THE INTRODUCTION OF ANIMALS AS AN ADAPTATION TO COLONIZATION OF ISLANDS: AN EXAMPLE FROM THE WEST INDIES

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Summary

We apply island biogeographic principles to the analysis of archaeological faunas from Caribbean Ceramic age sites, and use the results to better understand human adaptations to these island settings. Faunal samples reflect decreased diversity with distance from the mainland and a positive correlation between diversity and island size. Though the colonists were subject to the limitations described by island biogeographic principles, they were also able to exert some control by disproportionately enriching the diversity of species on small islands by introducing animals.

Résumé

Les introductions animales comme adaptation à la colonisation des îles : l'exemple des Caraïbes.

Nous appliquons les principes de la biogéographie insulaire à l'analyse de faunes archéologiques de sites caraïbes de la période céramique, et utilisons ces résultats pour mieux comprendre les adaptations humaines à ces environnements insulaires. Les échantillons de faune reflètent une diversité décroissante à mesure que la distance avec le continent augmente, et une corrélation positive entre la diversité et la taille de l'île. Bien qu'assujettis aux limitations décrites par les principes de la biogéographie insulaire, les colons étaient cependant capables d'exercer un contrôle en enrichissant de façon disproportionnée la diversité des espèces sur des petites îles en y introduisant des animaux.

Zusammenfassung

Das Einführen von Tieren als Anpassung an Insellagen: ein Beispiel aus der Karibik.

Die Grundsätze der Biogeographie von Inseln werden auf die Analyse von Faunenkomplexen aus keramikzeitlichen Siedlungen der Karibik übertragen. Die Ergebnisse sollen zum besseren Verständnis der menschlichen Anpassung an diese Insellagen beitragen. Die Fund-inventare belegen eine schwindende Artenzahl mit zunehmender Entfernung vom Festland und eine positive Beziehung zwischen Artenzahl und Inselgröße. Obwohl die Siedler den biogeographischen Rahmenbedingungen unterworfen waren, konnten sie durch die Einführung von Tieren doch einige Kontrolle auf die Artenvielfalt kleinerer Inseln ausüben.

Key Words

Island biogeography, Adaptations, Introductions.

Mots clés

Biogéographie insulaire, Adaptations, Introductions d'animaux.

Schlüsselworte

Biogeographie von Inseln, Anpassung, Einführung von Tieren.

Native American colonization of the West Indian archipelago was fraught with uncertainties. These early colonists faced distant ocean voyages to islands with unfamiliar plants and animals. They did not know whether they would find resources they were accustomed to using in sufficient quantities to sustain life. All of the resources they required for food, medicine, and the raw materials for construction of tools, equipment, shelter, and clothing had to be met by the plants and animals of the island, its surrounding waters, and whatever was imported. The animals that were used for food and whose remains were incorporated in archaeological deposits are evidence for the ways the colonists coped with the differences they found in island faunas.

Despite the uncertainties native Americans faced, they did colonize the West Indies, Bahamas, and the Turks and Caicos islands (fig. 1). Whether they were pushed by population pressures on the mainland or were drawn by the potentials of the islands is still debated. Whatever the force that initiated migration, Amerindians moved into the West Indies from at least two fronts and came in at least three waves of migration (Rouse, 1992). The first and second waves of migration were of preceramic people and were limited in extent. The third and largest wave of migration

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Fig. 1: Map of the Caribbean.

began about 250 bc. This migration of people, originating from northeastern South America, progressed up the island chain reaching the Bahamas late in the prehistory of the Caribbean. The sequence of dates of the contexts associated with the faunal samples reflect this progress up the island chain with the Bahamian sites the most recent and the majority of Lesser Antillean sites from the early Ceramic age (tab. 1). These people produced pottery, practiced agriculture (Newsom, 1993), and colonized virtually all of the islands of the West Indies and the Bahamas by the time Europeans explored the Caribbean.

The adaptations of these Ceramic age people to the island ecosystem is the focus of this paper. The data upon which it is based are samples of animal remains excavated from sites representing the third period of settlement and located along a transect from islands close to the South American mainland up the island chain to the Bahamas. Very little evidence exists for cultural interchange between the islands and what is now the southeastern United States.

A better understanding of the kinds and diversity of plants and animals that were found by early colonists on islands such as the West Indies is provided by research stimulated by the seminal work on island biogeography by MacArthur and Wilson (1967). Their predictions are: 1) that large islands support more species than small ones; and 2) that species numbers decline with increased remoteness of the island. In view of these predictions, we anticipate that people would take advantage of available animal diversity and therefore: 1) that the faunal assemblages from sites located on larger islands would be more diverse than assemblages from smaller islands; and 2) that diversity in the faunal assemblages would decrease with distance from the mainland.

We also expect that people could overcome the limitations of the island faunas by augmenting them with introduced animals. Early introduction of wild, tame, and domestic animals onto islands is becoming well documented. Marsupials and rodents were introduced from Papua New Guinea to New Ireland as early as 19,000 years ago (Flannery and White, 1991). Good cases are made for the introduction of foxes to the California Channel Islands (Collins, 1991) and of a variety of animals to islands in the Mediterranean (Groves, 1989; Blondel and Vigne, 1993) and Outer Hebrides (Serjeantson, 1990). A rich array of animals of both wild and domestic animals were also introduced into and among the West Indian Islands (Wing, 1993). We address the importance of these introductions in enhancing the endemic faunas and whether they serve as an adaptation for colonization of island archipelagoes.

Materials and methods

Site Selection

We have applied new methods in zooarcheology to the study of faunal samples from the West Indies and as a result we feel confident that they represent the primary vertebrates used by the occupants of each site. One of the most important methods is recovery of animal remains with fine gauge sieves (3 and 1.5 mm). Though this is by no means a new method, it has only recently been used in the West Indies (Payne, 1972). Faunal samples recovered with fine gauge screen give us a new improved view of animal catches in the West Indies. Older samples, recovered with large gauge sieves or simply gathered, are composed of remains of large animals and one would have to conclude from these samples that sea turtles were the primary resource used in the Caribbean. However, with the better recovery methods it is now clear that prehistoric catches included diverse species and the majority were small individuals. We use the width of vertebral centra of fishes as a gauge of their size in life. The means of these measurements range from 2 to 6 mm and these come from fishes estimated to weigh between 60 and 569 g (Wing and Brown, 1979). Only samples recovered with a fine gauge sieving strategy are included in this study.

The other guidelines used for our choice of archaeological faunal samples are intended to insure both the greatest comparability of the context and the widest geographic distribution of the samples. The faunal samples come from 18 sites located on 12 islands, five in the Lesser Antilles, two in the Virgin Islands, two in the Greater Antilles, and three in the Bahamas, Turks and Caicos (tab. 1; fig. 1). Most of these samples came from the early Ceramic age deposits on each island. The samples are midden refuse and the animal remains in them represent primarily food remains. Some animals such as dogs are usually recovered from burials in the West Indies. Remains from burials are not included in this study and therefore animals that were traditionally buried will be under represented.

Identification and Quantification

Identifications are made by direct comparison of each specimen with modern reference specimens in the collections of the Florida Museum of Natural History and the method of quantification used is minimum numbers of individuals (MNI). Our calculations of MNI are based on the individual animals from an occupation zone, a discrete feature, or widely separated levels. We use MNI for this analysis for one important reason. These faunal assemblages are composed of species with different numbers of skeletal elements. If we used the count of identified speci-

Table 1 : The faunal samples analyzed, their island location, dates of the deposits and reference are presented. C14 dates are listed as the mean and standard deviation BP. In the absence of C14 dates, chronological dates spanning the years of the production of dated pottery types associated with the faunal remains are given. (* personal communications).

ISLAND	SITE NAME	DATE	REFERENCE
Bahamas			
1. Samana Cay	SM-2 and SM-7	AD 1000-1500	Watford*, Hoffman*
2. Crooked Island	CR-8 and CR-14	AD 1000-1500	deFrance, 1991
Turks and Caicos			
3. Middle Caicos	MC-6 and MC-12	AD 750-1500	Wing and Scudder, 1983
Greater Antilles			
4. Hispaniola	En Bas Saline (Fea. 4 & 25)	AD 1400-1500	Deagan*
5. Puerto Rico	Maisabel	AD 200-600	deFrance, 1988
Virgin Islands			
6. St. John	Trunk Bay	AD 100-800	Wild*
	Calabash Boom	AD 1050 ± 60	Caesar*
7. St. Thomas	Tutu (2044 D & F)	1430 ± 90 bp (BETA-62568)	Righter*, Wing *et al.*, nd.
Lesser Antilles			
8. St. Martin	Hope Estate	2275 ± 60 bp (PITT-0219)	Haviser*
9. Saba	Kelbeys Ridge	AD 670-1350	Hoogland*
	Spring Bay (Unit 31)	655 ± 30 bp (GrN-16773)	Hoogland*
10. Nevis	GE-5	AD 0-600	Wilson*
	GE-1	1280 ± 60 bp (BETA-19327)	Wilson*
11. Barbados	Silver Sands	650 ± 100 (I-16215)	Drewett, 1991
12. Grenada	Pearls	AD 200	Fandrich, 1990; Stokes, 1991

mens (NISP) as the basic method of quantification, we would bias the results in favor of those species with the largest number of skeletal elements, all other things being equal. Samples, composed of species from all vertebrate classes with different numbers of identifiable skeletal elements, need to be quantified in some way that reduces these innate biases. Though minimum numbers of individuals may not be perfect, it is the best method we know at this time.

Sample size

Sample size is always a critical issue because samples must be large enough to accurately reflect the nature of the population sampled. We include only those that have over 130 MNI and then tested the sample sizes to insure that the diversity measures we use in the analysis are not correlated with sample size. The methods we use to test for adequate sample size are the random sampling method and sample size rarefaction.

We used the random sampling method described by Kintigh (1989) and McCartney and Glass (1990) to test whether our samples are random collections from a population. We simulated random samples from the summed generic abundance for all sites together and counted the number of genera "collected" for hypothetical sample sizes from 0-3000. The distribution shows a classic rarefaction curve where accumulation of new genera progresses at an increasingly slow rate with increased sample size. When the data from each site are plotted against this curve, we find that the sites from the two large islands, Hispaniola and Puerto Rico, and the site on the island closest to the mainland, Grenada, fall within the distribution while the cluster of sites from smaller islands falls significantly below the line (fig. 2). This indicates that sites on large islands and the island close to the mainland are representative of the overall population in terms of sample size and generic richness but the sites on smaller islands fall well below the expected richness. Species richness in the samples from the two smallest islands, Saba and Samana Cay, fall farthest below the line. This also indicates that island size effect on generic richness is large. Because of this island size effect on expected richness it is also necessary to view sample size for each island separately. We employed the method of sample size rarefaction to compare the adequacy of each of the samples (Wing and Wing, 1995).

The other critical issue about sample size, in addition to representing the population they sample, is whether they correlate with the measures used in this analysis, generic

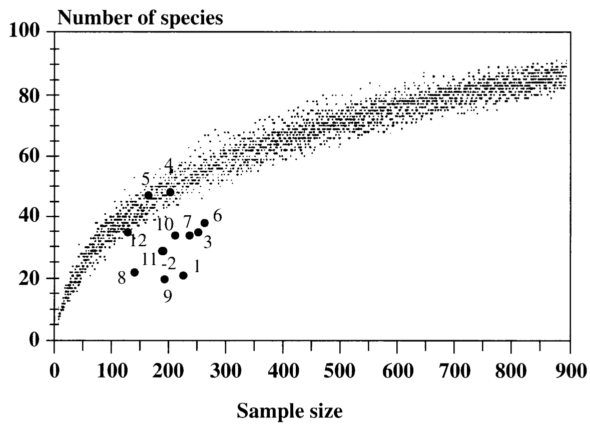

Fig. 2: Simulated random samples from the summed generic abundance for all sites together and a count of the number of genera "collected" for hypothetical sample sizes from 0 to 3000.

richness. To test for correlation we use a Spearman's rank correlation of sample size with generic richness. None of the correlations between the total samples (MNI) or the marine component subsamples (MNI) and generic richness are significant showing that sample size and richness are not linked (MNI for the total sample vs. total generic richness p =.1885, vs. marine generic richness p =.3800, and vs. terrestrial generic richness p =.3559; MNI for the marine component vs. marine generic richness p =.2418). Only the correlation between the small terrestrial samples and terrestrial richness are significant (p =.0256) indicating a possible reduction in the power of our regression analysis for this group. As a conservative measure, we evaluate terrestrial subsamples in a descriptive sense only and focus on the relative importance of terrestrial fauna within the samples as a whole. These tests indicate that the size of the total samples adequately represent the animals that were central to the vertebrate animal protein portion of the diet of settlers on each island. Undoubtedly, other rare species were occasionally used and some of these may have had great cultural significance but as subsistence is based upon staples these samples fit our analysis requirements.

Analysis

Our strategy is to analyze the samples from each site for patterns of diversity as measured by richness of the marine and terrestrial components. The genera are grouped according to their habitat preference, marine or terrestrial, and then the terrestrial genera are further subdivided according to whether they are endemic or introduced. Richness, numbers of genera, is divided by sample size (MNI) for the sites on each island (fig. 3). We arranged these data for each island in sequence along the transect from the island closest to the South American mainland, up through the Lesser Antilles, the Virgin Islands, the eastern Greater Antilles, and finally to the most remote islands in the chain, the Bahamas.

To examine the source and importance of introduced animals, we present the abundance as measured by MNI of introduced animals as a fraction of the total terrestrial subsample which has to be seen in the light of the overall importance of terrestrial animals in the faunal assemblages (figs. 4 and 5). This does not address the diversity but only the relative importance of introduced animals in the terrestrial component. Diversity and relative abundance both address importance in a faunal assemblage; the first relates to breadth in the food quest and the second relates to the importance of a targeted species.

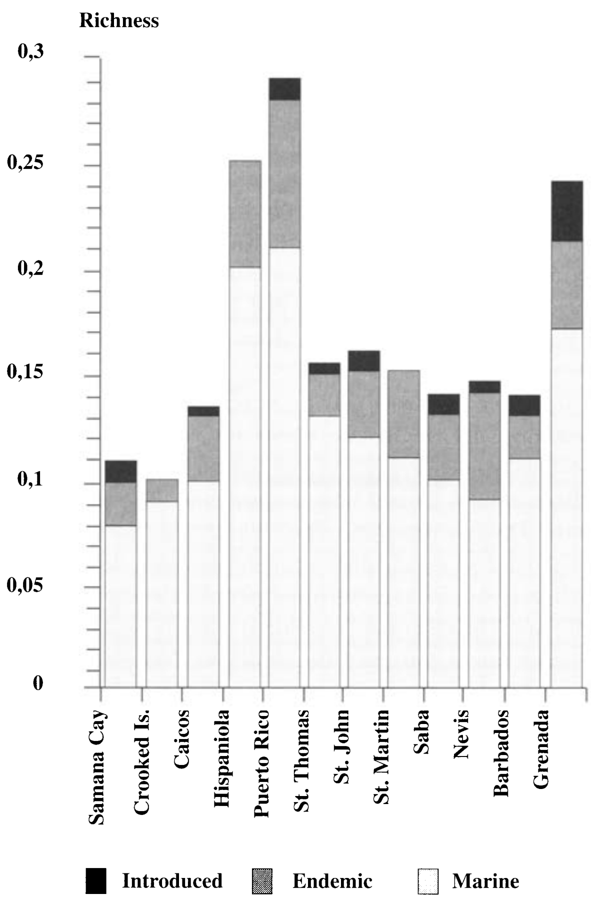

Fig. 3: Generic richness divided by sample size (MNI) presented along the gradient from Samana Cay to Grenada.

Table 2: Animals introduced among the West Indian islands during prehistoric times (Olson, 1978; Morgan and Woods, 1986; Wing 1989; Schwartz and Henderson, 1991).

SOURCE	DESTINATION	SPECIES
South America	entire Caribbean Hispaniola, Puerto Rico, Antigua, Curaçao Lesser Antilles Grenada, St. Lucia Grenada Virgin Islands, Lesser Antilles	domestic dog *Canis familiaris* guinea pig *Cavia porcellus* agouti *Dasyprocta leporina* opossum *Didelphis marsupialis* armadillo *Dasypus novemcinctus* tortoise *Geochelone carbonaria*
Hispaniola	Puerto Rico, Virgin Islands	hutia *Isolobodon portoricensis*
Puerto Rico	Virgin Islands	insectivore *Nesophontes edithae*
Greater Antilles	San Salvador, Middle Caicos, Saba	pond turtle *Trachemys* sp.
Large Bahama Islands	Samana Cay	cony *Geocapromys* sp.

Results and discussion

Faunal richness along the island chain reveals highest diversity on the island closest to the mainland, Grenada, and on the two Greater Antillean islands, Hispaniola and Puerto Rico (fig. 3). This greater diversity (.24 to .29) is due to the combined effect of more diverse terrestrial and marine components. Faunal diversity in the assemblages from the Lesser Antilles, excluding Grenada, and the Virgin Islands is lower and quite uniform (.14 to .16). While the faunas from the small and most remote islands of the Bahamas and Turks and Caicos are the least diverse (.10 to .135).

Introduced animals play an important role in the terrestrial diversity on Grenada where these animal constitute almost half of the diversity of that component (tab. 2). Two of these animal gained wide importance. These are the agouti, *Dasyprocta leporina*, which was introduced throughout the Lesser Antilles and the domestic dog, *Canis familiaris*, which accompanied people throughout the Caribbean. The other two introduced animals are opossum, *Didelphis marsupialis*, and the armadillo, *Dasypus novemcinctus*. Of these two, only the opossum was transported further up the island chain to St. Lucia.

The sites from the Greater Antilles have a more diverse endemic land fauna. The introduced animal on Puerto Rico is the hutia, *Isolobodon portoricensis*, which despite its name originated from Hispaniola. This animal is abundantly represented in many sites from these two islands and was introduced further into the Virgin Islands.

The greater diversity in the assemblages from Grenada and the Greater Antilles is not determined by the terrestrial component alone but equally by a more diverse marine component. When the marine component is subdivided into estuarine, reef, and pelagic animals; pelagic species contribute the least, reef species are uniformly the most abundant and diverse throughout the island chain, and estuarine animals are disproportionately more diverse on Grenada and the larger islands and their immediate neighbors (Wing and Wing, 1995). The size of estuaries is proportional to the size of the land masses and the rivers that flow from them. It is, therefore, expected that greater diversity of this faunal component would be associated with island size. However, the slightly elevated diversity of this component in the Virgin Islands does not relate to island size alone. The Virgin Islands, excluding St. Croix, are situated close to Puerto Rico on a relatively shallow water shelf surrounded by many small islands. This situation provides more extensive estuarine habitats than the size of the islands alone would support. Likewise, the slightly greater estuarine component from the sites on Middle Caicos probably results from the extensive shallow water lagoon encompassed by the arc of Caicos islands of which Middle Caicos is only one.

These patterns of diversity reflect the predictions of island biogeography on a broad scale. They meet our anticipations of more diverse faunas on large islands, such as the Greater Antilles, than the small islands of the Lesser Antilles and Bahamas. Our second expectation is also met by the evident decline in diversity with distance from a source of species. Richness is much higher on Grenada and diminishes progressively from the Lesser Antilles to the Bahamas. Within the Lesser Antilles, excluding Grenada, however, we do not see a gradual decline in diversity with either increased distance from the mainland or decreased size of the island though these factors may be responsible for the slight variation in richness between these islands. Instead, richness is quite uniform throughout the faunas from the Lesser Antilles and the Virgin Islands.

Diversity alone does not describe the importance of animals to prehistoric economies. The relative abundance of each species in the faunal assemblage is also an important consideration. A significant trend of increased importance in terms of MNI of marine animals and therefore decreased importance of land animals is seen in sites located progressively further from the South American mainland (fig. 4). In this trend marine animals (MNI) make up 90% or more of the samples from the Greater Antilles, Virgin Islands, and Bahamas but 76% or less in the Lesser Antilles except in the oceanic island of Barbados where the marine component is 89%.

The animals that play a major role in the more terrestrial characteristics of the Lesser Antillean site are the endemic rice rats (Oryzomyines) and to a lesser extent ground birds such as the pigeons (Columbidae). Rice rats, now extinct, were distributed throughout the Lesser Antilles and Jamaica but were absent from the rest of the West Indies. These rodents were especially important during the early ceramic period, the Saladoid, when they constituted 22%, on average, of the entire vertebrate assemblages and as much as 50% at the inland site of Hope Estate, St. Martin (Wing, 1993). This level of exploitation may not have been sustainable as their relative abundance dropped to an average of 11% in the later ceramic period, the Ostionoid. Rice rats of two different size occur at the Trants site on Monserrat (Reitz and Wing, nd.). This suggests that they were transported between islands at least in this one case (ibid.; Woods, 1989: 756). We treat them all as endemic in this paper.

Against this background of diminished importance of land animal resources with distance from the mainland one can nevertheless see a clear pattern of exploitation of introduced animals (fig. 5). These animals constitute 40 percent or more of the terrestrial component in the site on Grenada and the sites in the Virgin Islands. In Barbados introduced animals constitute 20 percent of the terrestrial animals. In the rest of the islands introduced animals make up 11 percent or less of the terrestrial component.

On Grenada these animals are primarily dogs and agouti. Dogs throughout the West Indies are usually associated with burials and not with food refuse. The early chron-

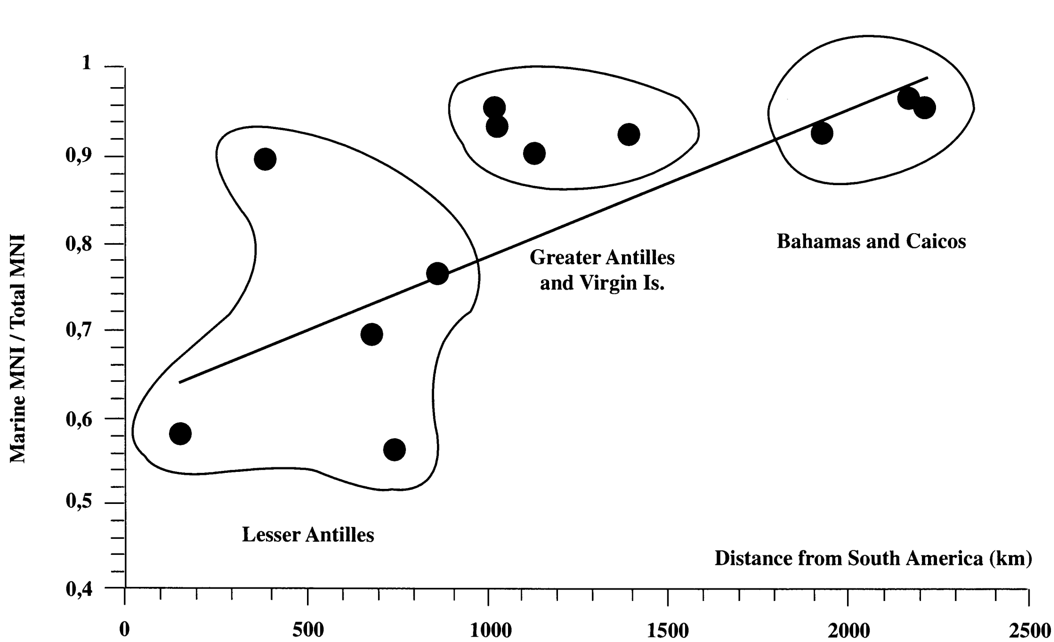

Fig. 4: The size of the marine component divided by the total sample as measured by minimum numbers of individuals and plotted against the distance from the mainland of South America.

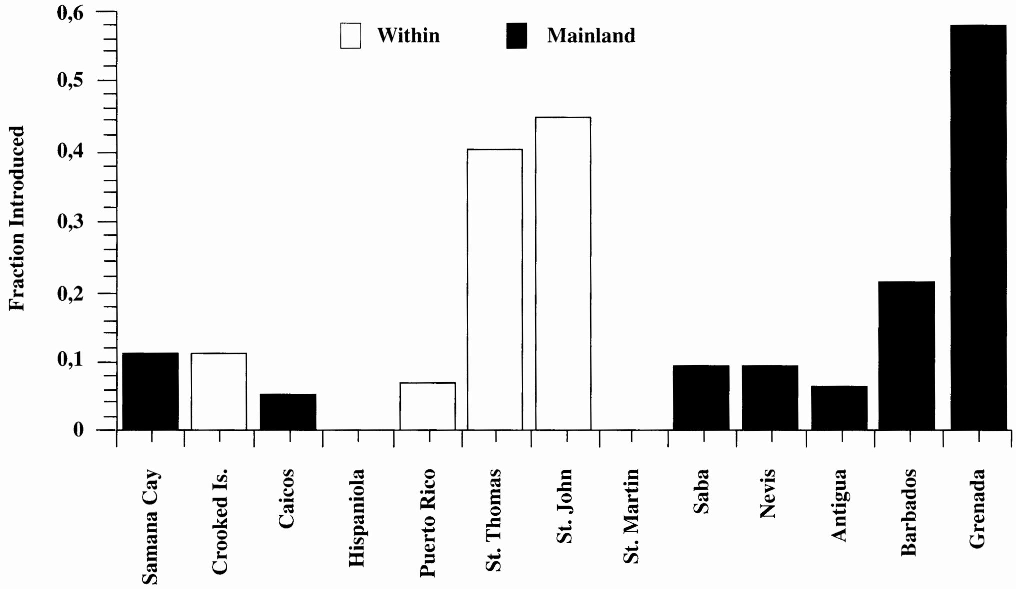

Fig. 5: The fraction of the land animals that were introduced from within the West Indian islands and from the South American mainland presented on a gradient from Samana Cay to Grenada.

icler provide conflicting reports on the roles of dogs in the West Indies (Sauer, 1966: 59). Oviedo describes them as being small nervous dogs that did not bark and were used in hunting. Las Casas agrees that they were small dogs but claimed that they were eaten. The dog remains from Grenada may be intrusive from a disturbed burial or dogs may have been used for food and not maintained and buried at death on this island. The agouti were probably more important as a food animal. They are highly esteemed for food wherever they occur with people (Redford and Robinson, 1991). They are attracted to the produce of garden plots and may have been hunted to protect the agricultural enterprise and at the same time adding animal protein to the diet (Linares, 1976). They are occasionally kept as pets. The burial of an agouti excavated from the Sugar Factory Pier site may have been a pet or had some special status. Burial of agouti may have been more widely practiced than our data from midden deposits indicate.

The hutia was an important addition to the faunas from the Virgin Islands. They became more important in the later ceramic period, the Ostionoid, perhaps as a managed resource to compensate for overexploitation of endemic animals (Wing *et al.*, nd.). Hutia were endemic to Hispaniola and were introduced to Puerto Rico where they occur in particular abundance in inland sites. They were then transported on to the Virgin Islands where they assumed greater importance in these small neighboring islands. We have no evidence that they were carried on to the Lesser Antilles or that the agouti was introduced into the Virgin Islands. However, pond turtles originating in the Greater Antilles do appear in a Lesser Antillean site, Saba, as well as in the Bahamas and Turks and Caicos. The large islands of the Greater Antilles were a source of animals enhancing the faunas of neighboring islands but did not substantially alter the faunas of more distant islands.

In conclusion, human exploitation of animal resources is limited by the diversity of species in island archipelagoes which conform to island biogeographic principles. Both the mainland and large islands in the archipelago provide a source of animals to adjacent islands. Some of these animals such as the hutia and agouti were of particular importance to those economies. Other animals such as the dog and guinea pig had important cultural roles in the island economies but are rare in midden remains. Their importance as well as some of the other introduced forms may not be accurately documented by their remains in midden samples. Even acknowledging possible underrecording of introduced animals they clearly were important to the colonizing effort though their impact in terms of diversity did not free people from the constraints described by island biogeography.

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