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ORIGINAL PAPER

Browsing into a Panamanian tropical rainforest: micro- and mesowear study of Central American red brocket deer

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Abstract

The *Mazama* genus is one of the more diverse genera among deer (Cervidae); its classification is controversial because of its complex phylogenetic relationships. The Central American red brocket deer (*Mazama temama*) is distributed from Central America to the northwest of South America. Studying the diet of mammals gives us information about the environment in which they live, considering that animals select food according to the resources available in the surrounding environment. Mesowear and microwear provide complementary data because they present direct evidence of feeding behaviour on different time scales. The use of extant animals as control samples or baselines allows for the interpretation of the results of a study performed using the archaeological record. For this reason, the aim of this paper was to study the diet of extant *M. temama* from Darien and to compare it with our previous results on ancient deer from Pedro Gonzalez Island archaeological site (6060–5620 cal yr BP) and extant individuals from San Jose Island (Panama). Evidence from the meso- and microwear analyses of *M. temama* from Darien suggests that they were browse-dominated mixed feeders during the last years of their lives and during the days before their death. There was no evidence of seasonal variation in their diets and between sexes. This paper exemplifies the potential of studying extant materials housed in museum collections as a reference to compare them to archaeological remains. The use of the same methods allows to construct baselines to better understand the archaeological record in the Neotropics.

Keywords Darien Province · *Mazama temama* · Dietary ecology · Palaeoecology

Introduction

Central American red brocket (*Mazama temama* Kerr 1792)

The *Mazama* genus includes species of small neotropical deer with simple antlers adapted for movement in environments of dense forests and closed vegetation (Eisenberg 2000). This genus is one of the most diverse genera among deer, with 10 extant recognised species. The genus *Mazama* is characterised by a rapid diversification and morphological convergences (Duarte et al. 2008; Gutiérrez et al. 2017). In the particular case of Central American brocket deer (*Mazama temama*), some authors of the twentieth century considered it a subspecies of *M. americana*; however, different cytogenetic studies demonstrated differences between them and recognised *M. temama* as a valid species (Wilson and Reeder 2005). Pinto Sandoval et al. (2022) characterised (morphologically and genetically) an extant individual of Central American

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red brocket deer from Veracruz and three from Campeche (Mexico) to complete a description of the species by proposing a neotype. The authors found that the karyotypic differences between the neotype and other specimens suggest the existence of more than one species of Central American red brocket in Mexico (Pinto Sandoval et al. 2022).

Three subspecies are currently recognised within *M. temama* using pelage coloration as the primary diagnostic character. In a recent geometric morphometrics study of Central American red brocket deer, a divergence in skull size was found between individuals from Mexico and Guatemala relative to specimens from Honduras, Nicaragua, Costa Rica and Panama. For this reason, the authors suggested that *M. t. temama* (Kerr, 1792) and *M. t. reperticia* Goldman, 1913 should remain valid names for the two morphological and ecologically differentiated groups (Escobedo-Morales et al. 2022).

Central American red brocket deer are distributed from Central America to northwest of South America—Mexico, Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama and Colombia (Eisenberg 1989; Bello-Gutiérrez et al. 2010; Sarria 2012; Gallina et al. 2019; Ramírez-Chaves et al. 2021). Central American red brockets prefer well-preserved forests sites, perennial and sub-perennial forests, cloud forests, low-dry forests and low-flooded forests. Occasionally, they have been found in transformed forests, secondary forests and croplands, although in some conservation areas, they avoid deforested sites and agricultural fields (Bello-Gutiérrez et al. 2010; Gallina et al. 2019). They are considered habitat specialists because of their preference for forests, and their presence is indicative of well-preserved ecosystems (Gallina et al. 2019). The diet of the Central American red brocket deer varies among regions and ecosystems; in the tropics, it behaves like a specialist frugivore, while in the mountain cloud forests, it behaves like a browser with a broader consumption spectrum (Weber 2005; Villarreal-Espino-Barros et al. 2008; Flores-Vazquez 2021). *Mazama temama* is listed as Data Deficient at the *IUCN Red List of Threatened Species* (Bello et al. 2016).

Dietary traits, microwear and mesowear

Studying the diet of mammals provides information about the environment in which they live, considering that animals choose their food according to the resources available in the surrounding environment (Evans and Pineda Munoz 2018). Other aspects could be determined, for example their feeding behaviours to cope with external environmental phenomena (e.g. very harsh winters or dry summers), diet preferences and other life events (Evans and Pineda Munoz 2018). Studying the diet of animals found in archaeological records, by extension, will uncover information about human palaeoecology, subsistence and behaviour (Rivals et al. 2016).

There are several approaches to studying the diet of ungulates. In extant populations, direct observation (Villarreal-Espino-Barros et al. 2008; Flores-Vazquez 2021), faecal microhistological analyses (Villarreal-Espino-Barros et al. 2008; Flores-Vazquez 2021) and stomach content analyses (Gayot et al. 2004; Weber 2005) are the most often used methods. In the case of fossil populations from palaeontological or archaeological sites, stable isotope analyses (Carr 1996; Emery et al. 2000; Rivera-Araya and Pilaar Birch 2018; Freiwald et al. 2019), dental calculus analyses (Weber and Price 2016) and tooth wear (Uno et al. 2018; Rivals et al. 2020) are useful approaches. The combination of these methods gives us more information; in particular, mesowear and microwear provide complementary data because they present direct evidence of feeding behaviour at different time scales (Rodríguez-Hidalgo et al. 2016; Sánchez-Hernández et al. 2016; Rivals and Tornero 2020). Mesowear results from attrition and abrasion over a long period of time reflects the average annual diet of an individual (Fortelius and Solounias 2000; Rivals et al. 2013; Amano et al. 2016; Ackermans et al. 2020). Microwear, due to its high turnover rate, indicates the type of diet during the last days or weeks before an individual's death (Grine 1986). In addition, palaeoenvironmental conditions, food preferences and dietary ecology can be inferred weeks or even days before an animal dies (Solounias and Semprebon 2002; Davis and Pineda Munoz 2016; DeSantis 2016; Xafis et al. 2017).

Both microwear and mesowear allow for discrimination among the three main dietary categories of herbivores, i.e. browser, grazer and mixed feeder, as defined by Hofmann and Stewart (1972). In the case of mesowear, leaf browsing herbivores have an attritive wear pattern (producing sharp molar cusps) and grazing animals with high abrasive diets have blunt molar cusps (Fortelius and Solounias 2000). Microwear has been used to differentiate the dietary categories in extant ungulates and in fossil records by studying the microscopic features visible on tooth enamel (Solounias and Semprebon 2002). The quantity of scratches and pits allows the three main categories to be distinguished. Solounias and Semprebon (2002) analysed extant ungulate populations to establish a database correlating microwear patterns and dietary traits. This database is widely used as a reference to establish dietary traits in samples with unknown diets.

Due to the high turnover rate of the microwear pattern, it has the particularity to be sensitive to seasonal, local and individual variations in diet (Rivals et al. 2015; Semprebon et al. 2016). The number of scratches is sensitive to seasonal variations and reflects seasonal changes in diet. For this reason, each season is expected to produce a specific microwear signal, particularly in scratch variability (Rivals et al. 2009, 2011; Rodríguez-Hidalgo et al. 2016). The number of scratches recorded in a population can be used to evaluate the variability and infer the time (one season or various seasons) involved. In other words, it allows for the estimation of 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 and accumulated hunted animals in a given locality (Rivals and Semprebon 2011; Rivals and Takatsuki 2015). The longer the hunting period during which the animals were killed, the more diverse the range of food and the microwear signal (Rivals et al. 2011; Rodríguez-Hidalgo et al. 2016). Microwear is capable of identifying whether archaeological assemblages are the result of a short death event (seasonal) or of multiple ones over longer periods of time (separated or successive seasons) (Rivals et al. 2015).

A source of knowledge to better understand microwear patterns and their variations in palaeontological and archaeological collections are reference collections. These are built using extant/historical individuals housed in museum collections (Solounias and Semprebon 2002; Rivals and Takatsuki 2015; Stuhlträger et al. 2021) or controlled experiments (Ward and Mainland 1999; Mainland 2003a; Winkler et al. 2021; Martin et al. 2022). The weakest point of reference collections is that they do not always have a large number of individuals from controlled populations and excellent records of age, date of death, sex and location (Rivals et al. 2016). Controlled experiments are frequent in dental microwear texture analyses (DMTA) of domestic animals (Winkler et al. 2021; Martin et al. 2022). In this kind of experimental work, the objective is to understand the role of different food items in the formation of microwear patterns on the surface of teeth (Winkler et al. 2020; Martin et al. 2022; Mihlbachler et al. 2022). In traditional microwear analyses, this approach is also used, for example to study the feeding systems of ancient agropastoral societies (Mainland 2003a, b; Gallego-Valle et al. 2020).

Microwear, mesowear and neotropical cervids

Cervids, in particular white-tailed deer (*Odocoileus virginianus*), in pre-Columbian times represented an important resource for humans across America (Berg and Bursey 2000; Stahl and Athens 2002; Emery and Kennedy Thornton 2008; Blasco Martín et al. 2019). Studying the past diet of deer explains past subsistence strategies and seasonality. At three Panamanian archaeological sites with different chronologies (Cerro Mangote 7800–4600 cal BP, Sitio Sierra 2200–500 cal BP and Cerro Juan Díaz 300 BCE–1600 CE), microwear and mesowear analyses were applied to infer the duration and seasonality (wet versus dry season) of human interactions with white-tailed deer (Martínez-Polanco et al. 2020). This approach has also been used to identify dietary changes in dwarf deer (*Mazama* sp.) at Playa don Bernardo, an island archaeological site also located in Panama (Pedro Gonzalez Island, Pearl Island Archipelago). Extant *O. virginianus* individuals from the Florida Keys and Coiba Island and individuals of the undescribed *Mazama* species that were collected on the island of San Jose were analysed to establish a baseline as a reference to reconstruct the palaeodiet of deer from archaeological sites (Martínez-Polanco et al. 2022). It is highly probable that *Mazama* sp. found on Pedro Gonzalez and San Jose islands are descendants or related to Darien (Panama-Colombia) *M. temama* populations.

The use of extant animals as control samples or baselines allows for the interpretation of the data from the archaeological record. The use of the same methodology both in archaeological and zoological collections will provide more accurate results and align with the ecological characteristics of the study area. For this reason, the aim of this paper was to study the diet of the extant *M. temama* from Darien and to compare it with our previous results of the ancient deer from the archaeological site Pedro Gonzalez Island (6060–5620 cal yr BP) and the extant individuals from San Jose Island (Panama).

Materials and methods

Study area

The province of Darien is located east of the Republic of Panama, near the border with Colombia (Fig. 1). This province is mostly covered by lowland tropical rainforests with a great diversity of fauna and flora. The province has an annual rainfall of 1700–2000 mm and an altitude ranging from 0 to 1800 m above sea level. Local temperatures vary seasonally between 17 and 35 °C. The dry season is from January to March, and the wet season is between April and December. Some Darien mammals have South American characteristics (Handley 1972).

Materials

In this research, the available dental material of Central American red brocket deer from Darien at the mammal collection of the American Museum of Natural History (AMNH) and the Smithsonian National Museum of Natural History (NMNH) were evaluated. The second lower molars (m2) in intermediate dental wear, which were not fragmented and/or damaged, were selected. The individuals included in this study were labelled *Mazama americana*, the specimens from NMNH were *M. americana reperticia* ($n=10$) and the individuals from ANHM were *M. americana temama* ($n=6$) (Anthony 1916). All of them were collected at several localities in the Province of Darien in Panama (Fig. 1; Table 1). In total, 16 individuals were studied: 9 females and 7 males. These individuals were collected between 1914 and 1964, 8 in the dry season (January to March) and 8 in the wet season (April to December). Individuals from the wet season were

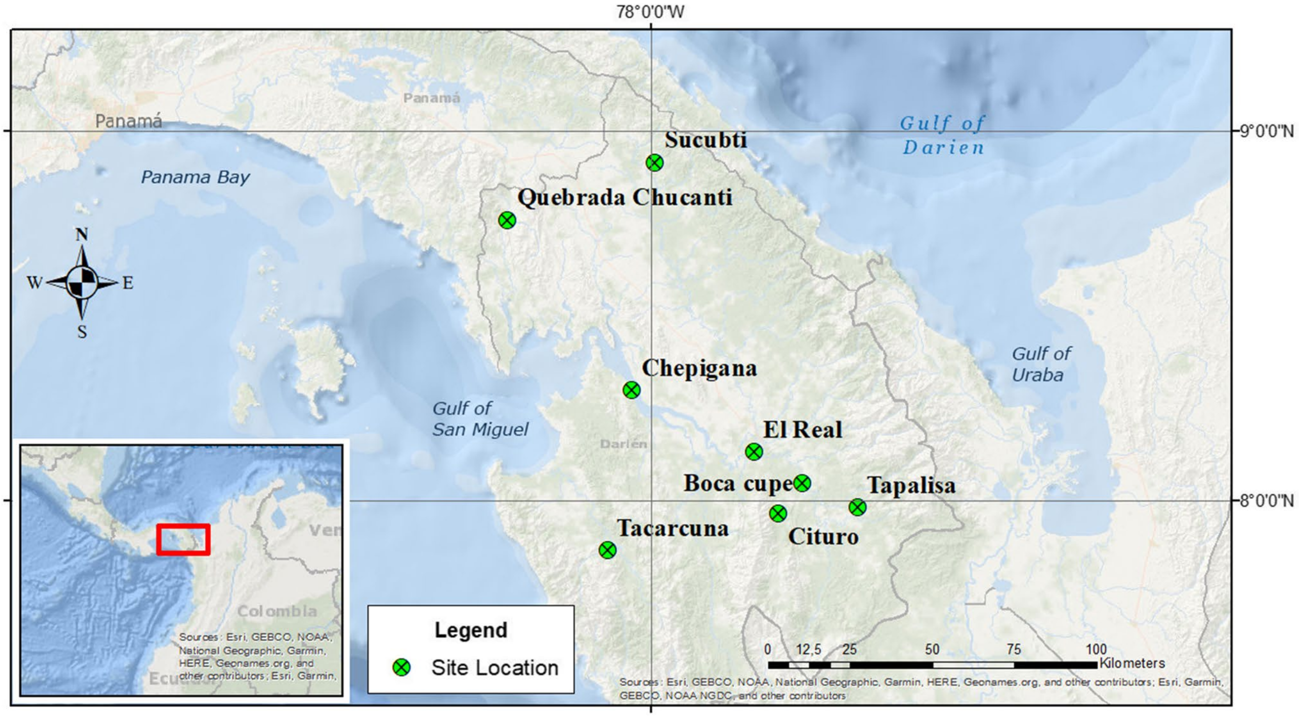

Fig. 1 Geographical location of extant Central American red brocket (*Mazama temama*) from Darien, Panama. Based on the online catalogues of the NMNH and ANHM

Table 1 Geolocation information of Central American red brocket deer (*Mazama temama*) from Darien, Panama, based on the online catalogues of the NMNH and ANHM. Abbreviations: *M* male, *F* female

Collection	ID	Season	Sex	Locality	Latitude (N)	Longitude (W)
NMNH	240435	Wet	M	Sucubti	8° 54′ 53″	77° 59′ 12″
NMNH	290887	Dry	M	Quebrada Chucanti	8° 45′ 35″	78° 23′ 23″
NMNH	310686	Dry	F	Tacarcuna	7° 52′ 03″	78° 07′ 03″
NMNH	310687	Dry	M	Tacarcuna	7° 52′ 03″	78° 07′ 03″
NMNH	310688	Wet	F	Tacarcuna	7° 52′ 03″	78° 07′ 03″
NMNH	338359	Dry	F	El Real	8° 08′ 00″	77° 43′ 00″
NMNH	338360	Dry	M	El Real	8° 08′ 00″	77° 43′ 00″
NMNH	339085	Wet	M	Tacarcuna	7° 52′ 03″	78° 07′ 03″
NMNH	339086	Wet	F	Tacarcuna	7° 52′ 03″	78° 07′ 03″
NMNH	339088	Wet	F	Tacarcuna	7° 52′ 03″	78° 07′ 03″
ANHM	38123	Dry	F	Tapalisa	7° 59′ 00″	77° 26′ 00″
ANHM	38192	Wet	F	Boca cupe	8° 03′ 00″	77° 35′ 00″
ANHM	38193	Wet	F	Cituro	7° 58′ 00″	77° 39′ 00″
ANHM	37618	Wet	M	Chepigana	8° 18′ 00″	78° 03′ 00″
ANHM	37616	Dry	M	El Real	8° 08′ 00″	77° 43′ 00″
ANHM	37615	Dry	F	El Real	8° 08′ 00″	77° 43′ 00″

collected in five different years (1914, 1915, 1954, 1958 and 1963), while those from the dry season were collected in four (1915, 1950, 1959 and 1964). In this paper, we presumed that the sampled individuals belonged to *M. temama*, and according to Escobedo-Morales et al. (2022) the subspecies is *M. t. reperticia*.

Methods

Mesowear

Mesowear analyses involve the observation of cusp morphology to evaluate the abrasiveness of food items (Fortelius and Solounias 2000). We followed the protocol of

Milhlbachler et al. (2011), in which cusp sharpness and relief were scaled from 0 (sharp cusps and high relief) to 6 (blunt surfaces). Mesowear was scored on the lower m2 of adult individuals. Young and old adults were discarded because the mesowear signal was not stable across age groups (Rivals et al. 2007). Mesowear was scored on each specimen and then averaged for each sample (Mihlbachler et al. 2011; Rivals et al. 2013, 2017). In total, we studied a sample of 16 individuals. We compared the mesowear scores between males and females using a *t*-test if the assumptions were fulfilled or an *F*-test if not.

Microwear

We followed the method proposed by Solounias and Semprebon (2002) and Semprebon et al. (2004). This method follows several steps: (1) selecting teeth; (2) making a mould of the occlusal surface using a material appropriate for high-resolution dental impressions, such as polyvinylsiloxane; (3) making a cast using transparent epoxy and (4) analysing and quantifying the microwear pattern under a stereomicroscope. 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 using an ocular reticle.

The quantification of pits and scratches allowed three dietary categories to be distinguished: browsers (number of scratches in the range of 0–17), grazers (number of scratches in the range of 17.5–29.5) and mixed feeders, which present some overlapping values (Solounias and Semprebon 2002). According to Solounias and Semprebon (2002), scratches discriminate better dietary categories than pits. This is because there is no overlap in the scratch ranges between browsers and grazers. The average number of pits, however, overlaps between browsers and grazers, especially in the lower range (less than 20 pits). For this reason, the average number of pits alone is not reliable for discriminating browsing from grazing ungulates (Solounias and Semprebon 2002). Solounias and Semprebon (2002) plotted the average number of scratches (x) and the average number of pits (y) and observed that browsers were grouped together on one side of the bivariate plot (with a low number of scratches), while the grazers were grouped on the other side (with a high number of scratches). A database was constructed based on microwear results from extant ungulate taxa, which we used as a reference (Solounias and Semprebon 2002). In this article, the R code proposed by Rivals (2019) was used to create bivariate plots. In total, we studied a sample of 13 individuals. To compare the variability of the scratches and pits, we use a *t*-test if the assumptions are fulfilled or an *F*-test if not.

There were other features that could be identified on the enamel bands: 1. Cross scratches are oriented with different directions to the majority of the scratches; 2. Large pits (LP) are double-sized pits. 3. Gouges are similar to large pits but are 2 or 3 times larger and deeper and present irregular edges. 4. The scratch textures were ranked using the scratch width score (SWS): 0 (fine scratches), 1 (mixture of fine and coarse scratches) or 2 (coarse scratches). The SWS was obtained by taking each individual value and averaging them (Solounias and Semprebon 2002; Semprebon et al. 2011). For a detailed explanation of each feature, see Solounias and Semprebon (2002). We separately recorded the qualitative characteristics of the traces (small and large pits, gouges and cross scratches).

Scratch variability

To test for the existence of a seasonal signal in the sample, we used two methods to measure variations in the microwear pattern: the coefficient of variation (CV) and the standard deviation (SD) of the number of scratches. To obtain the CV, we calculate the ratio of the standard deviation to the mean. According to Rivals et al. (2025), variability of the number of scratches is related to the duration of mortality events. In the case of archaeological studies, this period was related to the duration of human occupations when the animals were hunted. In comparison to extant reference samples, the CV and SD values allow to differentiate, from the lowest to the highest values, among short seasonal events, long-continued events and two separate short events (Rivals et al. 2015). In total, we studied a sample of 13 individuals. We used the R package cvequality (v. 0.1.3) (Marwick and Krishnamoorthy 2019) to test for significant differences in scratch values between seasons, running the modified signed likelihood ratio test (M-SLRT) for equality of CVs (Krishnamoorthy and Lee 2014).

Results

Mesowear

The mean of the mesowear scores showed low values (MWS = 1.25), signifying that the Central American red brocket deer diet at Darien was similar to that of extant browsers or browse-dominated mixed feeders (Fig. 2). In Table 2, the mesowear scores discriminated by season and genera can be observed. The results indicate a mixed feeder diet tending to be dominated by browsing in the last years of the life of the individuals (Table 2; Fig. 2). The *F*-test showed no significant differences among the mesowear scores between specimens from

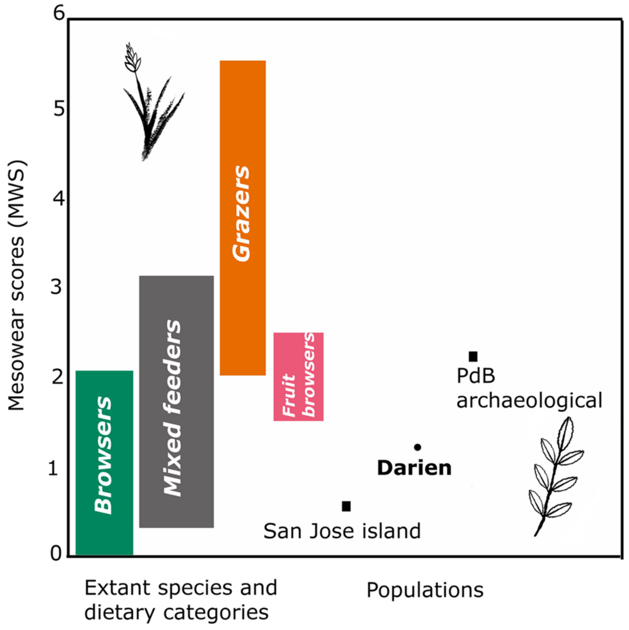

Fig. 2 Mesowear results for Central American red brocket deer (*Mazama temama*) from Darien in comparison with data on ungulates with known diet from Fortelius and Solounias (2000), Rivals et al. (2013, 2017), the ancient deer from Playa don Bernardo (PdB) and the extant deer population of San José Island, Pearl Island Archipelago, Panama (Martínez-Polanco et al. 2022)

AMNH/NHMN previously referred to as two subspecies ($F = 3.50$; $p = 0.18$) and between males and females ($F = 1.60$; $p = 0.52$). We also compared seasons, and there were no significant differences ($F = 1.84$; $p = 0.43$).

Microwear

The enamel surfaces were characterised by a microwear pattern with more or less the same number of scratches and pits (Fig. 3). We did not find evidence of individuals with cross scratches and gouges. The scratch width score (SWS) was 0.15 (Table 2). The percentage of large pits in the complete sample (dry and wet seasons) was 7.69%. When we considered only the individuals coming from the rainy season, the percentage was higher, reaching 12.50%, and large pits were absent in case of the individuals that died during the dry season. The puncture pits were absent from the total sample studied. We observed a low number of scratches and an intermediate number of pits (Table 2). The Darien sample was located in the medium part of the 95% confidence ellipse of the leaf browsers (Fig. 3). Microwear analyses indicated that deer were typical browsers at the time of death. The *F*-test showed no significant differences between specimens from AMNH/NHMN previously referred to as two subspecies (scratches: $F = 1.28$; $p = 0.85$ and pits: $F = 5.99$; $p = 0.10$) and between males and females, both in the number of scratches ($F = 2.72$; $p = 0.22$) and pits ($F = 1.06$; $p = 0.88$). We also compared seasons and did not find significant differences in the number of scratches ($F = 4.33$; $p = 0.12$) and pits ($F = 1.20$; $p = 0.85$). According to the modified signed likelihood ratio test, there were no significant differences in number of pits across seasons ($MSLRT = 0.08$; $p = 0.76$).

Plant residue

In 4 individuals of the 13 examined under the stereomicroscope (i.e. 30.76% of the total sample), identified plant residues were found. These individuals were collected in

Table 2 Summary of mesowear and microwear data of Central American red brocket deer (*Mazama temama*) from Darien, Panama. Abbreviations: *n* sample size, *MWS* mesowear score, *NS* number of scratches, *NP* number of pits, *%LP* percentage of specimens with large pits, *SWS* scratches width score (from 0: fine scratches only to 2: coarse scratches only), *M* mean, *SD* standard deviation, *CV* coefficient of variation

Season	Mesowear			Microwear				%LP	SWS
	n		MWS	*n*		NS	NP		
Dry season (January–March)	8	M	0.75	6	M	12.16	11.66		
		SD	1.16		SD	1.32	5.08	0	0
		CV	1.55		CV	0.1	0.43		
Wet season (April–December)	8	M	1.75	7	M	12.00	11.85		
		SD	1.58		SD	2.76	5.58	12.50	0.28
		CV	0.9		CV	0.23	0.47		
Female	9	M	1.33		M	11.87	10.5		
		SD	1.32	8	SD	1.72	5.01	12.50	0
		CV	0.99		CV	0.14	0.47		
Male	7	M	1.14		M	12.4	13.8		
		SD	1.67	5	SD	2.88	5.16	0	0.25
		CV	1.46		CV	0.23	0.37		
All individuals	16	M	1.25	13	M	12.07	11.76		
		SD	1.43		SD	2.13	5.13	7.69	0.15
		CV	1.15		CV	0.17	0.43		

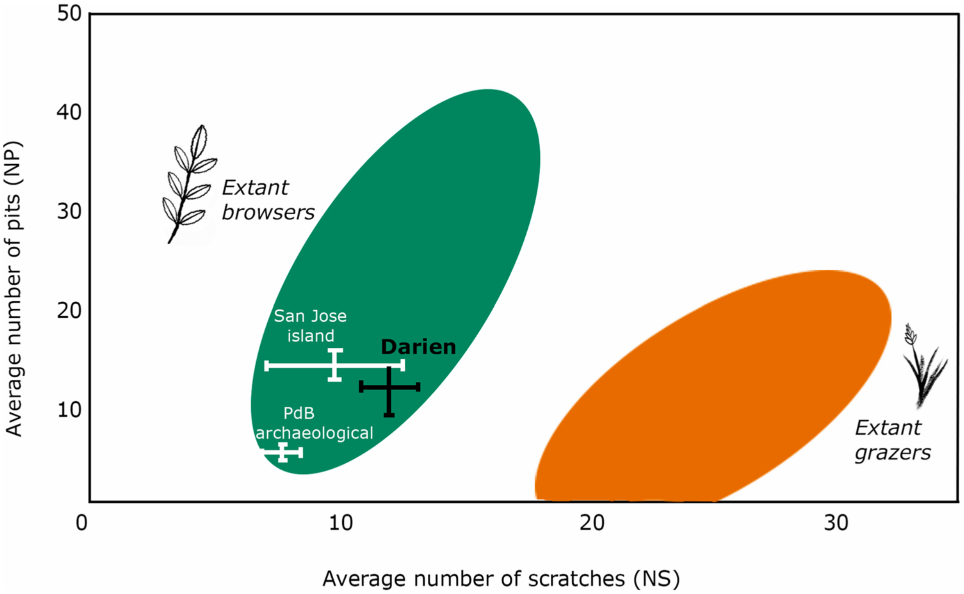

Fig. 3 Bivariate plot of the average numbers of pits and scratches of Central American red brocket deer (*Mazama temama*) from Darien, the ancient deer from Playa don Bernardo (PdB) and the extant deer population of San José Island, Pearl Island Archipelago, Panama (Martínez-Polanco et al. 2022). Error 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)

the wet season at three different locations and belonged to both museum collections. The structures that were observed seemed to have a large amount of silica and corresponded to some epidermal structures of leaves and/or spikelet bracts of some grasses, perhaps grasses of the C_4 photosynthetic pathway (Diego Giraldo-Cañas—expert in neotropical grasses, personal communication). The structures were long epidermal cells, papillae, microtrichomes (apparently two-celled), unicellular macrotrichomes (at least the proximal portion appears) and perhaps of the marginal or costal roughness type (Fig. 4).

Scratch variability

The scratch variation, quantified by the SD and CV, presented low values (Table 2). According to the modified signed likelihood ratio test, there were no significant differences in the number of scratch across seasons ($MSLRT = 2.54$; $p = 0.11$).

Discussion

We did not find differences among the mesowear scores and microwear traits (pits and scratches) between specimens from AMNH/NHMN previously referred to as two subspecies. This makes sense if we take into account the results of Escobedo-Morales et al. (2022) 2D geometric morphometric analysis that point to the presence of a single subspecies in the Darien area of Panama.

We compared our results with those of Playa don Bernardo ancient dwarf deer (6060–5620 cal yr BP) from Pedro Gonzalez Island and twentieth century *Mazama* sp. from San Jose Island and Darien *M. temama* (Martínez-Polanco et al. 2022). The mesowear results indicate that *Mazama* from San Jose, as the Darien *Mazama* extant population, were all browsers for several months or years before their death (Fig. 2). However, the microwear results showed that the Darien population of deer tended to be more browse-dominated mixed feeders than that of San Jose, which was the most browse-dominated in the samples previously studied (Fig. 3). As soon as Preceramic people arrived on Pedro Gonzalez, ca 6000 cal yr BP, 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 (Martínez-Polanco et al. 2022).

Considering scratches, the extant population from San Jose Island exhibited a higher range of variation compared to the ancient and Darien populations. According to the databases of AMNH and NMNH, individuals from San Jose Island were collected during the wet season (August 1944 and November 1945). This could mean that the San Jose deer were less selective in their diet composition in one season than the Darien deer, who exhibited a lower scratch variation in the wet and dry seasons (Fig. 3). This evidence could be an argument in favour of *M. temama* as a habitat specialist because of the limited composition of its diet on the mainland. In the case of the San Jose island deer population, food availability was already reduced for the size of the island (44 km^2) but the animals included a wide range of plants in their diets.

The absence of puncture pits was also observed at San Jose and Playa don Bernardo, Pedro Gonzalez Island (Martínez-Polanco et al. 2022), indicating that they did not consume fruit, as observed in extant populations of other

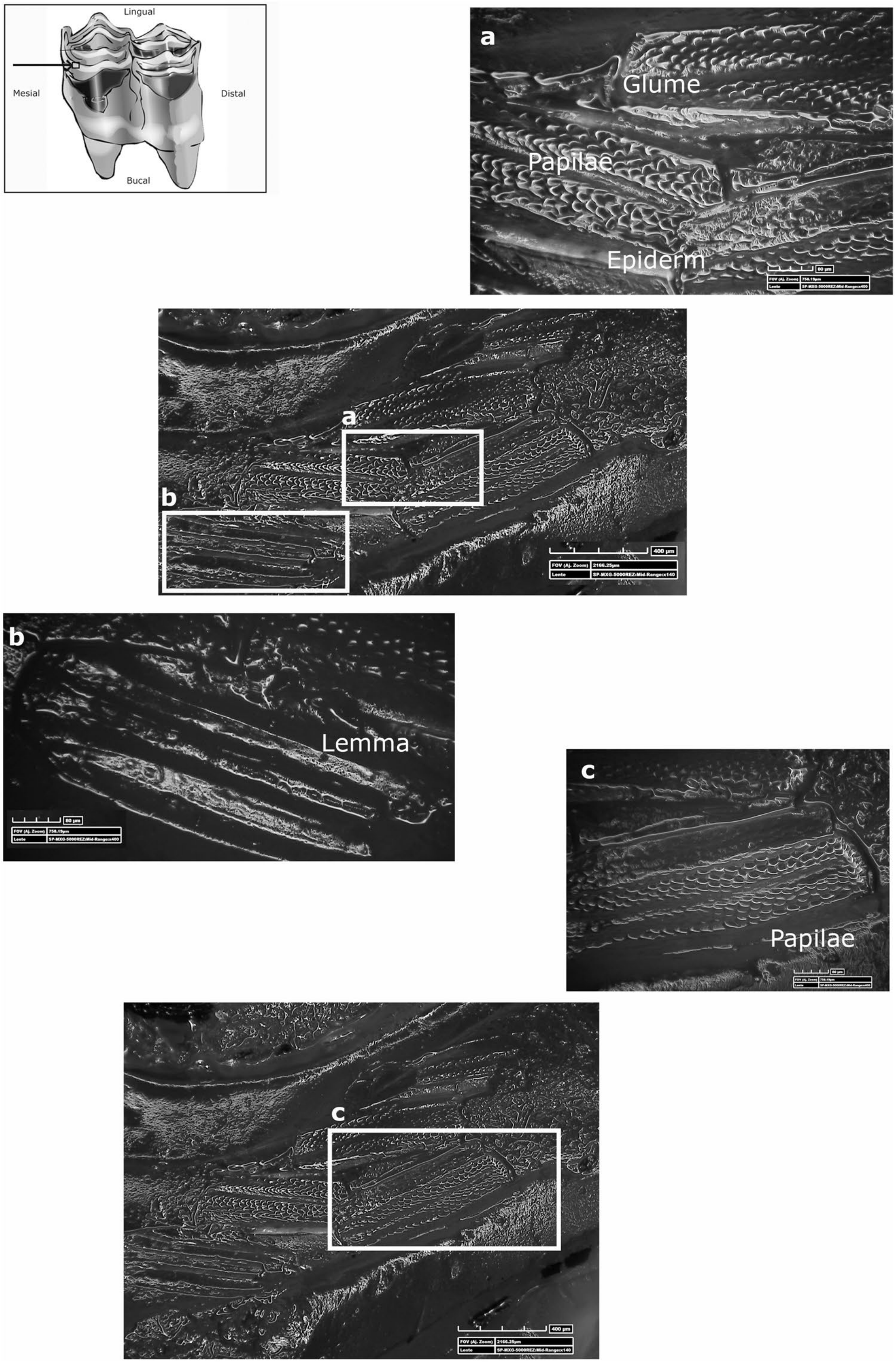

Fig. 4 Examples of vegetal remains on the occlusal surface of m2 of Central American red brocket deer from Darien, Panama (specimen NMNH-339085). Plant part determination by Céline Kerfant and photos by Lena Asryan

Mazama species, such as *M. nemorivaga* (Eisenberg 1989; Bodmer and Ward 2006; Rossi et al. 2010), *M. americana* (Gayot et al. 2004), *M. gouzoubira* (Gayot et al. 2004) and *M. temama*, at Calakmul Region in Mexico (Weber 2005). Additionally, they all tended to be browsers at the time of death (Martínez-Polanco et al. 2022).

A recent study of the diet of *M. temama* in San Bartolo Tutotepec mountain cloud forest (Hidalgo, Mexico) reported the consumption of vegetative parts—leaves and stems—in greater proportions, while reproductive parts, such as flowers or fruit, were consumed in much lesser proportions (Flores-Vazquez 2021). This study also showed that *M. temama* prefers herbaceous and shrubby strata. It is very likely that this food preference is related to the nutrients, as well as the digestibility and palatability that the plant species of these strata contain, to satisfy the metabolic needs of the organisms (Flores-Vazquez 2021). This result coincides with another study of *M. temama* from the north-eastern mountains of Puebla in Mexico (Villarreal-Espino-Barros et al. 2008).

The diet of the Central American red brocket deer varies among regions and ecosystems. For instance, the diet of *M. temama* in the Calakmul Region (south-eastern Mexico) shows seasonal differences in the number of species consumed during the dry season and during the wet season (Weber 2005). A study of the diet of *M. temama* from San Bartolo Tutotepec did not reflect a significant difference between the diversity of plants that composed the diet of the Central American red brocket deer during the rainy and dry seasons. The results suggested that the nutritional requirements of Central American red brocket deer were met in both seasons and that there was no different need for nutrients between seasons (Flores-Vazquez 2021). According to the author, this may be due to the fact that mountain mesophyll forests present a constant climate and variations in their floristic composition in the different seasons of the year are minimal, which allows Central American red brocket deer to have access to food resources throughout the year (Flores-Vazquez 2021). However, in the rainy season, the most frequently consumed species was *Miconia anisotricha*, while in the dry season, the most important species was *Symplocos coccinea* (Flores-Vazquez 2021). The scratches and pit variability in the Darien samples also indicate a constant climate that favours minimal changes in the floristic composition between seasons, which is reflected in the diet of brocket deer.

Considering that there are few studies of the diet of Central American red brocket in Central America, it is inevitable to compare it with the most common species in this area, the white-tailed deer (*Odocoileus virginianus*). Previous studies of deer diets using meso and microwear in extant populations showed that the diet of modern white-tailed deer at Isla Coiba is similar to extant browsers or browse-dominated mixed feeders, while the diet of white-tailed deer from the Florida Keys is more browser-like. *Odocoileus virginianus* from Coiba and the Florida Keys similarly have a high variation in the number of pits (Martínez-Polanco et al. 2022). Rotti et al. (2018), who studied the microwear of extant deer from Peru and Venezuela from the collection of Museo de La Plata (Argentina), also showed that deer were browsers at the moment of their death (Rotti et al. 2018).

A study of extant collections of white-tailed deer from PNN El Tuparro (Colombian, Orinoquia) showed that they consume plants and herbs from forests and also from savannas, but their consumption changes depending on the season. Mesowear indicates a mixed feeder diet tending to be grass-dominated throughout their lives, and microwear shows that individuals browsed during the last days or week before their death (Martínez-Polanco et al. under review).

A study of the diet of ancient white-tailed deer from Panama at Cerro Mangote (7800–4600 cal BP) and Cerro Juan Díaz (300 BCE–1600 CE) showed that deer were typically browsers. Both methods—mesowear and microwear—show the same tendency, and deer were likely hunted mostly during the wet season (May to November) (Martínez-Polanco et al. 2020). In the case of Sitio Sierra (2200–500 cal BP), another archaeological site, the microwear signal evidenced the opposite trend, indicating that deer were hunted in the dry season since scratch and pit variations had a higher frequency in these samples than in those from Cerro Mangote and Cerro Juan Diaz (Martínez-Polanco et al. 2020). The micro- and mesowear analyses of extant and ancient white-tailed deer suggested browsing or browse-dominated mixed-feeding and showed regional differences in mesowear of PNN el Tuparro, and the mixed feeder diet tended to be grass dominated (Martínez-Polanco et al. 2020; Martínez-Polanco et al. under review).

According to the model of scratch variability and seasonality, differences between the dry and wet seasons were expected. However, we did not find evidence of this in the case of *M. temama*. This is probably because the animals did not radically change their diets across seasons. This model was proposed for temperate ecosystems and not specifically for Neotropics (Rivals et al. 2015). However, in the case of *O. virginianus*, it seems that the model works for both ancient and extant populations (Martínez-Polanco et al. 2020). For this reason, it is important to extend this kind of study to other *Mazama* species, to test the model but also to better know the dietary habits of these species using a technique not commonly used by biologists and that could be helpful to understand the behaviour of these cryptic species.

Conclusions

Microwear and mesowear analyses of *M. temama* from Darien showed that they were browse-dominated mixed feeders during the last months/years of their lives and the days/weeks before death. No differences were identified in the diet of males and females either. There was no evidence of seasonal variation in the diet according to the microwear signal. Extant San Jose deer tended to be more browser dominated than those from the Darien population. According to the microwear analyses, the three populations (Darien, San Jose and Playa don Bernardo) did not consume fruit as other *Mazama* species are accustomed to. This paper is an example of the potential of studying extant populations housed in museum collections as a reference to compare them to archaeological materials.

The use of the same methodologies allowed the construction of baselines to better understand the archaeological record in the Neotropics. At the same time, dietary ecology information on species is difficult to study.

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Declarations

Conflict of interest The authors declare no competing interests.

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