

# Behind white-tailed deer teeth: A micro- and mesowear analysis from three Panamanian pre-Columbian archaeological sites

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#### **Abstract**

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The white tailed-deer (Odocoileus virginianus Zimmermann 1780) is one of the largest mammals in Holocene America. It was a primary resource for pre-Columbian communities in the wooded savannas of Panama for several millennia. The oldest remains yet found refer to the Late Preceramic period (6000-4500 cal yr BP), when people were already farming (i.e. at Cerro Mangote). Deer bones, antlers, and inferentially, sinews and skins, were used for tools, ornaments, musical instruments, and furniture. A prominent role in regional (i.e., Greater Coclé) symbolism is evidenced by the frequent representation of these cervids on ceramic, gold, and bone art objects at hierarchized villages and burial grounds during the period 2300-500 cal yr BP. We infer the duration and seasonality of human-deer interactions across a region characterized climatically by ~4 month intense dry seasons, and ~8 month unpredictable wet seasons. We combine microwear and mesowear analyses of deer teeth at three pre-Columbian sites with different time spans -Cerro Mangote (AG-1) (5900-3020 cal yr BP), Sitio Sierra (AG-3) (2300-500 cal yr BP), and Cerro Juan Díaz (LS-3) (2300-400 cal yr BP)-. The two dental wear methods indicate that the white-tailed deer was a browser at these sites. The microwear results, based on the degree of variability in the numbers of microwear traits such as scratches and pits, show that white-tailed deer hunting was restricted to wet seasons at Cerro Mangote and Cerro Juan Díaz while, at Sitio Sierra, different kinds of occupational events involving white-tailed deer occurred throughout the year.

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# **Key words**

Odocoileus virginianus; microwear; mesowear; Sitio Sierra; Cerro Mangote; Cerro Juan Díaz; Panama

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#### 1. Introduction

#### 1.1 The white-tailed deer

The white-tailed deer (Odocoileus virginianus Zimmermann 1780) is one of 77 the largest extant mammals in tropical America whose body mass averages 78 50 kg for males, and 30 kg for females (Emmons, 1999). This species is 79 notably protean in its choice of habitat, being able to adapt to vegetated 80 81 deserts, savannas, prairies, mountains, and both temperate deciduous, and tropical dry and evergreen forests (Smith, 1991). Generally, the white-82 tailed deer avoids densely wooded biomes. Behaviorally, it is plastic, and 83 trophically, it is opportunistic especially in regard to its consumption of 84 human food crops. It chooses relatively nutritious and highly digestible 85 plants and plant parts, such as young leaves (Eisenberg, 1989; Smith, 86 87 1991; Teer, 1994; Arceo et al., 2005; Gallina et al., 2010). However, it also 88 feeds on grasses, sedges, nuts, fungi, fruits, and fallen flowers (Eisenberg, 1989; Smith, 1991; Gallina et al., 2010; Ramírez Lozano, 2012). 89

Habitat use by this deer species is predicated upon the quality, quantity, 90 and heterogeneity of available forage (Sánchez-Rojas et al., 1997; Gallina 91 et al., 2010; Ramírez Lozano, 2012). Diet varies among seasons due to 92 discontinuities in the availability of food, cover, and water (Sánchez-Rojas 93 et al., 1997). In high rainfall periods, a large quantity of food resources 94 95 becomes available to the deer although, paradoxically, dietary diversity may 96 be diminished at the beginning of the rains when the deer become more selective, choosing young leaves of trees, shrubs, and vines (Sánchez-Rojas 97 et al., 1997; Bello et al., 2001; 2004; Arceo et al., 2005). Dry seasons are 98 critical periods during which the deer orientate their foraging towards the 99 most nutritious fruits, and leaves trees, shrubs and herbs that are then 100 available (Sánchez-Rojas et al., 1997; Bello et al., 2001; 2004; Arceo et al., 101 102 2005).

# 1.2 Pre-Columbian targeting of white-tailed deer on the Pacific watershed of Panama

Zooarchaeological data show that the white-tailed deer was a targeted 105 mammal species across the ancient anthropogenic savannas of central 106 Pacific Panama for at least 8000 cal years (Cooke et al., 2007; 2008). It 107 merits the term "apex species," not only for its primary role in human 108 dietary well-being and in social feasting events (Martínez-Polanco and 109 Cooke, 2019), but also for affording a ready supply of raw material for 110 111 making tools and personal ornaments. In addition, after about 2300 cal yr BP, adult male white-tailed deer became prominent actors in the symbolic 112 realm of the Greater Coclé culture area being often depicted in diverse ways 113 on painted and modelled ceramic art and on goldwork (Cooke, 2004b; 114 2011; Cooke and Jiménez-Acosta, 2010).

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This paper concentrates on three pre-Columbian sites located within 15 km 116 of the active Pacific coast of Parita Bay - Cerro Mangote (AG-1), Sitio Sierra 117

(AG-3), and Cerro Juan Díaz (LS-3) (Figure 1), which is the most north-118 westerly extension of the much more extensive Panama Bay. Politically, 119 Parita Bay belongs today to the provinces of Herrera and Coclé, and, 120 geographically, it represents the north-eastern corner of the Azuero 121 Peninsula. Known in popular parlance as the dry crescent (Arco Seco), its 122 eponym (Parita) refers to the paramount chieftain who held sway over 123 several chiefdoms that abutted onto Panama Bay during the immediately 124 pre-Conquest years (1515 and 1522) (Haller, 2004; Isaza Aizpurua, 2007; 125 2013; Cooke et al., 2008). The term dry crescent refers to the fact that 126 strong north-south trade winds accentuate desiccation during the usually 4 127 to 5 month dry season in this region (Cooke et al., 2008). All over the 128 129 isthmus, wet season precipitation is heavily influenced by orography, and, in the vicinity of Parita Bay, convectional up-lift, and electric storms are less 130 pronounced than elsewhere. During the wet season (May-December), the 131 landscape is green and lush, and seasonal swamps form in low-lying areas. 132 Fresh water is provided by rivers, which rise in the central mountain range 133 (Cordillera Central), or down the north-south hilly spine of the Azuero 134 135 Peninsula. During the sunny dry season (strongest in January-April) the 136 water table falls dramatically and evapo-transpiration is very rapid. Some streams (but not the largest rivers) dry out, and vegetation cut for clearing 137 fields burns quickly (Cooke et al., 2008). By April, the landscape has 138 become brown and parched (Cooke et al., 2008). Vegetation history has 139 documented an early Holocene onset of fire-induced forest removal in the 140 central Pacific lowlands and foothills, except for gallery forests included 141 142 some tall trees (e.g. barrigón (Bombax barrigon) and higuerón (Ficus 143 spp.)), which remain lush and tall along stretches of major rivers, such as 144 the Santa María, Parita and La Villa, in whose watersheds the referred three 145 sites are located (Piperno, 2011b) (See Figure 2 a. and f.). Surviving wooded patches contain many fire-tolerant taxa that have xeromorphic 146 characteristics (i.e. microphyllous leaves, thorns, leaves, and thick bark) as 147 well as drought-adapted tree species, such as chumico (Curatella 148 149 americana), and nance (Byrsonima crassifoloia), which often occur in large 150 stands (Linares, 1977: Figure 3). This was the kind of anthropogenic environment that nurtured human-white-tailed deer symbiosis during most 151 of the Pre-Columbian Era. 152

Our objective in this article is to use microwear and mesowear analysis of teeth in order to infer the duration and seasonality (wet versus dry season) of human interactions with white-tailed deer at three Panamanian archaeological sites with different chronologies and unequal population size and density – Cerro Mangote (AG-1), Sitio Sierra (AG-3), and Cerro Juan Díaz (LS-3).

# 2. Regional setting

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160 Cerro Mangote (AG-1), Sitio Sierra (AG-3), and Cerro Juan Díaz (LS-3) are 161 now located respectively eight, 13 and four km inland from the active 162 coastline of Parita Bay in central Pacific Panama, (provinces of Coclé and 163 Herrera) (Figure 1). The Pre-Columbian landscape in the vicinity of the

three sites would not have been identical, but would have comprised 164 165 variable combinations of wooded savanna (with extensive open and/or grassy areas), dry forest remnants especially on hills, tidal flats, 166 mangroves, freshwater seasonal swamps, and mature gallery forest along 167 larger rivers (Cooke et al., 2008). Since about 6000 cal years ago, the 168 deltas of the Santa María and Parita rivers have been prograding seawards. 169 Delta formation is particularly rapid at the outlet of the Santa María because 170 of its particularly large sediment load due to its length of 145 km from its 171 source in the central cordillera, to Parita Bay (Clary et al., 1984; Weiland, 172 1984; Cooke and Ranere, 1999; Isaza Aizpurua, 2007; 2013). 173

Cerro Mangote (AG-1): is today located in Aguadulce District, Coclé 174 Province, Panama at the edge of Parita Bay, and just landward of a zone of 175 high tidal flats (Clary et al., 1984; Cooke and Ranere, 1999). It is situated 176 on the flattish summit (~48 m a.s.l) of a small hill located on the north 177 bank of the Santa María River (Figure 1). The active marine shore would 178 have been only 2 km away at the time people stopped living there on a 179 regular basis (Cooke, 1984; Cooke and Ranere, 1999). Excavations were 180 conducted by McGimsey in 1955 and by Ranere in 1979 (McGimsey, 1956; 181 182 1958; Ranere, 1979; McGimsey et al., 1986; Cooke and Ranere, 1992c). It is a small site (ca. 2250 m<sup>2</sup>) that was used exclusively as a dwelling for a 183 maximum of 2880 years (5900-3020 cal yr BP) (Table 1). The shell-bearing 184 kitchen middens spread across the hill's summit are assigned exclusively 185 to the Late Preceramic in the regional cultural sequence (McGimsey, 1956; 186 1958; Ranere, 1979; McGimsey et al., 1986; Cooke and Ranere, 1992c). 187 Burial activities, however, continued long after the abandonment of the 188 189 dwelling site, by which time pottery was in use (4425-2010 cal yr BP) (Smith-Guzmán, personal information, August 2019). Isotope proportions 190 191 (C and N) calculated from human bone collagen infer a predominantly terrestrial diet that included significant amounts of C<sub>3</sub> plants, but with input 192 from C<sub>4</sub> plants, whose source is likely to have been maize (Norr, 1995; 193 194 Cooke et al., 1996). Cerro Mangote had a small catchment area, over 195 which the mammals most frequently hunted were white-tailed deer and 196 raccoon (Procyon lotor) (whose isthmian subspecies is known to prefer 197 mangroves), green and black iguanas (Iguana iguana and Ctenosaura similis), and several bird species from marine edge, mangrove, dry forest, 198 biomes (Cooke et al., 2013a). Aquatic foods comprised and riverine 199 inshore molluscs and crabs, and almost exclusively marine fish with a clear 200 bias towards the capture of oligonaline marine catfish (Ariidae), snook 201 202 (Centropomus spp.), and toadfish (Batrachoides spp.), as well as smaller 203 sleepers (Dormitator latifrons) from inshore pools. Non-fish vertebrates provided as much dietary meat as fish (Cooke and Ranere, 1989; 1992a; 204 Cooke, 1992; Mayo and Cooke, 2005). 205

Ranere's (1979) interpretation of the stratigraphy at Cerro Mangote is that there are only two major culture-bearing zones, which he named the "Red Zone" and the "Brown Zone". During the red zone occupation, which is estimated to have lasted from ca 5900 cal yr B.P. to ca 5500 cal yr B.P., the intensity of human settlement was not sufficient to modify the natural (red clay) character of the soil development with organic matter. The more intense brown zone occupation apparently added much larger amounts of organic matter, and built up from ca 5500 B.P. to ca 4500 cal yr B.P. or whenever the first Monagrillo complex pottery entered the record (Willey and McGimsey, 1954; Ranere, 1979; Cooke and Ranere, 1992c). Table 1 presents radiocarbon data for the site and a description of each occupation zone.

Sitio Sierra (AG-3): is located 4 km south-east of La Loma village 218 (Aguadulce District, Coclé Province, Panama), on the north bank of the 219 River Santa María, and 12.5 km straight line distance from its current 220 marine outlet (Figure 1). This site was excavated by Richard Cooke from 221 1971 to 1975 (Cooke, 1979; 1984; Isaza Aizpurua, 1993; 2007). This 222 village was established by the end of the second millennium BP, and people 223 were still living there at the time of the conquest (1515-1519 CE). It 224 appears to have been occupied continually based on the unbroken ceramic 225 sequences (Cooke, 2011). There is no evidence that it was a high-ranked 226 village in a chiefdom known to be under the aegis of Escoria at Spanish 227 contact (Cooke et al., 2003; Cooke, 2011). The subsistence pattern of this 228 229 population at about 1500 cal yr BP comprised fishing (30% freshwater and 230 70% marine fish) and hunting mostly deer, iguanas, and freshwater turtles (Cooke and Ranere, 1989; Cooke et al., 1996; Cooke and Ranere, 1999; 231 Cooke et al., 2007; 2008; 2013a). Carbonized macrobotanical remains were 232 found in some quantity in houses and rubbish dumps at AG-3. Nearly 99% 233 belong to maize, and many fragments of legged maize-grinding tables 234 (metates) and grinding stones (manos) were deposited on structure floors, 235 236 and in trash heaps. Squash (Cucurbita sp.) pollen and phytoliths were 237 identified in domestic contexts. Carbonized palm nuts (Attalea butyracea) 238 were probably collected in nearby fields where these palms are usually left standing today during de-vegetation for pastures and fields (Dickau, 2005; 239 2010) (see Figure 2 c.). 240

In the 1975 excavations, two major areas were opened, and worked by décapage: Cut A and Cut B. Table 1 presents a list of the features employed for this study together with their inferred functions. In most cases, animal remains were found on in pit fills, and in refuse lenses found adjacent to houses or thrown over their living floors (Cooke, 1979:35).

246 Cerro Juan Díaz (LS-3): is located on the coastal plain bordering Parita Bay and on both banks of the tidal valley of the Parita River. The site is 247 dominated by a 42 m-high hill located in Los Santos Province (Figure 1). 248 249 Today, Cerro Juan Díaz is 4.3 Km inland from the active marine shore although, when the settlement was thriving, it would have been 0.25 - 1 250 Km closer to the coast (Cooke et al., 1998). Fieldwork was carried out by 251 an international team under Cooke's supervision from 1992 to 2001. Eleven 252 field "operations" were performed here, each one with different dimensions 253 ranging from 2 x 1 m test pits to an 800 m<sup>2</sup> décapage excavation (Cooke 254 et al., 1998; 2000). Cerro Juan Díaz is a residential-cum-mortuary site 255 (2300-400 cal yr BP), where dwelling floors, kitchen middens, and trash 256

pits, alternate with graves, many of which have multiple burials with 257 individuals treated for death in different ways (Díaz, 1999; Cooke et al., 258 2000). Residential areas, shell and bone artifact workshops (Mayo, 2004; 259 Mayo and Cooke, 2005), and several ritual zones including burials and 260 associated features, such as stone-walled ovens, were located. Also, there 261 262 is evidence for low-level modification of the hill's topography by the ancient inhabitants of the site who, for example, leveled the southern section of the 263 hill where some of the burials were placed, and which probably functioned 264 as a social or ritual space used for gatherings (Cooke et al., 1998; 2000). 265 Some grave units at Cerro Juan Díaz contained individuals buried with 266 special artifacts, such as hammered gold plaques, carefully crafted marine 267 268 shell necklaces and other personal ornaments made of marine shells, including thorny oyster (Spondylus spp.), and preforated teeh of carnivores 269 including jaguar (Panthera onca), puma (Puma concolor), and ocelot 270 (Leopardus pardalis) (Sánchez, 1995; Cooke et al., 1998; Díaz, 1999). The 271 subsistence economy of this population was mixed: marine shellfish 272 gathering; fishing in inshore waters and tidal rivers; agriculture heavily 273 274 biased towards maize; hunting emphasizing iguanas, birds, white-tailed 275 deer, and smaller terrestrial mammals (Jiménez-Acosta and Cooke, 2001; Cooke et al., 2007; 2013a; Isaza Aizpurua, 2007; Cooke and Jiménez-276 Acosta, 2008). 277

In sum, Cerro Juan Díaz presents a complex stratigraphy produced by multiple activities carried out in the same settlement over at least 1900 years (i.e., burials and associated activities, dwellings, kitchen refuse, workshops, and social and residential areas). In table 1, we present the radiocarbon dates and a brief description of the operations.

#### 3. Materials and Methods

#### **3.1 Materials**

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We selected all available white-tailed deer dental material from the three 285 sites. For mesowear analysis, we sampled 124 teeth (Cerro Juan Díaz 286 n=70; Sitio Sierra n=20; Cerro Mangote n=34). In order to perform 287 microwear analysis, 102 teeth were employed (Cerro Juan Díaz, n=57; Sitio 288 289 Sierra, n=18; Cerro Mangote, n=27). In both cases, we selected only adults, taking into account the degree of wear of the teeth, not including 290 291 the most worn ones, and also the teeth without wear. In the case of Cerro Juan Díaz, we selected teeth from operations 1, 3, 4, 5 and 31. We sampled 292 all contexts at Sitio Sierra (A3, A2-1 / A2-2, A1-1 / A1-2, B4, B3, and B2). 293 At Cerro Mangote, we focused our sample on the brown zone, which 294 295 represents the more intense occupation in the site.

#### 3.2 Methods

### 297 **3.2.2 Microwear and mesowear**

Analyses of microwear and mesowear allow different kinds of dietary inferences. Broadly speaking, microwear distinguishes among browsers, grazers, and mixed feeders (Solounias and Semprebon, 2002). Since plant species, and their component parts, vary with regard to hardness and

abrasiveness, distinct patterns are etched into the tooth enamel in the form 302 of microscopic pits and scratches (Solounias and Semprebon, 2002). 303 Patterns are produced quickly, and are continuously overwritten. 304 305 Consequently, they indicate the type of diet during the last days or weeks before an individual's death (Grine, 1986). In addition, paleoenvironmental 306 conditions, food preferences, and dietary ecology can be inferred weeks, or 307 even days, before an animal dies (Solounias and Semprebon, 2002; Davis 308 and Pineda Munoz, 2016; DeSantis, 2016; Xafis et al., 2017). 309

Microwear patterns are also sensitive to seasonal, local and individual 310 variations in diet (Semprebon et al., 2016). This variability depends to a 311 degree upon how long it took a death assemblage to accumulate (Rivals et 312 al., 2009) and, by inference, how long, or at which season of the year, 313 314 people lived in a given locality (Rivals and Semprebon, 2011; Sánchez-Hernández et al., 2014; Rivals and Takatsuki, 2015). In addition, microwear 315 is capable of identifying whether archaeological assemblages are the result 316 of a short death event, or of multiple ones over longer periods of time 317 (Rivals et al., 2015). Taking into account that, firstly, scratches in the 318 enamel are sensitive to seasonal variation, and, secondly, that each season 319 320 may be associated with specific foods, it stands to reason that that each 321 season produces a specific microwear signal. The more seasonal are the mortality events, the more diverse will be the range of food and the 322 microwear signal (Rivals et al., 2011; Rodríguez-Hidalgo et al., 2016). By 323 using the standard deviation and the coefficient of variation, analysis of 324 scratch variability permits distinguishing short or long mortality events 325 (Rivals et al., 2015). 326

On the other hand, mesowear reflects the physical characteristics of the 327 328 plants that the animals consume, which are visible on the occlusal relief and 329 overall shape of the molar cusps (Fortelius and Solounias, 2000). For example, browser diets show little abrasion and molars are characterized by 330 sharp buccal cusp apices. Conversely, grazers have abrasive diets and they 331 ingest grit. Thus, their molars have more rounded and blunt apices. To sum 332 up, mesowear results from attrition and abrasion over a long period of time, 333 and reflects the annual diet of an animal (Fortelius and Solounias, 2000; 334 Rivals et al., 2013; 2017; Amano et al., 2016). 335

Tooth mesowear: Mesowear analysis involves the observation of cusp morphology, and proceeds by describing the sharpness and the relief of molar tooth cusps (Fortelius and Solounias 2000). These attributes are scaled from 0 (more sharp) to 6 (more blunt); mesowear is scored on each specimen and then averaged for each sample (Mihlbachler et al., 2011; Rivals et al., 2013; 2017).

Tooth microwear: We follow the method proposed by Solounias and Semprebon (2002) and Semprebon et al. (2004). Microwear analysis comprises several steps: 1) selecting teeth, 2) making a mould 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 348 scratches) were quantified on the enamel bands, and on the mesiobuccal 349 cusp of the second molar within a standard (0.4 x 0.4 mm) area by using 350 an ocular reticle. Counting the scratches allows distinguishing three dietary 351 categories: browsers (numbers of scratches in the range of 0-17), grazers 352 (numbers of scratches in the range of 17.5-29.5), and mixed feeders which 353 present some overlapping values (Solounias and Semprebon, 2002). In 354 order to compare the variability of the scratches and the pits, we performed 355 a two-way variance analysis (ANOVA) without replication when the data 356 meet the assumptions to carry out the test, while, in the opposite case, we 357 performed a Kruskal-Wallis test and a Mann-Whitney pairwise test in order 358 359 to identify differences between groups. In this article, the R code proposed by Rivals (2019) was used to create the bivariate plots. 360

Scratch variability: We also quantified the variability of the number of scratches, in order to estimate the relative duration of the occupation of the sites by following Rivals et al. (2015). This tool allows to distinguish among three types of human occupations (A. Seasonal or shorter events; B. Longer- than- a- season events; C. Two separated events) according to their position on the heat map of the scratches' coefficient of variation (X-axis) and the scratches' standard variation (Y-axis).

#### 4. Results

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369 Tooth mesowear: In Table 2 we present the results of the mesowear analysis. Mesowear analysis shows very low values indicating that white-370 tailed deer diet at the archaeological sites was low in abrasiveness -- a 371 situation that is similar to that of present-day typical browsers or browse-372 dominated mixed feeders. It is likely that Cerro Mangote deer were heavier 373 browsers than those hunted at the other sites, although the difference is not 374 375 statistically significant (Figure 3). However, the Kruskal-Wallis test shows 376 that there are no significant differences between the three sites (H=0.06; p=0.96). 377

Tooth microwear: The number of scratches and pits is low in the three cases (Table 2), locating their values in the lower part of the 95% confidence ellipse in comparison to the modern browsers (Figure 4). Microwear analysis indicates that deer were typical browsers at the time of death. There is no significant difference in the number of scratches among the three sites (F=1.82; g|=2; p=0.16). However, there are significant differences in pits among the three sites (Table 1). The number of pits is highest at Sitio Sierra (H=6.06; p=0.04). Table 3 summarizes graphically the differences in pit variation among the samples from Sitio Sierra, Cerro Mangote and Cerro Juan Díaz, and shows that there no differences in the case of Cerro Mangote and Cerro Juan Díaz.

Scratch variability: Scratch variability at Cerro Mangote is low (see Figure 5) falling in Area a on the heat map, and thus corresponding to seasonal or shorter events. In the case of Cerro Juan Díaz, it is not possible clearly to distinguish scratch variability because it falls on the boundary between

areas a and b. On the other hand, scratch variation at Sitio Sierra is notably higher than at the other sites, falling in area b of the heat map, and thus indicating several events at different time of the year or events distributed over one or several years (Figure 5).

#### 5. Discussion

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This study presents mesowear and microwear analyses of white tailed deer teeth from three Panamanian pre-Columbian sites located in the so-called dry crescent of the central Pacific lowlands of the isthmus. The low scratch and pit variation in the samples from Cerro Mangote and Cerro Juan Díaz suggests that white-tailed deer were more likely to have been hunted at these sites during the rainy season (May-December) when the deer were more selective about their diet, and focused on the young leaves of particular shrub and vine taxa (Sánchez-Rojas et al., 1997; Bello et al., 2001; 2004; Arceo et al., 2005). On the other hand, at Sitio Sierra, deer were likely hunted mostly during the dry season since pits and pit variation have a higher frequency in these samples than in those from Cerro Mangote and Cerro Juan Diaz. A wide diversity of available plant species and plant parts (e.g. fruits, seeds, leaves and woody forage) from several taxa of shrubs and trees, are conducive to a more variable white-tailed deer diet during the dry months (Sánchez-Rojas et al., 1997; Bello et al., 2001; 2004; Arceo et al., 2005).

414 Martínez-Polanco and Cooke (2019) presented a detailed zooarchaeological and taphonomical study of the white-tailed deer at Sitio Sierra. They 415 describe a communal feasting event at which deer meat was consumed in 416 large quantity. Socially, holding communal feasts of this nature would have 417 been more practical and appealing between late December and late April, 418 than during the rainy and stormy months. Dry season is the time of year 419 420 when the communities of the Pacific-side Ngäbe (formerly Western Guaymí) 421 held their stick-throwing competitions - the krun (Ngäbere) or balsería (Spanish) -, which were attended by many people from dispersed hamlets 422 scattered over the landscape, and which offered great prestige to the 423 individual or kin group that had been able to accrue sufficient food and 424 fermented maize beverages - known as do kwaga in Ngäbere and chicha 425 fuerte in Panamanian Spanish) - for feeding a throng of guests (Young, 426 427 1976).

428 The Maya, whose realms were situated further north on the Central 429 American isthmus, linked the white-tailed deer to agriculture, the sun, rain, and the cyclical nature of time - features that they believed were the 430 supernatural correlates of fecundity and prosperity (Pohl, 1981; Brown, 431 2001). According to Pohl (1981) the Maya still hold feasts in mid-December 432 in the hope of a good harvest the following year, and no harvest ceremony 433 can be held until the agricultural cycle has been formally concluded. The 434 Maya situation described by Pohl lends support to the hypothesis that the 435 feasting event identified at Sitio Sierra was timed for the early dry season 436 when cobs are harvested rapidly in order to diminish weevil (Curculionidae: 437

Sitophilus zeamais) and avian attacks (e.g., in Panama's case, parrots and parakeets [Amazona, Aratinga, and Pionus spp.] (Cooke et al., 2013a)).

Cerro Mangote is a considerably older dwelling-site than Cerro Juan Diaz 440 and Sitio Sierra (likely maximum span, 7800-5500 cal yr BP), and, covering 441 2250m<sup>2</sup> 1956), its lifestyle and subsistence 442 (McGimsey, 443 understandably quite different from that of the Sitio Sierra nucleated village. The earliest Late Preceramic inhabitants of this hill-top settlement 444 consumed maize according to microbotanical data (Piperno, 2011b) -- an 445 issue discussed in greater detail below --, and two coeval rock-shelters did 446 so also. At one of these -- the Aquadulce Shelter (AG-13) --, located ca 18 447 km inland from the Parita Bay shoreline in a narrow coastal plain (Ranere 448 449 and Hansell, 1978; Piperno et al., 2000). At this site, Late Preceramic 450 cultigens included, in addition to maize, squash (Cucurbita moschata), lerén (Calathea allouia), bottle gourd (Lagenaria siceraria), arrowroot (Maranta 451 arundinacea), manioc (Manihot esculenta), and, possibly, an American yam 452 (Dioscorea sp.) (Piperno, 2011a). These domesticates would have needed 453 rain to germinate and sprout. 454

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483 484 The multi-cultigen Late Preceramic agriculture in the lands bordering Parita Bay was enhanced by palms, such as the American oil palm (Elaeis oleifera), whose easily-collected and bunched orange-red fruits provide an oil, which would have afforded an important source of calories (see Figure 2 e.). Carbonized remains of the American oil palm have only been identified at the Aquadulce Shelter among the Parita Bay sites, and they dominated the macrobotanical assemblage here during all periods, including the Late Preceramic (Dickau, 2010) -- meriting the consideration that the intensive exploitation and processing of this palm's fruits was a major wet season activity at the Aguadulce Shelter (Cooke and Ranere, 1992b). Ecologically, this makes sense since the American oil palm forms large stands in poorly drained soils, which leave the palms under water during the rainiest periods. Such habitats surround the Aquadulce Shelter today. Carbonized parts of the fruits of coyol or wine palm (Acrocomia aculeata), whose fruits have an edible mesocarp, a hard oily kernel, edible hearts, and a sap used today for making palm wine (See Figure 2 d.). Carbonized seeds of the fruits of the fire-resistant nance tree (Byrsonima crassifolia), which today is made into drinks and flavoured desserts, and would have provided an important source of vitamins in the past, were found under the shelter, too. Lastly, phytolith and pollen evidence shows that maize was used at the Cueva de los Ladrones rockshelter (LP-1) from the very bottom of its Late Preceramic occupation (7800-7630 cal yr BP) (Piperno et al., 1985; Piperno, 2011b). At this early stage of maize's evolution, of course, it would not have been as productive as varieties used at the later villages (Cooke, 1984: 283-286; Dickau, 2010: Table 2). At such an early stage of development, of course, maize would have been far less productive than varieties used at Panamanian villages until about 2300 cal yr BP (Galinat, 1980; Cooke, 1984:283-286). The discovery at El Gigante rockshelter, in Honduras, of robustly domesticated productive staple grain landraces with 10-14 rows, which were directly AMS-dated between 4,340 and 4,020 cal yr

BP (Kennett et al., 2017), suggests that the timing of the appearance in the regional diet of productive staple maize landraces has not yet been identified on the isthmus of Panama.

Archaeologists who work in Panama have discussed whether Cerro Mangote 488 was occupied preferentially during the dry season, and whether its 489 490 temporary residents participated in a seasonal round, moving from site to site and changing subsistence activities as the optimality of resources varied 491 seasonally (Piperno and Pearsall, 1998: 293; Cooke, 2005: 142). The 492 question is whether the denizens of coastal sites such as late Preceramic 493 Cerro Mangote (7800-5500 cal yr BP) and the Early Ceramic Monagrillo site 494 (4500-3200 cal yr BP) would have preferentially fished during the dry 495 months when this activity was purportedly more practical. But, there are 496 multiple issues with this supposition. Artisanal fishing practiced today 497 around Parita Bay does not offer a perfect analogy with pre-Spanish fishing 498 practices since it relies mostly on dug-out and gunwaled canoes with 499 outboard motors. Before the recent globalization of fishing practices in 500 Panama, however, modern fisherfolk often preferred to stay in port during 501 the dry season because of the strength of on-shore winds and the real 502 503 dangers of capsizing. Falling into shallow waters in Parita Bay would have 504 been dangerous in ancient times because of the threat caused by large inshore sharks, such as hammerheads (Sphyrna spp.), tiger-shark 505 (Galeocerdo cuvier) and bull-shark (Carcharhinus leucas) (Cooke et al., 506 2016). Estuary-loving American crocodiles (Crocodylus acutus) would have 507 represented another genuine threat to life in those pre-firearm days. It is 508 understandable why these afore-named marine animals were so prominent 509 510 in the painted and modelled ceramic art of the Greater Coclé semiotic 511 tradition, which materialized in the last five centuries BCE (Cooke, 2011), 512 because, on a cognitive level, these animals would have required supernatural appearement mediated by shamans (Cooke, 2004a; Cooke 513 and Jiménez-Acosta, 2010). 514

At the time of the shell-bearing middens, in which our deer samples were 515 laid down at Cerro Mangote, between 8000 and 5500 cal yr BP, fishing was 516 bimodal, comprising a focus on fish taxa whose body masses averaged 0.7 517 518 kg weight, and were likely taken in mangrove channels and tidal rivers close by the site, and a second strategy concentrating on smaller fish, such as fat 519 sleepers (Eleotridae: Dormitator latifrons), which became entrapped in 520 desiccating albina pools when the rains stopped, when they could be easily 521 have been caught by hand or with scoops (Cooke and Ranere, 1999). 522 Fishing strategies around Parita Bay had changed, however, by 4500 cal yr 523 BP (Cooke, 1992): thereafter, human consumption focused on small fish 524 525 under about 200 g live weight, which move into estuarine waters in large shoals, and are most economically trapped with inter-tidal barrier tidal traps 526 that do not require complex technology (Cooke and Tapia, 1994; Zohar and 527 Cooke, 1997; 2019). Until the last decade, when globalization caused great 528 changes in traditional fishing in Panama, a sizable proportion of catches 529 around Parita Bay was salted and wind-and-sun dried, and then exported or 530 carried to inland communities. In pre-Columbian times, salt would have 531

been most economically obtained by scraping the salt-laden dried out 532 533 surface of the albinas during dry periods, and then boiled down in clay vessels. Arguments have been made that the coast to interior movement of 534 fish was prevalent in pre-Conquest times (Carvajal-Contreras et al., 2008) 535 and it is substantiated by finds of the bones of small thread-herrings 536 (Clupeidae: Opisthonema libertate), long-fin herrings (Pristigasteridae: 537 Ilisha fuerthii) and croakers (Sciaenidae: Ophioscion typicus) in the Early 538 Ceramic middens at the Cueva de los Ladrones rock-shelter, located 20 km 539 inland (Cooke, 2001; Carvajal-Contreras et al., 2008). 540

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Dry seasons at Cerro Mangote, then, would have facilitated both drying and salting fish, and collecting sleepers in albina pools, but that does not mean that fishing was ignored during the wet months. A dry season occupation of Cerro Mangote may also have coincided temporally with trapping over-wintering shore birds, e.g., whimbrel (Numenius phaeopus), willet (Catoptrophorus semipalmatus), and small calidrid sandpipers, as well as iguana-hunting by night in the mangroves (Cooke, personal observation in mangroves near Cerro Mangote). All these taxa were reported in the middens at Cerro Mangote (Cooke et.al 2007; Cooke et al., 2013b). But, there again, arguing for rigid seasonality in this case is counter-intuitive: exploiting birds and iguanas could have been practiced by people who stayed year-round at the site. In sum, dry and wet seasons favoured different subsistence activities at Cerro Mangote, and wet season occupation is substantiated by the mass collection of the mangrove crab (Gecarcinidae: Cardisoma crassum) (Ranere, 1979; McGimsey et al., 1986). This crab species is very abundant at the beginning of the wet season (late April-June), when vast numbers congregate at the landward edges of mangroves, where they can be trapped using collective methods (Bright, 1966).

Even though the maize planted at Cerro Mangote (Norr, 1995; Dickau, 2010; Piperno, 2011a) would not have yet attained the foliage density and kernel-size of later varieties, the large number of grinding implements in the kitchen midden (some with maize phytoliths incrusted on them) is consistent with constant maize use, and the existence of nearby fields (McGimsey, 1956; Ranere, 1979; Piperno, 2011a). It is well known that crops planted in fields or garden plots increase the deer population because deer prefer second-growth vegetation, and would thus have benefitted from the disturbance of primary forest cover for opening garden plots and fields (Smith, 1991; Teer, 1994; Geist, 2000; Gallina et al., 2010; Cherry et al., 2018). It is interesting to pointed out that even the palm fruit availability in the area our results do not evidence that deer consumed it.

Lastly, as an addendum, the fact that isotope data for intensive maize consumption at Cerro Mangote (Norr, 1995; Cooke et al., 1996: 114 figure 5), which is very similar to Sitio Sierra's, would appear to be at odds with the early maize that, we argue, would have been sown in Cerro Mangote's fields or garden plots, on-going evaluation of the burials at this site by Smith-Guzmán (personal communication, August 2019) is confirming that their calibrated [INTCAL 13] <sup>14</sup>C age spans the time period between 2475

BCE and 230 CE. Therefore, Norr's published isotope estimates for high maize consumption at Cerro Mangote should correspond temporally, not to the shell-bearing middens there, but to a time-span during when largekernelled and multi-rowed productive races were likely being consumed.

At Cerro Juan Díaz, seasonality for deer hunting could not be evidenced 582 583 from the microwear analysis. Two alternatives stand out: firstly, Cerro Juan Díaz represents a village occupied all year round, and secondly, inferring 584 only wet season hunting is a sampling issue because we used samples from 585 different excavation units or "operations," which could belong to dissimilar 586 occupational events. This may explain their location on the boundary 587 between area A and B on the heat map (Figure 5). But the discovery at 588 Cerro Juan Diaz of several funerary precincts spanning at least 1800 589 590 calendar years, some of which show evidence for discrete burial groups with connotations of kinship relationships and ancestor-worship (Cooke and 591 Sánchez Herrera, 1997; Cooke et al., 1998; 2000; Díaz, 1999), argues 592 593 strongly for long-term sedentary occupation.

### 6. Conclusion

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Microwear and mesowear analyses address the issue of the times of year 595 when deer hunting was practiced at three sites bordering Parita Bay in the 596 strongly seasonal dry crescent of Pacific Panama: Cerro Mangote (AG-1), 597 598 Cerro Juan Díaz (LS-3), and Sitio Sierra (AG-3). At two sites located in two 599 different watersheds with markedly different calibrated radiocarbon ages, and very different population sizes -- Cerro Mangote and Cerro Juan Díaz --, 600 the tooth wear data infer that the ubiquitous white-tailed deer were likely 601 hunted mostly during the wet season (May to November). On the contrary, 602 results from Sitio Sierra show that white-tailed deer were hunted 603 preferentially during the early dry season (December to April) when 604 605 productive varieties of maize would have been nearing collection or already 606 harvested, and rapidly consumed during seasonal festivities evinced by our taphonomic studies. 607

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**Table captions** Table 1. Cerro Mangote (AG-1), Sitio Sierra (AG-3) and Cerro Juan Díaz (LS-3) context descriptions and dates. The dates were calibrated by using INTCAL13. Table 2. Summary of mesowear and microwear data for the archaeological white-tailed deer (Odocoileus virginianus) from Cerro Mangote (AG-1), Sitio Sierra (AG-3) and Cerro Juan Díaz (LS-3). Abbreviations: n: sample size; MWS: Mesowear score; NS: Number of scratches; NP: Number of pits; M: mean; SD: Standard deviation; CV: coefficient of variation. Table 3. Mann-Whitney pairwise pit comparison between Cerro Mangote (AG-1), Sitio Sierra (AG-3) and Cerro Juan Díaz (LS-3). 

# Table 1.

Site						Measured	
code	Context	Context description	Method	Material	Lab. Number	date <sup>1</sup>	Cal BP (2σ) <sup>2</sup>
AG-	Above red clay	Preceramic dump site	Radiometr	charcoal	Y-458d	$6810 \pm 110$	5974-5531 BCE
AG-	Red zone	Preceramic dump site	Radiometr	charcoal	β-1219	$6670 \pm 215$	6014-5215 BCE
AG- 1 AG-	Red zone	Preceramic dump site	Radiometr ic Radiometr	Protothaca	TEM-206/Beta- 1703	$6330 \pm 170$	5617-4859 BCE
1 AG-	Red zone	Preceramic dump site	ic Radiometr	Crassostrea	TEM-174	$5990 \pm 180$	5317-4488 BCE
1 AG-	Red zone	Preceramic dump site	ic Radiometr	Crassostrea	TEM-176	$5440 \pm 130$	4532-3982 BCE
1 AG-	Red zone	Preceramic dump site	ic Radiometr	Crassostrea	TEM-175 TEM-207,/Beta-	$5140 \pm 120$	4241-3666 BCE
1 AG-	Red zone	Preceramic dump site	ic Radiometr	Crassostrea	1702 TEM-208/Beta-	$4630 \pm 150$	3661-2926 BCE
1 AG-	Brown zone	Preceramic dump site	ic Radiometr	Crassostrea	1704	$3980 \pm 160$	2901-2039 BCE
1 AG-	Brown zone	Preceramic dump site	ic Radiometr	charcoal	β-1218	$3555 \pm 100$	2196-1641 BCE
3 AG-	A2-1 / A2-2	Kitchen refuse Floor of a	ic Radiometr	charcoal	I-8556	$1475 \pm 110$	335 – 770 CE 350 BCE – 209
3 AG-	B1	circularstructure Floor of a	ic Radiometr	charcoal	I-9702	$2015 \pm 80$	CE 177 BCE – 224
3 AG-	B1	circularstructure Oval domestic	ic Radiometr	charcoal	I-9703	$1975 \pm 80$	CE 21 BCE – 395
3 AG-	A1-1 / A1-2	structure Oval domestic	ic Radiometr	charcoal	CEI-9701	$1835 \pm 90$	CE
3 LS-	A1-1 / A1-2	structure	ic	charcoal	I-8613	$1715 \pm 90$	90 – 540 BCE
3 LS-	OP.1	Kitchen refuse	AMS Radiometr	Maize	TO-4594	$1470 \pm 90$	390-764 CE
3 LS-	OP.3	Kitchen refuse	ic Radiometr	charcoal	1-18679	$1730 \pm 80$	87-107 CE
3 LS-	OP.3	Kitchen refuse	ic Radiometr	charcoal	1-18222	$1370 \pm 80$	474-485 CE
3 LS-	OP.3	Kitchen refuse	ic Radiometr	charcoal	1-18287	1310±80	583-894 CE
3 LS-	OP.3	Kitchen refuse	ic Radiometr	charcoal	1-18288	1450± 80	415-694 CE
3 LS-	OP.3	Kitchen refuse	ic Radiometr	charcoal	1-18675	1330± 110	435-450 CE
3 LS-	OP.3	Kitchen refuse	ic Radiometr	charcoal	1-18672	1380± 80	433-489 CE
3 LS-	OP.3	Kitchen refuse	ic Radiometr	charcoal	1-18671	1570± 80	265-273 CE
3 LS-	OP. 4	Kitchen refuse	ic Radiometr	Charcoal Carbonized	β-121163	1260 ±90	635-976 CE
3 LS-	OP. 4	Kitchen refuse	ic Radiometr	tallo Carbonized	β-121162	1180 ±60	690-983 CE
3 LS-	OP. 4	Kitchen refuse	ic Radiometr	food Carbonized	β-121157	$1110 \pm 50$	777-1019 CE
3 LS-	OP. 4	Kitchen refuse	ic Radiometr	food	β-121156	1010 ±60	894-1162 CE
3 LS-	OP. 4	Kitchen refuse	ic Radiometr	Charcoal	β-121164	$950 \pm 60$	990-1214 CE
3 LS-	OP.31	Kitchen refuse	ic Radiometr	charcoal	1-18681	$750 \pm 80$	1049-1399 CE
3	OP.31	Kitchen refuse	ic	charcoal	1-18682	650± 110	1058-1458 CE

 $<sup>^{1}</sup>$  conventional C-14 age BP  $\pm$  1-sigma range.  $^{2}$  calibrated 2-sigma range BCE/CE.

**Table 2.** 

CITE	Mesowear			Microwear		
SITE		n	MWS	n	NS	NP
LS-3	М	70	1.17	57	11.59	7.5
	SD		1.31		2.52	4.52
	CV		1.12		0.21	0.6
AG3	M	20	0.95	18	10.75	9.61
	SD		0.82		3.12	4.11
	CV		0.86		0.29	0.42
AG-1	M	34	1.02	27	10.92	7.25
	SD		1.02		1.89	3.86
	CV		1.02		0.17	0.53

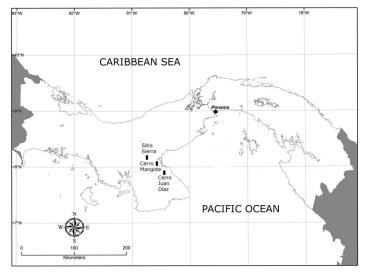
# **Table 3.**

	Sito Sierra (AG-3)	Cerro Juan Díaz (LS-3)
Cerro Juan		
Díaz (LS-3)	0.02	-
Cerro		
Mangote		
(AG-1)	0.01	0.94

## 1059 Figure captions

- 1060 Figure 1.
- 1061 Geographical location of Cerro Mangote (AG-1), Sito Sierra (AG-3) and
- 1062 Cerro Juan Díaz (LS-3) and pictures of the areas during the wet and dry
- seasons. Images Cooke's personal archive.
- 1064 **Figure 2.**
- Some examples of typical plant species of the dry crescent of the central
- 1066 Pacific lowlands of the isthmus of Panama.
- a. Barrigon (Bombax barrigon), a tall deciduous tree of the remnant gallery
- 1068 forest along the Santa María river near Sitio Sierra (AG-3). Image:
- 1069 Martínez-Polanco, M.F. April, 2015, Cocle province.
- b. Ciruelo (Spondias purpurea), a cultivated deciduous tree, which produces
- an edible fruit (hog-plum in English). Stakes of this species are planted to
- make living fences between pastures, usually reinforced with barbed wire
- 1073 fences. The juicy fruits are eaten by birds, cows, horses and humans.
- 1074 Image: Martínez-Polanco, M.F. April 2014, Cocle province.
- 1075 c. Corozo gunzo (Attalea butyracea). This palm species was planted around
- 1076 pre-Columbian settlements, and is still protected in pastures, which have
- 1077 been cleared for homogenizing forage. The fronds are much appreciated for
- 1078 roof- and wall-thatching. Image: Cooke, R. 1975, Cocle province.
- 1079 d. Wine palms (Acrocomia aculeata). Image: Dickau, R. 2005. Ancón,
- 1080 Panama City.
- 1081 e. American oil palm (*Elaeis oleifera*). Image: Dickau, R. 2005. Casita de
- 1082 Piedra, Chiriquí,
- 1083 f. Gallery woods along Santa Maria River in the late dry season. The tall
- palms are coconuts (Cocos nucifera) which were observed by the Spanish
- around Parita Bay in the early sixteenth century CE and appear to have
- 1086 been in the process of colonizing the Pacific coast of Panama. Image:
- 1087 Martínez-Polanco, M.F. April 2015, Cocle province.
- 1088 Figure 3.
- 1089 Mesowear results for the archaeological white-tailed deer (Odocoileus
- 1090 virginianus) from Cerro Mangote (AG-1), Sitio Sierra (AG-3) and Cerro Juan
- 1091 Díaz (LS-3). Data on modern ungulates from Fortelius and Solounias (2000)
- 1092 and Rivals et al. (2013, 2017).
- 1093 Figure 4.
- 1094 Bivariate plot of the average numbers of pits and scratches in the
- 1095 archaeological white-tailed deer (Odocoileus virginianus) from Cerro

Mangote (AG-1), Sitio Sierra (AG-3) and Cerro Juan Díaz (LS-3). 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). Figure 5. Heat map (boundary lines of the three regions with the error probability) and the fossil samples from Cerro Mangote (AG-1), Sitio Sierra (AG-3) and Cerro Juan Díaz (LS-3). a. Seasonal or shorter events; b. Longer than a season events; c. Separated events (data from Rivals et al. 2015). 



**DRY SEASON** 

**WET SEASON** 



Sitio Sierra AG-3



Cerro Mangote AG-1

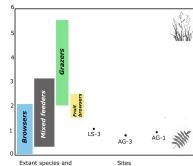


Ce LS

Cerro Juan Díaz LS-3







dietary categories

Mesowear scores (MWS)

5.0

