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## Quantitative paleodietary reconstruction with complex foodwebs: An isotopic case study from the Caribbean



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### A B S T R A C T

Stable isotope analysis has a long history in Caribbean archaeology. The Caribbean region, however, possesses a highly complex isotopic ecology, including both a large number of isotopically variable food sources, and a high degree of isotopic overlap between different food groups. As such, to date, most regional paleodietary studies have been limited to descriptive and qualitative conclusions concerning the relative contributions of different food sources. In this study we apply an iterative Bayesian multi-source mixing model (FRUITS) to skeletal stable isotope data from the prehistoric population of Tutu, St. Thomas, USVI, to test the feasibility of such models to generate quantitative and probabilistic individual paleodietary reconstructions. The isotope data set includes both bone collagen ( $\delta^{13}\text{C}_{\text{co}}$  and  $\delta^{15}\text{N}_{\text{co}}$ ) and apatite ( $\delta^{13}\text{C}_{\text{ap}}$ ) data. The results of two different dietary models using four and five distinct food groupings, respectively, are compared and assessed relative to other relevant archaeological evidence pertaining to past diet at the site. We highlight the potentials and limitations of multi-source mixing models for regional paleodietary studies, and their relevance to ongoing debates within Caribbean archaeology concerning the relative importance of different food sources such as manioc, maize, and seafood.

### 1. Introduction

Recent years have seen a notable increase in the use of mixture models, many of which employ Bayesian principles, in isotopic studies of paleodiet (Fernandes et al., 2014, 2015; Lubetkin and Simenstad, 2004; Moore and Semmens, 2008; Newsome et al., 2004; Parnell et al., 2010, 2013; Phillips, 2001; Phillips and Gregg, 2003; Stock and Semmens, 2013). Many of these applications have been made in continental settings (e.g. Fernandes et al., 2015; Pestle et al., 2016a, 2016b), however, which tend to possess comparatively simple foodwebs featuring little overlap in the isotopic signatures of source groups. In comparison, few examples of the use of such models are to be found in Caribbean paleodietary literature (the only exceptions being Pestle, 2010a and Chinique de Armas et al., 2015). In large part, the paucity of Caribbean applications can be attributed to the incredible complexity of the region's foodweb (Pestle, 2010b, 2013). Not only do the floral and faunal foodwebs of the region comprise hundreds and hundreds of edible taxa but the isotopic signatures of different food groups (established based on taxon, ecological niche, supposed trophic position) are non-overlapping. This stands in stark opposition to many of the continental regions in which stable isotope analysis was first developed and

applied. The huge number of potential sources and the lack of discrete, non-overlapping clusters of ecologically similar organisms tend to produce overly broad and non-definitive solutions in multi-source mixture models.

The lack of such studies is unfortunate, as these Bayesian tools can provide quantitative and probabilistic solutions to individual diet and, “offer a powerful means to interpret data because they can incorporate prior information, integrate across sources of uncertainty and explicitly compare the strength of support for competing models or parameter values” (Moore and Semmens, 2008: 471). The capability to compare models/competing hypotheses could be of particular utility in the Caribbean, where some long-held assumptions about diet (e.g. the primacy of manioc/cassava) are/have been challenged (e.g. Mickleburgh and Pagán-Jiménez, 2012; Pagán-Jiménez, 2013). Moreover, these approaches are inherently stronger in that they are model-bound, and allow testing of possible alternatives fitting the observed data following Bayesian principles, instead of traditional approaches that fit possible explanations of diet only after patterns in the data are defined (See Pestle et al., 2016b). Finally, these models have significant interpretive value in that they move discussions beyond isotopes or macronutrients to actual assessment of food intake, a metric that would

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have been cognizable to the human populations under study.

To address this apparent lacuna, we present here the results of an iterative Bayesian modeling study of a previously analyzed and well-studied Caribbean population from the Tutu site, St. Thomas, USVI. The Tutu site was chosen given: a) the existence of a robust corpus of human isotope data, b) the high degree of preservation of the human bone samples from which the isotopic data were derived, c) that St. Thomas is a relatively small island, without major river systems, thereby eliminating the confounding possibility of freshwater food sources, and d) the existence of independent evidence for paleodiet (in particular, zooarchaeological analysis, [Wing et al., 2002](#)) against which the results of modeling might be compared. It was our intent to employ successively more complex dietary models so as to gauge the effects of using more and more “realistic” and complex models, all the while comparing the resulting data with the independent sources of paleodietary data. The hope was that the consilience of modeling and archaeological data could serve to validate the use of such models in future Caribbean studies.

Ultimately, the results of our study show multi-source mixture modeling (in this case, FRUITS, [Fernandes et al., 2014](#)) to be useful for characterizing individual level dietary variability, in spite of the notable complexity of the region's foodweb. The limits of such modeling approaches in the region are, however, also evident from the results of this study, and we attempt to present both the pros and cons of this method in as transparent a manner as possible.

## 2. Background

### 2.1. Site context

The site of Tutu is located on the island of St. Thomas, US Virgin Islands (USVI), in an inland valley about two km from the coast ([Fig. 1](#)). St. Thomas lies in the Virgin Islands at the easternmost end of the Greater Antilles archipelago in the northern Caribbean Sea. The island

is situated roughly 55 km east of Puerto Rico and 200 km from the northern end of the Lesser Antilles, at a strategic location in terms of trade between the two major Antillean archipelagos. Geologically, St. Thomas was formed by the uplift of submerged volcanoes capped by marine limestone, and possesses rugged topography with many low-lying hills and sparse flat land. The climate is maritime tropical with little year-round variation in temperature but substantial seasonal fluctuations in rainfall, including pronounced dry periods. The arid conditions and sloping terrain limit permanent freshwater bodies on the island primarily to small fast-moving streams with seasonally variable output. Similar to the insular Caribbean in general, and the smaller islands of the Antilles in particular, the biomass and diversity of terrestrial fauna, especially of mammals, on St. Thomas is quite limited. The island does however provide ready access to a diverse array of marine ecosystems and resources including lagoon, littoral, coral reef, and offshore resources.

Archaeological excavations at Tutu were carried out in the early 1990s prior to development of the land for use as a shopping center ([Righter, 2002](#)). The excavations and subsequent investigations of the recovered assemblages from the site represent one of the largest archaeological research projects carried out in the USVI. This research revealed the presence of a large Amerindian village with a central plaza area surrounded by domestic structures and refuse middens ([Righter, 2002](#)). Owing to the size and multi-period occupation of the site, the quantity of recovered materials (especially the relatively large number of burials containing well preserved skeletal remains), and the large-scale interdisciplinary research design, the Tutu site has provided unique insights into continuity and change of pre-Columbian Antillean lifeways ([Righter, 2002](#)).

The Ceramic Age of the Caribbean is generally divided into an earlier and later phase ([Rouse, 1992](#)), which in the Lesser Antilles and eastern Greater Antilles, correspond to approximately 300 BCE to 600 CE (Early Ceramic) and 600 CE to 1500 CE (Late Ceramic), respectively. Ninety-two radiocarbon dates in total have been obtained

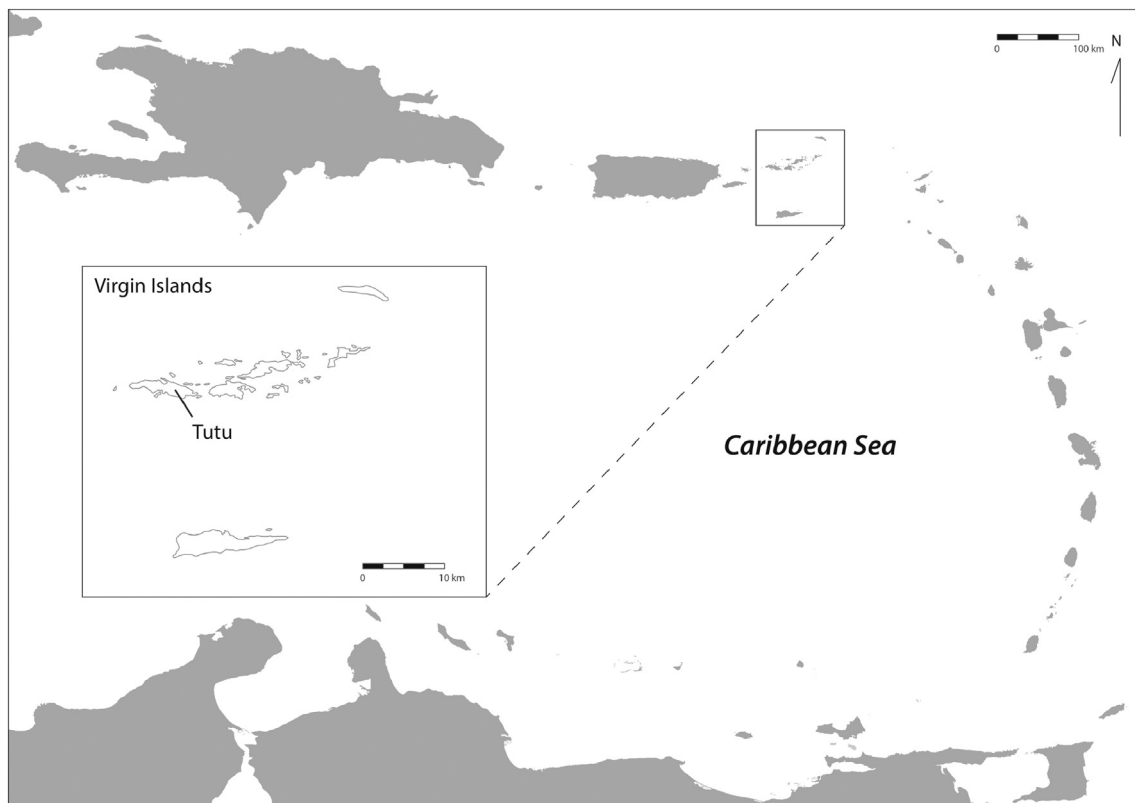


Fig. 1. Map of Caribbean region showing location of St. Thomas, with inset displaying Tutu site's location.

from the Tutu archaeological village site, and these indicate that it was settled as early as the first century AD and ultimately abandoned sometime before 1500 CE. There is little evidence for occupation between 950 CE and 1150 CE (Richter, 2002) suggesting that the site may have been abandoned for a time prior to subsequent resettlement.

In addition to artefactual remains, over forty burials were recovered during excavations at Tutu. In total, the Tutu skeletal sample is comprised of 20 subadults and 22 adults, with adults defined as those individuals with an estimated age at death of 16 years or older (Sandford et al., 2002).

Considering just the dated skeletal remains, the excavators of the Tutu site divide the overall corpus of analyzed individuals into two chronological groups. Those in the first group, dating to the period before 1000 CE, were affiliated by the excavators with the Saladoid, whereas those dating to after 1150 CE were associated with the Ostionoid cultural manifestation. For the purposes of the present work, we have not chosen to employ these cultural labels (given their problematic nature, see Curet, 2005, Pestle et al., 2013, Rodríguez Ramos, 2005, 2007, Rodríguez Ramos et al., 2007) and instead simply treat the two groups as early and late individuals, respectively.

## 2.2. Previous paleodietary research at Tutu

Paleobotanical analyses of charred macrobotanical and phytolith remains from Tutu revealed that although the inhabitants relied on a mixed diet of plants throughout the site's occupation, there were some differences in resource exploitation between the site's earlier and later inhabitants (Pearsall, 2002; Piperno, 2002). Piperno, working with phytoliths from all periods of the site's occupation, found that, "subsistence was based largely on root and tree crops, with some substantial input also from seed crops like squash," (Piperno, 2002:140). Pearsall (2002), while identifying some diachronic consistency in preserved macrobotanical remains, for example in the frequency of roots and tubers, also identified a shift from early to late consisting of a marked decrease in the frequency of porous endosperm fragments.

Zoarchaeological analyses (Wing and Wing, 2001; Wing et al., 2002) of both the vertebrate and invertebrate portions of the Tutu faunal collections have yielded interesting insights into long-term subsistence and dietary strategies at Tutu. The faunal evidence indicates that marine resources (including herring, jack, grouper, grunts, snapper, parrotfish, and marine crabs, as well as marine invertebrates such as the West Indian topsnail [*Cittarium pica*]) contributed more to dietary protein than terrestrial sources (hutia [*Isolobodon portoricensis*], insectivore [*Nesophontes edithae*], birds, reptiles, and land crabs) throughout the site's occupation, but that changes did occur in the composition of marine diet. Overall changes in aquatic resource utilization include decreases through time in: a) the average weight of reef fishes (e.g. jacks, grouper, snapper, and grunt), b) the size distribution of obligate reef taxa, c) the contribution of reef fishes to the total estimated aquatic vertebrate, and d) the mean trophic level of reef fishes (Wing and Wing, 2001).

The skeletal remains from the site have been subjected to a variety of analyses, including osteological, dental, trace element, and stable and radiogenic isotope analyses (Farnum and Sandford, 2002; Laffoon, 2012; Larsen et al., 2002; Mickleburgh, 2007, 2014; Norr, 2002; Sandford et al., 2002), a number of which provide useful detail on diet. Dental anthropological analyses of the Tutu skeletal materials included studies of patterns of pathology and wear, and these studies have revealed several interesting patterns of health and disease (Larsen et al., 2002; Mickleburgh, 2007, 2013, 2014). Generally, poor oral health and relatively high frequencies of carious lesions were reported for this population, the latter probably attributable to the consumption of starch-rich foods (Larsen et al., 2002; Mickleburgh, 2007). A slight decrease in caries rates from the earlier to later period may be associated with the proposed greater reliance on marine resources in the later period (Larsen et al., 2002; Mickleburgh, 2007). Microbotanical

analyses of starch grains in dental calculus of three individuals (two dating to the early phase: B16 and B32A) has identified the presence of a wide range of taxa and the consumption of both wild and cultivated plants such as cocoyam (*Xanthosoma* sp.), wild legumes (Fabaceae), and maize (*Zea mays*) at Tutu (Mickleburgh and Pagán-Jiménez, 2012).

Trace element concentrations were obtained from human femoral bone samples and soil samples from the Tutu site (Farnum and Sandford, 2002). Using multiple techniques to assess diagenesis, these researchers found no widespread or substantial contamination of the bone materials based on trace element concentrations. These results provide greater confidence in the interpretation of the isotopic analyses of these remains, and also aid in dietary reconstructions at the site. Human remains from the later component possessed higher Sr/Ba bone concentrations than the remains from the earlier component (Farnum and Sandford, 2002). This pattern is consistent with a shift towards less reliance on terrestrial food resources in later periods, although this shift still falls within the mixed marine and terrestrial consumption ranges.

Stable isotopes analyses of carbon and nitrogen in bone collagen and carbon isotopes in bone apatite have also been conducted on a subset of the Tutu skeletal assemblage (Norr, 2002). These results are in accordance with other lines of evidence indicating a broad-based subsistence strategy and mixed reliance on marine and terrestrial resources. The overall dietary pattern is homogenous throughout the sample, indicating shared dietary practices between males and females, adults and children (Norr, 2002). In contrast to the trace element study, the isotopic results revealed no major shift in diet between the earlier and later periods (Norr, 2002). Comparisons with published dietary isotope results from other contemporaneous sites in the Caribbean show that the ancient inhabitants of Tutu generally consumed less terrestrial resources than most Greater Antillean populations but less reef, and more pelagic, marine resources than most Lesser Antillean populations (Norr, 2002; Pestle, 2010a, 2010b; Stokes, 1998) with the possible exception of Lavoutte, St. Lucia (Laffoon et al., 2016).

Subsequent analyses of stable carbon and oxygen and radiogenic strontium isotopes of dental enamel samples from Tutu have contributed to paleodietary and paleomobility assessments (Laffoon, 2012; Laffoon and Hoogland, 2012; Laffoon et al., 2013). Enamel apatite  $\delta^{13}\text{C}$  values are consistent with previously reported bone  $\delta^{13}\text{C}$  values (Norr, 2002) and confirm that  $\text{C}_3$  resources (including, for example, manioc, other tubers, legumes, and tree fruits) likely dominated local diets, and that  $\text{C}_4/\text{CAM}$  plants (including maize, cacti, and pineapple) played a lesser role. Enamel  $\delta^{18}\text{O}$  values did not indicate the presence of long-distance (possibly South American mainland) migrants, although the sample size to date is quite small (Laffoon et al., 2013). Strontium isotope ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) results indicated the presence of at least seven nonlocals at Tutu, most of which are likely nonlocal to the island of St. Thomas (Laffoon, 2012). At least three of these nonlocals also possess somewhat distinct bone collagen  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, suggesting that dietary patterns may have varied relative to individual origins (Laffoon, 2012; Laffoon and Hoogland, 2012).

## 3. Methods

### 3.1. Isotopic data

Carbon and nitrogen stable isotope data for all twenty-two individuals under consideration here were gleaned from the previously published work of Norr (2002). Methods for extraction and analysis of these samples are available in the same publication.

### 3.2. Model choice

Individual isotopic data were analyzed using the Bayesian multi-source mixture modeling software FRUITS v2.1.1 (Food Reconstruction Using Isotopic Transferred Signals, [Fernandes et al., 2014]). This analysis allows for probabilistic and uncertainty-integrated

**Table 1**

Human sample demographic information and measured and converted isotope data (burials are assigned E or L prefixes to designate early and late components, respectively).

Burial	Age	Sex	Place of origin	$\delta^{13}\text{C}_{\text{co}}$ (‰)	$\delta^{15}\text{N}_{\text{co}}$ (‰)	$\delta^{13}\text{C}_{\text{ap}}$ (‰)	$\Delta^{13}\text{C}_{\text{ap-co}}$ (‰)	$\delta^{13}\text{C}_{\text{bulk}}$ (‰, $\pm 0.4$ )	$\delta^{15}\text{N}_{\text{prot}}$ (‰, $\pm 1.2$ )	$\delta^{13}\text{C}_{\text{prot}}$ (‰, $\pm 1.9$ )
E3	Adult	Female	Local	-14.4	12.9	-10.9	3.5	-21.3	9.3	-18.0
E4/7	Adult	Female	Nonlocal	-16.3	10.1	-11.0	5.3	-21.4	6.5	-20.5
E10	Adult	Female	Nonlocal	-15.8	12.7	-10.6	5.2	-21.0	9.1	-20.0
E13	Adult	Female	Local	-15.7	12.8	-9.2	6.5	-19.6	9.2	-20.7
E16	Adult	Female	Local	-15.2	12.5	-10.5	4.7	-20.9	8.9	-19.3
E39	Juvenile	Indeterminate	Local	-15.3	11.6	-9.7	5.6	-20.1	8.0	-19.9
L1	Adult	Female	Local	-15.9	13.4	-8.4	7.5	-18.8	9.8	-21.5
L2	Adult	Female	Local	-15.5	12.6	-9.6	5.9	-20.0	9.0	-20.2
L5	Adult	Female	Local	-16.5	12.2	-11.5	5.0	-21.9	8.6	-20.5
L6	Juvenile	Indeterminate	Local	-15.6	12.9	-9.4	6.2	-19.8	9.3	-20.5
L8A	Juvenile	Indeterminate	Unknown	-16.4	11.2	-10.1	6.3	-20.5	7.6	-21.1
L8B	Juvenile	Indeterminate	Unknown	-15.0	11.8	-9.7	5.3	-20.1	8.2	-19.5
L9	Adult	Male	Nonlocal	-15.2	12.1	-10.1	5.1	-20.5	8.5	-19.5
L12	Adult	Male	Local	-14.7	12.9	-10.9	3.8	-21.3	9.3	-18.4
L19	Adult	Female	Local	-15.8	12.9	-11.0	4.8	-21.4	9.3	-19.8
L20	Juvenile	Indeterminate	Local	-15.6	11.7	-10.1	5.5	-20.5	8.1	-20.1
L22B	Juvenile	Indeterminate	Local	-15.4	11.4	-11.2	4.2	-21.6	7.8	-19.1
L29	Adult	Female	Unknown	-14.9	12.3	-10.6	4.3	-21.0	8.7	-18.8
L30	Adult	Male	Local	-15.6	12.7	-11.4	4.2	-21.8	9.1	-19.3
L31	Adult	Female	Nonlocal	-17.3	10.3	-11.0	6.3	-21.4	6.7	-21.8
L33	Adult	Male	Local	-14.9	11.6	-11.8	3.1	-22.2	8.0	-18.1
L38	Adult	Male	Nonlocal	-12.9	11.1	-10.8	2.1	-21.2	7.5	-16.0

quantification of dietary inputs. FRUITS was chosen because of its capability for incorporating food macronutrient, elemental, and isotopic composition data, as well as source and consumer uncertainty, in its calculations, and because of its ability to simultaneously solve for both plant (carbohydrate rich and protein poor) and animal (protein and fat rich, but typically carbohydrate poor) foodstuffs. Ultimately three models (hereafter referred to as the 4-, 5-, and 7-source models) were employed, with the results of each presented and compared independently with zooarchaeological data from the site.

### 3.3. Human (consumer) data

Measured isotopic data (Norr, 2002) for the twenty-two individuals from the Tutu site are presented in Table 1. For inclusion in FRUITS, these measured data were first converted so as to account for fractionation, producing the corrected isotope values also found in Table 1. The offset (fractionation) factor for  $\delta^{13}\text{C}_{\text{ap}}$  was stipulated as  $10.1 \pm 0.4\text{‰}$ , following Fernandes et al. (2012). For  $\delta^{15}\text{N}_{\text{co}}$ , we employed a trophic fractionation value of  $3.6 \pm 1.2\text{‰}$ , as recommended by several experimental studies of omnivorous animals (Ambrose, 2002; DeNiro and Epstein, 1981; Hare et al., 1991; Howland et al., 2003; Sponheimer et al., 2003; Warinner and Tuross, 2009). Finally, for the purposes of this analysis, we determined the consumer-foodstuff offset (and error) for  $\delta^{13}\text{C}_{\text{co}}$  using the linear regression method described in Pestle et al. (2015). All measured values were input into FRUITS with stipulated instrumental uncertainties of  $0.1\text{‰}$  for all isotope systems.

### 3.4. Routing and priors

To account for differential elemental routing, all nitrogen in bone collagen was stipulated as coming from dietary protein (the only macronutrient that contains nitrogen), the carbon in hydroxyapatite was stipulated as reflecting (an average of) all dietary carbon, and the carbon composition of bone collagen was set to reflect a roughly 3:1 ratio ( $74 \pm 4\%$ , 26%) of dietary protein to energy (Fernandes et al., 2012). Consumption of protein was limited to between 10% and 45% of protein as energy (using the FRUITS prior data option), reflecting the lower and upper limit of possible human protein intake (WHO, 2007).

### 3.5. Source (foodweb) data

Source specification began with isotopic data on edible Caribbean plant taxa derived from several regional studies (Keegan and DeNiro, 1988; Pestle, 2010b; Schwarcz et al., 1985; Stokes, 1998; von Fischer and Tieszen, 1995). All modern data had their  $\delta^{13}\text{C}$  values corrected by  $+1.5\text{‰}$  to account for the Suess/fossil fuel burning effect (Keeling et al., 1979; Marino and McElroy, 1991). Cluster analysis of these data produced two distinct groups: one consisting of  $\text{C}_3$  plants ( $n = 112$ ), and possessing a bulk  $\delta^{13}\text{C}$  of  $-25.5 \pm 1.7\text{‰}$  and a  $\delta^{15}\text{N}$  of  $3.3 \pm 2.1\text{‰}$ , and the other comprised of  $\text{C}_4$  and CAM plants ( $n = 28$ ), with an average bulk  $\delta^{13}\text{C}$  of  $-10.4 \pm 1.3\text{‰}$  and  $\delta^{15}\text{N}$  of  $5.1 \pm 2.9\text{‰}$ .

Compilation of faunal data isotope values began with the list of documented taxa presented in Wing et al. (2002). This list of attested Tutu taxa was cross-referenced against a corpus of published faunal foodweb values for the Caribbean (Burton et al., 2001; Cardona et al., 2009; Coltrain et al., 2004; Fry et al., 1982; Godley et al., 1998; Keegan and DeNiro, 1988; March and Pringle, 2003; Moncreiff and Sullivan, 2001; Norr, 2002; Pestle, 2010b; Reich and Worthy, 2006; Schimmelmann, 1985; Schoeninger and DeNiro, 1984; Stokes, 1998; Stoner and Waite, 1991; van Klinken, 1991). Only those 356 taxa whose presence was documented in the Tutu assemblage were included in the resulting faunal source groupings. Tissue corrections (between measured and edible animal tissues) are fully detailed in Pestle (2010b, Table 38).

For the purpose of source group building, taxa were next grouped according to the habitat determinations (inshore, intertidal, land, pelagic, reef) of Wing et al. (2002). Isotope values were averaged for taxa within these groupings, and more inclusive groups were produced for the models featuring fewer sources (the 4- and 5-source models, see below). Sample sizes for these groupings are presented in Table 2.

### 3.6. Macronutrient and elemental composition

Macronutrient composition of each food group was determined by reference to a range of comparable foodstuffs in the USDA National Nutrient Database for Standard Reference (USDA, 2013).  $\text{C}_3$  plants were represented using USDA numbers 20014, 20314, 11134, 9315, 9266, and 9176;  $\text{C}_4$ /CAM plants using USDA numbers 20014, 20314, 11134, 9315, 9266, and 9176; land animals using USDA reference numbers 5160, 5161, 5162, 15,139, 5151, and 5152; and marine animals were

**Table 2**  
Model food grouping macronutrient and tissue isotope values (4-source and 5-source models).

Food grouping	Group <i>n</i>	Macronutrient concentration (%)		Tissue $\delta^{13}\text{C}$ (‰)			Tissue $\delta^{15}\text{N}$ (‰)
		Protein	Energy	Bulk	Protein	Energy	Protein
<b>4-source model</b>							
Land animals	25	69 ± 18	31 ± 18	-19.7 ± 4.1	-21.7 ± 4.1	-26.7 ± 4.1	5 ± 3.7
Marine animals	268	76 ± 15	24 ± 17	-12.0 ± 3.9	-14.5 ± 3.9	-16.2 ± 3.9	7.1 ± 4.0
C <sub>3</sub> plants	112	6 ± 6	94 ± 10	-25.5 ± 1.7	-27.5 ± 1.7	-26.4 ± 1.7	3.3 ± 2.1
C <sub>4</sub> /CAM plants	28	6 ± 6	94 ± 10	-10.4 ± 1.3	-12.4 ± 1.3	-11.3 ± 1.3	5.1 ± 2.9
<b>5-source model</b>							
Land animals	25	69 ± 18	31 ± 18	-19.7 ± 4.1	-21.7 ± 4.1	-26.7 ± 4.1	5 ± 3.7
Intertidal/inshore	121	76 ± 15	24 ± 17	-12.7 ± 4.1	-15.2 ± 4.1	-16.9 ± 4.1	5.7 ± 5.0
Reef/pelagic	147	76 ± 15	24 ± 17	-10.8 ± 3.0	-13.3 ± 3.0	-15.0 ± 3.0	8.3 ± 2.0
C <sub>3</sub> plants	112	6 ± 6	94 ± 10	-25.5 ± 1.7	-27.5 ± 1.7	-26.4 ± 1.7	3.3 ± 2.1
C <sub>4</sub> /CAM plants	28	6 ± 6	94 ± 10	-10.4 ± 1.3	-12.4 ± 1.3	-11.3 ± 1.3	5.1 ± 2.9

**Table 3**  
Individual model results (4-source and 5-source models; burials are assigned E or L prefixes to designate early and late components, respectively).

	4-source model								5-source model									
	Land animals	sd	Marine animals	sd	C <sub>3</sub> plants	sd	C <sub>4</sub> /CAM plants	sd	Land animals	sd	Intertidal/inshore	sd	Reef/pelagic	sd	C <sub>3</sub> plants	sd	C <sub>4</sub> /CAM plants	sd
E3	20.6%	13.8%	21.2%	11.2%	46.2%	9.8%	12.0%	8.1%	16.4%	13.5%	12.7%	10.4%	12.4%	9.4%	49.1%	11.7%	9.4%	7.2%
E10	25.0%	18.7%	16.8%	9.3%	44.7%	16.8%	13.5%	8.5%	17.1%	13.5%	11.0%	9.1%	11.8%	8.8%	50.3%	12.0%	9.7%	7.4%
E13	24.0%	13.6%	17.1%	11.0%	44.2%	11.1%	14.8%	10.6%	15.5%	12.3%	13.1%	10.0%	12.7%	9.5%	46.3%	11.8%	12.5%	8.8%
E16	24.7%	16.5%	13.8%	9.1%	47.8%	14.8%	13.7%	9.1%	16.6%	13.3%	12.1%	10.0%	12.0%	9.2%	49.0%	12.4%	10.3%	7.8%
E39	24.0%	13.3%	19.4%	10.2%	41.8%	12.1%	14.8%	9.6%	16.0%	13.0%	11.7%	8.9%	13.1%	8.8%	47.4%	12.2%	11.8%	8.4%
E47	14.6%	10.3%	18.6%	9.4%	55.4%	11.2%	11.4%	7.7%	16.3%	12.8%	9.6%	8.0%	10.9%	7.9%	53.6%	12.3%	9.5%	7.1%
L1	27.9%	16.2%	16.9%	11.9%	32.5%	13.5%	22.7%	10.4%	18.2%	13.9%	13.0%	10.0%	12.2%	9.1%	42.4%	12.7%	14.2%	9.7%
L2	15.9%	10.3%	24.1%	11.3%	46.9%	13.4%	13.1%	8.7%	18.5%	14.0%	11.3%	9.1%	13.2%	9.4%	45.1%	12.8%	11.9%	8.6%
L5	22.1%	14.9%	14.3%	9.2%	53.1%	15.8%	10.6%	7.1%	18.2%	15.8%	11.2%	9.4%	9.7%	7.6%	52.3%	14.9%	8.6%	6.6%
L6	21.1%	13.7%	16.9%	10.7%	46.4%	11.6%	15.7%	9.7%	17.2%	12.8%	12.6%	9.7%	12.1%	8.8%	46.1%	12.4%	12.0%	8.6%
L8A	13.8%	12.7%	17.0%	9.6%	54.7%	13.2%	14.5%	9.2%	16.1%	11.7%	10.1%	8.2%	11.2%	8.2%	51.2%	12.2%	11.3%	8.1%
L8B	19.8%	14.1%	16.9%	9.7%	46.1%	14.8%	17.1%	10.0%	16.6%	12.4%	11.1%	8.8%	13.6%	9.4%	47.1%	11.3%	11.7%	8.4%
L9	16.6%	14.6%	18.3%	10.6%	48.0%	11.5%	17.2%	9.8%	15.8%	12.8%	11.3%	9.0%	13.1%	9.1%	48.4%	12.3%	11.3%	8.1%
L12	26.6%	18.2%	21.6%	15.2%	40.0%	13.0%	11.8%	7.2%	15.1%	12.8%	12.5%	9.9%	12.7%	9.5%	50.3%	12.5%	9.5%	7.1%
L19	20.2%	14.6%	15.0%	9.9%	53.5%	11.0%	11.3%	7.6%	14.5%	11.9%	11.7%	9.2%	11.8%	8.2%	53.1%	11.4%	8.9%	6.9%
L20	24.8%	14.9%	13.8%	9.6%	47.4%	12.0%	14.1%	8.7%	17.2%	13.4%	10.6%	8.7%	12.7%	8.9%	48.4%	12.6%	11.2%	8.0%
L22B	27.6%	14.4%	16.9%	9.3%	43.4%	14.4%	12.2%	8.3%	15.4%	12.7%	10.0%	8.4%	11.9%	8.5%	53.6%	12.0%	9.1%	7.2%
L29	26.6%	14.8%	13.6%	9.8%	44.6%	15.0%	15.3%	9.3%	15.7%	12.9%	10.9%	8.7%	13.7%	9.2%	49.8%	12.0%	10.0%	7.6%
L30	16.0%	12.7%	20.0%	12.3%	54.0%	10.0%	10.1%	7.4%	16.3%	13.3%	10.4%	8.3%	11.6%	8.7%	53.1%	12.4%	8.6%	6.8%
L31	17.9%	15.9%	14.1%	8.8%	54.9%	16.0%	13.1%	9.1%	16.2%	11.9%	9.3%	7.7%	9.7%	7.4%	55.6%	11.9%	9.3%	7.1%
L33	18.9%	12.8%	17.8%	9.7%	54.1%	11.0%	9.2%	5.6%	15.9%	14.0%	10.8%	8.9%	11.8%	8.7%	52.9%	12.7%	8.7%	6.9%
L38	14.8%	13.6%	23.9%	10.1%	50.4%	12.5%	10.9%	7.8%	15.6%	13.0%	12.1%	10.2%	14.9%	10.2%	46.8%	12.2%	10.6%	8.1%

represented using USDA numbers 15101, 15031, 15250, 15177, 15046, 15157, 15164, 15023, 15055, and 15167. Dry weights for each 100 g of reference foodstuff were calculated (by subtraction of the water portion), and the protein and energy (fats plus carbohydrates) composition of that dried food was then determined and converted to a percentage. These values were then averaged within each food grouping producing the mean and standard deviation of macronutrient composition for each food group. Elemental composition (particularly %C) of each foodstuff/macronutrient group was based on formulae provided in Morrison et al. (2000). Digestibility was determined following Hopkins (1981). Isotopic offsets between measured bulk food isotope values and the isotopic values of specific dietary macronutrients were derived from Tieszen (1991) and used as macronutrient-specific inputs for FRUITS. Final macronutrient and tissue isotope values for the model food groupings are presented in Table 2.

### 3.7. Model complexity

As mentioned above, three successively more complex and realistic models were employed in the present study. The first and simplest iteration, the 4-source model, divided the possible foodstuffs into four

categories, C<sub>3</sub> plants (*n* = 112), C<sub>4</sub>/CAM plants (*n* = 28), land animals (*n* = 25), and marine animals (*n* = 268). The 5-source model included the same sources, except that the marine animal grouping was divided, on the basis of the habitat characterizations of (Wing et al., 2002) into two separate sources, intertidal/inshore marine (*n* = 121) and reef/pelagic marine (*n* = 147). The 7-source model further divided the two marine groupings of the 5-source model into four possible sources, intertidal (*n* = 23), inshore (*n* = 98), reef (*n* = 139), and pelagic (*n* = 8).

### 3.8. Statistical analysis

Statistical comparison of consumer isotope values and simulated foodstuff contributions were made using Student's *t*-tests, with Levene's correction for those comparisons for which sub-sample variances were unequal. Correlations between model inputs and results, as well as between the results of different model iterations were made by means of Pearson's *r* tests. While a more traditional alpha of 0.05 was used in the comparison of isotope values, due to the possibility of overfitting with large sample sizes (i.e. the 10,000 simulation runs of the FRUITS models), we instead employed an alpha of 0.01 for any comparisons of

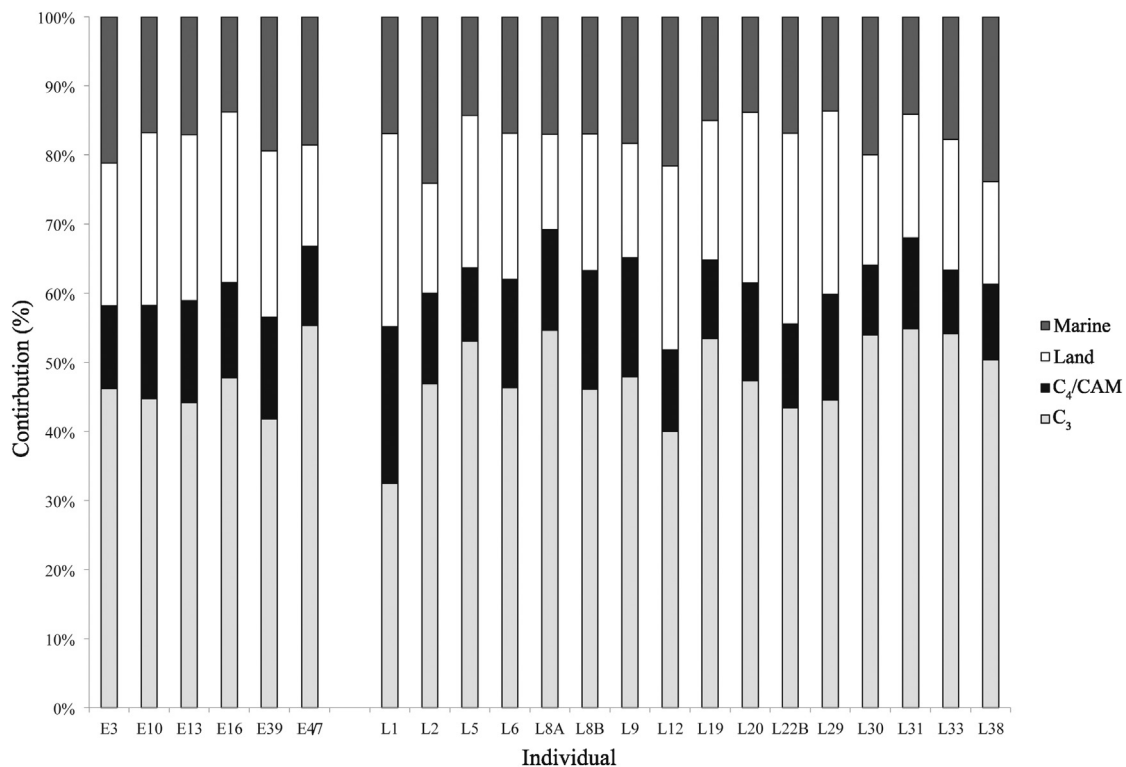


Fig. 2. Individual mean modeled dietary contributions for 4-source model (burials are assigned E or L prefixes to designate early and late components, respectively).

model outputs.

## 4. Results

### 4.1. 4-Source model

Results of the simpler, 4-source, model are presented in Table 3 and Fig. 2. Considering all individuals of both time periods together, plants accounted for an average of  $61.3 \pm 15.7\%$  of total dietary intake, with meat accounting for the remaining  $38.7 \pm 17.8\%$  of diet, a highly significant difference ( $t = 4.47$ ,  $df = 42$ ,  $p < 0.01$ ). There is, however, variation of nearly 20% in the relative contribution of plants and meats among the analyzed individuals, from individual 12, who consumed  $51.8 \pm 14.9\%$  plants and  $48.2 \pm 23.7\%$  meat, to individual 8A, who ate  $69.2 \pm 16.1\%$  plants and  $30.8 \pm 15.9\%$  meat.

On average, C<sub>3</sub> plants formed the single largest component of the average diet at the Tutu site, at  $47.7 \pm 13.1\%$  of total diet, far outweighing C<sub>4</sub>/CAM plants, which accounted for an average of  $13.6 \pm 8.7\%$  of dietary intake. The observed difference in plant intake was highly significant ( $t = 10.17$ ,  $df = 42$ ,  $p < 0.01$ ). As above, however, there is substantial (22.9%) variation in C<sub>3</sub> plant consumption among the individuals in the sample, from a minimum of  $32.5 \pm 13.5\%$  to a maximum of  $55.4 \pm 11.2\%$ . The ability to quantify individual variation in specific food group consumption is one of the obvious strengths of the sort of mixture modeling employed here.

Not only do C<sub>4</sub>/CAM plants represent a far less important contributor to average diet at the Tutu site, but the range of modeled contribution is also far smaller, at 13.6%. Taken together, the results of the 4-source model suggest that C<sub>3</sub> plants were preferred/consumed in preference to C<sub>4</sub>/CAM plants by an average 3.7:1 ratio. No individual showed evidence of C<sub>3</sub> plants playing a smaller dietary role than did their C<sub>4</sub>/CAM equivalents, as individual ratios of C<sub>3</sub>:C<sub>4</sub>/CAM plants varied from 1.4:1 to 5.9:1.

While land animals ( $21.1 \pm 14.4\%$ ) accounted for a greater portion of the average diet of all Tutu individuals than did marine animals ( $17.6 \pm 10.4\%$ ), the observed difference was not significant ( $t = 0.92$ ,

$df = 42$ ,  $p = 0.37$ ). Differences among individuals in the samples are large, however, including individuals who consumed more marine animals than land animals (individual 38: marine  $23.9 \pm 10.1\%$ , land  $14.8 \pm 13.6\%$ ) and individuals who had the inverse pattern of consumption (individual 29: marine  $13.6 \pm 9.8\%$ , land  $26.6 \pm 14.8\%$ ).

### 4.2. 5-Source model

At the highest level, the results of the 5-source model, presented in Table 3 and Fig. 3, are not dissimilar to those of the 4-source solution. These similarities are indicative of the general robustness of the models employed.

To begin with, plant consumption was determined to make up  $60.1 \pm 14.6\%$  of average dietary intake, with animals accounting for the remaining  $39.9 \pm 18.3\%$  of average diet. This difference was highly significant ( $t = 4.1$ ,  $df = 42$ ,  $p < 0.01$ ). As compared with the 4-source model, however, variation was only 8% among the analyzed individuals for these two food categories. The average modeled plant and meat contributions from the 5-source model are not significantly different than those of the 4-source run ( $p = 0.79$  for plants and  $p = 0.83$  for meat).

C<sub>3</sub> plants again were determined to have been the single largest component of individual diet, accounting for  $49.6 \pm 12.3\%$  of average diet, although there is substantial variation (13.2%) between the individuals with the minimum and maximum modeled C<sub>3</sub> plant contributions. As above, C<sub>4</sub>/CAM plants played a significantly ( $t = 12.6$ ,  $df = 42$ ,  $p < 0.01$ ) smaller role in the diet at Tutu, averaging  $10.5 \pm 7.8\%$ , with only a 5.6% difference between maximum and minimum modeled contributions. The individual variation is substantial, in that C<sub>3</sub>:C<sub>4</sub>/CAM plant intake ratios runs from 3:1 for individual 1 to 5.8:1 for individual 30. Modeled C<sub>3</sub> and C<sub>4</sub>/CAM contributions for the 5-source model do not differ significantly from those of the 4-source iteration above ( $p = 0.62$  for C<sub>3</sub> and  $p = 0.22$  for C<sub>4</sub>/CAM).

Turning to patterns of animal consumption, the division of the marine group specified in the 4-source model into two separate

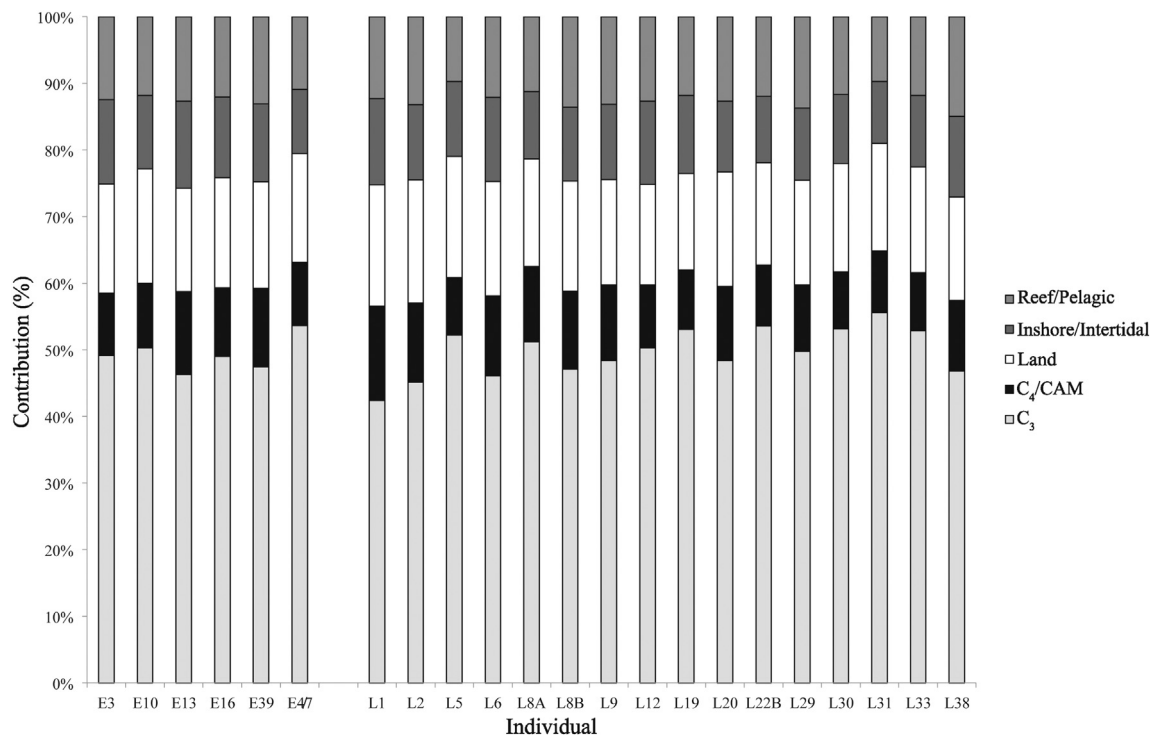


Fig. 3. Individual mean modeled dietary contributions for 5-source model (burials are assigned E or L prefixes to designate early and late components, respectively).

categories in the 5-source run has several ramifications. First, the average contribution of land animals to the 5-source modeled diets at Tutu fell from  $21.1 \pm 14.4\%$  to  $16.4 \pm 13.1\%$  in the 4-source model, a non-significant difference ( $p = 0.26$ ). This 5-source average does, however, mask significant intra-sample variation in modeled land animal consumption, which ranges from a low of  $14.5 \pm 11.9\%$  for individual 19 to a maximum of  $18.5 \pm 14.0\%$  for individual 2. Not surprisingly, the decrease in the 5-source modeled land animal consumption is matched by an increase (albeit not significant,  $p = 0.10$ ) from  $17.6 \pm 10.4\%$  to  $23.5 \pm 12.7\%$  in the average modeled intake of marine animals.

The obvious strength of the 5-source model is the ability to discriminate between consumption of marine animals of different ecological niches/habitats. On average, reef/pelagic marine animals ( $12.2 \pm 8.9\%$ ) would appear to have formed a greater part of the diet at Tutu than did intertidal/inshore organisms ( $11.3 \pm 9.1\%$ ), but the observed difference was not significant ( $p = 0.74$ ). Overall, it would appear that some of the intake attributed to land animal consumption in the 4-source iteration is, in the 5-source model, attributed instead to the intertidal/inshore marine group, which features lower, and hence more “terrestrial appearing”,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values than the animals in the reef/pelagic grouping. As above, however, this average statement hides the fact that sixteen of the twenty-two Tutu individuals showed greater reliance on reef/pelagic animals than intertidal/inshore species, whereas the other six had greater modeled contributions of intertidal/inshore than reef/pelagic taxa.

#### 4.3. 7-Source model

Unfortunately, attempts at running a full 7-source model, which separated the intertidal/inshore and reef/pelagic categories used in the 5-source model into 4 distinct sources, proved impossible. Ultimately, it was determined that the substantial overlap/isotopic similarity of the various marine animal groupings (intertidal and inshore, pelagic and reef) resulted in uninformative modeled solutions. In cases such as this, where multiple sources are isotopically indistinguishable, FRUITS ceases operation and the software does not proceed with generating

modeled solutions. As such, the 5-source model was the most specific model that could be generated.

#### 4.4. Temporal patterns

We found no significant differences in either isotope values or modeled dietary contributions between the site's six early and sixteen late inhabitants. This overall temporal homogeneity is, as discussed below, somewhat surprising given apparent temporal differences in zooarchaeological data.

#### 4.5. Demographic patterns

Beginning with sex, there were significant differences between females ( $n = 11$ ) and males ( $n = 5$ ) for both  $\delta^{13}\text{C}_{\text{co}}$  and  $\Delta^{13}\text{C}_{\text{ap-co}}$ . Females had significantly lower  $\delta^{13}\text{C}_{\text{co}}$  values than males,  $-15.8 \pm 0.8\text{‰}$  versus  $-14.7 \pm 1.0\text{‰}$  ( $t = -2.3$ ,  $df = 14$ ,  $p = 0.04$ ), and significantly larger  $\Delta^{13}\text{C}_{\text{ap-co}}$  values,  $5.4 \pm 1.1\text{‰}$  versus  $3.7 \pm 1.1\text{‰}$  ( $t = 2.8$ ,  $df = 14$ ,  $p = 0.01$ ). Interestingly, however, these different isotopic values did not equate to significant differences in modeled dietary contributions in either of the two successful model runs, due to large variance and small sample size. Turning to age-based subdivisions, we found no significant differences in either isotope values or modeled dietary contributions between the site's six subadult and sixteen adult inhabitants.

#### 4.6. Place of origin

Finally, comparison of local and nonlocal individuals as judged on the basis of Sr isotope analysis (Laffoon, 2012) revealed an additional isotopic difference within the sample. The fourteen local individuals had significantly higher  $\delta^{15}\text{N}_{\text{co}}$  values ( $12.4 \pm 0.6\text{‰}$  versus  $11.3 \pm 1.1\text{‰}$ ) than the five nonlocals ( $t = 2.9$ ,  $df = 17$ ,  $p = 0.01$ ). As above, however, the isotopic differences did not equate to significant differences in modeled dietary contributions in either of the two successful model runs, due to large variance and small sample size.

**Table 4**  
Comparison of summary model results with zooarchaeological data of Wing et al., 2002.

	Land	Marine	Inshore/intertidal	Reef/pelagic
Early				
Wing et al.	41.0%	59.0%	23.0%	36.0%
4-source model	55.2%	44.8%	–	–
5-source model	40.7%	59.3%	29.1%	30.2%
Late				
Wing et al.	17.0%	83.0%	51.0%	32.0%
4-source model	53.8%	46.2%	–	–
5-source model	41.1%	58.9%	28.2%	30.7%

#### 4.7. Comparison with other paleodietary proxies

Despite the inability to run the 7-source iteration, simpler iterations of FRUITS modeling nonetheless produced two sets of quantitative data that can be compared directly with the site and phase level faunal data (Table 4) previously published by Wing et al. (2002). In this case, the use of the average modeled dietary contributions is of an appropriate scale for comparison with the zooarchaeological data in that both measures are representative of the community diet of multiple individuals living at the Tutu site over a long period of time. Unfortunately, however, as Wing and colleagues only present MNI, rather than biomass, data on the faunal taxa, the comparison made is far from one-to-one, as while the isotopic results speak to the relative proportions of foods consumed, the MNI-based data speak only to counts of animals in different taxa, each of which might contribute widely differing amounts of edible tissue.

Nonetheless, in the early deposits at Tutu, Wing et al. (2002, Table 4.4) found that 41% of the faunal remains were terrestrial and 59% were marine organisms, as calculated on the basis of MNI. The 4-source model places the average distribution at 55.2% land and 44.8% marine, roughly 15% adrift of the observed faunal values. In contrast, the 5-source model produced values that were nearly identical to the zooarchaeological data: 40.7% land and 59.3% marine, a difference of < 1%. When the zooarchaeological data is grouped in a manner equivalent to the 5-source model, the similarities between the two datasets remain strong. While Wing and colleagues found frequencies of land animals of 41%, inshore/intertidal 23%, and reef/pelagic 36%, the 5-source model predicted average dietary proportions of 40.7%, 29.1%, and 30.2%, respectively. The differences between the zooarchaeological and modeled isotopic data for these faunal categories range from 0.3–6.1%.

Comparing the zooarchaeological analysis of the sole later deposit (9S) with the modeled dietary contributions yields less satisfactory results. Wing et al. (2002, Table 4.4) found that 17% of the later period faunal remains were terrestrial and the remaining 83% was marine, as calculated on the basis of MNI. The 4-source model places the average distribution at 53.8% land and 46.2% marine, over 35% astray of the observed faunal values. The 5-source model also failed to produce values similar to the observed faunal breakdown, finding that 41.1% of the average diet was terrestrial and 58.9% marine. While closer, these values are still 25% off of the observed faunal values. Grouping the faunal data in a manner equivalent to the 5-source mode fails to improve the situation, as while Wing and colleagues found that the late deposit consisted of 17% land animals, 51% inshore/intertidal, and 32% reef/pelagic, the 5-source model predicted average dietary proportions of 41.1%, 28.2%, and 30.7%, respectively. The differences between the zooarchaeological and modeled isotopic data for these faunal categories range from 1.3–24.1%. It should be noted that some of these discrepancies could be a result of the fact that the zooarchaeological data for the later period are based on the analysis of just one deposit, which may not be representative of general late period diet.

The differences between dietary reconstructions based on the two classes of data (isotopes versus faunal remains) may result from a

number of factors. First, the two lines of evidence may represent different averaging periods for local diet. Second, preservation and/or recovery biases differentially affect different kinds of zooarchaeological remains (e.g. fish versus mammal bone or bony animals versus invertebrates), which may distort reconstructions of the contributions of fauna from different niches. Finally, the extremely robust and heavy diagnostic remains of certain classes of fish (e.g. parrotfish or pufferfish) may skew results such that those species are overrepresented in reconstructions based on MNI and/or weight.

#### 4.8. Correlations

Considering first the relationship between model inputs (in particular consumer isotope data) and model results for the 4-source model, we found a number of significant correlations, most of which were intuitive. For example,  $\delta^{13}\text{C}_{\text{ap}}$  was positively correlated with  $\text{C}_4/\text{CAM}$  consumption ( $r = 0.87$ ,  $df = 22$ ,  $p < 0.01$ ) and negatively correlated with  $\text{C}_3$  plant consumption ( $r = -0.64$ ,  $df = 22$ ,  $p < 0.01$ ) while  $\Delta^{13}\text{C}_{\text{ap-co}}$  was positively correlated with  $\text{C}_4/\text{CAM}$  consumption ( $r = 0.68$ ,  $df = 22$ ,  $p < 0.01$ ). These are all easily understood given the carbon isotope dissimilarity of  $\text{C}_3$  ( $-25.5 \pm 1.7\text{‰}$ ) and  $\text{C}_4/\text{CAM}$  plants ( $-10.4 \pm 1.3\text{‰}$ ). Furthermore,  $\delta^{13}\text{C}_{\text{co}}$  was significantly positively correlated with modeled marine animal contribution ( $r = 0.55$ ,  $df = 22$ ,  $p < 0.01$ ), which again can be seen as a consequence of the substantial enrichment of marine animals in  $^{13}\text{C}$  as compared with their terrestrial counterparts. It is noteworthy, however, that there was no equivalent negative correlation of any significance between  $\delta^{13}\text{C}_{\text{co}}$  and land animal consumption ( $r = 0.03$ ,  $df = 22$ ,  $p = 0.9$ ). Confusingly, while  $\delta^{15}\text{N}_{\text{co}}$  was significantly negatively correlated with modeled  $\text{C}_3$  plant consumption ( $r = -0.55$ ,  $df = 22$ ,  $p < 0.01$ ), there were only non-significant correlations with modeled land ( $r = 0.47$ ,  $df = 22$ ,  $p = 0.03$ ) and marine animal contributions ( $r = 0.06$ ,  $df = 22$ ,  $p = 0.78$ ). That the correlation with land animal consumption was positive is, by itself, noteworthy, given that the land taxa have lower  $\delta^{15}\text{N}$  values than their marine equivalents.

The observed relationships between consumer isotope values and the results of the 5-source model also were broadly intuitive. As above,  $\delta^{13}\text{C}_{\text{ap}}$  was positively correlated with  $\text{C}_4/\text{CAM}$  consumption ( $r = 0.98$ ,  $df = 22$ ,  $p < 0.01$ ) and negatively correlated with  $\text{C}_3$  plant consumption ( $r = -0.86$ ,  $df = 22$ ,  $p < 0.01$ ) while  $\Delta^{13}\text{C}_{\text{ap-co}}$  was positively correlated with  $\text{C}_4/\text{CAM}$  consumption ( $r = 0.64$ ,  $df = 22$ ,  $p < 0.01$ ).  $\delta^{13}\text{C}_{\text{co}}$  was significantly positively correlated with the modeled contributions of both intertidal/inshore marine ( $r = 0.46$ ,  $df = 22$ ,  $p = 0.03$ ) and reef/pelagic marine animals ( $r = 0.83$ ,  $df = 22$ ,  $p < 0.01$ ), but was not again, significantly negatively correlated with modeled land animal consumption ( $r = -0.30$ ,  $df = 22$ ,  $p = 0.18$ ). Finally,  $\delta^{15}\text{N}_{\text{co}}$  was significantly positively correlated with the consumption of intertidal/inshore marine animals ( $r = 0.75$ ,  $df = 22$ ,  $p < 0.01$ ), a testament to the enriched  $\delta^{15}\text{N}$  of these marine taxa, but was also positively correlated, albeit not significantly, with modeled land animal consumption ( $r = 0.20$ ,  $df = 22$ ,  $p = 0.37$ ).

Finally, comparisons of the outputs of the two models showed some generally similar trends, particular in modeled patterns of plant consumption. To begin with, the modeled plant contributions of both models were significantly positively correlated ( $r = 0.54$ ,  $df = 22$ ,  $p = 0.01$ ), as were the modeled  $\text{C}_3$  ( $r = 0.69$ ,  $df = 22$ ,  $p < 0.01$ ) and  $\text{C}_4/\text{CAM}$  ( $r = 0.85$ ,  $df = 22$ ,  $p < 0.01$ ) contributions of the two different models. In terms of animal consumption, however, the models showed no significant correlations in terms of their respective determinations of land animal consumption ( $r = 0.02$ ,  $df = 22$ ,  $p = 0.93$ ), nor were there significant relationships between the modeled marine consumption of the 4-source model and either the intertidal/inshore ( $r = 0.26$ ,  $df = 22$ ,  $p = 0.24$ ) or reef/pelagic categories ( $r = 0.47$ ,  $df = 22$ ,  $p = 0.03$ ) of the 5-source run, although the latter was tantalizingly close to significant.

## 5. Discussion

Comparing the 4- and 5-source models, three points merit specific consideration. First, there is a high degree of correspondence between the results of the two models in terms of the estimated relative contributions of plant and animal foods, and within the plant food category between  $C_3$  and  $C_4$ /CAM plants. Second, in terms of animal food consumption, although the two models produced slightly different estimations of the contribution of land animals to diets, the differences were not statistically significant. Third, the associated errors in outputs are broadly similar between the two models, while the 5-source model generated somewhat smaller ranges of contributions from the different food sources than the 4-source model. Considering these patterns, and the fact that the more complex 5-source model is likely more realistic and permits incorporation of a greater number of food sources, we tentatively suggest that this model is preferable, although the decision of which model is more appropriate should be based on the nature of the research question and the quality and quantity of available foodweb isotope data.

As previously stated, one of the most obvious benefits of these models is that they permit detailed explorations of intra-population variation and direct quantitative comparisons between individual diets. This is illustrated in Fig. 4, which displays the individual food-group estimates of the 4-source model for two individuals (L1 and L2) with distinct dietary patterns.

Despite the observed variance in estimated percentages of different foodstuffs (i.e. considering not just the mean results but the associated standard deviations and ranges), we can still make some statements about diet that are interpretively meaningful. For example, based on both models, for all of the analyzed individuals,  $C_3$  plants made larger

contributions to diet than  $C_4$ /CAM plants. Based on the 4-source model, land animals made larger contributions than marine animals for the majority of individuals ( $n = 16$ ; 73%). Based on the 5-source model, the trend is reversed and for all individuals the mean estimated contribution of marine animals exceeds that of land animals, however, when focusing on the error ranges as opposed to the mean estimates, the proportions are very similar and overlap substantially. This suggests that the differences in the relative contributions of land versus marine animals for the Tutu population as a whole were not very large.

Turning to the implications of these results for current debates in Caribbean archaeology, a few interesting patterns emerge. First,  $C_4$ /CAM foods are consistently present in Tutu diet, with all individuals appearing to consume at least some  $C_4$ /CAM plants, but with no indication that these were major important staple crops (maximum individual value for 22.7% for simple model, 14.2% for middle model). It must be noted that the  $C_4$ /CAM grouping includes not only maize, but also other edible and potentially important foods such as chenopods, pineapple, cacti, and agave. This serves to further lessen the potential importance of maize, as the maximum contribution of maize to any/all individuals' diet cannot exceed that of the food group of which it is a part. Thus, the maximum estimates of  $C_4$ /CAM contribution likely overstate the importance of maize to Tutu diet. These results are of particular interest because they provide complementary evidence by which to interpret newly reported microbotanical (starch grain) data from the Caribbean which clearly indicates an early arrival and widespread distribution of maize throughout the prehistoric insular Caribbean but do not provide any indication of relative contributions or overall importance of maize to individual diets. The modeled results of our study provide probabilistic estimates indicating that despite the widespread presence of maize it remained but one component of a

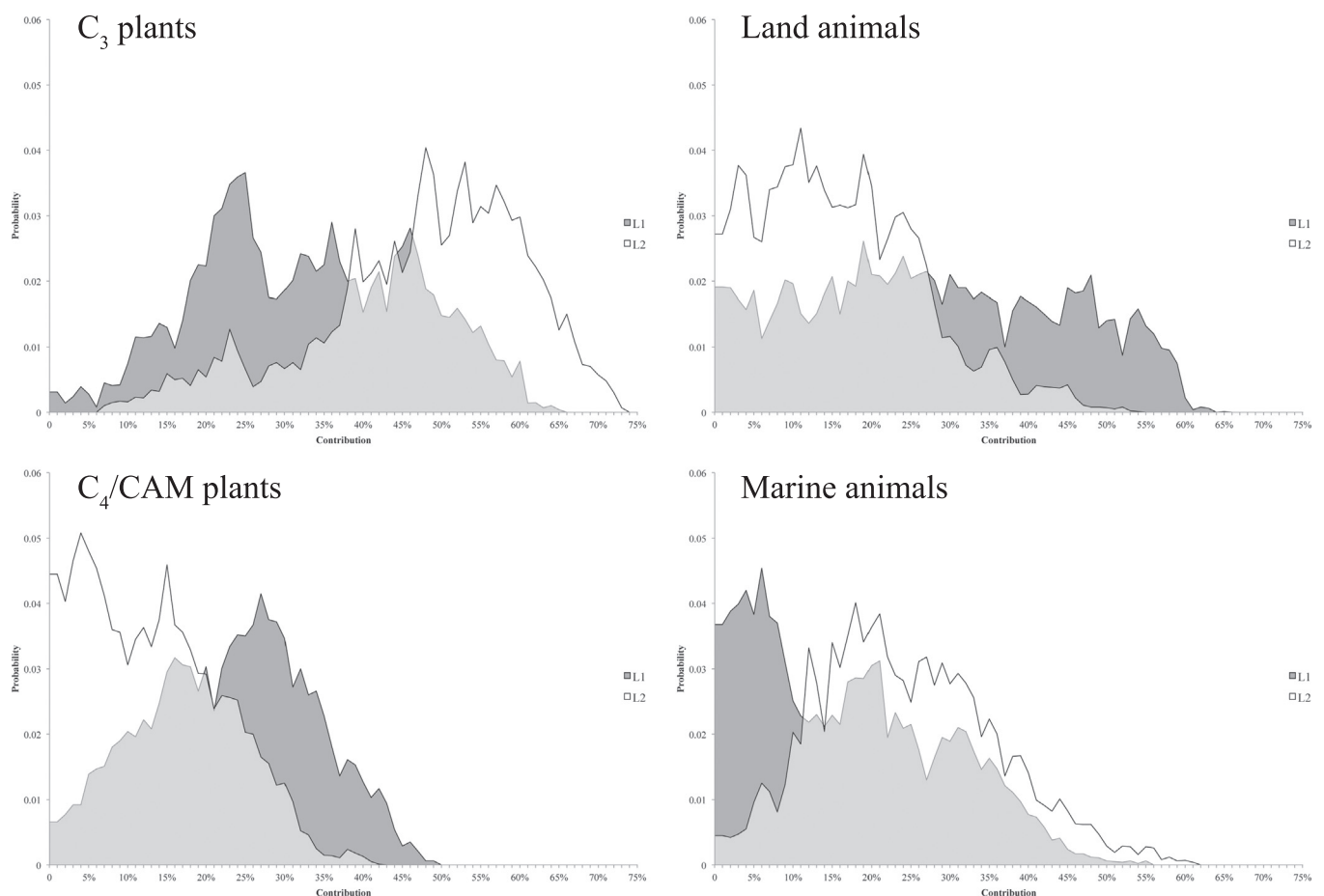


Fig. 4. Modeled output of 4-source model for individuals L1 and L2, displayed as probability distributions for each food grouping.

broader plant based subsistence that was dominated by  $C_3$  plants. The dominance of  $C_3$  plants should not be taken as prima facie evidence of the dominance of manioc, however, as just as the  $C_4$ /CAM category includes many plants that are not maize, the  $C_3$  grouping is similarly taxonomically broad, if not broader.

Second, although prehistoric Caribbean populations in general, and populations inhabiting the smaller Antillean islands in particular, are often characterized as marine-oriented or highly reliant on marine resources (Stokes, 1998), based on the modeled results presented here, land animal foods were also very important food resources and may have contributed as much or more to overall diets for the Tutu population. Recall that in the 4-source model, land animals accounted for  $21.1 \pm 14.4\%$  of diet versus  $17.6 \pm 10.4\%$  for marine animals, and that for the 5-source model, land animals ( $16.4 \pm 13.1\%$ ) were not significantly less important than marine animals ( $23.5 \pm 12.7\%$ ). This is particularly notable for a small island such as St. Thomas, which, like many Antillean islands, is considered impoverished in medium and large terrestrial fauna (especially mammals), and highlights one of the inherent biases of regional zooarchaeological assemblages which tend to be dominated by shellfish and to a lesser extent fish remains. As shell tends to preserve far better in Caribbean climates and soil than does bone, previous reconstructions of diet that emphasize the primacy of invertebrate taxa in local diets may, in light of these isotopic data, have overestimated the dietary importance of shellfish.

Third, despite statistically significant differences in isotope values between certain demographic groups within the Tutu population, similarly significant differences were not observed among the modeled dietary outputs. This pattern may be reflective of dietary patterns in which inter-individual variation in diets were minimal owing to communally based consumption practices, although further evidence is required to explore this suggestion more rigorously. The diachronic consistency of modeled diet is similarly interesting, in part because it contradicts observed changes in zooarchaeological and human skeletal elemental (Sr/Ba) data from the site. It is possible in this case that the breadth of the food groupings and the overlap between/among them could be serving to mask some chronological variation. The application of multi-source mixing models to other well-dated stable isotope datasets from the Caribbean region should permit exploration of whether this pattern (the lack of systematic intra-population dietary variation) is manifested at larger temporal and spatial scales within the Antilles.

That significant differences in isotope signatures do not manifest uniformly as significant differences in modeled dietary inputs reflects a potential added value of a modeling approach. In essence, the use of a model such as FRUITS permits us to assess the dietary significance/meaning of observed isotopic differences in light of the reality that: a) multiple, distinct combinations of different foodstuffs can produce similar isotopic signatures, and b) that non-significantly different dietary combinations can produce significantly different isotope values. As humans chose food based on criteria other than their isotopic composition, the use of modeling allows us to evaluate whether significant variations in diet, rather than isotopes, may have existed in past study populations.

We would conclude by noting that one of the primary limitations of the proposed model(s) as currently applied is the substantial variance of the modeled output estimates. We propose that the incorporation of compound-specific isotope analyses, especially of specific essential amino acids (that by definition derive entirely from protein consumption), should generate more precise (and accurate) estimates of the relative contributions of different food sources. In summary, the continued application, development and refinement of quantitative and probabilistic models for paleodietary assessment, and improved integration with other multiple lines of relevant evidence, show great promise for elucidating human dietary patterns for the Caribbean region and beyond.

## 6. Conclusion

As the present case study from Tutu shows, multi-source mixture modeling, while subject to a range of methodological and interpretive limitations and biases, would appear to hold significant potential for the reconstruction of Caribbean paleodiet. Indeed, as the present example amply demonstrates, this method represents the best available means for quantifying individual diets, in spite of issues of poor preservation and the complexity of the region's foodweb. While confirming certain aspects of artifact/ecofact-based dietary reconstruction (e.g. the limited role of maize or the apparent importance of terrestrial protein), our analysis also revealed insights that to which other dietary proxies are not sensitive. In particular, the diachronic consistency of diet at Tutu and the dearth of significant variation among various sub-groups (as judged by age, sex, and place of origin) are findings that are both noteworthy and otherwise unobtainable. Looking forward, we would humbly suggest that multi-source mixture modeling should become part of the normal toolkit of scholars interested in the reconstruction of paleodiet in the Antilles.

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