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Human ecological impacts on islands: Exemplified by a dwarf deer (Cervidae: *Mazama* sp.) on Pedro Gonzalez Island, Pearl Island Archipelago, Pacific Panama (6.2–5.6 kya)

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ABSTRACT

The present study's primary goal is to apply analyses of stable isotopes and tooth micro- and mesowear to the question of dietary change among a mid-Holocene population of small brocket deer (Cervidae: *Mazama*) in response to anthropogenic alteration of the natural insular vegetation for approximately 450 calendar years (6060-5620 cal yr BP). The brocket deer remains were found in shell-bearing middens on Pedro González in the Pearl Island archipelago. This island is the third largest of many platform or continental islands in Pacific Panama that were periodically affected by rising post-glacial seas during Pleistocene warm periods and became hills in drowned plains during glacial periods, which were extensive on the Pacific side of the isthmus. Our study is based on pre-Columbian *Mazama* deer remains recovered from excavations in the ancient middens of Pedro González and on modern skeletons of *Mazama* deer belonging to three United States museum collections. For comparative purposes we added museum specimens of extant white-tailed deer (*Odocoileus virginianus*) of reduced size from the Florida Keys and Coiba Island (Pacific Panama). Our results show that the diets of 1) present-day white-tailed deer from Coiba and the Florida Keys and 2) the brocket deer (*Mazama*) still present on San José Island were browsers. On the other hand, as soon as Preceramic people arrived on Pedro Gonzalez ca 6000 cal yr BP, the local brocket deer's diet gradually included more and more abrasive plants in response to changes in vegetation cover related to increasing anthropogenic clearance for cultivation.

1. Introduction

Pedro González Island (14.9 km^2) is a continental or platform island in the Pearl Island Archipelago located in Panama Bay, Pacific Panama. Archaeologists began a foot survey of this island in 2007 (Cooke et al., 2007) and two years later they discovered a buried shell-bearing midden deposit lacking ceramics alongside a beach named Playa don Bernardo. This sandy beach faces north-east and gave its name to the archaeological site (Fig. 1). The most unusual finds in the earliest test pits were bones of a very small deer and of dolphins. Neither had been recorded

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before in Panamanian pre-Columbian deposits. A radiocarbon age derived from *Delphinus* carbonised bone of about 4292 cal BC (β-278902: 5330 ± 40; ^{14}C BP; calibrated with OxCal v. 4.4 (Bronk Ramsey, 2009) and IntCal20 (Reimer et al., 2020)) was consistent with the deposit's Preceramic material culture. From 2008 to 2010 further test pits attaining 4.20 m depth enlarged the archaeofaunal and artifact samples (Cooke et al., 2016a, 2021; Martín et al., 2016).

The dwarfed brocket deer arrived on Pedro González Island before the human population when San José and Pedro Gonzalez briefly formed a single large island, as sea level rose (Martín et al., 2016; Redwood, 2020). The archaeological record vouches for its immediate exploitation by humans (Pearson et al., 2020), Butchery marks, human tooth marks on bones, elements subjected to heat and fire, and bone fractures indicate that the dwarf deer excavated at Playa don Bernardo were consumed by humans (Martínez-Polanco et al., 2015). Some of the bones and antlers were also used as raw materials for fashioning artefacts such as: awls, scrapers and gorges (Martín et al., 2016; Martínez-Polanco et al., 2015).

Proteomic research established that the *Mazama* deer on Pedro Gonzalez and on San José Island in the 1940s belonged to the same historic population (Buckley et al., 2017). Formerly, attempts were made by mammalogists to assign the 20th. Century population on San José Island to a particular *Mazama* species: Kellogg (1946) to *M. permira*, Handley (1966) to *M. gouazoubira* and Rossi et al. (2010) to *M. nemorivaga* (Cuvier, 1817). But these efforts were based on observed similarities in pelage color (Handley, 1966) – an unreliable criterion – or on guesswork (Rossi et al., 2010). The most objective and acceptable method for identifying the species of the 20th century San José Island *Mazama* is comparative molecular genetics among recently collected specimens although there are conservationist restraints on this practice.

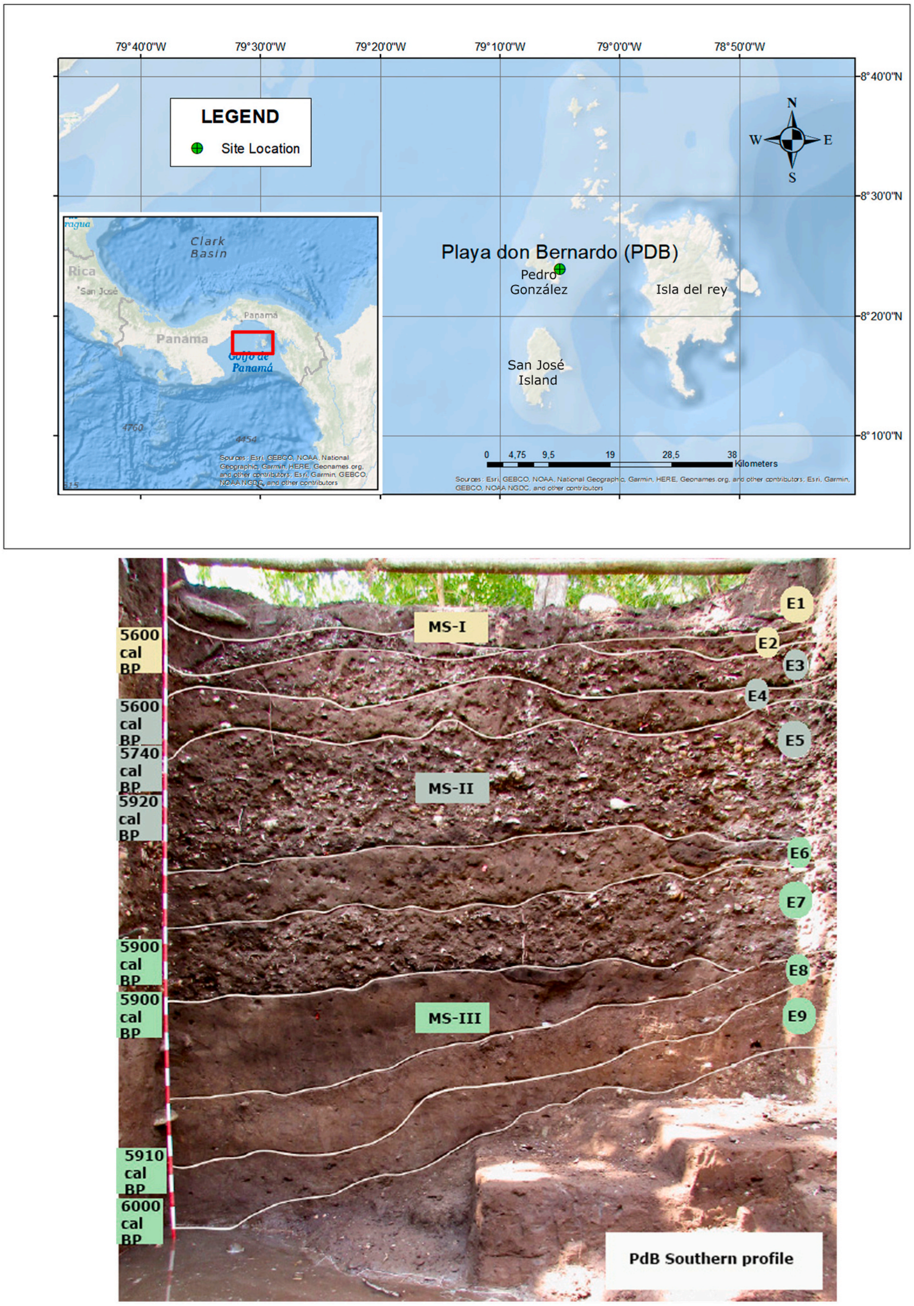

Fig. 1. Geographical location of Playa don Bernardo archaeological site, at Pedro González island, Pearl Island Archipelago, Panama. Southern profile indicating the natural strata (E1 through E9), the macrostrata (MS-I through MS-III) and the dates, Photograph: J.G. Martín personal archive.

If aDNA cannot be sequenced from Precolumbian Pearl Island brocket remains, as seems likely, the only other feasible methodology would be geometric morphometrics.

1.1. White-tailed deer (Odocoileus virginianus)

In the Americas, the most common cervid species is the white-tailed deer (*Odocoileus virginianus*; Zimmermann 1780), which is often used as a proxy for examining human-modified ecosystems in the past. This species can grow up to 50 kg in males and 35 kg in females in tropical areas (Eisenberg, 1989; Emmons, 1999; Gallina et al., 2010, 2019a; Smith, 1991). These deer are very adaptable and adjust their diet to seasonal changes, prioritizing the consumption of sprouts (Arceo et al., 2005; Ramírez Lozano, 2012; Sánchez-Rojas et al., 1997). They are widely distributed and are known to adapt their body mass and behaviour to islands as we mentioned earlier. There are two native populations of white-tailed deer in the Caribbean, one on the US Florida Keys and the other on Margarita Island in Venezuela (Heffelfinger, 2011; Molinari, 2007). These populations have long been isolated and thus evince morphological differences such as reduction in size (30–40 kg in Florida and 27–31 kg on Margarita Island) and distinctive cranial traits (Heffelfinger, 2011; Molinari, 2007). In the Panamanian Pacific, whitetails are native to the 490 km^2 island of Coiba situated 24 km off the west coast of Panama. This deer is smaller than other central American whitetails, with an average of weight of 22.5 kg (Heffelfinger, 2011).

1.2. Carbon isotopes

Carbon isotopes are a commonly used tool to indicate the types of plants that are consumed by terrestrial mammals. C_3 plants (trees, shrubs, cool/wet herbaceous and grassy vegetation) show greater depletion in heavy ^{13}C, and C_4 plants (warmer/drier grasses including maize) show greater enrichment in ^{13}C, and CAM plants (primarily succulents and xerophytes) show intermediate $^{12}C/^{13}C$ ratios (Harrison and Katzenberg, 2003; Krueguer and Sullivan, 1984). C_3 plants predominate in the Playa don Bernardo geographical area. CAM plants are uncommon as they are generally native to hot and arid environments. A few C_4 plants, such as grain amaranths, would have been available in mainland highland Panama, but the most conspicuous C_4 resource is maize (Sugiyama et al., 2020b). The white-tailed deer is well known for its predilection for feeding in fields where maize is grown, and the presence and intensity of crops can be determined through isotopic signals on archaeological deer bones and teeth (Barrera-Bassols and Toledo, 2005; Götz, 2014; Linares, 1976; Mateus-Gutiérrez and López-Arévalo, 2020; Pohl, 1990; Retana-Guiascón and Padilla Paz, 2018). In Mayan areas, several researchers have used stable isotope signals of carbon, nitrogen, oxygen and strontium to study ancient deer populations (Carr, 1996; Emery et al., 2000; Emery and Thornton, 2008; Freiwald et al., 2019; Rivera-Araya and Pilaar Birch, 2018; Sharpe et al., 2018; Sugiyama et al., 2018; Thornton, 2011; White et al., 2001, 2004). In particular, carbon isotopes reflect different degrees of anthropogenic impact and can be identified through the relative frequency of C_3 and C_4 resources; "wild" animals have C_3 diets, those that occasionally feed in fields have mixed C_3 and C_4 diets, and it is likely those with C_4 diets were fed maize (White et al., 2004). At Panamanian archaeological sites such as Cerro Mangote, Sitio Sierra and Cerro Juan Díaz, the consumption of maize by deer has been observed with different intensities, even at Cerro Mangote, a Late Preceramic site (7900-4600 cal BP) where the maize variety grown was initially poorly developed (Sugiyama et al., 2020a, 2020b).

1.3. Dental microwear and mesowear

Analyses of microwear and mesowear allow different kinds of dietary inferences. Mesowear reflects the physical characteristics of the plants that the animals consume, which are visible on the occlusal relief and overall shape of the molar cusps (Ackermans et al., 2020; Fortelius and Solounias, 2000). Browser diets show little abrasion and molars are characterized by sharp buccal cusp apices. Conversely, grazers have abrasive diets and they also ingest grit. Thus, their molars have more rounded and blunt apices. Mesowear results from attrition and abrasion over a long period of time, and reflects the annual diet of an animal (Amano et al., 2016; Fortelius and Solounias, 2000; Rivals et al., 2013). Cusp sharpness varies with age. Young individuals that have not yet developed substantial wear facets have sharp cusps, whereas dentally senescent individuals have well-worn cusps. However, for intermediate age groups, mesowear is less sensitive to age and more strongly related to diet (Rivals et al., 2007).

Microwear distinguishes among browsers, grazers, and mixed feeders (Solounias and Semprebon, 2002). Since hardness and abrasiveness of plant species and their component parts vary, distinct patterns are etched into the tooth enamel in the form of microscopic pits and scratches (Solounias and Semprebon, 2002). Patterns are produced quickly and are continuously erased and overwritten. Consequently, they indicate the type of diet during the last days or weeks before an individual's death (Grine, 1986). In addition, paleoenvironmental conditions, food preferences, and dietary ecology can be inferred weeks, or even days, before an animal dies (Davis and Pineda Munoz, 2016; DeSantis, 2016; Solounias and Semprebon, 2002; Xafis et al., 2017).

Microwear patterns are also sensitive to seasonal, local and individual variations in diet (Semprebon et al., 2016). This variability depends to a degree upon how long it took a death assemblage to accumulate (Rivals et al., 2009) and, by inference, how long, or at which season of the year, people lived in a given locality (Rivals and Semprebon, 2011; Rivals and Takatsuki, 2015; Sánchez-Hernández et al., 2014). In addition, microwear is capable of identifying whether archaeological assemblages are the result of a short death event, or of multiple ones over longer periods of time (Rivals et al., 2015). Taking into account that, (1) scratches in the enamel are sensitive to seasonal variation, and, (2) that each season may be associated with specific foods, it stands to reason that each season produces a specific microwear signal. The more seasonal are the mortality events, the more diverse will be the range of food and the microwear signal (Rivals et al., 2011; Rodríguez-Hidalgo et al., 2016).

The archaeological record reveals that the arrival of a human group into a new environment can have profound impacts, especially on islands' very fragile and closed ecosystems (Grayson, 2001; Rick et al., 2013). Examples include the local extinction of native fauna that may be caused by hunting or the introduction of novel predators (Anderson, 2009; Steadman et al., 2002). More serious problems arise if the colonizers are farmers who bring exotic plants with them and introduce new practices such as slash-and-burn forestry (Fitzpatrick, 2015; Fitzpatrick and Keegan, 2007; Giovas et al., 2012; Hofman and Rick, 2018; Laffoon et al., 2015; Louys et al., 2021; Takamiya, 2006).

Given that diet directly reflects the availability of plants in the environment where animals live (Evans and Pineda Munoz, 2018; Faith and Lyman, 2016), environmental changes caused by humans can be traced through the diet of dwarf deer using a methodological combination that offers a high level of resolution: stable isotope analysis, and dental mesowear and microwear (Rivals et al., 2016). Stable isotope analysis of teeth allows for understanding the first year of an animal's life while that of bone records the lifetime average (Rivera-Araya et al., 2019). On the other hand, mesowear reflects the last years in an individual's life (Ackermans et al., 2020; Fortelius and Solounias, 2000), and microwear provides a snapshot of the environment days before the animal's death (Davis and Pineda Munoz, 2016; DeSantis, 2016; Solounias and Semprebon, 2002; Xafis et al., 2017).

Since Playa don Bernardo settlers translocated maize to Pedro Gonzalez Island, one suspects that the diet of dwarfed deer would reflect this change, as has been observed in white-tailed deer in different parts of Central America and northern South America (Barrera-Bassols and

Toledo, 2005; Götz, 2014; Linares, 1976; Mateus-Gutiérrez and López-Arévalo, 2020; Pohl, 1990; Retana-Guiascón and Padilla Paz, 2018; Sugiyama et al., 2020b). However, *Mazama* tend to be ecologically narrowly focused on well-conserved forest habitats that are rarely found in disturbed areas (Bello-Gutiérrez et al., 2010; Gallina et al., 2019b; Reyna-Hurtado and Sanchez-Pinzón, 2019). Given there is no precedent study of the island *Mazama* deer from Playa don Bernardo, we do not know if their behavioral traits were similar to other white tail or *Mazama* species. For this reason, the main objective of this paper is to identify dietary changes in dwarf deer at Playa don Bernardo related to island colonization. We test whether dwarfed deer, like the white tails, could be a good proxy for identifying modified versus non-modified ecosystems. To establish a baseline as a reference for diet, we studied both extant *Odocoileus virginianus* individuals from the Florida Keys and Coiba Island and the undescribed *Mazama* species that were collected on the island of San José by US military personnel in the 1940s and were sent to various museum collections.

2. Materials and methods

2.1. The Playa don Bernardo site

Soil auger soundings indicate that the Preceramic shell-bearing midden at Playa don Bernardo covers ca. 1300 m^2. A vertical zonation into three Preceramic Macrostrata was developed based on the fact that conjoining faunal remains spanned several of the original arbitrary stratigraphic divisions (Cooke et al., 2016:739). Macrostratum I (MS-I) contains packed marine shells mixed with moderate amounts of vertebrate bone; Macrostratum II (MS-II) is a more laminated and heterogeneous unit containing irregular patches of marine shell fragments; Macrostratum III (MS-III) is edaphically quite homogeneous. It is characterised by sporadic marine shell and dense vertebrate bone in an excellent state of preservation. MS-III becomes sandier and more humid with depth (Cooke et al., 2016:739). This vertical zonation was used to study the deer remains found in excavations prior to 2015 (Martínez-Polanco et al., 2015; Sugiyama et al., 2020b).

For the analyses that follow we selected deer remains from all 2007–2010 excavation units (L-19, L-20, B-17, Cut-1) in accordance with the vertical zonation into three Macrostrata proposed by Cooke and colleagues in 2010 because this zonation allows a comparison between different occupational moments. However, another vertical zonation strategy was developed during a salvage excavation conducted in 2015 by JGM and his student assistants when Playa don Bernardo was threatened with eradication (an event that never happened). In this case, 10 cm arbitrary levels were used to compare the distribution of faunal taxa and lithic materials found in the 7 × 4 m excavation (Pearson et al., 2020).

2.2. Materials

2.2.1. Stable isotopes analysis

For bone and dentin collagen extraction, we sampled 30 elements (MS-II n = 7; MS-III n = 23) and for carbonate, 41 samples (MS-II n = 8; MS-III n = 33). When multiple samples were from the same macrostrata, the left humerus was selected to avoid re-sampling the same individual. In 12 cases, where bone, dentin, and enamel were available from the same individual, all three were sampled to reconstruct early age (enamel) versus later age (bone) isotope results. In the case of the first lower molars (m1) of young adults only non-fragmented and undamaged teeth were selected. For the humerus and mandible we selected only adult individuals.

Samples were extracted from bones and teeth, at the Institut Català de Paleoecologia Humana i Evolució Social (IPHES). Sample preparation was carried out at the Archaeology Laboratory at George Mason University and were analyzed at the Smithsonian Museum Conservation Institute Stable Isotope Mass Spectrometry Laboratory. The carbonate samples were analyzed with the FTIR-ATR at the Smithsonian Institution Museum Conservation Institute.

For a maximized evaluation of the isotope data we added the results obtained in this project to those previously published by Sugiyama and colleagues (Sugiyama et al., 2020a, 2020b). This strategy allowed us to increase the sample size, to facilitate comparison between macrostrata and to include data from MS-I. To evaluate those differences, we used a Mann–Whitney *U* test and a Mann–Whitney pairwise comparison.

2.2.2. Mesowear and microwear

2.2.2.1. Mesowear archaeological sample. For mesowear analysis, second lower molars (m2) which were not fragmented and/or damaged were selected. Due to the strong sensitivity of tooth sharpness relief to ontogenetic age in young individuals (without substantial wear facets) and in dentally senescent individuals (high wear facets), only adult (permanent) teeth with wear facets were selected because they represent an intermediate dental wear pattern (Rivals et al., 2007). Unworn (and marginally worn) teeth, extremely worn teeth, and those with broken or damaged cusp apices were omitted from mesowear analyses. After a careful revision of all teeth samples, we selected all the dental material available for the deer only from macrostrata II and III since we do not have samples from macrostratum I. We sampled 85 teeth (MS-II n = 20; MS-III n = 65).

2.2.2.2. Microwear archaeological sample. The second lower molars (m2) in an intermediate dental wear stage, which are not fragmented and/or damaged, were selected for microwear analysis. We sampled a total of 92 teeth, 57% of which were discarded because of badly preserved enamel or taphonomic defects (features with unusual morphology and size, or fresh features made during the collecting process or during storage) (King et al., 1999). All acceptable samples were from macrostratum II and III. Thus, the final sample was reduced to 40 elements (MS-II n = 15; MS-III n = 25).

2.2.2.3. Extant sample mesowear and microwear. We also sampled modern individuals from museum collections, selecting second lower molars (m2) in an intermediate dental wear stage, which were not fragmented and/or damaged. We evaluated the mesowear and microwear of *O. virginianus* from Isla Coiba in Panama (n = 6; American Museum of Natural History -AMNH-), Florida Keys (n = 12; Smithsonian National Museum of Natural History -NMNH-) and San José Island (n = 4; AMNH & NMNH).

2.3. Methods

2.3.1. Stable isotopes analysis

Bone and dental fragments were sampled as isolated items or were extracted using a diamond tip drill bit. Structural carbonate from bone, dentin, and enamel was extracted according to modified methods of Bryant et al. (1996). Fine bone/dental powder ground by agate mortar and pestle was soaked in 2–3% sodium hypochlorite (NaClO) solution overnight to remove organic components. Neutralized samples were soaked for 4 h in 1M acetic acid solution buffered with 1M calcium acetate (pH~4.5) to remove secondary carbonate phase (Garvie-Lok et al., 2004; Pellegrini and Snoeck, 2016). Dried, neutralized samples were weighed into Exetainer vials, reacted with concentrated (SG > 1.92) phosphoric acid (H_3PO_4), and analyzed on a Thermo Gas Bench II connected to a Thermo Delta V Advantage mass spectrometer. Stable isotope values are reported using standard delta notation: $\delta X = [R_{sample}/R_{standard} - 1] * 1000$, where X is the heavy isotope of interest (i.e. ^{13}C), R is the ratio of interest (i.e. $^{13}C/^{12}C$), the standard is VPDB for carbon, and values are reported as permil (‰). The $\delta^{13}C_{carbonate}$ values were calibrated against NBS-19 and LSVEC carbonate reference materials and have an error of ±0.2‰ (1σ) based on repeated measures of internal standards and samples.

Pre-treated carbonate samples were examined for diagenesis using a Thermo Nicolet 6700 Fourier-Transform Infrared bench with a DTGS detector and a Golden Gate attenuated total reflectance attachment (FTIR-ATR). We followed the Preservation Index of IRSF proposed by France et al. (2020) for well-preserved bone 2.5–4.3, dentin 3.1–4.3 and enamel 3.1–4.0. We further omitted samples with a C/P ratio <0.1 (Smith et al., 2007; Wright and Schwarcz, 1996).

Taking into account that enamel and bone experience slightly different isotopic fractionation during biomineralization, we used the values found by Warinner and Tuross (2009) to transform our values in order to compare bone and teeth directly. This experiment analyzed pigs fed with maize, and observed that the enamel apatite was enriched over bone apatite by 2.3‰ in carbon and 1.7‰ in oxygen (Warinner and Tuross, 2009). While pig diet is different from that of island deer, this kind of study does not exist in cervids and data from Warinner and Tuross (2009) is the closest approximation currently available.

2.3.2. Mesowear and microwear

2.3.2.1. Mesowear. Following Fortelius and Solounias (2000) mesowear was scored macroscopically on the buccal side of upper molars, preferably the paracone of M2, taking into account cusp shape and relief. These attributes were scaled from 0 (sharp and high cusps, mostly browsing) to 6 (blunt cusps, mostly grazing). Mesowear was scored on each specimen and then averaged for each sample (Mihlbachler et al., 2011; Rivals et al., 2013, 2017). In addition to the upper M2, we also included the lower m2 because that tooth position is more abundant in our archaeological sample (Rivals et al., 2007). Young individuals (unerupted teeth without wear facets) and old individuals (heavy worn teeth) were excluded according to Rivals et al. (2007). To evaluate differences between macrostrata, we used the student *t*-test. As some sample have small sizes a significance level assessed at p = 0.1 (Mudge et al., 2012).

2.3.2.2. Microwear. We followed the methodology proposed by Solounias and Semprebon (2002) and Semprebon et al. (2004). Microwear analysis comprised several steps: 1) selecting teeth, 2) making a mold of the occlusal surface using a material appropriate for dental impressions, such as polyvinylsiloxane, 3) making a cast using transparent epoxy. In order to observe the epoxy casts under incident light, we used a Zeiss Stemi 2000C stereomicroscope at 35 × magnification. The microwear features (pits and scratches) were quantified on the enamel bands, and on the mesiobuccal cusp of the second molar within a standard (0.4 × 0.4 mm) area by using an ocular reticle. Counting the scratches enables three dietary categories to be distinguished: browsers (numbers of scratches in the range of 0–17), grazers (numbers of scratches in the range of 17.5–29.5), and mixed feeders which present some overlapping values (Solounias and Semprebon, 2002). In this article, the R code proposed by Rivals (2019) was used to create the bivariate plots. Error bars correspond to the standard error of the mean (±1 SEM). Ellipses correspond to the Gaussian confidence ellipses ($p = 0.95$) on the centroid for the extant leaf browsers and grazers from the database of Solounias and Semprebon (2002). This is a standard significance test for levels of confidence used in microwear analysis that allows comparison between different ungulate species both extinct and extant. To evaluate differences between macrostrata, we used a Mann–Whitney *U* test and, as for mesowear, due to small sample size the significance level was set at $p = 0.1$ (Mudge et al., 2012).

3. Results

3.1. Stable isotopes analysis

We obtained 24 of the 41 samples of bone carbonates (MS-II n = 6; MS-III n = 18) (Table 1) and 12 samples of enamel carbonates (MS-II n = 2; MS-III n = 10) (Table 2) that showed FTIR-ATR values indicative of well-preserved bioapatite (see Fig. 1).

The results for the carbonates are summarized in Tables 1 and 2 and Fig. 2. These tables and the figure include data published by Sugiyama et al. (2020). In MS-II, enamel $\delta^{13}C_{carbonate}$ values average −12.8‰ and in MS-III the values average −12.5‰. For the bones, $\delta^{13}C_{carbonate}$ values average −11.4‰ in MS-I, −11.5‰ in MS-II and −12.0‰ in MS-III. These results suggest a primarily C_3 diet in all macrostrata (Fig. 2).

After applying tooth to bone offset corrections following Warinner and Tuross (2009), we found significant differences among the distributions of $\delta^{13}C_{carbonate}$ values between macrostrata ($U = 149.5$; $p = 0.0065$). Fig. 3 and Table 3 in which the tooth and bone offset corrections are presented, show two notable trends: (1) there are significant differences between the enamel $\delta^{13}C_{carbonate}$ and bone $\delta^{13}C_{carbonate}$ within each macrostratum, but (2) there are no significant differences between the enamel $\delta^{13}C_{carbonate}$ and bone $\delta^{13}C_{carbonate}$ when comparing across macrostrata. In Table 3 the Mann-Whitney pairwise comparison is presented.

Table 1

Raw values, descriptive statistics, and ATR-FTIR results of deer bone $\delta^{13}C_{carbonate}$ for the archaeological deer from Playa don Bernardo by macrostratum. Abbreviations: MS: Macrostratum; n: sample size; SD: Standard deviation; C/P: carbonate/phosphate ratio; IR-SF: infra-red splitting factor *Data from Sugiyama et al., (2020b).

MS	ID	$\delta^{13}C$ (‰, VPDB)	C/P	IR-SF
I	10-1767*	−11,1	**0,2**	**3,5**
II	9–809	−12,0	0,2	3,6
	3676	−12,4	0,2	3,5
	3569	−12,1	0,2	3,7
	3571	−11,0	0,2	3,7
	3576	−11,2	0,2	3,3
	10–139	−11,2	0,2	3,4
	9-824*	−12,1	0,2	3,4
	10-1017*	−11,1	0,2	3,3
	10-1750*	−10,0	0,3	3,5
	9-411*	−11,7	0,2	3,6
	9-445*	−11,7	0,2	3,5
	9-461*	−11,5	0,2	3,4
	Mean	**−11,5**	**0,2**	**3,5**
	SD	**0,7**	**0,0**	**0,1**
	Min.	**−12,4**	**0,2**	**3,3**
	Max.	**−10,0**	**0,3**	**3,7**
III	10–1881	−11,7	0,3	3,4
	10–2065	−11,8	0,2	3,5
	1286	−12,9	0,2	3,8
	10–265A	−11,2	0,2	3,7
	1287	−12,4	0,2	3,8
	10–510	−11,2	0,3	3,3
	199	−13,1	0,2	3,9
	1066	−13,2	0,2	3,8
	1484	−11,5	0,2	3,8
	1480	−12,1	0,2	3,4
	3624	−11,8	0,3	3,2
	3239	−11,1	0,2	3,6
	3169	−11,9	0,2	3,7
	3024	−12,3	0,3	3,3
	3168	−12,7	0,2	3,7
	3011	−11,4	0,2	3,5
	3010	−12,9	0,2	3,7
	1146	−12,4	0,2	3,7
	10-1284*	−12,1	0,3	3,3
	10-1885*	−11,4	0,2	3,5
	10-584*	−11,9	0,3	3,3
	9-223*	−11,7	0,2	3,5
	10-137*	−12,2	0,3	3,3
Mean		**−12,0**	**0,2**	**3,5**
SD		**0,6**	**0,0**	**0,2**
Min.		**−13,2**	**0,2**	**3,2**
Max.		**−11,1**	**0,3**	**3,9**

Table 2
Raw values, descriptive statistics, and ATR-FTIR results of deer enamel $\delta^{13}C_{carbonate}$ for the archaeological deer from Playa don Bernardo by macrostratum. Abbreviations: MS: Macrostratum; n: sample size; SD: Standard deviation; C/P: carbonate/phosphate ratio; IR-SF: infra-red splitting factor *Data from Sugiyama et al., (2020b).

MS	ID	$\delta^{13}C$ (‰, VPDB)	C/P	IR-SF
I	10-1001*	−13,4	0,3	3,3
II	9–515	−13,5	0,2	3,3
	9–809	−11,6	0,3	3,3
	11-842*	−12,3	0,2	3,6
	10-2229*	−11,7	0,2	3,5
	10-1812*	−11,7	0,2	3,3
	9–491A*	−13,0	0,2	3,4
	10-679*	−13,0	0,1	3,4
	10-672*	−14,4	0,2	3,3
	10-619*	−14,1	0,1	3,4
	Mean	−12,8	0,2	3,4
	SD	1,1	0,0	0,1
	Min.	−14,4	0,1	3,3
	Max.	−11,6	0,3	3,6
III	10–1881	−14,5	0,2	3,2
	10–2065	−11,9	0,2	3,2
	1286	−12,7	0,2	3,5
	10–265A	−11,5	0,2	3,3
	1287	−11,8	0,2	3,3
	10–510	−12,1	0,2	3,2
	199	−12,6	0,2	3,3
	1066	−12,5	0,2	3,4
	1484	−11,5	0,2	3,2
	1480	−12,3	0,2	3,4
	10-1807*	−12,9	0,2	3,4
	10-511*	−13,1	0,2	3,2
	10-577*	−12,0	0,2	3,4
	10-1777*	−12,9	0,1	3,5
	11-4*	−13,4	0,2	3,3
	Mean	−12,3	0,2	3,3
	SD	0,9	0,0	0,1
	Min.	−14,5	0,2	3,2
	Max.	−11,5	0,2	3,5

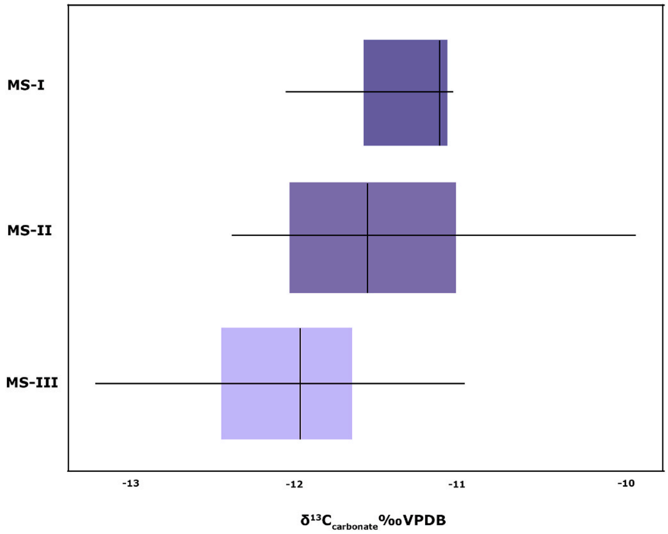

Fig. 2. Box plot of the bone $\delta^{13}C_{carbonate}$ archaeological deer from Playa don Bernardo compare by macrostratum.

3.2. Mesowear and microwear

3.2.1. Mesowear

Table 4 shows results of the mesowear analysis. The dwarf deer in MS-III present low mesowear scores indicative of a low abrasive diet (Fig. 4.a.) similar to extant browsers/fruit browsers or browse-dominated mixed feeders. Alternatively, the higher mesowear score in MS-II characterizes higher levels of abrasion (Fig. 4.b.) and a diet more akin to extant grazers or grass-dominated mixed feeders (Fig. 5). The student t-test shows that there are significant differences (90% confidence level) between the two macrostrata ($t = 1.68$; $p = 0.09$).

The two samples from Playa don Bernardo have higher mesowear values than comparative data from extant species (Fig. 5). The diet of modern *O. virginianus* diet at Isla Coiba is similar to extant browsers or browse-dominated mixed feeders while Florida Keys white-tailed deer diet is more browser like. The diet of 20th century *Mazama* from San José Island is the most browse-dominated in the samples (Table 4; Fig. 5).

3.2.2. Microwear

The number of scratches and pits is low in the two macrostrata (Table 4). The values are located in the lower part of the 95% confidence ellipse of the extant browsers (Fig. 6). Microwear analysis indicates that deer were typical browsers at the time of death. There is a significant difference (90% confidence level) in the number of scratches between the two macrostrata ($U = 127$; $p = 0.09$) and there are no differences for the pits ($U = 187$; $p = 1$) according to the Mann–Whitney U test.

All the extant (20th century) island *Odocoileus* and *Mazama* deer teeth that we studied were inferred to be browsers at the time of death since they clustered in the middle part of the ellipse. Conversely, the Playa don Bernardo *Mazama* teeth gravitate towards the lower part of the ellipse. Also, 20th century deer exhibit a greater variation in the number of the scratches than at 6000 yr old Playa don Bernardo (Fig. 6). The *O. virginianus* from Coiba and Florida Keys have in common a high variation in the number of pits (Fig. 6).

4. Discussion

4.1. The island environment, geological and faunal resources and human dietary emphases

When human groups arrived on Pedro González about 6000 years ago, they encountered an island covered with dry forests. It was depauperate in mammals. There is no archaeofaunal evidence for felids, procyonids, mustelids, canids, and peccaries. Exploited mammals were mostly small (less than 10 kg body mass): opossums (*Didelphis*), spiny rats (*Proechimys* and *Diplomys*), pacas (*Cuniculus*), capuchin monkeys (*Cebus*), squirrels (*Sciurus*), and a rabbit (*Sylvilagus*). The only deer taxon on the island was the undescribed dwarf *Mazama* species that is a primary subject of this paper. They were a top-ranked meat resource and their bones and antlers were used as raw material to make artefacts (Martín et al., 2016; Martínez-Polanco et al., 2015). Coastal and terrestrial birds were taken but not as frequently as one would expect given the present-day importance of the Pearl Islands for vast nesting colonies of cormorants (*Phalacrocorax olivaceus*), brown pelicans (*Pelecanus occidentalis*) and boobies (*Sula* spp.) (Cooke et al., 2013). Reptiles made up a surprisingly large proportion of terrestrial vertebrate diversity and biomass: marine turtles (*Eretmochelys imbricata* and *Chelonia mydas*), non-poisonous snakes (e.g., *Boa constrictor*, tiger rat snake [*Spilotes pullatus*] and puffing snake [*Phrynonax poecilonotus*]) and green iguanas (*Iguana iguana*) – all components of regular human sustenance. Marine fish from rock and coralline reefs, coastal flats, sandy beaches, and the epipelagic zone were responsible for a large proportion of the island's animal protein and fats and oil. Marine molluscs – highly selected by the islanders – increased in dietary importance as terrestrial vertebrate resources declined. Dolphins (*Tursiops truncatus* and *Delphinus delphis*) were exploited and, arguably, were scavenged on beaches rather than killed at sea (Cooke et al., 2016b, 2021; Cooke and Jiménez-Acosta, 2009; Isaza-Aizpurúa et al., 2022; Pearson et al., 2020).

The dwarf deer (*Mazama* sp.) did not radically change its diet as a direct result of human activities. Rather, subtle dietary shifts occurred between MS-III and MS-II. The minimum number of dwarf deer

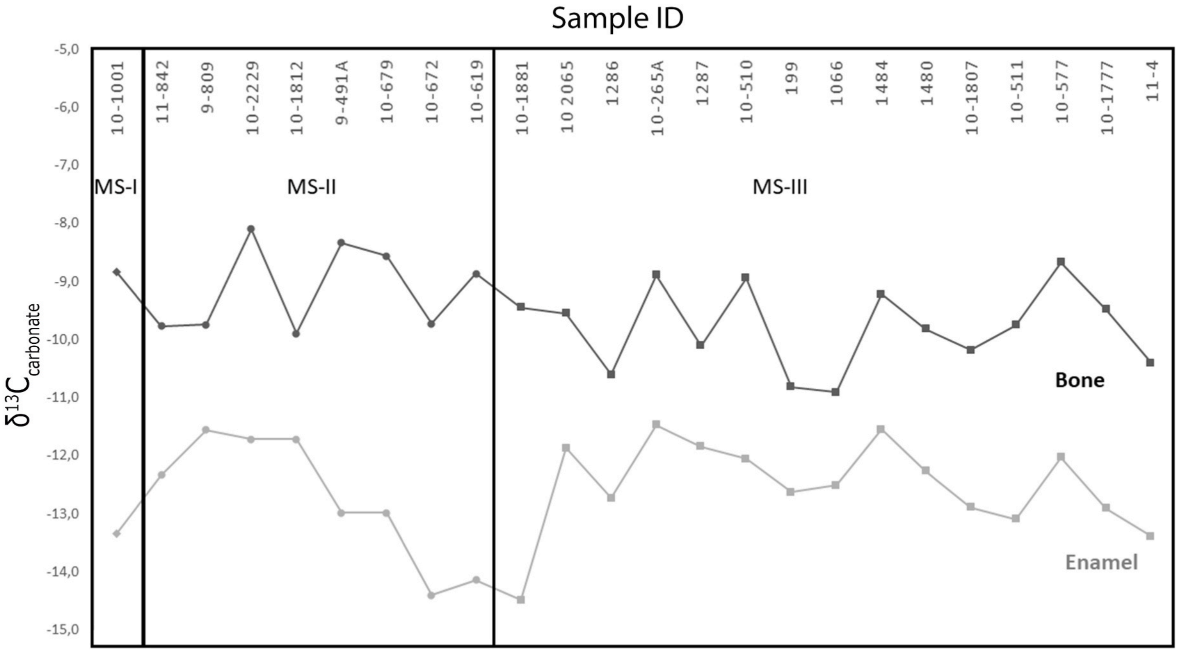

Fig. 3. Archaeological deer from Playa don Bernardo bone $\delta^{13}C_{carbonate}$ vs. deer enamel $\delta^{13}C_{carbonate}$ after bone offset corrections following Warinner and Tuross (2009), compared by macrostratum. X-axis shows sample numbers as indicated in Tables 1 and 2.

Table 3
Mann-Whitney pairwise comparison of bone $\delta^{13}C_{carbonate}$ vs. deer enamel $\delta^{13}C_{carbonate}$ p-values after bone offset corrections following Warinner and Tuross (2009) compared by macrostrata. Bold values indicate significance at $\alpha < 0.05$.

	MS-II Bone	MS-II Enamel	MS–III–Bone	MS-III Enamel
MS-II Bone				
MS-II Enamel	0.0021			
MS-III-Bone	0.0570	**0.0002**		
MS-III Enamel	**0.0002**	0.7243	**0.0000**	

Table 4
Summary of mesowear and microwear data for the archaeological deer from Playa don Bernardo by macrostratum. Abbreviations: MS: Macrostratum; n: sample size; MWS: Mesowear score; NS: Number of scratches; NP: Number of pits; M: mean; SD: Standard deviation; CV: coefficient of variation.

MS		Mesowear		Microwear		
		n	MWS	n	NS	NP
II	M	20	2.75	15	8.60	4.96
	SD		1.89		2.16	2.18
	CV		0.68		0.25	0.44
III	M	65	1.98	25	7.26	5.16
	SD		1.79		2.19	2.92
	CV		0.90		0.30	0.56
Coiba Island	M	6	1.66	6	8.83	10.41
	SD		2.06		1.29	4.27
	CV		1.24		0.14	0.41
Florida Keys	M	12	1.16	12	11.37	13.70
	SD		1.58		3.69	7.15
	CV		1.36		0.32	0.52
San José Island	M	4	0.50	4	9.87	14.12
	SD		1.29		1.73	1.43
	CV		2.58		0.17	0.10

individuals deposited in MS-III was nine, of which eight were adults (Martínez-Polanco et al., 2015). *Mazama* sp. from MS-III was "C_3 and browser type," and involved feeding on low abrasive plants, implying the existence of a forest vegetation cover on the island. Considering that microwear patterns occur rapidly and are continuously overwritten, they reflect the diet of a deer during the last days or weeks before people hunted it at Playa don Bernardo. Hence they allow inferring specific paleoenvironmental conditions, i.e, that the number of available plant shoots (generally considered to be browse) was higher during the rainy season. The microwear signal shows that the animals were browsers at the time of their death by hunting, and, by extension, it can be inferred that human occupation was at its peak during this season.

During the subsequent occupation phase (MS-II), deer MNI once again totalled nine, although there were three juveniles in this unit (Martínez-Polanco et al., 2015). Although deer diet still focused on C_3 resources, a larger number of abrasive plants such as grasses were consumed. The meso- and microwear patterns suggest an increase in the quantity of herbaceous plants that passed into the diet (Figs. 5 and 6). Although differences due to climate change cannot be totally ruled out, in this case it is more likely that human impacts had a greater effect on changes in the landscape as dwarf deer diet shows. The process reflects environmental changes related to the slashing-and-burning of the forest and to the preparation of land for cultivation. The lithic assemblage evidences that people increased consumption of plant foods through time and may have begun cultivating maize near the site (Pearson et al., 2020).

The observed environmental change apparent in MS-II also corresponds to a transition in the lithic tool industry. The introduction of agate from a local source and of novel heat treatment technology improved tool quality allowing for the production of standardized microlithic artefacts (Bustamante et al., 2021). Increasing bi-polar reduction coincided with the cultivation of tubers and small hard-shell maize and suggests that composite grater boards using agate chips may have been used for the preparation of both types of plants. This technological advancement may have precipitated the increased cutting of trees and forest cover on MS-II and MS-I (Pearson et al., 2020).

The final occupation phase (MS-I) registered only four deer, one of which was a juvenile (Martínez-Polanco et al., 2015). Isotope data continue to infer that these deer continued on a C_3-based diet. Changes in the vegetation cover also affected other species such as opossums, spiny rats, pacas, and monkeys that, like the dwarf deer, gradually disappeared from the archaeological record. An increase in shellfish consumption in MS-I with respect to the other macrostrata underlines a

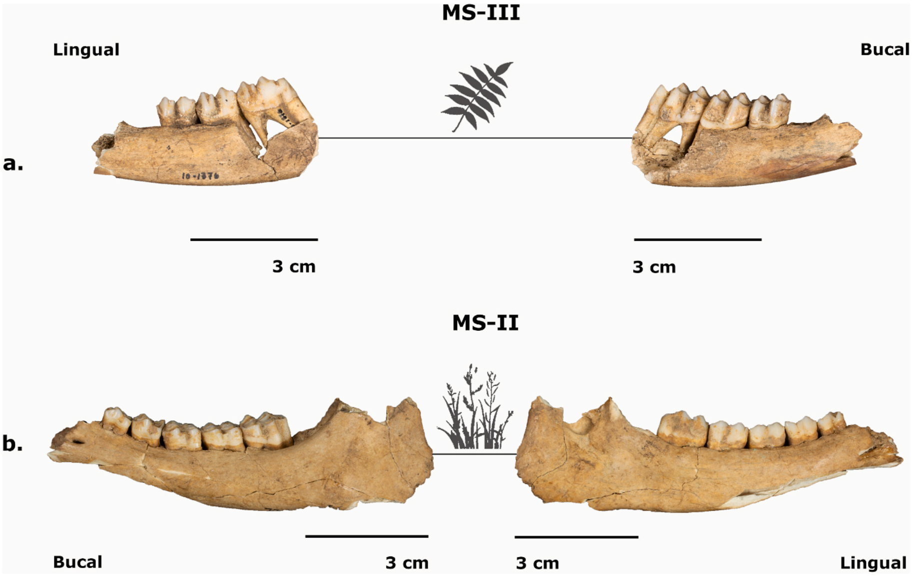

Fig. 4. Examples of different mesowear patterns. a. Right lower mandible showing low abrasive diet for Playa don Bernardo dwarf deer from MS-III and b. Left lower mandible showing high mesowear score for Playa don Bernardo dwarf deer from MS-II, indicating higher levels of abrasion.

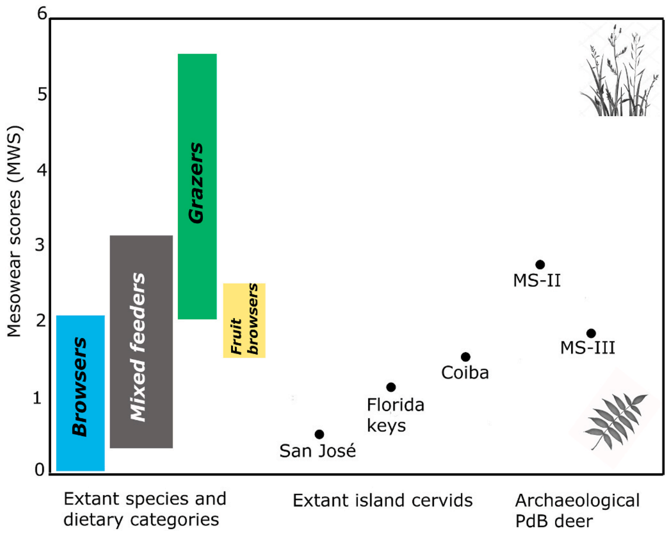

Fig. 5. Mesowear results for the archaeological deer from Playa don Bernardo MS-II and MS-III and extant island cervids, San José Island, Florida Keys and Coiba. Data on modern ungulates from Fortelius and Solounias (2000) and Rivals et al. (2013, 2017).

dietary change stimulated by vertebrate loss (Cooke et al., 2016b, 2021; Martín et al., 2016; Pearson et al., 2020).

4.2. Implications for the diet of dwarf deer from Playa don Bernardo

Cervid feeding ecology contributed to the stability of dwarf deer diet throughout Playa don Bernardo's occupation. In general, small ruminants, such as *Mazama*, are inefficient digesters of the structural components of plants (e.g., cellulose and lignin) (Gwynne and Bell, 1968; Hobbs et al., 1983). Likewise, their reduced size implies comparatively higher energy requirements (Hobbs et al., 1983). That is why small cervids prioritize consumption of tender green parts, flowers, and fruits, due to their high energy value and easy digestibility. This type of diet characterizes "concentrate feeders" and allows maximizing energy input per unit of time (Hobbs et al., 1983). This may explain why dwarf deer did not radically change their diet during human occupations at Playa don Bernardo. Studies of *M. gouazoubira* in Argentina show that the dietary importance of different plant parts shifts from season to season. Graminoids constitute a minority portion of the diet and, when they are consumed, select the apical shoots and the most tender leaves (Richard and Juliá, 2004). The Playa don Bernardo dwarf deer population did not consume fruit according to the microwear analysis, an important nutritional source for other *Mazama* species (e.g., *M. nemorivaga* Bodmer and Ward, 2006; Eisenberg, 1989; Rossi et al., 2010).

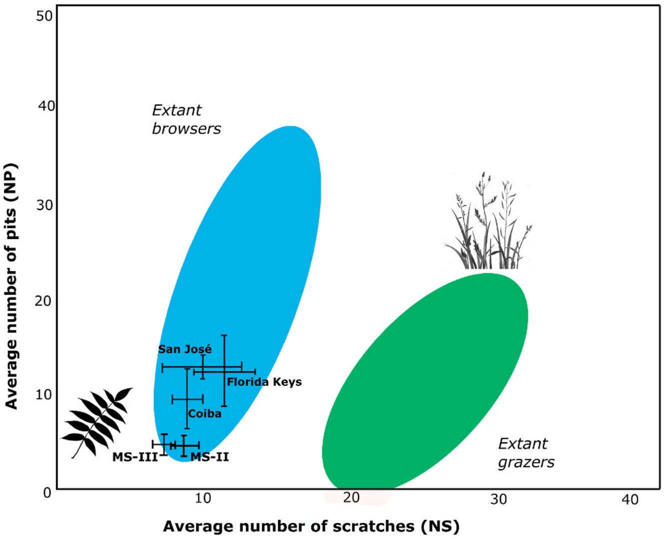

Fig. 6. Average numbers of pits and scratches in the archaeological deer from Playa don Bernardo (Playa don Bernardo) MS-II and MS-III and extant island cervids, San José Island, Florida Keys and Coiba. Error bars correspond to standard error of the mean (±1 SEM). Ellipses correspond to the Gaussian confidence ellipses ($p = 0.95$) on the centroid for the extant leaf browsers and grazers from Solounias and Semprebon (2002).

Although it is true that the sample size is small, this work illustrates certain patterns in the enamel carbon stable isotopes from both macrostrata MS-II and MS-III, which show that, at the time their teeth were mineralizing, juvenile deer consumed mostly C_3 plants. On the other hand, bone carbon stable isotopes indicate that, during later years of life, they consumed progressively larger quantities of grasses (some of them

C_4) (Fig. 3). A similar trend has been reported for Argentinian *M. gouazoubira* whose calves are hidden in dense vegetation, and around 3–4 weeks of age start their first outings with their mothers to feed in open areas (Richard and Juliá, 2004). Isotopes vary according to the portion of the plant that is consumed. It is possible that during the first week of a dwarf deer's life on Playa don Bernardo its diet included more leaves than other plant parts. Both enamel and bone carbon stable isotopes from the deer in MS-II suggest that the increasing diversity of plants they consumed may be related to alterations to forest composition induced by the ancient inhabitants of Playa don Bernardo.

The mesowear results indicate that Playa don Bernardo dwarf deer from MS-II shifted their dietary habits by consuming more abrasive plants such as grasses throughout their lives. This behaviour contrasts with that of white-tailed deer from archaeological sites in mainland Panama (Martínez-Polanco et al., 2020b) and of extant deer from Coiba Island and the Florida Keys) and *Mazama* deer from San José, which were all browsers for several years before death (Fig. 5).

If we compare the Playa don Bernardo microwear results with those of extant deer populations, it is observed that all tend to be browsers at the immediate time of death, despite occasional grazing over their total lifespan. In extant populations, a greater variation in the number of scratches could be related to the time of year at which the animals were collected. This trend is different in the case of the dwarf deer from Playa don Bernardo, where the lower variation in the number of scratches is related to the timing of specific foraging behaviour. This implies that people hunted dwarf deer seasonally and exclusively during the rainy season.

Cerro Mangote is an archaeological site whose middens are coeval with those of Playa don Bernardo. It is located on the Panamanian mainland near Parita Bay, and provides an alternate overview of an anthropologically highly disturbed environment where deer isotope values directly reflect the nature of the human occupation. People hunted and consumed white-tailed deer during the Preceramic occupation of this site and they also planted maize, an activity that increased deer populations and facilitated hunting (Martínez-Polanco et al., 2020a, 2020b; Sugiyama et al., 2020b). Isotope analyses of white-tailed deer show that they consumed C_4 plants (Sugiyama et al., 2020b), while palaeobotanical analyses reveal large-scale slash-and-burn forestry (Piperno, 2011a, 2011b; Piperno et al., 1991; Piperno and Jones, 2003). The strongly differential food preferences among *Mazama* and *Odocoileus* populations underlines the customary dietary differences between the two genera that could serve as proxies for inferring the conservation status of habitats in proximity to other archaeological sites.

To sum up, the present study has highlighted the contrasting strategies that different species of cervids employ to adapt and respond to human interventions. The white-tailed deer is a highly adaptable species with a fairly opportunistic diet, which means that it can respond quickly to rapid changes (Gallina et al., 2010; 2019a). Conversely, species of the genus *Mazama* are more focused on well-conserved forest habitats that are rarely found in disturbed areas (Bello-Gutiérrez et al., 2010; Gallina et al., 2019b; Reyna-Hurtado and Sanchez-Pinzón, 2019). These characteristics make them more vulnerable to both hunting and environmental changes, as shown by the case of preceramic Playa don Bernardo dwarf deer.

4.3. Evidence for the occupation season at Playa don Bernardo

The hypothesis that human occupation on Pedro González Island was seasonal, taking place during the wet season (April–December), has been aired in the literature (Cooke et al., 2016). The first supporting line of influence is the presence of maize starch and phytoliths. Several small grinding stones and flat bases were recovered in the Preceramic strata at Playa don Bernardo. Five were analyzed for starch grain and phytolith presence. Four grinding stones occurred in Macrostratum I in Cut L-19 (2008) and one in Macrostratum II in Cut 1 (2010). Other starches were similar to those of genera *Canna*, *Dioscorea*, *Heliconia*, and *Maranta*, all of which contain species with edible tubers. Based on these analyses, Cooke and colleagues (2016) inferred that Playa don Bernardo inhabitants cultivated plots on Pedro González Island during the wet season (April through December) (Cooke et al., 2016b).

The second and third lines of evidence supporting wet season occupation involve the presence and absence of bird species. In one of the Playa don Bernardo middens, a coracoid of the sooty shearwater (*Puffinus griseus*) was found. This species nests in the south Pacific and after breeding disperses as far as the northern Pacific. It does not normally come to land on the islands of the archipelago during its annual migrations between June and September (wet season), but canoeists could capture them resting on the sea. The Pearl Islands are well known to ornithologists for the large colonies of marine birds, which take advantage of fish abundance during dry season upwelling generated by northerly trade wind activity. Boobies (*Sula* spp.) nest from October to April, frigate birds (*Fregata magnificens*) in February and March and brown pelicans (*Pelecanus occidentalis*) between January and April (Cooke et al., 2013). Since bones of these taxa do not appear in the middens at Playa don Bernardo, the non-utilization of breeding colonies can be used as an argument to support wet season settlement as long as the rejection was not cultural (Pearson et al., 2020).

Differences between the lithic assemblage in MS-III and MS-II/MS-I suggest that different human groups may have occupied the island at different times (Pearson et al., 2020). These occupations could have occurred during the rainy season when there is high availability of plant sprouts, which is consistent with our microwear results. Taking into account that Pedro Gonzalez is located in an area where annual and multiannual climate variability is driven by the interaction of the intertropical convergence zone (ITCZ) and the El Niño Southern Oscillation (ENSO), it is possible that its occupation and abandonment patterns are related to these climatic events (Cooke et al., 2016b; Martín et al., 2016; Pearson et al., 2020).

A negative aspect of the current state of archaeological research in the Pearl Islands and in Panama east of the Canal, in general, is very irregular archaeological survey and only skeleton knowledge of Preceramic settlements notwithstanding the fact that paleo-vegetational research in the upper River Tuyra valley demonstrates slash and burn activities in eastern Darien province for 4000 years (Piperno, 1994). We simply do not know where the first settlers at Playa don Bernardo came from. The island of Pedro González is located closer to the coast of Darien (40 km) than to the coastline of Panama Bay (50–135 km), and so Darien may have been the area of origin of the ancient inhabitants of Playa don Bernardo. Survey has been very sectorized on the largest island (Isla del Rey or Terarequi (250 sq. km) (Cooke et al., 2007; Linné, 1929). This island is now heavily vegetated with intransigent xeric thorn scrub, and this would hinder further surveys. Even on 14 sq. km Pedro Gonzalez, a large sector in the southwestern side has not been investigated making the uniqueness of Playa don Bernardo questionable.

5. Conclusions

This is the first time that the diets of Neotropical cervids that inhabit, or inhabited islands have been studied using a multiproxy approach. We showed that the diets of extant *Odocoileus* and *Mazama* deer on islands are browser-based. At Playa don Bernardo on Pedro González Island the dwarf *Mazama* species consumed mostly C_3 plants, but its lifetime diet varied according to the nature and duration of contiguous human activities. Some animals' diets were opportunistically similar to those of extant grazers including on grass, but they did not include significant maize in their diets, as Panama mainland white-tailed deer do. It is possible that human occupation was most intense during the wet season. However, when human colonizers arrived on Playa don Bernardo, the dwarf deer experienced a slight change in their diet to include more abrasive plants. This may indicate an influence from vegetal cover changes related to the land being cleared for cultivation. Dwarf deer preferentially continued to utilize their preferred habitats, although they included grasses in their diets, which they would not have chosen before the human occupation.

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Author contributions

MFMP: Design of the work, acquisition, analysis and interpretation of the data and writing original draft. FR: Acquisition and interpretation of the data and revision of the manuscript. NS: Acquisition and interpretation of the data and revision of the manuscript. CAMF: Acquisition and interpretation of the data and revision of the manuscript. SACM: Data acquisition. MJA: Data acquisition. JGM: Conception of the work and revision of the manuscript. RGC: Design and conception of the work, interpretation of the data, and revision of the manuscript.

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