions remain as to its presence in pre-Columbian societies, including its taxonomic classification (Emmons 1990; Woods 1993; Emmons and Feer, 1997; Patton and Emmons 2015), and the degree to which it would have been managed by pre-Columbian groups (Giovas et al. 2012). Agouti was a valuable resource for Lesser Antilles pre-Columbian groups, seemingly incorporated in many aspects of daily life. On Carriacou’s two largest sites, Sabazan and Grand Bay, agouti remains occurs consistently in middens, from the beginning of occupation in approximately ca. A.D. 400, to site abandonment in ca. A.D. 1250 for Grand Bay and ca. A.D. 1400 for Sabazan. In the Caribbean, archaeological agouti remains are identified through morphological analysis at the genus level and often assumed through association as *D. leporina*, despite the lack of clarity regarding the agouti’s taxonomic classification. Making clear the taxonomic identification of archaeological agouti is significant because it can contribute to delineating the continental area involved in human interactions based on the animal’s range. Genetic analysis is the only way of substantiating morphological species identification for archaeological Caribbean agouti and clarify the nature and number of translocated agouti species.
1.2. Thesis Structure

This project aims to reconstruct the diversity of agouti-human interactions connecting to the Lesser Antilles, particularly Carriacou. Results contribute to this broad objective by addressing tangible unknowns about pre-Columbian Caribbean agouti including 1) the taxonomic classification for the Pre-Columbian Caribbean agouti analyzed in this study 2) population structure of pre-Columbian agouti and 3) the agouti’s population viability on Carriacou. Clarifying which agouti specie(s) were present in the pre-Columbian Caribbean allows us to use that species range to specify the continental area interacting with the Caribbean. Population structure for pre-Columbian agouti, including population viability on islands, can delineate patterns of inter-island interactions among human groups.

The diversity of taxa which were translocated to the Caribbean and broad home ranges of many of these taxa throughout northern South America and Trinidad (Newsom and Wing 2004; Lord et al. 2020) point to extensive patterns of human interaction across the continent. Lithic materials (Cody 1993; Epstein 1988; Watters 1997a; Costa et al. 2004; Garcia-Casco et al. 2013; Queffelec et al. 2018), pottery styles (Hofman et al. 2007, 2008, 2011), and petroglyph motifs (Dubelaar 1986; 1995, Roe 2009) further evidence the extant of these interactions, which reached from Guatemala and Belize in the North, to Amazonia and the Andes in the South. Genetic analyses of pre-Columbian guinea pig (C. porcellus) (Kimura et al. 2016; Lord et al. 2018, 2020), evidence the occurrence of two Caribbean haplotypes, suggesting the possibility of separate introductions from different source populations. However, so far, analyses of commensals, materials, and artifacts have only broached the extensive patterns of human interaction. Additional data from a broader range of datasets are needed to better appreciate and refine the complexities of human interactions in the Caribbean. This study contributes to reconstructing pre-Columbian interactions by incorporating genetic data from agouti, a novel commensal taxon. Incorporating genetic analyses of agouti to the study of pre-Columbian interactions may more concisely outline the continental area with which Caribbean groups may have interacted, produce an estimate for the frequency of agouti imports from the continent to the Caribbean, and delineate interaction patterns between specific Caribbean islands.
Patterns of human interaction suggest that pre-Columbian Caribbean agouti may have originated from multiple continental populations and may even represent different species of *Dasyprocta*. I hypothesize that the Caribbean agouti analyzed in this study originated from different continental populations, likely from the Guianas (Roe 1989: 272; Hofman et al. 2007, 2008, 2011: 78), Trinidad (Boomert 2010), or Venezuela (Hofman et al. 2007, 2008, 2011). Agouti is native to this area of northern South America, which shares many cultural connections with the Pre-Columbian Caribbean. Although it is understood that Pre-Columbian South America and the Caribbean were connected through exchange, previous analyses, concentrated primarily on artifact and stylistic correspondences (e.g., Hofman 2010; Hofman et al. 2007; Cody 1993; Garcia-Casco et al. 2013) have not been sufficiently refined as to show specific patterns of interaction. Genetic analyses of commensal fauna offer the possibility of much greater specificity in terms of reconstructing human interactions; each commensal taxon contributes objectively to this purpose. Among the Caribbean’s many continental translocates, agouti’s prominence consolidates the necessity of its use for improving the understanding human interactions in the Ceramic Age Lesser Antilles. Caribbean agoutis are generally assigned to the species *D. leporina*, although this identification has never been verified independent of morphological means. Following the agouti’s complex continental population structure and species’ overlapping home ranges, I hypothesize that many Caribbean translocates indeed belong to *D. leporina*, but that other species of *Dasyprocta* are also represented in the Caribbean. It is unclear whether Caribbean agouti was translocated to one or a few islands, then disseminated from these founding populations through pre-existing interaction networks, or if it was translocated directly from the continent throughout the Lesser Antilles. In line with the apparent ubiquity of pre-Columbian interaction across the islands, and the evidence of dissemination of guinea pig from founding populations (Kimura et al. 2016; Lord et al. 2018, 2020), I hypothesize that agouti was similarly disseminated throughout the Lesser Antilles from founding populations on one or a few islands.

In order to test my hypotheses, I analyzed 25 samples of agouti from the Carriacou sites of Grand Bay (ca. A.D. 390 to 1250) and Sabazan (ca. A.D. 400 to 1400) specifically the CytB gene of mtDNA. Another five agouti samples were included in this study for exploratory testing (a total of 30 specimens tested), one each from La Ramée (Basse-Terre); Toulourous (Marie-Galante); Belle Plaine (Grande-Terre); Macabou (Martinique);
and BK77 Grand Case (Saint-Martin). Sabazan and Grand Bay are the largest known pre-Columbian sites on Carriacou (Fitzpatrick et al. 2014), with diverse continental taxa exhibited at each site, including *Dasyprocta*. The CytB is a region of mitochondrial DNA functions as part of the electron transport chain. The circular nature and high copy number of mtDNA allows it a better chance of survival in ancient degraded biological materials and is conducive for the analysis of ancient Caribbean agouti samples. van Vuuren et al. (2004) sequenced 411 bp from the CytB region of 31 *D. leporina* specimens from French Guiana and Brazil. Modern reference sequences of agouti CytB from French Guiana and Brazil show the presence of a minimum of two clades (A and B) (van Vuuren et al. 2004), which are today sympatric in French Guiana. The established continental population structure reported by van Vuuren et al. (2004) will provide valuable comparative material for this study’s analysis of archaeological agouti sequences.

Based on the existing genetic and archaeological data, I anticipate that genetic results from this project should contain high levels of variation, demonstrating that the individuals originated from different populations. Genetic results may reflect variation similar to that reported by van Vuuren et al. (2004) in the analysis of modern agouti from French Guiana. In the case that my hypothesis is incorrect, and the agoutis originate all from one population, results would show low levels of variation. I hypothesize that the Caribbean samples belong to different *Dasyprocta* species. Sequences should show significant alignment with two or more of the three *Dasyprocta* species whose mitochondrial CytB has been sequenced. Alternatively, in the case that the Caribbean sample belongs to an agouti species whose mitochondrial CytB has not yet been sequenced, Caribbean samples should show more significant divergence. If Caribbean samples correspond exclusively to *D. leporina*, results should show significant alignment with modern reference *D. leporina* sequences. In the case that agouti were disseminated throughout the Lesser Antilles from founding populations on one or a few islands, I anticipate that genetic results from this project should be homogeneous between all of the islands. Direct translocations of agouti from the continent to various Lesser Antillean islands may be reflected by greater genetic variation, unless they are all coming from a single/same source population.

Below, in Chapter 2, I establish the theoretical framework for this project, the commensal model. In Chapter 3, I characterize pre-Columbian Caribbean history, archaeology and
biogeography, with specific attention to Carriacou, and the sites of La Ramée, Basse Terre; Tourlourous, Marie-Galante; Belle Plaine, Grande Terre; Macabou, Martinique; and BK77 Grand Case, Saint-Martin. In Chapter 4, I characterize the nature of pre-Columbian Caribbean translocates, and further expand upon the description of the agouti in Chapter 5. In Chapter 6, I describe my methods, and in Chapter 7, my results. I discuss my findings in Chapter 8. Finally, I conclude in Chapter 9 by synthesizing the findings in my study and offer new directions for future research.
Chapter 2.

The Commensal Model and its Genetic Application

This research employs a genetic commensal model as a conceptual basis to reconstruct pre-Columbian Caribbean interactions. Commensals are organisms that share close relationships to humans, affecting or providing functions for them in a variety of ways, and as such, can be utilized to investigate questions relating to past human populations (Matisoo-Smith 1994, 2017; Storey et al. 2012a). In particular, commensals were often traded or transported alongside human groups, including in the Caribbean, and can thus be used to reconstruct human interactions. Ancient DNA (aDNA) has proven useful tool for reconstructing the interactions of ancient human populations, including through commensal proxies. Below, I characterize the methods utilized to reconstruct human interactions based on the commensal model. I also review the use of genetic variations of commensals to determine the origins and interactions of populations through time, focusing on the mtDNA and the CytB. Finally, I discuss challenges for the analyses of ancient biological materials.

2.1. The Commensal Model for Reconstructing Human Interactions

Any commensal organism can be used to substantiate human mobility, as long as the assurance of anthropogenic involvement has been ascertained in translocation. Translocation is defined as the “intentional or accidental introduction of organisms to new ecosystems by humans” (Hofman and Rick 2018). To this definition, it is important to specify the introduction of live organisms. Identifying live translocation versus carcass imports is significant because these two practices entail varying socio-cultural and economic significance for the target import and further, have differing ecologic repercussions. However, the differentiation between these two practices is not one that is often acknowledged in the literature (but see Grouard 2002; Newsom and Wing 2004: 72; Giovas 2017), in part because it is difficult to evidence.

The translocation of commensals is an ancient and ongoing practice, dated in the archaeological record to approximately to 20,000 years B.P. (Flannery and White 1991).
Prehistoric translocations were sometimes substantial, with many commensal species used for reshaping the local ecology (e.g., Anderson 1952; Kirch 1982). Translocations are particularly visible on islands, or other physically isolated areas, where native animals and plants are distinct from nearby ecosystems (Hofman and Rick 2018). Many translocations have lasting impacts on native ecosystems (Grayson 2001), in particular in insular systems. Native island species are particularly sensitive to change due to their often small, non-replenishable populations and limited ability to adapt to environmental changes, increasing their vulnerability to new threats and predators (Hofman and Rick 2018).

Combined biological, paleontological, archaeological, and historical evidence (summarized in Figure 2.1) are required to secure the occurrence of prehistoric translocations (Hofman and Rick 2018). Biological evidence is required in terms of identifying an organism’s natural range and capacity for dispersal. Over-water dispersals typically require additional effort, such as swimming, rafting on makeshift natural constructions (Hofman and Rick 2018), or distribution by proxy, such as by wind or fauna (e.g., Forget and Milleron 1991). Morphology and behavior of the organism are also to be considered. Small, docile animals have a greater chance of being translocated, although prehistoric translocations of large and wild fauna have also been recorded (e.g., Vigne et al. 2012). Understanding reproductive behaviors is significant in identifying plant translocations. Flora that propagate using root suckers (e.g., Seelenfreund et al. 2010) or that have large seeds (e.g., O’Farill et al. 2011) are less prone to over-water natural dispersals. Introduced domesticates are an obvious signature of anthropogenic involvement, but commensals do not have to be domesticated to be translocated; undesirable “cargo” species can stowaway leading to unintentional translocation (e.g., Leach 2005; Kirch 2000: 18).

In terms of paleontological evidence, the absence of a taxon from the paleontological record and its sudden appearance coinciding with human arrival is revealing of anthropogenic involvement (Newsom and Wing 2004: 51). Translocations are implied archeologically, when a shared phylogeny ranges over broad distributions, in particular in the case of physically isolated areas (e.g., Martin et al. 2015). Demographic profiles, especially irregularities or aberrances in the distribution of taxa are also to be considered. Historic or ethnographic accounts of synanthropic patterns between humans and commensals advises an increased likelihood of translocation (e.g., Panagiotakopulu
In the absence of archaeological evidence, historic or ethnographic accounts can directly testify to translocations; for example, the only record for the translocation of elephants to Britain are the descriptions by Polyaenus and Cassius Dio (Strategems, 8.23.5; Historia Romana, 60.21, in Witcher 2013). Finally, translocations can be inferred through the construction of a linguistics phylogeny, where common names can indicate a shared history (e.g., Emory 1946; Green 1966, 1981; Pawley 1966).

Figure 2.1. Lines of evidence for identifying the occurrence of prehistoric translocations.

In recent year studies have turned towards incorporating genetic data from commensal species, which provide a number of advantages over human remains. Fauna are often preferred for commensal studies focusing on reconstructing human mobility. The
reproductive capacities of many plants allow them greater capacity for natural dispersal (Hofman and Rick 2018), making their translocation more difficult to establish. Archaeological plant materials typically contain only small amounts of endogenous aDNA (Storey et al. 2012a; Nistelberger et al. 2016), with amplification further hindered by secondary compounds—glycosides and alkaloids—that act as PCR inhibitors (Lan and Lindqvist 2018). Commensal remains often appear in archaeological contexts in higher quantities than human remains, although these of course remain a valued limited resource (Pálsdóttir et al. 2019). This abundance is of particular significance for more sensitive environments where preservation issues can limit the potential for extraction of aDNA. Commensals are also less prone to contamination than human remains, although DNA from chickens and pigs, which have been used to study Pacific human mobility (Storey et al. 2012b; Allen et al. 2001), and cattle are frequently present in commercial PCR reagents and can contribute to inadvertent contamination (Leonard et al. 2007).

2.2. Genetic Variations for Reconstructing Prehistoric Interactions

Analysis of genetic variations in ancient translocated flora and fauna can provide insight to the origins and interactions of ancient populations. This method was first applied in the Pacific using the Polynesian rat (*R. exulans*) (Matisoo-Smith 1994; Matisoo-Smith and Robins 2004) before being expanded to integrate other taxa such as for example chickens (*G. gallus*) (Storey et al. 2012b) and pigs (*Sus* sp.) (Allen et al. 2001). By identifying changes in non-recombining DNA such as mtDNA, or the Y-chromosome, archaeologists can trace maternal or paternal lineages and construct the phylogeny of a species. Polymorphisms and single Nucleotide Polymorphisms (SNPs) (commonly occurring polymorphisms which affect only single nucleotides (National Institute of Health 2020) act as biological markers which can indicate the geographic provenience of fauna and flora, from which can be inferred ancient human interactions.

The circular nature and high copy number of mtDNA allows it better chance of survival in ancient degraded biological materials, especially in challenging regions such as the tropics (e.g., Kehlmaier 2010; Grealy et al. 2016; Schroeder et al. 2018). Although the development of High Throughout Sequencing (HTS) has allowed the sequencing of entire ancient mitochondrial and nuclear genomes (e.g., Dabney et al. 2013; Green et al.
2010; Meyer et al. 2012; Grealy et al. 2017), individual regions of mtDNA are still a valuable resource in aDNA research.

Due to its high degree of conservation the CytB region of mtDNA, which functions as part of the electron transport chain, is a pragmatic choice for species identification (e.g. Clare et al. 2007) but is less often used to identify population variation. In contrast to hypervariable regions such as the control region D-Loop, CytB polymorphisms often reflect long-standing multi-generation changes and cannot fully characterize the level of variation between populations. However, CytB has been found in some cases to possess high levels of variation (Benton 2013, Kimura et al. 2016) and is thus adequate in providing estimates for population diversity.

2.3. Challenges for Genetic Analyses

Genetic analyses of ancient materials are often hindered by the fragility of biological materials, and their potential to for contamination. Below, I recapitulate the main challenges for the genetic analyses of ancient materials.

2.3.1. DNA Degradation and Preservation

Because of the sensitive structure of DNA, endogenous molecules are usually present in ancient biological materials only in small, low quality fragments (Briggs et al. 2007; Allentoft et al. 2012; Dabney et al. 2013). DNA degradation is caused by a wide range of internal chemical phenomena, which are triggered immediately after cell death. First, cells lose their ability for generating enzymatic repair, after which autolysis causes lysosomes to release digestive enzymes, which cleave the DNA’s sugar phosphate backbone. Skeletal tissues such as bone, dentine, and antlers are transformed through the physio-chemical processes of diagenesis (Kendall et al. 2017). A variety of taphonomic factors, including the physical nature of the tissue –collagen content, porosity, and crystallinity–, depositional environments–humidity, salinity, and pH–and microbes impact the loss of DNA.

DNA degradation cannot be viewed purely as a product of time (Burger et al. 1999; Poinar 2002; Sawyer et al. 2012; Allentoft et al. 2012). Temperature, more particularly heat, accelerate the degradation process (Lindahl 1993; Adler et al. 2011; Allentoft et al. 2012).
The challenge of aDNA retrieval from samples from tropical regions is well documented (e.g., Kumar et al. 2000; Reed et al. 2003), while samples from cold or temperate climates offer an increased chance for aDNA retrieval (e.g., Willerslev et al. 2007; Meyer et al. 2016). For this reason, aDNA studies have for the most part focused on archaeological samples originating from sites with annual mean temperature <20°C (Kistler et al. 2017). Although today, recovery of aDNA from tropical regions is still a delicate procedure, the increased understanding of ancient materials and the processes to which they are subject to (Nieves-Colón 2018), as well as methodological and technological advances (e.g., Meyer and Kircher 2010; Dabney et al. 2013; Grada and Weinbrecht 2013) has allowed for an increased success in analyzing aDNA from hot and humid environments, including from the Caribbean (Lalueza-Fox 2001, 2003; Mendisco et al. 2015; Kimura et al. 2016; Frantz et al. 2016; Lord et al. 2018, 2020; Schroeder et al. 2018; Nieves-Colón et al. 2020; Oswald et al. 2020; Nägele et al. 2020).

Chemical degradation in aDNA manifests in a wide range of processes (Dabney et al. 2013). Hydraulic depurination (the cleaving of the DNA's sugar phosphate backbone from a purine nucleic base) is one of the main causes in aDNA fragmentation (Dabney et al. 2013). Depurination results in the formation an abasic site, followed by non-enzymatic breakage. The process is catalyzed by acidic solutions (Lindahl and Andersson 1972; Graham 2007). Oxidation products of pyrimidines, known as hydantoins, form noncoding base derivatives. Hydantoins block the polymerase reaction, preventing the amplification and sequencing of DNA. Crosslinks (Pääbo 1989) are another type of blocking damage that occurs when a covalent link is created between two DNA strands or exogenous material and endogenous DNA. The un-conventional structure created by crosslinks prevents accurate sequencing by “blocking” the enzymatic reaction in PCR (Dabney et al. 2013). Hydrolytic deamination (the rupture of DNA by a water molecule resulting in the loss of nucleotides) primarily affects cytosine to thiamine transitions (Lindahl 1993; Hofreiter et al. 2001). Substitutions are located primarily at the DNA fragment ends. Chemical degradation appears in PCR products as misreads, transitions, deletions, or additions of nucleotides, and may even completely block the polymerase reaction.
2.3.2. Polymerase Fidelity

Chemical degradations are not the only processes which put in question the fidelity of the polymerase reaction. *Taq* polymerase, used for PCR amplification is the cause of damage-independent mis-insertions, which occur approximately every 1,000 bases (Graham 2007). “Jumping” PCR (Pääbo et al. 1990), promoted by DNA damage, causes the polymerase to jump from one template to another ensuing in the fusing of two templates. Chimeric sequences are subsequently amplified by PCR. The fidelity of DNA polymerase can be verified through multiple double-strand sequencing.

2.3.3. Contamination

The slightest handling of aDNA material carries the risk of contamination, whether in the field or in the lab. The risks for contamination begin even before recovery, as endogenous DNA is already subjected to contamination from exogenous microbial DNA during the degradation process (Willerslev and Cooper 2004). The power of PCR amplification has greatly magnified these risks, so that now even the most minuscule quantities of contaminant material can be replicated and expanded to produce erroneous results. Due to our shared biology with ancient hominins, human remains are especially affected by contamination. However, caution towards samples of any nature remains essential to avoid contamination.

2.4. Conclusion

The commensal model is an effective framework, proven successful at reconstructing human mobility in a number of settings, including the Caribbean (e.g., Laffoon et al. 2013, 2017; Giovas et al. 2016; Kimura et al. 2016; Frantz et al. 2016; Lord et al. 2018, 2020; Oswald et al. 2020). Improvements in DNA extraction methodologies, as well as the better understanding of degradation and contamination are expanding the range of aDNA capture and enlarging its application to diverse proxies, chronologies and geographies. Once aDNA is recovered, it can be analyzed in biogeographic and archaeological contexts. This study uses agouti as a basis for a Caribbean genetic commensal model. The biogeography and culture history of the pre-Columbian Caribbean, nature of Caribbean translocations, and more particularly of agouti, which I
detail in the following chapters, is significant for the construction and interpretation of a productive commensal model.
Chapter 3.

The Prehistory and Archaeology of the Lesser Antilles

Understanding the biogeography and culture history of the pre-Columbian Lesser Antilles is essential for building a comprehensive commensal model, allowing for a productive interpretation of continental origins and patterns tying the islands to the continent. The richness and diversity of imported faunal resources on Carriacou, an island located in the Grenadines, strongly suggests the involvement of Trinidad, north-eastern South America, and possibly Central America in frequent exchanges (Giovas 2012; Giovas 2016). Archaeological evidence and faunal remains on Basse-Terre, Marie-Galante, Grande-Terre, Martinique and Saint-Martin also point to close ties between these islands and the continent. Continental goods, including agouti, may have been translocated to one or a few of these islands, then disseminated through pre-existing interaction networks, or alternatively, would have been translocated directly from the continent throughout various islands in the Lesser Antilles. In this chapter, I discuss the Lesser Antilles’ geographic setting, ecology, and culture history, with particular emphasis on Carriacou. I also provide background for the sites of Grand Bay and Sabazan on Carriacou, La Ramée (Basse-Terre); Tourlourous (Marie-Galante); Belle Plaine (Grande-Terre); Macabou (Martinique); and BK77 Grand Case (Saint-Martin), which are central to this study.

3.1. Geographic Setting and Ecology

The Caribbean islands, located in and around the Caribbean Sea east of Central America, are commonly sub-divided into four archipelagos: the Bahamas, the Greater Antilles, the Lesser Antilles, and the Southern Caribbean Islands (Figure 3.1). The weather patterns and current systems summarized below are important in considering interactions between the islands and the continent. The tropical climate alternates between a wet and a dry season, occasionally disrupted by the occurrence of extreme environmental events, such as hurricanes, tsunamis, earthquakes, and volcanic eruptions (Cooper 2013). The shallow surrounding sea stabilizes temperature
throughout the region, although local contexts characterize each island with its own distinctive climate and ecology (Newsom and Wing 2004: 12 – 13).

This project will focus on the Lesser Antillean archipelago, extending ca. 800 km from Anguilla in the North to Trinidad in the South, the second largest of the four Caribbean archipelagoes. Geologically, the Lesser Antilles is a relatively recent formation, divided into a double arc of islands: an inner igneous arc of volcanic islands and an external sedimentary arc of limestone islands. Part of the archipelago is still volcanically active (Macdonald 1999, Serrand and Bonnissent 2018). The geology of the islands shapes their topography, climate, and vegetation (Newsom and Wing 2004). The external limestone arc is characterized by a lower topography, xeric vegetation and shallow surrounding waters. The internal volcanic arc is characterized by high elevations, with sharp cliffs falling into deep waters. The vegetation is overall mesic, except along the coasts and on smaller, lower-elevation islands which receive less rainfall and have a generally drier vegetation (DeWalt et al. 2016). Mangroves also border the coasts and protected bays of many of these islands (Newsom and Wing 2004: 78, 169).

The majority of the Caribbean islands sit in the Trade wind belt (Amador 1998), which produces a steady easterly flow across the region (Figure 3.2). In the southern Lesser Antilles, the prevailing winds are steadiest in winter and spring. The region’s oceanographic system is dominated by the Caribbean Current, which flows clockwise from the Lesser Antilles towards the Yucatan Channel to the Gulf Stream. The Current is fed by Atlantic waters, notably the North Equatorial (NEC) and North Brazil (NBC) Currents, and NBC Rings, which are funneled through the islands (Johns et al. 2002). The influx of fast flowing waters through the southeastern Caribbean passages, coupled with oceanographic and atmospheric influences, creates a swift flow (>25 cm/s) west of the Lesser Antilles (Wilson and Johns 1997; Centurioni and Niiler 2003; Richardson 2005).
Figure 3.1. The Caribbean, in relation to the Central and South American continents.
Note: Map courtesy of C. Giovas.
Figure 3.2.  The Caribbean’s main wind and current systems.
Note: Map background from Google Maps, accessed May 2020. (Google Maps 2020a)
3.2. Caribbean Culture History

The culture history of the pre-Columbian Caribbean is typically organized into four core periods (Rouse 1986, 1989): the Lithic and Archaic Ages (ca. 4000 B.C. – A.D. 550), which are typically grouped together due to the insignificant number of sites that are relied on for analysis (e.g. Fitzpatrick 2015; Keegan and Hofman 2017; Napolitano et al. 2019), the Early Ceramic Age (ca. 550 B.C. – A.D. 400/600) and Late Ceramic Age (ca. A.D. 400/600 – European contact). Although the earliest sites in the Caribbean, from Trinidad in the Lesser Antilles, have been dated as far back as ca. 6500 B.C. (Napolitano et al. 2019), low sea-levels exposed a land bridge during the Early Holocene, connecting the island to the continent (Boomert 2000; Tankersley et al. 2018), setting it apart culturally, ecologically, and geologically from the rest of the Caribbean (Boomert 2000; Farrell et al. 2018). Below, I describe the cultural landscape characterizing each of the four major Ages; synthesizing the existing literature, I condense the Lithic and Archaic Ages into a single “Archaic” phase.

3.2.1. The Archaic Age (ca. 4000 B.C. – 550 B.C.)

Around 4000 B.C., the first human groups, possibly from Meso- (Rouse 1992; Wilson et al. 1998; Wilson 2007) and South America (Callaghan 2003; Siegel 2015; Págan-Jiménez et al. 2015) traversed the Caribbean Sea by watercraft to settle islands throughout the Caribbean. The earliest archeological dates are from Cuba, Hispiniola, and Puerto Rico in the Greater Antilles (Napolitano 2019). In the northern Lesser Antilles, a few islands including Guadeloupe, Saint Martin, Barbuda, Antigua and Montserrat were colonized in the Archaic period after ca. 3000 B.C., but most of the southern Lesser Antilles islands, including Carriacou, lack conclusive evidence for Archaic occupation (Fitzpatrick 2006). It is evident that settlement of this area was postponed until the Ceramic Age, possibly due to volcanic activity (Callaghan 2010). Exceptionally, Grenada and Barbados possess some of the earliest verified dates South of the Guadeloupe passage, and were possibly occupied during the Archaic Age (Callaghan 2010; Fitzpatrick 2011; Napolitano 2019; Hanna 2019). Early Archaic groups seem to have clustered on the region’s largest (between 8900 km² (Puerto Rico) and 105,000 km² (Cuba)) and thus, most resource abundant islands in the Greater Antilles and their accompanying satellite islands in the northern Lesser Antilles. The islands
most proximate to the South American continent, Tobago, Aruba, Bonaire, and Curaçao were also colonized during this time (Fitzpatrick 2006; Napolitano 2019).

Archaic age groups were presumably egalitarian. Sites are primarily located on the coast. Groups were semi-mobile and relied in part on hunting and gathering practices. Archaic diets reflect great variety, suggesting the exploitation of local resources, which groups may have followed seasonally across the islands (Hofman and Hoogland 2003; Hofman et al. 2006). Yet, Archaic age groups also regulated their environment and engaged in food production. Both inter-island and continental translocations have been verified as taking place before ca. 550 B.C. Two inter-island faunal translocations have been identified and continental flora have been recorded in Archaic Caribbean sites on Cuba (de Armas et al. 2015; Pajón et al. 2007, from Keegan and Hofman 2017: 169), Puerto Rico (Rouse and Alegria 1990: 22), Nevis (Newsom 1993), and Trinidad (Pagán-Jiménez et al. 2015). Many of these translocated plants appear to have been cultivated (Newsom 1993: 226; Newsom and Wing 2004). Some wild resources also appear to have become cultivated at this time, such as marunguey (or coontie) (Zamia sp.), prevalent among Archaic assemblages from Hispaniola (Veloz Maggiolo and Vega 1982). Axes, hammers, scrapers, choppers (Alegria et al. 1955), mortars, and pestles (Boomert 2000; Pajón et al. 2007, in Ulloa Hung and Valcárcel Rojas 2013; Pagán-Jiménez et al. 2015) suggest systems of plant and landscape management. In addition, the sudden increase in concentration of charcoal particles in core sediments convey the possibility of human-induced disturbance, where fire would have been used for landscape management (Burney and Burney 1994; Siegel et al. 2005, 2015).

3.2.2. The Ceramic Age (ca. 550 B.C. – A.D. 1500)

From its beginnings in the 1920s (Fewkes 1922) until the 1990s, Caribbean archaeology has been dominated by the Culture History approach (Pestle et al. 2013), in which human groups are classified through material culture, notably ceramic designs, to reconstruct culture histories and migration routes. The Ceramic Age, during which ceramics become prolific across the pre-Columbian Caribbean, have garnered most of the focus of Caribbean archaeology. This emphasis is, in part, due to the poor preservation of archaeological materials which is characteristic of tropical regions (Sinelli 2013): “Irving Rouse once calculated that more than 90% of all pre-Columbian artifacts from the West Indies are made of clay” (Keegan 2000: 135). This focus is further
exacerbated by the scarcity of materials from the preceding Archaic Age, which was for a long time considered aceramic (e.g. Alegría 1965; Keegan 1994).

Ceramic classifications have for the most part standardized the classifications of pre-Columbian Caribbean groups. In particular, the classification system developed by Caribbean prehistory scholar Irving Rouse is commonly referenced in the literature. Although these classifications are recognized as problematic (Curet 2004; Wilson 2007; Rodríguez Ramos et al. 2010; Hofman and Carlin 2010; Hofman and Hoogland 2011; Curet 2014; Mol 2014; Fitzpatrick 2015; Keegan and Hofman 2017), they are still used to this day. Rouse’s ceramic classification system is organized into 1) styles (individual or local variances); 2) subseries (variances on an extended regional or chronological scale); and 3) series (the broadest classification, it encompasses multiple subseries) (Rouse 1952, 1963, 1986, 1992). These classifications are central to the phylogeny of Caribbean groups. In line with the focus of this thesis, I review the ceramic styles for the southern Lesser Antilles in the following paragraphs.

Starting around ca. A.D. 400, rare Archaic Age pottery (e.g. Alegría 1965; Keegan 1994) was replaced in the northern part of the region by stylistically distinctive and abundant Cedrosan Saladoid ceramics, thought to have originated from the Saladero series of eastern Venezuela (Rouse and Cruxent 1963). Cedrosan Saladoid ceramic assemblages are characterized by the variety and excellence of their wares, often decorated in polychromatic white-on-red (WOR) slip designs and zone incised crosshatching (ZIC). In the southern Lesser Antilles, Cedrosan Saladoid ceramics are relatively rare, in line with the later occupation of the islands, which started around ca. A.D. 400. Beginning around ca. A.D. 500/600, the Lesser Antilles evolved towards the regional style known as Troumassoid, divided into distinct regional substyles. In the northern Lesser Antilles, ceramic assemblages were defined as Mamoran Troumassoid. In the southern Lesser Antilles, ceramic assemblages progressed from the Troumassan Troumassoid (ca. A.D. 500/600 – 1000/1200) to the Suazan Troumassoid (ca. A.D. 1000 – 1500) (Rouse 1992). Troumassan and Suazan styles suggest influence from the Orinoco Basin in Venezuela (Hofman et al. 2007, 2008, 2011). Troumassan ceramics were thicker and not as finely made as Saladoid wares, decorated with red-and-black paint. Pedestal bases are diagnostic, three-legged griddles are introduced. Suazan ceramics privileged crude, coarse, often undecorated utilitarian wares, with finger-indented or inwardly thickened rims and scratched surfaces. Vessels often have legged
or pedestal bases. Finer, polished wares occur but are rare; decorations include red paint and incisions of simple geometric forms (Keegan and Hofman 2017: 222). Around A.D. 1250, the intrusion of Cayo ceramics in some of the southern Lesser Antillean islands is associated with the ‘Island Caribs,’ a group identified in the Lesser Antilles at the time of European contact (Boucher 1992), possibly a condensation of several groups which may have inhabited the Lesser Antilles during this time (Keegan 1996; Hofman 2013; Hanna 2019). Cayo ceramics are characterized by conical bodies with flat rims, decorated with small round perforations and may have been affiliated to the Koriaban complex of the Guianas (Boomert 1986, 1995, 2004, 2011).

**The Early Ceramic Age (ca. 550 B.C. – A.D. 400/600)**

The Early Ceramic Age is characterized by the rapid dispersal of the Saladoid people, who originated from the Orinoco basin in South America (Siegel 1989, 1996; Wilson et al. 1998; Wilson 2007; Keegan 2009). This dispersal descended from Puerto Rico through the previously uninhabited Lesser Antillean chain to Trinidad and Tobago. Trade, exchange, and mobility were ubiquitous throughout the islands and between the continent. The population expansion marking this period was accompanied by emerging socio-political complexity, with technologies (Drewett 2000, 2007, 49–65; Schultz 1995) and ritual artifacts (McGinnis 1997; Oliver 2009) showing increased regionalization over time, anticipating the rise of the complex Taíno chiefdoms during the late Ceramic Age.

Across the Antilles, people targeted sites in proximity to freshwater drainages, coastal plains, and horticultural land. Groups relied primarily on hunting and collecting marine resources (fish and marine invertebrates), but also hunted small terrestrial fauna (Newsom and Wing 2004; Stokes 2005; LeFebvre 2007; Krigbaum et al. 2013), and cultivated wild and domesticated plants (Berman and Pearsall 2000; 2008; Lane et al. 2008; Mickelburgh and Pagán-Jiménez 2012). Settlement layout was circular or semi-circular, with large, multi-family homes clustered around a central plaza, which served for burials (Siegel 1992, 1996; Keegan 2009). Patterns in spirituality and cosmology (Oliver 1997; Curet and Oliver 1998; Siegel 2010), lithics and other minerals (Chanlatte Baik 1981; Siegel and Severin 1993), as well as translocated fauna and flora (Newsom and Wing 2004; Wing 2008; Giovas 2017), which become abundant during this period, demonstrate a strong link to South America.
The Late Ceramic Age (ca. A.D. 400/600 – 1500)

Population expansion continued across the Late Ceramic Age, with the colonization of Jamaica and the Bahamas after ca. A.D. 550 (Callaghan 2008; Napolitano et al. 2019). Neither the Cayman Islands (Scudder and Quitmyer 1998) nor the North American continent (Fitzpatrick 2015) appear to have been reached by pre-Columbian Caribbean Amerindians, possibly due to the Cayman Islands’ low topography (Fitzpatrick 2015) in the case of the former, or the presence of pre-established, and perhaps hostile, groups in the case of the latter (Widmer 1988; Keegan 1995). Across the Caribbean, population size and the numbers of sites increased and grew more dispersed. Small settlements reached deeper inland, typically clustering around major coastal settlements (Curet 2005; Torres 2012). Many islands lacking permanent freshwater sources were settled for the first time, including Carriacou. In terms of subsistence, marine foods, in particular shallow inshore taxa, were privileged (e.g. Carlson and Keegan 2004; Delsol and Grouard 2016; Giovas 2016; Serrand and Bonnissent 2018), except on larger islands where some sites show preference for the more plentiful and diverse terrestrial fauna, such as the Coralie Site on Grand Turk (e.g. Carlson and Keegan 2004: 90).

Much of the developments in political organization, material culture, and ceremonial practices that characterized the Early Ceramic seem to have been prolonged and amplified throughout this time, perpetuating the cultural divide between northern and southern Caribbean. Petroglyphic motifs (Dubelaar 1986; 1995, Roe 2009; Hanna 2018), adornos (Roe 1989:272; 1995; Hofman et al. 2011: 78), and ceramic styles in the southern Caribbean primarily reflect influence from South America, in particular Venezuela and the Guianas. In the northern Caribbean, substantial population increase and complex regional dynamics lead to the emergence of the Taíno, socially complex chiefdoms that were present in the Greater Antilles at European contact. Pottery styles became coarser and less ornate, craftsmanship focused instead on objects of ceremonial purpose designed for the elite (e.g. Oliver 1997, 2000), demonstrating the increased significance of ritual. Ceremonial courts (bateys), ritual paraphernalia used in hallucinogenic ritual (e.g., cohoba ritual), and carved figurines of deities (zemis), became prominent in the Late Ceramic Age (Curet and Stringer 2010). The southern Lesser Antilles appears to have remained distinct from these more stratified societies, although ritual paraphernalia on certain islands (Kaye et al. 2004; Fitzpatrick et al. 2009a) point to the ubiquity of interactions which dominated the region.
3.3. Geographic Setting, Ecology, and Culture History of Carriacou

Carriacou is located in the Grenadines in the southern Lesser Antilles, located approximately 250 km off the coast of Venezuela. The largest island in the Grenadines, Carriacou is 32 km². The geology is volcanic with overlaying limestones (Pavia et al. 2013). The island’s interior is dominated by steep hills that extend almost 300 m above sea level. The climate is tropical and semi-arid, with temperatures averaging 30°C. Most of the rainfall occurs in summer and fall, the remainder of the year is typically very dry (Buckmire et al. 1985). The low topography limits orographic rainfall (Giovas 2013: 48). There are no permanent water sources on Carriacou, although natural accumulations of rainwater during the wet season provide some relief to the enduring drought. Carriacou’s terrestrial habitats include inland dry deciduous forest, rocky intertidal patches, seagrass beds, sand flats and coastal scrub. Marine habitats encompass shallow inshore reefs and waters to deep pelagic waters (Giovas 2013: 49-59).

The assemblages found on Carriacou fit within the ceramic classifications developed for the Windward Islands (Rouse 1992; revised by Petersen et al. (2004)), ranging from ca. 500 B.C. to A.D 1500. Ceramics, exotic continental fauna, and zoomorphic ceramics and adornos suggest strong influence from the continent, while objects of personal adornment, ritual paraphernalia, and guinea pig, believed to having been translocated from Puerto Rico, simultaneously tie Carriacou to islands in the North (Kaye et al. 2004; Fitzpatrick et al. 2009a; Waldron 2011; Quetta et al. 2012; Giovas et al. 2012; Giovas 2013; Lord et al. 2020). The first evidence of human occupation appears on the island during the terminal Saladoid (Early Ceramic Age) period, at ca. A.D. 400 (Fitzpatrick et al. 2009a; Napolitano 2019) making it among the earliest known settlements in the southern Lesser Antilles. The relative paucity of the Saladoid sherds, typically thin and finely painted wares, indicates that the Carriacou was settled only in the late Early Ceramic Age, during the Terminal Saladoid period (ca. A.D. 390 – 500) (Keegan 2000). Population size appears to drastically increase during the Troumassan Troumassoid period (ca. A.D. 500 – 1200) (Fitzpatrick et al. 2009a), with the abundance of coarser, less finely-made Troumassan ceramics (Giovas 2013: 69; Fitzpatrick et al. 2009b). By the Suazan Troumassoid (ca. A.D. 1000 – 1500), some sites are abandoned, and occupation of Carriacou’s two largest sites, Sabazan and Grand Bay, ends.
Table 3.1.  Colonization and occupation of Carriacou in relation to socio-cultural developments in the Caribbean

<table>
<thead>
<tr>
<th>Calendar Date</th>
<th>Carriacou Cultural Chronological Period (Ceramic Series)</th>
<th>Caribbean Cultural Chronological Period</th>
<th>Carriacou Socio-Cultural Developments</th>
<th>Caribbean Socio-Cultural Developments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre 550 B.C.</td>
<td>n/a</td>
<td>Archaic</td>
<td>n/a</td>
<td>Sites in the Greater Antilles, the northern Lesser Antilles, Grenada and Barbados become occupied. First continental translocations of flora.</td>
</tr>
<tr>
<td>550 B.C.</td>
<td>Early Saladoid/ Cedrosan Saladoid</td>
<td>Early Ceramic</td>
<td>n/a</td>
<td>Population expansion, increase in number and size of sites across the Caribbean. Regionalization between northern and southern Caribbean. Increased interactions between the islands and the continent, faunal translocations.</td>
</tr>
<tr>
<td>A.D. 400/600</td>
<td>Early Saladoid/ Cedrosan Saladoid</td>
<td>Early Ceramic</td>
<td>occupation of Carriacou begins, around ca. A.D. 400. Ornate, finely-made ceramics. First translocations of continental commensals.</td>
<td></td>
</tr>
<tr>
<td>A.D. 500/600</td>
<td>Troumassan Troumassoid</td>
<td>Late Ceramic</td>
<td>Increase in the number and size of sites, population growth.</td>
<td></td>
</tr>
<tr>
<td>A.D. 1000</td>
<td>Suazan Troumassoid</td>
<td>Late Ceramic</td>
<td>Increase in number of sites, particularly inland. Socially complex chiefdoms in the northern Caribbean, strong regional identity. Southern Caribbean maintains close ties to South America.</td>
<td></td>
</tr>
<tr>
<td>A.D. 1250 – 1400</td>
<td>Suazan Troumassoid</td>
<td>Late Ceramic</td>
<td>Ceramics become less refined, prioritizing utilitarian wares. Occupation Sabazan and Grand Bay ends.</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Appearance of Cayo ceramics on some of the islands in the Lesser Antilles.</td>
</tr>
</tbody>
</table>
3.3.1. The Sabazan and Grand Bay Sites

The sites of Sabazan and Grand Bay are located on the southern, windward coast of Carriacou, approximately 1.5 km directly overland from one another (Fitzpatrick and Giovas 2011) and are the largest known pre-Columbian sites on the island (Fitzpatrick et al. 2014). Similar environmental characteristics, as well as corresponding cultural assemblages, subsistence practices and radiocarbon dates tie the sites to one another and suggest contemporaneous pre-Columbian activity (Giovas 2013: 77). Significant coastal erosion at both sites has slashed much of the coastline (Bullen and Bullen 1972; Fitzpatrick et al. 2004; Kaye et al. 2005; Giovas et al. 2019), simultaneously emphasizing the magnitude of cultural deposits and damaging their integrity. Both sites have also been substantially disturbed by human economic activities (Wells 1902; Richardson 1975; Fitzpatrick et al. 2006), looting (Kaye 2003), tourism (Fitzpatrick et al. 2004), hurricanes (Kaye et al. 2005) and livestock grazing (Richardson 1975; Giovas 2013: 50).

Figure 3.3. Map of Carriacou with locations of Sabazan and Grand Bay sites. Note: Map courtesy of C. Giovas.
Sabazan Site Background

Sabazan is a large coastal village, occupied in Pre-Columbian times ca. A.D. 400 – 1400 (Fitzpatrick et al. 2004; Fitzpatrick and Giovas 2011), with the remains of a colonial-period plantation partially overlaying the prehistoric site (Giovas 2013: 63). The site is located in a sheltered crook of highland that separates it from Grand Bay and protects it from the regions’ dominating easterly trade winds (Newsom and Wing 2004: 13). The site itself is nestled at the bottom of a valley which slopes down toward shallow surrounding reefs, with easy access to pelagic waters (Giovas 2016). An ephemeral stream and pond in proximity to the site allow for rainwater accumulation during the rainy season. The vegetation is xeric (Newsom and Wing 2004: 109), mostly composed of dry woods that are inhabited by native fauna and historically introduced livestock (Giovas 2013). Taking into account the significant erosion that has affected the site, sherd scatter and midden placements, Giovas et al. (2019) estimate site size to have once covered at minimum 8000 m$^2$. Sabazan contains surface sherd, shell, and bone scatters, hearths, post-holes and burials (Giovas 2013). Other evidence of settlement includes the presence of deep, stratified midden deposits, up to 1.5 m in thickness. These deposits become progressively shallower as they extend inland, demonstrating site expansion beginning around approximately ca. A.D. 800. Population increase is also suggested through increasingly rapid accumulation of deposits. Ceramic styles are characterized by a combination of late Saladoid, Troumasssan Troumassoid, and Suazan Troumassoid (Fitzpatrick et al. 2009a, 2014; Giovas 2016). Worked shell and bone objects found at the site include one fishhook, and “bowtie” sea turtle (Cheloniidae family) and deer (Mazama americana) bone artifacts (Fitzpatrick et al. 2009a; Giovas 2013).

Sabazan Site Excavation

Fieldwork at Sabazan was completed between 2003 and 2014, with an additional field period in 2018 consisting of pedestrian and geophysical surveys, as well as five 30 x 30 cm test pits (Giovas et al. 2019). Excavations began in 2005 with a 50 cm x 50 cm column sample. Subsequently, three 1 x 1 m trenches (Trench 1, Trench 2, Trench 3) were opened in 2007 (Figure 3.4). Trench 1 was subsequently enlarged in 2008 to 2 x 1 m. The main excavations were conducted approximately 40-50 m inland, within dry forest vegetation (Giovas 2016). Trench locations were selected based on the density of artifact scatter and the obstructions caused by vegetation (Giovas 2013). The trenches were excavated stratigraphically by hand-troweling, with 10 cm arbitrary levels dividing
stratigraphic layers where necessary. All excavated sediment was sifted using nested 6.4 mm and 1.6 mm mesh screens. In addition to the trenches, a number of column samples and features have been excavated. Faunal samples excavated from Sabazan were initially wet screened using seawater, then cleaned and rinsed with fresh water and dried in the sun. Samples were stored for approximately two weeks in non-air-conditioned facilities, in plastic zipper-sealed bags, before being returned to North America.

Figure 3.4. Map of Sabazan site showing location of trenches.
Note: From Giovas (2013: 94). Reproduced with permission.
Grand Bay Site Background

The Grand Bay site is a large pre-Columbian coastal village site, located on the eastern side of Carriacou, to the south of the bay which shares its toponym. Radiocarbon dates place pre-Columbian site occupation ca. A.D. 380 – 1250 (Fitzpatrick et al. 2004; Fitzpatrick and Giovas 2011), although the site may have been reused for burials after its abandonment until ca. A.D. 1450 (personal communication Fitzpatrick 2012, in Giovas 2013: 62). Ceramic analysis suggests an increase in population during the Troumassoid period (Kaye et al. 2011; Casto 2015: 16), similar to Sabazan. Covering an estimated total 6000 m$^2$ (Giovas 2013: 71), the site extends 120 m along the coastline (Fitzpatrick et al. 2007). Grand Bay is located on a small grassland covered ridge, overgrown with manchineel (*Hippomane mancinella*), cactus, and thorny scrub. The ridge on which the site sits is directly exposed to the easterly trade winds. Grand Bay provides easy access to diverse marine environments, with rocky outcrops, seagrass and sandflats (Giovas 2013: 72), but coral reefs are located 1.5 km offshore. Isotopic evidence from bone collagen ($\delta^{13}$C$_{co}$ and $\delta^{15}$N) and bone apatite ($\delta^{13}$C$_{ap}$) confirms the marine protein contribution to diet at Grand Bay (Krigbaum et al. 2013). A number of gullies in close proximity to the site might have allowed for rainwater to accumulate.
during the rainy season. Evidence for settlement includes the presence of hearths, numerous burials, and deep, stratified midden deposits. Over 60 potential post-holes, suggest the presence of large architectural features. The abundance of raw shell material evokes the occurrence of manufacturing activities. Artifacts found at the site include an armadillo-shaped ceramic pestle (Quetta et al. 2011), vomit spatulas, inhaling bowls (Fitzpatrick et al. 2009a, 2009b), and three-pointer stones or zemis (Kaye et al. 2004).

**Grand Bay Site Excavation**

Fieldwork at the Grand Bay site began in 2004, and to date, has received most of the archaeological attention on Carriacou (Fitzpatrick et al. 2014). The site is divided into eight 5 x 5 m trenches set on a North-South axis, themselves subdivided into 25 1 x 1 m units (Figure 3.6). Trenches 561, 562, 563, 592, and 622 were partially excavated, with some units remaining untouched or inaccessible. Trenches 415 and 446 were fully excavated. The trenches’ locations targeted both residential structures (Trenches 561, 562, 563, 592, and 622) and midden deposits (Trenches 415 and 446). All trenches were excavated in arbitrary 10 cm levels by hand-troweling. Four squares from Trenches 415 and 446 were sifted using 6.4 mm screens, and one quad (50 x 50 cm column) from each of these four squares was sifted using nested 6.4 mm and 1.6 mm mesh screens. In addition to the trenches, a number of features and portions of the site at high-risk of erosion have also been excavated. Faunal samples excavated from Sabazan were initially wet screened using seawater, then cleaned and rinsed with fresh water and dried in the sun. Samples were stored for three up to seven years in plastic zipper-sealed bags in non-air-conditioned facilities before being returned to North America.
Sabazan and Grand Bay Mammalian Assemblages

Mammals constitute 6.5% NISP of Sabazan total vertebrate NISP and 2.3% of vertebrate NISP of the preliminary analysis conducted on the Grand Bay assemblage (LeFebvre 2005, 2007; Giovas 2013: 197, 223). Agouti (*Dasyprocta* sp.), opossum (*Didelphis* cf. *marsupialis*), and rice rat (*Oryzomyini* tribe) are recurrent at both sites, two of which, the agouti and the opossum, are continental translocates (Newsom and Wing 2004: 87). In addition, a number of other South American species are found on Carriacou: armadillo (*Dasypus* sp.) at Sabazan and guinea pig (*C. porcellus*) and peccary (*Tayassu/Pecari* sp.) at Grand Bay (Giovas et al. 2012). Genetic analyses of
pre-Columbian guinea pig (*C. porcellus*) (Kimura et al. 2016; Lord et al. 2018, 2020), evidence the occurrence of two Caribbean haplotypes, suggesting the possibility of separate introductions from different source populations. One of the haplotypes was shared exclusively in the Caribbean between samples from Tibes and Carriacou so that Carriacou guinea pigs were likely translocated from Puerto Rico (Lord et al. 2020). Agouti remains are recorded from the Early Period of occupation (ca. A.D. 400 – 850) and may be present in earlier, yet to be excavated, Initial Period deposits, persisting throughout the remaining period of settlement (Giovas 2013: 197). Overall however, like most continental translocates in the Caribbean, agouti does not possess any significant presence at Sabazan (Giovas 2013: 34) and represents <1% of total Sabazan vertebrate and invertebrate NISP (Giovas 2013: 197). Most of the faunal assemblages at Grand Bay were never analyzed in detail, but, similar to Sabazan, agouti is recorded early in site occupation. The mammalian assemblages from Sabazan and Grand Bay demonstrate clear connection between Carriacou and the continent, with diverse taxa exhibited at each site.

### 3.4. Pilot Testing Sites

Six samples from six islands, Carriacou (Grand Bay); Basse-Terre (La Ramée); Marie-Galante (Tourlourous); Grande-Terre (Belle Plaine); Martinique (Macabou); and Saint-Martin (BK77 Grand Case), were included within this study for exploratory testing. Below, I provide the geographic setting, ecology, and culture history for these sites, excluding Carriacou, whose background is specified above (see Section 2.3).

#### 3.4.1. La Ramée, Basse-Terre

Basse-Terre is one of the islands of Guadeloupe, in the northern Lesser Antilles. La Ramée is located to the North of the island, in the commune of Sainte-Rose. The following data originates from the archaeological report by Casagrande et al. (2010). The La Ramée site is situated in proximity to the coast, on an eroded surface which slopes towards the northern Grand Cul-de-Sac Marin bay. Two rivers, Rivière de la Ramée to the west and Rivière Salée to the east run in proximity to the site. South-east, the site is delineated by a tree hedge and a colonial aqueduct, destined to feed the mill of La Ramée. The La Ramée site was first surveyed in the 1990s and 2000s. Excavations
were completed in 2007, over a 6248 m² area. 37 trenches were opened using mechanized shovels. Radiocarbon dates place site occupation between ca. A.D. 320 to 1000. The oldest dates from the site occur in an isolated area, indicating that site occupation likely took place in different phases. La Ramée was initially inhabited in the Early Ceramic, then likely expanded to its final size within the Late Ceramic. Excavations identified seven “locus” concentrating archaeological materials. Architectural elements include hundreds of postholes, middens, one burial, and “combustion structures,” built with calibrated blocs. Artifacts found at the site include sherds, shell and lithic tools, lithic materials, and three-pointer zemis. Ceramics are Cedrosan Saladoid evolving towards Mamoran Troumassoid styles. Body ornaments are rare, with only two lithic pearls recovered. Vertebrate faunal remains (11217 NISP) include mammals (1425 NISP), fish (6798 NISP), birds (380 NISP), and reptiles (2614 NISP).

3.4.2. Tourlourous, Marie-Galante

Marie-Galante is an administrative dependence of Guadeloupe, located to its south-eastern coast, in the northern Lesser Antilles. Tourlourous in the south-east of the island, 100 m from the sea. The site was discovered in the 1960s (Barbotin 1970).
In 2001, developmental projects lead to preventive diagnostic investigation of site. In 2002, the site was excavated with two backhoes, in 10 and 20 cm levels. Mechanized excavations were complemented with manual excavation and screening of 1 m² “test zones.” A second preventive excavation of 1273 m² was undertaken in 2012, prior to the expansion of a municipal stadium which now overlays the site. The two excavations revealed multiple occupation phases, between the 3rd and 13th centuries, late Cedrosan Saladoid (ca. A.D. 237 – 778) succeeded by Troumassan Troumassoid in the later centuries (Serrand et al. 2018). The site encompasses numerous structures (>150), primarily postholes, a midden, and a double burial. Evidence for shell manufacture at the site is plentiful and diverse; worked shell includes tools, beads, pendants, rings, and three-pointer zemis (Serrand et al. 2018). Vertebrate fauna consists primarily of fish, turtles, and small mammals, and includes three worked bones (Colás 2003).

Figure 3.7. Satellite image of the Toullourous site.  
Note: From Google Maps, accessed June 2020. (Google Maps 2020d)
3.4.3. Belle Plaine, Grande-Terre

Grande-Terre is one of the islands of Guadeloupe, in the northern Lesser Antilles. Belle Plaine is located to the north west of the island, in the commune of Les Abymes. The Belle Plaine site is located in a marshy region on the western coast of the Grand Cul-de-Sac Marin bay. The area is generally impoverished of pre-Columbian sites (Delpuech et al. 2003: 102 – 104). The data following originates from the archaeological report by Stouvenot (2010) and Stouvenot and Yvon (2010).

Figure 3.8. Satellite image of the Belle Plaine site.  
Note: From Google Maps, accessed June 2020. (Google Maps 2020e)
The Belle Plaine site, discovered in 2006, is the midden from a large village. It is located on a knoll approximately 10 m high. The site, over 40 cm deep, covers a 40,000 m² surface. The site is covered in “prairie” vegetation which is maintained by livestock grazing. The sea is 2 km away, separated from the site by mangrove forests difficult to travel on foot. Radiocarbon dates place site occupation between ca. A.D. 1040 to 1274. A probing unit measuring 2 x 1 m was excavated by hand-troweling in 15-20 cm arbitrary levels. Artifacts found at the site include plain undecorated wares, but lithic tools and materials are rare. Ceramics are identified as Mamoran Troumassoid. Faunal remains show a strong preference towards molluscs, vertebrates are much rarer and include fish, and rice rat (Oryzomys tribe).

3.4.4. Macabou, Martinique

Martinique is located in the northern Lesser Antilles. The site of Macabou is located in the most south-eastern cape of the island, in the commune of Le Vauclin. The site, covering 20,000 m², is located on a knoll bordering a mangrove. A sandy bay extends against the entire north and eastern lengths of the site, offering access to rocky outcrops and reefs. The vegetation is xeric, reflecting the overall aridity of the climate. Excavations first started in 1972, 1977, and 1979, and were more recently resumed from 2005 to 2008. Six areas were opened during the first excavation. Excavations continued with 15 survey plots measuring from 1 to 16 m². Archaeological deposits extend as far as 95 cm in depth. Sediment were sifted with water through 2,7 mm screens. Radiocarbon dates place site occupation between ca. A.D. 1100 to 1400, including late Troumassan Troumassoid and early and late Suazan Troumassoid components. The site includes habitation structures, middens, fire-pits, and human burials (Grouard 2015). The site presents a rich diversity of vertebrate and invertebrate fauna. Mammalian species include rice rats, dogs, bats (Chiroptera), manatees (Trichechus manatus) and agouti, which are well represented (NISP 53, MNI 12) (Grouard 2013: 145).

3.4.5. BK77 Grand Case, Saint-Martin

Saint-Martin is located at the very northern border of the Lesser Antilles. The Grand Case site is located in the north-east of the island on a sandbar imbedded near Grand Case bay, 200 m from the sea. The site is in slight elevation, 3 m high on a knoll, and covers a surface of 10,000 m². Grand Case is a large village from the Late Ceramic,

Figure 3.9. Satellite image of the Grand Case site.
Note: From Google Maps, accessed June 2020. (Google Maps 2020f)

The site is organized into a central habitation zone surrounded by midden. Burials are arranged around the central plaza. Architectural elements include ovens, destined for the high-level production of lime, workbenches, and postholes indicating wood-pillar habitations. Charred remains of diverse mollusk, crustacean, and fish species recovered
from the Grand Case middens point to the village’s reliance on marine resources. Ceramics, primarily plain utilitarian wares, correspond to the Troumassoid style. The site houses evidence for the full production sequence of lithics. Operations of shell manufacture and pearl production have also been identified.

### 3.5. Conclusion

Around ca. 4000 B.C., human groups, originating from continental America migrated to the Greater Antillean Archipelago, subsequently colonizing nearly every island in the Caribbean. The arrival of human groups and ensuing interaction lead to major cultural changes, which, over time, exposed growing regional differences between the northern and southern Caribbean. Throughout the remainder of the Caribbean’s pre-Columbian’s history, the northern Caribbean manifested an increasingly marked regional identity, while the southern Caribbean, in particular the southern Lesser Antilles where Carriacou, Basse-Terre, Marie-Galante, Grande-Terre, Martinique are located, maintained its intimacy with the continent. Saint-Martin, located in the Lesser Antilles, shares a closer cultural affiliation to islands in the North. Many items on Carriacou, including ritual paraphernalia, objects of personal adornment, exotic continental fauna, and zoomorphic ceramics and *adornos* (Kaye et al. 2004; Fitzpatrick et al. 2009a; Waldron 2011; Quetta et al. 2012; Giovas et al. 2012; Giovas 2013; Lord et al. 2020) evidence interaction both with the northern Caribbean and the continent. The agouti’s prevalence among Caribbean translocates at Sabazan and Grand Bay, Carriacou’s two largest sites, offers an ideal opportunity for investigating the human interactions which connected Carriacou to the continent through genetic research. Agouti also occurs over a broad geographic range in the Lesser Antilles, including on Basse-Terre, Marie-Galante, Grande-Terre, Martinique, and Saint-Martin, and offers the potential for uncovering the interactions connecting islands to the continent and each other.
Chapter 4.

Translocates in the Caribbean

In the Caribbean, translocations of fauna and flora have been shown to occur as early as the Archaic, accelerating throughout the Early and Late Ceramic. Translocates would likely have been sources of subsistence (Lefebvre et al. 2019), companionship (Plomp 2011), possible pest control (personal communication Voss 2017, in Giovás 2019b), or used as forms of adornment (Giovás 2013: 71), and more generally, were manipulated to alter and ameliorate newly settled landscapes (Stahl 2009; Boivin et al. 2016). Despite the Caribbean’s high levels of ecological diversity, most islands lack large, endemic fauna, which might have initiated the need for many of these translocations (Stahl 2009; Giovás 2017). In the following chapter, I discuss the chronology of pre-Columbian Caribbean translocations. I review the lines of evidence by which Caribbean translocations can be identified. I also consider the degree of management, function, distribution, and ecological impacts of translocates.

4.1. Chronology of Translocations

Both inter-island and continental translocations have been verified as taking place before 550 B.C Flora native to Central America such as sapodilla (Manilkara sp.) (Pearsall 1983; Newsom 1993: 144), yellow sapote (Pouteria campechiana) (Rouse and Alegria 1990: 22), wild avocado (Persea americana) (Rouse and Alegria 1990: 22 – 23), sweet potato (Ipomoea batatas) (Pagán-Jiménez et al. 2015), chili pepper (Capsicum spp.) (Pagán-Jiménez et al. 2015), maize (Zea mays) (Pagán-Jiménez et al. 2015), and evening primrose (Oenothera sp.) (Newsom 1993) have been recorded in Archaic Caribbean sites in the Antilles. Many of these plants appear to have been cultivated (Newsom 1993: 226; Newsom and Wing 2004). Only two inter-island faunal translocations have been identified, and continental translocations of fauna remain unknown. Remains of hutia (Isolobodon portoricensis), a species native to Hispaniola, were found in an Archaic Age layer at the Angostura site, on Puerto Rico (Rivera-Collazo 2015). Remains of the large flightless DeBooy’s rail (Nesotrochis debooyi), were uncovered at archaeological sites on Saint Thomas, Saint Croix, Saint John, and maybe Virgin Gord in the Virgin Islands, where it does not occur paleontologically (Wetmore...
1918, 1937; Brodkorb 1974; Olson 1974; Olson and Pregill 1982). Although the home range of the DeBooy’s rail is still uncertain (Steadman et al. 2013), its presence in paleontological deposits in Puerto Rico suggests it would have been native to that island. Saint Thomas possesses verified Archaic dates (Napolitano et al. 2019), indicating a possible Archaic translocation from Puerto Rico, although further chronometric investigations are needed for the islands and sites on which the rail occurred archaeologically.

Around ca. 400 B.C., the magnitude of translocations substantially increased with the arrival of Early Ceramic Age groups. Many fauna were translocated, including guinea pig (C. porcellus) (Giovas et al. 2012; LeFebvre and DeFrance 2014), opossum (Didelphis cf. marsupialis) (Grouard 2002; Giovas et al. 2012, 2016; Wing 2012), armadillo (Dasypus cf. novemticus) (Keegan, 1991; Wing 1991, 2001; Haviser 1997; Grouard 2002; Giovas et al. 2012), dog (C. lupus familiaris) (Grouard et al. 2013) or possibly other canids (Stahl 2013), and most importantly for this research, agouti (Dasyprocta sp.) (Wing 2001, 2012; Giovas et al. 2012), see Newsom and Wing (2004) for a comprehensive review of translocated fauna. Peccary (Tayassu/Pecari sp.) (Fandrich 1991; Narganes Storde, 1985, 2005; Giovas et al. 2012), brocket deer (Mazama sp.) white-tailed deer (Odocoileus virginianus) (Grouard 1997; Fitzpatrick et al. 2009a; see Giovas 2017), jaguar (Panthera onca) (Narganes Storde 1985, 2005; Rodriguez Lopez 1991) have also been recovered from a number of islands, primarily as worked bone and teeth. The offshore islands of the Southern Caribbean present the greatest introduced species richness, including exotic species that can be found in none of the other Caribbean archipelagoes: tapir (Tapirus terrestris), ocelot (Leopardus pardalis), capuchin monkey (Cebus paella), red howler monkey (Alouatta seniculus), margay cat (Leopardus wiedii), crab-eating fox (Cerdocyon thous), and long-tailed weasel (Mustela frenata) (Antczak 1995; Newsom and Wing 2004: 72). Most of these exotic fauna were recovered as modified bone or were bones pertaining to the head (Antczak 1995). Some reptiles, such as freshwater turtles (Testudinidae family) and iguana (Iguana iguana) (Grouard 1997) may also have been translocated. The home ranges of many of these Caribbean translocates are spread throughout Central and South America (Newsom and Wing 2004), indicating the potential for broad patterns of human interaction. Recent genetic analyses suggest that Caribbean guinea pigs likely would have originally derived
from Peruvian populations and been brought to the Caribbean through pre-existing human interaction networks (Edana et al. 2020).

4.2. **Identifying Pre-Columbian Caribbean Translocations**

Most Caribbean faunal translocations are inferred through their absence from paleontological contexts (e.g., LeFebvre et al. 2019). Direct radiocarbon analyses of various faunal skeletal elements have allowed for greater resolution into the beginnings of continental faunal translocations (e.g., Giovas et al. 2012), although dating of associated artifacts can also be used (e.g., Lefebvre et al. 2019), further binding the movement of commensals to pre-Columbian human mobility. Most Caribbean faunal translocates are non-volant mammals and lack the capacity for long-distance swimming. The distance between the islands and the continent, strong current dividing the islands (Wilson and Johns 1997; Centurioni and Niiler 2003; Richardson 2005), and inability of many of the translocated fauna to overcome these conditions affirms the likelihood of anthropogenic transport. The large seed sizes for many floral translocates, such as avocado or sapodilla, undermines the likelihood that these would have been dispersed through natural means. The natural continental ranges of many flora and fauna in Central and South America further reaffirms the nature of many Caribbean translocates (Newsom and Wing 2004). However, some translocates' natural ranges include some islands in the Caribbean (e.g., hutia (subfamily Capromyinae), peccary, and opossum. Other species (e.g., Green Iguana (*Iguana iguana*) may have dispersed through an anthropogenic-assisted translocation (Pregill et al. 1994: 32), natural over-water dispersal (Censky et al. 1998), or a combination of the two (Stahl 2009), complicating their status as pre-Columbian translocates.

4.3. **Distribution**

The archaeological distribution of pre-Columbian translocates has been proposed (e.g., Wing and Wing 1995; Newsom and Wing 2004; Wing 2008) as following the principles of biogeography offered by MacArthur and Wilson (1967), which suggests that frequency of occurrence of a translocated taxon decreases progressively as it moves farther away from its home range. However, while the occurrence of some translocates, like the agouti, decreases as sites shift farther away from South America (Newsom and Wing
2004: 206), others, like the guinea pig, which is found primarily in the Greater Antilles (LeFebvre and deFrance 2014), oppose this model completely. Instead, the variation in introduced species richness underlines the cultural demarcation between the northern and southern Caribbean and their varying connections with the continent. The Lesser Antilles boasts the greatest diversity of translocated taxa, with a clear interruption at the northern end of the archipelago, underlining this area’s close connection to the continent (Hofman et al. 2011). Present-day distributions of known pre-Columbian translocates are likely affected by post-contact introductions (e.g., opossum), so that it is unclear whether current populations represent pre-Columbian or colonial translocations, or the mixing of both populations. However, some taxa (e.g., guinea pig, deer) no longer occur on the islands where they were introduced prehistorically.

4.4. Function

Most commensal translocates including opossum, agouti, armadillo, guinea pig, and opossum appear archaeologically in middens as disarticulated remains and lack any cultural modification beyond those associated with consumption (e.g., butchery, burning) (e.g., Wing 1996; Grouard 2002, 2010; Steadman and Stokes 2002; Newsom and Wing 2004; Giovas et al. 2012, 2016; Wing 2012; LeFebvre and deFrance 2014; Laffoon et al. 2016), so that a supraculinary function is often difficult to envision, let alone evidence. Armadillo is described by DuTertre (1667: 514) as having been a major source of subsistence on Grenada at the time of European contact.

Dogs are also found in middens (Carlson and Steadman 2009), however, they appear consistently as burials alongside human burials during the Early Ceramic Age (Newsom and Wing 2004; Grouard et al. 2013), which suggests that they possessed a supra-dietary function. Dogs would likely have been used for both food and companionship (Roe 1995; Plomp 2011) and may also have functioned as valuable social exchange items, such as in the neighboring Amazon (e.g., Fock 1962; Vaughn Howard 2001; Mans 2012). In some cases, guinea pig may have been associated to non-domestic refuse contexts (Curet and Pestle 2010), although their status within the Caribbean remains unclear (deFrance 2010; LeFebvre and deFrance 2014). Some species, such as peccary (*Taysassu/Pecari* sp.) and deer (*Mazama* sp. and *Odocoileus* sp.) may have been imported to the islands exclusively as carcasses, destined exclusively for craft production (Narganes Storde 1985, 2005; Giovas et al. 2012; Laffoon et al. 2014, 2016;
Giovas 2019b). Dog (Newsom and Wing 2004: 137; Grouard et al. 2013) and agouti (Grouard 2007; Giovas 2019b) remains have also been recovered as worked bone.

Alternatives for the functions of faunal translocates, have also been proposed using the animals’ behaviors and biology. Robert Voss (personal communication Voss 2017, in Giovas 2019b) suggested that the opossum’s natural tolerance to Bothrops spp. venom (Voss 2013; Voss and Jansa 2012) and tendency to prey on snakes would have made it an ideal biological tool for pest control. Ethnographic accounts support the pertinence of this argument. Opossums were present on Martinique in colonial times (Ballet 1894: 4), where they are not found archaeologically. They may have been introduced to Martinique to control the infestations of venomous snakes described in ethnohistorical accounts (Ballet 1894: 468). These same accounts remark on the absence of snakes from Guadeloupe, where opossum has been recovered archaeologically, post ca. A.D. 400 (Grouard 2002). Similarly, other commensals might have been employed for various forms of pest control. Armadillo has been recovered from archaeological contexts in the southern Lesser Antilles (Keegan 1991; Wing 1991, 2001; Havisier 1997; Steadman and Jones 2006; Giovas et al. 2012) and Guadeloupe (Grouard 2002). D. novemcinctus are generalist insectivores (Redford 1985) and may have been introduced as a way of controlling the ants and termites that are said to have plagued the crops and settlements of pre-Columbian groups (Ballet 1894: 59, 63). da Silveira Anacleto (2007) notes that Nasutitermes, whose type species, N. corniger is native to the Southern Caribbean Islands and the Antilles (Evans et al. 2013), are dominant to D. novemcinctus’s diet.

4.5. Domestication and Management

Among the dozens of translocates, only the dog and the guinea pig were domesticated (Newsom and Wing 2004), although archeologists have speculated that a number of Caribbean translocates, notably agouti and hutia, were assisted by human management (Newsom and Wing 2004; Lefebvre and deFrance 2018). Management may be understood as the: “intentional human influence over an animal and/or its environment in such a way that promotes increased abundance and availability for exploitation” (LeFebvre et al. 2019). Archaeologist generally assume pre-contact indigenous people managed the commensal animals they introduced, however, for the most part, the precise relationships between translocated species and humans remains unclear. At issue is the intensity of potential management by human and their intentions for doing so.
(Lefebvre and deFrance 2018). Resolving such issues requires robust zooarchaeological sampling across wide chronological and geographic scales, and the incorporation of multiple datasets (e.g., LeFebvre et al. 2019). Hutia has so far been the only non-domesticate whose management in the Caribbean has been carefully investigated (Lefebvre and deFrance 2018; LeFebvre et al. 2019). However, Caribbean commensals are the current focus of a number of studies (e.g., LeFebvre et al. 2019; Lord et al. 2020; Oswald et al. 2020) which may contribute towards the better understanding of human management.

No physical evidence for faunal captivity, such as remains of enclosures or accumulations of coprolites indicating the concentration of fauna, have persisted archaeologically (Giovas 2019b; Lefebvre et al. 2019), although historic accounts allude to the captive control of hutia in the Greater Antilles (Lovén 1935 in Giovas 2019b). Grouard (2007) suggests the islands themselves would have served as natural enclosures. Ethnohistorical accounts describe agouti roaming free in the mountains (Ballet 1894: 362). However, zooarchaeological evidence points to the potential management of certain translocates, showing the specific selection of mature hutia for exploitation at Palmetto Junction, in the Turks and Caicos (DuChemin 2005; Lefebvre et al. 2018). Garden hunting (Linares 1976), whereby hunters target animals attracted to cultivars and garden plots (e.g. Nokkert 2002: 65; Lefebvre et al. 2019), has repeatedly been proposed as a minimal, yet intentional, form of faunal management imported from South America’s tropical lowlands (Linares 1976), having the advantage of providing both animal protein and crop safety. According to modern day studies on South American subsistence crops (Stahl 2014), commensal species which may have been procured through garden hunting include agouti (Dasyprocta), paca (Cuniculus), collared peccary (Tayassu), armadillo (Dasypus), brocket deer (Mazama), tapir (Tapirus), and white-lipped peccary (Pecari), which are all known to have been translocated in the Caribbean (Giovas 2019b). Agoutis’ synanthropic nature and natural habitat, which includes plantations and secondary forests (Dubost 1988), would make it a prime target for this intentional food-harvesting strategy, potentially making its domestication superfluous (Linares 1976). Modern-day studies (Pérez and Pacheco 2006) on damage caused by wildlife on subsistence crops in Bolivia showed that agouti (D. variegata) were the most frequent wildlife species to visit crop fields. However, although harmful to crops, agouti were never responsible for total crop loss. In the Caribbean, faunal
translocates (primarily rodents) would have been used to complement and support comprehensive horticultural systems, providing a diverse, self-sustaining food source. The expansion of horticultural landscapes during the Early Ceramic would have facilitated the development of subsistence strategies reliant on the minimal tending of translocated fauna, achieved through garden hunting. Furthermore, many translocates no longer occur on islands where they were introduced prehistorically (e.g., Giovas et al. 2012; Giovas 2013: 52), suggesting that their past presence may have been nurtured by pre-Columbian groups, who declined following European contact.

4.6. Ecological Impacts

Anthropogenic modification and degradation of local landscapes is a well-documented phenomenon in pre-Columbian the Caribbean (Wing 2001; Fitzpatrick and Keegan 2007), a result of the increasing overexploitation of resources, land clearing, and the import of non-local fauna and flora. Translocated commensals in the Caribbean may have deeply impacted their ecological setting, a phenomenon that likely became exacerbated post ca. A.D. 500 as groups increased the number and magnitude of translocations (Newsom and Wing 2004). However, the disruption caused by Caribbean translocates is difficult to evidence from archaeological contexts, in particular because of the uncertainty regarding the exact timing of introductions and the establishment of viable populations. Island ecosystems are particularly vulnerable to species introductions (Fitzpatrick and Keegan 2007; Hofman and Rick 2018), accelerating the impact brought upon endemic fauna and flora. Understanding the ecological repercussions of each established translocate is significant for clarifying the overall environmental impact caused by pre-Columbian translocations in the Caribbean.

The introduction of new species has profound and often permanent impacts on local ecologies, which are aggravated when these environments are devoid of predators, limiting possible checks on translocates’ proliferation. The islands are for the most part devoid of endemic terrestrial carnivorous taxa (Gill 1978). Many commensal translocates have highly adaptable behavior, and are capable of spreading rapidly, especially in anthropogenically disturbed landscapes (Brown 1989; Stahl 2009). The impact of translocates is particularly visible through the elimination of endemic species. In the Caribbean, pre-Columbian anthropogenic impacts may have caused the extinction or local extirpation of a number of species (Veloz Maggiolo et al. 1976; Pregill et al. 1994;
Steadman et al. 2005), although none of these events can be directly tied to the introduction of translocates. Translocates may impact local environments by preying on endemic species and their young or by increasing competition for resources with local species. Dogs, which are the only carnivorous Caribbean translocates, would likely have been among the most intrusive to the islands. Contemporaneously, dogs have been shown to be extremely disruptive, preying on endemic island fauna (Borroto-Pàez 2009). In some cases, agouti (*Dasyprocta* spp.) (Smythe 1978: 6; Marcondes-Machado 2009; Figueira et al. 2014; Jones et al. 2019), hutia (subfamily *Capromyinae*) (Borroto-Páez and Woods 2012: 72), and opossum (*Didelphis* spp.) (Julien-Laferrière and Atramentowicz 1990; Cáceres 2010) have been known to consume animal protein. Foraging translocates disrupt local habitats by overturning soils, perturbing the habitat of endemic insects and seedlings, and increasing opportunity for harmful and/or new invasive species to settle (e.g., Sherley and Lowe 2000). Alternatively, the removal of leaf-litter by foraging fauna can be beneficial, facilitating new growth (e.g., Lambert et al. 2004: 86). Peccary, a Caribbean translocate found in the Southern Caribbean Islands and the Antilles, are renowned root and tuber foragers (Kiltie and Terborgh 1983; Barreto et al. 1997), although their status as live translocates (versus as carcass imports) in the pre-Columbian period is unclear (Giovas 2019b). Many Caribbean translocates (e.g., *Didelphis* sp.) (Grelle and Garcia 1999; Cantor et al. 2010), green iguana (Moura et al. 2014; Lasso and Barrientos 2015), crab-eating fox (Cazetta and Galetti 2009), tapir (Galetti et al. 2001; Talamoni and Assis 2009), and agouti (Forget and Milleron 1991; Peres and Baider 1997; Pires and Galetti 2012; Cid et al. 2014) are noted seed dispersers, which might have facilitated the spread and of regeneration of forest growth, although tapir and fox were likely imported as carcass parts.

**4.7. Conclusion**

Pre-Columbian groups translocated numerous and diverse continental species of flora and fauna to the Caribbean, as early as the Archaic, although some species may have been imported exclusively as carcasses. The complexity of translocates’ status and function is blurred by their occurrence as disarticulated remains in archaeological middens. Uncertainties regarding the management of many translocates persist, although it is likely that strategies would have varied across time and from island to island. Ethnographic and biological information about individual taxa provides theoretical
frameworks regarding their functions. Translocates also impacted local ecologies in a number of ways, but the lack of clarity regarding their status as live translocations, timing of introductions, and number and density of taxa makes their impact difficult to demarcate from other anthropogenic activities. Regardless of these uncertainties, commensal translocates shared close relationships with pre-Columbian human groups and are thus effective means for tracing prehistoric human interactions. The magnitude of translocations in the Caribbean, particularly in the Antilles (Stahl 2009), provides an ideal opportunity for using commensals to reconstruct human interactions.
Chapter 5.

Agouti for a Genetic Commensal Model

Throughout Caribbean history, human groups formed complex interactions, linking the Caribbean islands to each other and the continent through seafaring (Keegan et al. 2008; Fitzpatrick 2013; Mol 2014; Hofman et al. 2014; Fitzpatrick 2015; Keegan and Hofman 2017; Hofman et al. 2018). Generally, interactions were facilitated by the proximity of islands to each other. Most of the islands are “intervisible,” meaning they can be seen from one island to the next and in the case of the southern Caribbean Islands (e.g., Curacao) from the continent (Hofman et al. 2007; Torres and Rodriguez Ramos 2008), with the only wider channel separating the Virgin Islands from Saba and Anguilla (Hofman et al. 2006). Inter-island mobility was thus integral to pre-Columbian groups, extending to nearly every aspect of everyday life (Shearn 2020). Alongside the interactions of these human groups, commensals would have been sourced, traded, or transported and are thus valuable proxies for reconstructing human interactions.

The insularity of the Caribbean provides isolation from continental organisms, while its proximity to the continent facilitated the transport of commensals through human seafaring in pre-Columbian times. In addition, the magnitude of seafaring interactions, most visible in the Antilles (Stahl 2009), allows for an almost unique opportunity for tracing human mobility. The degree of interaction in the Caribbean necessitates the application of genetic research: “archeometric studies such as isotope analysis and extraction of ancient and modern DNA are indispensable to untangle the Gordian knot of pre-Columbian Antillean descent and residence rules” (Hoogland et al. 2010: 152).

Previous Caribbean genetic-based commensal models have been successful in extracting and amplifying DNA from ancient samples (e.g., Frantz et al. 2016; Kimura et al. 2016; Lord et al. 2018, 2020; Oswald et al. 2020). However, despite the variety of species translocated in pre-Columbian times, only a couple of taxa (guinea pig and hutia) have been used as proxies for a genetic-based commensal approach for reconstructing pre-Columbian human interactions, in part because of the poor preservation of aDNA which characterizes tropical regions.
Perhaps better than any other Caribbean translocate, the agouti is an ideal proxy for substantiating human mobility in the Lesser Antilles, in particular for reconstructing continental connections to Carriacou. In this chapter I discuss the biological and cultural characteristics that make the agouti an ideal candidate for genetic application of the commensal model. Furthermore, the agouti embodies many of the questions which pertain to continental translocates in the Caribbean, including its potential to establish viable populations, its degree of management by human groups, function among pre-Columbian groups and uncertain taxonomic classification. I review biological traits relating to the agouti’s morphology, behavior, and taxonomic classification. I also discuss the agouti’s identity as a pre-Columbian Caribbean translocate, including its distribution, function, level of management, and ecological impacts.

5.1. Agouti Morphology and Behavior

There are currently eleven species of agouti, divided into a number of subspecies in the genus *Dasyprocta*, the sole agouti genus in the family Dasyproctidae (Wilson and Reeder 2005), although the entire genus is in need of taxonomic revision (Emmons and Feer, 1997; Voss et al. 2001; Patton and Emmons 2015). *Dasyprocta* spp. are medium-sized rodents, measuring approximately 425-655 mm head to tail and weighing 2 – 6 kg (Vietmeyer 1991; Nowak 1991; Jorge and Peres 2005). The head is oval, with a long snout and rounded ears. The body is rounded, supported by slender legs, and finished by a stumpy tail. Pelt colors vary between dark brown, black, and ochre.
Figure 5.1.  **Agouti (Dasyprocta sp.).**
Note: Brian Gratwicke, *Agouti*, 2012. CC BY 2.0.

Agoutis are primarily frugivorous but with some degree of omnivory (Jones et al. 2019, but see Ranjeeta Lall et al. 2018). Fruits and seeds constitute the vast bulk of their diet (Smythe 1978: 24; Ranjeeta Lall et al. 2018) although they also consume roots and leaves (Smythe 1978: 5 – 6), grubs (Silvius 2002; Dubost and Henry 2006), and animal matter (Smythe 1978: 6; Marcondes-Machado 2009; Figueira et al. 2014; Jones et al. 2019). Agoutis possess many effective adaptive traits (Govoni and Fielding 2001), including behavioral plasticity (Vietmeyer 1991: 202; ter Steege et al. 1996: 49, 66; Ferrer et al. 2012; Praxedes 2018; Magalhães and Srbek-Araujo 2019), multiple breeding seasons (Vietmeyer 1991: 202; van Vuuren et al. 2004), precocial nature (Vietmeyer 1991: 202), and lack of dependence on lactation by pups (Singh et al. 2018). Successful modern introductions of agouti to Brazil (Cid et al. 2014) have highlighted the agouti’s high capacity for adaptability and reproductive efficacy. Agoutis can be monogamous (Smythe 1978), steady mates providing dependable breeding opportunities and increased security. Although agoutis maintain territorially marked home-ranges, these were found to possess high overlap (Aliaga–Rossel et al. 2008). Males tolerate juvenile and female co-habitation, although demonstrate aggressive behavior towards other males (Aliaga–Rossel et al. 2008).
5.2. Agouti Taxonomy

There are currently eleven species of agouti, divided into a number of subspecies (Wilson and Reeder 2005), although the entire genus needs taxonomic revision (Emmons and Feer, 1997; Voss et al. 2001; Patton and Emmons 2015). Species from the genus Dasyprocta are difficult to distinguish morphologically, both as living animals (Souza et al. 2007; Ramírez-Chaves et al. 2018) or as skeleton remains, and also exhibit karyotypic stability (Lima and Langguth 1998; Patton et al. 2015: 736, but see Souza et al. 2007; Praxedes et al. 2018). Although the agouti remains found at pre-Columbian sites are almost entirely designated as *D. leporina*, Linnaeus, 1758, where assigned to species (e.g., Newsom and Wing 2004; Wing 1989, 2008; Grouard 2010), the taxonomic classification for pre-Columbian Caribbean agoutis has not yet been verified independent of morphological means. *D. punctata*, Gray, 1842, *D. guamara*, Ojasti, 1972, *D. fugilinosa*, Wagler, 1832, revised by Allen 1915; Tate 1939; Handley 1976, and *D. Mexicana*, De Saussure, 1860, whose home territories range from Mexico to Argentina, including Bolivia, Brazil, Colombia, French Guiana, Guyana, Panama, Peru, Surinam, and Venezuela, overlap within the Circum-Caribbean sphere (Emmons and Freer 1997; Wilson and Reeder 2005) also offer potential for having been translocated. Ultimately, no species should be discounted, as a wide network of Circum-Caribbean commensal trade would have likely extended throughout Central and northern South America and Trinidad (e.g., Laffoon et al. 2014; Kimura et al. 2016). Furthermore, hybridization between two agouti species is possible due *Dasyprocta* spp. similar morphology (Ramírez-Chaves et al. 2018) and overlapping ranges throughout Central and northern South America (Du Tertre 1656 in Ballet 1894: 3; Aliaga-Rossel et al. 2008; Wilson and Reeder 2005). Hybridization has been proposed for the Venezuelan *D. fugilinosa* agouti, which is a potential cross between *D. fugilinosa* and *D. punctata* (Patton et al. 2015: 743).

5.3. Agouti Native Distribution in Central and South America

Agouti was a favored food item in pre-Columbian Central and South America (Joyce 1916: 37; Prestes-Carneiro et al. 2019), where it is still consumed to this day (Vietmeyer 1991: 200; Ouhoud-Renoux 1998; Richard-Hansen 1998; Peres 2000; Cummins et al. 2014).
Dasyprocta spp. boast an extensive archaeological presence on the continent, from ancient pre-Columbian times till post-European contact, from Central to South America, including at sites in Mexico (Mason and Lope 2008), Brazil (Rosa and Jacobus 2010), Belize (Masson 1999), Amazonia (Saunaluoma and Virtanen 2015), and Peru (DeBoer 1971: 77). Today, Dasyprocta spp. still occurs throughout most of Central and South America (Wilson and Reeder 2005). Population structures and the home range of different species are vague, due to the agoutis confused taxonomic classification (Emmons 1990; Woods 1993; Emmons and Feer 1997; Patton and Emmons 2015). Of the five translocates whose home ranges overlap within the Circum-Caribbean sphere, D. leporina is the only validated species occurring in Guyana, Surinam, French Guiana, and Guianan Brazil (Voss et al. 2001), but occurs also in Venezuela. Modern genetic analyses of D. leporina by van Vuuren at al. (2004) showed the occurrence of two maternal clades (Clade A and B) living sympatrically in French Guiana and Brazil. D. fugilinosa occurs allopatrically around the source of the Orinoco in Guiana and southern Venezuela (Tate 1939; Handley 1976), but also in Colombia, northern Brazil, and Peru, and may occur in Surinam (but see Voss et al. 2001). D. punctata occurs from southern Mexico to Panama, as well as in Bolivia, southern Brazil and northern Argentina. D. guamara is endemic of the Deltaic System of Venezuela (Ojasti 1972; Linares and Belkis Rivas 2004). D. mexicana occurs in Mexico, see Wilson and Reeder (2005) for a comprehensive review of modern agouti distribution. However, it is likely that these distributions do not conform to those which occurred in pre-Columbian times.

5.4. Caribbean Agouti Distribution

Dasyprocta spp. are native to the Americas, with a widespread continental distribution ranging from southern Mexico to northern Argentina (Wilson and Reeder 2005). These rodents can be found in a variety of habitats (Merrit 1983), primarily dry and moist Neotropical forests (Silvius and Fragoso 2003) but can also plantations and secondary forests (Dubost 1988). The agouti’s complete absence from the Caribbean paleontological record and its sudden appearance in the Caribbean during times of increased human settlement (Morgan and Woods 1986) establishes its status as an anthropogenically-induced translocate. Although able swimmers (Govoni and Fielding 2001), it is unlikely that agouti would have been capable of long-distance sea crossings.
Like most translocates, agouti begins to appear in significant numbers after ca. A.D. 500, in association with Late Ceramic Age settlements (Newsom and Wing 2004), present at many sites in greater numbers than almost any other translocate (e.g., Giovas et al. 2012, 2016). Pre-Columbian agouti skeletal remains are prevalent across the Lesser Antilles, occurring on most islands (Figure 5.1). The agouti’s known, non-native distribution extends across the Lesser Antilles, occurring on most islands (Figure 2), up to Anguilla at the border of the Greater Antilles (Giovas 2019a). In the South, agouti can be found as far as Grenada (Newsom and Wing 2004: Table B.1), approximately 150 km from the agouti’s closest established native home range on Trinidad (Emmons and Feer, 1997: 226; Wilson and Reeder 2005). On Anguilla, the earliest known agouti is found at the Barnes Bay site (A.D. 600/800 – 1500) (Garder 2007), on Grenada, at the Pearls site, (A.D. 370 – 770) (Hanna 2019; Newsom and Wing 2004: Table B.1). Direct dating of archaeological agouti specimens is extremely limited, but based on the presence of agouti at Trants (480 B.C. – A.D. 320) (Montserrat), Hope Estate (450 B.C.– A.D. 650) (Saint-Martin), and Folle Anse (250 B.C. – A.D. 500) (Marie-Galante), agouti were present in the Caribbean outside of their native range as early as 450 B.C., but more likely around A.D. 300/500 at which time the magnitude of translocations substantially increased. Three species of agouti (*D. leporina, D. mexicana, and D. punctata*) have been identified in the present-day Caribbean (Wilson and Reeder 2005) although the current distribution of agouti is likely affected by the contemporary introductions of several species in the colonial era (Newsom and Wing 2004; Giovas et al. 2012), when agouti were notably used as food for slaves (Vietmeyer 1991: 200; Govoni and Fielding 2001). Abundances of agouti are described on the “big islands,” possibly referring to the Greater Antilles, where the agouti is not known archaeologically (Newsom and Wing 2004: 205) as early as 1656 (Labat 1656, in Ballet 1894: 3), perhaps alluding to the colonial imports of agouti used as game meat for slaves.
Figure 5.2. Agouti (*Dasyprocta* sp.) pre-Columbian distribution in the Caribbean, encompassed within the islands in the red boundaries. Agoutis are native to Trinidad, their status on Tobago remains unclear.

Note: Map courtesy of C. Giovas, modified with data from Giovas (2019a).
5.5. Agouti Cultural Role

Agouti remains are found consistently in midden deposits. Only a single agouti burial has been recorded, discovered at the Sugar Factory Pier on Saint Kitts (approximately ca. A.D. 400 – 600) (Goodwin 1976). The agouti was likely used for subsistence (Giovas 2019b), with a number of bones exhibiting charring or butchery marks (Grouard 2010; Delsol and Grouard 2016). Historic accounts (Du Tertre in Adélaïde 1972: 74; Breton in Ballet 1894: 4, 362) describe the agouti as one of the most common and most prized meats, smoked and boiled in cassava water on undisclosed Lesser Antillean islands (Breton in Ballet 1894: 355). Today, agoutis are still important for domestic consumption in South America (e.g., Ferrer et al. 2012). Agouti remains were also employed for artifact production (Delpuech et al. 2000: 39; Grouard 2007; Giovas 2019b). Ethnohistoric sources (Ballet 1894: 381 – 382; Joyce 1916: 174; Anonyme de Saint-Vincent in Adélaïde 1972: 85; Adélaïde 1972: 76) describe a coming of age ritual were young men were fought and scratched with agouti teeth. The use of agouti teeth as sharp tools is again mentioned in relation to festivity (Ballet 1894: 383; Joyce 1916: 170), sacrifice (Ballet 1894: 407), and healing (Ballet 1894: 345, 399). Rodents’ incisors are sharpened through occlusion throughout the animal’s life, continuously exposing hard enamel. The value of agouti and agouti bones and teeth within pre-Columbian ceremonies cannot be ascertained solely from ethnographic accounts. However, these accounts testify to the practical use of materials recovered from imported fauna in addition to their consumption, and hint at their potential use within ceremonial practices.

5.6. Pre-Columbian Agouti Management

Agouti are considered prime candidates for pre-Columbian management (Wing 1993; Crosby 2001; Newsom and Wing 2004), however, the degree of management of agouti by pre-Columbian groups is unclear, with contradictory evidence. On the one hand, ethnohistorical accounts describe agouti being hunted in the mountains, at a considerable enough distance from human settlements that hunters had to camp in the woods for a night (Ballet 1894: 362), suggesting large populations of wild agouti. Analysis of strontium ($^{87}$Sr/$^{86}$Sr) and lead isotopes ($^{206}$Pb/$^{204}$Pb) isotopes of agouti on Carriacou (Giovas et al. 2016) showed that live agouti were present on Carriacou and Nevis by ca. A.D. 600/800, suggesting that agouti may have established viable
populations on multiple islands. On the other hand, the agouti’s firm presence across the Lesser Antilles (Figure 5.1) may be explained by multiple introductions and sustained pre-Columbian management (Wing 1993, 2008; Newsom and Wing 2004; Grouard 2007; Giovas 2016; Giovas 2017). The agouti’s behavior is certainly well-suited for captivity: “From a standing start agouti reportedly can leap as high as 2 m or as far as 6 m; however, as long as they are well fed, there is little problem keeping them behind a wall only 1 m high.” (Vietmeyer 1991: 200). Furthermore, agouti no longer occur on many of the Lesser Antillean islands where it was prehistorically introduced (Wing 1993; Wing and Wing 1997), including Carriacou (Giovas 2013: 52; Giovas et al. 2016), which suggests that some form of human management contributed to its survival. At the same time, this absence also might be explained by the considerable landscape change and degradation brought on by European colonizers (Westermann 1953; Fitzpatrick and Keegan 2007). Labat (1656, in Ballet 1894: 3) noted the absence of agouti on Martinique, where it is known to occur archaeologically, at l’Anse Trabaud (ca. A.D. 800 – 1000) (Grouard 2011), Macabo (ca. A.D. 415 – 1275) (Grouard 2013: 151), and Diamant, Plage de Dizac (ca. A.D. 400 – 750) (Grouard and Bérard 2005).

5.7. Ecological Impacts of Agouti

The exact ecologic impact of pre-Columbian agouti has not been confirmed. Agoutis in captivity have been observed to kill and consume a live adult mouse (*Liomys pictus*) (Smythe 1978: 24) and dove (*Zenaida macroura*) (Jones et al. 2019, see also Figueira et al. 2014). Although the significance of animal matter in agouti diet is still unclear (Jones et al. 2019), it is highly unlikely that the agoutis’ meat consumption would have been significant enough to impact directly endemic Caribbean fauna. Agoutis are renowned seed dispersers (Forget and Milleron 1991; Peres et al. 2009; Gálvez et al. 2009; Pires and Galetti 2012; Cid 2014) and can carry seeds up to 200 meters from their source (Hallwachs 1986; Aliaga–Rossel 2008). In the Caribbean, translocated agouti likely facilitated tree recruitment for various species but may also have altered recruitment regimes in ways that altered forest species composition, affecting the habitats of endemic fauna (Eisenberg and Thorington 1973; Terborgh et al. 2001; Taylor et al. 2014). Agouti are notably key dispersers for *Hymenaea courbaril* (Hallwachs 1986; Asquith and Terborgh 1999; Gorchov et al. 2004), which may have been used for pre-Columbian canoe manufacture (Shearn 2020). As previously discussed, the agouti’s
efficient reproductive behavior would have facilitated its adaptation and propagation. Human hunting may have kept agouti populations in check, but endemic predators which would have preyed on agouti are rare. Pit vipers (*Bothrops* spp.), endemic to Martinique and Saint Lucia (Roughgarden 1995: 147; Hailey et al. 2011: 317), are opportunistic mammal specialists (Martins et al. 2002) which may have preyed on agouti; Du Tertre (1656 in Ballet 1894: 3) advises that the absence of agouti on Martinique may be caused by snakes. Introduced dogs were probably the most likely non-human predator of agoutis (e.g., Cid et al. 2014). Ocelot, a Caribbean translocate found on the Southern Caribbean islands (Antczak 1995, Newsom and Wing 2004: 72) are significant predators for agouti (Aliaga-Rossel et al. 2006), although ocelots may have been imported to the Caribbean only as carcass products.

### 5.8. Conclusion

Among the many translocates of the Lesser Antilles, the agouti’s obvious nature as a translocate, extensive number of remains, and broad distribution makes it an ideal proxy for a genetic application of the commensal model for reconstructing pre-Columbian interactions. Despite being a prominent Caribbean translocate, the taxonomic status of *Dasyprocta* spp. necessitates a complete revision (Emmons and Feer, 1997; Voss et al. 2001; Patton and Emmons 2015). Agoutis share close relationships with humans and are well-suited for captivity, indicating that they may have been managed by pre-Columbian groups, although the degree to which they were managed is still unclear. It is likely that agouti impacted local ecologies in a number of ways, notably altering forest composition on islands where they were translocated. The agouti’s complex continental population structure and species’ overlapping home-ranges offers the potential for individuals from different populations, representative of more than one species, being translocated to the Caribbean. In the following chapter, I describe the methods employed for the sampling and analysis of the agouti remains employed in this study.
Chapter 6.

Materials and Methods

Agouti is recurrent continental translocate throughout the Lesser Antilles and is present in greater numbers than almost any other translocate, including on Carriacou (Giovas et al. 2012). Genetic analyses of agouti are thus an effective measure for analyzing the connections tying continental groups to the Caribbean islands. Furthermore, genetic analyses can clarify pre-Columbian agouti taxonomy, which is often assumed by association, and has not yet been identified independently of morphological means. In the sections following, I describe the methods used for the undertaking of this project. DNA from modern agouti specimens was extracted as a positive control to confirm the functionality of primer design. A pilot test was run using samples from six islands in order to evaluate the presence/absence of DNA and determine a geographic focus for the project. Testing then focused on the Sabazan and Grand Bay sites from Carriacou.

6.1. Modern DNA Sampling and Extraction

Three samples of skin tissue (AGM1, AGM2a, AGM2b) from two taxidermically preserved agouti specimens (Dasyprocta sp., accession numbers M013269 and M009188) were obtained from the Beaty Biodiversity Museum (University of British Columbia). The agouti specimens did not have species-level identification and lacked provenience information. For the most part, these modern agouti specimens were stored at room temperature. However, the specimens were frozen to -30°C for 48 hours twice during a dermestid beetle outbreak and thawed 24 hours between the two freezes. Specimens were fumigated and treated, including with dichlorvos. A tissue sample (<1 g) was cut using new gloves and razor blades, changing gloves and blades between specimens. The samples were then stored at -20°C until extraction. Modern extraction and PCR setup was conducted in a laboratory dedicated to the analysis of modern DNA at Simon Fraser University. DNA was extracted from the tissue using the DNeasy Blood and Tissue Extraction Kit from Qiagen (Hilden, Germany), following the manufacturer’s protocol.
6.2. Primer Design

For the purpose of this project, six genus-specific primers covering almost all of the Cytochrome B (CytB) Open Reading Frame (ORF) were designed using NetPrimer (www.premierbiosoft.com/netprimer). The three overlapping primer sets amplify regions localized between nt 114 and nt 387 of the *Dasyprocta* mitochondrial CytB ORF (see Figure 6.1). Primer template consisted of the agouti (*D. leporina*) CytB ORF, available on GenBank- Accession Number AF437811, which is used throughout this project as the primary reference sequence. The efficiency and specificity of the primer sets was tested by applying them to the modern agouti samples. Different combinations of primers were used to generate PCR products of different lengths, such as F114 and R387 (274 bp, for modern DNA only); F114 and R215 (102 bp); F114 and R252 (139 bp); and F156 and R387 (232 bp) (see Table 7.1).

**Table 6.1.  *Dasyprocta leporina* CytB project primers.**

<table>
<thead>
<tr>
<th>Primer Name</th>
<th>Sequence</th>
<th>Primer Length (bp)</th>
</tr>
</thead>
<tbody>
<tr>
<td>F114</td>
<td>GCATCTGCCTARTAATACAAATCCTT</td>
<td>26</td>
</tr>
<tr>
<td>R215</td>
<td>TCTCGGCAAATGTGTGTAACG</td>
<td>21</td>
</tr>
<tr>
<td>F156</td>
<td>AATACATTACACCGCAGATACAACC</td>
<td>25</td>
</tr>
<tr>
<td>R252</td>
<td>GGCAGTAARTATCGGATAGATCAT</td>
<td>25</td>
</tr>
<tr>
<td>F282</td>
<td>TTACCTACACATCGGACGAGGAA</td>
<td>23</td>
</tr>
<tr>
<td>R387</td>
<td>TATGAAGCCGGTGGCCATTAC</td>
<td>21</td>
</tr>
</tbody>
</table>
6.3. Archaeological DNA Sampling

6.3.1. Field Protocol for Zooarchaeological Samples

Sampling for this project focused on identifying agouti (Dasyprocta sp.) remains offering potential for extraction of aDNA. To establish the islands with the most potential for successful DNA retrieval and amplification, six samples from six islands Carriacou (Grand Bay); Basse-Terre (La Ramée); Marie-Galante (Toulourous); Grande-Terre (Belle Plaine); Martinique (Macabou); and Saint-Martin (BK77 Grand Case) were processed in an initial round of testing.

In total, 25 samples were processed from Carriacou (NISP 25, MNI 23, see Table 6.5). All zooarchaeological samples excavated from the Sabazan and Grand Bay sites were initially wet screened using seawater, then rinsed with freshwater and cleaned of adhering sediments by gentle brushing or with a metal dental pick. Bone samples that will be exported from their country of origin are required to be cleaned from any adhering sediment due to biohazard concerns. Samples were stored at room temperature in non-ventilated facilities, in plastic zipper-sealed bags (Sabazan for up to three weeks, Grand Bay for three to seven years, depending on samples), before being transported to North America. Many samples were passed through an X-ray scanner during airport security.
screenings. Samples were stored at Simon Fraser University in plastic zipper-sealed bags of mixed vertebrate bones. Zooarchaeological identifications for the Carriacou samples were completed by Dr. Christina Giovas. Zooarchaeological samples from Basse-Terre (NISP 1, MNI 1), Marie-Galante (NISP 1, MNI 1), Grande-Terre (NISP 1, MNI 1), Martinique (NISP 1, MNI 1), and Saint-Martin (NISP 1, MNI 1) (see Table 6.5) were wet screened with freshwater using 2 mm screens, then dried in the shade. For the Basse-Terre, Grande-Terre, Martinique, and Saint-Martin samples, the extraction of vertebrate materials from sieve residue was completed in laboratory by Brigitte David and Dr. Sandrine Grouard, and on the excavation site for Marie-Galante. Zooarchaeological identifications of samples from these islands were completed by Dr. Sandrine Grouard.

Although standard practice and required for foreign import, these measures are not favorable for archaeological samples destined for the extraction of genetic material, in particular bone (Hedges and Millard 1995). The washing or soaking of bone forces the access of exogenous DNA through porosities in the bone, creating a greater chance for contamination, especially for samples originating from hot climates were the bone mineral is already weakened (e.g. Bollongino et al. 2008). To minimize degradation and contamination of freshly excavated samples destined towards aDNA extraction, certain highly rigorous measures have been proposed during and immediately following excavation (Leney 2006; Llamas et al. 2016). These measures include the use of disposable gloves, surgical masks and hairnets during excavation, protection of the site from the intrusion of natural elements such as sunlight and wind, clean tools, a specialized staff, and control elements such as thorough records and site sampling (Llamas et al. 2017). Although these measures were not used in previous excavations of Grand Bay and Sabazan, growing investment in genetic testing of Caribbean materials (e.g. Lalueza-Fox 2001, 2003; Kimura et al. 2016; Mendisco et al. 2015; Frantz et al. 2016; Lord et al. 2018, 2020; Schroeder et al. 2018; Oswald et al. 2020) suggests that similar procedures be considered, at least in some proportion, during future excavations.

6.3.2. Pilot Testing and Carriacou Sampling Protocol

Sampling for this project focused on identifying agouti (*Dasyprocta* spp.) remains offering potential for extraction of aDNA. To establish the islands with the most potential for successful DNA retrieval and amplification, six samples from six islands Carriacou
(Grand Bay); Basse-Terre (La Ramée); Marie-Galante (Tourtourous); Grande-Terre (Belle Plaine); Martinique (Macabou); and Saint-Martin (BK77 Grand Case) were processed in an initial round of testing. The six samples were processed twice, the first time, using universal primers in order to ascertain the presence of DNA, then, using the genus-specific primers developed for this project. Pilot testing resulted in a 50% success rate, with DNA retrieved from the Saint-Martin (BK77 Grand Case), Martinique (Macabou), and Carriacou (Grand Bay) samples. We were not able to retrieve any DNA from the three samples from Guadeloupe, likely due to a lack of preserved endogenous DNA.
Table 6.2. Site chronology and sample provenience for pilot test islands.

<table>
<thead>
<tr>
<th>Lab Number</th>
<th>Island</th>
<th>Site</th>
<th>Raw $^{14}$C Date for Site (2σ)</th>
<th>Cal B.C. /A.D.</th>
<th>Skeletal Element</th>
<th>Side</th>
<th>Successfully Amplified</th>
</tr>
</thead>
<tbody>
<tr>
<td>AG1</td>
<td>Carriacou</td>
<td>Grand Bay</td>
<td>1020BP +20 – 990 BP +20 – 1310 BP ±40</td>
<td>A.D. 990 – 1190</td>
<td>Innominate (Ilium)</td>
<td>R</td>
<td>Y</td>
</tr>
<tr>
<td>AG2</td>
<td>Basse Terre</td>
<td>La Ramée</td>
<td>Unavailable</td>
<td>A.D. 320 – 1000</td>
<td>Incisor</td>
<td>Unknown</td>
<td>N</td>
</tr>
<tr>
<td>AG3</td>
<td>Marie-Galante</td>
<td>Tourlourous</td>
<td>Unavailable</td>
<td>A.D. 237 – 13th century</td>
<td>Femur</td>
<td>R</td>
<td>N</td>
</tr>
<tr>
<td>AG4</td>
<td>Grande Terre</td>
<td>Belle Plaine</td>
<td>810 BP ±35 – 880 BP ±35</td>
<td>A.D. 1040 – 1274</td>
<td>Incisor</td>
<td>Unknown</td>
<td>N</td>
</tr>
<tr>
<td>AG5</td>
<td>Martinique</td>
<td>Macabou</td>
<td>Unavailable</td>
<td>A.D. 415 – 1275</td>
<td>Maxilla and molar</td>
<td>R</td>
<td>Y</td>
</tr>
<tr>
<td>AG6</td>
<td>Saint Martin</td>
<td>BK77 Grand Case</td>
<td>Unavailable</td>
<td>A.D. 835 – 1160</td>
<td>Femur</td>
<td>Unknown</td>
<td>Y</td>
</tr>
</tbody>
</table>

Note: All samples belong to agouti (*Dasyprocta* sp.), class Mammalia.
Analysis then turned to towards previously excavated samples from the Carriacou sites of Sabazan and Grand Bay (see Appendix A1 and A2 for sample provenience). Zooarchaeological materials collected from surface scatter and upper disturbed layers were not included for consideration in sampling. Preliminary visual assessment of bone has been shown as useful to predict samples with higher potential for aDNA extraction (e.g., Hansen et al. 2017). Sampling aimed primarily at large, dense, bones in apparent good condition. Porous, calcined, and weathered surface bones were excluded from analysis (see Appendix A3 for sample description). The sampling strategy targeted repeating skeletal elements and element portions to minimize the risk of analyzing reiterated genetic data. Non-repeating elements included for sampling were chosen only when originating from distinct stratigraphic layers where specimen interdependence could be excluded, i.e., selected specimens were extremely unlikely to come from the same animal. Because Sabazan offered fewer repeating agouti bones in apparent good condition, sampling largely focused on Grand Bay zooarchaeological finds. Sampling also allowed complete chronological coverage (from approximately ca. A.D. 400 to 1400) of Carriacou’s pre-Columbian settlements. In total, twenty-five samples, nineteen from Grand Bay and six from Sabazan were targeted for extraction. Nineteen of these samples originate from stratigraphic layers with associated radiocarbon dates (see Appendix A4 and A5 for sample chronology). The extraction of aDNA from samples is a destructive process. Preceding extraction, all samples were weighed, measured, described and photographed to provide a pre-destruction record (Appendix A3).
Table 6.3. Site chronology and sample provenience for Carriacou samples.

<table>
<thead>
<tr>
<th>Lab Number</th>
<th>07CSZ000063</th>
<th>Find #</th>
<th>Site</th>
<th>Screen Fraction (mm)</th>
<th>Date</th>
<th>Period</th>
<th>Skeletal Element</th>
<th>Side</th>
<th>Successfully Amplified</th>
</tr>
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<tbody>
<tr>
<td>AG7</td>
<td>07CSZ000063</td>
<td>n/a</td>
<td>Sabazan</td>
<td>6.4</td>
<td>A.D. 730 – 990</td>
<td>Initial/Early-Middle</td>
<td>Ilium</td>
<td>R</td>
<td>N</td>
</tr>
<tr>
<td>AG8</td>
<td>07CSZ000166</td>
<td>n/a</td>
<td>Sabazan</td>
<td>6.4</td>
<td>A.D. 890 – 1010</td>
<td>Middle- Late/Final</td>
<td>Femur</td>
<td>L</td>
<td>Y</td>
</tr>
<tr>
<td>AG9</td>
<td>07CSZ000075</td>
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<td>Sabazan</td>
<td>6.4</td>
<td>A.D. 1040 – 1160</td>
<td>Late/Final</td>
<td>Innominate</td>
<td>L</td>
<td>Y</td>
</tr>
<tr>
<td>AG10</td>
<td>07CSZ000006</td>
<td>n/a</td>
<td>Sabazan</td>
<td>6.4</td>
<td>A.D. 1280 – 1400</td>
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<td>Auditory Bulla</td>
<td>L</td>
<td>Y</td>
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<tr>
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<td>6.4</td>
<td>A.D. 890 – 990</td>
<td>Middle</td>
<td>Incisor</td>
<td>L</td>
<td>Y</td>
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<tr>
<td>AG12</td>
<td>07CSZ000091</td>
<td>n/a</td>
<td>Sabazan</td>
<td>6.4</td>
<td>A.D. 1020 – 1150</td>
<td>Late/Final</td>
<td>Scapula</td>
<td>R</td>
<td>Y</td>
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<td>Grand Bay</td>
<td>6.4</td>
<td>A.D. 390 – 590</td>
<td>Initial/Early</td>
<td>Auditory Bulla</td>
<td>R</td>
<td>Y</td>
</tr>
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<td>AG14</td>
<td>n/a</td>
<td>05CGB001042BOA</td>
<td>Grand Bay</td>
<td>6.4</td>
<td>A.D. 990 – 1190</td>
<td>Middle- Late/Final</td>
<td>Femur</td>
<td>L</td>
<td>Y</td>
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<td>AG15</td>
<td>n/a</td>
<td>08CGB001751BOA</td>
<td>Grand Bay</td>
<td>6.4</td>
<td>A.D. 390 – 590</td>
<td>Initial/Early</td>
<td>Auditory Bulla</td>
<td>R</td>
<td>Y</td>
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<td>AG16</td>
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<td>11CGB001770BOA</td>
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<td>Auditory Bulla</td>
<td>R</td>
<td>Y</td>
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<td>AG17</td>
<td>n/a</td>
<td>11CGB001743BOA</td>
<td>Grand Bay</td>
<td>6.4</td>
<td>A.D. 390 – 590</td>
<td>Initial/Early</td>
<td>Auditory Bulla</td>
<td>R</td>
<td>Y</td>
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<td>AG18</td>
<td>n/a</td>
<td>11CGB001714BOA</td>
<td>Grand Bay</td>
<td>6.4</td>
<td>A.D. 470 – 880</td>
<td>Initial/Early-Middle</td>
<td>Auditory Bulla</td>
<td>R</td>
<td>Y</td>
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<td>AG19</td>
<td>n/a</td>
<td>08CGB001556BOA</td>
<td>Grand Bay</td>
<td>6.4</td>
<td>A.D. 470 – 880</td>
<td>Initial/Early-Middle</td>
<td>Auditory Bulla</td>
<td>R</td>
<td>Y</td>
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<td>AG20</td>
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<td>08CGB001644BOA</td>
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<td>A.D. 470 – 880</td>
<td>Initial/Early-Middle</td>
<td>Auditory Bulla</td>
<td>R</td>
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<td>A.D. 470 – 880</td>
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<td>R</td>
<td>Y</td>
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<tr>
<td>Lab Number</td>
<td>Find #</td>
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<td>Date</td>
<td>Period</td>
<td>Skeletal Element</td>
<td>Side</td>
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<td>05CGB000883BOA</td>
<td>Grand Bay</td>
<td>6.4</td>
<td>A.D. 990 – 1190</td>
<td>Middle- Late/Final</td>
<td>Femur</td>
<td>L</td>
<td>Y</td>
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<td>AG24</td>
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<td>Grand Bay</td>
<td>6.4</td>
<td>A.D. 990 – 1190</td>
<td>Middle- Late/Final</td>
<td>Femur</td>
<td>L</td>
<td>Y</td>
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<tr>
<td>AG25</td>
<td>n/a</td>
<td>05CGB000894BOA</td>
<td>Grand Bay</td>
<td>6.4</td>
<td>A.D. 990 – 1190</td>
<td>Middle- Late/Final</td>
<td>Femur</td>
<td>L</td>
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<td>Grand Bay</td>
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<td>A.D. 990 – 1190</td>
<td>Middle- Late/Final</td>
<td>Femur</td>
<td>L</td>
<td>Y</td>
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<td>AG27</td>
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<td>Grand Bay</td>
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<td>A.D. 990 – 1190</td>
<td>Middle- Late/Final</td>
<td>Femur</td>
<td>L</td>
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<td>6.4</td>
<td>A.D. 990 – 1190</td>
<td>Middle- Late/Final</td>
<td>Femur</td>
<td>L</td>
<td>Y</td>
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<td>05CGB001045BOA</td>
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<td>Femur</td>
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<td>A.D. 700 – 1200</td>
<td>Initial/Early-Middle- Late/Final</td>
<td>Femur</td>
<td>L</td>
<td>Y</td>
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</tbody>
</table>

Note: Occupation periods for Sabazan and Grand Bay were condensed from Giovas (2013: 192 – 193) in order to minimize overlap of calibrated ^14C dates. Date ranges are as follows: Initial/Early (ca. A.D. 400 – 850), Middle (ca. A.D. 850 – 1000), Late/Final (ca. A.D. 1000 – 1400). Information for AG1 which originates from Grand Bay but was processed during pilot testing can be found in Table 6.3. All samples belong to agouti (*Dasyprocta* sp.), class Mammalia.
6.3.3. Taxonomic Quantification

Samples of *Dasyprocta* utilized in this project were quantified using standard measures of NISP and MNI (Grayson 1984; Lyman 1985). For Sabazan, taxon MNI was calculated by 10 cm arbitrary levels, stratigraphic layer, and trench, for Grand Bay, by 10 cm arbitrary levels and by trench. Faunal percentages were not calculated because of the sampling focus on the single genus *Dasyprocta*.

**Table 6.4.** Taxonomic quantification for archaeogenetic samples from pilot test islands and Carriacou.

<table>
<thead>
<tr>
<th>Island</th>
<th>Site</th>
<th>NISP</th>
<th>MNI</th>
<th>Original Specimen Weight (g)</th>
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</tr>
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<td>Tourlourous</td>
<td>1</td>
<td>1</td>
<td>1.11</td>
</tr>
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<td>Belle Plaine</td>
<td>1</td>
<td>1</td>
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</tr>
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<td>Macabou</td>
<td>1</td>
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<td>1.16</td>
</tr>
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<td>BK77 Grand Case</td>
<td>1</td>
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<td>Sabazan</td>
<td>6</td>
<td>5</td>
<td>8.44</td>
</tr>
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<td>Grand Bay</td>
<td>19</td>
<td>18</td>
<td>36.52</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>30</td>
<td>28</td>
<td>48.60</td>
</tr>
</tbody>
</table>

The majority of samples, 63%, originate from Grand Bay. The established sampling protocol was almost completely successful in associating each specimen with a unique individual, thus maximizing the retrieval of non-repeating genetic data. The two exceptions were for samples AG8 and AG11 (Sabazan) and AG1 and AG14 (Grand Bay) which may be not be independent from each other.

6.4. Archaeological DNA Extraction

6.4.1. Contamination Controls

aDNA extraction and post-PCR analysis were conducted using standard procedure in dedicated aDNA and post-PCR labs at Simon Fraser University, Canada. This project was the first to process agouti DNA in the Simon Fraser University Ancient and Modern Laboratories, limiting the potential for contamination from previous testing. aDNA and post-PCR labs were located in separate buildings. One DNA extraction blank control and one PCR negative control were added for each set of eight to ten samples, to assess the
absence of contamination, punctual or systematic. Modern analysis of agouti was undertaken in a separate lab dedicated to the analysis of modern DNA in order to prevent contamination from modern sources. All samples were handled by myself and another lab member (H.G.Z.) in full protective gear, including double layered nitrile or latex gloves, consistent with the standards outlined in Yang and Watt (2005).

6.4.2. Sample Decontamination and Preparation

Intact bone samples were photographed individually in polyethylene weigh boats. Samples were obtained through chipping of the bones with razors and forceps and weighed individually, with sample weights ranging between 63 and 612 mg. Each sample was immersed in 100% commercial bleach solution (~5% sodium hypochlorite w/v) for 6 minutes. The bleach was poured off and the samples were rinsed twice with 14 mL of distilled water, the first time for 30 seconds, the second for 6 minutes. Samples were transferred to a UV crosslinker where they were exposed to ultraviolet light at 4 800 Jm⁻² dosage for thirty minutes. After drying, the samples were crushed with a hammer, which was cleaned between each the processing of each specimen.

6.4.3. DNA Extraction

A modified silica-spin column method (Yang et al. 1998) was used for aDNA extraction. Samples and 3.5 mL of lysis buffer (0.5 M EDTA pH 8.0, 0.25% SDS, and 0.5 mg/mL proteinase K) were transferred to 15 mL tubes. A blank control was added control was added for each set of eight to ten samples. The tubes were sealed with parafilm, paper towel, aluminum foil, and transferred into a 50°C rotating incubator where they were left overnight. Samples were removed from incubator and centrifuged for six minutes at 4.4 krmp. Approximately 3 mL of the supernatant was then transferred to Amicon Ultra-4 100 KD centrifugal filters (MilliporeSigma, Burlington, MA, USA). The 15 mL tubes with residual bone suspensions were placed in storage at -20° C. The Amicon tubes were spun for 90 minutes at 4.4 k rpm, until the solution was reduced to 100 μl. 500 μl of PB was added to the samples and centrifuged for six minutes at 4.4 krmp. Approximately 3 mL of the supernatant was then transferred to Amicon Ultra-4 100 KD centrifugal filters (MilliporeSigma, Burlington, MA, USA). The 15 mL tubes with residual bone suspensions were placed in storage at -20° C. The Amicon tubes were spun for 90 minutes at 4.4 k rpm, until the solution was reduced to 100 μl. 500 μl of PB was added to the samples and mixed using a pipette. Samples were placed into Qiaquick spin columns with collection tubes and spun for 1 minute at 6 krpm. 400 μl of PE washing buffer was added to the spin columns. Samples were spun in the centrifuge for three minutes at 13 krpm before being transferred into conical collection tubes. 100 μl of EB elution buffer was added to the samples before being incubated at 70°C for four
minutes, at which point the DNA was eluted. The aDNA column was centrifuged for one minute at 13 krpm from which was recovered the 1st elute. 100 μl of EB buffer was again added to the aDNA column before being incubated at 70°C for four minutes and centrifuged for one minute at 13 krpm from which was extracted the 2nd elute. 1st and 2nd elutes were placed in storage at -20°C.

6.4.4. PCR Set Up and Amplification

PCR amplifications were performed in a 30 μl of reaction volume consisting of 1.5 x PCR Gold Buffer (Applied Biosystems, Carlsbad, CA, USA), 2 mM MgCl₂, 0.2 mM each dNTP, 0.3 μM forward primer, 0.3 μM reverse primer, 1 mg/mL BSA, and 1.5 U AmpliTaq Gold (Applied Biosystems, Carlsbad, CA, USA) and 3 μl of DNA solution using an Eppendorf Personal or Gradient thermocycler (Eppendorf, 187 Mississauga, ON, Canada) and thermocycling program consisting for 60 cycles, at 95°C for 30 seconds, 52°C for 30 seconds and 70°C for 40 seconds with an initial denaturing at 95°C for 12 minutes. A negative control was included in each PCR run in order to monitor PCR reagent contamination. Following amplification, SYBR Green I (Life Technologies, Carlsbad, CA, USA) was added to 5 μl of PCR product and electrophoresed on a 2% agarose gel, visualized with a Dark Reader transilluminator (Clare Chemical Research, Dolores, CO, USA). All post-PCR laboratory work were conducted in laboratory dedicated to post-PCR analyses.

6.4.5. Sequencing and Analysis

Samples and sequencing primers were sent to Eurofins Genomics (Toronto, ON). Typically, two sequencing reactions from opposite directions (double-stranded sequencing) are performed to confirm sequence authenticity (Cooper and Poinar 2000; Winters et al. 2011). For this project, multiple overlapping PCR amplifications and bi-directional sequencing were initially proposed, to generate multiple overlapping and verifiable sequence reads, which would have produced longer DNA sequence assemblies for each sample. Although all samples have already been amplified through PCR, double-stranded sequencing could not be completed due to lab work restrictions for the prevention of COVID-19. The sequences obtained from each sample were manually trimmed to remove primer sequences and low-quality bases using Nucleobytes 4Peaks (by A. Griekspoor and Tom Groothuis, nucleobytes.com) and Clustal Omega.
Sequencing produced only short fragments that could not be overlapped. All sequences were aligned against human (Genbank accession number GU170818) mitochondrial CytB sequences in order to confirm the absence of contamination. Modern and ancient edited sequences obtained in this study were aligned against one another by sequencing primer and also against the 34 GenBank reference Dasyprocta spp. sequences of the CytB using Clustal Omega. Sequence were processed through Basic Local Alignment Search Tool (BLAST) (Altschul et al. 1990) and matched to reference Dasyprocta spp. GenBank reference sequences. Sequences were translated into protein sequences using ExPASy (5'3' Frame 1) (Gasteiger et al. 2003) in order to evaluate the impact of polymorphisms on amino acid translations.

6.4.6. Phylogenetic Analyses

Due to the lack of overlap in archaeological sequences, phylogenetic analysis was conducted independently for each group of amplified and sequenced fragments. Three Maximum Likelihood phylogenies were constructed using sequences (amplification F114-R252, sequencing F114, amplification F114-R252, sequencing R252, amplification F156-R387, sequencing F156, see Table 7.1). The sequences for samples AG1, AG5, and AG6 were too short to form an accurate phylogeny. Archaeological sequences aligned with Dasyprocta spp. reference sequences obtained from GenBank (n=33) using Clustal Omega. None of the full mitochondrial genomes of the eleven currently recognized Dasyprocta species (Wilson and Reeder 2005) have been sequenced. The mitochondrial CytB gene is the focus of intense sequencing due to it widespread used in phylogenetic and phylogeographic studies. Consequently, sequences of the CytB gene are available for Dasyprocta azarae, Dasyprocta fuliginosa (one sequence each), and D. leporina and (32 sequences). Archaeological and reference sequences were aligned using Clustal Omega. All trees were built using Phylogeny.fr (Dereeper et al. 2006) and viewed with TreeDyn (Chevenet et al. 2006). HKY85, a standard nucleotide substitution model, was determined the best-fit model for nucleotide substitution.

6.5. Conclusion

For this project, pre-Columbian agouti remains from Carriacou, Basse Terre, Marie-Galante, Grande Terre, Martinique, and Saint Martin were selected. The
zooarchaeological sample selection protocol was successful in associating each specimen with a unique individual (NISP 30, MNI 28), thus maximizing the retrieval of non-repeating genetic data. Primers were designed and verified using modern agouti skin tissue. Zooarchaeological samples were processed in dedicated aDNA labs, using standard procedure to extract and analyze the aDNA. aDNA samples were handled with great caution in order to minimize the potential for contamination. In the following chapter, I provide evidence for the absence of contamination and describe the results obtained from my analyses.
Chapter 7.

Results

This section details the results obtained from the extraction of DNA from modern and archaeological *Dasyprocta* spp. samples. First, I discuss the preservation of DNA in the examined modern and archaeological samples. I then provide evidence for the absence of contamination. I describe the polymorphisms found among archaeological sequences. I discuss species identification for modern and archaeological samples. Finally, I discuss phylogenetic trees constructed using archaeological and modern *Dasyprocta* spp. reference sequences.

7.1. PCR Amplification and DNA Preservation in Modern and Archaeological Samples

In total, 50 sequences were obtained from the three modern and 30 archaeological samples. Three sequences were obtained from the three modern agouti samples, representing two individuals. 47 sequences were obtained from the 30 archaeological samples (NISP 30, MNI 28, see Table 6.5), three from BK77 Grand Case, Saint Martin, three from Macabou, Martinique, six from Sabazan, Carriacou, and 35 from Grand Bay, Carriacou (see Table 7.1. below). Sequences will be stored in the Simon Fraser laboratories after the double stranded sequencing has been completed.
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<th>Reverse PCR Primer</th>
<th>Sequencing Primer</th>
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<td>Island</td>
<td>Site</td>
<td>Lab Number</td>
<td>Sequence Read Number</td>
<td>Forward PCR Primer</td>
<td>Reverse PCR Primer</td>
<td>Sequencing Primer</td>
<td>Amplicon Length (bp)</td>
<td>PHRED Score</td>
</tr>
<tr>
<td>------------</td>
<td>-----------</td>
<td>------------</td>
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<td>--------------------</td>
<td>--------------------</td>
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<td>---------------------</td>
<td>-------------</td>
</tr>
<tr>
<td>Carriacou</td>
<td>Grand Bay</td>
<td>AG27</td>
<td>AGH27</td>
<td>F156</td>
<td>R387</td>
<td>F156</td>
<td>232</td>
<td>56</td>
</tr>
<tr>
<td>Carriacou</td>
<td>Grand Bay</td>
<td>AG28</td>
<td>AGS28</td>
<td>F114</td>
<td>R252</td>
<td>R252</td>
<td>139</td>
<td>36</td>
</tr>
<tr>
<td>Carriacou</td>
<td>Grand Bay</td>
<td>AG28</td>
<td>AGH28</td>
<td>F156</td>
<td>R387</td>
<td>F156</td>
<td>232</td>
<td>55</td>
</tr>
<tr>
<td>Carriacou</td>
<td>Grand Bay</td>
<td>AG29</td>
<td>AGS29</td>
<td>F114</td>
<td>R252</td>
<td>R252</td>
<td>139</td>
<td>41</td>
</tr>
<tr>
<td>Carriacou</td>
<td>Grand Bay</td>
<td>AG29</td>
<td>AGH29</td>
<td>F156</td>
<td>R387</td>
<td>F156</td>
<td>232</td>
<td>56</td>
</tr>
<tr>
<td>Carriacou</td>
<td>Grand Bay</td>
<td>AG30</td>
<td>AGS30</td>
<td>F114</td>
<td>R252</td>
<td>R252</td>
<td>139</td>
<td>37</td>
</tr>
<tr>
<td>Carriacou</td>
<td>Grand Bay</td>
<td>AG30</td>
<td>AGH30</td>
<td>F156</td>
<td>R387</td>
<td>F156</td>
<td>232</td>
<td>57</td>
</tr>
</tbody>
</table>
The high 87% success rate for PCR amplification and sequencing (26/30) for short mtDNA fragments (from 79 bp to 232 bp) clearly demonstrates the good preservation of aDNA so that even the four oldest samples, AG13, AG15, AG16, and AG17 dated ca. A.D. 390-590, generated DNA sequences. AG16 and AG17 even generated longer DNA fragment of 232 bp. Only four samples (La Ramée, Basse Terre (AG2), Tourlourous, Marie-Galante (AG3), Belle Plaine, Grande Terre (AG4), and Sabazan, Carriacou (AG7)) failed completely to amplify, likely due to the poor preservation of endogenous DNA in these samples.

Overall, the sequencing quality of these ancient DNA data is very high, as shown in the clean peaks of the electropherograms (Figures 7.5-7.10). Sequences for samples AG1, AG5, and AG6 were poorer, with many indistinct peaks that required heavy trimming and editing. The length of the edited sequences for archaeological samples ranged from 16 to 143 bp (average 69 bp) and for modern samples from 24 to 204 bp (average 126 bp). Three samples from the multi-island pilot testing produced only ultra-short sequences (Figure 7.8), but for the most part, where not used for analysis. The quality and length of the remaining archaeological sequences was suitable for analysis.

### 7.2. Contamination Analysis

All sequences were mapped against a human mitochondrial genome (Genbank accession number GU170818) mitochondrial CytB sequences with no significant alignment, suggesting the obtained sequence are not from contaminant human DNA. Electrophoretic analysis of archaeological fragments amplified with primers F156-R387 (sequencing F156) (Figure 7.1) showed the presence of a <100 bp fragment in blank control BKH1 lane 7. The amplification products from this run migrated as fragments of 200 to 300 bp, consistent with the predicted size of 231 bp. The presence of a <100 bp fragment in BKH1 is likely due to an amplification artifact and is unrelated to contamination.
7.1. Electrophoresis of amplified DNA of archaeological samples AG26-AG30. DNA fragments were separated on a 2% agarose gel. Lane 1 shows a molecular weight marker. Archaeological samples in lanes 2-6 (AG26, AG27, AG28, AG29, AG30) and positive controls in lanes 9 and 10 (AG11 and AG14) migrated as fragments of 200 to 300 bp, consistent with the predicted size of 231 bp. In lane 7, the blank control BKH1, a possible primer dimer, migrated as a fragment below 100 bp. Artifacts are also present in the archaeological sample AG26 and the positive control AG11. Blank (BKH2) and Negative (NEG) controls were negative.

Blank and negative controls from all other runs were negative for any DNA. No contamination, either punctual or systematic, was detected in this study as all PCR setups show no false positive amplification from the blank controls and negative controls. DNA extraction, PCR amplification and sequencing, were repeated for all samples by another lab worker (H.G.Z.) with the same success, demonstrating strong reproducibility. In addition, analysis of archaeological sequences (amplification F156-R387, sequencing F156) revealed the occurrence of polymorphisms (see Figure 7.4) that are consistent with the absence of contamination.

7.3. Species Identification

BLAST sequence alignment results for archaeological sequences showed 100% identity with D. leporina, except at the identified polymorphic sites (Figure 7.4). Fragments amplified with primers F114-R252 (sequencing F114) and F156-R387 show 92-95% identity with D. fuliginosa and 90-92% identity with D. azarae. The ultra-short sequences from samples AG1, AG5, and AG6 did not produce any significant alignment with reference sequences. BLAST sequence alignment of modern agouti AGM2 showed...
similar identity matches with the three species of agouti, with >92% identity for \textit{D. leporina}, >93% for \textit{D. azarae}, and >94% for \textit{D. fuliginosa}. The short (24 bp) sequence obtained from AGM1 showed no significant alignment with reference sequences.

Maximum Likelihood trees with bootstrap values were created using archaeological sequences and 34 reference agouti CytB sequences, to 1) evaluate the taxonomic relationship of archaeological samples in relation to the three currently sequenced modern reference \textit{Dasyprocta} spp; and 2) visualize the placement of the archaeological sequences within the modern \textit{D. leporina} clades. The archaeological sequences could not be assembled due to lack of overlap so that individual trees had to be constructed for each group of fragments. The sequences from samples AG1, AG5, and AG6 were too restricted in length to form an accurate phylogeny. Three trees were made for fragments amplified with primers F114-R252 (sequencing F114), F114-R252 (sequencing R252), and F156-R387 (sequencing F156). Reference sequences include the 32 available CytB sequences for \textit{D. leporina} and the one available CytB sequence for \textit{D. fuliginosa} and \textit{D. azarae} (Appendix B).

In order to evaluate the taxonomic relationship of archaeological samples and the placement of the archaeological samples within the modern \textit{D. leporina} clades, three trees were built using archaeological sequences and \textit{Dasyprocta} spp. modern reference sequences. Archaeological samples clustered in the \textit{D. leporina} clade, but reflect the ambiguity caused by the shortness of the sequences, and lack additional reference sequences for \textit{D. fuliginosa} and \textit{D. azarae}. In trees of fragments amplified with primers F114-R252, \textit{D. fuliginosa} is clustered with archeological and \textit{D. leporina} reference sequences (see Figure 7.3 and Appendix C).
Figure 7.2. Maximum likelihood tree of archeological sequences (amplification F156-R387, sequencing F156) and *Dasyprocta* spp. modern reference sequences. Archaeological samples originate from Carriacou. Branch support values are in percentages, with minimum 90% branch support value. Archaeological samples are located in a *D. leporina* clade, supported by a 93% value. *Rattus sordidus* is used as a comparative outgroup.

The tree built using sequences (amplification F114-R252, sequencing R252), which did not present with any polymorphic sites, showed clearly the two *D. leporina* clades. Archaeological samples clustered all in Clade A (Figure 7.3 below). Trees containing sequences with polymorphic sites (amplification F114-R252, sequencing F114), and (amplification F156-R387, sequencing F156) were less accurate, due to the presence of
the polymorphisms which confused the phylogeny (see Figure 7.2 and Appendix C). None of the trees offered enough support to show the potential Sub-Clades.
Figure 7.3. Maximum likelihood tree of archeological sequences (amplification F114-R252, sequencing R252) and Dasyprocta spp. modern reference sequences. Archaeological samples originate from Carriacou. Branch support values are in percentages, with minimum 50% branch support value. Archaeological samples are clustered in the single lower clade (Clade A), supported by a 63% value. *Rattus sordidus* is used as a comparative outgroup.

### 7.4. Archaeological Sequence Polymorphisms

A total of eight polymorphisms were detected in six Caribbean archaeological samples (AG5, AG6, AG11, AG16, AG17, AG25, see Figure 7.4), based upon sequence alignment of archaeological samples sequences.
Figure 7.4. Sequence alignment of archaeological sequences (AG1-AG6 amplification F114-R215, sequencing R215; AG8-AG14 amplification F114-R252, sequencing F114; AG14+AG-30 amplification F156-R387, sequencing F156) and reference D. leporina CytB ORF (accession number AF437811). Archaeological sample AG5 originates from Martinique, AG6 from Saint-Martin, AG1 and AG8-AG30 from Carriacou. Red highlighted nucleotides show variation among archaeological samples. Blue highlighted nucleotides show variation between archaeological samples and AF437811 reference sequence.

Five of the eight polymorphisms were identified in four Carriacou samples (Table 7.2), one sample from Sabazan and three from Grand Bay. Sequences were of good quality, with clear peaks visible on the electropherograms (Figures 7.5-7.10). The three remaining polymorphisms were located in the Martinique and Saint-Martin samples.

Table 7.2. Polymorphisms identified in archaeological samples. Red highlighted nucleotides show variation between archaeological samples. Blue highlighted nucleotides show variation between archaeological samples and AF43781 reference sequence.

<table>
<thead>
<tr>
<th>Site</th>
<th>Island</th>
<th>Lab number</th>
<th>Position of Polymorphism</th>
<th>Sample Codon Sequence</th>
<th>Reference Codon Sequence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Macabou</td>
<td>Martinique</td>
<td>AG5</td>
<td>114</td>
<td>AGG A CTT</td>
<td>AGG CCT</td>
</tr>
<tr>
<td>BK77</td>
<td>Grand Case</td>
<td>Saint-Martin</td>
<td>AG6</td>
<td>152</td>
<td>C-T</td>
</tr>
<tr>
<td>BK77</td>
<td>Grand Case</td>
<td>Saint-Martin</td>
<td>AG6</td>
<td>156</td>
<td>AGT</td>
</tr>
<tr>
<td>Sabazan</td>
<td>Carriacou</td>
<td>AG11</td>
<td>205</td>
<td>TAT</td>
<td>CAT</td>
</tr>
<tr>
<td>Sabazan</td>
<td>Carriacou</td>
<td>AG11</td>
<td>220</td>
<td>TGG</td>
<td>CGG</td>
</tr>
<tr>
<td>Grand Bay</td>
<td>Carriacou</td>
<td>AG16</td>
<td>302</td>
<td>AAG</td>
<td>AGG</td>
</tr>
<tr>
<td>Grand Bay</td>
<td>Carriacou</td>
<td>AG17</td>
<td>271</td>
<td>TTT</td>
<td>CTT</td>
</tr>
<tr>
<td>Grand Bay</td>
<td>Carriacou</td>
<td>AG25</td>
<td>263</td>
<td>ATT</td>
<td>ATC</td>
</tr>
</tbody>
</table>

Insertions and deletions of nucleotides, such as those located at AG5 nt 114 and AG6 nt 152, are highly improbable and instead likely reflect damage caused to the DNA, or sequencing errors. Typically, two sequencing reads from two directions are done to confirm the authenticity of the polymorphisms (Cooper and Poinar 2000; Winters et al. 2011), but in this case, could not be completed due to lab work restrictions set for the prevention of COVID-19. Additional testing is needed to confirm and potentially identify further polymorphisms. Authenticity of polymorphisms is further discussed in Chapter 8.
Figure 7.5  Electropherogram of AG11 and AG14 of agouti (*Dasyprocta* sp.) CytB sequences. SNP identified as cytosine to thiamine transition in AG11, Carriacou (upper) with comparative archaeological reference sequence AG14, Carriacou (lower).
Figure 7.6. Electropherogram of AG11 and AG12 of agouti (*Dasyprocta* sp.) CytB sequences. SNP identified as cytosine to thiamine transition in AG11, Carriacou (upper) with comparative archaeological reference sequence AG12, Carriacou (lower).
Figure 7.7. Electropherogram of AG16 and AG14 of agouti (*Dasyprocta* sp.) CytB sequences. SNP identified as guanine to adenine transition in AG16, Carriacou (upper) with comparative archaeological reference sequence AG14, Carriacou (lower).
Figure 7.8. Electropherogram of AG17 and AG18 of agouti (*Dasyprocta* sp.) CytB sequences. SNP identified as cytosine to thiamine transition in AG17, Carriacou (upper) with comparative archaeological reference sequence AG18, Carriacou (lower).
Figure 7.9. Electropherogram of AG25 and AG24 of agouti (*Dasyprocta* sp.) CytB sequences. SNP identified as cytosine to thiamine transition in AG25, Carriacou (upper) with comparative archaeological reference sequence AG24, Carriacou (lower).

Figure 7.10. Electropherogram of AG6 and AG5 agouti (*Dasyprocta* sp.) CytB sequences. SNP identified as cytosine to thiamine transition in AG6, Saint-Martin (upper) with comparative archaeological reference AG5, Martinique (lower).
7.5. Comparison of Reference Sequences

Archaeological sequences were aligned with modern *Dasypodita* spp. CytB reference sequences. None of the six archaeological sequence polymorphisms identified in this study were found to occur in any of the modern *Dasypodita* sp. reference sequences. Two *D. leporina* clades (Clades A and B) were identified in the modern reference *D. leporina* CytB sequences, corresponding to those reported by van Vuuren et al. (2004). Three diagnostic nucleotide positions define the Clades (Figure 7.11). All archaeological samples from this project were restricted to Clade A.
Figure 7.11. *D. leporina* reference sequence Clades A and B, with archaeological and modern reference samples. Archaeological sample AG5 originates from Martinique, AG6 from Saint-Martin, AG1 and AG8-AG30 from Carriacou. Clade A is in green, Clade B in purple. Archaeological sequences are clustered in Clade A. Red highlighted nucleotides show variation among archaeological samples. Blue highlighted nucleotides show variation between archaeological samples and modern reference sequences. Sequence AF437801’s position within clades A and B shifts between Clade A and Clade B. van Vuuren et al. (2004) report AF437801 in Clade A.
Further analysis of the modern reference and archaeological sequences suggested the presence of two previously unreported Sub-Clades within Clade A (Sub-Clades A1 and A2). Together with three of the modern samples, archaeological samples from this project clustered in the presumed Sub-Clade A1.

Figure 7.12. *D. leporina* reference sequence potential Sub-Clades, with archaeological and modern reference samples. Archaeological samples AG14+-AG30 originate from Carriacou. Sub-Clade A1 is in yellow, Sub-Clade A2 in turquoise. Archaeological sequences (AG1-30) are clustered in Sub-Clade A1. Red highlighted nucleotides show variation among archaeological samples. Blue highlighted nucleotides show variation between archaeological samples and modern reference sequences.

7.6. Conclusion

This study offers the first genetic evidence for pre-Columbian agouti. Results demonstrate the authenticity of amplification products which were all consistent with the
absence of contamination. All three modern samples were successfully amplified; however, modern sequences were too short and/or unspecific to produce any significant alignment. Archaeological samples had a very high success rate of amplification, with only four samples out of 30 failing to amplify. BLAST alignments and phylogenetic trees support the taxonomic identification of archaeological samples as *D. leporina*. Alignment of archaeological sequences showed a number of polymorphisms occurring between archaeological samples. Alignment of modern *D. leporina* sequences showed the occurrence of two clades (Clade A and B), as reported by van Vuuren et al. (2004), with archaeological sequences clustering in Clade A. Additionally, two possible Sub-Clades were tentatively identified, with archaeological sequences clustering in presumed Sub-Clade A1. Further testing is required in order to confirm archaeological polymorphisms. Additional testing may also identify further polymorphisms. In Chapter 8, I offer a comprehensive review of these results with respect to my hypothesis, and discuss their significance for the genetic, archaeological, and ecological study of the pre-Columbian Caribbean.
Chapter 8.

Discussion

Agouti (Dasyprocta sp.) was translocated from the continent to the Caribbean, alongside other commensal fauna and flora, starting around ca. A.D. 500 (Newsom and Wing 2004: 107). As with other translocates and human groups of the pre-Columbian Caribbean, the geographic origin(s) and interaction networks through which prehistoric Caribbean agoutis circulated are still in question. By identifying genetic variations in ancient agouti, this research contributes to clarifying the extent of the pre-Columbian interactions occurring between Carriacou and the continent. This is the first study to use ancient agouti DNA as a proxy for human interaction, demonstrating the potential for successful genetic research in environments with challenging conditions for aDNA preservation, such as the Caribbean. This research also contributes to the clarification of ongoing questions affecting pre-Columbian Caribbean agoutis, such as its taxonomic classification, population structure and population viability on Carriacou. I previously hypothesized that pre-Columbian Caribbean agouti sampled in this study 1) originated from different populations; 2) represented more than one species; and 3) that agouti was disseminated throughout the Lesser Antilles from founding populations on one or a few islands. Below, I discuss the authenticity of ancient agouti polymorphisms and the use of the agouti CytB in tracking pre-Columbian Caribbean human interactions. I consider species identification through genetic analysis for Caribbean pre-Columbian agouti and modern samples. Finally, I examine the implications of this research for pre-Columbian agouti supply and dissemination in the Caribbean, population viability on Carriacou, and continental origins.

8.1. Authenticity of Polymorphisms

The authenticity of the presumptive polymorphisms found in archaeological sequences was verified using nucleotide to protein translation to determine the impact of polymorphisms on the coding sequence. Changes in codon sequence that impact the coding for amino acids are more likely caused by damage to the aDNA or a sequencing error, due to the highly conserved nature of CytB. Changes in codon sequence with no impact on amino acids have a higher potential of being authentic polymorphisms.
Figure 8.1. Nucleotide to amino acid translation of the reference agouti CytB Open Reading Frame (accession number AF437811).

Note: Translated through ExPASy (5’3’ Frame 1) (Gasteiger et al. 2003).

Table 8.1. Impact of polymorphisms on amino acid translations.

<table>
<thead>
<tr>
<th>Lab Number</th>
<th>Position of Polymorphism</th>
<th>Reference Sequence Amino Acid</th>
<th>Polymorphic Change</th>
<th>Effect on Translated Product</th>
</tr>
</thead>
<tbody>
<tr>
<td>AG5</td>
<td>114</td>
<td>Arginine/Proline</td>
<td>Insertion</td>
<td>Unlikely</td>
</tr>
<tr>
<td>AG6</td>
<td>152</td>
<td>Proline</td>
<td>Deletion</td>
<td>Unlikely</td>
</tr>
<tr>
<td>AG6</td>
<td>156</td>
<td>Serine</td>
<td>Serine</td>
<td>No Change</td>
</tr>
<tr>
<td>AG11</td>
<td>205</td>
<td>Histidine</td>
<td>Tyrosine</td>
<td>Unlikely</td>
</tr>
<tr>
<td>AG11</td>
<td>220</td>
<td>Arginine</td>
<td>Tryptophan</td>
<td>Unlikely</td>
</tr>
<tr>
<td>AG16</td>
<td>302</td>
<td>Arginine</td>
<td>Lysine</td>
<td>Conservative</td>
</tr>
<tr>
<td>AG17</td>
<td>271</td>
<td>Leucine</td>
<td>Phenylalanine</td>
<td>Unlikely</td>
</tr>
<tr>
<td>AG25</td>
<td>263</td>
<td>Isoleucine</td>
<td>Isoleucine</td>
<td>No Change</td>
</tr>
</tbody>
</table>

Insertions and deletions of nucleotides, such as those found in samples AG5 and AG6, cause significant changes in nucleotide structure and as a result, in the coding for amino acids. Substitutions of one nucleotide for another, as found in the remaining polymorphisms, can have little to high impact, depending on the nucleotide’s placement within the codon. The polymorphisms AG6 nt 156 and AG25 nt 263 do not perturb the coding for amino acids, and as such, that for protein. AG16 nt 302 which codes for lysine in the place of arginine, is a conservative substitution, meaning that the amino acids involved have similar molecular structures which do not overly perturb protein coding.

Further testing is necessary to secure the presence of these substitutions and clarify the status of remaining polymorphisms. The polymorphisms located at AG5 nt 114 and AG6 nt 152, whose high impact on amino acid and protein coding is highly unfeasible, likely reflects damage caused to the DNA, or a sequencing error. The remaining five polymorphisms have an unknown effect on amino acid coding.
8.2. Agouti CytB for a Caribbean Commensal Model

This study reports the extraction and amplification of DNA from thirty pre-Columbian agouti samples. Only four samples failed to amplify, three from the pilot test islands (La Ramée, Basse Terre (AG2), Tourlourous, Marie-Galante (AG3), and Belle Plaine, Grande Terre (AG4)) and one from Sabazan, Carriacou (AG7)). None of the samples from the Guadeloupe region were successfully amplified. 26 out of the 30 samples were successfully amplified. This high success rate (over 86%) for DNA recovery is uncommon with Caribbean samples, because hot and humid environments offer challenging conditions for the preservation of aDNA. Previous aDNA studies conducted in the Caribbean have typically achieved below 50% success rate, even with the use of powerful Next Generation Sequencing (NGS) technologies (e.g., Lalueza-Fox et al. 2003; Mendisco et al. 2015; Lord et al. 2018). In this project, failure to amplify was likely due to the absence of endogenous DNA, since two independent attempts for DNA extraction were performed. The provenience, weight and physical condition of bone samples did not exhibit any notable distinction from successfully amplified samples. Pilot test samples (AG1, AG5, and AG6) only yielded very short (47 bp on average) sequences with little informative value. The short size of the sequences is due to the relative position of the PCR primers used for these fragments, designed specifically for pilot testing to verify the presence of DNA.

Despite the high conservation of the CytB, sequencing data showed the occurrence of eight individual polymorphisms in six samples. Two potential polymorphisms, predicted to severely disrupt the open reading frame, were immediately discounted, likely caused by damage or a sequencing error. Five polymorphisms were found in four samples out of the 24 successfully amplified Carriacou samples (NISP 22, MNI 22) and one polymorphism was found in the individual from Saint-Martin (NISP 1, MNI 1 see Table 6.5). Molecular clocks use the linear mutation rate of DNA to estimate the timing of divergence between populations and species. The rate of change of the CytB in voles (*Microtus longicaudus*) (Conroy and Cook 2000) and squirrels (*Tamiasciurus* spp.) (Arbogast et al. 2001), rodents closely related to agouti, is estimated to slightly under 10% per million years. There is approximately 0.2% of polymorphisms in the 26 sequenced archaeological agouti, suggesting that the pre-Columbian CytB polymorphisms occurred over a period of approximately 20,000 years, likely well before the translocation of agouti to the Caribbean.
van Vuuren et al. (2004) sequenced 411 bp from the CytB region of 31 *D. leporina* specimens from French Guiana and Brazil. Modern reference sequences of agouti CytB from French Guiana and Brazil show the presence of a minimum of two clades (A and B) (van Vuuren et al. 2004), which are today sympatric in French Guiana and Brazil. Based upon the molecular clock, the *D. leporina* maternal clades are estimated to have separated between 160,000 and 260,000 years ago (van Vuuren et al. 2004).

Phylogenetic trees and alignment of archaeological and modern reference sequences showed that archaeological samples from this project all clustered within Clade A. Further analysis of the modern reference sequences and archaeological sequences identified the presence of two previously unreported potential Sub-Clades within Clade A (A1 and A2). Together with three of the modern samples, archaeological samples from this project clustered in presumed Sub-Clade A1. This clustering, supported by five polymorphic sites (Figures 7.11 and 7.12), indicates that the Caribbean agouti is likely to have originated from a single continental population. The sympatric nature of maternal Clades and potential Sub-Clades of modern reference agouti in French Guiana and Brazil did not provide any resolution as to the geographic origin of Caribbean agouti.

I previously hypothesized that pre-Columbian Caribbean agouti originated from different populations. Based upon the timing from the molecular clocks, it is likely that Clades A and B and presumed Sub-Clades A1 and A2 developed prior to the occurrence of the SNPs found in the Caribbean samples. SNPs developed subsequently in isolated Clade populations, but likely prior to the agoutis’ translocation to the Caribbean. Caribbean agouti were thus translocated from a single isolated population, exclusively from Sub-Clade A1. It is vital that continental archeological agouti samples be sequenced in order to determine what clades are present on the continent and the potential source populations for pre-Columbian Caribbean agouti.

8.3. **Species Identification for Archaeological Caribbean Agouti**

Agouti species are osteologically similar, which complicates morphological identification of fragmented archaeological remains. Eleven species of agouti are currently recognized, although agouti taxonomy is in need of revision (Emmons and Feer 1997; Voss et al. 2001; Patton and Emmons 2015). I previously hypothesized that pre-Columbian Caribbean agouti specimens may represent more than one species.
Sequencing data for all samples support species identification for *D. leporina* on Carriacou, Saint Martin, and Martinique. Phylogenetic trees confirmed these results, with archaeological samples clustering in the *D. leporina* clade. The clustering of archaeological samples in the modern *D. leporina* clades reported by van Vuuren (2004) also supports identification of Caribbean agoutis as *D. leporina*. However, the lack of reference CytB mitochondrial sequences from nine of the eleven agoutis species excludes the possibility for conclusive results. Furthermore, although it has not been recorded, hybridization between two agouti species is a possibility (Patton and Emmons 2015: 743) so that the archeological samples used in this study may reflect an unknown species or sub-species. The ultra-short sequences from samples AG1, AG5, and AG6 did not produce any significant alignment. However, the polymorphic site sample AG6, corresponding to Clade A reported by van Vuuren (2004) supports its identification as *D. leporina*. Overall, the results from this study contradict my hypothesis and support a species identification of *D. leporina* for 26 of 30 analyzed specimens from three islands. This consistency within islands and between islands located at significant distance apart (over 600 km in a straight line) strongly suggest *D. leporina* was widespread in the pre-Columbian Lesser Antilles and that archaeological agouti specimens in this region most likely belong to *D. leporina*. The following paragraphs of this Chapter will rely upon this identification in discussing pre-Columbian human interactions.

### 8.4. Species Identification for Modern Agouti

No species designation or collection locality information was attached to either of the two modern agoutis from the Beaty Biodiversity Museum, University of British Columbia. Nor was such information available from the morphology of the specimens due to the likeness of many agouti species in appearance, size, and pelt color (Souza et al. 2007; Ramírez-Chaves et al. 2018, but see Matson and Shump 1980). Sequencing data of modern agouti did not produce any conclusive BLAST alignment results. Modern agouti AGM2 showed similar identity matches with *D. leporina, D. fuliginosa*, and *D. azarae*. The ambiguity in identity match does not permit for a reliable species identification. It is also possible that the sample originates from an agouti species whose mitochondrial data has not yet been sequenced. The short sequence obtained from AGM1 showed no significant alignment with reference sequences and was inconclusive.
8.5. Implications for Pre-Columbian Agouti Supply and Dissemination in the Caribbean

I previously hypothesized that agouti was disseminated throughout the Lesser Antilles from founding populations on one or a few islands. Although it cannot be excluded that the agouti would have been translocated directly from northern South America or Trinidad to Martinique and Saint Martin, genetic analyses from this study strongly suggest a genetic bottleneck. In this case, Caribbean agouti populations would have been entirely supplied from founding populations on one or a few islands. The richness and diversity of imported faunal resources and ritual paraphernalia (Kaye et al. 2004; Fitzpatrick et al. 2009a; Giovas et al. 2012; Giovas 2013; Lord et al. 2020) found on Carriacou suggest that it may have shared privileged connections to the continent and northern Caribbean, and thus may have served as a gateway supply for agouti for the remainder of the Caribbean. However, it is also necessary to investigate the potential of other neighbouring islands, particularly in the southern Caribbean, as being the primary gateway sources of supply in agouti. At present, the absence of comparative genetic data from archaeological continental agouti does not allow for conclusively establishing the nature of agouti dissemination in the Caribbean. The continental home range of Clade A and the presumed Sub-Clade A1 may provide further indication as to the dissemination of agouti in the Caribbean. A broad continental range may indicate greater potential for direct translocation from the continent to the islands, due to a more widespread access by human groups. On the contrary, a limited continental range, to which fewer human groups might have access, may indicate greater potential for the creation of founding populations of agouti on one or a few islands, which later, would have been disseminated to the remainder of the Caribbean.

The CytB is a gene encoded in mtDNA, transferred only through the maternal lineage. As such, in the case of a genetic bottleneck, it is possible to speculate that only a few female agoutis, originating from a single population, would have been transported and used to establish viable populations in the Caribbean. The natural dispersal and subsequent colonization of islands by a single or small number of pregnant females has been hypothesized by ecologists and archaeologists (e.g., Davis 1987: 118; Vigne 2014; Hofman et al. 2015; Cox et al. 2016: 197, 384; Hofman and Rick 2018), but may have also been used as a mechanism of anthropogenically-stimulated dispersal. Pre-
Columbian groups may thus have specifically targeted pregnant agouti females for transport in order to facilitate the rapid and successful propagation of populations.

8.6. Implications for Viable Agouti Populations on Carriacou

In the case of a genetic bottleneck, with only a few translocated individuals, it is likely that agouti would have established viable populations very early on in the history of human occupation of Carriacou, soon after island settlement around ca. A.D. 400/600. Analysis of strontium \( ^{87}\text{Sr}/^{86}\text{Sr} \) and lead isotopes \( ^{206}\text{Pb}/^{204}\text{Pb} \) isotopes of agouti on Carriacou (Giovas et al. 2016) showed that agouti found in middens had a local Sr signature, and thus were most likely born on the island, indicating viable breeding populations by ca. A.D. 600/800. The agouti’s highly adaptable nature also favors the likelihood of its rapid establishment. In the case that agouti would have established viable populations on Carriacou rapidly around ca. A.D. 400/600, it could have affected local ecologies in a number of ways (see Chapter 5, Section 7). Introduced agouti would have necessitated little hands-on management from human groups, although this does not preclude the possibility for management having taken place. In either case, it is likely their commensal relationship with humans aided their establishment on the island (Newsom and Wing 2004; Ferrer et al. 2012). Clarifying the degree to which pre-Columbian Caribbean agouti were managed is important for reconstructing human interactions and also provides a basis for evaluating the potential ecological impact of agoutis. Unfortunately, the present genetic data does not allow for insight into pre-Columbian agouti management at this stage. Comparative genetic data from domesticated agouti along with additional approaches (zooarchaeological, geochemical, biochemical) (see LeFebvre and deFrance 2018: 154–156) applied specifically to agouti remains, are necessary to successfully address the question of management.

Furthermore, the agouti’s relative prominence on a number of islands in the Lesser Antilles, including Antigua (Wing 1999: Table 4; Healy et al. 2005); Grenada (Newsom and Wing 2004: Table B-1), Guadeloupe (Grouard 2001), Martinique (Grouard and Bérard 2005; Grouard 2011, 2013), Montserrat (Steadman et al 1984; Reitz 1994), Nevis (Nokkert 2002), Saint Martin (Nokkert 1995; Grouard 2004), and Carriacou (Wing 2012; Giovas et al. 2012), suggests that agouti would have, at minimum, been well
assimilated in the Lesser Antilles (Giovas 2019a) and may even have been fully naturalized on a number of islands (Newsom and Wing 2004: 205).

In the Caribbean, the radiocarbon chronology of zooarchaeological remains, including agouti, is not systematically investigated. Strengthening the radiocarbon record for agouti specimens from islands across the Lesser Antilles might validate the potential for Carriacou or another island in Lesser Antilles to have functioned as the supply source of agouti for the remainder of the Caribbean. Importantly, the radiocarbon dates of Macabou (A.D. 415–1275) (Martinique), BK77 Grand Case (A.D. 730–1160) (Saint-Martin), and Belle Plaine (A.D. 1040–A.D. 1274) (Grande-Terre) occur within or post-date this ca. A.D. 400/600 window (see Table 6.2), which is consistent with the possibility that agoutis from these sites would have been supplied from Carriacou. The chronology of sites such as Indian Creek (200 B.C.–A.D. 1300) (Antigua), Tourlourous (A.D. 237–13th century) (Marie-Galante), La Ramée (A.D. 320–A.D. 1000) (Basse Terre), Morel (400 B.C.–A.D. 1400) (Grande-Terre), and Hope Estate (450 B.C.–A.D. 650) (Saint-Martin) extend decades prior to this window; a more precise dating of the agouti samples from these sites is needed. Isotopic evidence suggests that other commensal translocates, such as opossum (Didelphis cf. marsupialis) and dog (Canis lupus familiaris) had also established living populations in the Antilles (Giovas et al. 2016; Laffoon et al. 2017).

8.7. Implications for Pre-Columbian Agouti Continental Origins

The Caribbean archeological agouti analyzed in this study originated from a single population, and likely originated from a limited geographic area. The extent of this area can be delineated only with additional comparative genetic data from archaeological continental agouti. However, understanding the human interactions and the natural range of D. leporina may broadly delimit the continental origin of Caribbean archeological agouti.

The home range of D. leporina ranges from Venezuela to eastern Brazil, incorporating, the Guianas, Trinidad (Emmons and Feer, 1997: 226; Wilson and Reeder 2005). Its status on Tobago is unclear, although it is found archaeologically at the Millford (ca. 2900 years old) and Golden Grove (ca. 1200 to 900 years old) sites (Steadman and Stokes 2002). Raw materials, prestige goods, ceramic styles, and commensal
translocates in the southern Lesser Antilles point to strong ties with various areas in northern South America, Trinidad, and islands in the northern Caribbean. Across the Caribbean, zoomorphic ceramics and adornos depict continental fauna, similar to ceramic artifacts from Venezuela (Roe 1989: 272; Hofman et al. 2011: 78). Depictions of continental mammals concentrate in the southern Lesser Antilles, on Trinidad, Tobago, and in the Grenadines (Waldron 2011). Petroglyphic motifs further tie the Lesser Antilles to the Middle and Lower Orinoco and north-eastern Venezuela, and the Guianas (Dubelaar 1986; 1995, Roe 2009). In the southern Lesser Antilles, the Troumassan series, developed ca. A.D. 600, showed influence from the Orinoco Basin in Venezuela (Hofman et al. 2007, 2008, 2011) and Trinidad (Boomert 2010). This continental connection is emphasized during the Late Ceramic (Hofman et al. 2011), with the regionalization of the northern Caribbean, which, becomes increasingly distant from continental systems.

Although poorly mapped, archaeologists (Boomert 1987; Cody 1993; Rodríguez Ramos 2010; Stenborg 2016: 17) have also emphasized the related iconography and materials—semi-precious stones and guanin—of the Caribbean with Amazonia and the Isthmo-Colombian region, suggesting interactions with these regions prior or concurrent to the occupation of the Caribbean. Nephrite, turquoise, and amethyst, which may have originated from the Lower Amazon (Cody 1993; Epstein 1988; Watters 1997a; Costa et al. 2004), are reported in the Lesser Antilles, in various proportion on Antigua (Murphy et al. 2000), Guadeloupe (Durand and Petitjean-Roget 1991; Queffelec et al. 2018), Grenada (Cody 1990; Watters 1997a, 1997b; Guzzo Falci et al. 2020), Martinique (Bérard 2004), Saint Martin (Haviser 1999) and Montserrat (Watters and Scaglion 1994). Human interactions thus occurred throughout the continental home range of D. leporina, suggesting broad origin(s) for the pre-Columbian Caribbean agoutis.

Archaeological evidence also links the southern Lesser Antilles to islands in the North. Jadeitite, which is believed to have been sourced in part in the Dominican Republic and Cuba, has been recovered from a lapidary workshop at Pearls, Grenada, both as raw material and finished or partially finished beads (Cody 1991, 1993). Pearls also supplied amethyst beads to islands in the North (Guzzo Falci et al. 2020), demonstrating ongoing interaction. On Carriacou, ritual paraphernalia includes vomit spatulas and three-pointer stones (Fitzpatrick et al. 2009a; Kaye et al. 2010), typical of the northern Taíno chiefdoms in the Greater Antilles. Guinea pig, present in the Lesser Antilles on Antigua
(Wing et al. 1968; Healy et al. 2003); Nevis (Kaye et al. 2010); Saint-Lucia (Phulgence 2007, in LeFebvre and deFrance 2014); Curaçao (Newsom and Wing 2004: 73), and Carriacou (Giovas et al. 2012), likely would have been translocated to the area from the northern Antilles (Lefebvre and deFrance 2014, Lord et al. 2020). Overall however, the absence of any archaeological remains of agouti north of the Lesser Antilles (Newsom and Wing 2004: 205) suggests that the agouti would more likely have been a continental import from northern South America, most likely the Guianas, Trinidad, or Venezuela, as opposed to having been translocated from islands in the North. Importantly, the consistency of Clade A throughout the successfully amplified samples from three islands suggests that the agouti from Martinique and Saint-Martin may have been sourced directly from Carriacou, or another southern Lesser Antillean island from which agouti has not yet been analyzed.

8.8. Conclusion

This study analyzed ancient agouti mtDNA to determine the geographic origins of this continental translocate and contribute to the understanding of pre-Columbian continental connections to Carriacou. I hypothesized that Caribbean agouti would have been translocated from multiple populations. Results suggest that the pre-Columbian agouti on Carriacou likely originated from a single species, native to a defined geographic area in northern South America or Trinidad. As hypothesized, results are most consistent with agouti being disseminated throughout the Lesser Antilles from founding populations on one or a few islands. Speculatively, Carriacou may have functioned as supply source for agouti, from where it would have been disseminated to the rest of the Lesser Antilles. This study also suggests an approximate chronology for the establishment of viable agouti populations on Carriacou, soon after island settlement around ca. A.D. 400/600, which has repercussions for our understanding of Caribbean ecology. The radiocarbon dates from Belle Plaine (Grande-Terre), Macabou (Martinique), and BK77 Grand Case (Saint-Martin) are consistent with the possibility that agoutis from these sites would have been supplied from Carriacou. A more precise chronology of the agouti samples from La Ramée (Basse Terre) and Tourlourous (Marie-Galante) is needed to confirm the possibility that these individuals originated from Carriacou. I hypothesized that the Caribbean agouti analyzed in this study represented more than one species. Results offer the first substantiation of morphological species identification of Caribbean agouti as *D. leporina* by independent, molecular techniques, and demonstrate that the agouti
on Carriacou, Martinique, and Saint-Martin all belonged to the same species. Following from *D. leporina*’s home range and the stylistic connections with northern South America, it is possible to postulate that either the Guianas, Trinidad, or Venezuela would have been the source for pre-Columbian agouti supply, for Carriacou, Martinique, and Saint-Martin, but perhaps also for the remainder of the Lesser Antilles.
Chapter 9.

Conclusion and Future Directions

9.1. Conclusions

This project’s objective was to use ancient agouti mtDNA from islands in the Lesser Antilles to reconstruct human pre-Columbian continental connections to Carriacou. 30 archaeological agouti samples from six islands were tested. mtDNA from 26 samples from three islands, Martinique, Saint Martin, and Carriacou was successfully amplified and sequenced for a high success rate of over 86%, uncommon with Caribbean samples. Partial sequencing of the CytB region of Dasyprocta proved to be highly relevant for this study, aided by the pre-existing comparative genetic database of modern agouti CytB.

Agouti remains in the Caribbean are typically assigned to D. leporina. Following the agouti’s complex continental population structure and species’ overlapping home ranges, as well as the widespread human interaction networks which are known to have occurred throughout the Circum-Caribbean, I hypothesized that the Caribbean agouti analyzed in this study represent more than one species. Analysis of the Caribbean archaeological DNA sequences showed that samples most likely belonged exclusively to D. leporina. This is the first study to provide genetic evidence for species identification. Sequences of the modern agouti analyzed in this study were too short and/or unspecific for this study to provide species identification.

Archaeological evidence, notably artifact and cultural similarities, (Cody 1993; Roe 1989, 2009; Hofman et al. 2007, 2008, 2011) point to robust interactions between the Caribbean and various regions in northern South America and Trinidad. Following this evidence, I initially hypothesized that Caribbean agouti would have been translocated from multiple populations. However, alignment of the CytB agouti archaeological sequences with modern reference agouti sequences showed the clustering of the archaeological sequences in a single previously unreported presumed Sub-Clade, Sub-Clade A1. The genetic results from this study showed that agoutis were likely translocated to Carriacou, Martinique, and Saint Martin from a single continental
population, and may have originated from the Guianas, Trinidad, or Venezuela, which share many cultural connections with the Southern Caribbean.

I hypothesized that Caribbean agoutis were disseminated throughout the Lesser Antilles from founding populations on one or a few islands. The limited variation of mtDNA in samples from Martinique, Saint Martin, and Carriacou strongly suggest a genetic bottleneck, so that Caribbean agouti populations may have been entirely supplied from founding populations on one or a few islands. Speculatively, Carriacou may have functioned as a supply source for agouti, from where it would have been disseminated to the rest of the Caribbean. The radiocarbon dates from Belle Plaine (Grande-Terre), Macabou (Martinique), and BK77 Grand Case (Saint-Martin) are consistent with the possibility that agoutis from these sites would have been supplied from Carriacou. However, at present, because of the absence of comparative genetic data from archaeological continental agouti we cannot conclusively clarify the pathways of dissemination.

The limited variation of mtDNA implies that agouti may have established viable populations on Carriacou rapidly after island settlement around, ca. A.D. 400/600, so that new imports of agouti would have been unnecessary. These results reinforce the findings from previous studies (Giovas et al. 2016), indicating viable breeding populations by ca. A.D. 600/800.

9.2. Future Directions

In the following paragraphs, I suggest several future research avenues to strengthen the findings from this study. Future research may clarify the origins of pre-Columbian agouti in northern South America or Trinidad, confirm pre-Columbian agouti species identification, and the character of their supply and dissemination in the Caribbean. Additional samples from a broader diversity of commensal species may properly address the multitude of human interactions tying northern South America to the Caribbean. First and foremost, it is essential that the double stranded sequencing of all agouti sequences included in this study be completed to confirm the authenticity of sequences and SNPs. Further sequencing may also identify additional informative polymorphisms.

Comparative pre-Columbian continental agouti sequences from the coastal Guianas, Trinidad, and coastal Venezuela, are crucial for identifying the geographic origins of pre-
Columbian Caribbean populations. Sequences from a broader inland range may also be analyzed to exclude regions with unsupported genetic connections and identify related agouti populations. Continental testing should particularly target samples dated in the ca. A.D. 400/600 range to acquire an accurate understanding of continental population structure and distribution during the time of the first pre-Columbian agouti translocations. The established continental population structure reported by van Vuuren et al. (2004), and this study’s identification of potential Sub-Clades will greatly facilitate the identification of the pre-Columbian Caribbean’s agouti source population once genetic data from ancient continental populations has been acquired. South American archaeological collections offer diverse and plentiful collections with great potential for analysis (see Antczak et al. 2019).

In the Caribbean, site chronology is complex and radiocarbon dating often lacks rigor (Fitzpatrick 2006; Napolitano et al. 2019), in addition to which the radiocarbon chronology of zooarchaeological remains is not systematically investigated. Strengthening the radiocarbon record for agouti specimens from islands across the Lesser Antilles will allow the identification for the island which supported the earliest agoutis and which may have functioned as the supply source of agouti for the remainder of the Caribbean. Additional sequencing of agouti samples from Carriacou and other islands, notably those with confirmed overlapping or preceding radiocarbon dates (see Chapter 5.4 and 8.6) may also confirm whether an island would have been used as a supply source. Additional sequencing, preferably of hypervariable regions such as the D-loop control region, may confirm the nature of the dissemination of agouti in the Caribbean. Complete mitochondrial or nuclear genomes, sequenced using NGS technologies, would provide the highest resolution for population structure of Caribbean agouti.

The taxonomic review of the genus *Dasyprocta* is necessary, without which species identification analyses cannot provide conclusive results. Comparative genetic materials for all eleven currently recognized agouti species and several subspecies are necessary to authenticate the *D. leporina* identification of agoutis analyzed in this study. Additional testing of agouti samples from a broader range of islands may conclusively ascertain the taxonomic identification for all Caribbean pre-Columbian agouti.

Finally, genetic research in the Caribbean, which has so far included humans, dog, guinea pig, hutia, (Lalueza-Fox 2001, 2003; Kimura et al. 2016; Mendisco et al. 2015;
Frantz et al. 2016; Lord et al. 2018, 2020; Schroeder et al. 2018; Nieves-Colón et al. 2020; Oswald et al. 2020; Nägele et al. 2020) and now agouti, should be expanded to include other fauna and flora. The diversity of interactions in the Caribbean cannot be properly addressed by the genetic analysis of a few organisms. The variety of relationships which human groups may have entertained with various flora and fauna calls for broader analysis, both in the number of samples and diversity of species. The success of this study in extracting and sequencing aDNA demonstrates great potential for the continuation of aDNA research in the Caribbean and other tropical regions. Additional systematic genetic testing of archaeological samples from Carriacou and other islands may also explain the high success rate in amplification of the samples analyzed in this study, enabling improved sampling strategies regarding ancient materials from hot and humid environments destined towards genetic analysis.

This study contributes to the ongoing discussion regarding the relationships between humans and continental translocates in the Caribbean and emphasizes the potential of the commensal model for the global study of ancient translocations and island interactions. This study also informs the field of Neotropical ecology, by bringing to light new data informing continental agouti population structure, and by refining the timing of potential ecological repercussions brought on by translocates in the islands. Finally, this study contributes to the growing body of research using molecular analyses to solve the taxonomic classification of previously assumed or unconfirmed species of archaeological specimens, allowing for more precise interpretations of archaeological, ecological, and genetic materials in the Caribbean and South America. Results revitalize the rigour of archaeological practice in respect to commensal fauna.
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Woods, C. A.
Yang, D.Y., B. Eng, J.S. Waye, J.C. Dubar, and S.R. Saunders  

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## Appendix A.

Table A1. Provenience for archaeogenetic samples from the pilot test islands (excluding Carriacou). All samples belong to agouti (*Dasyprocta* sp.), class Mammalia. Additional archaeological reference information found on bags as detached reference data.

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Table A2. Provenience for archaeogenetic samples from Carriacou. All samples belong to agouti (*Dasyprocta* sp.), class Mammalia.

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</tr>
<tr>
<td>AG28</td>
<td>n/a</td>
<td>04CGB000239BOA</td>
<td>Carriacou</td>
<td>Grand Bay</td>
<td>446</td>
<td>19</td>
<td>02</td>
<td>n/a</td>
<td>n/a</td>
<td>L002</td>
<td>n/a</td>
</tr>
<tr>
<td>AG29</td>
<td>n/a</td>
<td>05CGB001045BOA</td>
<td>Carriacou</td>
<td>Grand Bay</td>
<td>415</td>
<td>20</td>
<td>04</td>
<td>n/a</td>
<td>n/a</td>
<td>L002</td>
<td>n/a</td>
</tr>
<tr>
<td>AG30</td>
<td>n/a</td>
<td>08CGB001534BOA</td>
<td>Carriacou</td>
<td>Grand Bay</td>
<td>562</td>
<td>n/a</td>
<td>02</td>
<td>n/a</td>
<td>n/a</td>
<td>F0157</td>
<td>n/a</td>
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</table>
Table A3. Zooarchaeological sample description of agouti (*Dasyprocta* sp.) skeletal elements from the pilot test islands and Carriacou. Description includes length (measurement of sample along its longest side in mm) and original sample weight (g). Measurements were taken using a right angle 300mm ruler. Photos were taken with a Nikon D90, copies of the photos are stored in the Simon Fraser laboratories.

<table>
<thead>
<tr>
<th>Sample Name</th>
<th>Skeletal Element</th>
<th>Side</th>
<th>Sample Description</th>
<th>Length (mm)</th>
<th>Original Sample Weight (g)</th>
<th>Cultural Modification</th>
<th>Photo Number</th>
<th>Photo Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>AG1</td>
<td>Innominate</td>
<td>R</td>
<td>Right innominate. Partial ilium and acetabulum. Iliac crest is broken off.</td>
<td>Currently unavailable</td>
<td>1.95</td>
<td>None</td>
<td>IMG_0156.CR2 - IMG_0168.JPG</td>
<td>9/12/2019</td>
</tr>
<tr>
<td>AG2</td>
<td>Incisive</td>
<td>Unknown</td>
<td>Upper incisor. Enamel is in good condition. Occlusal and root tips have been broken off.</td>
<td>Currently unavailable</td>
<td>0.29</td>
<td>None</td>
<td>IMG_0212.CR2 - IMG_0222.JPG</td>
<td>9/12/2019</td>
</tr>
<tr>
<td>AG3</td>
<td>Femur</td>
<td>R</td>
<td>Right femur shaft, broken at proximal and distal end. Missing Epiphyses.</td>
<td>Currently unavailable</td>
<td>1.11</td>
<td>None</td>
<td>IMG_0198.CR2 - IMG_0211.JPG</td>
<td>9/12/2019</td>
</tr>
<tr>
<td>AG4</td>
<td>Incisive</td>
<td>Unknown</td>
<td>Lower incisor. Enamel is in good condition. Root tip has been broken off.</td>
<td>Currently unavailable</td>
<td>0.31</td>
<td>None</td>
<td>IMG_0223.CR2 - IMG_0240.JPG</td>
<td>9/12/2019</td>
</tr>
<tr>
<td>AG5</td>
<td>Maxillar with attached molar</td>
<td>R</td>
<td>Right maxillar fragment with attached molar. Posterior fragment, broken off ahead of the zygomatic process. Premolars are missing.</td>
<td>Currently unavailable</td>
<td>1.16</td>
<td>None</td>
<td>IMG_0171.CR2 - IMG_0197.JPG</td>
<td>9/12/2019</td>
</tr>
<tr>
<td>AG6</td>
<td>Femur</td>
<td>Unknown</td>
<td>Currently unavailable.</td>
<td>Currently unavailable</td>
<td>0.77</td>
<td>None</td>
<td>Currently unavailable</td>
<td>09/25/2019</td>
</tr>
<tr>
<td>AG7</td>
<td>Ilium</td>
<td>R</td>
<td>Right ilium, auricular surface excluding the acetabulum.</td>
<td>Currently unavailable</td>
<td>0.57</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>AG8</td>
<td>Femur</td>
<td>L</td>
<td>Left femur, proximal end and part of shaft. Head and part of greater trochanter missing. Possible carnivore gnawing.</td>
<td>Currently unavailable</td>
<td>2.57</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>AG9</td>
<td>Innominate</td>
<td>L</td>
<td>Ischium including acetabulum and sections of associated ilium and pubis.</td>
<td>Currently unavailable</td>
<td>1.89</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>AG10</td>
<td>Auditory Bulla</td>
<td>L</td>
<td>Complete left auditory bulla.</td>
<td>Currently unavailable</td>
<td>0.88</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>AG11</td>
<td>Incisor</td>
<td>L</td>
<td>Upper incisor. Enamel is in good condition. Occlusal tip has been broken off.</td>
<td>Currently unavailable</td>
<td>1.65</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>Sample Name</td>
<td>Skeletal Element</td>
<td>Side</td>
<td>Sample Description</td>
<td>Length (mm)</td>
<td>Original Sample Weight (g)</td>
<td>Cultural Modification</td>
<td>Photo Number</td>
<td>Photo Date</td>
</tr>
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</tr>
<tr>
<td>AG12</td>
<td>Scapula</td>
<td>R</td>
<td>Left scapula. Head, coronoid process, neck and part of the blade with spine are present.</td>
<td>Currently unavailable</td>
<td>0.88</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>AG13</td>
<td>Auditory Bulla</td>
<td>R</td>
<td>Complete right auditory bulla.</td>
<td>20</td>
<td>1.48</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>AG14</td>
<td>Femur</td>
<td>L</td>
<td>Complete left femur. Unfused missing epiphyses, at both proximal and distal ends.</td>
<td>65</td>
<td>3.04</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>AG15</td>
<td>Auditory Bulla</td>
<td>R</td>
<td>Right auditory bulla, virtually complete. Hole in chamber.</td>
<td>22</td>
<td>1.15</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>AG16</td>
<td>Auditory Bulla</td>
<td>R</td>
<td>Right auditory bulla, virtually complete. Hole in chamber.</td>
<td>23</td>
<td>1.02</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>AG17</td>
<td>Auditory Bulla</td>
<td>R</td>
<td>Complete right auditory bulla. Eroded external acoustic meatus.</td>
<td>22</td>
<td>0.87</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>AG18</td>
<td>Auditory Bulla</td>
<td>R</td>
<td>Right auditory bulla, virtually complete. Distal end is broken off.</td>
<td>15</td>
<td>0.91</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>AG19</td>
<td>Auditory Bulla</td>
<td>R</td>
<td>Complete right auditory bulla. Distal end is eroded.</td>
<td>22</td>
<td>1.41</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>AG20</td>
<td>Auditory Bulla</td>
<td>R</td>
<td>Complete right auditory bulla.</td>
<td>20</td>
<td>1.48</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>AG21</td>
<td>Auditory Bulla</td>
<td>R</td>
<td>Right auditory bulla. 1/2 of the chamber is missing.</td>
<td>20</td>
<td>0.84</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>AG22</td>
<td>Auditory Bulla</td>
<td>R</td>
<td>Complete right auditory bulla.</td>
<td>20</td>
<td>1.39</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>AG23</td>
<td>Femur</td>
<td>L</td>
<td>Left femur, proximal end and part of shaft. Epiphyses are unfused. Broken off mid-shaft.</td>
<td>50</td>
<td>3.54</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>AG24</td>
<td>Femur</td>
<td>L</td>
<td>Left femur, proximal end and part of shaft. Missing Epiphyses. Eroded neck and greater trochanter. Broken off near distal end.</td>
<td>64</td>
<td>3.14</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>Sample Name</td>
<td>Skeletal Element</td>
<td>Side</td>
<td>Sample Description</td>
<td>Length (mm)</td>
<td>Original Sample Weight (g)</td>
<td>Cultural Modification</td>
<td>Photo Number</td>
<td>Photo Date</td>
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</tr>
<tr>
<td>AG25</td>
<td>Femur</td>
<td>L</td>
<td>Left femur, proximal end and part of shaft. Missing Epiphyses. Eroded neck and greater trochanter. Brocken off near distal end.</td>
<td>68</td>
<td>3.37</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>AG26</td>
<td>Femur</td>
<td>L</td>
<td>Left femur, proximal end and part of shaft. Missing Epiphyses. Eroded greater trochanter. Broken off at distal end.</td>
<td>68</td>
<td>3.30</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>AG27</td>
<td>Femur</td>
<td>L</td>
<td>Left femur shaft, broken at proximal and distal end. Missing Epiphyses.</td>
<td>57</td>
<td>2.95</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>AG28</td>
<td>Femur</td>
<td>L</td>
<td>Proximal end of left femur. Missing Epiphyses. Greater trochanter is broken off, shaft is split in half and broken off near proximal end.</td>
<td>35</td>
<td>0.46</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>AG29</td>
<td>Femur</td>
<td>L</td>
<td>Left femur, distal end and part of shaft. Missing Epiphyses. Broken of near proximal end.</td>
<td>53</td>
<td>2.26</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
<tr>
<td>AG30</td>
<td>Femur</td>
<td>L</td>
<td>Left femur shaft. Missing Epiphyses.</td>
<td>54</td>
<td>1.96</td>
<td>None</td>
<td>Currently unavailable</td>
<td>Currently unavailable</td>
</tr>
</tbody>
</table>
### Table A4. Sample chronology for sites from the pilot test islands (excluding Carriacou).

<table>
<thead>
<tr>
<th>Sample Name</th>
<th>Island</th>
<th>Site</th>
<th>Uncalibrated, Reported $^{14}$C Date for Site (2σ)</th>
<th>Cal B.C./A.D.</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>AG2</td>
<td>Basse Terre</td>
<td>La Ramée</td>
<td>Unavailable</td>
<td>A.D. 320 –1000</td>
<td>Casagrande et al. 2010</td>
</tr>
<tr>
<td>AG3</td>
<td>Marie-Galante</td>
<td>Tourlourous</td>
<td>Unavailable</td>
<td>A.D. 237 –13th century</td>
<td>Serrand et al. 2018</td>
</tr>
<tr>
<td>AG5</td>
<td>Martinique</td>
<td>Macabou</td>
<td>Unavailable</td>
<td>A.D. 415 –1275</td>
<td>Vidal 2007</td>
</tr>
</tbody>
</table>

### Table A5. Sample chronology for archaeogenetic samples from Carriacou. Chronology for samples from layers with no associated $^{14}$C date is calculated using associated $^{14}$C dates from closest neighboring layers.

<table>
<thead>
<tr>
<th>Sample Name</th>
<th>Site</th>
<th>Associated $^{14}$C Date</th>
<th>Uncalibrated, Reported $^{14}$C Date (2σ)</th>
<th>Cal B.C. /A.D.</th>
<th>Period</th>
<th>Associated $^{14}$C Sample Number</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>AG1</td>
<td>Grand Bay</td>
<td>Y</td>
<td>1020BP ±20 – 990 BP ±20 – 1310 BP ±40</td>
<td>A.D. 990 – 1190</td>
<td>Middle-Late/Final</td>
<td>UCIAMS-94045, UCIAMS-94044, Beta-233647</td>
<td>Giovas 2013:105</td>
</tr>
<tr>
<td>AG7</td>
<td>Sabazan</td>
<td>Y</td>
<td>1,158BP ±45</td>
<td>A.D. 730 – 990</td>
<td>Initial/Early-Middle</td>
<td>AA81055</td>
<td>Giovas 2013:106</td>
</tr>
<tr>
<td>AG8</td>
<td>Sabazan</td>
<td>N</td>
<td>1100 BP ±20 – 1080BP ±15</td>
<td>A.D. 890 – 1010</td>
<td>Middle-Late/Final</td>
<td>OS-71464, OS-71465</td>
<td>Giovas 2013:106</td>
</tr>
<tr>
<td>AG9</td>
<td>Sabazan</td>
<td>N</td>
<td>960BP ±15 – 970±15</td>
<td>A.D. 1040 – 1160</td>
<td>Late/Final</td>
<td>OS-71407, OS-71408</td>
<td>Giovas 2013:106</td>
</tr>
<tr>
<td>AG10</td>
<td>Sabazan</td>
<td>Y</td>
<td>657±44</td>
<td>A.D. 1280 – 1400</td>
<td>Late/Final</td>
<td>AA81054</td>
<td>Giovas 2013:106</td>
</tr>
<tr>
<td>AG11</td>
<td>Sabazan</td>
<td>Y</td>
<td>1100BP ±20</td>
<td>A.D. 890 – 990</td>
<td>Middle</td>
<td>OS-71464</td>
<td>Giovas 2013:106</td>
</tr>
<tr>
<td>AG12</td>
<td>Sabazan</td>
<td>Y</td>
<td>970 BP ±15</td>
<td>A.D. 1020 – 1150</td>
<td>Late/Final</td>
<td>OS-71408</td>
<td>Giovas 2013:106</td>
</tr>
<tr>
<td>Sample Name</td>
<td>Site</td>
<td>Associated ¹⁴C Date</td>
<td>Uncalibrated, Reported ¹⁴C Date (2σ)</td>
<td>Cal B.C. / A.D.</td>
<td>Period</td>
<td>Associated ¹⁴C Sample Number</td>
<td>Source</td>
</tr>
<tr>
<td>-------------</td>
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<td>--------------------------</td>
<td>-------------------------------</td>
<td>-------------------------------</td>
</tr>
<tr>
<td>AG14</td>
<td>Grand Bay</td>
<td>N</td>
<td>1020 BP +20 – 990 BP +20 – 1310 BP ±40</td>
<td>A.D. 990 – 1190</td>
<td>Middle-Late/Final</td>
<td>UCIAMS-94045, UCIAMS-94044, Beta-233647</td>
<td>Giovas 2013: 105</td>
</tr>
<tr>
<td>Sample Name</td>
<td>Site</td>
<td>Associated ¹⁴C Date</td>
<td>Uncalibrated, Reported ¹⁴C Date (2σ)</td>
<td>Cal B.C. /A.D.</td>
<td>Period</td>
<td>Associated ¹⁴C Sample Number</td>
<td>Source</td>
</tr>
<tr>
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</tr>
<tr>
<td>AG23</td>
<td>Grand Bay</td>
<td>Y</td>
<td>1020BP +20 – 990 BP +20 – 1310 BP ±40</td>
<td>A.D. 990 – 1190</td>
<td>Middle-Late/Final</td>
<td>UCIAMS-94045, UCIAMS-94044, Beta-233647</td>
<td>Giovas 2013:105</td>
</tr>
<tr>
<td>AG24</td>
<td>Grand Bay</td>
<td>Y</td>
<td>1020BP +20 – 990 BP +20 – 1310 BP ±40</td>
<td>A.D. 990 – 1190</td>
<td>Middle-Late/Final</td>
<td>UCIAMS-94045, UCIAMS-94044, Beta-233647</td>
<td>Giovas 2013:105</td>
</tr>
<tr>
<td>AG25</td>
<td>Grand Bay</td>
<td>Y</td>
<td>1020BP +20 – 990 BP +20 – 1310 BP ±40</td>
<td>A.D. 990 – 1190</td>
<td>Middle-Late/Final</td>
<td>UCIAMS-94045, UCIAMS-94044, Beta-233647</td>
<td>Giovas 2013:105</td>
</tr>
<tr>
<td>AG26</td>
<td>Grand Bay</td>
<td>Y</td>
<td>1020BP +20 – 990 BP +20 – 1310 BP ±40</td>
<td>A.D. 990 – 1190</td>
<td>Middle-Late/Final</td>
<td>UCIAMS-94045, UCIAMS-94044, Beta-233647</td>
<td>Giovas 2013:105</td>
</tr>
<tr>
<td>AG27</td>
<td>Grand Bay</td>
<td>Y</td>
<td>1020BP +20 – 990 BP +20 – 1310 BP ±40</td>
<td>A.D. 990 – 1190</td>
<td>Middle-Late/Final</td>
<td>UCIAMS-94045/ UCIAMS-94044/ Beta-233647</td>
<td>Giovas 2013:105</td>
</tr>
<tr>
<td>AG28</td>
<td>Grand Bay</td>
<td>Y</td>
<td>1020BP +20 – 990 BP +20 – 1310 BP ±40</td>
<td>A.D. 990 – 1190</td>
<td>Middle-Late/Final</td>
<td>UCIAMS-94045/ UCIAMS-94044/ Beta-233647</td>
<td>Giovas 2013:105</td>
</tr>
<tr>
<td>AG29</td>
<td>Grand Bay</td>
<td>Y</td>
<td>1020BP +20 – 990 BP +20 – 1310 BP ±40</td>
<td>A.D. 990 – 1190</td>
<td>Middle-Late/Final</td>
<td>UCIAMS-94045/ UCIAMS-94044/ Beta-233647</td>
<td>Giovas 2013:105</td>
</tr>
<tr>
<td>AG30</td>
<td>Grand Bay</td>
<td>N</td>
<td>n/a</td>
<td>A.D. 700 – 1200</td>
<td>Initial/Early-Middle-Late/Final</td>
<td>n/a</td>
<td>Personal Communication, Fitzpatrick, Giovas, Harris, Kappers, May 2020</td>
</tr>
</tbody>
</table>
Appendix B.

Table B1. Genbank accession numbers of modern reference *Dasyprocta* CytB sequences used in this study.

<table>
<thead>
<tr>
<th>Accession Number</th>
<th>Species</th>
<th>Location</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>AF437783</td>
<td><em>Dasyprocta leporina</em></td>
<td>Brazil: Amazonas</td>
<td>van Vuuren et al 2004</td>
</tr>
<tr>
<td>AF437785</td>
<td><em>Dasyprocta leporina</em></td>
<td>French Guiana: Sokoumou</td>
<td>van Vuuren et al 2004</td>
</tr>
<tr>
<td>AF437786</td>
<td><em>Dasyprocta leporina</em></td>
<td>French Guiana: Maroni</td>
<td>van Vuuren et al 2004</td>
</tr>
<tr>
<td>AF437787</td>
<td><em>Dasyprocta leporina</em></td>
<td>French Guiana: Crique Paracou</td>
<td>van Vuuren et al 2004</td>
</tr>
<tr>
<td>AF437788</td>
<td><em>Dasyprocta leporina</em></td>
<td>French Guiana: Saint Georges</td>
<td>van Vuuren et al 2004</td>
</tr>
<tr>
<td>AF437789</td>
<td><em>Dasyprocta leporina</em></td>
<td>French Guiana</td>
<td>van Vuuren et al 2004</td>
</tr>
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Appendix C.

2. **Figure C1.** Maximum likelihood tree of archeological sequences (amplification F114-R252, sequencing F114) and *Dasyprocta* spp. modern reference sequences. Archaeological samples originate from Carriacou. Branch support values are in percentages, with minimum 50% branch support value. *Rattus sordidus* is used as a comparative outgroup.